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BIOLOGY

# ECOLOGICAL METHODS IN FOREST PEST MANAGEMENT



DAVID WAINHOUSE

## Ecological Methods in Forest Pest Management

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**David Wainhouse**

*Forest Research, Surrey, UK*

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# Preface

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This book is about the management of forest pests and aims to provide a critical appraisal of the theory and practice of key methods of management. These include, for example, semiochemicals, biological or microbial control and plant resistance. The appropriate application of these 'ecological methods' in the development of Integrated Pest Management (IPM) programmes depends on a clear understanding of pest biology and population dynamics, as well as an appreciation of the ecology and economic importance of managed forests. The *extensive* management of forests is often contrasted with *intensive* management in agriculture where IPM programmes have the aim of reducing insecticide use. But in forestry, where chemical pesticides are much less commonly applied, the main impetus for the development of IPM comes from the need to use environmentally sensitive and sustainable methods of control appropriate to both semi-natural and plantation forests. Such forests are increasingly likely to be managed for multiple purposes. As well as timber production therefore, maintaining or enhancing biodiversity and providing for public recreation and amenity are likely to be important objectives of management.

A major theme throughout the book is that details of pest ecology and of forest ecology and management matter in the application of IPM. The general bias towards examples of IPM from north temperate forests largely reflects coverage in the literature. However the principles, and to a large extent the practice, are applicable worldwide. Books with a particular emphasis on tropical pests include Wagner *et al.* (1991) and Speight and Wylie (2001).

Many of the examples and case studies relate to insect pests, but the term 'pest' is used in its widest sense to include fungal pathogens and brief reference is also made to mammalian herbivores. This inclusive approach is helpful for example in illustrating different aspects of resistance, reinforcing the point that resistance mechanisms are often effective against different kinds of organisms. A wider discussion of forest pests is particularly convenient when considering bark beetles (Scolytidae) because some of the most significant ones can vector pathogenic fungi, an association that affects both their population dynamics and their impact on forests. Possible interaction between organisms can also be an important consideration in the management of forests. For example, silvicultural operations may increase the incidence or spread of disease-causing organisms and, as a consequence, predispose trees to attack by insect pests.

Forests in many countries have been altered by exploitation and management and by the increasing use of plantations of exotic species for wood production. The species composition, distribution and extent of forests and the way they are managed can have an important influence on the nature and severity of pest problems and these are considered in Chapter 1. The increasing use of plantations of non-native trees in different countries and the globalisation of trade have significantly increased the risk of introducing exotic pests. The devastating effects that such pests can have on these plantations has highlighted the importance of regulating international trade in plants and plant products, a subject considered in Chapter 2. Spatial and temporal variation in pest attack can occur on a local or regional scale. Differences in the age or species composition of forests or the direct effects of site and climate on both trees and pests can contribute to this variation and may be used in the development of indices of risk. Risk-rating of forests and monitoring of pest populations in those most at risk can provide an early warning of outbreaks. Chapter 3 explores such approaches to improving the effectiveness and efficiency of pest management in extensive forest areas.

In discussing the role of silviculture (chapter 4), most emphasis is given to the ways in which normal silvicultural practices can be adapted to reduce pest attack, but examples are also given of how pest populations can sometimes be reduced by avoiding or modifying silvicultural practices. The role of resistance in forest pest management (chapter 5) is often underestimated. This is partly because the long juvenile period of trees and the largely polygenic expression of resistance would seem to limit the scope for breeding for increased resistance. However, unlike agricultural crops, trees are undomesticated and characterised by high levels of intraspecific variation. This can often be exploited in pest management. In chapters 6 and 7, the main focus is on the principles and practice of biological and microbial control in forests. In these chapters, there is also a discussion of potential non-target effects that may follow the release of introduced natural enemies, reflecting increasing interest in this topic. Semiochemicals, in particular the use of pheromones in monitoring, mating-disruption and mass-trapping are considered in chapter 8. The final chapter, on IPM, brings together elements of the previous ones, discussing them in the context of the economic and environmental impact of pests, the economics of control and the role of decision support systems. Detailed case studies are provided and future developments in IPM discussed in relation to multiple-use forest management and the potential effects of climate change on pests and pest management. In all chapters, references cited have been chosen to reflect recent discussion of a subject but most of them provide access to key original studies.

I am indebted to Don Reynolds and David Lonsdale who read through all the chapters making many improvements to the flow of the text. Invaluable comments on the content and emphasis of particular chapters were made by John Borden, Clive Braiser, Jenny Cory, Julian Evans, Roger Farrow, Bob Haack, Gary Kerr, Steve Lee, Nick Mills, Jose Negron and Joan Webber. I am most grateful to the following authors for supplying photographs (or even offering to take new ones!) – Roddie Burgess, Erik Christiansen, Rodney Croteau, Penelope Edwards, Joe Elkinton (especially for tracking down Fig. 2.15), Hugh Evans, Roger Farrow, Brian Federici, Ursula Kölzer, Bo Långström, Åke Lindelöv, Kevin Thorpe, Henrik Nordenhem, Ming Pei, Matti Rousi, Armand Séguin and Steven Strauss. Special thanks to Valmai and Owen for their tolerance and unfailing support.

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# Acknowledgements for reproduction of figures

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## Acta Forestalia Fennica

**Fig. 5.4.** Fig. 2 in Rousi, M. (1990). Breeding forest trees for resistance to mammalian herbivores – a study based on European white birch. *Acta Forestalia Fennica*, **210**, 1–20.

## AI Applications

**Fig 9.10.** Fig. 1 in Fedra, K. (1995). Decision support for natural resources management: models, GIS, and expert systems. *AI Applications*, **9**, 3–19.

## Annual Review of Phytopathology

**Fig 5.21.** Fig. 2 in Carson, S. D. and Carson, M. J. (1989). Breeding for resistance in forest trees – a quantitative genetic approach. *Annual Review of Phytopathology*, **27**, 373–395.

## Australian Forestry

**Fig. 2.12.** Fig. 3a in Peters, B. C. (1990). Infestations of *Cryptotermes brevis* (Walker) (Isoptera:Kalotermitidae) in Queensland, Australia 1. History, detection and identification. *Australian Forestry*, **53**, 79–88. By permission of the Institute of Foresters of Australia.

## BioScience

**Fig. 2.16.** From Fig. 1 and Fig. 4 in Brasier, C. M. (2001). Rapid evolution of introduced plant pathogens via interspecific hybridisation. *BioScience*, **51**, 123–133. Copyright, American Institute of Biological Sciences.

**Fig. 7.3.** From Fig. 1 a and b in Federici, B. A. and Maddox, J. V. (1996). Host specificity in microbe-insect interactions insect control by bacterial, fungal, and viral pathogens. *Bioscience*, **46**, 410–421. Copyright, American Institute of Biological Sciences.

## Blackwell Publishing

**Fig. 2.2b. and Fig 2.14.** Respectively Fig. 1 and Fig. 5 in Withers, T. M. (2001). Colonization of eucalypts in New Zealand by Australian insects. *Austral Ecology*, **26**, 467–476.

**Fig. 2.5.** Fig. 5 in Matsuki, M., Kay, M., Serin, J., Floyd, R. and Scott, J. K. (2001). Potential risk of accidental introduction of Asian gypsy moth (*Lymantria dispar*) to Australasia: effects of climatic conditions and suitability of native plants. *Agricultural and Forest Entomology*, **3**, 305–320.

**Fig. 3.11.** Unnumbered Fig. in Waring, R. H. and Pitman, G. B. (1983). Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. *Zeitschrift für angewandte Entomologie*, **96**, 265–270.

**Fig. 3.17.** Fig. 5 in Morewood, P., Gries, G., Liška, J., Kapitola, P., Häußler, D., Möller, K. and Bogenschütz, H. (2000). Towards pheromone-based monitoring of nun moth, *Lymantria monacha* (L.) (Lep., Lymantriidae) populations. *Journal of Applied Entomology*, **124**, 77–85.

**Fig. 3.21.** Fig. 1 in Battisti, A. (1994). Voltinism and diapause in the spruce web-spinning sawfly *Cephalcia arvensis*. *Entomologia Experimentalis et Applicata*, **70**, 105–113.

**Fig. 4.4.** Fig. 4b in McCracken, A. R. and Dawson, W. M. (1998) Short rotation coppice willow in Northern Ireland since 1973: development of the use of mixtures in the control of foliar rust (*Melampsora* spp.). *European Journal of Forest Pathology*, **28**, 241–250.

**Fig. 4.7.** Unnumbered Fig. on page 155 in Jactel, H., Menassieu, P., Raise, G. and Burban, C. (1996). Sensitivity of pruned maritime pine (*Pinus pinaster* Ait) to *Dioryctria sylvestrella* Ratz. (Lep., Pyralidae) in relation to tree vigour and date of pruning. *Journal of Applied Entomology*, **120**, 153–157.

**Fig. 4.12.** Fig. 4 in Gara, R. I., Millegan, D. R. and Gibson, K. E. (1999). Integrated pest management of *Ips pini* (Col., Scolytidae) populations in south-east Montana. *Journal of Applied Entomology*, **123**, 529–534.

**Fig. 4.14.** Unnumbered Fig. in Eidmann, H. H. (1992). Impact of bark beetles on forests and forestry in Sweden. *Journal of Applied Entomology*, **114**, 193–200.

**Fig. 4.20.** Fig. 2 b and Fig. 4 a in Schroeder, L. M. and Lindelöw, Å. (2002). Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and Forest Entomology*, **4**, 47–56.

**Fig. 5.11.** Fig. 1 in Christiansen, E. (1985). *Ips/Ceratocystis* – infection of Norway spruce: what is a deadly dosage? *Zeitschrift für angewandte Entomologie*, **99**, 6–11.

**Fig. 5.16.** Fig. 1, Fig 4.1a and Fig. 5a in Hodkinson, I. D., Flynn, D. H. and Shackel, S. C. (1998). Relative susceptibility of *Salix* clones to chrysomelid beetles: evidence from the Stott willow collection at Ness. *European Journal of Forest Pathology*, **28**, 271–279.

**Fig. 5.20b.** Fig. 3 in Roche, B. M. and Fritz, R. S. (1998). Effects of host plant hybridization on resistance to willow leaf rust caused by *Melampsora* sp. *European Journal of Forest Pathology*, **28**, 259–270.

**Fig. 8.1.** Fig. 1 in Schlyter, F. and Anderbrant, O. (1989). Mass attack of trees by *Ips typographus* induced by sex-specific pheromone: a model of attack dynamics. *Holarctic Ecology*, **12**, 415–426.

**Fig. 8.4.** Fig. 2 a and b in Thorpe, K. W., Mastro, V. C., Leonard, D. S., Leonhardt, B. A., McLane, W., Reardon, R. C. and Talley, S. E. (1999). Comparative efficacy of two controlled-release gypsy moth mating disruption formulations. *Entomologia Experimentalis et Applicata*, **90**, 267–277.

**Fig. 8.10.** Fig. 1 in Bakke, A. (1983). Host tree and bark beetle interaction during a mass outbreak of *Ips typographus* in Norway. *Zeitschrift für angewandte Entomologie*, **96**, 118–125.

**Fig. 8.11.** Fig. 2 in Bakke, A. (1989). The recent *Ips typographus* outbreak in Norway – experiences from a control programme. *Holarctic Ecology*, **12**, 515–519.

**Fig. 8.12.** Fig. 2 in Weslien, J. (1992). Effects of mass trapping on *Ips typographus* (L.) populations. *Journal of Applied Entomology*, **114**, 228–232.

**Fig. 8.13.** Unnumbered Fig. in Borden, J. H. (1992). Two tree baiting tactics for the management of bark beetles with semiochemicals. *Journal of Applied Entomology*, **114**, 201–207.

**Fig. 9.16.** Fig. 1 in O'Neill, M. and Evans, H. F. (1999). Cost-effectiveness analysis of options within an Integrated Crop Management regime against great spruce bark beetle, *Dendroctonus micans*, Kug. (Coleoptera: Scolytidae). *Agricultural and Forest Entomology*, **1**, 151–156.

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**Fig. 7.11.** Fig. 8.1 in Stenlid, J. and Redfern D. B. (1998). Spread within the tree and stand. In *Heterobasidium annosum biology, ecology, impact and control* (ed. S. Woodward, J. Stenlid, R. Karjalainen and A. Hüttermann), pp. 125–141. CAB International, Wallingford.

### **Canadian Journal of Plant Pathology**

**Table 5.2.** Fig. 1 a and b in Fleming, R. A. and Person, C. O. (1982). Consequences of polygenic determination of resistance and aggressiveness in nonspecific host:parasite relationships. *Canadian Journal of Plant Pathology*, **4**, 89–96. Reproduced by permission from the Canadian Phytopathological Society.

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### **Canadian Forest Service**

**Fig. 3.12.** Fig. 2 and Table 3 in Shore, T. L. and Safranyic, L. (1992). *Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands*. Forestry Canada. Pacific and Yukon Region. Pacific Forestry Centre. BC-X-366 12pp. Reproduced with permission of Natural Resources Canada, Canadian Forest Service. Copyright owner Her Majesty the Queen in Right of Canada.

### **Elsevier**

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**Fig. 1.7.** Fig. 2 in Booth, T. H., Jovanovic, T. and New, M. (2002). A new world climatic mapping programme to assist species selection. *Forest Ecology and Management*, **163**, 111–117. With permission from Elsevier.

**Fig. 3.2.** Part of Fig. 4 and redrawn composite based on Fig.5 in Gray, D. R., Régnière, J. and Boulet, B. (2000). Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Quebec. *Forest Ecology and Management*, **127**, 217–231. With permission from Elsevier.

**Fig. 3.4.** Fig. 1 in Mattila, U., Jalkanen, R. and Nikula, A. (2001). The effects of forest structure and site characteristics on probability of pine twisting rust damage in young Scots pine stands. *Forest Ecology and Management*, **142**, 89–97. With permission from Elsevier.

**Fig. 3.6.** Fig. 4, Fig. 5 and part of Fig. 3 in Coulson, R. N., McFadden, B. A., Pulley, P. E., Lovelady, C. N., Fitzgerald, J. W. and Jack, S. B. (1999). Heterogeneity of forest landscapes and the distribution and abundance of southern pine beetle. *Forest Ecology and Management*, **114**, 471–85. With permission from Elsevier.

**Fig. 4.21.** Fig. 2c in Wichmann, L. and Ravn, H. P. (2001). The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. *Forest Ecology and Management*, **148**, 31–39. With permission from Elsevier.

**Fig 5.3.** From Agrios, G. N. (1988). *Plant pathology*. 3rd edition. Academic Press, San Diego. With permission from Elsevier.

**Fig. 5.5.** Fig. 5 b and c in Woodward, S. and Pearce, R. B. (1988b). Wound-associated responses in Sitka spruce root bark challenged with *Phaeolus schweinitzii*. *Physiological and Molecular Plant Pathology*, **33**, 151–162. With permission from Elsevier.

**Fig. 5.7.** Fig. 1 (upper graph) in Nielsen, U. B., Kirkeby-Thomsen, A. and Roulund, H. (2002). Genetic variation in resistance to *Dreyfusia nordmanniana* Eckst. infestations in *Abies nordmanniana* (Stev.) Spach. *Forest Ecology and Management*, **165**, 271–283. With permission from Elsevier.

**Fig. 5.8.** Fig. 2 a and b in Phillips, M. A. and Croteau, R. B. (1999). Resin-based defences in conifers. *Trends in Plant Science*, **4**, 184–190. With permission from Elsevier.

**Fig. 5.10 and Fig. 5.11 (inset).** Fig. 3 and Fig. 2 respectively in Christiansen, E., Waring, R. H. and Berryman, A. A. (1987). Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management*, **22**, 89–106. With permission from Elsevier.

**Fig. 5.22.** Fig. 3 b and Fig. 5 in Peña, L. and Séguin, A. (2001). Recent advances in the genetic transformation of trees. *TRENDS on Biotechnology*, **19**, 500–506. With permission from Elsevier.

**Fig. 8.6.** Fig. 3 (site 1) in Raty, L., Drumont, A., de Windt, N. and Grégoire, J.-C. (1995). Mass trapping of the spruce bark beetle *Ips typographus* L.: traps or trap trees? *Forest Ecology and Management*, **78**, 191–205. With permission from Elsevier.

**Fig. 9.2.** Fig. 4 and Fig. 5 a in Candy, S. G., Elliott, H. J., Bashford, R., Greener, A. (1992). Modelling the impact of defoliation by the leaf beetle, *Chrysophtharta bimaculata* (Coleoptera: Chrysomelidae), on height growth of *Eucalyptus regnans*. *Forest Ecology and Management*, **54**, 69–87. With permission from Elsevier.

**Fig. 9.3.** Fig. 3 and Fig. 4 in Elliott, H. J., Bashford, R., Greener, A., and Candy, S. G. (1992). Integrated pest management of the Tasmanian *Eucalyptus* leaf beetle, *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae). *Forest Ecology and Management*, **53**, 29–38. With permission from Elsevier.

**Fig. 9.5. and Fig. 9.9.** Fig. 5 and Fig. 4 respectively in Alfaro, R. I., Taylor, S., Brown, G. and Wegwitz, E. (1999). Tree mortality caused by the western hemlock looper in landscapes of central British Columbia. *Forest Ecology and Management*, **124**, 285–291. With permission from Elsevier.

**Fig. 9.15.** Fig. 4 in Hudak, J. (1991). Integrated pest management and the eastern spruce budworm. *Forest Ecology and Management*, **39**, 313–337. With permission from Elsevier.

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**Fig. 2.2a.** Fig. 1 in Sailer, R. I. (1978). Our immigrant insect fauna. *Bulletin of the Entomological Society of America*, **24**, 3–11.

**Fig. 3.14.** Fig. 1 in Liebhold, A. M., Simons, E. E., Sior, A. and Unger, J. D. (1993b). Forecasting defoliation caused by the gypsy moth from field measurements. *Environmental Entomology*, **22**, 26–32.

**Fig. 3.19.** Fig. 2 (maps for 1985–7) in Liebhold, A. M., Elkinton, J. S., Zhou, G., Hohn, M. E., Rossi, R. E., Boettner, G. K., Boettner, C. W., Burnham, C. and McManus, M. L. (1995). Regional correlation of gypsy moth

(Lepidoptera: Lymantriidae) defoliation with counts of egg masses, pupae, and male moths. *Environmental Entomology*, **24**, 193–203.

**Fig. 3.22.** Fig. 2 in Malinoski, M. K. and Paine, T. D. (1988). A day-degree model to predict Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae), flights in southern California. *Environmental Entomology*, **17**, 75–79.

**Fig. 5.13.** Fig. 7 b in Mutikainen, P., Walls, M., Ovaska, J., Keinänen, M., Julkunen-Tiitto, R. and Vapaavuori, E. (2000). Herbivore resistance in *Betula pendula*: effect of fertilization, defoliation, and plant genotype. *Ecology*, **81**, 49–65.

**Fig. 5.15.** Fig. 2 and part of Fig. 4 a in Tomlin, E. S. and Borden, J. H. (1997). Multicomponent index for evaluating resistance by Sitka spruce to the white pine weevil (Coleoptera: Curculionidae). *Journal of Economic Entomology*, **90**, 704–714.

**Fig. 6.1.** Fig. 4a in Smitley, D. R., Bauer, L. S., Hajek, A. E., Sapio, F. J. and Humber, R. A. (1995). Introduction and establishment of *Entomophaga maimaiga*, a fungal pathogen of gypsy moth (Lepidoptera: Lymantriidae) in Michigan. *Environmental Entomology*, **24**, 1685–1695.

**Fig. 6.9.** Fig. 1 in Ryan, R. B. (1997). Before and after evaluation of biological control of the larch casebearer (Lepidoptera: Coleophoridae) in the Blue Mountains of Oregon and Washington, 1912–1995. *Environmental Entomology*, **26**, 703–715.

**Fig. 8.2.** Fig. 1 and Fig. 2 in Sharov, A. A., Liebhold, A. M. and Ravlin, F. W. (1995). Prediction of gypsy moth (Lepidoptera: Lymantriidae) mating success from pheromone trap counts. *Environmental Entomology*, **24**, 1239–1244.

**Fig. 8.8.** Fig. 2 in Ross, D. W. and Daterman, G. E. (1998). Pheromone-baited traps for *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae): Influence of selected release rates and trap designs. *Journal of Economic Entomology*, **91**, 500–506.

**Fig. 8.14.** Fig. 1 a, b and c in Miller, D. R., Borden, J. H. and Lindgren, B. S. (1995). Verbenone: Dose-dependent interruption of pheromone-based attraction of three sympatric species of pine bark beetles (Coleoptera: Scolytidae). *Environmental Entomology*, **24**, 692–696.

**Fig. 9.12.** Fig. 3a in Fang, Y. and Hart, E. R. (2000). Effect of cottonwood leaf beetle (Coleoptera: Chrysomelidae) larval population levels on *Populus* terminal damage. *Environmental Entomology*, **29**, 43–48.

## Entomological Society of Canada

**Fig. 1.8.** Fig. 1 in Ericsson, T., Danell, Ö. and Andersson, B. (1994). Genetic variation of *Pinus contorta* var. *latifolia* breeding material in Sweden. *Canadian Journal of Forest Research*, **24**, 723–729.

**Fig. 1.9.** Fig. 2 (1989) in Karlman, M., Hansson, P. and Witzell, J. (1994). *Scleroderris* canker on lodgepole pine introduced in northern Sweden. *Canadian Journal of Forest Research*, **24**, 1948–1959.

**Fig. 1.10.** Fig. 2 in Roberds, J. H. and Bishir, J. W. (1997). Risk analyses in clonal forestry. *Canadian Journal of Forest Research*, **27**, 425–432.

**Fig. 3.3.** Fig. 4 in Su, Q., MacLean, D. A., Needham, T. D. (1996). The influence of hardwood content on balsam fir defoliation by spruce budworm. *Canadian Journal of Forest Research*, **26**, 1620–1628.

**Fig. 3.5.** Fig. 4 in Dupont, A., Bélanger, L. and Bousquet, J. (1991). Relationships between balsam fir vulnerability to spruce budworm and ecological site conditions of fir stands in central Quebec. *Canadian Journal of Forest Research*, **21**, 1752–1759.



**Fig. 3.10.** Fig. 1 in Marchand, P. J. (1983). Sapwood area as an estimator of foliage biomass and projected leaf area for *Abies balsamea* and *Picea rubens*. *Canadian Journal of Forest Research*, **14**, 85–87.

**Fig. 3.13.** Fig. 1 and Fig. 7 in Turgeon, J. J. and Régnière, J. (1987). Development of sampling techniques for the spruce budmoth *Zeiraphera canadensis* Mut. and Free. (Lepidoptera: Tortricidae). *Canadian Entomologist*, **119**, 239–249.

**Fig. 3.16.** Fig. 1 in Sweeney, J. D., McLean, J. A. and Shepherd, R. F. (1990). Factors affecting catch in pheromone traps for monitoring the western spruce budworm, *Choristoneura occidentalis* Freeman. *Canadian Entomologist*, **122**, 1119–1130.

**Fig. 3.20.** Fig. 3 in Hansen, E. M., Bentz, B. J. and Turner, D. L. (2001). Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Canadian Entomologist*, **133**, 827–841.

**Fig. 4.5.** Fig. 5 a and b (selected data) in Schmid, J. M., Mata, S. A. and Schmidt, R. A. (1991). Bark temperature patterns in ponderosa pine stands and their possible effects on mountain pine beetle behaviour. *Canadian Journal of Forest Research*, **21**, 1439–1446.

**Fig. 4.6.** Fig. 1 and Fig. 4 in Taylor, S. P., Alfaro, R. I., DeLong, C., Rankin, L. (1996). The effects of overstory shading on white pine weevil damage to white spruce and its effects on spruce growth rates. *Canadian Journal of Forest Research*, **26**, 306–312.

**Fig. 4.8.** Fig. 1 (graphs for Rover and Madias) in Morrison, D. J., Pellow, K. W., Nemeč, A. F. L., Norris, D. J. and Semenoff, P. (2001). Effects of selective cutting on the epidemiology of armillaria root disease in the southern interior of British Columbia. *Canadian Journal of Forest Research*, **31**, 59–70.

**Fig. 4.10.** Fig. 2 in Crook, G. W., Vézina, P. E. and Hardy, Y. (1979). Susceptibility of balsam fir to spruce budworm defoliation as affected by thinning. *Canadian Journal of Forest Research*, **9**, 428–435.

**Fig. 4.11.** Fig. 4b in Bergeron, Y., Leduc, A., Morin, H. and Joyal, C. (1995). Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research*, **25**, 1375–1384.

**Fig. 4.13.** Fig. 2c (selected data), Fig. 3 (selected data) and Fig. 4 (sapwood) in Kelsey, R. G. (1994). Ethanol synthesis in Douglas-fir logs felled in November, January, and March and its relationship to ambrosia beetle attack. *Canadian Journal of Forest Research*, **24**, 2096–2104.

**Fig. 4.16.** Fig. 6a in Conway, B. E., Leefers, L. A. and McCullough, D. G. (1999). Yield and financial losses associated with a jack pine budworm outbreak in Michigan and the implications for management. *Canadian Journal of Forest Research*, **29**, 382–392.

**Fig. 5.1.** Fig. 1 in Loehle, C. (1988). Tree life history strategies: the role of defences. *Canadian Journal of Forest Research*, **18**, 209–222.

**Fig. 5.6.** Fig. 1 (no. 1 and 6) in Alfaro, R. I., Kiss, G. K. and Yanchuk, A. (1996a). Variation in the induced resin response of white spruce, *Picea glauca*, to attack by *Pissodes strobi*. *Canadian Journal of Forest Research*, **26**, 967–972.

**Fig. 5.17a.** Fig. 1 in Wu, H. X., Ying, C. C. and Muir, J. A. (1996). Effect of geographic variation and jack pine introgression on disease and insect resistance in lodgepole pine. *Canadian Journal of Forest Research*, **26**, 711–726.

**Fig. 5.17b.** Fig. 7b in Wu, H. X. and Ying, C. C. (1998). Stability of resistance to western gall rust and needle cast in lodgepole pine provenances. *Canadian Journal of Forest Research*, **28**, 439–449.

**Fig. 6.2.** Fig. 3 in Smith, S. M., Hubbes, M. and Carrow, J. R. (1987). Ground releases of *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) against the spruce budworm (Lepidoptera: Tortricidae). *Canadian Entomologist*, **119**, 251–263.

**Fig. 6.3 and Fig. 6.4.** Fig. 8 and Fig. 7a-c respectively in Smith, S. M., Carrow, J. R. and Laing, J. E. (ed.) (1990). Inundative release of the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae), against forest insect pests such as the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae): the Ontario project 1982–1986. *Memoirs of the Entomological Society of Canada No. 153*.

**Fig. 7.6.** Fig. 1 top part only in Fleming, R. A. and van Frankenhuyzen, K. (1992). Forecasting the efficacy of operational *Bacillus thuringiensis* Berliner applications against spruce budworm *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), using dose ingestion data: initial models. *Canadian Entomologist*, **124**, 1101–1113.

**Fig. 7.7. and Fig. 7.9.** Fig. 4a and Fig 2 respectively in van Frankenhuyzen, K., Nystrom, C., Dedes, J. and Seligy, V. (2000b). Mortality, feeding inhibition, and recovery of spruce budworm (Lepidoptera: Tortricidae) larvae following aerial application of a high-potency formulation of *Bacillus thuringiensis* subsp. *kurstaki*. *Canadian Entomologist*, **132**, 505–518.

**Fig. 9.4. and Fig. 9.7.** Fig. 6 and Fig. 1 respectively in Gross, H. L. (1992). Impact analysis for a jack pine budworm infestation in Ontario. *Canadian Journal of Forest Research*, **22**, 818–831.

**Fig. 9.6.** Fig. 8 in Gavin, D. G. and Peart, D. R. (1993). Effects of beech bark disease on the growth of American beech (*Fagus grandifolia*). *Canadian Journal of Forest Research*, **23**, 1566–1575.

**Fig. 9.8.** Fig. 6 (histogram data as percent) in Orbay, L., Mclean, J. A., Sauder, B. J., and Cottell, P. L. (1994). Economic losses resulting from ambrosia beetle infestation of sawlogs in coastal British Columbia, Canada. *Canadian Journal of Forest Research*, **24**, 1266–1276.

**Fig. 9.14.** Fig. 2 in Czokajlo, D., Wink, R. A., Warren, J. C., and Teale, S. A. (1997). Growth reduction of Scots pine, *Pinus sylvestris*, caused by the larger pine shoot beetle, *Tomicus piniperda* (Coleoptera, Scolytidae), in New York State. *Canadian Journal of Forest Research*, **27**, 1394–1397.

## The Forestry Chronicle

**Fig. 7.1.** Fig. 1 in Cunningham, J. C. and van Frankenhuyzen, K. (1991). Microbial insecticides in forestry. *Forestry Chronicle*, **67**, 473–480.

**Fig. 8.9.** Fig. 3 and Fig. 5 in Lindgren, B. S. and Fraser, R. G. (1994). Control of ambrosia beetle damage by mass trapping at a dryland log sorting area in British Columbia. *Forestry Chronicle*, **70**, 159–163.

**Fig. 9.1.** Fig. 2, Fig. 3 and Fig. 4 in Fox, G., Beke, J., Hopkin, T. and McKenney, D. (1997). A framework for the use of economic thresholds in forest pest management. *Forestry Chronicle*, **73**, 331–339.

**Fig. 9.11.** Fig. 4 b in MacLean, D. A., Beaton, K. P., Porter, K. B., MacKinnon, W. E. and Budd, M. G. (2002). Potential wood supply losses to spruce budworm in New Brunswick estimated using the Spruce Budworm Decision Support System. *Forestry Chronicle*, **78**, 739–750.

## Forestry Commission

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*Ips typographus*, *Anoplophora glabripennis*, *Cryptococcus fagisuga* and *Lymantria dispar*, Forest Research Photographic Library © Crown Copyright.

**Fig 3.7.** Fig. 5 in Grayson, A. J. (ed) (1989). *The 1987 storm: Impacts and responses*, Forestry Commission Bulletin 87. HMSO, London.

## International Forestry Review

**Fig. 1.4.** Fig. 3 in Burgess, T. and Wingfield, M. J. (2002). Quarantine is important in restricting the spread of exotic seed-borne tree pathogens in the southern hemisphere. *International Forestry Review*, **4**, 56–65. Reproduced with permission of the International Forestry Review.

## Kluwer Academic Publishers

**Fig. 1.2.** Fig. 1 in Koch, N. E. and Skovsgaard, J. P. (1999). Sustainable management of planted forests: some comparisons between Central Europe and the United States. *New Forests*, **17**, 11–22. With kind permission of Kluwer Academic Publishers.

**Fig. 5.24.** Fig. 2 in Hu, J. J., Tian, Y. C., Han, Y. F., Li, L. and Zhang, B. E. (2001). Field evaluation of insect-resistant *Populus nigra* trees. *Euphytica*, **121**, 123–127. With kind permission of Kluwer Academic Publishers.

**Fig. 6.7. and Fig. 6.10.** Fig. 4 and Fig. 3 respectively in Long, G. E. (1988). The larch casebearer in the intermountain northwest. In *Dynamics of forest insect populations patterns, causes, implications*. (ed. A. A. Berryman), pp. 233–242. Plenum Press, New York. With kind permission of Kluwer Academic Publishers.

**Fig. 8.3.** Fig. 3 in Leonhardt, B. A., Mastro, V. C., Leonard, D. S., McLane, W., Reardon, R. C. and Thorpe, K. W. (1996). Control of low-density gypsy moth (Lepidoptera: Lymantriidae) populations by mating disruption with pheromone. *Journal of Chemical Ecology*, **22**, 1255–1272. With kind permission of Kluwer Academic Publishers.

## Nature

Quotation on page 16 in Anon (1999). 100 years ago. *Nature*, **399**, 309. Reprinted by permission from Nature. Macmillan Publishers Ltd.

## New Zealand Journal of Forestry Science

**Fig. 2.10.** Fig. 2 in Bulman, L. S., Kimberley, M. O. and Gadgil, P. D. (1999). Estimation of the efficiency of pest detection surveys. *New Zealand Journal of Forestry Science*, **29**, 102–115.

**Fig. 2.11.** Fig. 6 in Carter, P. C. S. (1989). Risk assessment and pest detection surveys for exotic pests and diseases which threaten commercial forestry in New Zealand. *New Zealand Journal of Forestry Science*, **19**, 353–374.

## Oxford University Press

**Fig. 2.3.** Fig. 2.9 in Shigesada, N. and Kawasaki, K. (1997). *Biological invasions: theory and practice*. Oxford University Press, Oxford.

**Fig. 4.17.** Fig. 2 in Gibbs, J. N., Greig, B. J. W. and Pratt, J. E. (2002). Fomes root rot in Thetford Forest, East Anglia: past, present and future. *Forestry*, **75**, 191–202.

**Fig. 8.5.** Fig. 9.10 in Speight, M. R. and Wainhouse, D. (1989). *Ecology and management of forest insects*. Clarendon press, Oxford.

## The Quarterly Review of Biology

**Fig. 5.2.** Fig. 1 in Herms, D. A. and Mattson, W. J. (1992). The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*, **67**, 283–335. Copyright © 1992. The University of Chicago.

## Royal Entomological Society

**Fig. 6.5.** Fig. 4.5 in Kidd, N. A. C. and Jarvis, M. A. (1997). The impact of parasitoids and predators on forest insect populations. In *Forests and insects*, (ed. A. D. Watt, N. E. Stork and M. D. Hunter), pp. 49–68. Chapman and Hall, London.

**Fig. 6.11.** Fig. 13.1 in Roland, J. (1998). The population dynamics of *Operophtera brumata* (Lepidoptera: Geometridae). In *Insect populations in theory and practice*. 19th Symposium of the Royal Entomological Society. (ed. J. P. Dempster and I. F. G. McLean), pp. 309–321. Kluwer Academic Publishers, Dordrecht.

## Silvae Genetica

**Fig. 4.1.** Fig. 4 in Ledig, F. T. and Smith, D. M. (1981). The influence of silvicultural practices on genetic improvement: height growth and weevil resistance in eastern white pine. *Silvae Genetica*, **30**, 31–36.

## Silva Fennica

**Fig. 4.15.** Fig. 1a and Fig.7 in Långström, B. and Hellqvist, C. (1991). Shoot damage and growth losses following three years of *Tomiscus*-attacks in Scots pine stands close to timber storage site. *Silva Fennica*, **25**, 133–145.

**Fig. 9.20.** Fig. 5a and b - Virtanen, T., Neuvonen, S., Nikula, A., Varama, M. and Niemelä, P. (1996). Climate change and the risks of *Neodiprion sertifer* outbreaks on Scots pine. *Silva Fennica*, **30**, 169–177.

## Society of America Foresters

**Fig. 1.3.** Fig. 3 in Plochmann, R. (1992). The forests of central Europe a changing view. *Journal of Forestry*, June, 12–16 and 41.

**Fig. 2.1.** Fig. 2 in Liebhold, A. M., MacDonald, W. L., Bergdahl, D. and Mastro, V. C. (1995). Invasion by exotic forest pests: A threat to forest ecosystems. *Forest Science Monograph*, **30**, 1–49.

**Fig. 3.8.** Fig. 3 in Hard, J. S. (1985). Spruce beetles attack slowly growing spruce. *Forest Science*, **31**, 839–850.

**Fig. 3.9.** Fig. 1 (selected data) - Mitchell, R. G., Waring, R. H. and Pitman, G. B. (1983). Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science*, **29**, 204–211. -

**Fig. 5.20a.** Fig. 1 in Manley, S. A. M. and Fowler, D. P. (1969). Spruce budworm defoliation in relation to introgression in red and black spruce. *Forest Science*, **15**, 365–366.

**Fig. 5.23.** Photograph of hybrid poplar plantation on Oregon in Strauss, S. H., Campbell, M. M., Pryor, S. N., Coventry, P. and Burley, J. (2001b). Plantation certification and genetic engineering FSC's ban on research is counter productive. *Journal of Forestry*, **99**, December, 4–7.

**Fig. 6.8.** Fig. 1 in Ryan, R. B., Tunnock, S. and Ebel, F. W. (1987). The larch casebearer in North America. *Journal of Forestry*, **85**, July, 33–39.

**Fig. 8.15.** Fig. 1 (in part) in Clarke, S. R., Salom, S. M., Billings, R. F., Berisford, C. W., Upton, W. W., McClellan, Q. C. and Dalusky, M. J. (1999). A scentsible approach to controlling southern pine beetles - Two new tactics using verbenone. *Journal of Forestry*, **97**, July, 26–31.

**Fig 9.18 and Fig 9.19.** Fig. 3/4 and Fig. 6 respectively in Sharov, A. A., Leonard, D., Liebhold, A. M., Roberts, E. A. and Dickerson, W. (2002). "Slow the spread" a national program to contain gypsy moth. *Journal of Forestry*, **100**, July/August, 30–35.

### South African Forestry Journal

**Fig. 5.18.** Fig. 4 in Richardson, K. F. and Meakins, R. H. (1986). Inter- and intra-specific variation in the susceptibility of Eucalypts to the snout beetle *Gonipterus scutellatus* Gyll. (Coleoptera: Curculionidae). *South African Forestry Journal*, **139**, 21–31.

### Springer-Verlag

**Fig. 1.6.** Fig. 1 c and Fig. 2 in Roland, J. (1993). Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, **93**, 25–30.

**Fig. 3.1.** Fig. 2 in Weber, U. M. (1997). Dendroecological reconstruction and interpretation of larch budmoth (*Zeiraphera diniana*) outbreaks in two central alpine valleys of Switzerland from 1470–1990. *Trees*, **11**, 277–290.

**Table 3.3. (inset Fig.).** Fig. 1 in Armour, H., Straw, N., and Day, K. (2003). Interactions between growth, herbivory and long-term foliar dynamics of Scots pine. *Trees*, **17**, 70–80.

**Fig. 5.9.** Fig. 6 a and b in Wainhouse, D., Cross, D. J. and Howell, R. S. (1990). The role of lignin as a defence against the spruce bark beetle *Dendroctonus micans*: effects on larvae and adults. *Oecologia*, **85**, 257–265.

**Fig. 5.14.** Fig. 1 b and Fig. 2 in Edwards, P. B., Wanjura, W. J. and Brown, W. V. (1993). Selective herbivory by Christmas beetles in response to intraspecific variation in *Eucalyptus* terpenoids. *Oecologia*, **95**, 551–557.

**Fig. 5.20c.** Fig. 4 d in Fritz, R. S., Nichols-Orians, C. M., and Brunsfeld, S. J. (1994). Interspecific hybridization of plants and resistance to herbivores: hypotheses, genetics, and variable responses in a diverse herbivore community. *Oecologia*, **97**, 106–117.

### Taylor and Francis

**Fig. 3.18.** Fig. 5 and Fig. 6 in Weslien, J., Annala, E., Bakke, A., Bejer, B., Eidman, H. H., Narvestad, K., Nikula, A. and Ravn, H. P. (1989). Estimating risks for spruce bark beetle (*Ips typographus* (L.)) damage using pheromone-baited traps and trees. *Scandinavian Journal of Forest Research*, **4**, 87–98.

**Fig. 4.3b.** Fig 3 (1993+94) in Eidmann, H. H., Nordenhem, H. and Weslien, J. (1996). Physical protection of conifer seedlings against pine weevil feeding. *Scandinavian Journal of Forest Research*, **68**, 68–75.

**Fig. 4.18.** Fig. 4 (site 8) in von Sydow, F. (1997). Abundance of pine weevils (*Hylobius abietis*) and damage to conifer seedlings in relation to silvicultural practices. *Scandinavian Journal of Forest Research*, **12**, 157–167.

**Fig. 7.10.** Fig. 1 in Solter, L. F., Keena, M., Cate, J. R., McManus, M. L. and Hanks, L. M. (2001). Infectivity of four species of nematodes (Rhabditoidea: Steinernematidae, Heterorhabditidae) to the Asian Longhorn beetle, *Anoplophora glabripennis* (Motchulsky) (Coleoptera: Cerambycidae). *Biocontrol Science and Technology*, **11**, 547–552.

# Forests and pest management

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Forest pest management differs in a number of important respects from the management of pests of agricultural crops or those affecting orchard trees. The differences are related in particular to the area scale of forestry which, together with the often long rotation times, affects logistic and economic aspects of management. Rotation times are usually measured in decades so that trees are exposed to a range of different pests and pathogens during the juvenile and mature stages of growth. The methods used in pest management may also be influenced by the increasingly important role of forests in recreation and amenity, as well as the need to protect rare species or habitats.

The different options for management and control that are considered in the following chapters, except perhaps silvicultural management, are discussed in most textbooks on pest management. The emphasis given to particular methods however, and the way in which they are integrated into a pest management programme depends on the nature of the forest, the objectives of forest management and, importantly, on key ecological or life-history characteristic of the pests. This is not to say that forest pest management lacks general principles but rather that the variety of pests and the scale and complexity of the forest environment require an adaptive approach to management. In other words, details matter. Examples of how the characteristics of forests such as their extent, species composition and the intensity of management can influence not only the nature of pest and pathogen problems, but also the opportunities for, and constraints on, pest management are discussed in the following sections.

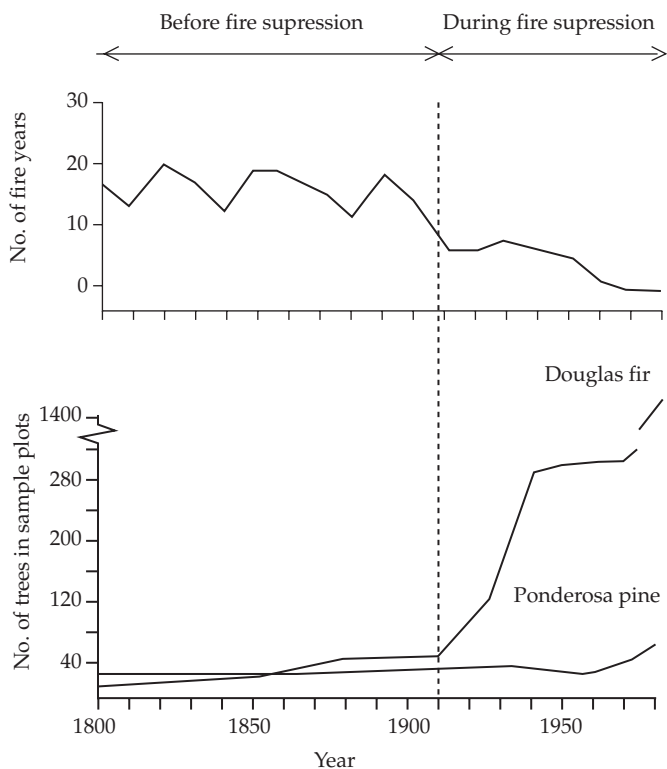
### 1.1 Natural and managed forests

Natural and semi-natural forested landscapes dominate large geographical areas in different parts

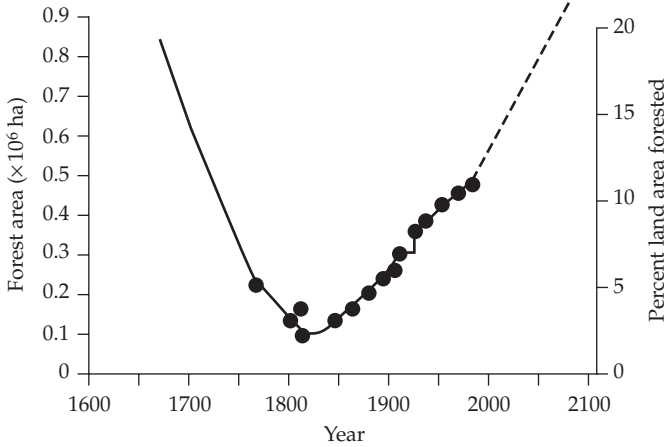
of the world (FAO 2001). The characteristics of these different forests such as their species composition, density, growth rate and age structure are determined to a large extent by environmental factors. The circumpolar boreal forest of North America and Eurasia, grows in regions characterised by low temperatures and snow accumulation in the winter and represents around 20% of the world's forested area. Conifers form the major component of these northern forests but a relatively small number of tree species, 9 in North America and 12 in Fennoscandia and Russia, are dominant (Gordon 1996; Messier and Kneeshaw 1999). In equatorial regions on the other hand, tropical rainforests are noted for their extremely high diversity, with around 70–100 mainly broadleaved tree species per hectare growing in regions characterised by a warm and stable climate with seasonal variation marked by differences in rainfall (Evans 1992). These tropical forests still occupy hundreds of millions of hectares in Central and South America, central Africa and Asia (FAO 2003). Within countries, forests are characterised by the different native species that are adapted to the climatic and edaphic conditions within the region. In North America for example, conifer forests are widespread in northern and western regions, mixed hardwood forests are characteristic of the north-east and in the drier southern regions, pines predominate. In central Europe, beech and oak are among the most important species in native broadleaved lowland forest. Australian forests by contrast are dominated by eucalypts of which there are around 700 species, with fire playing an important role in shaping the forest communities. Most of these forest ecosystems have been influenced to some extent by the activities of people and some forest landscapes have been completely transformed by management and exploitation.

Some changes to forests have been gradual and have occurred through extensive management. So while the area of forests may not have changed to any great extent, the character and species composition of forests has been much altered. In northern Sweden for example, fire has played an important role in the development of multi-storied old-growth forests. In these boreal forests, the 'natural' mean fire-return interval varies from around 50 to 160 years depending on forest type, but fire frequency has been significantly reduced by management and this has influenced the distribution and abundance of fire-dependent hardwood species (Östlund *et al.* 1997). Similar gradual changes in species composition have been observed in parts of North America as a result of selective logging and fire control (Fig. 1.1). In many regions however, there have been dramatic changes to the extent and characteristics of forests through clearance or unsustainable management. The rate at which native forests and woodlands are being lost varies in different regions of the world. In British Columbia, Canada, the current rate of loss of

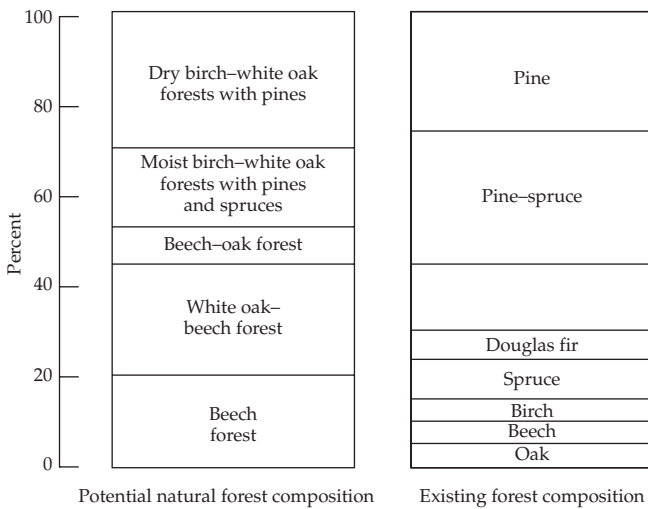
productive forest per decade has been estimated to be less than 0.02%, whereas in California, USA, it is around 0.5% and in Mexico around 13%. In the Amazon basin in South America, current estimates of loss suggest that over 2 million ha, about 6% of the lowland rainforest, would be lost in an equivalent period (Ledig 1992; Pimm 1998). In Europe as a whole, forest exploitation and clearance began centuries ago, with <20% of the native forest of central and western Europe remaining by 1300 (Niemelä and Mattson 1996). This pattern has been repeated to a greater or lesser extent in other temperate forest regions. More recently, that trend has been reversed in many countries but has resulted in forested landscapes dominated by semi-natural stands or plantations (Fig. 1.2). In central Europe, the process of reforestation has in effect converted pre-existing native forest dominated by hardwoods to forests dominated by conifers (Fig. 1.3). As well as restoring forested landscapes, plantations also play an essential role in meeting the projected future demands for timber for fuelwood, for structural and industrial



**Figure 1.1** The effect of fire suppression on species composition of unlogged forests in western Montana, USA. Historic fire sequences derived from fire scars in sample trees show the effect of management on fire frequency. The reduction in fire frequency altered stand structure and species composition, allowing an increase in shade-tolerant Douglas fir (from Anderson *et al.* 1987).



**Figure 1.2** The exploitation and recovery of forest resources in Denmark between 1600 and 2100. The predicted (—) registered (●) and projected (---) trends reveal a pattern of deforestation followed by afforestation using plantations. Similar trends have occurred elsewhere in central Europe and on different timescales, in other countries. In central Europe, along with a recovery in forested areas, is a trend for multiple-use forest management (from Koch and Skovsgaard 1999).



**Figure 1.3** The potential natural composition of forests on glacial sands in a region of the north German lowlands and the current composition after reforestation (from Plochmann 1992).

uses and for conversion into pulp for paper making (Evans 1992; Evans 1999; Nambiar 1999; Sutton 1999).

The increasing commercial importance of plantations is reflected in the major expansion that occurred in the middle of the twentieth century so that now, planted forests occupy millions of hectares worldwide (Table 1.1).

The species selected for plantation establishment reflect the characteristics of the sites available and the planned use of both forest and timber. In commercial plantations, industrial uses such as sawn timber or pulpwood predominate but planted forests can also play a role in environmental protection by reducing soil erosion, for example, and they may provide public amenity as in social and community

**Table 1.1** Approximate regional total plantation area in 2000

	Million hectares
Asia	116
Europe	32
North and Central America	18
South America	10
Africa	8
Oceania (including Australasia)	3

Sources: FAO (2003), [www.fao.org/forestry](http://www.fao.org/forestry).

forests (Evans 1992). Species most commonly used in plantations come from forests in different parts of the world reflecting a change from the direct and often destructive exploitation of natural forests to indirect



exploitation through the selection and establishment of desirable tree species in plantations (Table 1.2). In some extreme cases, entire forest industries may be based on a single introduced species. A good example is provided by radiata pine which was established as an important forest tree in New Zealand in the early 1900s and which now comprises over 90% of the 1.3 million ha of plantation forests (Fig. 1.4) (Kershaw 1989; Bulman 1992).

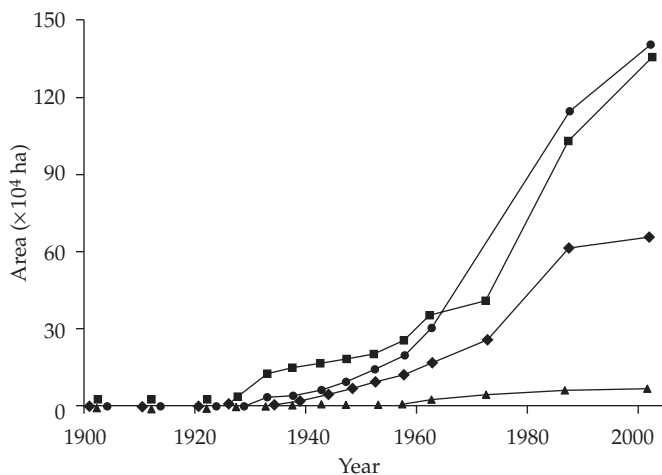
For many industrial plantations, high productivity is often an important factor in species selection. Although native trees are widely used in plantations in both temperate and tropical regions, exotic species can offer a wider choice

and so increase the chances of finding trees that will produce desirable wood of the right quality and quantity on the sites available. Radiata pine in New Zealand provides an illustrative example, with the growth of this species far exceeding that of native species (Table 1.3). Radiata pine can also be established on difficult sites and so it can be of value in land restoration. In south central Chile, plantations of this species have been established in the coastal ranges on soils that have been eroded through excessive agricultural use over 150 years. Native genera such as *Nothofagus*, *Araucaria* and *Fitzroya* are difficult to establish on such soils and also have very long rotation times (Toro and Gessel 1999).

**Table 1.2** Some important plantation species

Forest region	Plantation species
<b>Tropical/Subtropical</b>	
Conifers	<i>Araucaria</i> , <i>Cupressus</i> , <i>Cunninghamia</i> , <i>Pinus</i> spp.— <i>patula</i> , <i>caribaea</i> , <i>elliottii</i> , <i>merkusii</i> , <i>kesiya</i> , <i>oocarpa</i> , <i>massoniana</i> , <i>yunnanensis</i>
Hardwoods	<i>Tectona</i> , <i>Acacia</i> , <i>Gmelina</i> , <i>Leucaena</i> , <i>Grevillea</i> , <i>Meliaceae</i> , <i>Terminalia</i> , <i>Albizzia</i> , <i>Prosopis</i> , <i>Casuarina</i> , <i>Cordia</i> , <i>Triplochiton</i> , <i>Eucalyptus</i> spp.— <i>grandis</i> , <i>camaldulensis</i> , <i>globulus</i> , <i>saligna</i> , <i>tereticornis</i> , <i>robusta</i> , <i>citriodora</i> , <i>urophylla</i> , <i>deglupta</i> , <i>excorta</i>
<b>Temperate</b>	
Conifers	<i>Picea</i> , <i>Pseudotsuga</i> , <i>Abies</i> , <i>Larix</i> , <i>Pinus</i> spp.— <i>sylvestris</i> , <i>radiata</i> , <i>nigra</i> , <i>pinaster</i> , <i>halapensis</i> , <i>contorta</i> , <i>taeda</i>
Hardwoods	<i>Quercus</i> , <i>Fagus</i> , <i>Populus</i> , <i>Eucalyptus</i> spp.— <i>globulus</i> , <i>viminalis</i>

Sources: Zobel et al. 1987; Evans 1992.



**Figure 1.4** The increasing importance of radiata pine in afforestation in the southern hemisphere in the twentieth century. Australia ◆, Chile ●, New Zealand ■, South Africa ▲ (from Burgess and Wingfield 2002).

**Table 1.3** Productivity of the exotic radiata pine compared to native New Zealand species

Species	Mean annual increment m <sup>3</sup> ha <sup>-1</sup> year <sup>-1</sup>
<i>Pinus radiata</i>	20–25
<i>Agathis australis</i>	6
<i>Nothofagus</i> spp.	6
<i>Beilschmiedia tawa</i>	1–2
<i>Podocarpus cupressinum</i>	1–2

Source: Chou 1991.

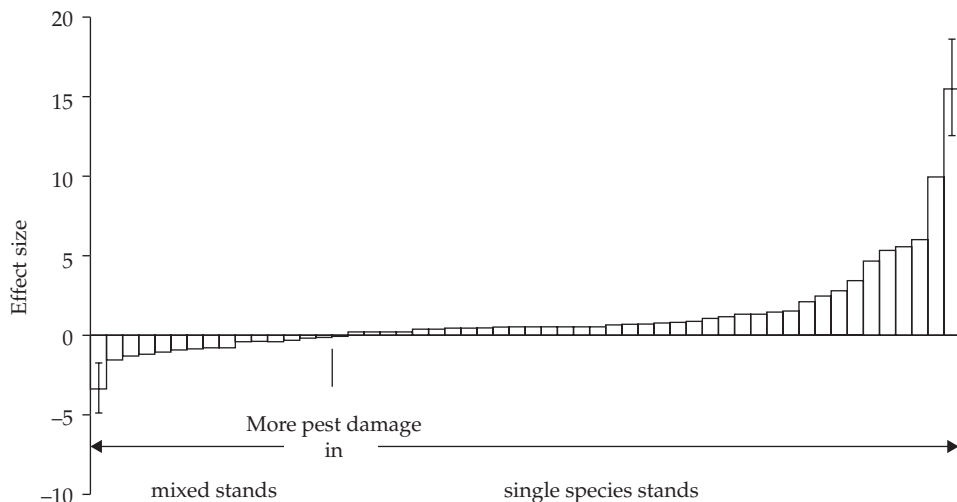
Despite the many advantages of exotic trees in plantation forestry, there are some drawbacks. They can, for example, alter the 'look' of the landscape and so have an impact on landscape values and some species have the ability to invade natural and semi-natural ecosystems (Richardson 1998; Richardson and Higgins 1998; Ledgard 2001). In parts of northern Europe lodgepole pine, which has been introduced from North America, can be difficult to distinguish from the native Scots pine. The seeds of the introduced species are readily dispersed over relatively large distances by wind, raising concerns that if it were to become widely dispersed within the environment, it would appear to have the potential to spread throughout the boreal zone of Fennoscandia and Russia (Knight *et al.* 2001; Sykes 2001). From the pest management point of view, a particular concern is the possibility that introduced tree species may prove to be susceptible to native pests and pathogens. There is also a risk that pests from the trees' region of origin may be introduced, a topic discussed more fully in the following chapter.

## 1.2 Pests and pathogens in natural and managed forests

An important consideration for both forest and pest management is whether the historical changes observed in the structure, composition and extent of forests have affected their overall susceptibility to biotic damage. For example, management-induced changes in the species composition and structure of native forests, or their fragmentation through agricultural and urban encroachment, might alter the frequency or spatial extent of pest or

pathogen outbreaks. The more abrupt changes in species composition associated with the establishment of plantations, especially when exotic species are used, also have the potential to alter the distribution and relative abundance of pests. The development of plantation forestry itself may pose more generalised risks however, because plantation monocultures are frequently regarded as inherently more susceptible to outbreaks of pests and pathogens than 'natural' forests (Andow 1991; Watt 1992; Jactel *et al.* in press; Pautasso *et al.* in press). This perception arises partly as a result of comparison with the extremely simplified and highly disturbed agricultural monocultures where direct insecticidal control of pests is often required. The general assumption is that 'simple' ecosystems such as monocultures are less 'stable' than complex natural ones (Elton 1958; Pimentel 1961). Some studies however, have shown that relatively simple robust communities in temperate regions can recover from periodic disturbance whereas some complex ones in equatorial regions are sensitive to it, making it difficult to generalise about the relationship between complexity and stability (see Begon *et al.* 1996 for discussion). As far as forest insects are concerned, outbreaks do not appear to be less frequent in complex tropical forests and tropical insects seem to fluctuate in abundance just as much as those from temperate zones (Gray 1972; Wolda 1978, 1983, 1992). Natural monocultures such as pines and Douglas fir in the United States and southern beech in New Zealand's South Island occur over extensive areas. These monocultures can often be even-aged as a result of regeneration following fire or other natural disturbance such as windthrow, but they do not appear to be inherently more vulnerable to pest damage than mixed species. There seems therefore to be no general evidence of a simple positive relationship between diversity and stability that is likely to be of value in predicting susceptibility to pest outbreaks in managed forests. Nevertheless, at the experimental level, a number of studies suggest that insect abundance or damage can be higher in single than in mixed-species stands (Fig. 1.5).

Factors that may influence pest abundance in monocultures include concentration of potential food resources, making them easier to find and



**Figure 1.5** Results of a meta-analysis of 54 studies comparing insect abundance or damage in single species and mixed forest stands. Calculation of the 'effect size' took into account the difference in mean values for the two stand types, standard deviation and sample size. A positive value indicates higher densities or damage in single species stands. The studies covered a range of tree species and forest insects (from Jactel *et al.* in press).

exploit, and reduction in effectiveness of natural enemies. Natural enemies for example, may be more abundant and effective in diverse and complex plant cultural systems because they can utilise a greater range of prey. Natural enemies could also feed on non-prey food resources such as nectar, pollen and honeydew, which may be more abundant in mixed forests, and which can increase their longevity and fecundity (Jervis *et al.* 1996). How important these factors are for particular forest pests is likely to depend on the relative importance of natural enemies versus food resources in their population dynamics. Particular aspects of the composition, structure, location or extent of forests, that influence the amount or risk of damage by particular pests are likely to be most important in practice. These aspects are considered further in Chapters 3 and 4. Examples of the ways in which some past and present forest management practices may have indirectly influenced pest damage are discussed in the following sections of this chapter. Particular attention is given to one aspect of plantation monoculture where evidence of the importance of diversity is unambiguous, that of tree to tree 'genetic diversity' and its possible reduction through tree selection or the use of clones.

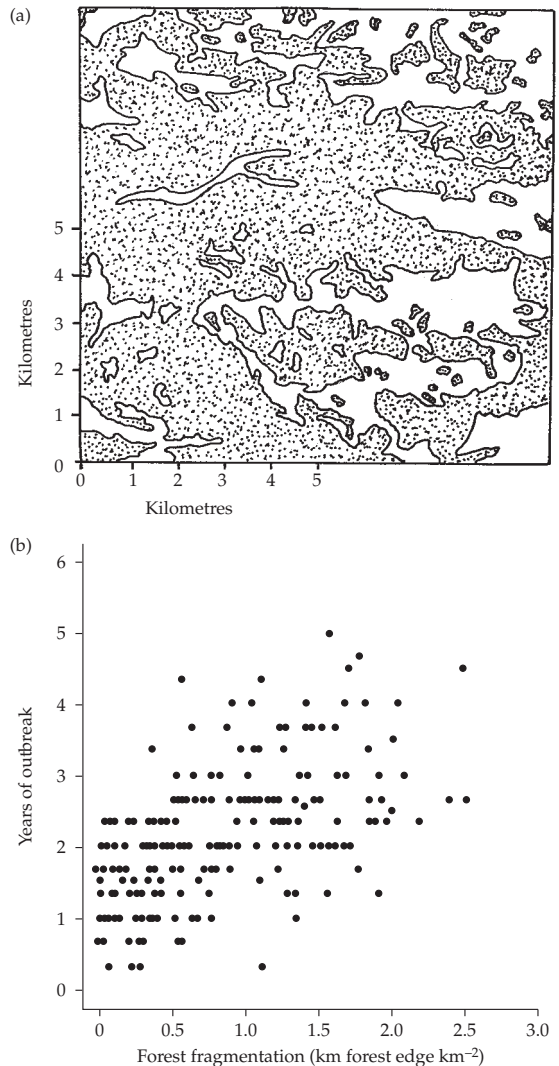
### 1.2.1 Management and exploitation of natural and semi-natural forests

Fire is an important disturbance factor in many parts of the world and when fire frequency is reduced by management there can be long-term effects on the structure and species composition of forests. Demonstrating a direct relationship between changes to the forest and susceptibility to attack by pests and pathogens is not straightforward however. Over long time periods, other factors such as those related to changes in climate may have had an effect on pest population dynamics. Despite these difficulties, an effect of change in species composition seems to have been demonstrated for the western spruce budworm, *Choristoneura occidentalis*, whose main hosts in western North America are Douglas fir and true firs. This defoliator can have a significant impact on the composition and structure of the forest by killing understorey trees and reducing the growth rate and coning of overstorey trees. Over large forested regions of south-western USA, tree-ring analysis of old-growth stands of Douglas fir and white fir has enabled the reconstruction of past outbreaks of *C. occidentalis* showing that they seem

to have become more widespread, synchronous and intense in the late twentieth century (Swetnam and Lynch 1993). Part of the reason for this was the selective logging of ponderosa pine in the Anglo-American settlement period of approximately 1850–1910 and fire suppression after 1900 that resulted in a significant change in the structure and composition of the forest. The continuous mixed-conifer forest that regenerated contained a higher proportion and density of budworm host trees than existed in pre-settlement times (see Fig. 1.1 for similar example). More direct influences of forest management on species composition can also influence susceptibility of forests. In the pine forests of the southern United States, longleaf pine was the dominant species prior to European settlement but large areas were subsequently converted to loblolly pine. This species is less resistant to southern pine beetle, *Dendroctonus frontalis*, and this change of species has contributed to making this bark beetle one of the most significant forest pests of the region (Coulson *et al.* 1999b).

The fragmentation of forests resulting in the break-up of large contiguous areas into semi-isolated blocks, also has the potential to influence pest population dynamics. In Canada, outbreaks of the forest tent caterpillar, *Malacosoma disstria*, occur in boreal mixed forest containing trembling aspen. Outbreaks can spread over thousands of square kilometres and tend to be cyclic in character. Evidence from historical records of defoliation in northern Ontario suggests that increases in the duration of outbreaks may well be linked to the production of smaller blocks of forest. The degree of fragmentation can be quantified by relating the length of forest edge to the area of forest and this suggests that outbreaks last almost a year longer for each 1-km increase in forest edge per square kilometre (Fig. 1.6). An important contributory factor to the change in population dynamics of *M. disstria* appears to be the way in which fragmentation limits natural enemy dispersal. Isolated areas of forest with a high density of *M. disstria* may remain relatively free from natural enemy attack so that in these areas, populations of the defoliator decline more slowly (Roland 1993; Roland *et al.* 1997). The creation of forest edges also appears to have a more direct effect on the population

dynamics of *M. disstria* because a nucleopolyhedrovirus that can cause some outbreaks to collapse is more rapidly inactivated on edge trees through higher exposure to UV light (Roland and Kaupp 1995).



**Figure 1.6** The effect of forest fragmentation on the duration of outbreaks of *Malacosoma disstria* in northern Ontario, Canada. (a) An example of a fragmented forest (stippled) along the interface between the continuous northern boreal forest and a more southerly region of encroaching forest clearance. (b) Mean duration of outbreaks in relation to forest fragmentation or habitat heterogeneity measured as the amount of forest edge per unit area of forest (from Roland 1993).

During the study of *M. disstria*, it was evident that the population dynamics of other boreal forest defoliators did not appear to be affected. Indeed, for pests with limited ability to disperse, fragmentation may actually reduce the likelihood of outbreaks occurring. How general the effects of forest fragmentation are on the dynamics of forest pests, as opposed to effects on habitat quality or biodiversity, remains to be determined by further research.

### 1.2.2 Management of plantation forests

The tree species and sites selected for plantation establishment have the potential to influence the nature and extent of biotic damage. In extreme cases, tree species may prove to be inherently unsuitable for plantation establishment. Growing mahogany (*Swietenia* spp.) in plantation monoculture in its native tropical areas is generally unsuccessful because of the impact of mahogany shoot borers (*Hypsipyla* spp.). This problem might have arisen because of the increased density of planting of a tree that would normally be distributed throughout the forest at a relatively low density but the exact mechanism is not known (Newton *et al.* 1993). For tree species more suited to plantation establishment, susceptibility to particular pests could still be increased by inadvertently selecting a subset of susceptible trees from within an extended natural range. In addition, establishing plantations in a new location may expose trees to new potential pests for the first time.

#### *Species and species selection*

Trees have characteristic natural ranges that are largely defined by the climatic and edaphic conditions to which they are adapted. It is the inter- and intra-specific variation in these adaptive traits that provides the raw material for selection of trees with appropriate ecological adaptations to the sites available for planting. As well as 'matching' species to sites, other important selection criteria for commercial plantations include silvicultural traits such as form and growth rate (Zobel and Talbert 1984; Zobel *et al.* 1987; Evans 1992).

The ranges of different tree species vary enormously in size. Scots pine has both a temperate and boreal distribution and has the distinction of

having the largest continuous range of any forest tree species, extending over 125° of longitude (Critchfield and Little 1966). In contrast, some trees have quite restricted ranges. Radiata pine for example, is one of the most widely used exotics in plantation forestry and yet only grows naturally over 7000 ha in the summer fog belt of coastal California and on two Mexican offshore islands (Moran *et al.* 1988; Savill *et al.* 1997). The range of the Serbian spruce is even more restricted, occurring in a total area of less than 60 ha in the former Yugoslavia (Kuittinen *et al.* 1991).

Within a tree's natural range, variation in climate related to such factors as latitude, altitude and topography, can give rise to regional phenotypes that may be recognised as distinct varieties or even subspecies. Variation related to the local area of origin may also be recognised and used to describe the provenance of the trees (see Zobel and Talbert 1984 for definitions). Some of the climatic variables such as mean annual rainfall and its seasonal distribution together with mean maximum and minimum temperatures can be used to identify the broad geographical location of sites where particular tree species are likely to grow well (Fig. 1.7). However, it is difficult to predict exactly how well trees will 'perform' in a new location both silviculturally and in relation to resistance to pests and pathogens. It is essential therefore that planting trials are conducted prior to the widespread planting of introduced species.

Most tree species, and conifers in particular, are genetically highly heterogenous. In those with discontinuous or isolated populations however, genetic diversity can sometimes become reduced. In radiata pine, between-population diversity is very high but overall, genetic diversity is relatively low compared to some other conifers (Moran *et al.* 1988). The process of selecting native or exotic trees from part of their range for plantation establishment is, therefore, likely to influence the genetic structure of the population (Gömöry 1992). However, given the high levels of variability in most tree populations and their selection primarily for silvicultural traits, this process is unlikely to reduce overall variability for pest resistance traits. The limited range and genetic diversity of radiata pine populations for example, has not prevented



**Figure 1.7** Areas of the world likely to be suitable for establishment of plantations of loblolly pine (▨) identified by a world climatic mapping programme (WORLD). The programme utilises climatic variables related to the amount and seasonal timing of rainfall and variation in temperature (maximum, minimum and annual mean). Description of the climatic requirements of a tree species allows suitable locations to be identified. The natural distribution of loblolly pine (circled) is in south-eastern USA (from Booth *et al.* 2002).

the extremely successful use of this species as a plantation tree.

Trees planted outside their range as exotic species are often highly productive. This is due in part to appropriate species and provenance selection but the fact that introduced trees have 'escaped' attack by pests within their native range is also likely to be important (Gadgil and Bain 1999). These trees can of course be utilised as hosts by insect herbivores native to the region of introduction and the extent to which this is likely to occur can be broadly predicted by species–area relationships (see Brändle and Brandl 2002 for a recent review). The number of invertebrate herbivores associated with native and introduced trees in Britain (Table 1.4) reveals a pattern that has been found in several similar studies in different regions. They show that, in general, many more insect species are found on widely distributed and abundant trees species than on those such as introduced species whose distribution is more restricted. More detailed analysis of the species–area relationship

has enabled the identification of factors, apart from area or other measures of 'abundance', that could influence the number of species feeding on trees. Those that are of particular significance for 'exotic' plantation trees include geographical isolation (Nilssen 1978), chemical distinctiveness (Claridge and Wilson 1982), and 'taxonomic relatedness' to local tree species (Connor *et al.* 1980; Kennedy and Southwood 1984). In Britain, the 'relatedness' of *Nothofagus* spp. to oaks appears to explain why it has acquired a relatively large number of insect species despite being introduced relatively recently and only planted on a relatively small scale (Welch 1981). One of the factors contributing to the relative freedom of pines in the southern hemisphere and eucalypts grown outside Australia from attack by native pests is their distinctiveness from native flora.

While species–area relationships are useful in predicting the likely extent of the 'herbivore load' on exotic trees, they are not helpful in predicting which particular species may cause economic damage. Some species for example have made

**Table 1.4** Number of plant-feeding invertebrates associated with some native and introduced trees in Britain

Native trees	Number of species	Introduced trees
<i>Salix</i> spp.	450	
<i>Quercus petraea</i> , <i>Q. robur</i>	423	
<i>Betula pendula</i> , <i>B. pubescens</i>	334	
<i>Pinus sylvestris</i>	172	
<i>Populus</i> spp.	153	
<i>Fagus sylvatica</i>	98	
	78	<i>Nothofagus</i> spp.
	70	<i>Picea</i> spp.
<i>Fraxinus excelsior</i>	68	
<i>Tilia cordata</i> , <i>T. platyphyllos</i>	57	
<i>Acer campestre</i>	51	
<i>Carpinus betulus</i>	51	
	43	<i>Acer pseudoplatanus</i>
	38	<i>Larix</i> spp.
<i>Juniperus communis</i>	32	
	11	<i>Castanea sativa</i>
<i>Ilex aquifolium</i>	10	
	9	<i>Aesculus hippocastanum</i>
	7	<i>Juglans regia</i>
<i>Taxus baccata</i>	6	
	5	<i>Quercus ilex</i>

Source: Modified from Peterken 2001 after Kennedy and Southwood 1984.

unexpected extensions to their host range. In northern Britain, the winter moth, *Operophtera brumata*, a polyphagous species that causes periodic defoliation of oaks, has more recently caused outbreaks on isolated populations of Sitka spruce (Stoakley 1985; Vanbergen *et al.* 2003).

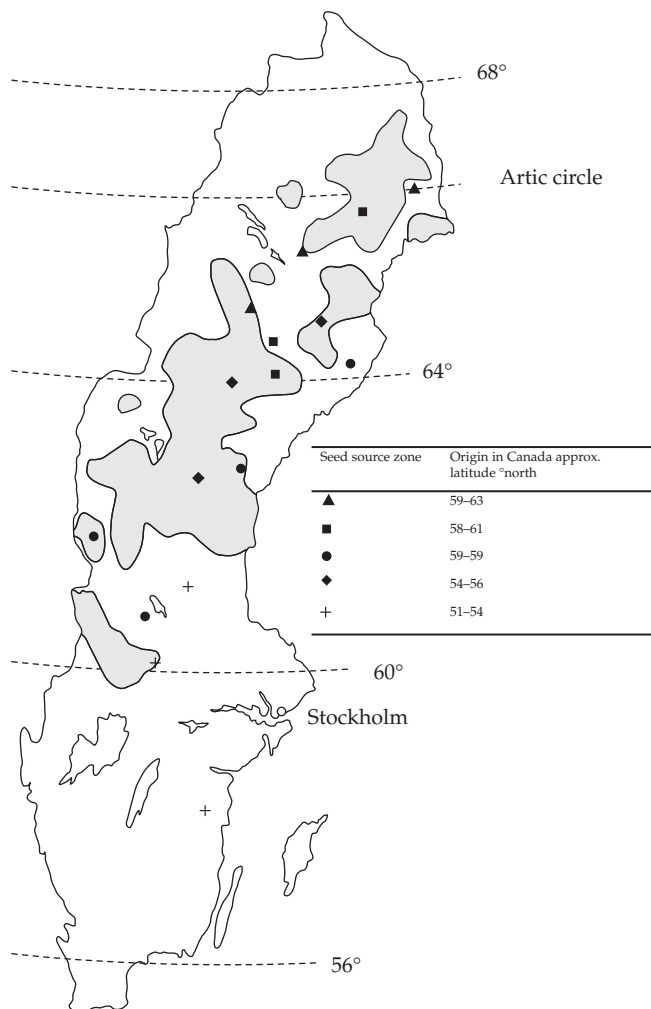
One of the most notorious examples of damage caused by a native pathogen on an introduced tree is that of the North American Weymouth or white pine and white pine blister rust, *Cronartium ribicola*, (Liebhold *et al.* 1995; Maloy 1997; Karlman 2001). White pine was introduced into parts of Europe from as early as the mid-sixteenth century where it became increasingly widespread. It proved to be highly susceptible to the rust which appears to have transferred from relatively resistant pines whose native range is in eastern Asia. The rust was subsequently introduced into North America on infected white pine seedlings in the early 1900s, spreading throughout the range of white pine and resulting in

the most extensive forest disease control effort in forestry in the United States. This example illustrates the importance of effective plant quarantine regulations, which were not in place at the time of these introductions. Introduced pests and pathogens are a threat not only to exotic plantations but to natural and semi-natural forests as well. Examples include the chestnut blight pathogen, *Cryphonectria parasitica*, and gypsy moth, *Lymantria dispar*, in North America, pine wood nematode, *Bursaphelenchus xylophilus*, in Japan and the Dutch elm disease pathogen, *Ophiostoma novo-ulmi*, in North America and Europe (Gibbs 1978; von Broembsen 1989; Niemelä and Mattson 1996).

#### Sites and site selection

Local site conditions can affect both trees and pests and when trees are planted on new sites, the resulting interactions can be difficult to predict. Site factors such as the availability of water and nutrients, pH and rooting quality of the soil, and the degree of exposure can all affect the growth and establishment of trees. Temperature and day length can affect insect development and activity and fungi are likely to be affected by rainfall as well as temperature. The needle blight pathogen, *Dothistroma pini*, is relatively benign in natural populations of radiata pine in California, the United States, where the climate is dry but in New Zealand, transmission rates of the introduced pathogen in the moist climate are high and it can cause significant damage in some plantations of radiata pine (Woollons and Hayward 1984).

The resistance of trees to pests and pathogens is often polygenically controlled (Section 5.3). One of the consequences of this is that variation in the environment related to planting site or other factors can influence resistance expression. It may often be necessary therefore, to conduct trial plantings of the selected species and provenances on a range of sites in the region of establishment, not only to determine effects on growth and form but also to assess their susceptibility to local pests and diseases. The establishment of trials of lodgepole pine in different parts of Sweden provide a good example. Seeds were collected from 'plus' trees in wild stands in western Canada in zones identified as suitable seed sources for target planting areas within Sweden (Fig. 1.8). In these trials, some seed origins proved to be



**Figure 1.8** Location of trials of lodgepole pine seed origins in Sweden. Planting of this species (shaded area) is permitted north of about 60°N. Seedling material was grouped (inset) according to collection zone within the tree's range in western Canada. Each group consisted of several hundred half-sib families collected from open-pollinated 'plus' trees distributed among several different stands. Each group was tested in randomised block trials located at three different forest sites in the appropriate target zone (from Ericsson *et al.* 1994; Karlman *et al.* 1994).

susceptible to damage by *Scleroderris* canker caused by *Gremmeniella abietina*. Young trees were particularly vulnerable when planted on sites in northern Sweden subject to environmental extremes related to altitude and latitude (Fig. 1.9). Stem cankers caused by this disease occur on trees damaged by exposure above the snow cover at high elevations or in cold air depressions and seem to be more common on good quality sites formerly occupied by spruce.

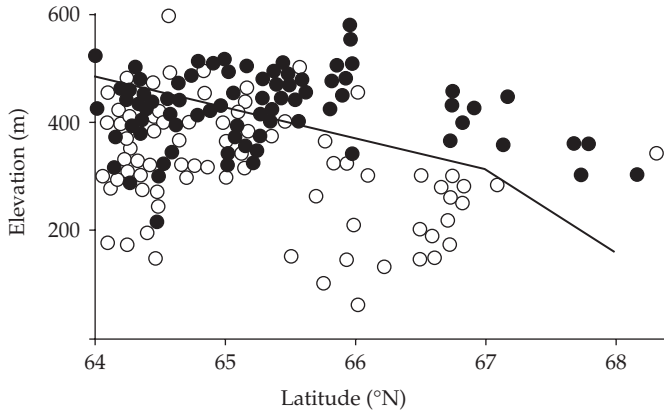
In practice, really comprehensive trials across a range of sites is rarely if ever possible and of course results of small-scale trials may not reflect what will happen in large-scale plantings. Trials are expensive, time consuming and in north temperate

regions, unlikely to cover the whole rotation age and so will not detect damage by pests that attack later in the rotation. However, it should be possible to retain older trial stands of introduced species once commercial planting has begun in order to provide longer-term information on pest vulnerability (Englemark *et al.* 2001).

#### *Tree improvement and clonal forestry*

Although the selection of a subset of trees within a species' range has the potential to alter the genetic structure of the population, for most species this is unlikely to increase the susceptibility of plantations to pests and diseases. The more intensive selection associated with tree improvement programmes





**Figure 1.9** The degree of *Sclerotinia* canker attack in 110, 6–13-year-old lodgepole pine plantations in northern Sweden. The association between damage and exposure to severe climatic conditions, defined partly by the latitude and altitude, resulted in recommendations (line) on the limit of new plantings. ○ disease-free or slightly diseased; ● moderate to severe damage (from Karlman *et al.* 1994).

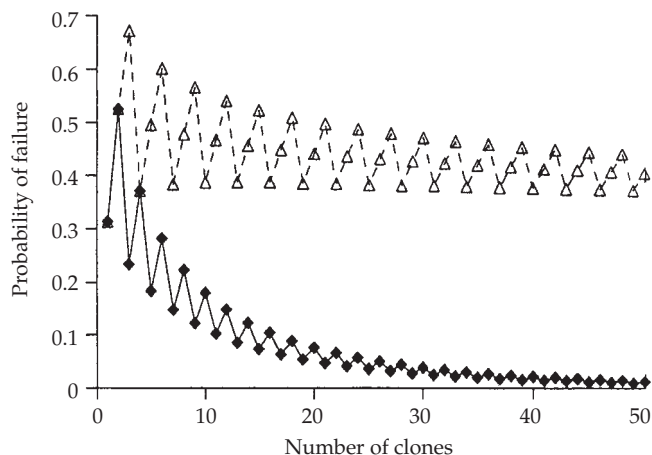
may, however, pose a greater risk. Tree improvement programmes are often based on selection and breeding to increase stem diameter growth and improve form or timber quality. By selecting a subset of 'plus' trees from the wild population or the products of seed orchards in established breeding programmes, a genetic bottleneck might be created, altering the genetic structure of the population and perhaps increasing susceptibility to pests and diseases. In fact, most breeding programmes are designed to maintain a broad genetic base and in the few cases where this has actually been tested, major changes in genetic variability have not been observed (Chaisurisri and El-Kassaby 1994; El-Kassaby and Ritland 1996).

Improvements in tree growth through selection and breeding programmes are often utilised by vegetative propagation of elite plants. In fact, natural clones exist in a number of tree populations such as some temperate broadleaves, where clonal growth occurs through root suckers. In eastern North America, individual clonal aspen may occupy areas of up to 40 ha (Kemperman and Barnes 1976). In England, the introduced field elm rarely produces viable seed and populations are maintained by vegetative reproduction through root suckers (Richens 1983). One of the most common forms of clonal forestry is with eucalypts, particularly associated with the extensive plantings in Brazil, and their use can double volume yields compared to plantations of seed origin (Zobel 1993). Poplar clones are important in many temperate and subtropical countries and clones of conifers

such as spruce and pine are increasingly being developed (Ritchie 1991; Sonesson 2001). While there are clearly significant advantages to the use of clonal trees in forestry, clones can be especially vulnerable to pest outbreaks. For example, monoclonal plantations of poplar in Europe were destroyed by the fungus *Marssonina brunnea* (Zuffa *et al.* 1993).

The risks associated with the use of clonal plants can be significantly reduced by planting many different clones and particular attention has focussed on how many unrelated clones are needed to reduce the risk to a level comparable to that of plantations of seedling origin. The importance of the number of different clones is reflected in the fact that some countries specify in law the minimum number to be used in plantation establishment (Muhs 1993). Risk can be quantified by estimating the probability of failure over a rotation. Failure is usually defined in relation to the level of loss acceptable to forest managers in terms of reductions in tree growth, deformation or mortality. Risk is influenced by a number of different factors and it is difficult and costly to investigate these experimentally over a complete rotation. However, it has been explored using models which have given useful insights into the risks associated with clonal plantations.

In a series of papers, Roberds and Bishir (Roberds *et al.* 1990; Bishir and Roberds 1995; Roberds and Bishir 1997) developed a model based on a population genetics approach. They described the relationship between the number of clones and the risk of catastrophic failure, assuming a simple



**Figure 1.10** The probability of failure of plantations composed of different numbers of clones during a rotation of 50 years. Plantations were assumed to fail when the proportion of surviving ramets was at or below a minimum acceptable level based on silvicultural and other considerations and in the two examples corresponds to 0.50 (▲) and 0.67 (△). Failure probabilities were derived from a model with certain assumptions about mortality of ramets, the genetic control of resistance and the probability of pest attack and ramet survival, details of which are given in the original paper. Despite the simplifying assumptions in this special-case example, results from this and other studies suggest that 30–40 clones provide the same level of protection against failure as a larger number of clones (from Roberds and Bishir 1997).



**Figure 1.11** Willows planted in a mosaic of different clones (Photo Ming Pei).

genetically controlled resistance trait that was selectively independent of desirable traits for which the clones were originally selected (Fig. 1.10). The possible effects of the spatial arrangement of clones were not considered in their model but spatial effects can be important in the management of pests and pathogens. Possible arrangements include random mixtures or a mosaic of different clonal subsets and indicate an important role for silvicultural management in reducing risk of pest damage (Fig. 1.11). In willows for example, mixtures of clones that vary in their acceptability to the leaf beetle, *Phratora vulgatissima*, can delay the rate of colonisation and population build-up

because adults spend time searching for acceptable clones and some of them may leave the stand altogether (Peacock *et al.* 1999).

### 1.3 Forests and the management of pests and pathogens

As we have seen, the characteristics of forests in different countries and their particular history of exploitation and management have produced distinctive combinations of natural, semi-natural and plantation forests. The four examples shown in Fig. 1.12 provide striking contrasts and serve to draw attention to the wider context of pest



**Figure 1.12** Four contrasting examples of forest structure and management. (a) Restoration of native Caledonian pine forest in Scotland. (b) Intensively managed, fast growing plantation of *Eucalyptus* in South America. (c) Bark harvested from cork oaks in southern France. (d) Seminatural sub-boreal forest in Sweden.

management, taking into account the characteristics of pests in different kinds of forest, the intensity of forest management and their relative importance for recreation and amenity as well as reservoirs of biodiversity. These different kinds of forest reflect

different phases in the development of forest management (Table 1.5) and despite the long history of exploitation all may still be represented today within a single country. As the examples discussed in this chapter show, the characteristics

**Table 1.5** Transitions in the exploitation and management of forests

Exploitation of forests	Period
Wild Forest	10 000 BC–present
Managed forest	100 BC–present
Planted forest	1800–present
Planted forest, intensively managed	1960–present
Planted forest, tree breeding	1970–present
Cloning	1990–present
Genetic modification	2000?–future

Source: Sedjo 2001.

of these different forests and the ways in which they are exploited and managed can influence the nature and impact of forest pests and pathogens. Their effective management will depend on the development of programmes of Integrated Pest Management (IPM) that recognise the ecological characteristics of the pests and that are appropriate to the scale and diversity of forests as well as to their economic and environmental value. Some generalised examples illustrate these points.

Effective plant quarantine regulations are an important component of IPM. For those countries where commercial forestry is based on extensive plantations of exotic species, it is particularly

important to identify and take appropriate measures to minimise the risk of introducing specific pests from within the tree's natural range. Should these exotic pests be accidentally introduced, 'classical' biological control and search for resistant seed sources within the tree's native range may be appropriate management responses. For countries with extensive areas of semi-natural forests, dominant native pests may have a significant impact on a regional scale and for these pests, monitoring and risk-rating can increase the efficiency of management by focussing control efforts on restricted high-risk areas. For smaller or more intensively managed forests on the other hand, silvicultural manipulation can make an important contribution to pest management. Behaviour-modifying chemicals such as aggregation or sex pheromones may be useful in monitoring and control but only for those groups of insects where these signalling chemicals play a significant role in their ecology. These and other ecological methods in the management of forest pests and pathogens are discussed in the following chapters. How they may be combined into a truly integrated approach to pest management and how they are influenced by current and possible future changes in forest management are discussed in the final chapter on Integrated Pest Management.

# Plant health

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One of the most spectacular examples of the impact and spread of an introduced forest insect pest is that of the gypsy moth, *Lymantria dispar*, in the eastern United States. This European insect was imported to a Boston suburb by a French amateur entomologist from where it escaped in around 1869 (Leibhold *et al.* 1995). An early account of its transformation from curiosity to one of the most important pests of trees in North America was published in 1899 (Anon. 1999).

Thirty years ago, a French entomologist, named Leopold Trouvelot, was living at Medford, in Massachusetts. He was engaged in carrying on a series of experiments on rearing moths . . . He imported the Gipsy moth, and by some accident, some of the insects escaped from his custody into his own or the neighbours' gardens . . . Had prompt measures been taken, the insect might possibly have been exterminated; but it does not seem to have attracted any attention till about 1880, when the people then living in or near M. Trouvelot's former residence began to be troubled with swarms of caterpillars, though what they were, and whence they came, was then unknown. For several years the neighbouring houses suffered severely, apple- and pear-trees and shade-trees being stripped of their leaves and killed, and the caterpillars creeping all over and into the houses. Nevertheless, they spread very slowly along the street, and into surrounding woods till 1889, when the insects multiplied so much that the caterpillars stripped all the trees in the immediate neighbourhood of M. Trouvelot's old house, and then marched forth in armies sufficient to blacken the streets, in search of fresh provender. A terrible account of the ravages of the caterpillars is given by those who witnessed them. (from Nature 25 May 1899. Reprinted by permission from Nature)

This engaging report highlights a number of important aspects of the ecology and management of an introduced pest, in particular its identity and origin and the relatively long establishment period before populations rise to outbreak levels causing visible and often extensive damage. Following this

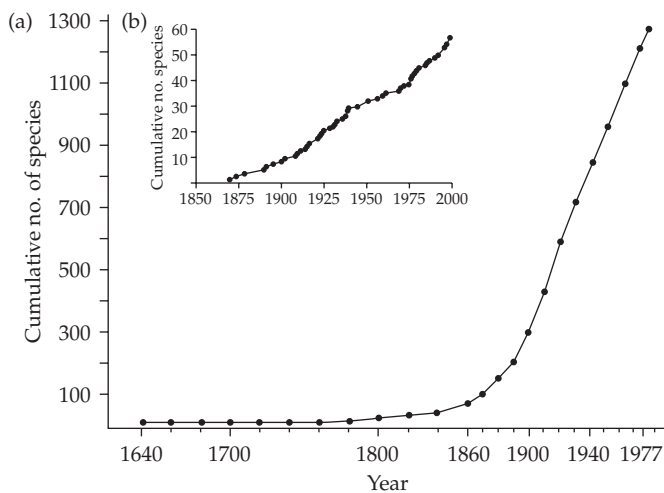
and other early examples of pest introduction, plant quarantine, or phytosanitary regulations have been enacted worldwide. The word quarantine itself has a Latin root meaning 40 and refers to the number of days' isolation imposed on ships arriving in fourteenth-century European ports whose passengers could transmit epidemic diseases (Kahn 1989). Plant quarantine is now usually discussed under the broader topic of plant health which now covers a wide range of measures designed to minimise the risk of new introductions of specific kinds of pest as well as methods that can be used to manage and in some cases eradicate them following establishment.

## 2.1 International movement of pests and pathogens

The introduction of the gypsy moth, *Lymantria dispar* to North America resulted from a deliberate importation. But most introductions of alien pests and diseases are accidental in the sense that they occur as a consequence of the movement during international trade of the plants and plant products with which they are normally associated (Fig. 2.1). As a result of such movements over the last 200 years or so, countries worldwide now harbour many non-native pests and pathogens. In the United States, the number of non-native arthropod species introduced rose rapidly after 1800, largely reflecting the increasing levels of international trade (Fig. 2.2(a)). In New Zealand, a similar accumulation of insects of Australian origin has occurred on introduced *Eucalyptus* spp. (Fig. 2.2(b)). Of course, not all of these introduced species are pests, but those that are have sometimes proved to be extremely damaging in the new environment. Almost a third of the 70 or so important forest insect pests in North America are in fact



**Figure 2.1** The main movements of forest products in international trade (from Liebhold *et al.* 1995, after Laarman and Sedjo 1992). Canada, the United States, Finland, Germany and Sweden account for around 50% of world exports of forest products and the United States, Germany, Japan, China and the United Kingdom, about 45% of world imports (from Hicks 2001).



**Figure 2.2** (a) The number of insects and mites introduced into the 48 contiguous states of the USA from 1640–1977 (from Sailer 1978). (b) Cumulative colonisation of *Eucalyptus* spp. in New Zealand by Australian insects over the last 100 years. *Eucalyptus* is planted as an exotic in New Zealand and about a third of the introduced insects are regarded as serious pests (from Withers 2001).

introduced species (Pimentel 1986). Many of these introductions took place before plant health regulations were recognised as important. Such measures, however, cannot provide a complete barrier to introductions but their implementation has slowed the general rate of introduction and has excluded

key pests against which specific quarantine measures have been targeted. Nevertheless, the introduction and establishment of pests and pathogens continues worldwide and such trends have raised concerns of global homogenisation of the earth's biota (Lodge 1993) (Table 2.1).

**Table 2.1** Some selected examples of alien pests and pathogens that have had a major impact on trees in the area of introduction

Pest	Main hosts	Likely origin	Introduction	Approx. date of introduction or first report
<b>Insects</b>				
<i>Lymantria dispar</i> (Asian form)	Polyphagous especially larch, alder oak and willow	Russian Federation	Western North America	1991–2
<i>Sirex noctilio</i>	Pines	Europe	New Zealand Tasmania Mainland Australia Uruguay Argentina Brazil South Africa Chile	1900 1952 1961 1980 1985 1988 1994 2001
<i>Heteropsylla cubana</i>	<i>Leucaena</i> spp. Leguminous plants native to Central and South America but widely planted in tropical regions	Central and South America	Hawaii Pacific islands, Australia and Asia Mauritius and Reunion Kenya, Tanzania and Madagascar	1984 1985–8 1991 1992
<i>Cinara cupressi</i>	<i>Cupressus lusitanica</i> native to Guatemala and Mexico and widely planted in Africa. Other Cupressaceae	Unknown; occurs in Europe, North America and near east	Malawi Kenya, Zambia and Zimbabwe	1986 1990
<i>Tomicus piniperda</i>	Pines	Europe	Ohio, USA	1992
<i>Anoplophora glabripennis</i>	Maple and other hardwoods	China	USA Austria	1996 2001
<i>Oracella acuta</i>	Pines	USA	China	1998
<i>Trachymela sloanei</i>	Eucalyptus	Origin unknown; native to Australia	California, USA	1998
<b>Pathogens</b>				
<i>Ophiostoma novo-ulmi</i>	Elms	North America Europe	Europe New Zealand	1960s 1989
<i>Bursaphelenchus xylophilus</i>	Pines	North America	Japan Portugal	Early 1900s 1999

Sources: Gibbs (1978), Speight and Wainhouse (1989), Ciesla (1993), Liebhold *et al.* (1995), Savotikov *et al.* (1995), Sun *et al.* (1996), Mota *et al.* (1999), Gadgil *et al.* (2000a), Haack and Poland (2001), Paine and Millar (2001), Ciesla (2003), Tomiczek (2003).

## 2.2 The ecology of invasions

Our knowledge of the movement of pests around the world is, not unexpectedly, dominated by examples of successful establishment and conspicuous

damage. Pests that fail to establish in particular regions excite little comment. It is likely however, that many more organisms are introduced into different geographical regions than successfully establish and not all of those that do become

established actually cause economic damage. In trying to assess the threat posed by particular pests and pathogens, it would be useful to know whether there are characteristic features of the life history and ecology of some species that make them particularly successful invaders and whether some habitats are more vulnerable to invasion than others. These and other aspects of the ecology of invasions in relation to forestry are discussed in detail by von Broembsen (1989), Liebhold *et al.* (1995), and Niemelä and Mattson (1996). Niemelä and Mattson (1996) addressed these complex ecological questions by comparing the relative success of invasion of North American forests by European insects and European forests by insects of North American origin.

Forests in Europe and North America are composed of broadly similar kinds of trees but many more insect species from Europe have successfully invaded North American forests than vice versa (Niemelä and Mattson 1996). This asymmetry in establishment of introduced insects seems to be due in part to the fact that North American forests are extensive and have a greater variety of tree species available as potential host plants while forests in Europe are less diverse and more fragmented. The differences in the extent and diversity of forests between these two regions partly reflect the greater impact of glaciation cycles on European forests together with the reduction in area of these forests as a result of large-scale clearances for agriculture (Section 1.1). Traits that have enabled European forest insects to survive in fragmented and impoverished forests are likely to have pre-adapted them to survival and establishment when introduced into new areas. Differences in life-history traits between European and North American insects also appear to have been important. For example, insects with parthenogenetic reproduction are more likely to establish at low population density than sexually reproducing ones and parthenogenesis is in fact more common among European than North American phytophagous insects. Other aspects of pest biology likely to have survival value in the invasion of new habitats are considered under the three key aspects of the invasion process: *arrival*, *establishment* and *spread* (Elton 1958; Dobson and May 1986; Williamson 1996).

### 2.2.1 Arrival

Some insect pests and pathogens are capable of long-range dispersal and so can reach new geographical regions by natural spread (Pedgley 1982; Nagaranjan and Singh 1990). Adults of the spruce budworm, *Choristoneura fumiferana*, fly at night above the forest canopy and under the right meteorological conditions, can be displaced downwind and even concentrated in forest areas in sufficient numbers to cause outbreaks (Miller *et al.* 1978; Greenbank *et al.* 1980; Dickinson *et al.* 1983, 1986). Insects can also be transported over long distances on prevailing winds. Some of the native Australian insects found in New Zealand are likely to have been transported over the intervening 1800 km on the trans-Tasman air currents (Withers 2001). The sudden appearance of the psyllid, *Heteropsylla cubana* over large geographical areas in Asia was also likely to have been the result of mass movement on air currents (Ciesla 1993). The most important factors influencing arrival however, are those accidents of life history that link organisms to international trade.

Insects that complete part of their life-cycle in bark or wood represent a particular risk of international movement. Larvae of insects in some families of beetles (e.g. Bostrichidae, Buprestidae, Cerambycidae, Curculionidae, Scolytidae, Platypodidae), moths (Sesiidae, Cossidae) and wasps (Siricidae) bore into wood and so may occur in imported logs and timber (Wallenmaier 1989). However, they can also be found in the low-quality timber employed in the construction of wooden crates or pallets which are used to transport a much wider range of goods not normally subject to quarantine inspection. Some insect species may also 'hitchhike' along trade routes and remain undetected long enough to allow introduction and establishment. For example, egg-masses of the gypsy moth, *Lymantria dispar*, can be deposited on inanimate objects such as vehicles parked within infested areas that may subsequently be exported and females of the Asian form, which can fly, have laid eggs on the superstructure of ships in east Russian ports and were subsequently transported to western North America (Schaefer and Wallner 1992).



### 2.2.2 Establishment

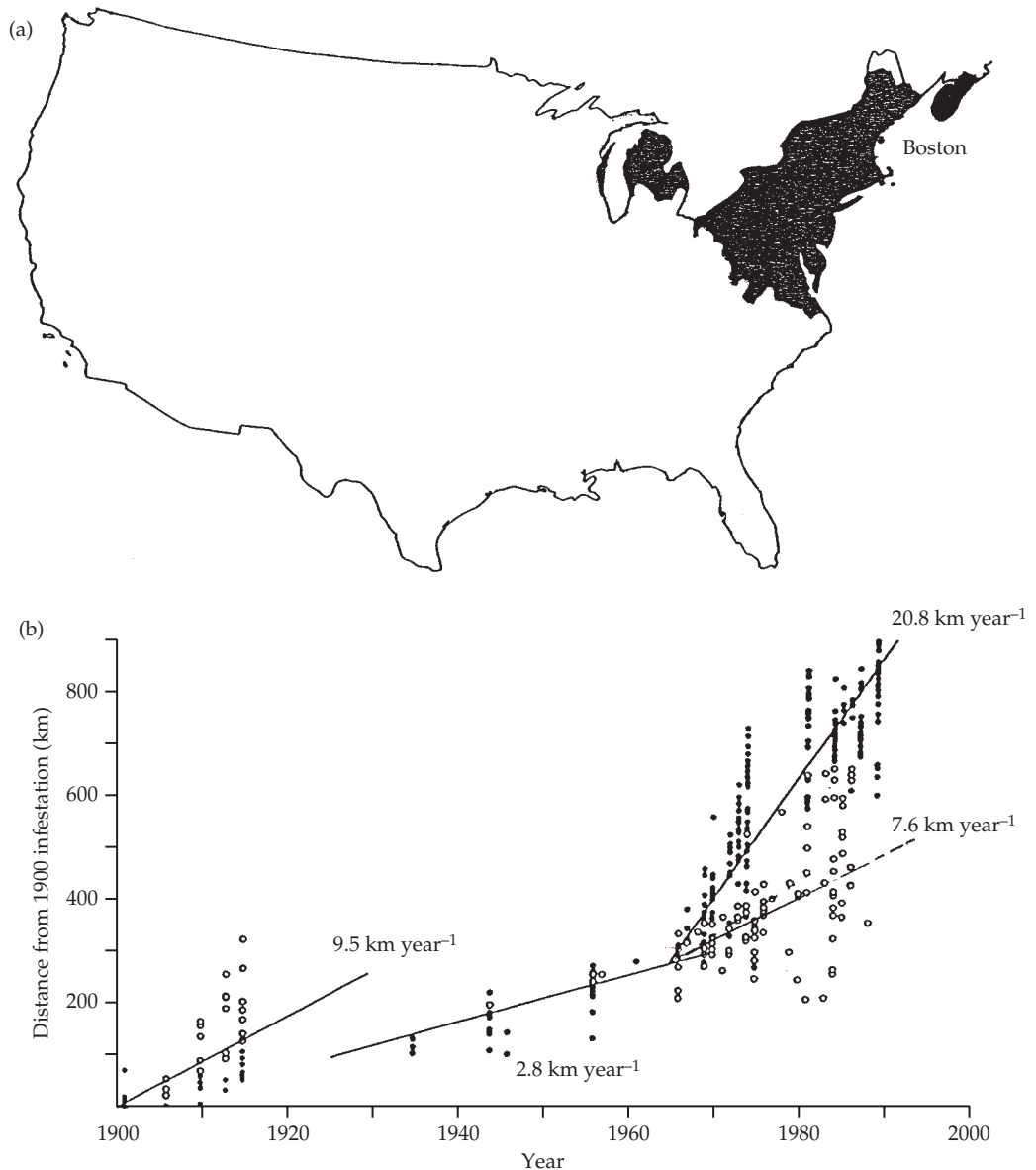
Exotic organisms that become established tend to get noticed. But this does not necessarily mean that they are inherently 'successful' invaders since there is usually no information on the number of times they have arrived and failed to become established. Special factors that influence establishment success or failure are therefore difficult to identify. The frequency of introductions is likely to be an important factor and chance events at the introduction site, such as suitability of weather for insect flight and the proximity of suitable host trees, seem certain to affect establishment success (Crawley 1989). The probability of establishment also increases with initial population size. The minimal initial insect population size below which extinction is likely to occur has been estimated at 10–20 (Shigesada and Kawasaki 1997). But this will be influenced by such factors as sex ratio, age structure, genetic diversity, and breeding system as well as local environmental conditions (Mooney and Drake 1989; Williamson 1989). Parthenogenetic insects such as some scale insects and sawflies have the potential to establish at very low population densities, but even some sexually reproducing species may have traits that favour establishment. The spruce bark beetle, *Dendroctonus micans*, for example is a species in which sib-mating occurs in the natal gallery prior to dispersal so that, in theory, establishment could follow the introduction of a single female.

### 2.2.3 Spread

When organisms are first introduced, there is often an initial 'establishment phase' during which little expansion from the site of introduction seems to take place, due in part to the fact that population densities are initially very low (Shigesada and Kawasaki 1997). Before pests are finally detected however, some spread even at a relatively low level is likely to have been going on for some time. After this initial phase, the rate of subsequent movement depends on a number of different, often interacting, factors including population growth rate, the mechanism of dispersal, the distribution of suitable host plants and the direction of prevailing winds. Organisms capable of long-distance dispersal may quickly establish new populations remote from the parent colony and

such species are likely to be more difficult to contain, control or eradicate. When the chestnut blight pathogen, *Cryphonectria parasitica*, was introduced to the eastern United States, it spread at 30–40 km per year, invading the natural range of chestnut in 40 years. The overall rate of spread of *L. dispar* from its point of introduction in north-eastern United States has, in comparison, been relatively slow (Liebhold *et al.* 1995). The rate of spread has not been uniform however, and the likely causes of this variation illustrate the range of factors that can influence this important process. The map of the current distribution of *L. dispar* shows a number of interesting features (Fig. 2.3(a)). Spread to the north of the introduction site has been less extensive than that to the west and south and there are many sporadic isolated infestations. There is also a discrete population in Michigan resulting from a secondary introduction. Liebhold *et al.* (1992) analysed spread based on historical records of infested counties and identified three distinct periods with different rates of spread (Fig. 2.3(b)). The slow rate of expansion in the period 1916–1965 probably reflects the effectiveness of domestic quarantine that prohibited movement of gypsy moth life stages and established a 'barrier-zone' in which there were intensive control measures. After 1965, the overall rate of spread was clearly much higher but also seemed to be more variable. Several factors seem to have contributed to this. In the new areas being invaded, there was an improvement in the 'quality' of habitat for *L. dispar*, increased human-aided transport of life stages and probably also some reduction in the effectiveness of containment measures. The rate of spread in very cold counties with mean minimum January temperatures of less than  $-13.8^{\circ}\text{C}$  was much slower than in those with less extreme temperatures, suggesting that spread was affected by the reduced population growth that resulted from high mortality of overwintering egg-masses. However, later studies have suggested that habitat quality, based on the abundance of preferred host species in the areas being invaded, is much more important in determining the rate of spread (Sharov *et al.* 1999).

Importing countries are clearly exposed to *ecological risks* that depend in part on the life-history characteristics of potential invaders that affect the likelihood of arrival, establishment and spread. The degree of risk is also influenced by the



**Figure 2.3** The distribution and spread of *Lymantria dispar* in north-eastern North America. In this species, where females are flightless, natural dispersal occurs when first instars are carried short distances on air currents. Human-aided transport results from the accidental movement of life stages, particularly egg-masses. (a) the area generally infested in 1991. (b) temporal spread relative to infestation in 1900 around Boston. From 1900 to 1915 spread occurred at a rate of  $9.5 \text{ km year}^{-1}$  slowing to  $2.8 \text{ km year}^{-1}$  from 1916 to 1965. In the period 1966–1990 the rate of spread was relatively high ( $7.6\text{--}20.8 \text{ km year}^{-1}$ ), especially in counties with less-extreme winter temperatures (mean minimum January temperatures  $> -13.8^\circ\text{C}$  (●) or  $< -13.8^\circ\text{C}$  (○)). Counties also differed in the 'quality' of habitat for *L. dispar* (modified from Shigesada and Kawasaki 1997 after Liebhold *et al.* 1992).

geographical location, nature of the forest estate and patterns of trade of the country concerned. But by taking plant health measures, countries are also exposed to *economic risks* that result from changes to

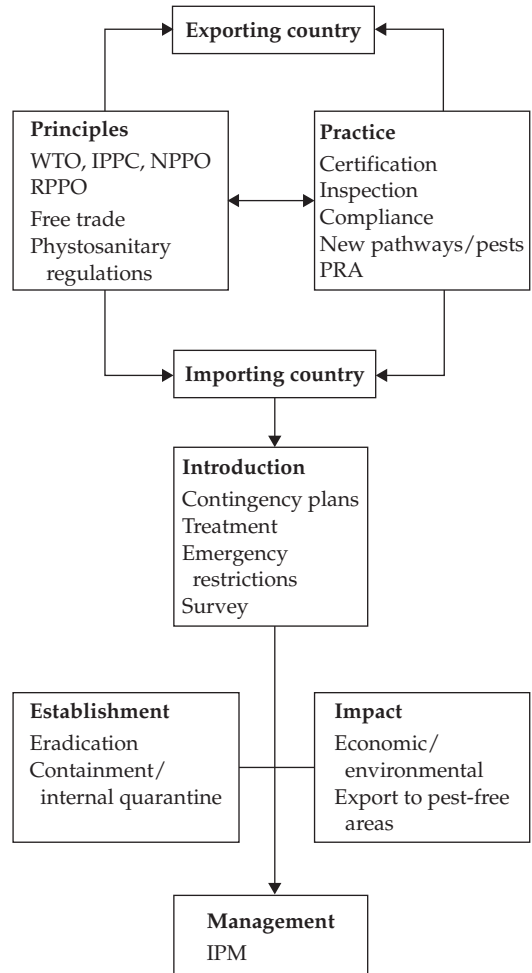
international trading patterns, and both importing and exporting countries will be affected. Balancing these risks has been an important theme of recent developments in plant health legislation.

### 2.3 Plant health: the organisational framework

Co-ordinated efforts to reduce the risk of introducing exotic pests began to be implemented in the first half of the twentieth century through the mechanism of national 'forestry acts' relating to quarantine or phytosanitary measures. Although pests and pathogens continue to be introduced around the world, such measures have in general proved to be highly effective. In New Zealand, legislation enacted in the 1940s led to the development of a quarantine system that has kept extensive plantations of the exotic radiata pine relatively pest and pathogen free (Bulman 1992).

Effective management of phytosanitary risks involves collaboration between international trading partners in the operation of standardised procedures to minimise the probability of introduction and to ensure compliance (Fig. 2.4). National governments are the legislative authorities for phytosanitary measures, but voluntary international standards provide a basis for accommodating the requirements of free trade between nations. The International Plant Protection Convention (IPPC), a multilateral treaty with some 140 contracting governments, has been pivotal in the development of such standards. The IPPC is administered through the Plant Protection Service of the Food and Agriculture Organisation (FAO)—an agency of the United Nations. The guiding principles for assessing risk and formulating appropriate risk-reducing phytosanitary measures are outlined in Table 2.2. For members of the World Trade Organisation (WTO) current guidelines are outlined in the Agreement on the Application of Sanitary and Phytosanitary Measures—the SPS Agreement—for which the IPPC is the source for international standards (Smith *et al.* 1997; Campbell 2001; www.wto.org).

Trading countries within similar geographical regions, and especially those that share common borders, often cooperate through the medium of Regional Plant Protection Organisations (RPPO) within the IPPC. There are currently nine such groupings (Table 2.3) that tend to have the same concerns as National Plant Protection Organisations but may also develop their own regional standards for



**Figure 2.4** Principles and practice of Plant Health. Voluntary international standards accommodate the requirements for free trade following guidelines from the World Trade Organisation (WTO). The International Plant Protection Convention (IPPC) sets phytosanitary standards, with measures enacted under the authority of National (NPPO) or Regional (RPPO) Plant Protection Organisations. Practical application of measures includes certification and inspection of imports in relation to quarantine pests or plant material. Discovery of novel pests or pathways generates new Pest Risk Analysis (PRA). Following introduction, contingency plans are enacted, including appropriate treatment of infested material, survey of port environs and other areas after tracing movement of infested timber or products. Eradication may be attempted following establishment of some pests or alternatively, containment and management.

phytosanitary measures. National Plant Protection Organisations therefore, tend to implement phytosanitary measures within the context of a regional group that faces common phytosanitary risks

**Table 2.2** Plant quarantine principles as related to international trade**General principles**

*Sovereignty*—sovereign right of countries to utilise phytosanitary measures to regulate entry of potentially infested material

*Necessity*—only those measures necessary to prevent introduction of quarantine pests

*Minimal impact*—least restrictive measures with minimal impact on international trade consistent with pest risk involved

*Transparency*—publication of phytosanitary restrictions

*Modification*—phytosanitary measures can become more or less restrictive in response to changed conditions

*Harmonisation*—phytosanitary measures based on international standards within IPPC framework

*Equivalence*—equivalence of different phytosanitary measures with the same effect

*Dispute settlement*—preferably resolved at technical bilateral level

**Specific principles**

*Co-operation*—between countries to prevent spread and introduction of quarantine pests

*Technical authority*—countries to provide one official plant protection organisation

*Pest risk analysis*—based on biological and economic evidence to identify quarantine pests

*Managed risk*—phytosanitary measures formulated on basis of risk management

*Pest-free areas*—subject to verification, to prevent trade restrictions when quarantine pest present elsewhere in the country concerned

*Emergency action*—on basis of preliminary pest risk analysis subject to detailed review

*Notification of non-compliance*—notification to exporting countries

*Non-discrimination*—phytosanitary measures applied without discrimination between countries

Source: Modified from Ikin 1991.

**Table 2.3** Regional Plant Protection Organisations

Organisation	Year established	Member governments
Asia and Pacific Plant Protection Commission (APPPC)	1956	24
Caribbean Plant Protection Commission (CPPC)	1967	22
Comité de Sanidad Vegetal del Cono Sur (COSAVE)	1980	5
Comunidad Andina (CA)	1969	5
European and Mediterranean Plant Protection Organisation (EPPO)	1951	43
Inter-African Phytosanitary Council (IAPSC)	1954	51
North American Plant Protection Organisation (NAPPO)	1976	3
Organismo Internacional Regional de Sanidad Agropecuaria (OIRSA)	1953	8
Pacific Plant Protection Organisation (PPPO)	1995	21

Source: <http://www.ippc.int/IPP/En/rppo.jsp>.

but often following guidelines and standards for phytosanitary measures developed by IPPC.

In practice, RPOs are often the important operational level of plant quarantine and can be an important 'arena' for the development of specific quarantine procedures. For example, to avoid the need for Phytosanitary (Plant Health) Certificates for the separate countries in the single market of the European Union (EU), 'Plant Passports' have been introduced. These certify that material is free from quarantine pests and pathogens and so allow free movement within the EU.

## 2.4 Plant health in practice

### 2.4.1 Quarantine pests

Providing information on quarantine pests is an important step in identifying known risks and so as a general principle, phytosanitary measures should target named quarantine pests. The Regional Plant Protection Organisation, EPPO for example, distinguishes between quarantine pests not present in any part of the EPPO region (the 'A1' list) and those that are already present in some part of it (the 'A2' list) and publishes standard data sheets on them

(Smith *et al.* 1997). Lists of quarantine pests are by their nature subject to addition and amendment. Applying phytosanitary measures only in relation to named pests associated with specific commodities is therefore regarded as less satisfactory than the alternative 'generic' approach based on measures targeted on plants or plant products containing or likely to contain quarantine pests.

### 2.4.2 Quarantine material

One obvious example of high-risk material is bark attached to imported conifer wood since it could harbour bark beetle pests (Haack 2001). Within the EU and in many other regions, bark on conifer

wood originating from certain parts of the world is therefore prohibited. Some examples of prohibited materials subject to regulation within the EU are given in Table 2.4.

### 2.4.3 Pest Risk Analysis

Since the early 1990s, Pest Risk Analysis (PRA) has provided the internationally agreed basis for the justification of phytosanitary measures (Smith *et al.* 1997). PRA provides a formal mechanism for assessing whether phytosanitary measures need to be taken against a particular pest and how rigorous those measures should be. The process itself is essentially qualitative. This is partly because it is

**Table 2.4** Selected examples of plants and plant products prohibited in EU Member States or those subject to special requirements following introduction and movement into and within them

Prohibited	Origin
<b>Plants, other than fruits and seeds, of:</b>	
<i>Abies, Cedrus, Chamaecyparis, Juniperus, Larix, Picea, Pinus, Pseudotsuga, Tsuga,</i> and <i>Castanea, Quercus</i> with leaves	Non-European countries
<i>Populus</i> with leaves	North American countries
<b>Isolated bark of:</b>	
Conifers	Non-European countries
<i>Populus</i>	Countries of the American continent

Special requirements	Origin	Principal target organism	Treatment
<b>Wood, including that without its natural round surface, of:</b>			
Conifers (except <i>Thuja</i> )	Canada, China, Japan, Korea, Taiwan, and the United States	<i>Bursaphelenchus xylophilus</i> (pine wood nematode)	Evidence from indicator system of heat treatment to minimum wood core temperature of 56°C for 30 min
Conifers in the form of packing cases, crates, drums pallets, box pallets or other load boards, dunnage spacers, and bearers	Canada, China, Japan, Korea, Taiwan, and the United States	<i>Monochamus</i> spp. vectors of pine wood nematode	Stripped of bark, free from non-European <i>Monochamus</i> grub holes (i.e. those larger than 3 mm across) and <20% moisture content when manufactured
<i>Acer saccharum</i> other than for the production of veneer	North American countries	<i>Ceratocystis coerulescens</i> (sap streak disease of maple)	Evidence by marking of kiln drying (e.g. kiln-dried, KD) to <20% moisture content at time of manufacture
<b>Plants, other than seed, of:</b>			
<i>Ulmus</i> intended for planting	North American countries	Elm yellows (=elm phloem necrosis mycoplasma)	Official statement that no symptoms of elm yellows observed at or near place of production

Source: Council Directive 2000/29/EC.

difficult to predict the dynamics of a pest in a new environment and partly because it is necessary to balance scientific information and expert opinion with non-scientific factors such as the likely effects of phytosanitary measures on trade. Risk in the context of PRA refers not only to the probability of introduction through a given pathway, but also the likelihood of establishment and of damage following establishment. EPPO has published a series of guidelines that describe the current (FAO) standard for different aspects of PRA (Anon 1993a,b, 1997, 2001). An analysis of the risk to the EU from possible introduction of the pine wood nematode, *Bursaphelenchus xylophilus*, the cause of pine wilt disease and cerambycid beetles in the genus *Monochamus* that can vector it, provides a detailed example of a PRA (Evans *et al.* 1996).

Pest Risk Analysis is concerned with risks from particular pests but since they are usually carried in some way, a proper assessment of risk must also include the commodities or pathways by which they may be introduced. Thus a PRA may be 'pest-initiated', with the focus on a single pest, or 'commodity-initiated', allowing individual assessment of the risk of any of several pests that may be associated with the commodity. The need for a PRA can be highlighted in a number of different ways. A common example would be an unusually high level of interceptions or the discovery of possible new pathways of introduction. When egg-masses of the Asian strain of the gypsy moth, *Lymantria dispar* (Asian gypsy moth), were transported on ships from the Russian far east to western North America in 1991, it was evident that a new pathway had been discovered. When ships were being loaded in Russian ports, the flying females of this strain, which were attracted to lights, laid eggs on the superstructure of the ships and on the cargo. The discovery of this new pathway has focussed attention on those species capable of being transported on the external surface of containers (Gninenko and Gninenko 2002; Gadgil *et al.* 2000b). New threats may arise however, in less obvious ways. For example, independent ecological studies may reveal unsuspected risks or changes in the natural distribution of known pests may open up new routes of introduction through existing trade patterns. The Siberian silk moth, *Dendrolimus*

*sibiricus*, is native to China and south-eastern Siberia but has been spreading north and west for over a century. This pest now poses a threat to European forests not only as a result of natural spread but through existing trade with parts of Russia from which the pest was previously absent (Orlinskii 2001; Gninenko and Orlinskii 2002).

Pest Risk Analysis consists essentially of three stages—*initiation*, *pest risk assessment* and *pest risk management*. The PRA process is initiated once it has been established that it relates to a distinct individual pest, that the PRA area can be clearly defined and that no appropriate PRA is already available either nationally or internationally. The main pest risk assessment, the second stage of the process, is concerned not only with the risk of introduction and establishment but also with the likelihood of economic or other impact. Pest risk assessment is conducted in two parts. First there is a *qualitative* assessment of whether the pest presents a risk by considering such factors as the occurrence of hosts in the PRA area, the suitability of the climate, whether the organism needs to link up with a vector and the possible economic impact. A checklist of the information needed for a full assessment is given in Table 2.5. When appropriate information on the pest is lacking, relevant supporting information may be available for closely related pests. Taking Australia and New Zealand as an example of a PRA area, potentially suitable areas for development of Asian gypsy moth can be determined using CLIMEX or similar models that give predictions of the 'favourableness' of the climate for a particular pest (Fig. 2.5). Predictions are made by integrating the pest's response to factors affecting development such as temperature, moisture and day length based on long-term means at a particular geographical location (Sutherst *et al.* 1991, 1999). Information on climatic suitability can then be integrated with information on host availability and as in the example in Fig. 2.5, on a quantitative assessment of pest performance on different hosts.

The second part of the assessment is a *quantitative* evaluation of the probability of entry and establishment and of the likelihood of economic impact and is carried out when the first part of pest risk assessment indicates a clear threat. Probability is 'quantified' using a scoring system for factors such

**Table 2.5** Check-list of the main information used to assess a possible quarantine pest

1. The organism	5. Potential of the pest for establishment in PRA area
Name and taxonomic position	Ecoclimatic zones
Relationship with known quarantine pests	Occurrence in protected cultivation
Methods of identification	Climatic conditions affecting survival
Methods of detection	Climatic conditions in PRA area
2. Biological characteristics of the pest	6. Control of the pest
Life cycle	Control measures in regular use
Dissemination and dispersal	Records of eradication
Survival of adverse conditions	7. Transport of the pest
Adaptability	Methods of natural spread
3. Geographical distribution of the pest	Pattern of international trade in major host plants
Present occurrence in PRA area	Records of interception on host in international trade
World distribution	Records of international movement not on host
Area of origin	Specific pathways
Overlap of world distribution of pest with that of major hosts	8. Economic impact of the pest
4. Host plants of the pest	Type of damage
Host plants in areas where pest now occurs	Recorded economic impact on each major host
Host plants from above list growing in PRA area	Effect on exported commodities
Nature of host range (i.e. specificity)	Effect of control measures on control of non-target pests
	Side effects from use of plant protection products
	Costs of control

Source: Anon. 1993a.

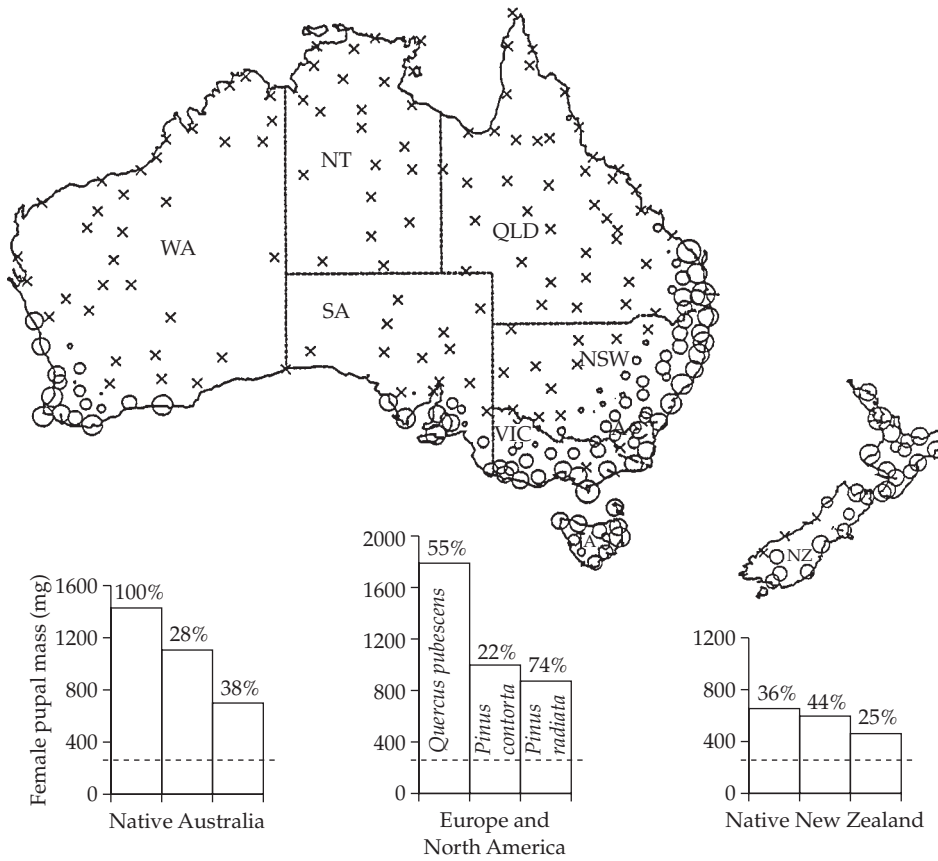
as the number of possible pathways, survival during transit, ease of detection on imported material and whether the pest is likely to transfer to a suitable host when imported. Assessment of likely economic impact will obviously be influenced by the amount of damage observed within the pest's native range as well as by the extent of the area at risk. Obviously a weakness in making this and other assessments in the PRA process is the difficulty in predicting pest behaviour in a new environment, especially for those organisms that are not considered to be important pests in their native range. Examples of such pests include the European woodwasp, *Sirex noctilio*, introduced into plantations of pine in the southern hemisphere (Eldridge and Simpson 1987) and the pine wood nematode, *Bursaphelenchus xylophilus*, a widely distributed but innocuous species in North America that has killed millions of native pines in Japan since its introduction (Yamane 1981; Mamiya 1983; Ikeda 1984; Wingfield *et al.* 1984). The final stage of the PRA process is pest risk management which provides the basis for decisions on whether phytosanitary measures are required and which ones are most appropriate. Emergency PRAs for newly discovered pests or pathways allow for the

application of interim phytosanitary measures pending more detailed analysis.

Pest Risk Analysis is a dynamic area of work and information on newly introduced pests or newly identified pathways within the shifting patterns of international trade is increasingly available on the websites of National and Regional Plant Protection Organisations. Compiling a PRA can be time consuming, but by bringing together scattered information on pests and pathways into a standardised format, PRAs can often identify gaps in knowledge where further research is needed. The process is likely to benefit from the development of a computerised Decision Support System (Cohen *et al.* 1995).

#### 2.4.4 Certification and inspection

Meeting exacting international plant health standards, such as the requirement to remove bark from conifer logs prior to export, is costly for most countries especially those that use labour-intensive methods (Fig. 2.6). Phytosanitary certificates that accompany imported wood and wood products are issued by exporting countries to certify that the material has been inspected and is free from harmful



**Figure 2.5** The predicted distribution of the Asian gypsy moth (AGM), *Lymantria dispar*, in Australia and New Zealand, based on a CLIMEX model. Circle area is proportional to predicted suitability of climate and crosses indicate no predicted survival. The model was based on known effects of climatic factors such as temperature and moisture conditions on the growth and development of AGM in different geographical areas within the existing distribution of the pest. Growth (female pupal weight) and per cent survival of AGM on three of the most favourable mature native trees from Australia (*Callistemon* sp. and *Eucalyptus* sp.) and preferred native Zealand (*Nothofagus* spp.) was compared with a preferred native host species (*Quercus pubescens*) and the exotic conifers *Pinus contorta* and *P. radiata*. The fecundity of females is proportional to pupal weight, with no eggs produced below a threshold (dotted line) of 233 mg. Native trees in New Zealand appear less vulnerable to AGM than those in Australia but *P. radiata*, the main plantation species in New Zealand, appears highly vulnerable (from Matsuki *et al.* 2001).

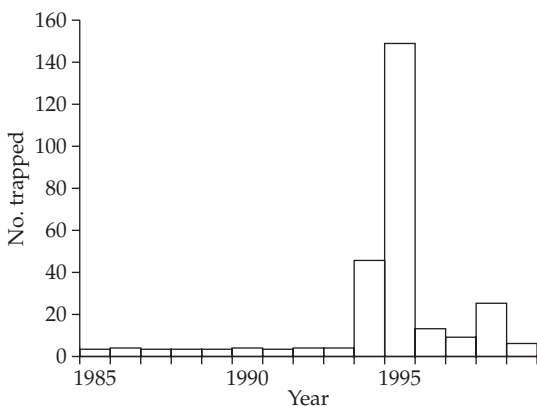


**Figure 2.6** Labour-intensive hand-peeling of logs prior to export. (Photo R. Burgess)

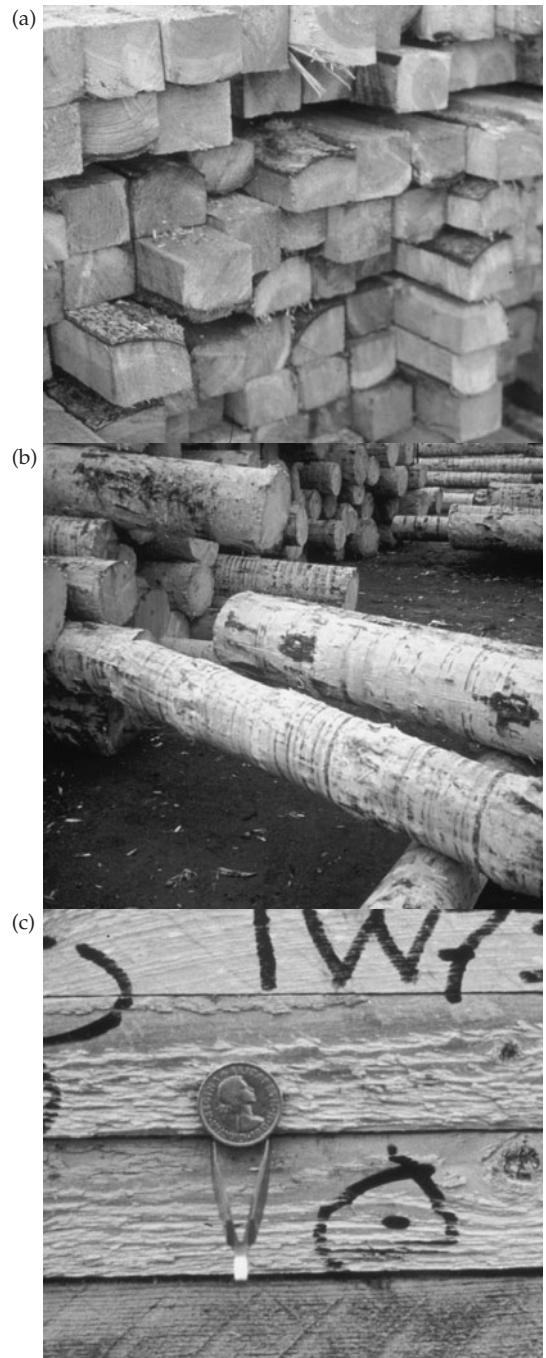


organisms in compliance with the relevant plant health regulations of the importing country. Phytosanitary certificates also provide a mechanism of traceback of 'pathways' through which quarantine pests may have been introduced. Sudden increases in the numbers of the spruce bark beetle, *Ips typographus*, trapped at UK ports were traced in international trading patterns and to low standards of inspection and certification in the exporting countries (Fig. 2.7). Compliance is monitored by a system of inspection to ensure that prohibited materials are excluded and that special requirements have been observed (Table 2.4, Fig. 2.8). In rare cases, regulations may be deliberately circumvented in ingenious ways (Fig. 2.9). Cargoes containing quarantine organisms may be refused entry especially when infestations are severe or consignments from a particular source are frequently contaminated.

Inspection of imported goods is usually done on a sampling basis because the volume of material is often very large. Cargoes identified as 'high risk' are often sampled more intensively and include those previously found to contain quarantine pests or those from regions of the world that are climatically similar to the importing country and that harbour potential pests. A recent survey in New Zealand shows how the degree of infestation of cargoes can vary between different countries



**Figure 2.7** Catches of *Ips typographus* in 200 pheromone traps deployed at 20–25 major ports in the UK. Increased catches in 1994–5 were largely attributed to greater trade with the Baltic States where standards of debarking timber were initially low (data from Gibbs and Evans (2000) and subsequent annual reports).



**Figure 2.8** (a) Low-quality prepared timber with prohibited natural round surface and attached bark. (b) Bark remaining on logs peeled by machine. (c) Holes made by wood-boring larvae (marked). (Photos R. Burgess)



**Figure 2.9** A bundle of low-quality prepared timber with bark attached. The ends of the planks have been modified to conceal the rounded external surface of the trunk that is likely to have attached bark. Endoscopes have now been developed to allow internal examination of timber bundles and such timber would be rejected at ports of inspection. (Photo R. Burgess)

**Table 2.6** Quarantine interceptions in New Zealand (1989–91) of mainly insects, fungi or bark by regional groupings of country of origin

Country of origin	Adjusted mean percent consignments infested
Central Asia	25.7
SE Asia	16.9
Europe	12.6
North Asia	10.2
Unknown	7.7
Australia	7.3
North America	7.0

Source: from Bulman 1992.

(Table 2.6). Although the highest interception rates were from Asia, the greatest risk was from organisms introduced from North America and Europe because these countries have a similar temperate climate.

The effectiveness of inspection depends on the nature of the material and on the manner in which it is transported. Bulk cargoes can often be fully inspected whereas fully loaded containers are difficult to inspect thoroughly and the intensity of inspection varies from country to country. In the USA, <2% of containers are inspected whereas in New Zealand, about 16% of full containers are currently subject to 'door' inspection. The effectiveness of this sampling technique has been tested in a detailed study in which containers that did not appear to contain quarantine organisms were fol-

**Table 2.7** Selected examples of the contamination of imported goods and associated packaging in containers arriving in New Zealand in 1993. Containers were identified as 'high-risk' of containing quarantine material of significance to forestry based on type of goods, packaging and area of origin. A sample of full containers was examined by 'door' inspection at the port and those that were apparently uncontaminated, were reinspected when unpacked at their final destination

	Containers contaminated (%)	
	Door inspection	Follow-up inspection
Goods		
Machinery	25.0	18.7
Sawn timber	22.2	11.1
Stone	41.0	13.0
Packing type		
Crates	43.5	15.3
Dunnage	20.0	12.5
Pallets	14.4	17.0
Overall	23	15

Source: Bulman 1998.

lowed to their destination and re-examined during unpacking (Table 2.7).

Of the high-risk containers, around 23% were contaminated by quarantine material (insects, insect damage, bark or fungi) but a further 15% were found to be contaminated to some extent after unpacking, although relatively few were serious enough to require treatment. While door inspections

at ports are currently considered adequate in New Zealand, further monitoring is needed to ensure 'acceptable' levels of detection. In this study quarantine material was treated by fumigation, burning or burial as appropriate but the relatively high rate of contamination found in this and similar surveys emphasises the importance of effective methods for treating infested cargoes.

#### 2.4.5 Quarantine treatments

Measures to reduce the risk of contamination are taken by the exporting country but quarantine treatment may be applied before or after export depending on the importance of the pest and the degree of risk. If contamination is infrequent and it is easy to detect pests in a commodity, treatments can be restricted to infested cargoes. Treatment of very high risk material prior to export is usually required by importing countries and some examples of EU requirements are given in Table 2.4. Kiln drying of prepared timber in sawmills is a highly effective though relatively costly means of eliminating quarantine pests. This method has been used to treat timber from areas affected by *B. xylophilus*, prior to export (Tomminen and Nuorteva 1992; Dwinell 1997). Some experiments have been done with gamma irradiation and heat treatment of unprocessed logs with limited success although irradiation appears to have potential for surface sterilisation of freshly felled material (Morrell 1995; Lester *et al.* 2000). Treating quarantine pests at ports of entry is most effectively done by fumigation with methyl bromide, details of which are discussed by Roth (1989). Methyl bromide however, is an ozone-depleting chemical whose use is being phased out and alternative treatments are urgently needed (Fields and White 2002).

The discovery of new pathways of pest introduction may lead not only to a requirement for treatment at ports of entry, but also to the introduction of emergency measures to require treatment prior to export. For example, within the EU, solid wood packing material (SWPM) made of unprocessed conifer wood has been found to contain *B. xylophilus*, and this material also appears to have been the means of introduction of the Asian longhorn beetle, *Anoplophora glabripennis*, to North America and

Europe (Haack *et al.* 1997a; MacLeod *et al.* 2002). This has led to the development of a new interim international standard for treatment of SWPM for use in international trade (FAO 2002).

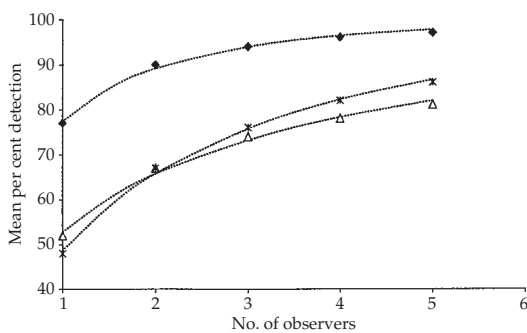
## 2.5 Managing introduced pests

Stringent quarantine regulations and inspection of imported goods are highly effective strategies for limiting the introduction of exotic pests and pathogens. Nevertheless, some manage to evade detection and become established in different countries. In New Zealand, the period 1958–88 saw the introduction and establishment of an annual average of 2.2 new insects and 2.4 fungi affecting commercial forests (Carter 1989). Some pests evade detection on recognised pathways but account also needs to be taken of novel pathways related to shifting patterns of trade and the emergence of new and unexpected pests. Because of the threat posed by *B. xylophilus*, there has been a reduction in trade from North America to western Europe. This has led to an increased trade with Russia and with Belarus, Ukraine and the Baltic states and as a consequence, has exposed western Europe to new plant health risks (Orlinskii 2001). An important way of ensuring a rapid coordinated response to the discovery of newly established quarantine pests is through the development of a contingency plan, as a policy and as an operational document (Hosking 1979; Hosking and Gadgil 1987). Typical plans might include details of responsible personnel, strategies for survey and delineation of affected areas, assessment and evaluation of control options and their implementation, details of equipment stores or suppliers and methods for dissemination of information to the public. A rapid and coordinated response, facilitated by a contingency plan is likely to give the widest choice of control options and where appropriate, the best chance of attempting eradication.

### 2.5.1 Detection and survey

For ports and other areas handling high-risk cargoes, routine surveillance may be necessary including, for example, the use of pheromone-baited traps to detect bark beetles (Fig. 2.7). If several detection traps were used within the restricted area of

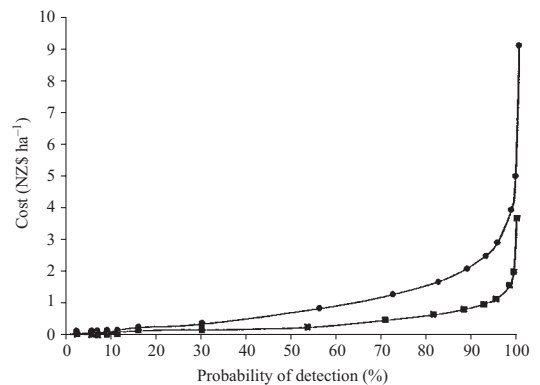
a port, they could significantly reduce the number of beetles dispersing into the surrounding area and so have an effect similar to that of mass-trapping (Section 8.2). Detection surveys can be extended to included port environs and nearby forest areas and carried out either as a routine or only after the discovery of heavily infested cargoes or of new unmonitored routes of entry for quarantine organisms. More widespread surveys may become necessary when it seems likely that infested material has been transported inland. Where adequate records exist, it is often possible to trace the movement of infested material along major transport routes to timber-processing areas or other industrial sites so that further sampling can be done in forests likely to have been exposed. Surveys should be designed to give the best chance of detection for a given effort with the intensity of sampling proportionate to the perceived risk. The main purpose of surveys is to define the extent of the infestation so that a programme of management can be initiated. The sampling methods used for surveys will depend to a large extent on pest biology. The use of pheromone-baited traps will obviously depend on the availability of synthetic pheromones whereas effective visual surveys require that disease symptoms or organism damage are distinctive. When foliage symptoms such as yellowing or browning are visible from the air, aerial surveys can be



**Figure 2.10** Predicted rates of detection of simulated pest damage in plantations and in mixed urban forested parks around a major port by between one and five independent observers. Damage was represented by paint or tags on stems, branches or foliage or by using coloured stakes to represent recently killed trees. Surveys were done by driving (◆) or walking (▲) along forest plantation roads or by walking through three parks (X) close to the port of Auckland, New Zealand (from Bulman *et al.* 1999).

a highly effective method of rapidly surveying large areas (Section 3.4.1). Since most of the survey area can be covered by aerial surveys, detection efficiency rather than sampling intensity determines the probability of detection (Carter 1989).

A quick response is usually needed when surveying for introduced pests and pathogens. Differences in the visibility of symptoms together with variation in spatial distribution within the forest mean that it is rarely possible to optimise survey methods. In plantations that are easily accessible, visual surveys from track or roadside are a convenient sampling technique and experimental trials have illustrated some of the factors that affect the efficiency and costs of sampling. Bulman *et al.* (1999) simulated biotic damage on plantation trees and in areas typical of partially wooded parks in urban areas around ports. Stems, branches or foliage were marked with paint or tags to represent damage and coloured stakes used to represent highly visible recently killed trees. The ability of observers to detect 'damage targets' at different distances from the road were compared when walking or travelling in vehicles moving at different speeds. Time-limited walking surveys were also done in urban parks. When surveying from vehicles, speed was important, with detection rates not unexpectedly decreasing with increasing speed and for both types of survey, with distance from the road. Detection rates close to the road were high



**Figure 2.11** Estimated cumulative costs and associated probabilities of detection of introduced pests of radiata pine. Combined probabilities of detection were calculated for aerial survey, roadside survey and random survey. Some of the assumed detection efficiencies have been tested experimentally (Bulman *et al.* 1999). Costs were calculated for high (●) and low cost (■) forest locations based on travelling distance to and from the forest (from Carter 1989).

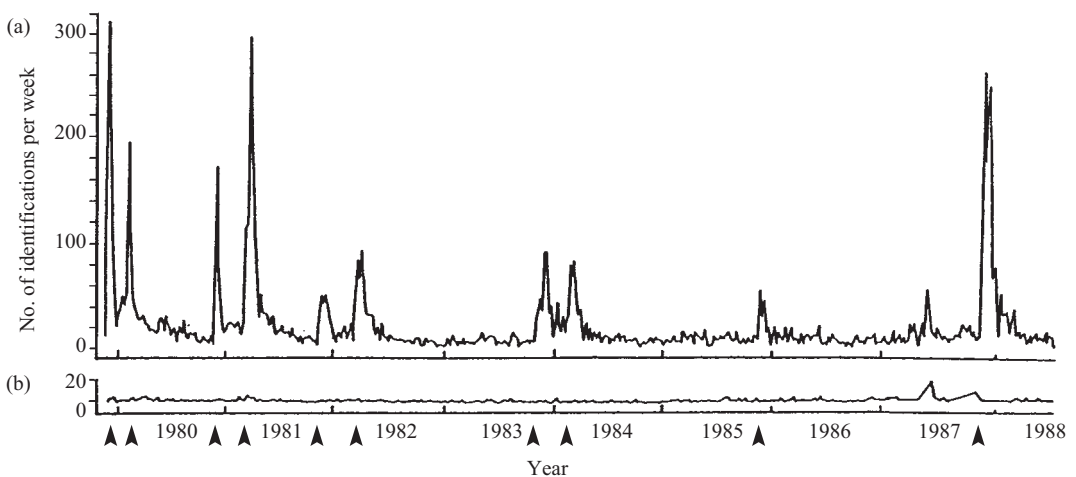
(>85%) for both low-speed driving (15 km h<sup>-1</sup>) and walking surveys but this dropped to 30–70% for damage 40 m from the road. The probability of detection tended to increase with the number of observers used and in the forest, drive-through surveys gave the best results overall (Fig. 2.10). Information was used from these studies to estimate the probability of detecting infestations in forests for different survey intensities. Different methods of survey (e.g. aerial and ground surveys) can be combined to increase the probability of detection. However achieving a high probability of detection is very costly (Fig. 2.11).

Introductions are often discovered accidentally or reported by the public or workers in the forest industry. Further information on pest distribution and frequency of occurrence can often be obtained following requests through the media for additional samples (Fig. 2.12). Such requests increase awareness of pest problems and can be supplemented by dissemination of more detailed information on pest biology and damage and on possible control, including activities such as aerial spraying about which there is likely to be public concern (Fig. 2.13).

### 2.5.2 Containment and eradication

Once the extent and severity of infestations is known, quarantine areas may be defined with appropriate restrictions on movement of pests and contaminated

material. Where information is available on pathways of movement and dispersal following introduction, measures to minimise further spread can be implemented. The effectiveness of measures to reduce spread will depend to a large extent on pest biology, in particular on the number of generations and the method and extent of dispersal. The example of the eucalypt leaf-mining sawfly, *Phylacteophaga froggatti*, in New Zealand illustrates the importance of early detection and of pest biology on the likely effectiveness of containment or eradication strategies (Fig. 2.14). This insect has highly effective wind-assisted dispersal and can be moved on vehicles and infected foliage. It has several generations per year in New Zealand and was too widely dispersed on discovery to attempt eradication. For some introduced pests that are not widely distributed, the establishment of clearly defined areas subject to internal quarantine can be highly effective in containing or at least slowing their spread. Within the EU, the designation of such areas, together with regular detection surveys in surrounding uninfested areas allows phytosanitary measures to be maintained for internal trade by designating the pest-free areas as Protected Zones. This strategy was adopted for management of the spruce bark beetle, *Dendroctonus micans*, introduced into England and Wales in the early 1970s. The beetle was well established when it was first discovered but it had spread relatively



**Figure 2.12** The effect of 10 publicity campaigns (▲) conducted through radio, TV and newspaper advertising in south-eastern Queensland requesting samples of suspected *Cryptotermes brevis* (West India drywood termite) frass or wings. Many different kinds of insects were identified in the samples (a), almost half of which contained ants or ant debris. A relatively small proportion of samples (b) contained the exotic termite. This analysis illustrates the strong but short-lived response to publicity (from Peters B. C. 1990).

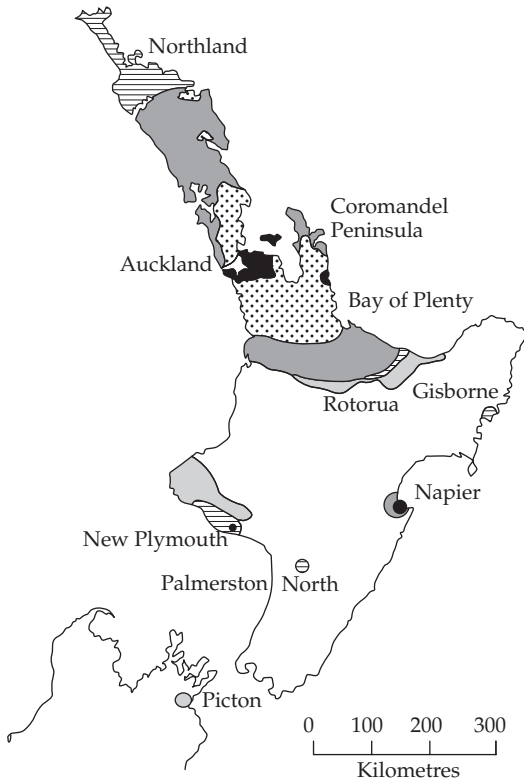


**Figure 2.13** Getting the message across in public awareness campaigns; posters and even beer mats can be effective! Internet sites are also now widely used.

slowly owing to its semi-voltine life cycle. The highly successful containment strategy adopted for this pest has prevented colonisation of the major spruce-growing areas of northern Britain for over 20 years (Box 9.5). This example, and that of the gypsy moth, *Lymantria dispar*, in North America (Box 9.7), demonstrates that slowing the rate of spread of well established introduced pests can be a cost-effective strategy for managing them.

Eradication is usually one of the main options to be considered when introduced pests are first discovered. Following introduction of the brown-tail moth, *Euproctis chrysorrhoea*, to north-eastern USA in

the nineteenth century, a direct, although somewhat labour intensive approach was adopted (Fig. 2.15)! Strictly defined, eradication is the elimination of every individual of a species from a geographical area that is sufficiently isolated to prevent reinvasion (Newsom 1978; Myers *et al.* 1998). However the term 'eradication', is sometimes misleadingly used to describe the local extermination of an isolated population within a much more widely infested area such as in the control of *L. dispar* in the eastern United States (Dreistadt and Weber 1989). Such operations are really part of a suppression and containment strategy. Eradication is an attractive and simple-sounding



**Figure 2.14** Spread of *Phylacteophaga froggatti*, a common pest on eucalypts in Australia, following its discovery in Auckland, New Zealand in 1985. The distribution is shown at the end of the following years: ● 1986, ⊙ 1988, ● 1989, ● 1990, ⊙ 1991 (from Withers 2001).

strategy that seems particularly appropriate for a newly introduced pest, offering the best opportunity to eliminate populations before they become widely established. The method therefore has considerable appeal to managers in affected industries not least because there is necessarily greater financial involvement of government or government agencies in eradication than for many other control programmes. The appropriateness of the method for particular pests, however, will depend on a number of different factors. These are discussed in detail by Dahlsten *et al.* (1989) and Myers *et al.* (1998).

The obvious economic benefits from successful eradication programmes include removing the need for long-term control, the elimination of damage to trees and avoiding loss of exports to areas that are free of the pest. Annual losses resulting from damage

caused by non-native forest pests in the United States have been estimated to be about \$2.1 billion (Pimentel *et al.* 2000). Usually however, the information required for a proper economic evaluation for particular pests is not available. In theory, the costs of eradication should be lower than the short- to medium-term cost of damage and control but in practice, these parameters cannot be realistically assessed in the face of a quarantine emergency involving pests or pathogens whose population dynamics in the new habitat are unknown. When new pests are introduced, quick action and decisions are necessary because delay could affect the prospects of success or failure. In general therefore, the precautionary principle usually operates, with eradication being attempted where appropriate, provided that the initial estimates of monetary and environmental costs are not excessive. Evaluation of environmental costs should include the possible consequences of extensive use of pesticides in the eradication programme (LeVein 1989). More detailed studies of economic impact may be possible while an eradication programme is in progress so that, where necessary, programmes can be reassessed. The importance of re-evaluation of large-scale containment and eradication programmes is illustrated by the campaign against the white pine blister rust, *Cronartium ribicola*. This fungus which is of Asian origin, causes disease of white pines and has a complex life-cycle involving secondary hosts in the genus *Ribes*. It was introduced to western North America on shipments of eastern white pine seedlings from France in 1910 and eventually spread throughout the range of western white pine from British Columbia to New Mexico causing significant losses. The extensive campaign to contain and control this disease was the largest in the history of US forestry and millions of dollars were spent unsuccessfully on control, including attempts to eradicate *Ribes* hosts (Maloy 1997).

Success in the eradication of insect pests is most commonly associated with the sterile-male release programmes aimed at the screwworm fly, *Cochliomyia hominivorax*, in the southern United States and Libya, North Africa (Knippling 1985; Myers *et al.* 1998). One of the most important factors in the success of the sterile-male technique is that the relative proportion of released males in



**Figure 2.15** Manual removal of the highly visible 'nests' of overwintering larvae of *Euproctis chryorrhoea* in north-eastern USA in an attempt to reduce the spread and eradicate this pest. Following introduction from Europe in the 1890s, this insect spread much more rapidly than *Lymantria dispar*, which had been introduced some years earlier. The hairy caterpillars, which posed a public health hazard, defoliated broadleaved trees and shrubs. While *L. dispar* continues to expand its range, *E. chryorrhoea* populations collapsed naturally and this insect is now restricted to isolated north-eastern coastal areas.

the population increases as the insect population declines. Sterile males therefore become increasingly effective in preventing successful mating of females and the population is driven to extinction. In contrast, in programmes of eradication relying on direct control with insecticides, spraying is most effective in reducing large populations but it becomes less efficient as the population declines. Eliminating the last few individuals therefore can be disproportionately costly, both economically and in terms of environmental impact, although of course very small populations are more vulnerable to extinction. Determining the end point of an eradication campaign is not straightforward because once pests are at very low density, it is difficult to detect them. Eradication may appear to have been achieved when in fact very low density populations still persist. Recovery from low

population density, explosive population dynamics and high dispersal ability are characteristics of many insects pests that reduce the likelihood of successful eradication programmes (Table 2.8).

Factors that influence the decision to attempt eradication include how widely established the pest is when first discovered, how well it appears to be adapted to the new environment and how much potential it has to reinvade. The perceived economic and environmental threat as well as the availability of appropriate control methods are also important considerations. Chemical or microbial insecticides may be used to target insect pests directly but for the eradication of pathogens, the destruction of diseased trees is usually the only option with a chance of success, although this can be very costly. For pathogens that are transmitted by insect vectors, destruction of trees is much less effective because a single tree missed can



allow a large number of insects to emerge and disperse over a wide area. It may therefore be several years after the end of intensive eradication programmes before success can be established.

Pests which are highly localised or which have specialised requirements, low reproductive rates or limited rates of dispersal can usually be eradicated more easily. The European house borer, *Hylotrupes bajulus*, which infests seasoned softwood, was eradicated from southern Australia following introduction in the 1950s. This was achieved largely by

**Table 2.8** Ecological or life-history characteristics likely to affect the success of eradication programmes against introduced pests

Probability of success	
Increased	Decreased
Localised/specialised requirements	Highly dispersive or readily transported by man
Restricted host range	Cryptic habit, difficult to detect
Low reproductive potential	Parthenogenesis or sib-mating
Poor dispersal	High reproductive potential
Species at limit of range	Reinvasion likely

inspecting and fumigating houses containing timber imported from Europe (Eldridge and Simpson 1987).

The apparently successful campaign to eradicate the white-spotted tussock moth, *Orgyia thyellina*, from largely urban areas in New Zealand is a model example (Box 2.1). New Zealand has a history of pest interceptions and introductions and contingency plans were in place to enable rapid response and planning. Key features of the campaign were a broad-based expert steering group, rapid response following initial discovery, the use of a microbial (*Bacillus thuringiensis*) rather than chemical insecticide and an effective publicity and information campaign. During and after the campaign, priority was given to environmental assessment of the effects of *Bt* and to monitoring for health effects in residents living in the control area.

## 2.6 Plant health and the emergence of new pests and pathogens

The increasing globalisation of trade is likely to lead to an increase in the international movement of both

### Box 2.1 Eradication of white-spotted tussock moth *Orgyia thyellina* in New Zealand

Prior to its discovery in New Zealand, *O. thyellina* had not been recorded outside its native range in Asia where it is not regarded as a serious pest.

It was discovered by a member of the public in 1996 but had apparently been present for at least a year. Surveys were used to define the infested area within the residential suburbs of Auckland. In common with other lymantriids, egg-masses on plant material or even inanimate objects were the likely means of introduction. The life-cycle is relatively complicated with spring and summer generation females that can disperse by flight and autumn generation females that are flightless and lay overwintering eggs. Rosaceae are the preferred hosts but larvae will also feed on willow, oak, birch and native beech.

Attempted eradication was complicated by the fact that the infested area was relatively large and lay within residential areas. The programme ('Operation Evergreen') was coordinated by an expert group and based in part on existing generalised contingency plans. Microbial control using *Bacillus thuringiensis* var. *kurstaki* (*Bt*) was selected as the most appropriate method for direct control over

such areas. In the first phase of control, nine ultra-low volume aerial applications were made over an area of 40 km<sup>2</sup>, starting after hatch of the overwintering eggs in 1996. There was also some targeted ground spraying. The main aim was to ensure that early first generation larvae were exposed to at least three applications of *Bt*. Further intensive spraying was done in 1997 within a more restricted area. Some initial monitoring of efficacy was done using live females in traps to attract males. But subsequent identification and synthesis of the sex pheromone, allowed thousands of traps to be deployed within the formerly infested area. Failure to catch male moths over an extended period indicated successful eradication.

A public awareness campaign was a particularly important part of the programme, with TV and radio advertising, public meetings and 'hot-line' information numbers. A 2-year health monitoring scheme was also operated for residents exposed to the microbial sprays. Programme costs were estimated at \$NZ12 million. Key references: Hosking 1998a,b; Gibbs 1996.

quarantine organisms and of organisms whose damaging potential is not yet recognised. But increasing trade is not the only factor favouring the emergence of new pest problems. If global temperatures increase in line with those predicted by climate change models (Section 9.4.2), pests may become established in areas that were previously unsuitable. With the more widespread planting of exotic species, native pests, and pathogens may adapt to the new hosts, not only having a local economic impact but posing a threat to the trees in their region of origin (Coutinho *et al.* 1998; Roux *et al.* 2000). For example, the eucalyptus rust, *Puccinia psidii*, seems to have originated on native

Myrtaceae in South America but causes serious damage in plantations of exotic eucalypts and now poses a threat to eucalypts in their native habitat as well as in plantations in other countries. An additional risk from pathogen introduction is that novel vector pathways may be established. This may be illustrated by the example of oak wilt caused by *Ceratocystis fagacearum* in North America. In its native region, this pathogen is vectored by sap-feeding nitidulid beetles which are relatively inefficient vectors. European oaks are highly susceptible to this pathogen and the oak bark beetle, *Scolytus intricatus*, is a potential highly effective vector (Gibbs *et al.* 1984; Yates 1984).

### Box 2.2 Dutch elm disease

Although elm is not a significant forest tree in Europe, the history of the development of Dutch elm disease provides a fascinating insight into disease dynamics and illustrates some unexpected consequences of the international movement of pathogens.

Dutch elm disease, so named because some of the earliest studies were done in Holland, was originally attributed to the wilt pathogen *Ophiostoma ulmi* transmitted by scolytid bark beetles (predominantly *Scolytus scolytus* and *S. multistriatus*). Elms are infected when spore-carrying beetles feed on twig bark in the tree crown during maturation feeding. The fungus enters through beetle feeding wounds and spreads through the xylem. As with other vascular wilts, disease transmission via root connections with infected trees is also possible. The presence of the pathogen and the tree's response to it results in disruption of xylem flow producing characteristic yellowing and wilting of foliage as the disease develops. The beetle vectors breed in the bark of moribund trees and adults of the next generation are often contaminated with spores from fruit-bodies of the fungus developing in the bark, completing the disease cycle during maturation feeding on healthy trees.

There have been two epidemics in Europe (Fig 2.16 (a)). During the first, caused by *O. ulmi*, some trees were killed by successive reinfection, perhaps 10–40% of elms in some countries, but many survived the death of some branches in the crown. The second epidemic was much more serious however, because it was caused by a related but much more aggressive species, *Ophiostoma novo-ulmi* and resulted in the death of most mature elms. The ultimate origin of the aggressive pathogen is uncertain but both *O. ulmi* and *O. novo-ulmi* are introduced species in Europe

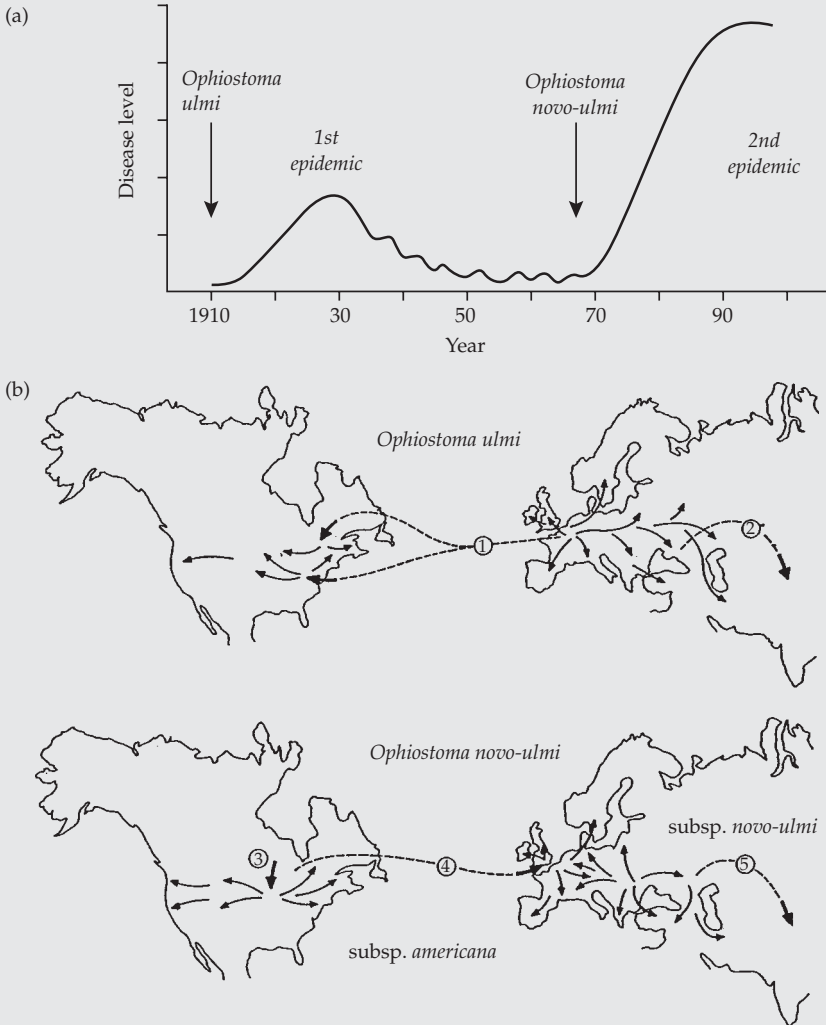
and the epidemics need to be interpreted in the context of the international movement of the causal organisms.

*Ophiostoma ulmi* spread through Europe, into south-west Asia and eventually into North America during the 1920s to 1930s (Fig 2.16 (b)). The epidemic eventually declined in Europe but not in North America where the native elms were much more susceptible, even to the less aggressive *O. ulmi*. In North America, the disease was transmitted by a native bark beetle, *Hylurgopinus rufipes* and the European *S. multistriatus* that had been previously introduced. Two subspecies of the aggressive *O. novo-ulmi* were implicated in the second epidemic—subsp. *novo-ulmi* (previously called the Eurasian or EAN form) and subsp. *americana* (previously the North American or NAN form). During the 1940s an aggressive fungus similar to subsp. *novo-novo-ulmi ulmi* appears to have been introduced to North America. Its introduction went unnoticed largely because the American elms were so susceptible to the original *O. ulmi*. The aggressive fungus subsequently evolved into subsp. *americana*, the fungus that was introduced into western Europe during the 1960s (Fig 2.16 (b)). At around this time, subsp. *novo-ulmi* in eastern Europe was moving westwards into western Europe and eastwards into Eurasia.

The movement of the pathogens, as well as their bark beetle vectors, via international trade has resulted in overlapping distributions of two highly pathogenic subspecies together with the original *O. ulmi* in central Europe. This has provided opportunities for the emergence of new pathogenic forms through hybridisation and introgression.

Key references: Gibbs (1978), Brasier (1990, 1995, 2000a, 2001), Brasier and Kirk (2001), Webber (2000), Konrad *et al.* (2002).

## Box 2.2 Continued



**Figure 2.16** (a) Two epidemics of Dutch elm disease in north-west Europe. The first, which was caused by *Ophiostoma ulmi*, declined naturally. In the 1970s to 1980s, a second epidemic caused by the more aggressive *O. novo-ulmi* killed millions of elms and mature trees disappeared from many towns and rural landscapes (Brasier 1996). (b) Movement of the two Dutch elm disease pathogens around the world. Small arrows represent natural migration from probable sites of introduction and large ones, subsequent spread via importation of infested timber. *O. ulmi*, responsible for the first epidemic, appeared in north-west Europe around 1910 and was introduced into North America in the 1920s (1) and Eurasia in the 1930s (2). An aggressive fungus similar to subsp. *novo-ulmi* was introduced to North America, probably during the 1940s (3) and subsequently evolved into subsp. *americana*. This subspecies was introduced into Britain around 1960 (4). From its presumed origin in eastern Europe, subsp. *novo-ulmi* spread naturally and was introduced into Asia during the 1970s (5). In western Europe, the distributions of *O. ulmi* and the two aggressive subspecies now overlap (from Brasier 1990).

The recent complex history of Dutch elm disease illustrates the potential for rapid evolutionary change within pathogen populations and the emergence of new pathogenic forms as an unpredictable

consequence of the international movement of plant pathogens (Box 2.2).

The introduction of exotic pathogens into a geographic area could result in hybridisation with

related native species already present provided that they have the potential to occupy a similar niche and that there is some degree of sexual compatibility. If an exotic pathogen or a new hybrid causes symptoms similar to those induced by native species their true nature may not initially be recognised, delaying identification as well as any measure to close pathways of introduction and initiate management programmes. An example of a recently discovered hybrid pathogen is that of *Phytophthora* disease of alder. This novel pathogen appears to have resulted from hybridisation

between *P. cambivora*, a pathogen of hardwood trees other than alder and a species close to *P. fragariae*, a specialised strawberry pathogen (Brasier *et al.* 1999). It illustrates the potential within some pathogenic organisms for evolution of novel hybrids or variants with new host ranges (Brasier 1995, 2001). The international movement of pathogens is likely to increase the opportunities for hybridisation and the possible emergence of new pathogenic forms and serves to emphasise the importance of plant health regulations in the management of pests and pathogens.

# Risk, monitoring and prediction

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The ability to anticipate where pest outbreaks are most likely to occur and to detect those outbreaks in their early stages of development can significantly improve the efficiency and effectiveness of pest management. Information on which forests are most at risk may allow monitoring to be concentrated in smaller and more clearly defined areas and detection of incipient outbreaks allows time for planning control measures. To make a qualitative or quantitative assessment of the risk of attack and likely extent and intensity of damage to the forest, it is necessary to consider not only the characteristics of forests or the particular sites where they grow but also the nature of the pests themselves.

The life history and outbreak characteristics of pests and pathogens, such as whether outbreaks tend to be localised or to spread rapidly to affect surrounding areas, have an important influence on their impact on forests and forest ecosystems. A slowly spreading root pathogen affects forests on a different temporal and spatial scale than an aggressive pathogen that can be spread over large areas by insect vectors. Bark beetles that normally feed on moribund host material and depend on high levels of environmentally-induced stress to allow successful breeding in living trees, typically only cause damage in localised areas. Aggressive bark beetles on the other hand, which are capable of pheromone-mediated mass-attack, can affect forests on a landscape scale. Some defoliating Lepidoptera even have the potential to cause outbreaks on a regional scale. Such differences are important in assessing the threat posed by different kinds of pest and pathogen as well as the need for and extent of monitoring.

The recognition that outbreaks of particular pests may be more likely to start within certain forests and that the amount of damage they cause can vary from site to site has spurred the development of

methods for characterising those forests. Although for most pests accurate prediction of the location or timing of outbreaks is not possible, broad estimates of the risk to particular forests can often be made and are of considerable practical value. Many different characteristics of managed or semi-natural forests such as tree species composition or age, or the attributes of sites such as altitude, degree of exposure or soil structure, have been associated with the risk of pest outbreaks. An important aspect of assessing risk is that the process of risk-rating itself may identify particular attributes of the stand that could be modified by appropriate silvicultural management with the aim of reducing risk or at least minimise losses. These aspects are discussed further in the chapter on the role of silviculture. The overall contribution that risk-rating, monitoring and prediction make to pest management will depend on the nature and extent of damage to trees, the value of the stand and the intensity of forest management.

### 3.1 Defining risk

In describing different aspects of risk, terms such as *risk*, *hazard*, *susceptibility*, *resistance* and *vulnerability* have been used and defined in a variety of ways. In forest management, risk and hazard are often used interchangeably but in other contexts, these terms have specific meanings. In industrial health and safety legislation, for example, hazard refers to something with the potential to cause harm and risk to the likelihood of harm from a particular hazard. Similar definitions have been adopted for hazard and risk posed by trees in urban environments (Lonsdale 1999). In the context of risk-rating for forest pests, terms have not been used consistently in different studies. 'Risk' may refer to the probability of an outbreak occurring or the probability of damage or loss

as a function of pest abundance and tree susceptibility (Paine *et al.* 1984; Shore and Safranyik 1992; Benz *et al.* 1993). 'Hazard' is often equated with risk or used more specifically as a measure of the amount of stand damage that would occur in the event of an outbreak (Paine *et al.* 1983; Reynolds and Hard 1991; Reynolds and Holsten 1994a). Other terms have also been used in different ways. 'Vulnerability' for example, may refer to the probability of tree mortality or growth reduction from a given level of insect attack (MacLean 1980; MacLean and Mackinnon 1997) or to the stand response to attack (Luther *et al.* 1997). 'Susceptibility' can be the probability of a forest being attacked (MacLean 1980; Luther *et al.* 1997), the ability of a stand to support an epidemic (Benz *et al.* 1993) or the amount of defoliation (MacLean and Mackinnon 1997) or stand characteristics that affect the likelihood of attack and damage (Shore and Safranyik 1992).

The terms used for different aspects of risk need to be clearly defined and yet be sufficiently inclusive to accommodate the considerable variation in sophistication, complexity and biological realism of different risk-rating methods. As far as possible in interpreting different published risk-rating methods, *risk* is used in this chapter to refer, depending on context, to the probability of an outbreak occurring or the likelihood of damage in a particular stand, taking into account pest population density and stand susceptibility. *Susceptibility* and *resistance* are broadly defined as the ability of stands, respectively, to support or resist development of pest outbreaks either through variation in tree-related characteristics such as resistance traits or density in the stand, or to stand characteristics such as species composition that can influence the development of outbreaks. *Vulnerability* refers to the probability of tree damage or mortality from a given level of insect attack. Use of the term *hazard* is avoided.

### 3.2 Pest ecology and risk assessment

Several attempts have been made to identify ecological characteristics that tend to be associated with forest insect pests (Nothnagle and Schultz 1987; Hunter 1991, 1995). Some traits such as overwintering in the egg stage or high reproductive and dispersal potential do seem to be commonly

observed among outbreak species. But describing pests in terms of their outbreak rather than their life-history characteristics has provided more useful general insights into their damaging potential and so can be a useful starting point for an overall assessment of risk.

The characteristic features of outbreaks such as their frequency, intensity, rate of spread, duration and area affected tend to vary with different kinds of pest. These different characteristics have been used to classify outbreaks into two basic types—*gradients* and *eruptions*—that reflect underlying differences in pest population dynamics (Berryman and Stark 1985; Berryman 1987, 1999). Gradient type outbreaks are characteristic of pests whose population density largely reflects a proportional or 'graded' response to local environmental factors. Outbreaks of gradient pests are characteristic of particular sites or locations where environmental conditions are especially favourable. Good examples are the so called 'silvicultural pests' whose damaging potential is largely determined by local forest management practices. The pine weevil, *Hylobius abietis*, for example, breeds in moribund or recently fallen trees, a resource that is usually scarce and unpredictable in unmanaged forests. In managed forests in northern Europe, clear-felling provides abundant root-stumps for larval development, resulting in high adult populations that attack seedling trees replanted on the site (Section 4.1). Tip and shoot moths associated with particular stages in the growth of even-aged plantations provide another example and outbreaks of these pests tend not to spread to other areas and subside once the resource has been utilised or conditions return to normal. Eruptive outbreaks also tend to develop locally but they can be self-perpetuating, spreading out from initial foci, sometimes over extensive areas. Scarce resources or the action of natural enemies are important factors keeping populations of eruptive pests at low density, but when the effect of these constraining factors is reduced outbreaks can develop rapidly. Aggressive species of bark beetles such as mountain pine beetle, *Dendroctonus ponderosae*, southern pine beetle, *D. frontalis*, and the spruce bark beetle, *Ips typographus*, are examples of eruptive pests. For these bark beetles, outbreaks may be triggered by the abundant resources available after windblow or when host resistance is reduced following prolonged periods of

dry weather. But at high population density, even relatively resistant trees can be successfully colonised following pheromone-mediated mass-attack so that outbreaks once started may be less sensitive to environmental conditions and can be self-sustaining as long as suitable hosts are available (Raffa and Berryman 1987; Raffa 1991; Paine *et al.* 1997).

The pattern of gradient and eruptive outbreaks over time is influenced by temporal changes in environmental factors such as the availability of food resources or by the operation of negative feedback processes that can regulate population growth, such as the action of natural enemies or the effects of induced resistance in host trees. Time delays in the operation of negative feedback processes can result in population cycles and these are usually associated with forest Lepidoptera. Cycles vary in periodicity and amplitude but, commonly, peaks in abundance occur every 8–11 years, although a few species have a relatively long period between peaks of abundance (Myers 1988, 1993; Berryman 1996). Regular cycles usually only occur in part of an insect's geographical range. In larch budmoth, *Zeiraphera diniana*, for example, populations cycle within the subalpine larch-cembra pine forests that grow in relatively dry valleys of the European Alps (Baltensweiler 1993; Weber 1997), whereas cycles of the autumnal moth, *Epirrita autumnata*, occur on mountain birch that forms the tree line in northern mountainous areas of Fennoscandia and north-western Russia (Ruohomäki *et al.* 2000). Some cyclic pests, however, are not confined to localised areas but spread over large areas of forest and may even cause damage on a regional scale as observed in spruce budworm, *Choristoneura fumiferana* (Myers 1988; Candau *et al.* 1998; Gray *et al.* 2000). Spatial synchrony in density fluctuations, which is a feature of the dynamics of some forest pests, may be caused by factors such as dispersal or weather factors that can entrain population fluctuations over extensive areas (e.g. Fig. 6.11) (Liebhold and Kamata 2000).

The classification of outbreaks, albeit in broad terms, provides a useful basis for assessing the damaging potential of particular pests and for determining whether risk needs to be measured on a local or landscape scale. This information can be of value in deciding which management or control

methods are likely to be most appropriate for the pests concerned.

### 3.3 Quantifying risk

An essential part of the process of constructing indices of risk is the identification of factors that appear to be associated with or reflect the level of risk. Quite commonly, the underlying causal relationship between such factors and, for example, local pest population dynamics or tree susceptibility, is unknown and therefore many risk indices are developed empirically. This is often done at a local level in the context of specific pest–tree interactions and the index is often constructed retrospectively as, for example, when stand or site characteristics are linked with the level of mortality after an outbreak. Indices derived in this way often do not take account of the vulnerability of the stand, that is, the relationship between pest population size and the amount of damage. A common problem with such indices is that they do not adequately reflect risk in other areas, that is, they lack predictive power. Constructing indices which allow susceptible trees or stands to be identified in advance usually requires much more information about the relationship between pest abundance and damage, and about the attributes of the stands that influence the transition from endemic to epidemic pest populations. Some stands of trees may be 'resistant' to the local build-up of pest populations, but they can sustain an outbreak once started and so are vulnerable to outbreaks of eruptive pests that spread into them from surrounding susceptible forests. Spatial scale, from local to the landscape or even the regional level, can therefore be important in assessing risk and consequently in managing pests.

Identifying potential risk factors often depends on knowledge and experience of particular forests and their associated pests since it is usually impracticable to test experimentally the large range of factors that may influence outbreaks. The relative importance of different risk factors is usually determined by trial and error but the Analytic Hierarchy Process, a method for analysing complex decision problems, may help in determining the relative importance of risk factors (Zahedi 1986; Saaty 1990; Vargas 1990). This method has not been widely applied in forest pest management but Reynolds and Holsten (1994b)

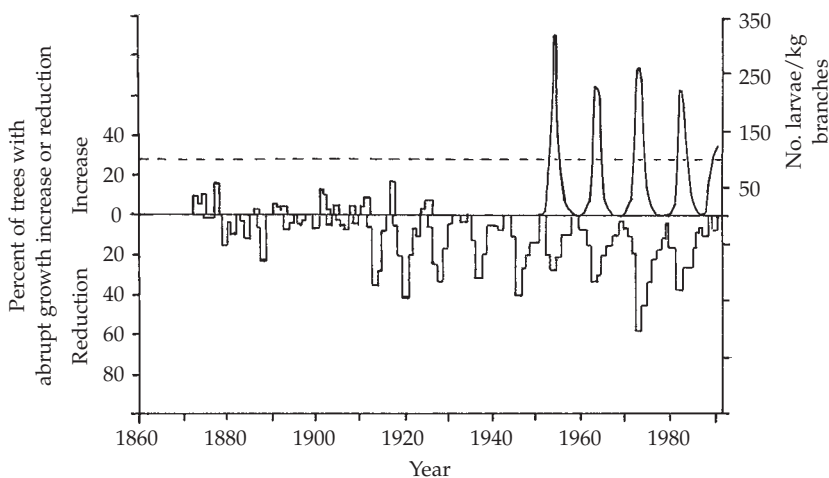
provide an outline example of its use for assessing risk factors for outbreaks of the spruce beetle, *Dendroctonus rufipennis*. Another way of identifying predictor variables for classifying risk is the method of Classification and Regression Trees (CART) analysis, a non-parametric method that can use variables measured on a range of different scales (Breiman *et al.* 1984; Verbyla 1987). The method is used to develop a binary decision tree by sequentially selecting predictor variables to split the data set into classes. At each decision stage, a predictor variable is selected that produces two new classes, each of which is more homogenous and which differ most from each other. Experimental examples of its application include determination of the soil characteristics that affect site susceptibility to the pathogenic fungus, *Heterobasidion annosum* (Baker 1993) and stand conditions that influence infestation by the roundheaded pine beetle, *D. adjunctus* (Negrón *et al.* 2000).

Some examples of different risk factors and the construction of risk indices are considered in the following sections.

### 3.3.1 Outbreak history

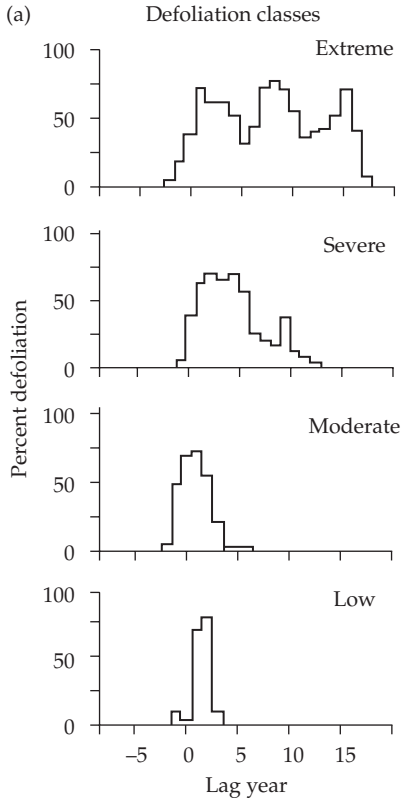
Records of outbreaks or cumulative levels of damage or defoliation compiled from annual surveys can be useful in identifying forests where outbreaks

appear to be more frequent (Shepherd 1994). Where such surveys reveal a cyclic pattern in pest population density within particular areas, it is obviously much easier to predict the location and timing of damage. One of the best studied examples of cyclic population behaviour is that of the larch bud moth, *Zeiraphera diniana*, an important pest in the European alps where high levels of damage occur every 7–10 years. For this budmoth, and particularly for other defoliators where population census data are more limited, historical records of the periodicity of outbreaks may be obtained from dendrochronological studies. In some cases, such studies may also allow the intensity and duration of outbreaks to be determined from the degree and duration of growth suppression (Fig. 3.1) (Swetnam and Lynch 1993; Jardon *et al.* 1994; Weber 1995; 1997; Rolland *et al.* 2001). While the degree of growth reduction can provide information on the intensity of an outbreak, it is important to remember that only trees surviving previous outbreaks are measured so that past mortality cannot be assessed. Where possible in such studies, measurements from non-host trees growing in the same location should be used to give an independent record of the effect of past variations in weather patterns on tree growth, allowing the effects of defoliation on the growth of host trees to be more readily interpreted (Fritts 1991).

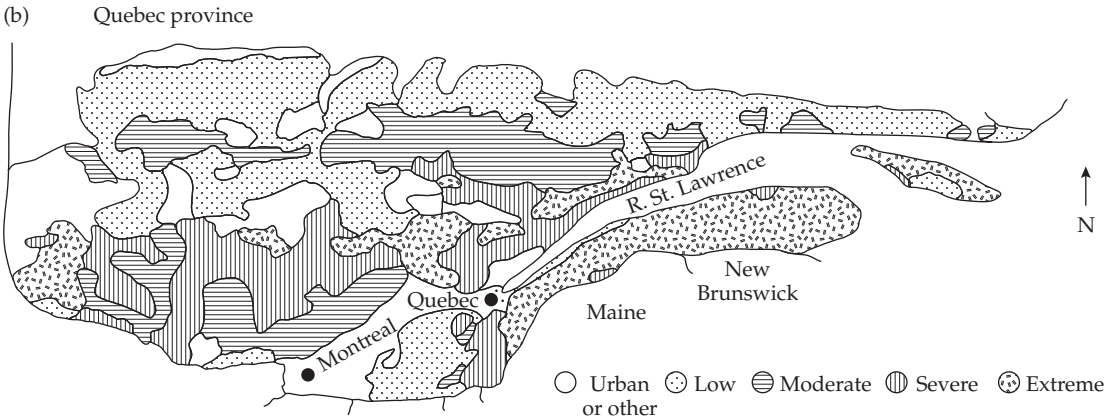


**Figure 3.1** Reconstructing past outbreaks of *Zeiraphera diniana* in the larch-cembra pine forests of the Upper Engadine valley in Switzerland. Larval population census was started in 1949. Cyclic changes in larval density correspond with changes in growth rings in sample larch trees in a stand where the trees were 115–140 years old. The percentage of trees with abrupt growth changes indicates the duration as well as the intensity of past outbreaks: 5–19% = weak, 20–39% = average and  $\geq 40\%$  = heavy outbreak. ----- defoliation threshold (from Weber 1997).





**Figure 3.2** In Quebec province, eastern Canada, outbreaks of *Choristoneura fumiferana* usually start in the south-west and progress northeastwards in a 28-year cycle. Variation in the timing and the intensity of defoliation and damage across the province can affect the accuracy of predictions from the budworm decision support system. (a) Four typical defoliation classes ranging from low to extreme. The relative timescale is determined from the difference between the observed and predicted first year of the outbreak at a particular geographical location based on spatial analysis of data collected from 58 km<sup>2</sup> cells across the province during a 28-year cycle. The typical defoliation classes broadly correspond with four impact zones. (b) The approximate geographical location of four budworm impact zones. *Low* impact — 1–2 years of intense defoliation with little growth loss. *Moderate* impact — 3–5 years of intense defoliation with significant growth loss and some mortality of suppressed trees. *Severe* impact — 6–10 years of intense defoliation with significant growth loss in most trees and mortality in some mature balsam fir. *Extreme* impact — more than 10 years of intense defoliation with death of most balsam fir and increasingly of spruce (from Gray *et al.* 2000).



Outbreak history may also be useful in predicting the timing or intensity of damage by pests that have an impact on a regional scale. Periodic and extensive outbreaks of the spruce budworm, *Choristoneura fumiferana*, occur in coniferous forests in North America. In a typical population cycle, there is an 18-year outbreak period during which

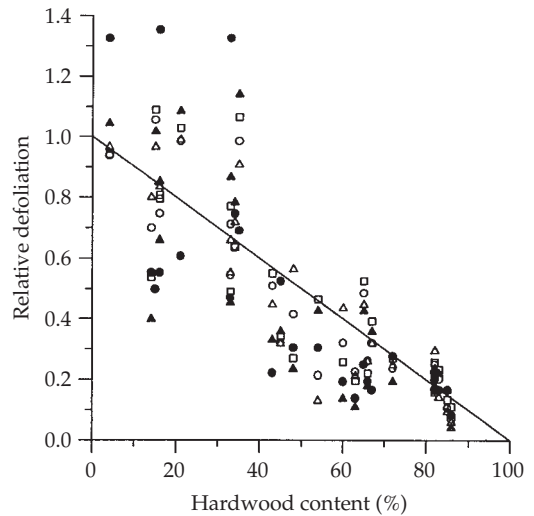
there is increasing defoliation over a 7-year period, with defoliation remaining severe for 2 years before declining gradually over the following 9 years. Around 12 years of endemic population densities then follow before the cycle begins again. Because of the extended geographic area over which outbreaks occur, the timing of the cycle varies with

geographical location. In Quebec, Canada, outbreaks usually start in the south-western part of the province and gradually spread north-eastwards. Within the province, there is also variation in the duration and severity of outbreaks, affecting the impact on forests and the need for and timing of control. During the 1965–1992 outbreak, the severity and duration of defoliation and data on mortality were obtained by annual aerial sketch map surveys from which it was possible to identify four distinctive patterns of defoliation severity (Fig. 3.2(a)). Spatial variation in the occurrence of these different defoliation classes broadly corresponded with regional variation in severity of impact (Fig. 3.2(b)). It was also possible to predict the timing of defoliation in a particular geographical location based on its appearance in other areas. These geo-referenced predictions of the intensity and timing of defoliation can be used in conjunction with forest level assessment of risk (e.g. Fig. 3.3) to improve significantly the management of this pest.

### 3.3.2 Forest composition and structure

The relative composition of stands can sometimes be a useful indicator of risk with effects usually determined in retrospective studies (Su *et al.* 1996; Alfaro *et al.* 2001). Mixed balsam fir and hardwood stands in Canada vary in their susceptibility to defoliation by *C. fumiferana*. A comparison of stands growing on the same site type revealed that defoliation of balsam fir was inversely related to hardwood content. As a consequence, during budworm outbreaks, stands dominated by balsam fir suffered much greater damage than stands made up of more than 40% hardwoods (Fig. 3.3).

Underlying factors that were thought to have contributed to the observed relationship were greater abundance of natural enemies, reduced budmoth oviposition and greater losses of dispersing larvae in stands of high hardwood content. The jack pine budworm, *C. pinus pinus*, is a related pest of sub-boreal forests in eastern North America where stand inventory has also proved to be a useful indicator of risk. Outbreaks of this defoliator occur at 6–12 year intervals and collapse after 2–4 years. In pine forests in Michigan, stand mortality



**Figure 3.3** Defoliation of balsam fir by *Choristoneura fumiferana* in stands with different hardwood content in northern New Brunswick, Canada. To standardise for variation in average severity of attack between years, defoliation was expressed relative to that occurring in pure softwood stands in the same year. Symbols represent different years between 1989 and 1993 during which defoliation was moderate to severe. Average defoliation ranged from 58 to 71% in stands with <40% of dominant/co-dominant hardwoods and 12–32% in those with >40% hardwoods (from Su *et al.* 1996).

**Table 3.1** Mean percentage of trees recently killed by *Choristoneura pinus pinus* in stands of jack pine in Michigan, USA. Stands, which were grouped by inventory variable, were growing on similar sites and assessed in 1994

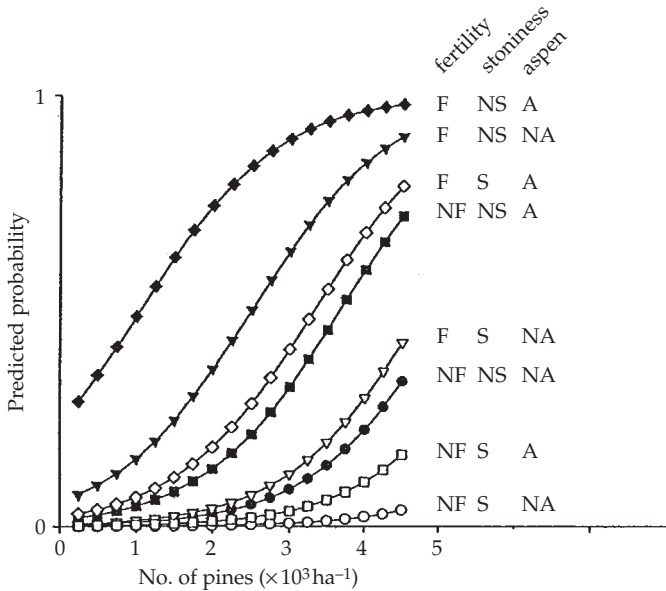
Inventory variable		Percent mortality $\pm$ SE
Age (years)	0–49	4.5 $\pm$ 1.1
	$\geq$ 50	10.7 $\pm$ 1.2
Site index (m)	0–15.2	4.5 $\pm$ 0.9
	>15.2	12.3 $\pm$ 1.4
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	0–16.0	5.7 $\pm$ 1.3
	16.1–25.2	9.0 $\pm$ 1.6
	>25.2	12.9 $\pm$ 1.8

*Site index*—average total height of free-growing healthy dominant or codominant trees in fully stocked even-aged stands.

*Basal area*—total cross-sectional area of dominant or codominant trees per unit area.

Source: McCullough *et al.* 1996.

during outbreaks was influenced by stand age, site index and basal area (Table 3.1). In this study, there was some evidence that relationships between tree mortality and some stand variables were non-linear



**Figure 3.4** The probability of occurrence of *Melampsora pinitorqua* in 109 young pine stands in northern Finland modelled by multiple logistic regression. The rust infects the growing shoots of young pines, resulting in stem deformation. Stands were classified as on fertile (F) or 'poor' (NF) sites where soils either contained small and large stones (S) or were fine-textured (NS). Stand composition was quantified in terms of the number of pines per ha and whether aspen was present (A) or absent (NA). Stands on fertile sites were 19 times more likely to have rust infection than those on non-fertile ones (from Mattila *et al.* 2001).

so that simple risk-rating systems may give misleading results if not adequately tested under a range of conditions.

Increasingly, forest inventory data are being incorporated into Geographical Information Systems (GIS)—integrated computer hardware and software systems that can store, manipulate and display spatially referenced information (Liebhold *et al.* 1993a; Johnson 1997). When combined with other site characteristics and maps of pest damage, this technique can provide a powerful means of detecting spatial association between stand and site characteristics and pest damage. It has been used experimentally to identify pine stands vulnerable to top-dying following defoliation by *C. pinus pinus* in Canada (Hall *et al.* 1998).

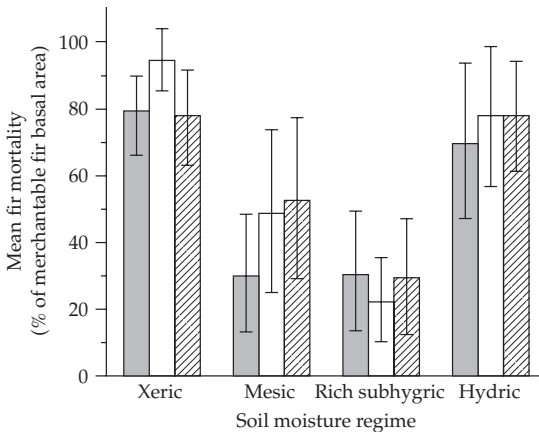
Factors associated with the management or exploitation of forests can also increase the risk of attack or damage by forest pests. The fragmentation that results from the break-up of large forested areas into smaller and separated forest blocks may increase the risk of damage for some species. For example, the higher susceptibility of older stands of jack pine to defoliation by *C. pinus pinus* seems to be due in part to the fact that road construction or clearfelling of adjacent stands exposes edge trees to the sun. This exposure increases the abundance of pollen cones in the trees, enhancing early budworm

survival and so contributing to the development of outbreaks (Nealis and Lomic 1994; Kouki *et al.* 1997). Other examples of risks associated with forest management practices are discussed in Chapter 5.

### 3.3.3 Site and environmental factors

Some examples of the importance of site factors and site selection in forest establishment and how they can affect the susceptibility to pests and diseases are discussed in Chapter 1. Site-related factors may affect directly on pests. For example, low temperatures can increase overwintering mortality and flooding can drown soil-dwelling stages. There may also be indirect effects mediated by tree growth rate or stand composition. The probability of disease caused by pine twisting rust, *Melampsora pinitorqua*, on certain sites in Finland, is predicted both by edaphic factors and composition of the forest (Fig. 3.4). Key risk factors were the fertility and stoniness of the sites, which affected the number of susceptible growing shoots, and the presence or absence of aspen which is an alternate host for this rust.

Mortality of balsam fir in forests that are moderately affected by outbreaks of *C. fumiferana* can be influenced by the soil moisture regime. In a study in Quebec, Canada, the effect of soil water regime



**Figure 3.5** Balsam fir mortality following moderate outbreaks of *Choristoneura fumiferana* in relation to four soil moisture regimes broadly defined as; *xeric*—rapidly drained thin glacial tills or sandy deposits; *mesic*—well drained deep tills or littoral deposits; *subhygric*—deep glacial tills or marine deposits moderately drained; *hydric*—deep glacial tills or marine deposits imperfectly drained. In central Quebec, Canada, the three eco-regions indicated by the different bars were defined by characteristic forest type and climate (from Dupont *et al.* 1991)

was found to be non-linear, with vulnerable stands growing on either very dry or very wet sites (Fig. 3.5). The relationship was found to be consistent within three different ‘eco-regions’ defined by their characteristic forest type and by climatic factors such as average annual temperature and rainfall. Nevertheless, the non-linear relationship observed in this example illustrates the care needed in using and interpreting such risk factors.

In some regions, factors associated with unusual or extreme weather conditions can be useful in assessing risk. In southern USA, lightning strikes on forests can occur frequently and are an important factor triggering outbreaks of southern pine beetle, *D. frontalis* (Fig. 3.6). Less frequent weather events such as ice storms or very high winds can severely damage large forest areas (Fig. 3.7). Following such extreme events, timber can be attacked by pests and pathogens resulting not only in degrade but also the formation of outbreak foci. The need to salvage and store large volumes of timber in order to prevent this, causes considerable logistical problems (Bakke 1989; Grayson 1989; Bunce and McLean 1990; Putz and Sharitz 1991; Hopkin *et al.* 2001; Ryall and Smith 2001). Infrequent events such as windblow are difficult to predict, but measures of ‘windiness’ that incorporate factors such as wind

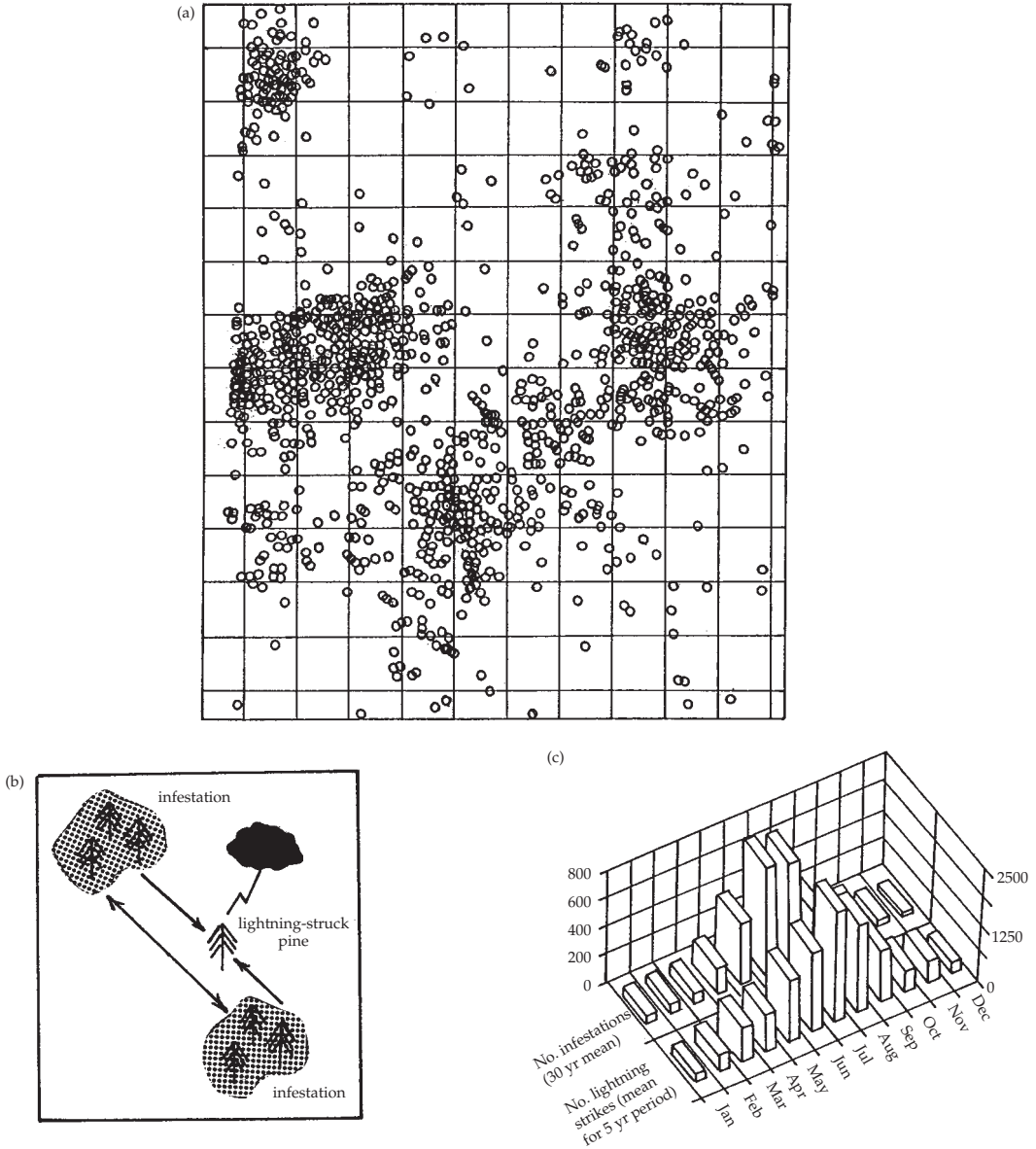
zone, elevation and exposure, together with some measure of tree anchorage can be used to identify sites with a high probability of damage (Coutts and Grace 1995; Quine *et al.* 1995).

### 3.3.4 Growth, vigour and complex indices

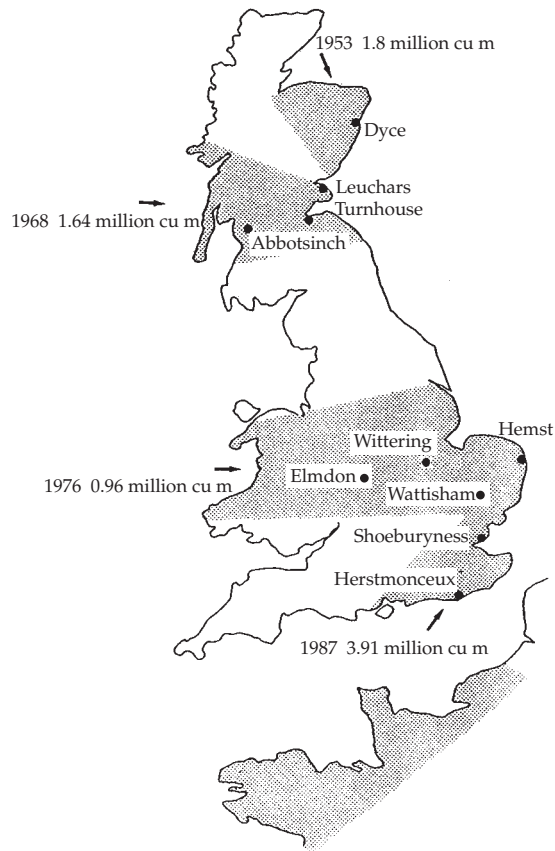
Estimates of the growth and ‘vigour’ of trees have been used as the basis of a number of indices of risk. This is partly because tree growth represents an integrated response to a range of factors linked to the forest stand and ‘site’ such as elevation, nutrient and water availability as well as competitive interactions between trees within the stand. Measures of tree ‘vigour’ range from determination of radial growth to the more physiologically-based estimates of stem growth efficiency and have been used particularly for assessing the risk of attack by bark beetles.

One of the simplest measurements of vigour is that of radial growth. In white spruce stands attacked by *D. rufipennis*, measurements of radial growth have shown that slowly growing spruce within a range of diameter classes were highly susceptible to attack (Fig. 3.8). Susceptibility of trees to bark beetles has also been related to a declining growth rate, expressed as the periodic growth ratio (PGR). This can be determined from the ratio of radial increment in the most recent 5-year period to that over the preceding 5 years and such measurements on a sample of dominant and codominant trees can give a ‘risk-rating’ for the stand as a whole. When this was done in lodgepole pine stands attacked by mountain pine beetle, *D. ponderosae*, trees with PGR values of  $<0.9$  were found to be highly susceptible (Mahoney 1978).

Measures such as stem growth efficiency (SGE), which standardise growth relative to photosynthetic efficiency, are considered to be a much more sensitive indicator of environmental stresses acting on the trees than simple measures of growth (Waring and Pitman 1980, 1983; Waring 1983; Stoneman and Whitford 1995). SGE measures biomass allocated to stem growth per unit amount of foliage and reflects both the effectiveness of the canopy in capturing light and the priority allocated to stemwood production. SGE can provide a useful index of tree ‘vigour’ because ‘fixed’ carbon is only allocated to stem growth after more important priorities such as formation of new leaves and roots have been satisfied. An example of how



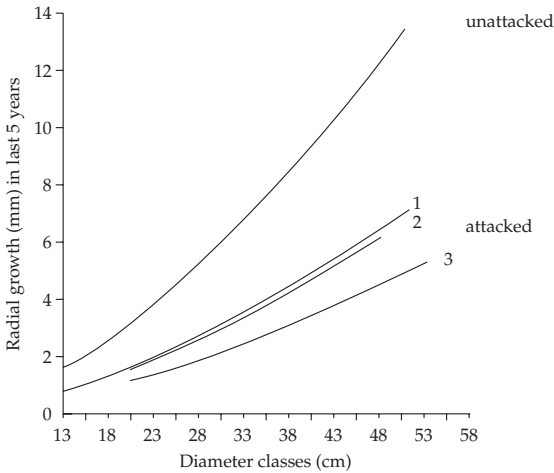
**Figure 3.6** Landscape and environmental factors in outbreaks of *Dendroctonus frontalis* in east Texas, USA. (a) Lightning strikes recorded during a storm over a forested area on a single day. The density of strikes results in vulnerable lightning struck trees within the 1-km dispersal range of the bark beetle. (b) As well as forming foci of infestation within the forest (habitat patch), lightning struck trees can provide 'stepping stones' between suitable habitat patches (from Coulson *et al.* 1999b). (c) The seasonal occurrence of infestations and lightning strikes. Infestations centred around lightning struck trees grow in size but typically stop expanding around the end of the summer season and adults disperse. Under epidemic conditions, separate infestations may coalesce, forming outbreaks ranging in scale from 100 to 1,000,000 ha that can alter the structure of the forest landscape itself.



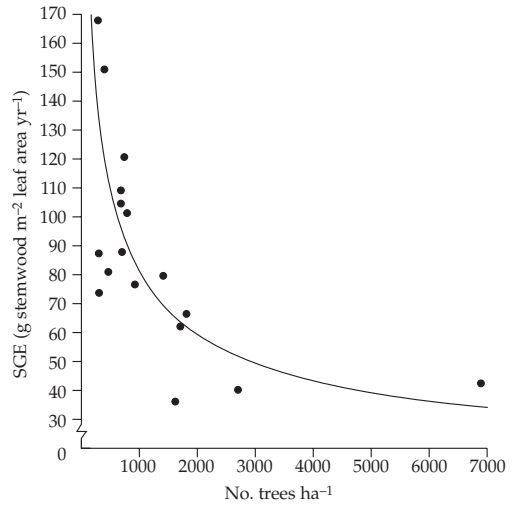
**Figure 3.7** Britain has a relatively severe wind climate with wind damage to trees recorded from as early as the thirteenth century. Areas of severe damage to trees during five exceptional storms since 1945 are indicated, together with volumes of windthrown timber and the location of meteorological stations. During these storms maximum gusts ranged from 47 to 52  $\text{ms}^{-1}$  (from Grayson 1989).

'competition stress' related to stand density influences tree vigour as estimated by SGE is shown in Fig. 3.9. Measurement of SGE in the field is made possible by the linear relationship between sapwood area and leaf area, a relationship which has been shown to hold for many different species on a range of sites (Waring *et al.* 1982; Marchand 1983). Once the ratio of leaf to sapwood area has been established for particular species (Fig. 3.10), SGE can be measured on individual trees from the increase in basal area as a proportion of sapwood area. When used as a basis for predicting mortality of lodgepole pine to *D. ponderosae*, trees with SGE exceeding 100 g of stemwood per square meter foliage per year were found to have a low risk of mortality (Fig. 3.11.).

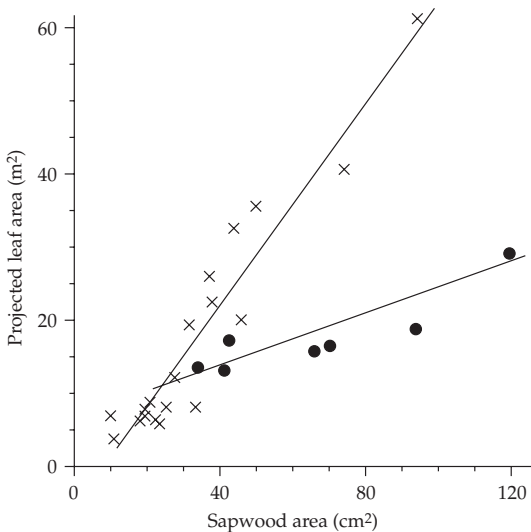
Many of the indices of risk, based on tree growth and 'vigour', have been developed for specific bark beetle–tree interactions because the size or growth rate of trees can reflect variation in tree resistance, a key influence on bark beetle population dynamics (Raffa 1991; Paine *et al.* 1997). Many of these indices however, have proved to be relatively poor at predicting risk at sites other than where they were developed (Amman 1985; Amman *et al.* 1988; Benz *et al.* 1993). This may be partly because they do not fully take account of variation in pest population density. In an attempt to address this problem, Shore and Safranyic (1992) developed a 'complex' risk index for *D. ponderosae* in lodgepole pine stands (Box 3.1).



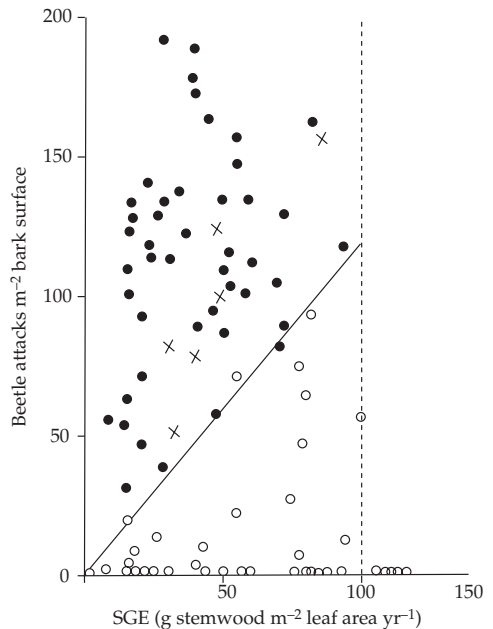
**Figure 3.8** Radial growth of mature white spruce in different diameter classes in a retrospective study of stands attacked by *Dendroctonus rufipennis* in Alaska, USA. In comparison to unattacked trees, those attacked by the bark beetle had much lower radial growth prior to attack, irrespective of diameter class. The different categories of attacked trees did not differ significantly in radial growth: 1-unsuccessfully attacked, 2-attacked and killed in the year of sampling, 3-killed in years prior to sampling (from Hard 1985).



**Figure 3.9** The influence of tree density on vigour estimated by stem growth efficiency (SGE) measured as grams of stemwood  $m^{-2}$  leaf area  $yr^{-1}$ . Tree density was manipulated by previous operational thinnings covering at least 4 ha, with measurements made on trees in adjacent thinned and unthinned stands of lodgepole pine in eastern Oregon, USA (from Mitchell *et al.* 1983).



**Figure 3.10** The relationship between projected (shadow) leaf area and sapwood conducting area (at breast height (b.h.)) for balsam fir (x) and red spruce (●) growing at several different sites in Vermont and New Hampshire, USA. As found in other studies, the relationships are species-specific. Correlation is often improved by measuring sapwood area at the base of the live crown rather than at b.h. (from Marchand 1983).



**Figure 3.11** The stem growth efficiency (SGE) of lodgepole pine in relation to the attack density of *Dendroctonus ponderosae* in Oregon, USA. The solid line shows the minimum density of attack predicted to kill trees of a given SGE. In this system, trees exceeding an SGE of 100 (dotted line) are unlikely to be killed by beetle attacks. (○) surviving trees, (●) killed trees, (x) trees with significant areas of bark killed during attack (from Waring and Pitman 1983).

### 3.4 Monitoring and prediction

One of the main functions of monitoring is to facilitate decision-making in pest management. Relevant information can be acquired in a number of different ways and at a number of different spatial scales, depending on the nature of the pest and the objective of monitoring. Risk-rating of stands can help to identify those where monitoring may be needed.

Detection surveys are designed to obtain information on presence or absence of pests. They may be used to detect exotic pests associated with imported timber or to reveal the presence of pests that are expanding their range. For example, within the European Union, certain quarantine pests may be widely distributed but nevertheless absent from a few member countries. These countries are able to maintain quarantine restrictions in relation to their status as a 'protected zone', provided that regular monitoring of areas designated as 'pest free' fails to detect the presence of the pest. Detection surveys

often need to be extensive and employ methods that are as sensitive as possible (e.g. the use of pheromone-baited traps) to give the best chance of detecting pests at low density. Extension services can also be a useful mechanism for detecting unusual or atypical pest activity that can alert managers to the possible presence of exotic pests.

In most situations, monitoring is done to provide advance warning of increases in the density of potentially damaging pests, to provide accurate information for timing of direct control measures or to monitor efficacy in post-treatment populations. The particular objectives of monitoring and whether it is being done for a limited period or as part of a long-term programme, influence the extent and intensity of monitoring and the level of precision required. Long-term monitoring of population abundance is most useful for pests whose populations characteristically increase over several years and so give one or two seasons' advance warning. But many important pests can increase rapidly in density from very low

#### Box 3.1 Risk index for *Dendroctonus ponderosae* in lodgepole pine stands

Construction of the risk index was based on the premise that risk was a function of stand susceptibility and beetle population 'pressure' measured by the number of infested trees in the area and their proximity to the stand being assessed. An heuristic or 'rule-of-thumb' approach was used based on knowledge and experience to select key factors and appropriate weighting to formulate the risk index (Fig. 3.12).

The susceptibility index ( $S$ ) can range from 0 to 100 and was based on four stand variables: the percentage of susceptible pine basal area ( $P$ ) and factors for age ( $A$ ), stand density ( $D$ ) and location ( $L$ ). Susceptible pines included those whose diameter at breast height  $\geq 15$  cm, but dominant or codominant trees over 80 years old were considered most susceptible. Stands where the density of all species was in the range 750–1500 stems per ha were considered to be more susceptible than stands with a higher or lower density of trees. Stands growing in more southerly areas and at lower altitudes where the beetle development time was shorter were also considered to be more susceptible. A multiplicative rather than an additive model was used to calculate the index, that is, the four variables were considered to have equal weight in contributing to the index.

The beetle population index depended on the number of beetle-infested trees in the stand being rated and in stands within 3 km of it, and the distance to the nearest infestation. The index is obviously highest when a large number of infested trees occurs within the stand itself. The beetle population index, as part of the overall risk index, has the potential to change much more rapidly than the susceptibility index and therefore requires more careful and regular monitoring. The relatively complex equation used to calculate the risk index reflects the fact that stand susceptibility and beetle population are related in a non-linear way to stand risk.

Most of the information needed to construct the risk index was available from existing forest inventory data. An important attribute of it was that variables relating to stand susceptibility such as basal area of susceptible pines and stand density could be subject to silvicultural manipulation. As discussed in Chapter 4, these include felling overmature stands, selective thinning and managing large areas of susceptible forest type to create a less susceptible forest mosaic. Beetle population size can be reduced by appropriate management of stands in surrounding areas, that is, by area-wide management and where necessary, by the control measures discussed in Chapters 4 and 8.

Key reference: Shore and Safranyic (1992).



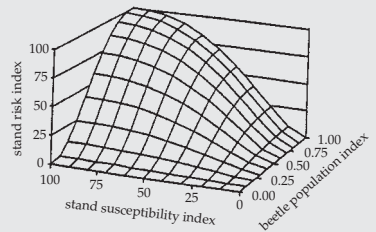
**Box 3.1 Continued**

**Susceptibility index**  
 Derived by multiplying the mean basal area of susceptible pines per ha as a percentage of the mean basal area of all tree species in the stand, by factors for age, stand density and location (latitude, longitude and elevation)

**Beetle population index**  
 Based on the relative size of the beetle population (number of infested trees) in the stand itself and within 3 km of it, and the distance to the nearest infestation.

Susceptibility index (S)	Beetle population index (B)									
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
10	<1	<1	2	3	5	6	7	8	8	8
20	<1	2	6	10	14	18	20	22	24	24
30	<1	4	10	17	24	30	35	39	40	41
40	1	6	14	24	33	42	49	54	56	57
50	1	7	18	30	42	52	61	67	70	71
60	2	9	20	34	48	61	70	77	81	82
70	2	10	22	38	53	67	78	85	89	91
80	2	10	24	40	56	71	82	90	95	96
90	2	10	24	41	58	73	85	93	98	99
100	2	11	25	42	59	74	86	94	99	100

$$\text{Risk index, } R = 2.74[S^{1.77} e^{-0.0177S}][B^{2.78} e^{-2.78B}]$$



**Figure 3.12** Risk index for *Dendroctonus ponderosae* in western Canada. The risk equation was derived by adopting an heuristic approach, selecting important variables and assigning weights based on logic and current knowledge and experience, and describes the non-linear relationships shown in the graph. The risk index can be obtained from the table for given levels of beetle population (B) and stand susceptibility (S). All variables in S can be altered by silviculture and B can be influenced by direct control measures. Note that the same risk index can be derived from a highly susceptible stand exposed to a moderate beetle population or vice versa and that both susceptibility and risk are relative indices that do not account for absolute basal area at risk. Both these aspects of the risk index may affect stand management decisions (adapted from Shore and Safranyic 1992).

levels and the methods and intensity of monitoring need to take this into account.

In large-scale programmes, cost is often an important consideration in determining the extent or intensity of monitoring, especially when time consuming and labour-intensive population census methods are used. Cost-effectiveness can be increased by appropriate combination of extensive and intensive monitoring. Initial extensive monitoring of pupae or adults, for example, can be followed by more intensive monitoring of eggs or even early instars but within a much smaller area identified as being at highest risk. For some pests, pheromone-baited traps may be used for the initial extensive surveys to identify the more restricted areas for population census. Catches in pheromone-baited traps can also be correlated with levels of pest damage and used to establish outbreak or control thresholds. In fact most monitoring operations depend on an established critical threshold density that represents the point at which significant damage will occur. Critical densities are often based on previous local experience of particular pest outbreaks. They will be influenced by such factors as the part of the tree attacked, the

susceptibility of the stand and its commercial value, and of course the outbreak characteristics of the pest itself. Some techniques for detecting and monitoring pests are discussed in the following sections.

**3.4.1 Mapping the distribution and intensity of damage**

Pest or disease outbreaks that occur in isolated or remote areas are usually not detected as quickly as outbreaks in more intensively managed forests. Early detection of isolated outbreaks may allow timely application of control measures to a relatively restricted area and may prevent development of uncontrollable outbreaks of eruptive pests. For this reason, some forest services conduct annual pest and disease surveys as part of forest health monitoring. Aerial surveys are particularly useful for covering extensive or inaccessible forest areas, with visual assessments of defoliation or discoloration of leaves proving in general to be more useful than remote sensing techniques such as photography or satellite imagery (Riley 1989). Further development of remote sensing techniques that would allow reliable

pre-visible detection of pest and disease activity from the air would, however, be particularly useful and a significant improvement over traditional aerial survey methods.

Aerial sketch mapping is particularly useful for delimiting affected areas. For sketch mapping as well as other forms of remote sensing, weather factors such as cloudiness can have a large effect on visibility or on image quality. This can be restrictive where surveys have to be carried out during a limited period of peak defoliation. In addition, rain or strong winds during peak defoliation can remove discoloured leaves and so affect subsequent defoliation estimates. In New Brunswick in Canada, sketch mapping of defoliation caused by spruce budworm, *Choristoneura fumiferana*, is conducted annually. Surveys are done from light aircraft flown at an altitude of 150–300 m in flight lanes separated by several kilometers over forests within known budworm infestation zones. The aim is to give an overview of the distribution and severity of budworm feeding throughout the province to allow identification of areas likely to require treatment. Producing accurate maps depends on adequate observer training, calibration of estimates with those based on ground surveys and also on precise navigation systems to reduce positional errors. Experimental comparisons between ground-based and aerial assessments of defoliation by *C. fumiferana* over several years indicates the kinds of error that are likely to occur in aerial sketch mapping (MacLean and MacKinnon 1996). Trained observers rated current defoliation in four classes from very light to severe in spruce/balsam fir forests and then compared results with ground-based estimates. In some years assessments were affected by poor weather during the period of peak refoliation, affecting both visibility and foliage retention. Overall, there was a tendency to underestimate defoliation in aerial surveys and also a tendency to miss patches of defoliation, especially when overall defoliation levels were low. Tree species differences were also evident, with more spruce than balsam fir classified correctly. *C. fumiferana* does not cause tree mortality at low levels of defoliation so for this particular pest, errors of this sort do not limit the value of aerial sketch mapping as a monitoring method.

Remote sensing techniques have been used on an experimental basis and show potential for future development. In particular, digital imagery

integrated with global positioning systems and GIS can be a powerful way of detecting and mapping the distribution of certain pests in remote areas. Methods used so far have been experimental and used with varying success. High resolution multispectral digital images from light aircraft have been used to detect damage by southern pine beetle, *Dendroctonus frontalis*, on shortleaf pine (Carter *et al.* 1998). Heavily damaged trees were readily located in reflectance images with wavelengths chosen to maximise contrast between yellow or brown and green foliage. However, on more recently attacked trees, visual symptoms included only mild chlorosis which could not be reliably detected because of natural variation in leaf chlorophyll content throughout the forest. Similar techniques have been used to successfully detect outbreaks of western pine beetle, *D. bevicornis* in mountainous areas of west Texas, USA (Everitt *et al.* 1997). Colour-infrared digital imagery has been used with some success to detect trees affected by oak wilt disease caused by *Ceratocystis fagacearum*. The ability to discriminate between diseased and healthy trees depended on differences in the reflectance of visible and near-infrared that are influenced by differences in the colour and density of leaves in the tree canopy (Table 3.2).

Satellite imagery has been used in a number of experimental studies to assess its potential in monitoring or detecting defoliation by forest pests with mixed success (Radeloff *et al.* 1999; Tømmervik *et al.* 2001; Heikkilä *et al.* 2002). Satellite imagery can also be used to acquire information about the forest itself rather than simply locating affected areas and

**Table 3.2** Light reflectance measurements from the canopy of healthy oak trees and diseased or dead trees affected by *Ceratocystis fagacearum*

Condition of oak trees	Canopy reflectance(%)		
	Green	Red	Near-infrared
Healthy	3.8	2.6	34.6
Diseased	5.3	4.3	26.0
Dead	8.5	6.6	7.9
Least significant difference ( $\rho = 0.5$ )	0.6	0.4	3.3

Note: Differences in reflectance were detected at the three spectral wavelengths allowing affected trees to be identified from the air using either colour-infrared photography or digital imaging  
Source: Everitt *et al.* 1999.

this may help to characterise forests at risk of attack (Luther *et al.* 1997).

### 3.4.2 Sampling populations

The aim in sampling populations in monitoring programmes is often to classify the population as being above or below a critical threshold rather than to obtain an accurate estimate of population density. Sequential sampling is a method of obtaining census data that allows populations to be classified as above or below a critical density while restricting the amount of sampling to that necessary to obtain the level of precision required (Box 3.2).

Overwintering stages such as pupae or eggs are present over a prolonged period and so can be a particularly convenient stage to sample and are sometimes used to monitor long-term changes in density (Table 3.3). Extensive monitoring of this kind is

particularly useful for detecting the few areas at risk identified by high pupal counts and at these sites, additional monitoring of later developmental stages can be done. This is necessary because a number of biotic and abiotic mortality factors can affect post-sampling survival of pupae or adults and, together with possible variation in fecundity and early instar survival, can introduce considerable variability into the relationship between pupal density and defoliation. Sampling the egg stage can remove some of the variability and is particularly convenient for defoliators with overwintering eggs. Even so, there can still be considerable variation in the relationship between egg numbers and subsequent defoliation as illustrated by sampling in stands affected by gypsy moth, *Lymantria dispar* (Fig. 3.14). Egg-masses of  $<125 \text{ ha}^{-1}$  are considered unlikely to result in defoliation. But within the range 250–2500 egg-masses  $\text{ha}^{-1}$ , there is such large variation in levels of defoliation (from 0 to 100%) that at these densities,

#### Box 3.2 Sequential sampling

When a reasonably large sample is taken from a population, the mean density and standard deviation can be calculated and compared statistically with the critical density ( $cd$ ) to provide the basis for a management or control decision. It is possible, however, that classifying the population as above or below the  $cd$  could have been done with fewer samples. The question of how many samples are required to classify the population with a given level of precision is addressed by sequential sampling.

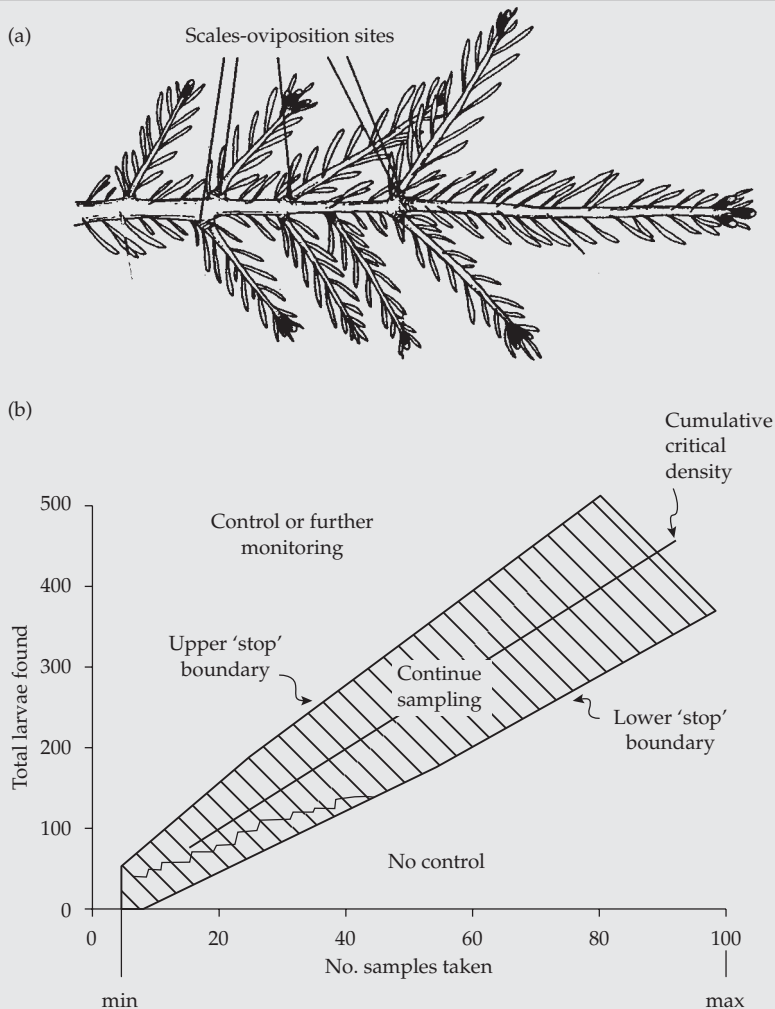
To develop a sequential sampling scheme, preliminary studies are necessary to define the appropriate sampling unit and to determine the relationship between the mean ( $m$ ) and variance ( $V$ ) such as that described by Taylor's Power Law ( $V = am^b$ ). The relationship needs to be determined for a number of different populations over a wide range of densities that includes the  $cd$ . The linear form of the equation,  $I_n(V) = I_n(a) + bI_n(m)$ , allows the constants  $a$  and  $b$  to be estimated. For the  $cd$ , the conventional 95% confidence interval is  $cd \pm 1.96 \sqrt{V/n}$  for sample size  $n$  and can be determined by substitution as follows  $cd \pm 1.96 \sqrt{a cd^b/n}$  (Binns *et al.* 2000).

Turgeon and Régnière (1987) provide an illustrative example of sequential sampling for eggs and larvae of the spruce budmoth, *Zeiraphera canadensis*. This insect

lays eggs under old bud scales that after overwintering, hatch in the spring in synchrony with budburst. The larvae feed exclusively on the current year's foliage. Preliminary sampling in stands of young white spruce helped to identify the appropriate part of the habitat to give representative and reliable samples as well as to define the appropriate sampling unit. From branch samples taken from the upper third of the crown (Fig. 3.13(a)), larvae were counted after egg hatch. The critical density was estimated to be a mean of five larvae per branch and the cumulative total for a series of samples shown in Fig. 3.13(b). The upper and lower 'stop' boundaries are determined from the confidence interval and expressed in relation to cumulative counts to avoid the need to calculate the mean after each set of samples. These boundaries represent the point at which sampling stops, allowing the population to be classified with the chosen level of precision. A representative minimum number of samples is taken and a maximum number set to avoid repetitive sampling when estimated means remain within the zone of uncertainty.

*Key references:* Taylor (1984), Turgeon and Régnière (1987), Fleischer *et al.* (1991), Kuno (1991), Binns and Nyrop (1992), Binns *et al.* (2000).

## Box 3.2 Continued



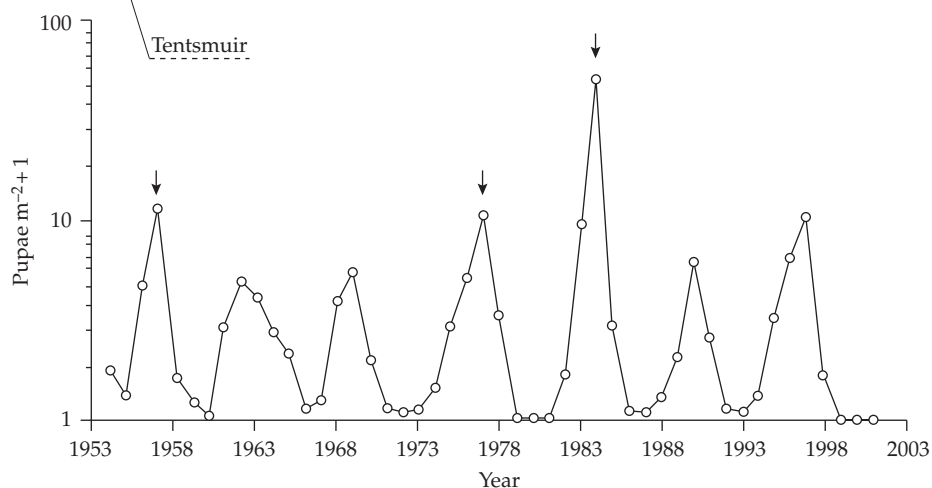
**Figure 3.13** Development of a sequential sampling programme for *Zeiraphera canadensis* on white spruce in New Brunswick, Canada. The programme was designed to determine whether the larval population density was above or below a critical density of five larvae per branch sample with a 95% confidence level. (a) The branch sampling unit. (b) A hypothetical series of cumulative counts (bold line) illustrates the point at which sampling stops, allowing the population to be classified as below the critical density (from Turgeon and Régnière 1987).

the relationship is of little value in decision-making. In this example, a number of factors could have contributed to the variation in defoliation for a given egg-mass density including the number of eggs within individual egg-masses (fecundity), first instar larval survival and the extent to which the larvae disperse. It may often be possible to increase sampling intensity to obtain more accurate estimates of the density of the stage sampled but there is usually a trade-off between precision and sampling costs.

For monitoring adult stages, pheromone-baited traps are particularly useful where appropriate lures are commercially available. Because pheromone-baited traps are largely species-specific, 'clean' samples are obtained that are easy to count although they do have the disadvantage that natural enemies that respond to the pheromone can also be trapped. For detection surveys, traps need to be efficient and baited with highly attractive lures that release pheromone over an extended period. There

**Table 3.3** Annual pupal surveys of *Bupalus piniaria* in UK forests on sites considered to be at risk from periodic outbreaks

Forest district	Unit	1994	1995	1996	1997	1998	1999
<b>England</b>							
Midlands	Cannock	1.2	1.6	4.0	6.0	0.8	0.4
	Swynnerton	0.8	2.0	8.8	2.0	0.0	0.4
Sherwood	Sherwood III	0.4	0.8	2.0	0.8	0.4	0.0
	Sherwood IV	0.8	2.8	2.4	1.6	1.2	0.4
<b>Scotland</b>							
Inverness	Culloden	0.0	0.0	0.4	0.4	3.6	0.8
Moray	Culbin	2.4	10.6	18.0	6.0	2.0	3.6
	Lossie	6.8	21.6	18.4	0.4	1.6	6.8
	Roseisle	2.8	11.2	14.8	4.4	1.2	2.8
	Speymouth	4.4	10.0	24.0	30.0	20.4	4.0
Tay	Montreathmont	—	—	22.4	23.2	1.2	2.4
Aberfoyle	Edensmuir	0.4	0.8	2.4	0.0	0.0	0.4
	Tentsmuir	1.6	6.0	14.0	32.8	2.8	1.2

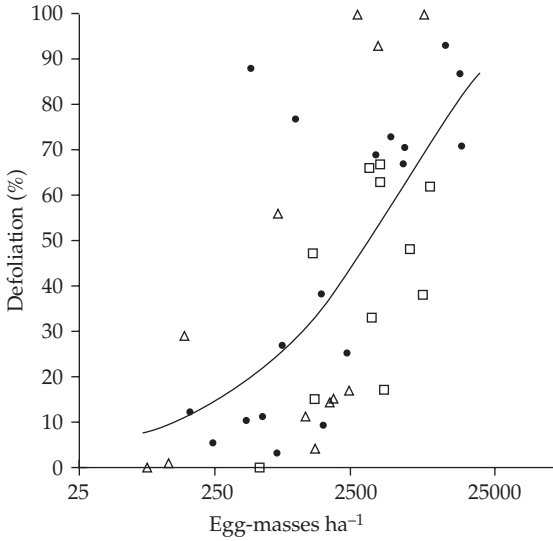


Note: The densities (pupae  $m^{-2}$ ) are the *highest* found within the forest in each year and subsequent egg sampling is triggered by a threshold density of around 25 pupae  $m^{-2}$ . The high populations at Tentsmuir in 1997 collapsed naturally. Inset—forest average pupal densities at Tentsmuir indicating years of chemical control (arrows).

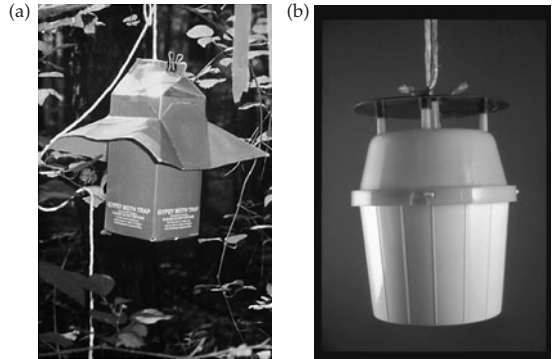
Source: Gibbs and Evans 2000; Armour *et al.* 2003 and unpublished.

is often little information on the absolute efficiency of commercially available traps, but some of the factors influencing trap catch are discussed by Muirhead-Thomson (1991). Some examples of the many different designs of pheromone-baited trap for Lepidoptera are shown in Fig. 3.15. In practice, traps used in monitoring tend to be those designed or available locally and cost is often an important consideration where large numbers are needed. The choice of trap, the pheromone dose and the level of maintenance will determine the operational charac-

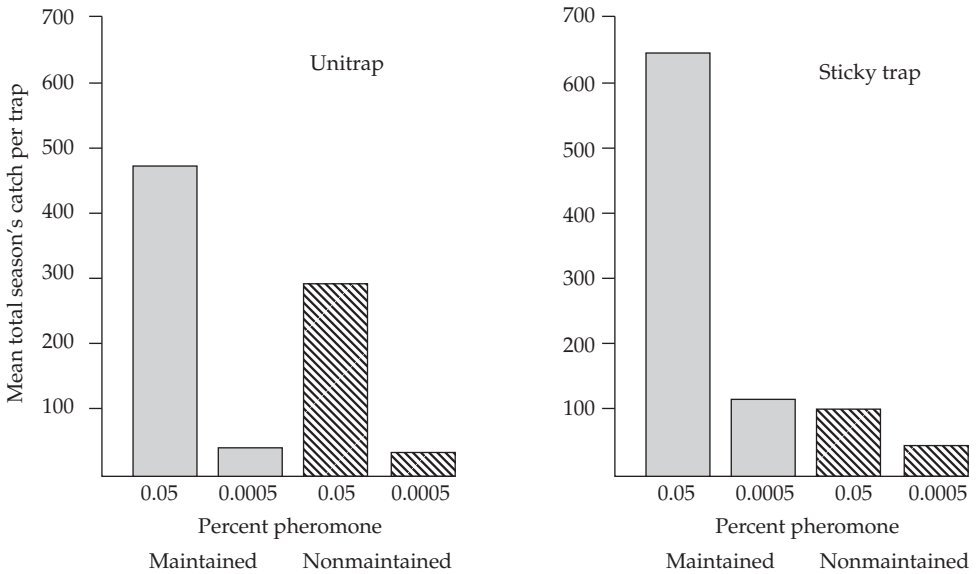
teristics of the trap (Fig. 3.16). For most kinds of monitoring, however, efficiency is a secondary consideration provided that a consistent relationship can be established between trap catch and some key indicator of damage in the current or following season (see Sanders 1988; Evenden *et al.* 1995a,b). Morewood *et al.* (2000), for example, correlated seasonal trap catches of nun moth, *Lymantria monacha*, with amounts of frass dropping from trees on which larvae were feeding (Fig. 3.17). In this example, the form of the relationship was not



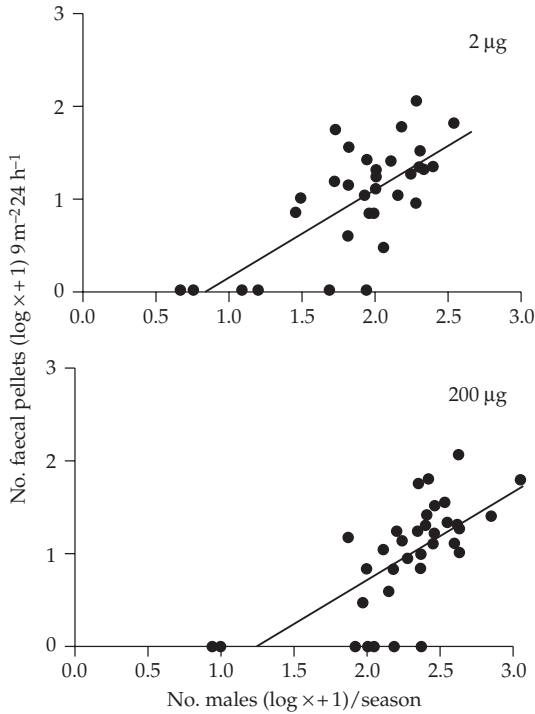
**Figure 3.14** Density of egg-masses of *Lymantria dispar* in relation to percent defoliation based on means of 0.01 ha circular plots in several different forests in Pennsylvania, USA. Symbols refer to different sampling years ( $\Delta$ 1989,  $\bullet$ 1990,  $\square$ 1991). The relationship was most appropriately described by a sigmoid curve (from Liebhold *et al.* 1993b).



**Figure 3.15** Some pheromone-baited traps used in monitoring Lepidoptera. (a) USDA milk carton trap (Photo K. Thorpe). (b) Unitrap. Some traps used to capture bark beetles are illustrated in Fig. 8.8.



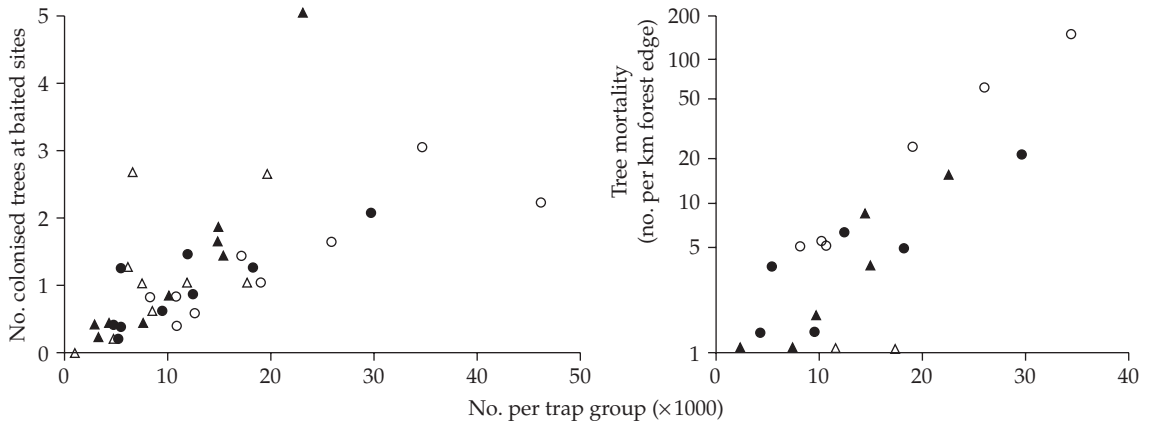
**Figure 3.16** Catches of *Choristoneura occidentalis* in delta sticky traps and non-sticky, high capacity unitraps in relation to pheromone dose and to trap maintenance. Moths were counted and removed from maintained traps every 2 days whereas non-maintained traps were left for the whole flight period. Maintained sticky traps caught significantly more moths than unitraps but when traps were not maintained, unitraps caught more than the sticky traps at the high pheromone dose (0.05%). Sticky traps became saturated at about 100 moths per trap (from Sweeney *et al.* 1990).



**Figure 3.17** Seasonal catches of male *Lymantria monacha* in four non-saturating pheromone-baited unitraps and number of frass pellets collected in 9 m<sup>2</sup> sampling area in 24 h. Several spruce and pine-dominated forests in Germany and the Czech Republic were sampled. The pheromone dose influenced the number of males caught but not the form of the relationship (from Morewood *et al.* 2000).

affected by the two widely different pheromone doses used. In general, however, when high doses are used traps with a low capacity may become saturated and have the potential to attract males from a wide area and so obscure local changes in pest density.

When monitoring bark beetles, it can be difficult to establish a relationship between trap catch and damage to the forest. Trap catches will be influenced by the type of trap used (Fig. 8.7) and the composition and release rate of the multicomponent pheromone. Trap location is also particularly important because beetles responding to traps can be concentrated within a small area, inducing attack on nearby trees. This problem is avoided when monitoring the spruce bark beetle, *Ips typographus*, by placing traps in open areas 10–20 m from stand edges. This has the effect of attracting beetles across intervening open areas without concentrating them at the forest edge where trees are likely to be attacked (Neimeyer 1992; Weslien 1992). The relationship between trap catch and successful attack on trees will be influenced by the intensity of attack required to overcome tree resistance. Nevertheless in an extensive study in Fennoscandia using standardised monitoring methods in similar kinds of forest, a surprisingly consistent relationship was found between trap catch and tree mortality (Fig. 3.18). Monitoring *I. typographus* in this way provided an estimate of damage only in the



**Figure 3.18** Monitoring *Ips typographus* at different sites within four Fennoscandian countries, Denmark (○), Norway (▲), Sweden (●) and Finland (△). The mean catch of *I. typographus* in groups of three pheromone-baited Norwegian drainpipe traps during the spring flight period in relation to (a) mean number of successfully colonised spruce trees at specific locations with a single pheromone-baited trap tree and (b) beetle-induced mortality within each study area as a whole estimated from the number of trees killed per km along forest edges adjoining recent clearfells. Catches of <15 000 per trap group represented a low risk provided only small amounts of breeding material were present in the forest (from Weslien *et al.* 1989).

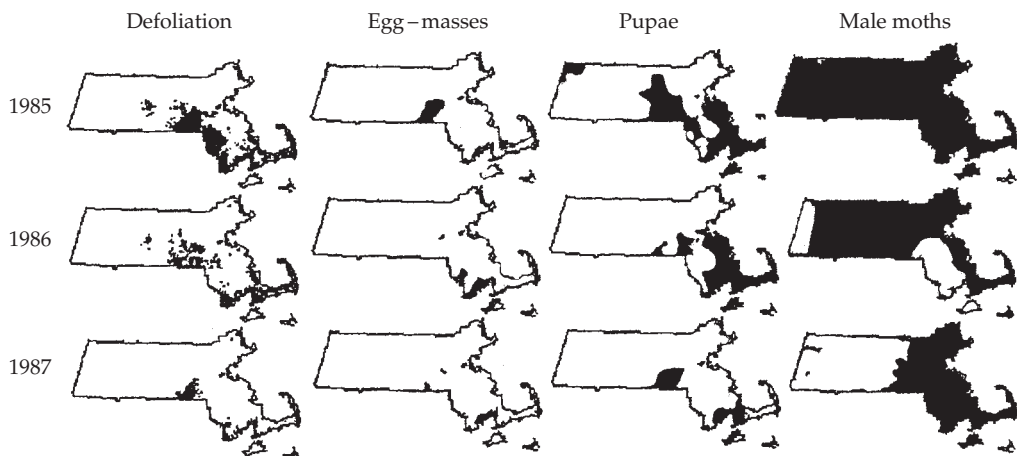
current season. Predicting levels of attack in the following season may be possible in some cases (Bakke 1992; Weslien 1992).

A few forest pests and pathogens have the potential to cause damage on a large scale, either by spreading out from foci of infestation or through the occurrence of synchronous outbreaks over large geographical areas. Monitoring such pests can be time consuming and expensive and it is usually not practicable to sample all stands within the area at risk. Geographical Information Systems (GIS) have been used experimentally to aid in monitoring and prediction of pest outbreaks on a landscape scale. The potential of GIS is illustrated by its use to compare the efficiency of different monitoring methods to predict defoliation by *L. dispar* within the State of Massachusetts, USA (Fig. 3.19). Aerial sketch mapping was used to provide the basic information on levels of defoliation. In sample plots distributed irregularly throughout the State, male moths were captured in pheromone-baited traps and egg-masses and pupae counted on samples of the surrounding oak trees. Geostatistical tools within GIS were used to interpolate population estimates at unsampled points on the basis of observed values in nearby sample plots. Although further refinement of the method is needed, counts of egg-masses and pupae were found to give the best prediction of defoliation

on a regional scale. Male moth catches, however, were poorly correlated probably because traps attracted males from too large an area, over an extended period, to reflect local densities.

### 3.4.3 Spread of pests and pathogens

Some examples of monitoring the spread of exotic pests from sites of introduction and around areas subject to internal quarantine are discussed in Chapters 2 and 9. In the United States, *L. dispar*, has spread to the south and west of its original introduction site in Boston but so far occupies only part of the mixed woodland habitat that appears capable of supporting significant populations. A strategy of managing this pest by reducing the rate of spread (the 'slow-the-spread' or STS campaign, Box 9.7) has been adopted, which depends on the detection and local eradication of isolated populations at the expanding front. In such populations, egg-mass densities are too low to detect and there is difficulty in identifying defoliation in aerial surveys as the boundaries of the affected areas are too variable to identify. Pheromone-baited traps have, however, proved to be an effective way of detecting the small number of male moths in these populations. Reliable estimates of the location of the boundary of the expanding population are necessary not only to



**Figure 3.19** The use of GIS to interpolate estimates of the size of *Lymantria dispar* populations based on different methods of monitoring at 150 locations in the State of Massachusetts, USA. Defoliation throughout the State was determined by aerial sketch mapping. The black areas represent respectively,  $\geq 30\%$  defoliation, 1.5–15.0 egg-masses/tree, 3.5–62.0 pupae/tree and 147–1997 males/trap (from Liebhold *et al.* 1995).

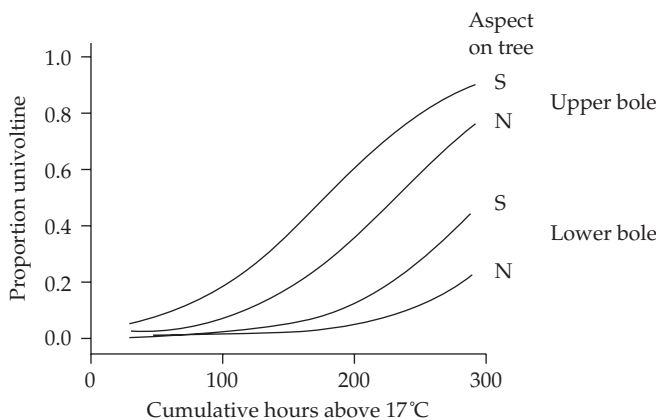


define areas where detection surveys are needed, but also to measure the effectiveness of the STS management strategy, to plan internal quarantine measures and to prepare pest management plans for the areas likely to be invaded. Sharov *et al.* (1995) defined the population boundary as a line dividing an area where populations are above or below a specific density threshold at a particular spatial scale but in practice, such boundaries can be difficult to measure. Using geostatistical methods, Sharov *et al.* (1997) showed that for *L. dispar*, a threshold density of 10 moths per trap per season defined a population boundary that was most stable in space and time.

The regular appearance of some pests can be predicted by monitoring regular climatic events. The timing of long-range dispersal of the teak defoliator, *Hyblaea puera*, in India can be predicted by the progress of the south-west monsoon. The monsoon begins by moving northwards along the western coast of India before turning eastwards across the states of Maharashtra and Madhya Pradesh. Moths first appear within  $\pm 2$  days of the arrival of the monsoon (Bhowmick and Vaishampayan 1986; Vaishampayan *et al.* 1987).

### 3.4.4 Phenology and development

Knowledge of the main factors determining the timing of key phenological events in insect life-history and an ability to predict how they vary from year to year or from place to place can be of value in managing pests. Temperature is the most important environmental factor influencing insect development and this can vary significantly in forests that can cover large and often topographically complex areas. In particular, variation in altitude and the aspect of sloping ground can result in considerable local variation in temperature and this can have a large influence on insect development rates. Throughout most of its range in North America, the spruce beetle, *D. rufipennis*, is predominantly semi-voltine, with the life-cycle taking 2 years. In some stands, however, univoltine development can occur and this can have a significant influence on outbreak potential. It is important therefore, to be able to predict where and when an annual cycle will occur. By studying the bark beetle life cycle in populations from several different regions, Hansen *et al.* (2001) were able to develop a temperature-based model to predict the proportion of the population with uni-voltine development. The best predictive variable was the cumulative number of hours above 17°C for the period 40–90

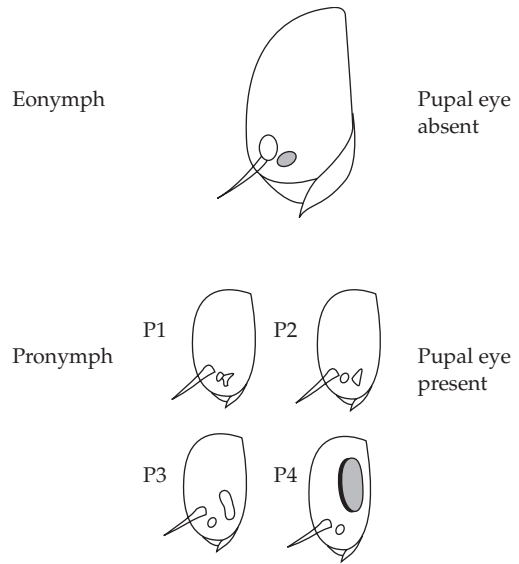


**Figure 3.20** The proportion of *Dendroctonus rufipennis* predicted to be univoltine when developing in spruce growing on ridges and slopes. Predictions of the model were based on the cumulative hours above an air temperature of 17°C from 40 to 90 days after peak beetle flight determined by captures in pheromone-baited traps. Examples are shown for development on the north and south sides of the lower and upper bole. Similar estimates were made for the mid-bole. Differences within trees and between ridges/slopes and valley bottoms are partly explained by night-time temperature inversions that cool the lower bole more than the upper and by the accumulation of cold air in valleys. By estimating the amount of bark 'habitat' on the lower, middle and upper parts of the north and south sides of an 'average' tree, the proportion of the population predicted to be univoltine could be determined for the whole stand (from Hansen *et al.* 2001).

days after peak flight (Fig. 3.20). Temperature accumulation was influenced by aspect (north, south) and height (lower, middle and upper) on the tree and whether the trees were in valley bottoms or up on ridges or slopes. These factors therefore, had a large effect on the proportion of the population with uni-voltine development.

One of the ways in which insects survive unfavourable conditions such as low temperatures in winter and high ones in summer is through diapause. Environmental cues such as daylength and to a lesser extent temperature are important in inducing diapause during which the insect stage is unresponsive to favourable developmental conditions (Tauber *et al.* 1986; Danks 1987). Diapause is usually terminated only after a period of 'diapause development' that helps to synchronise the life-cycle with the seasonal return of conditions favourable for both insect and host. In some insects, diapause may be prolonged and this appears to be a strategy for 'spreading the risk' where the availability of resources for emerging populations is highly variable from year to year. The factors influencing extended diapause are not well understood but when it occurs it can complicate prediction of population abundance based on samples of overwintering stages. In some species it may be possible to recognise individuals that have entered extended diapause and adjust estimates of 'population size' accordingly. In common with many *Cephalcia* spp., the spruce web-spinning sawfly, *C. arvensis*, has a life-cycle of variable length. Pupae occur as eonymphs, which have an extended diapause, or as pronymphs and the relative abundance of these stages can give important clues about the timing and size of the population likely to emerge (Fig. 3.21).

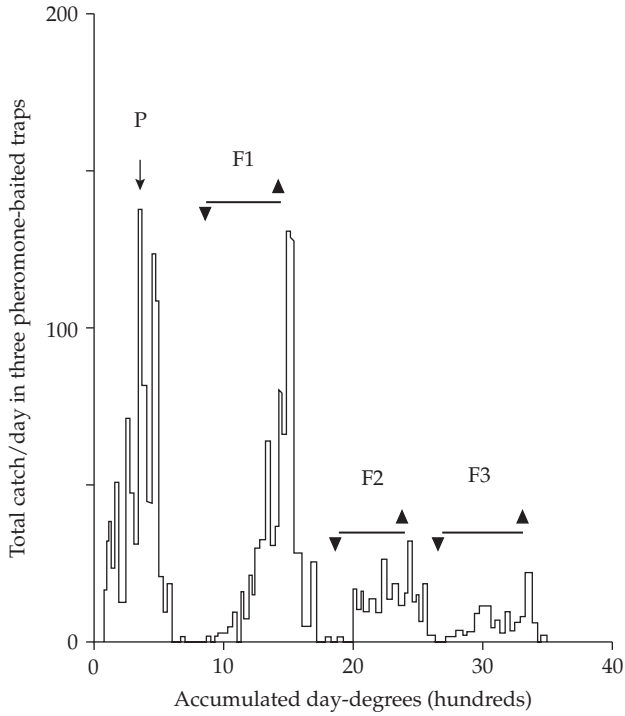
Once development resumes in insects following diapause, the rate of development (usually defined as the reciprocal of the time required to complete development of a particular stage) increases linearly over a relatively large range of temperature, allowing the developmental threshold to be determined by extrapolation (Gilbert and Raworth 1996). Because the development rate is proportional to temperature, 'physiological time' for development can be expressed as the accumulated heat sum above the developmental threshold for the



**Figure 3.21** Diapausing stages of *Cephalcia arvensis*. Prolonged diapause can occur in the eonymph stage and in pronymph stages P1 and P2 distinguished by the degree of development of the pupal eye. An annual cycle is indicated when the eonymph stage is reduced or absent and the P4 stage is evident a few days after larvae enter the soil (from Battisti 1994; after Eichhorn and Pausch 1986).

completion of a particular stage. This is commonly done using 'day degrees' (DD) calculated for each day by determining the difference in degrees between the species-specific development threshold and the daily mean temperature, that is,  $DD = (((T_{max} + T_{min})/2) - T_{threshold})$ .

Accumulated DD can be used to predict the timing of phenological events. The date from which DD are accumulated is sometimes referred to as the 'biofix' point. The most accurate predictions are usually obtained by selecting dates close to the key phenological event but in practice, biofix points usually reflect a trade-off between accuracy of prediction and the degree of forewarning needed (Fatzinger and Dixon 1996). Accuracy is usually most important for the application of direct control measures where there is a restricted 'window of opportunity' (Malinoski and Paine 1988; Fettig and Berisford 2002; Hanula *et al.* 2002). The Nantucket pine tip moth, *Rhyacionia frustrana*, is an important pest of pine Christmas tree plantations in the United States and provides an illustrative example. Insecticide treatments need to be targeted against



**Figure 3.22** Timing insecticide treatments against *Rhyacionia frustrana* on young radiata pine in California, USA. Male moths were caught in pheromone-baited traps deployed part way through the extended flight period of the overwintering generation (P). This first flight has no distinct beginning in the mild climate. The first moths caught in the F1–F3 generations (▼) were used as the ‘biofix’ point for the start of day degree (DD) accumulation and peak moth counts (▲) as the end point. This corresponded to 575 DD (horizontal bar). Peak egg hatch occurred an additional 111 DD after peak flight and this was the optimum time for insecticide treatment. The timing of treatment following the first flight (P) was based on accumulation of 111 DD after the peak trap catch (↓) (from Malinoski and Paine 1988).

early instars which are exposed on the surface of the shoots, but these larvae are difficult to detect. Damage to shoot tips is not evident until after the second to third instars have tunnelled into the shoots where they are protected from insecticide. For this pest, DD accumulation and pheromone-baited

trap catches were used together to determine the time of peak flight accurately (Fig. 3.22). The optimal treatment date is the time of peak egg hatch which occurs 111 DD after peak flight. More accurate timing of insecticide treatments reduced the number of applications needed to protect the high value trees.

# The role of silviculture

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The choice of where and what to plant when establishing plantation forests has the potential to influence subsequent damage by pests and diseases (Section 1.2). Silviculture can contribute to pest management therefore, by the selection of species that are adapted to the available sites and by avoiding those species that are known to be highly susceptible to native or previously introduced pests. In the United Kingdom, the European silver fir is extremely susceptible to the silver fir adelgid, *Adelges nordmannianae*, and this has effectively prevented the widespread planting of this otherwise desirable plantation species (Kerr 1999a). Similarly in New Zealand, introduction of the spruce aphid, *Elatobium abietinum*, has severely limited the use of spruce in plantation forestry (Miller and Knowles 1989; Nicol *et al.* 1998). Sometimes pest problems may only become evident after trees have been planted over large areas or where they are established on particular sites. In Scotland, plantations of lodgepole pine have proved to be highly susceptible to the pine beauty moth, *Panolis flammea*, a native defoliator that normally occurs at low density on Scots pine. Cyclic outbreaks on lodgepole pine cause high levels of mortality, particularly where trees are growing on sites characterised by deep peaty soils that are poorly drained (Leather and Barbour 1987; Hicks *et al.* 2001). In areas where outbreaks occur, the only long-term solution to this pest problem is to manage plantations on a shortened rotation and, where site conditions allow, to replant them with a non-host species such as Sitka spruce. The replacement of one tree species by another is a rather extreme example of how forest management can contribute to the management of pests of plantation forests. But in semi-natural forests, wide-ranging structural changes have also been proposed for the management of forest pests.

One of the longest running debates on the importance of silviculture in pest management concerns the spruce budworm, *Choristoneura fumiferana*, in North America. At issue is the extent to which forest management has actually contributed to the budworm problem and the role it now has in helping to ameliorate it. This pest is characterised by periodic outbreaks that appear to be synchronised over large geographical areas on a 30–35-year cycle. The debate centres on whether changes in the composition and structure of forests resulting from their exploitation and management after European settlement have increased susceptibility to *C. fumiferana*. In other words, were pre-settlement forests relatively more resistant to spruce budworm than those growing now? Similar arguments have been made in relation to western spruce budworm, *C. occidentalis* (Section 1.2.1). There have been three major outbreaks of *C. fumiferana* in the last century beginning around 1910, 1940 and 1970, progressively increasing in severity and affecting 11, 25 and 58 million ha, respectively (Miller and Rusnock 1993; MacLean 1996a). This increase in the severity of outbreaks has been attributed in part to an increase in the representation of susceptible balsam fir within stands as a result of both natural regeneration following clearfelling and fire suppression. The extent to which this ‘silvicultural hypothesis’ can explain the increasing severity of *C. fumiferana* depends on understanding how characteristics of the forest influence both budworm population dynamics and the susceptibility or vulnerability of the forest (Miller and Rusnock 1993). Long-term experiments could help to resolve some of these questions. In 1997, a silvicultural experiment was established in Alberta, Canada that has the aim of determining how the intensity and spatial pattern of thinning affects not only defoliation but also populations of budworm

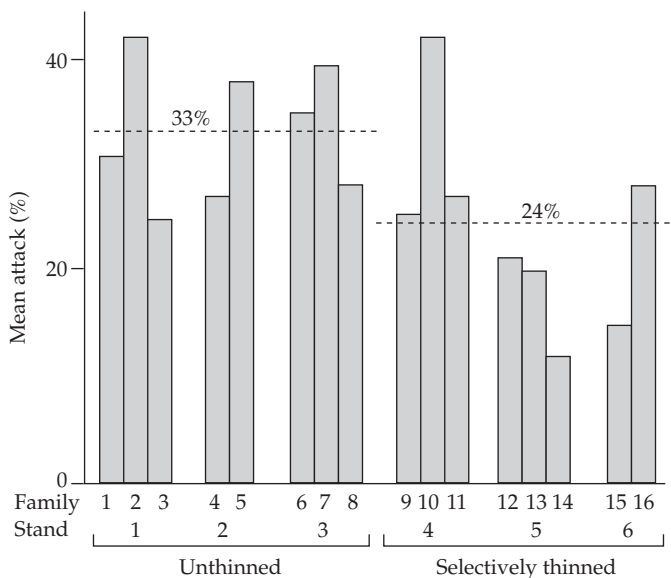
and of its natural enemies (Volney *et al.* 1999). The experiment is designed to last until 2067—beyond the life expectancy of even the younger collaborators!

Management of *C. fumiferana* on a local scale has depended on identifying stand risk factors that can be modified by silviculture to reduce the impact of outbreaks. Some of the risk factors are discussed in Chapter 3. The three factors that have been identified as particularly important and associated with increased mortality of mixed balsam fir forests are increasing stand age, reduced hardwood content (Fig. 3.4) and drainage characteristics of the site which results in unusually dry or wet conditions (Fig. 3.6). Silvicultural management has therefore been based on harvesting mature or overmature stands and, during thinning operations, favouring hardwoods and reducing the proportion of susceptible balsam fir in high-risk stands (MacLean 1996, 1998).

The use of thinning as a tool of silvicultural pest management has in fact been advocated for many different kinds of pest. During thinning, reducing tree density, as well as removing slowly growing or suppressed trees, increases the growth and vigour of stands and, in conifers, this can reduce susceptibility to bark beetles (Section 3.3.4). Removing pest-damaged or diseased trees can prevent the development of infestation foci and in stands where

natural regeneration is the predominant method of forest renewal, thinning may actually increase natural resistance to pests by altering the genetic composition of the stand. This effect has been demonstrated in managed and unmanaged stands of eastern white pine attacked by white pine weevil, *Pissodes strobi*, in the north-eastern United States. The stands originated when trees colonised abandoned fields and many of these unmanaged trees were deformed by repeated weevil attack on leaders. In managed stands however, weevil-attacked trees were selectively removed during thinning. Progeny of the more resistant trees that remain in managed stands will increase in frequency over time so that an overall increase in resistance of stands to weevil attack is anticipated (Fig. 4.1).

Damage by some pests can increase after silvicultural operations. One obvious example is the increased risk of windblow when stands growing on exposed sites are thinned, with a corresponding increase in the risk of damage by bark and wood colonising insects and fungi (Section 3.3.3). By reducing tree density, thinning may re-create open conditions typical of young stands and this can favour some pests and pathogens. Similarly, exposure of a forest edge caused by clearfelling or forest road construction leads in general to warmer, drier, windier and lighter conditions in comparison with



**Figure 4.1** The effect of selective thinning of white pine stands in New Hampshire, USA on resistance to *Pissodes strobi*. In unthinned stands, seeds were collected from dominant weevil-attacked trees that would normally be removed in thinning. In thinned stands, collections were made from dominant well-formed and unattacked trees. The progeny from individual trees (half-sib families) were planted in a common environment and when assessed at 12 years old, the progeny of trees from selectively thinned stands were significantly more resistant to weevil attack than those from unthinned stands. Dashed line represents the mean attack for thinned or unthinned stands (from Ledig and Smith 1981).

the forest interior and this can affect susceptibility of edge trees. In particular, the spruce bark beetle, *Ips typographus*, when present in the forest at endemic levels tends to kill spruce trees more commonly along forest-clearfell edges (Peltonen *et al.* 1997; Peltonen 1999). Thinning or harvesting operations can also lead to an increase in damage by pests that utilise the root-stumps or brash left on the site. Where more than one pest or pathogen can affect stands, thinning has the potential to produce conflicting effects by influencing the organisms in different ways. In oak stands in Pennsylvania, USA, defoliation by gypsy moth, *Lymantria dispar*, increases susceptibility of trees to the root rot fungus, *Armillaria* spp. Thinning stands considered to be at risk of future *L. dispar* attack is recommended as a way of reducing their susceptibility to defoliation. But thinning increases the number of root-stumps available for colonisation by *Armillaria* spp. and this could significantly increase the inoculum potential (Burrill *et al.* 1999). In this example, thinning experiments established that the incidence of the root pathogen was greater in unthinned but defoliated stands than in those that were thinned prior to defoliation.

These examples draw attention to the important point that the effects of thinning or other silvicultural operations are often complex, not only affecting tree density or species composition, but causing changes in microclimate, ground vegetation and the growth dynamics of the stand. These complex changes have the potential to affect different organisms in different ways and to have both positive and negative effects on damage levels. When developing silvicultural approaches to pest management therefore, the avoidance of certain practices can be as important as their application. The strategies adopted for particular pests should, as far as possible, be based on an understanding of key aspects of their ecology, of the stand factors that influence damage and on how changing them is likely to affect both pest abundance and the damage caused to the stand.

Silvicultural methods in pest management include not only thinning and felling but also those related to site preparation prior to planting and to post-harvest management of timber, as well as dealing with catastrophic events such as windblow.

## 4.1 Planting and establishment

Where forests are being re-established after clear-felling, pests and pathogens associated with trees of the previous rotation can attack the young transplants. Those pests whose damaging potential is significantly increased by the plantation environment or by the cycle of forest management are often referred to as 'silvicultural pests'. The pine weevil, *Hylobius abietis*, is a well-known example of a silvicultural pest, affecting conifer reforestation in north temperate forests of Europe and parts of Asia. In unmanaged forests, this weevil would normally occur at relatively low density because it breeds only in fallen or moribund trees that are usually relatively scarce. In managed forests, larvae feed within bark on the abundant root-stumps left in the ground after clearfelling, resulting in high local adult populations that cause significant mortality of unprotected plants. The basidiomycete fungus, *Heterobasidion annosum*, is an example of a 'silvicultural pathogen' and is one of the most important disease-causing fungi of north temperate conifer forests (Woodward *et al.* 1998). It is a primary coloniser of new stump surfaces and can spread from the stumps to the roots of adjacent trees, killing young trees or causing butt-rot later in the rotation. For both these organisms, 'destumping' after clear-fell to remove the breeding or food resource can be an effective, though labour intensive, method of control (Fig. 4.17).

Seedling trees used to replant forests are subject to abiotic stresses as a result of lifting, storage, or transport to the site. The resulting 'transplant shock' can reduce their resistance to, or tolerance of, pest and pathogen attack. Factors known to reduce establishment success and the early growth of transplants include lifting bare-rooted plants before they are fully dormant, prolonged cold storage and root desiccation (Margolis and Brand 1990; McKay 1997; South and Zwolinski 1997). Preparation of sites prior to planting can increase tree survival and may also reduce pest damage levels. Methods of cultivation designed to improve microsite conditions by reducing weed competition and increasing the availability of nutrients to young transplants include scarification and mounding. Scarification involves removing vegetation and accumulated organic matter to expose underlying soils whereas in mounding,

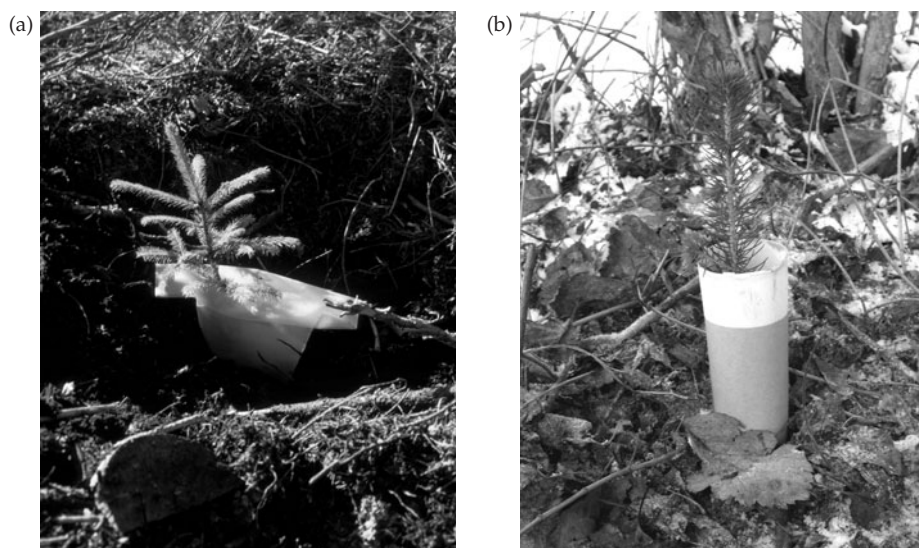
a patch of surface soil is removed and inverted to form the planting site (Fries 1993; Sutton 1993; Savill *et al.* 1997). Cultivation to improved planting sites prior to conifer reforestation can significantly reduce attack of young transplants by *H. abietis* (Fig. 4.18) (von Sydow 1997; Björklund *et al.* 2003).

After planting, physical protection by fencing whole compartments may be necessary for successful establishment in areas with high populations of mammalian herbivores such as deer or rabbits. Physical protection of individual trees has also been tried to minimise damage by some insect pests (Fig. 4.2). Barriers, in the form of 'collars' or 'sleeves' placed around transplants for at least two growing seasons, can provide protection from attack by *H. abietis* equivalent to that provided by insecticides (Fig. 4.3). However, barriers can be relatively expensive and the additional handling time to position them carefully can increase planting costs.

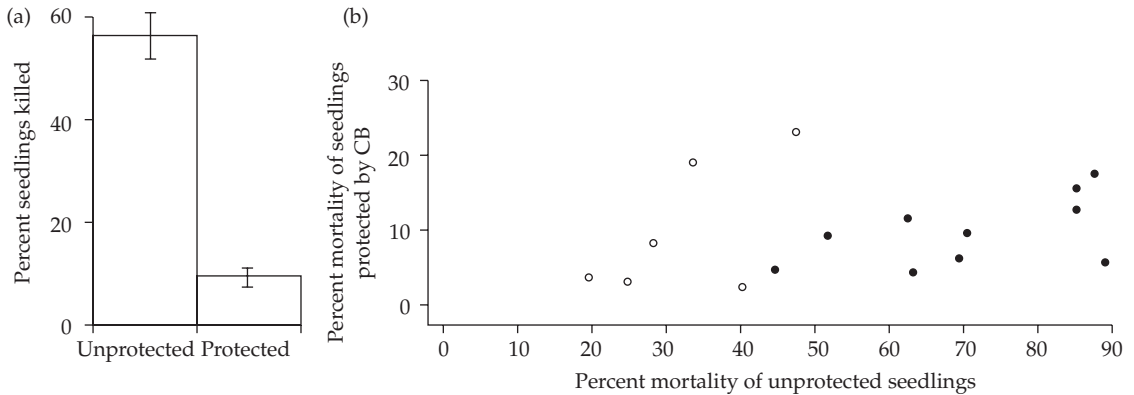
For some plantations, it may be possible to minimise the impact of particular pests by changing planting practice or design. In most stands, the initial planting density is determined by management objectives and the characteristics of the sites being

planted. It may however be possible to allow for unavoidable losses to pests and pathogens by planting at higher density so that pest impact on final yield is minimised. Increasing plant density may not be possible where elite plants from tree improvement programmes are used since they are more expensive and in limited supply. Managing forests on a 'continuous cover' rather than a clearfell system may reduce the impact of some pests on young trees. In continuous cover management, some mature trees are retained on the site at the end of a rotation and this appears to reduce damage to transplants by *H. abietis* (von Sydow and Örländer 1994; Helliwell 1997; Kerr 1999b). In tropical forests, planting mahogany under the shade of a 'nurse' crop has been suggested as a mechanism for reducing attack by the mahogany shoot borer, *Hypsipyla* spp., because artificial shade treatments have been shown to reduce oviposition and pupal mass (Mahroof *et al.* 2002).

The effect of plantation design on pest damage has been studied particularly in relation to the deployment of clonal willows and poplars in short-rotation forestry (Fig. 1.10). In clonal mixtures

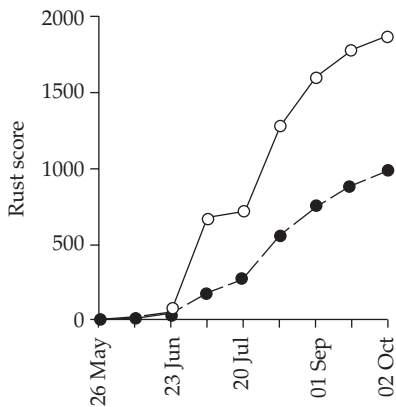


**Figure 4.2** Two kinds of protective barrier used experimentally for physical protection of conifer seedlings against attack by *Hyllobius abietis*. (a) The Teno-collar which has an upper rim folded downwards (Photo B. Långström). (b) The coated barrier is a cylinder of PVC-coated paper covered on the outside by polytetrafluoroethylene which has a slippery surface (Photo H. Nordenhem). Other types of shelter are illustrated in Lindström *et al.* (1986) and Eidmann and von Sydow (1989). In practice, the effectiveness of barriers is impaired if they are not properly located on the soil or where surrounding vegetation or brash forms a 'bridge' allowing access to the transplants. This problem increases as weeds grow on the site in the year after planting.



**Figure 4.3** Physical protection of conifer transplants against attack by *Hylobius abietis*. (a) Mortality of containerised Norway spruce over 2 years with or without the protection of coated barriers (CB) applied before planting (data from Eidmann *et al.* 1996). (b) Mortality in paired plots of protected and unprotected transplants planted on sites that were either scarified (○) or unscarified (●). The wide range of mortality in plots of unprotected transplants reflected local weevil population density although scarification of soil resulted in lower mortality rates. The limited range of mortality in corresponding plots of protected transplants demonstrated that mortality was independent of weevil population size. Most logging residues had been removed from the experimental sites (from Eidmann *et al.* 1996).

of willow, the onset and build-up of populations of the rust (*Melampsora* spp.) can be delayed in comparison with monoclonal plantings (Fig. 4.4). Before using particular planting designs commercially, it is important to establish that there are beneficial effects for management of all the key pests in the



**Figure 4.4** The effect of mono- and polyclonal stands of willow on development of rust caused by *Melampsora epitea* var. *epitea*. *Salix viminalis* 'Bowles Hybrid' was grown alone (○) or in intimate mixture with *S. x dasycardos* and *S. viminalis* '683' in 0.5 ha plots (●). In polyclonal mixture, the onset of disease was delayed, disease build-up was slowed and end-of-season disease levels were lower so that premature leaf fall was not induced. Highly susceptible clones, however, did not benefit from deployment in polyclonal mixtures (from McCracken and Dawson 1998).

system, or at least that designs do not make some pest problems worse. In willows, damage by both rust fungi (*Melampsora* spp.), and willow beetles (*Phratora* spp.), has been found to be less severe in mixtures of clones that differed in susceptibility than when clones were grown in monoculture, despite obvious differences in colonisation patterns and modes of dispersal between fungi and beetles (Peacock *et al.* 2001).

## 4.2 Managing established forests

Thinning or 'spacing' of stands is the principal silvicultural operation for optimising the productivity and quality of timber at final harvest (Evans 1992; Savill *et al.* 1997). In a series of thinnings throughout the rotation, the initial density of young stands is progressively reduced to maintain vigorous growth by reducing competition for light, water and nutrients. Reducing the density of trees in normal thinning operations also has some other important effects on the stand as a whole. For example, thinning produces an immediate effect on within-stand microclimate and can affect the understorey vegetation. In mixed species stands, thinning can also alter relative species composition. Some examples of the range of effects that may follow thinning are shown in Table 4.1.



The complexity of post-thinning changes in stands makes it difficult to predict the responses of different pests and to separate the influence of changes in tree density from those related to microclimate or effects on tree growth for example. There are therefore few generalised 'prescriptions' for silvicultural manipulation of stands for pest management. Appropriate silvicultural treatments may depend on particular site or stand characteristics and so may need to be developed empirically for particular pests. Although thinning is an important tool in the silvicultural management of pests and pathogens in established forests, other management techniques also have specialist applications including fertilisation and fire.

#### 4.2.1 Thinning and pruning

During normal selective thinning operations, diseased or infested trees would normally be removed and this helps to maintain stand health and remove

infestation foci. Thinning or pruning carried out specifically to remove trees attacked by pests or pathogens is usually referred to as 'sanitation thinning'. Pests for which this technique is particularly appropriate are those that attack individual trees such as stem-colonising scale insects and adelgids, 'solitary' bark beetles and some stem rust fungi, particularly those that develop relatively slowly over a number of years. In younger stands, the main aim is to remove trees that can act as a focus of infestation within the stand, on the assumption that this will reduce the rate of build-up and spread. Where relatively mature trees are attacked 'salvage thinning' operations may be aimed at removing trees before their commercial value is lost.

Changes to the timing or intensity of thinning or to the criteria for selecting trees to be removed provide the basis for using thinning as a silvicultural method of control. Some selected examples are discussed in the following sections in relation to the stand factors identified in Table 4.1.

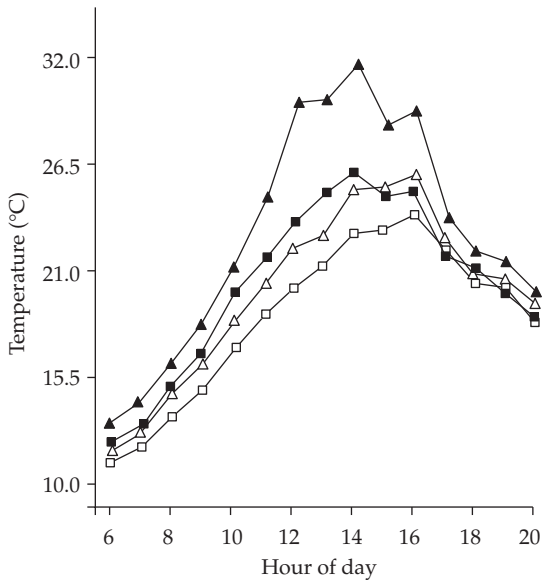
**Table 4.1** Some generalised and specific effects of thinning operations on trees, environmental conditions within stands or on pests and pathogens

Stand factor	Effect
<i>Microclimate, resources and biotic interactions</i>	<p>Increased bark temperature of standing and felled trees can affect behaviour and development of bark beetles.</p> <p>Reduced shading increases attack on leaders of understory spruce by <i>Pissodes strobi</i></p> <p>Increase in nitrogen mineralisation rate and uptake</p> <p>Changes in the amount and nutritional quality of foliage affects development rate of <i>Choristoneura fumiferana</i> and amount of foliage consumed.</p> <p>Removing infestation foci of stem colonising pests and pathogens.</p> <p>Increase in root-stumps for colonisation by insects and pathogenic fungi.</p>
<i>Tree density, growth rate and vigour</i>	<p>Reduced effectiveness of passive dispersal</p> <p>Removing large diameter trees reduces losses to <i>Dendroctonus ponderosae</i></p> <p>Reducing tree density reduces susceptibility to <i>Dendroctonus frontalis</i></p> <p>Survival of lower branches in thinned pine stands increases branch and stem infection by rust fungi</p>
<i>Species composition</i>	<p>Removing hardwoods in mixed conifer–hardwood forest increases defoliation on residual balsam fir by <i>C. fumiferana</i></p> <p>Reducing the density of N-fixing red alder in mixtures with Douglas fir decreases the nitrogen content of Douglas fir foliage with potential effects on insect herbivory</p>

Sources: Crook *et al.* (1979), McGregor *et al.* (1987), Schmid *et al.* (1991), Schowalter and Turchin (1993), Furuta and Aloo (1994), van der Kamp (1994), Carlyle (1995), Shainsky and Rose (1995), Bauce (1996), Taylor *et al.* (1996), Hindmarch and Reid (2001).

*Microclimate, resources and biotic interactions*

After thinning, previously shaded trees may be exposed to direct insolation, resulting in an increase in bark temperature (Fig. 4.5). This can increase the development of sub-cortical insects such as bark beetles, affecting voltinism or the occurrence of sister broods (e.g. Fig. 3.21). Some defoliators also appear to benefit from exposure of trees, particularly along



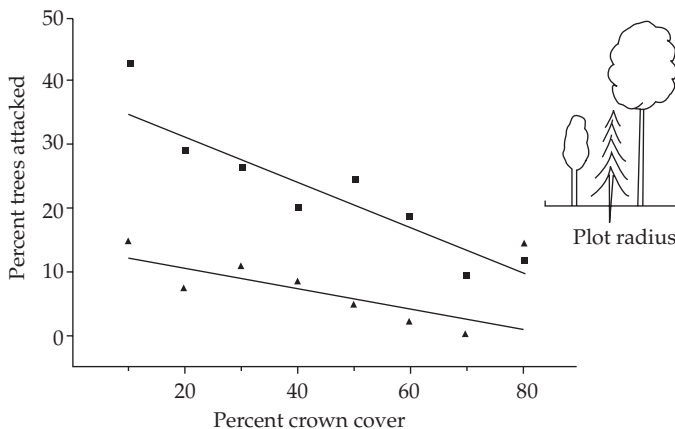
**Figure 4.5** Mean temperature in shaded bark crevices on the north (open symbols) and south (closed symbols) sides of mature ponderosa pine trees on a clear summer day. The trees, growing in South Dakota, USA, were in an unthinned stand (909 trees ha<sup>-1</sup>) (□ ■) or thinned to a density of 524 trees ha<sup>-1</sup> (▲ △) (from Schmid *et al.* 1991).

forest edges, as a result of nutritional and other changes in trees exposed to the sun (Nealis and Lomic 1994; Kouki *et al.* 1997).

The reduction in shade that follows thinning has a number of effects on white pine weevil, *Pissodes strobi*. In North America, this weevil attacks and kills the leading shoots of a number of conifer species including white and Sitka spruce and white pine. When vulnerable species are growing in mixed stands and are shaded by overstorey trees, weevil attacks tend to be less common (Fig. 4.6). Several factors may contribute to the effect of shade in reducing attack including a change in behavioural response of weevils to the host leaders, lower temperature of the bark and higher overwintering weevil mortality in shaded stands (Taylor *et al.* 1996). Removal of the overstorey during thinning operations is therefore likely to increase weevil attack, particularly in stands where it is already high. In managing stands there is likely therefore, to be a trade-off between increased levels of attack after thinning and increased growth of the overtopped conifers as a result of reduced competition.

The effects of thinning on soil temperature will depend among other things on the latitude of the forest, intensity of thinning and whether thinning waste is left on site, protecting the soil from the direct effects of the sun. In general, an increase in soil temperature after thinning enhances nitrogen mineralisation from thinning residues, leading to increased uptake by plants (Carlyle 1995).

Pruning can be used, like sanitation thinning, to remove infested material from the forest. In



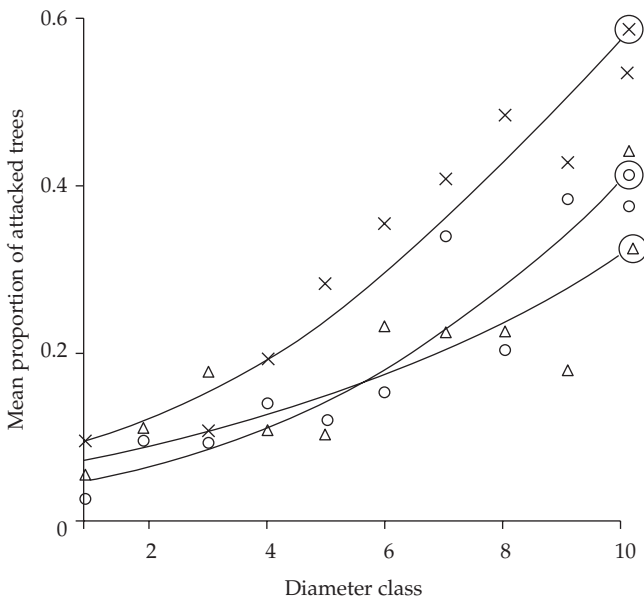
**Figure 4.6** Percentage of white spruce trees attacked by *Pissodes strobi* in mixed conifer-hardwood forests in British Columbia, Canada in relation to degree of shading. In experimental plots, shading by overtopping crown cover—the percentage of each plot covered by projected leaf area (inset)—reduced weevil attack in both heavily infested (■) and lightly infested stands (▲) (from Taylor *et al.* 1996).

particular, some conifer stem-infecting rust fungi initiate branch infections that gradually spread to cause cankers on the main stem, resulting in deformation and in some cases, significant mortality. In Canada, western white pine can be affected by white pine blister rust, *Cronartium ribicola*, which causes cankers that are usually within 2–3 m of the ground. Pruning branches protects healthy trees from infection by removing branch cankers before they reach the main stem. If stands are left untreated, most trees are killed within about 20 years (Hunt 1991).

For some species, pruning to improve stem quality of final crop trees in intensively managed plantations can actually increase the risk of damage from pests and pathogens. Removal of significant amounts of foliage during pruning depletes photosynthetic area like other forms of partial defoliation and in some conifers, this can increase susceptibility to attack by bark beetles and associated fungi (Christiansen and Fjone 1993; Solheim *et al.* 1993). In France, the practice of pruning the lower branches of maritime pines releases volatile resinous chemicals that attract adult moths of the European stem borer, *Doryctria sylvestrella*. This results in an increase in attack at the site of wounding, causing malformation of the trunk and formation of resin

pockets in the stemwood which has a significant economic impact. Interestingly, the larger more vigorous trees seem most susceptible to borer attack and this is increased further by pruning (Fig. 4.7). The risk of attack generally increases with the number of whorls that were pruned so that damage by this insect could be reduced by planting at high density to reduce lower branch survival and so confine pruning to the upper, less-valuable parts of the stem (Jactel and Kleinhentz 1997).

During thinning, the processes of felling and extraction can cause mechanical damage to the base of trees. Roots can also be damaged either directly, or through soil compaction by heavy machines. Wounds can result in the entry of stain or decay fungi that degrade the most valuable part of the tree (Hessburg *et al.* 2001; Vasiliauskas 2001). Mechanical damage can exacerbate attack by bark beetles such as the lodgepole pine beetle, *Dendroctonus murrayanae*, the red turpentine beetle, *D. valens*, and the spruce bark beetle, *D. micans*, as they are attracted to recent wounds near the bases of trees (Grégoire 1988; Safranyik *et al.* 1999). The number of damaged trees can accumulate over a rotation so that, in mature stands, a high proportion of the final crop trees may be affected. In high-risk stands, it may be necessary to modify thinning practices to



**Figure 4.7** Proportion of trees attacked by *Doryctria sylvestrella* in an experimentally manipulated stand of 12-year-old maritime pine in the Landes, south-western France. Vigorous trees of good form were selected and either pruned (x) or left unpruned (o) as controls. Some nearby trees that were silviculturally unsuitable for pruning were used as additional controls (Δ). Trees, which ranged in diameter from approximately 11–23 cm (at 1.3 m), were allocated to one of ten diameter classes (from Jactel *et al.* 1996b).

reduce the incidence of damage. The possibility of biological control of wound pathogens is discussed by Zimmermann *et al.* (1995).

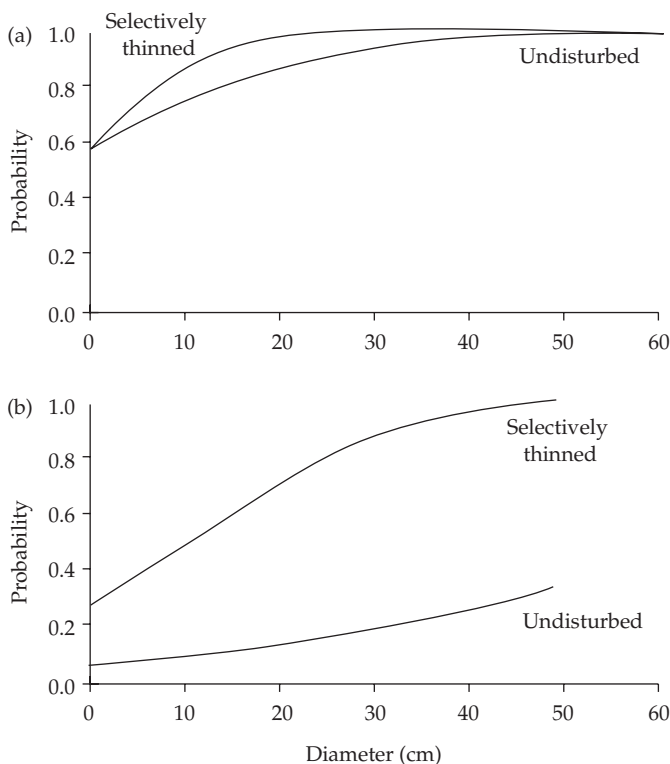
Experimental thinning of mixed conifer stands in Canada illustrates how the root pathogen, *Armillaria ostoyae*, can utilise root-stumps, creating new inoculum sources from which the pathogen can spread to neighbouring trees through root contact (Fig. 4.8). The increase in disease incidence following thinning was found to be much greater on sites where infection was generally low. On sites that were more favourable for the pathogen, with higher background levels of disease, thinning had much less effect on subsequent disease development.

#### *Tree density, growth rate and vigour*

A high density of trees within plantations may be conducive to the spread of some pest infestations. In Japan, the Sakhalin fir aphid, *Cinara todocola*, causes extensive damage to young firs. Winged females initially colonise new plantations, but within

stands the spread and establishment of new colonies occurs by short-range passive dispersal of wingless females. Increasing the spacing between trees can decrease both the percentage of trees infested and tree mortality (Furuta and Aloo 1994). Conversely, for insect pests such as shoot moths that tend to attack young trees in open stands before crown closure, thinning can actually increase attack and extend the period of vulnerability (Berisford 1988).

Thinning conifer stands to increase tree growth and 'vigour' has been particularly emphasised as a means of reducing the risk of bark beetle attack (Section 3.3.4). But demonstrating the positive effects of thinning in reducing mortality caused by bark beetles is not straightforward. Some studies have been conducted retrospectively in stands that were likely to differ in a number of characteristics at the time they were thinned. Since thinning treatments are not allocated at random in retrospective studies, some caution is needed in interpreting them. Some of these problems were overcome by



**Figure 4.8** Probability of occurrence of root lesions caused by *Armillaria ostoyae* based on a retrospective study in two mixed conifer forests in different biogeoclimatic zones in south-eastern British Columbia, Canada. Within forests, the amount of disease was determined for undisturbed areas and for areas selectively thinned at least 10 years previously. The background level of disease was much higher on sites classified as 'moist' (a), than on the 'dry' sites (b). On dry sites the effect of thinning was dramatically to increase incidence of disease in remaining trees. The site differences observed in this study could be used as a basis of risk assessment as discussed in Chapter 3 (from Morrison *et al.* 2001).

Schowalter and Turchin (1993) in a study of the effects of thinning and species composition on mortality caused by southern pine beetle, *D. frontalis*. Beetle populations were introduced into experimental plots with different thinning treatments and in each one, attack induced on a central pheromone-baited tree (Fig. 4.9). In the high-density plots of almost pure pine, most trees were killed but mortality was much lower in plots where pine density had been reduced by thinning or where the non-host hardwoods had been left intact among high-density pines.

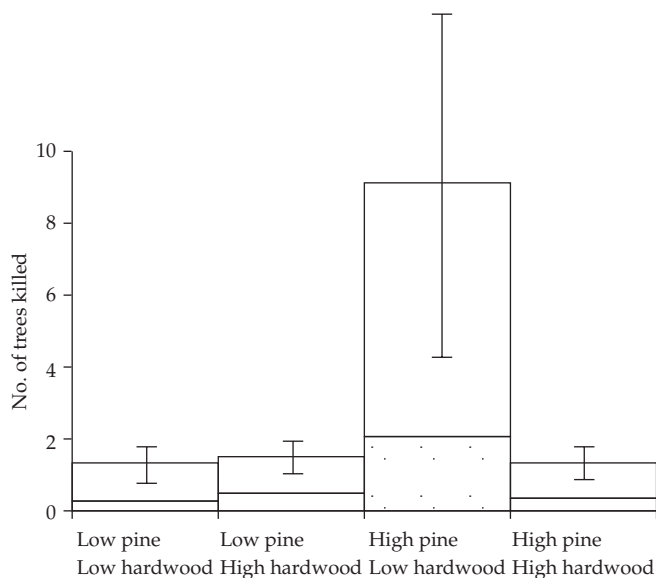
#### Species composition

Manipulation of species composition during selective thinning is usually done to favour those species that are needed to meet forest management objects. But species composition can also be manipulated to reduce the density of host species or to eliminate secondary hosts that help to maintain high populations of host-alternating species. The Douglas fir woolly aphid, *Adelges cooleyi*, for example, requires two hosts for the full life-cycle so that close proximity of spruce and Douglas fir can give rise to damaging populations (Anon. 1985). Defoliation of balsam fir and other susceptible conifers by the spruce budworm, *Choristoneura fumiferana*, in North America is influenced by the species composition of the forest

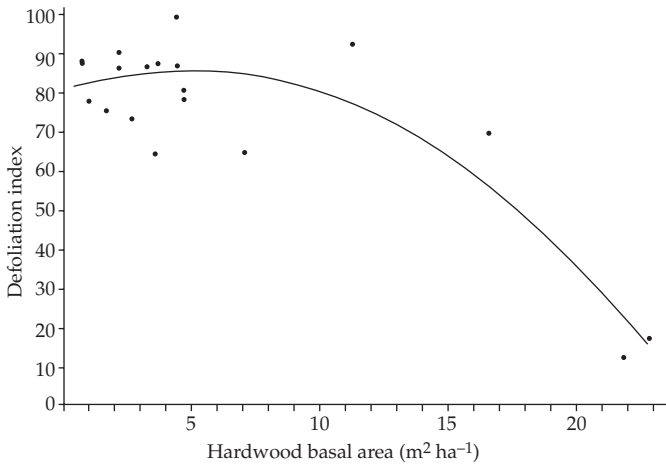
(Fig. 3.4). Mixed conifer–hardwood stands suffer less defoliation during outbreaks than those dominated by balsam fir or other susceptible conifers. Where thinning significantly reduces the hardwood component of stands, defoliation is likely to increase (Fig. 4.10). Management of this defoliator depends in part on maintaining the optimum species mix within stands. However, the influence of species composition also appears to extend to the surrounding forest mosaic (Fig. 4.11). One of the main factors influencing the forest mosaic in the study area was the period of time since the last fire. On burned areas, pioneer species such as jack pine and aspen predominate but as the interval since the last major fire increases, susceptible balsam fir becomes an increasingly important component of forests. These findings emphasise that silvicultural management of some pests may need to be done on a area-wide basis.

#### 4.2.2 Fertilisation

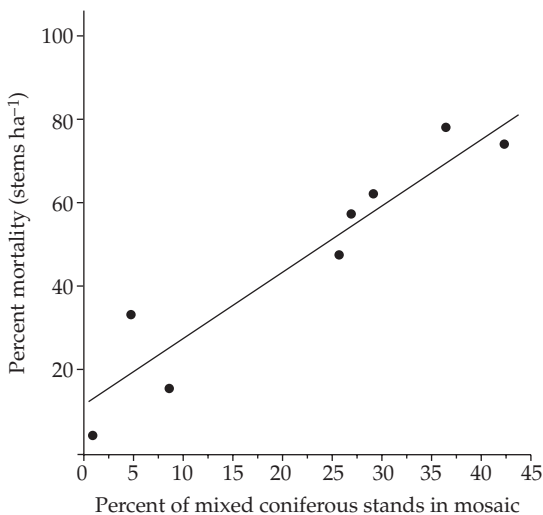
The use of fertilisers in forests is particularly associated with the establishment of new plantations on infertile sites (Savill *et al.* 1997). But fertilising trees has also been suggested as a way of increasing their resistance to some insect pests (e.g. Stark 1965). More



**Figure 4.9** An experimental test of the effect of thinning and species composition on mortality of pines caused by *Dendroctonus frontalis* at two sites in southern USA. Results were from different experimental stands in 1989 (□) and 1990 (□). Stands were 30–40 years old, composed predominantly of loblolly pine but with some mixed hardwood species present as a result of previous fire suppression. Stands had been thinned 3–5 years prior to experiments so that the original ‘high’ density of pine was reduced by about half to a ‘low’ density of 11–14 m<sup>2</sup> ha<sup>-1</sup> basal area. Hardwoods were effectively removed from some of the stands. Exposure of experimental plots to bark beetles was standardised by pheromone-baiting a tree in the plot centre and placing infested logs nearby (data from Schowalter and Turchin 1993).



**Figure 4.10** The effect of thinning mixed conifer–hardwood stands on defoliation of dominant and codominant balsam firs by *Choristoneura fumiferana* in Quebec, Canada. Stands were 30–50 years old and thinned to remove 30–40% of basal area, preferentially removing hardwoods and retaining white spruce and balsam fir as final crop trees. Stands were thinned 2 years before the peak of the budworm outbreak and those with the smallest hardwood component suffered the greatest intensity of subsequent attack on remaining balsam fir (from Crook *et al.* 1979).



**Figure 4.11** Mortality of balsam fir during an outbreak of *Choristoneura fumiferana* in Quebec, Canada. Where coniferous stands were intermixed with deciduous ones, they suffered lower mortality than when the forest mosaic was dominated by conifers. This effect was evident even after within-stand factors that influence mortality such as tree size and balsam fir abundance had been taken into account. Possible causes of reduced tree mortality when deciduous stands were present in the mosaic include increased losses during dispersal of adults and larvae, or more abundant natural enemies in deciduous stands (from Bergeron *et al.* 1995).

recent studies suggest however, that fertilisation is in fact more likely to increase rather than to decrease damage by insect pests because it usually increases nitrogen content or alters nutritional quality in other

ways. The response of insects to fertilisation of their host tree is influenced by a number of factors including degree of host specialisation, feeding habit and the intimacy of association with the host (Mattson 1980; Price 1991; White 1993; Kytö *et al.* 1996b). In general, insects that have an intimate association with their hosts such as galling insects, shoot borers and aphids often increase in abundance on young vigorous growth induced by fertilisation. Other species may be relatively unresponsive to the nitrogen content of their host or feed on parts of the tree where quantitative changes in nitrogen content in response to fertilisation are relatively small. The effects of fertilisation on forest pathogens have been less well studied but phosphorus fertilisation has been observed to increase levels of damage caused by some pathogens (Powers *et al.* 1981; Desprez-Loustau and Wagner 1997).

Fertilisation not only increases nitrogen concentration, but often decreases the concentration of carbon-based secondary chemicals (Koricheva *et al.* 1998; Wainhouse *et al.* 1998; Warren *et al.* 1999). This arises because less carbon is allocated to carbon-based secondary chemicals when growth is stimulated by fertilisation (see Figs 5.2 & 5.13). These are only general predictions, however, because trees vary in their response to fertilisation. Species such as eucalyptus for example, that are adapted to grow on nutrient poor soils, tend to be relatively unresponsive to fertilisers (Fox and Morrow 1992).

As well as affecting the nutritional and defensive quality of individual trees, fertilisation can have stand-level effects with the potential to influence damage by pests and pathogens. Some examples are illustrated in Table 4.2.

The many potential effects of fertilisation make it difficult to generalise about likely impact on pests and pathogens. In general however, fertilisation seems to be of limited value as a tool of management and may cause more pest problems than it solves.

### 4.2.3 Fire

Naturally occurring fires play an important role in the ecology of some forests and when fire frequency is reduced by management, changes to forest structure and composition occur that can alter the susceptibility of the forest to pest attack (Section 1.2.1). The deliberate and controlled use of fire—prescribed

burning—is an important way of maintaining or restoring forests whose characteristic structure and species composition would naturally depend on periodic fires (Attiwill 1994). Fires that are severe enough to damage trees almost always increase their susceptibility to pests. A number of studies have shown that even in fire-tolerant conifers, scorching of the bole can increase susceptibility to bark beetle attack (Bradley and Tueller 2001; Santoro *et al.* 2001). In some specialised habitats, however, controlled fires can contribute directly to pest management (McCullough *et al.* 1998). One often quoted example is burning the litter layer to control conifer seed pests in natural stands that are intensively managed for cone production (Miller 1978). The red cone pine beetle, *Conophthorus resinosae*, is an important pest in red pine stands whose susceptibility to fire is due to particular characteristics of the life cycle. The adult beetles tunnel into the buds of small branches which

**Table 4.2** Some observed and predicted effects of fertilisation on trees and forest stands and associated pests and pathogens. Effects on broad insect groups are based on overall trends observed in the literature. Examples of both positive or negative effects can however be found within the different feeding groups and, in many studies, fertilisation seems to have no effect

Individual tree effects			Forest stand effects
Nutrients	Secondary chemicals	Biomass and plant morphology	
Increase in leaf N content benefits aphids and other phloem-feeding insects, galling insects and some leaf-chewers (Lepidoptera and sawflies)	A reduction in the concentration of some carbon-based secondary chemicals such as phenolics can benefit defoliating insects	Rapid growth may reduce period of susceptibility	An increase in ground vegetation may favour natural enemies
Increase in N or P content benefits some fungal pathogens	An increase in resin droplets on young birch stems can increase resistance to some mammalian herbivores	Increase in leaf biomass may increase tolerance of defoliation	An increase in ground vegetation may increase competition and 'stress' on young trees
		Increased availability of new growth and size of leaves and shoots may benefit shoot borers and galling insects	
		Growth-related increase in number or size of resin ducts in conifers may have a negative effect on sawflies, bark beetles or weevils	

Sources: Björkman *et al.* (1991), Price (1991), Rousi *et al.* (1991, 1993), Kytö *et al.* (1996a,b, 1998), Desprez-Loustau and Wagner (1997), Wainhouse *et al.* (1998), Sun *et al.* (2000).

subsequently break off so that the adults overwinter on the forest floor. Red pines are fire-tolerant and managed stands are very open with little understorey. As a result, controlled burning of the natural litter layer—surface fires—is possible. When this is done before beetle emergence in the spring the fires cause high beetle mortality. In years when heavy cone crops are expected, surface fires seem to have some potential for reducing the density of a pest that is otherwise difficult to control. In practice however, the fires can be highly variable in their effects on trees and depend not only on the accumulation of sufficient fuel to maintain the fire but also suitable weather conditions.

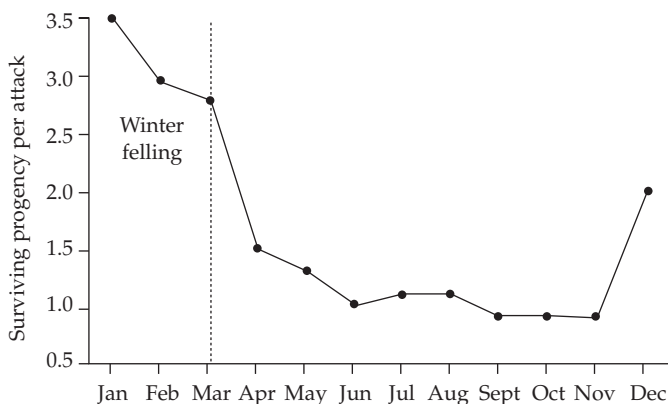
Fire is often used to destroy infested material following sanitation felling of diseased trees and has been used as part of a cut-and-burn strategy for treating spot infestations caused by *D. frontalis* (Section 8.3.2).

### 4.3 Felling and post-harvest

The maintenance of ‘forest hygiene’ or ‘clean silviculture’ is one of the earliest examples of silvicultural management of pests (Vité 1989). By removing brash and moribund trees during thinning or felling operations, the build-up of bark beetle populations that could attack living trees is prevented. Such measures are still an important way of reducing damage by these pests but are now applied more selectively, in part because of the importance of brash in nutrient cycling and because ‘deadwood’ is recognised as an important habitat for rare species (Section 9.4.1).

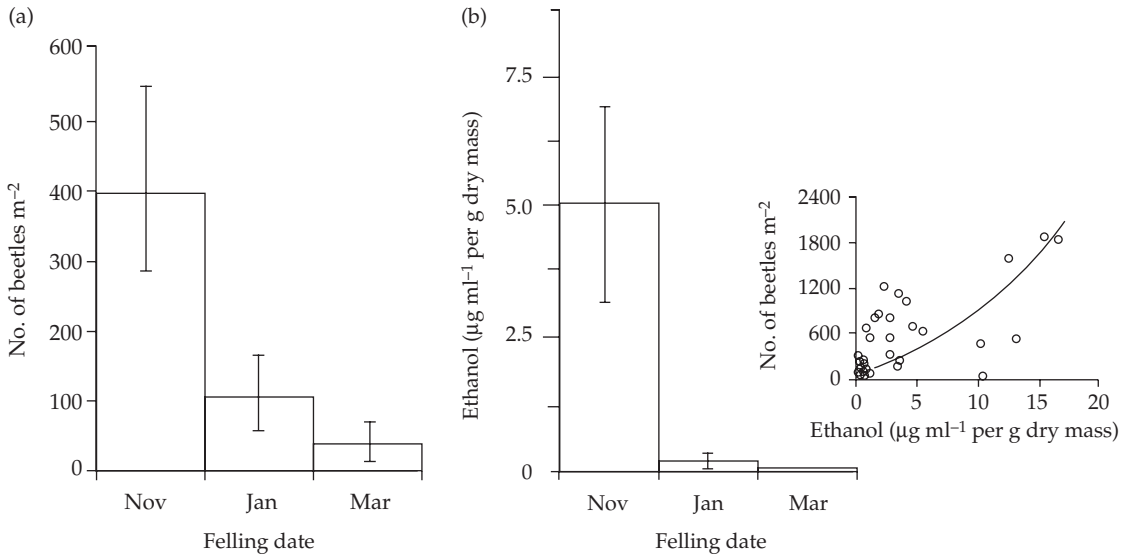
The seasonal timing of felling or thinning operations can influence the suitability of brash during the period when insects are active. For some species, adjusting the seasonal timing of operations can significantly reduce the risk of population increase. The pine engraver, *Ips pini*, is a non-aggressive bark beetle that breeds in brash and when successive felling operations occur within the same area their populations can build-up to high levels, leading to attack on living trees. Ponderosa pine in Montana, USA, can suffer prolonged drought stress and under these conditions, trees attacked by this insect can be killed. In this region, brash produced during the winter period does not dry out and is suitable for attack in the spring after emergence of the overwintering generation (Fig. 4.12). Brash produced during the summer, however, becomes unsuitable for breeding relatively quickly and that produced from late August to November dries significantly before being frozen overwinter and cannot be utilised by beetles in the spring. Population build-up of *I. pini* can therefore be minimised by imposing seasonal restrictions on felling operations in high-risk forests. Methods for quantifying logging residues remaining on sites after harvesting operations are discussed by O’Hehir and Leech (1997).

During harvesting operations, the timber itself is vulnerable to attack and degrade. Conifer logs for example can be used as breeding sites by bark beetles and this often results in blue-staining of the timber and increased bark beetle attack on surrounding trees. Logs are also vulnerable to attack by ambrosia beetles whose pin-hole galleries in the



**Figure 4.12** The effect of felling trees at different times of the year on suitability of pine brash for *Ips pini*, expressed as surviving progeny per initial attack. Rapid drying of the brash outside the winter felling period in Montana, USA reduces breeding success. Brash production should be minimised during the period January–May (from Gara *et al.* 1999).





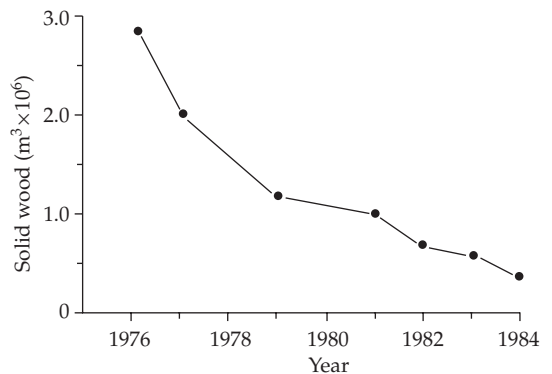
**Figure 4.13** (a) Attack density of *Gnathotrichus retusus* measured in August on Douglas fir logs from trees felled in the previous November–March and left in the forest in Oregon, USA. (b) Ethanol concentration in the sapwood measured in the spring when logs are attacked. Ethanol is a primary attractant for *G. retusus* as well as a number of other ambrosia beetles and it also stimulates attack (inset). Ethanol is formed in the phloem and sapwood of logs under anaerobic conditions and concentrations were highest in logs cut in November. Anaerobic conditions had not developed in logs cut in January and March (from Kelsey 1994).

xylem and associated fungal staining considerably reduce the commercial value of the logs. Attacks by ambrosia beetles are a particular problem in timber stores (Box 7.1). Logs become more attractive to ambrosia beetles as they age, largely because of the production of ethanol and in Douglas fir stands appropriate seasonal timing of felling can significantly reduce attack on logs (Fig. 4.13).

In some countries, laws have been enacted that limit the time that logs can be stored in the forest without protection from insect attack. These legal restrictions reinforce recommendations on good forestry practice and have proved to be highly effective in reducing the volume of logs in the forest when insects are active (Fig. 4.14). During felling operations, there are inevitably delays in the flow of timber from the forest so that measures for minimising pest attack are often necessary. Simply stacking timber provides some protection to the inner logs and is effective provided that logs from the outer part of stacks are removed after they have been attacked but before emergence has occurred. Additional methods include insecticidal treatment,

water sprinkling or using some form of covering (Jääskelä *et al.* 1997).

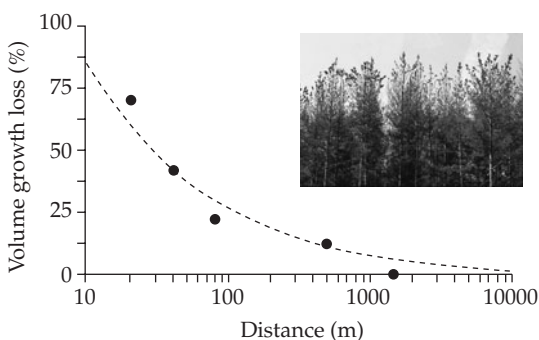
Once logs have been removed from the forest, they can still be a source of infestation so that careful siting of timber stores is necessary to minimise the risk of attack on forest trees. The pine shoot



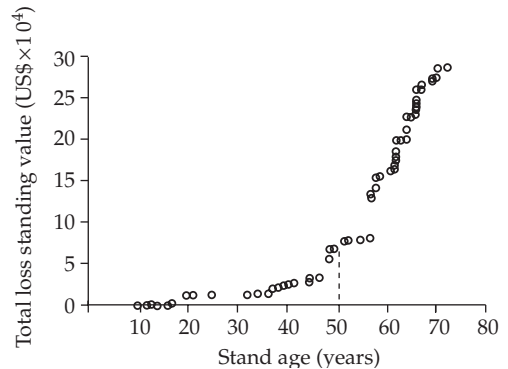
**Figure 4.14** The volume of conifer logs suitable for development of bark beetles stored at forest roadsides during spring and summer months in Sweden. Recommendations on good forestry practice, together with the effect of legal restrictions have significantly reduced log storage in the forest (from Eidmann 1992).

beetle, *Tomicus piniperda*, breeds in the bark of logs and moribund trees but after emergence, maturation feeding occurs in the shoots of living trees causing distortion and growth loss. In southern Sweden, damage caused by maturation feeding can be observed over a distance of 1 km from timber stores (Fig. 4.15).

Changing the rotation length can be a way of dealing with pests that attack mature or overmature stands. For managed stands, rotation length is usually determined to be the time of maximum mean annual increment in  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  (Fig. 9.1(a)). The felling of stands when mature or overmature is most often associated with conifers at risk of bark beetle attack, but mature forests may also be more vulnerable to defoliators, suffering higher mortality than younger stands at similar levels of defoliation. Conway *et al.* (1999) provide an example of the use of shortened rotations to minimise losses in stands of jack pine defoliated by the jack pine budworm, *Choristoneura pinus pinus*. In the study area in Michigan, USA, outbreaks usually last 2–4 years, with severe defoliation reducing tree growth, killing leading shoots—top kill—and causing death of some trees. Insecticides are not used to control outbreaks and management is largely through the application of silvicultural measures such as thinning, so as to reduce competition within stands,



**Figure 4.15** Relative growth loss caused by *Tomicus piniperda* in stands dominated by Scots pine growing at different distances from a timber yard in southern Sweden. Pine logs were stored at the yard over a 3-year period. Growth of sample dominant and codominant trees during the attack period was related to that prior to attack and expressed relative to that of the most distant stand. As well as causing growth loss, bark beetle feeding deforms the upper crown (inset) (from Långström and Hellqvist 1991).



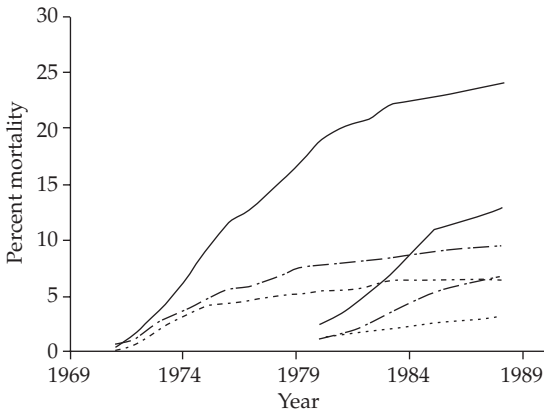
**Figure 4.16** The impact of outbreaks of *Choristoneura pinus pinus* on stands of jack pine in Michigan, USA. The total loss in value of merchantable timber increased with stand age. Around 75% of the total value loss in the sample stands occurred in those over 50 years old. Older stands obviously contained most merchantable timber but younger stands also suffered proportionately lower growth loss and mortality during outbreaks (from Conway *et al.* 1999).

and felling those that are overmature. Losses of merchantable timber volume during a 3-year outbreak averaged 14%, but most losses were concentrated within relatively few well-stocked older stands (Fig. 4.16). Management for a rotation age of 50 years was an effective way of minimising losses.

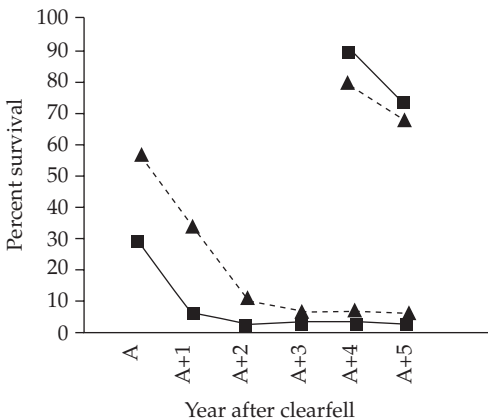
Pests and pathogens that utilise root-stumps after felling pose a threat to young trees replanted on the site. Root-stump removal soon after felling is a direct way of managing such pests and when done on an appropriate scale can be cost-effective (Fig. 4.17) (Greig 1984; Thies *et al.* 1994; Pratt 1998). Alternatively, an extended fallow period can help reduce the intensity of attack on young trees of the following rotation. This has been used with considerable success in the management of the pine weevil, *Hylobius abietis* (Fig. 4.18), and with more modest results for management of the decay pathogen, *Heterobasidion annosum* (Fig. 4.17).

#### 4.4 Salvage and long-term storage

For trees killed during pest outbreaks, losses can often be reduced by salvaging timber before significant degrade has occurred. In British Columbia, Canada, outbreaks of mountain pine beetle, *Dendroctonus ponderosae*, occur over millions of



**Figure 4.17** Cumulative mortality of second rotation Corsican pine caused by *Heterobasidion annosum* in eastern England. The disease was present in the previous crop of Scots pine planted on ex-agricultural land of high soil pH, conditions that favour disease spread through root contacts. Plots were planted in 1969 immediately after clearfelling or in 1975. More of the replanted trees were killed when root-stumps were left intact after felling (—). Mortality was much lower when root-stumps were removed, either of clearfell trees alone (---) or together with those of previous thinnings (- · - ·). When replanting was delayed by 6 years, mortality at corresponding ages was a little lower than that in plots replanted after clearfelling (from Gibbs *et al.* 2002).



**Figure 4.18** Survival of containerised Sitka spruce seedlings planted on a conifer clearfell site colonised by *Hyllobius abietis*. Seedlings were planted in the first growing season after felling (A) or after a four-year fallow period (A + 4). Seedlings, which had not been treated with insecticide, were planted with (▲) or without (■) scarification of the soil. Survival of seedlings planted after clearfelling was lower than that of seedlings planted after a four year fallow period. The beneficial effect of scarification was not evident after the fallow period, when weevil population density had declined (from von Sydow 1997).

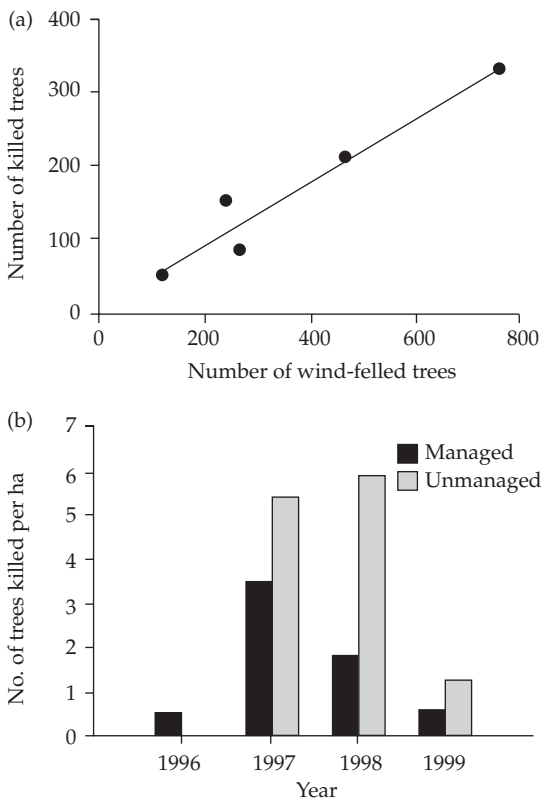
hectares of overmature lodgepole pine, necessitating salvage felling of large forest areas (Fig. 4.19). Timely removal may however be difficult where outbreaks are extensive or in remote areas. Similar problems arise where extreme weather conditions damage large areas of forest (Fig. 3.7). Salvaging and storage of windblown timber is important to prevent degrade by pest or pathogen attack but of greater concern is the possibility that areas of windblow will act as outbreak foci for bark beetles and other pests, resulting in damage over an even larger area (Section 3.3.3).

The size of the area affected by windblow, the initial size of the bark beetle population and the length of time that trees remain on site can all affect the likelihood of significant damage to standing trees. Following a storm in southern Sweden in November 1995, five million cubic metres of spruce and some pine were blown down. Most fallen timber was removed before the following summer but in a few unmanaged stands, fallen trees were left *in situ* to see what effect this had on local mortality caused by the spruce bark beetle, *Ips typographus*. Before the storm, populations of this bark beetle were at low endemic levels and unmanaged areas were relatively small, so the fallen trees were not expected to precipitate an outbreak. The number of trees killed by the bark beetle in the unmanaged areas during the 4-year period after the windblow was correlated with the number of windblown trees (Fig. 4.20a). Leaving the fallen trees in place doubled mortality overall during the 4 years as shown by comparison with managed forests (Fig. 4.20b). The beneficial effect of prompt removal of windblown trees is likely to be much greater in situations where endemic populations are already high, either through poor management or previous disturbance of the forest or where the resistance of standing trees has been reduced by environmental factors such as drought.

The effectiveness of these kinds of salvage operations in reducing damage to standing trees can be increased by careful timing of the removal of the fallen trees. Where the scale of the windblow and available resources allow, removing fallen trees after bark beetle attack has occurred in the spring but before adult emergence, allows the windblown trees to be used as trap trees and this reduces



**Figure 4.19** Regional scale outbreaks of *Dendroctonus ponderosae* in overmature lodgepole pine forests in British Columbia, Canada. Given the scale and severity of outbreaks, salvage felling is often the only practicable method of silvicultural management.

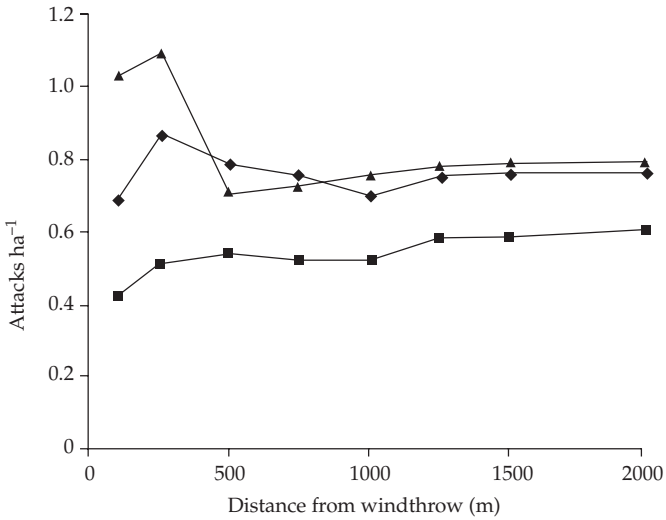


**Figure 4.20** The effect of stand management after windblow on the number of Norway spruce trees killed by *Ips typographus* in southern Sweden. (a) In the area affected by the storm, there was a linear relationship between the number of windblown trees and the number of trees killed by *I. typographus*. (b) In managed stands, fallen trees were removed before the summer but left in place in the unmanaged ones with the result that twice as many trees were killed by beetles in these stands over a 4-year period (from Schroeder and Lindelöw 2002).

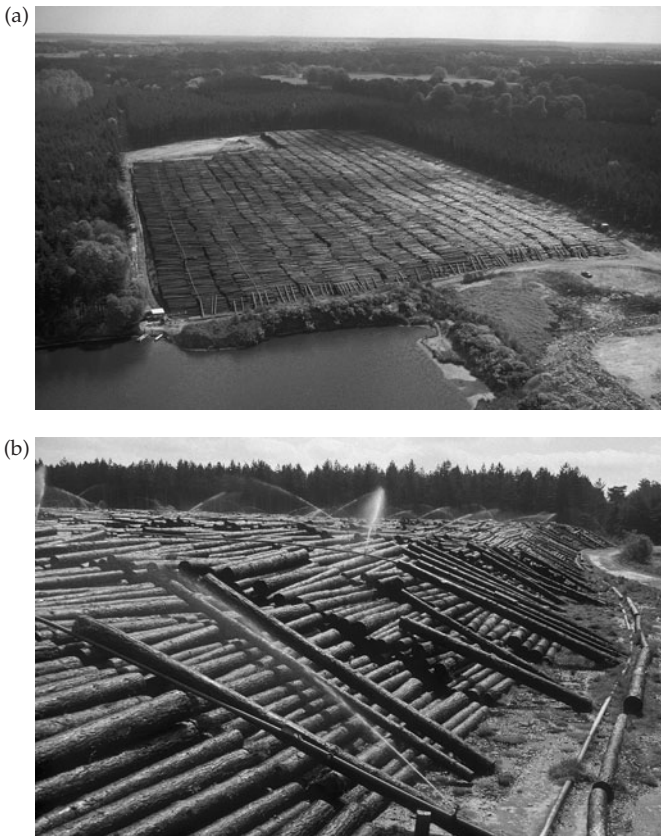
mortality of standing trees (Fig. 4.21). Where there is a delay in removing fallen trees, some protection from bark beetle attack may be possible using antiaggregation pheromones (Section 8.3.2). The use of pheromone-baited trap trees and strategies for ‘containment’ of local bark beetle populations are outlined in Section 8.3.1.

When large volumes of timber come on to the market unexpectedly as after windblow, market saturation can result in a significant reduction in timber prices (Holmes 1991). Market effects can be buffered by long-term storage of timber but protecting large volumes from degrade by insects and fungi presents considerable logistical problems. Wet storage has been used successfully on a number of occasions to store timber for several years. Timber can be stored in lakes but it can be difficult to get logs into and out of this limited storage area, and there is a risk of pollution by leachates from the logs. Storage of logs in stacks on dry land under sprinkler systems is a more practical solution (Fig. 4.22). This can be done most efficiently when stores can be sited near the source of timber, where there are facilities for continuous pumping from a local water supply and where threats to water quality and aquatic organisms from effluent water are minimised. The risk of pollution can be most effectively reduced where effluent water is contained and recycled.

The use of this technique and the factors that influence success have been discussed by Liese and Peek (1984), van dem Bussche (1993), Syme and Saucier (1995) and Webber and Gibbs (1996). The effectiveness of the method depends on good water



**Figure 4.21** Management of *Ips typographus* by removing fallen trees following a major windblow of spruce-dominated forests in North Jutland, Denmark. The number of trees attacked per hectare was influenced by distance from the windblow and the timing of tree removal. After the windblow in November 1981, trees in some stands were left *in situ* during the initial spring flight in the following year to act as trap trees and were then removed between mid-May and early-July before beetle emergence (■). In these stands, attack densities were lower than in those where trees had been either removed before the spring flight (◆) or after the start of emergence from the attacked windblown trees (▲) (from Wichmann and Ravn 2001).



**Figure 4.22** Storage of mainly pine logs under a sprinkler system in eastern England following extensive windblow in 1987. (a) The log store covered 4 ha and contained 70 000 m<sup>3</sup> of sawlogs. Water was pumped from and returned to the gravel pit shown lower left. (b) Irrigation pipes and sprays were adjusted to ensure that a saturated atmosphere was maintained around the logs. Logs were effectively stored for over 3 years (from Grayson 1989).

distribution over the whole stack. This is facilitated by, among other things, close stacking of logs of a standard length and the avoidance of 'eaves' during construction that can shelter lower logs. Properly constructed stacks are effective in preventing new attacks by bark and wood-boring insects and fungi and in preventing further development of existing blue-stain and to a lesser extent wood-decay fungi during prolonged storage. Fungal attack appears to be inhibited in part due to a rise in bacterial populations and the establishment of anaerobic conditions.

Conifers, including subtropical species, and some hardwoods have been effectively stored for long periods but small changes in wood quality do occur. Increases in the porosity of timber have been observed as well as reductions in strength although not enough to reduce the proportion of structural grade timber that can be obtained from the logs (Maun and Webber 1996).

Some examples of large-scale wet storage of timber that indicate the relative costs associated with storage are given in Table 4.3.

**Table 4.3** Examples of storage of logs under sprinkler systems in Europe. Cost-effectiveness is likely to be increased by only storing good-quality logs and minimising haulage costs to the storage site

	Eastern England one site	North-west Germany several sites	Jutland, Denmark one site
Species	Pine	Pine and spruce	Spruce
Storage dates	1988–92	1973–77	1982–86
Volume stored (m <sup>3</sup> )	63 340	1 204 000	18 000
Sale price m <sup>-3</sup>	£30	100DM	396Kr
Cost of water storage operations m <sup>-3</sup>	£10.4	14.6DM	52Kr

Source: Gibbs and Webber 1996.

# Resistance to attack by pests and pathogens

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Trees possess a variety of resistance mechanisms, from generalised to highly specific, that protect them from vertebrate and invertebrate herbivores and pathogenic organisms. The nature of these resistance mechanisms and their expression in leaves, bark and wood reflect to a greater or lesser extent the characteristics of the attacking organisms and the structural and physiological constraints associated with the different parts of the tree. While physical defences are important in protecting trees from attack by herbivores as well as by microorganisms, chemical defences, particularly the complex 'secondary chemicals', are usually key components of resistance mechanisms.

One of the broad aims of plant defence theory is to account for the resistance or defensive attributes that are characteristic of different plants. These attributes include the kinds of secondary chemicals that are important in defence, their distribution and concentration within plants, and importantly, the resources allocated to defence. The relevance of defence theory to the practical use of resistance in pest management may seem limited. But by focusing on the characteristics of different plant defence mechanisms and the physiological and environmental constraints on their expression, defence theory provides an essential framework for understanding the nature of resistance to different pests and pathogens and the potential and scope for utilising resistance in their management.

### 5.1 Defence and defence theory

The importance of secondary chemicals in defence can be inferred from observations of their distribution and concentration within plants (Edwards 1992). When secondary chemicals are concentrated in parts of the plant that are particularly exposed to attack, a role in 'preformed' defence is suggested.

Some plants may even store secondary chemicals in specialised containment structures and so provide an extensive reservoir that can flood damaged tissue as soon as it is attacked. Alternatively, some secondary chemicals may be present in small amounts but increase significantly in concentration during or after attack, suggesting a role in 'induced' defence.

Secondary chemicals have been particularly well studied in relation to defence against insect herbivores (Rosenthal and Berenbaum 1991; Harboure 1999). This is partly because coevolutionary interactions between insects and plants have resulted in complex behavioural and physiological adaptations. These have enabled insects to exploit secondary chemicals as token stimuli in host finding and in some cases to tolerate toxic secondary chemicals or even sequester them for their own defence against natural enemies (Ehrlich and Raven 1964; Rosenthal and Berenbaum 1992; Rowell-Rahier and Pasteels 1992; Bernays and Chapman 1994; Thompson 1994; Nishida 2002). Volatile secondary chemicals released from plants during insect feeding may also be used by insect predators and parasitoids to detect the presence of their prey and so contribute indirectly to the defence of the plant (Paré and Tumlinson 1999; Dicke and van Loon 2000). This emphasis on insect-plant interactions does, however, obscure the fact that secondary chemicals are equally important in defence against pathogens (Edwards 1992) and vertebrate herbivores (Grubb 1992).

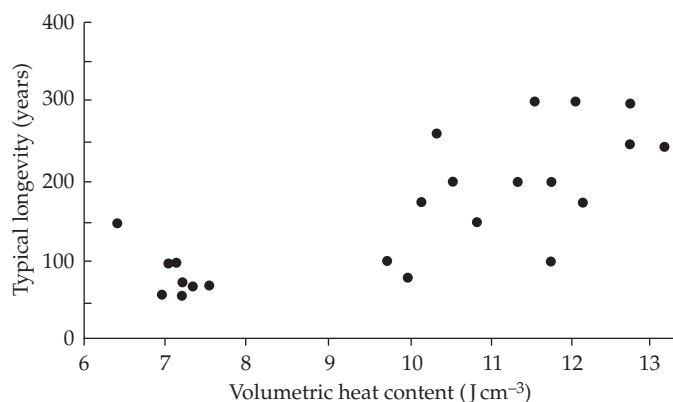
A broad distinction is usually made between the kinds of defensive secondary chemicals found in herbaceous plants and those that occur in long-lived and structurally complex trees that provide many different resources for organisms to exploit (Rhoades and Cates 1976; Rhoades 1979). In herbaceous plants, secondary chemicals tend to be biologically active at

relatively low concentrations. Different species typically contain specific toxins some of which, such as alkaloids and cyanogenic glycosides, are nitrogen-based chemicals. The highly toxic secondary chemicals commonly associated with herbs are often referred to as 'qualitative' defences. They are considered to be more susceptible to counter-adaptation by specialist insects than the 'quantitative' defences that occur in trees. Quantitative defences are typically carbon-based secondary chemicals such as terpenes and polyphenols that tend to be less acutely toxic and to have dose-dependent effects on herbivores. Similar kinds of quantitative defences occur widely among different tree species and may be present in such high concentrations that they are exploited commercially (Obst 1998). The distinction between qualitative and quantitative secondary chemicals is usually emphasised to draw attention to the fact that trees need defences which are not only effective against a range of different pests and pathogens but which are also difficult to counteract.

Most theories of plant defence emphasise that resources allocated to defence should reflect associated costs and benefits of reduced damage (Simms 1992). The distribution and concentration of secondary chemical defences should therefore, reflect the 'value' to the tree of its different parts, as well as the nature and frequency of herbivore damage. The implicit assumption is that defences are more or less costly to produce so that even in long-lived trees, there is a limit to the resources that can be allocated to defence. However, the true cost of defence is not easy to quantify. Defences that are produced only when required, that is, in response

to attack, are in general less costly than preformed defences present in high concentrations (Tallamy and Raupp 1991; Karban and Baldwin 1997). Secondary metabolism is integrated into the functioning of the plant as a whole and while some secondary chemicals may be primarily defensive, others also have additional functions in the plant (Gershenson 1994; Hartmann 1996). Phenolics, for example, help to protect plants from the damaging effects of UV light. Other attributes of plants that are not primarily defensive can also provide some protection from attack. For example, thick bark that evolved as a protection against fire can also give added protection against herbivores and pathogens, and a waxy leaf surface layer that reduces vulnerability to lethal abiotic stresses also provides a barrier to microbial invasion and insect attachment. Such 'neutral' defences cannot really be accounted for as a 'cost' of defence (Edwards 1989; Parker 1992).

The resources allocated to defence by different tree species reflect to some extent their life-history characteristics. Trees that are fast-growing pioneers with a relatively short lifespan tend to allocate less to defence than slow-growing and long-lived climax species (Coley 1983). This can be illustrated by comparing the volumetric heat content of wood from trees with different life spans (Fig. 5.1). Volumetric heat content provides an approximate measure of the amount of high-energy defensive secondary chemicals in wood and so can be used as an approximate measure of the resources allocated to defence. Trees that are long-lived tend to have wood with a high concentration of secondary



**Figure 5.1** The volumetric heat content of sawtimber-size stem wood of North American broadleaves that vary from short-lived fast-growing species to long-lived slow-growing ones (from Loehle 1988).



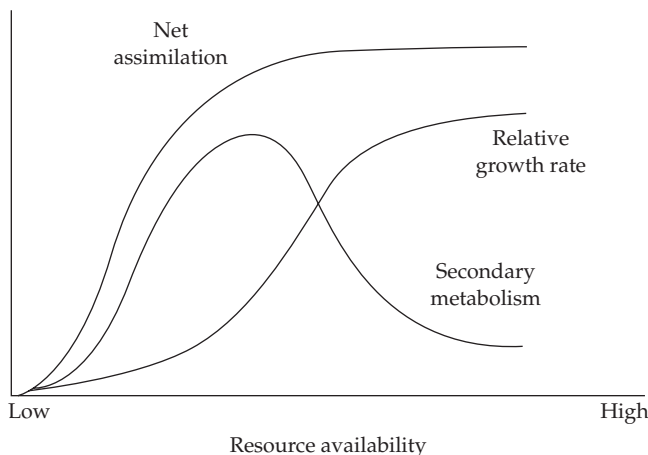
chemicals that is more resistant to wood-decay pathogens and wood-boring insects.

The growth of individual trees can also affect resources allocated to defence in a more direct way. Both growth and the synthesis of quantitative secondary chemicals are carbon-demanding processes and so have the potential to compete for the pool of carbohydrates produced by photosynthesis. One of the possible costs of investment in high concentrations of preformed or 'constitutive' carbon-based defences is therefore a trade-off with growth. Environmental factors have an important influence on tree growth rate and therefore the potential to affect the amount of carbon available for allocation to defence. The predicted relationship between growth and secondary metabolism as a function of resource availability is illustrated in Fig. 5.2. Nutrient deficiency, as well as many other environmental stresses, can restrict the growth of plants while having relatively little effect on their photosynthetic capacity per unit leaf area. As a result, carbohydrates accumulate in affected plants and more carbon can be allocated to synthesis of carbon-based secondary metabolites. For trees growing in nutrient poor habitats, where it would be difficult to replace parts lost to herbivory, this would seem to be an effective defence strategy. Circumstantial evidence for the influence of resource-availability on defence comes from the observation that some tree species growing in nutrient-poor soils have been found to have leaves that contain at least twice the concentration of

secondary chemicals as species growing in richer soils that support higher growth rates (McKey *et al.* 1978; Coley *et al.* 1985). More direct evidence of a trade-off between growth and defence comes from experimental manipulation of tree growth by altering soil fertility, light levels, or other environmental factors (Koricheva 1998).

## 5.2 Resistance and its expression

The terms defence and resistance are used interchangeably in this chapter in common with current usage. However, more emphasis is placed on the term *defence* in the wider context of generalised traits that protect trees from their natural enemies whereas *resistance* is emphasised in the more practical case of specific traits or mechanisms that are effective against particular pests. Plant resistance has been defined in a number of different ways, with particular definitions tending to reflect the nature and characteristics of the attacking organisms (Harris and Frederiksen 1984; Kennedy and Barbour 1992). Resistance can be defined as 'any inherited characteristic of a host plant which lessens the effects of parasitism' (Russell 1978)—interpreting parasitism in its broadest sense. In the study of resistance to pathogens there has in general been much more emphasis on the genetic basis of plant-pathogen interactions, especially in relation to the all or nothing responses observed in 'gene for gene' interactions (Table 5.1), on the complexities of pathogen 'recognition' and on induced responses to infection



**Figure 5.2** Proposed environmental sensitivity of net assimilation rate (NAR—net carbon gain per unit time per unit leaf area), relative growth rate ( $RGR = NAR \times LAR$ —ratio of total leaf area to total plant dry biomass) and secondary metabolism. Photosynthesis is less sensitive to resource limitation than growth processes so that at low levels of resources, excess carbohydrate can be diverted to secondary metabolism. Growth and secondary metabolism may be positively correlated. At higher levels of resource availability, where net assimilation reaches a maximum, RGR and secondary metabolism are negatively correlated indicating a physiological trade-off (from Herms and Mattson 1992).

**Table 5.1** Gene-for-gene interactions in a plant–pathogen system

Pathogen genotype	Host genotype		
	RR	Rr	rr
VV	–	–	+
Vv	–	–	+
vv	+	+	+

Note: R and r are alleles for resistance and susceptibility and V and v are alleles for avirulence and virulence, with capitals indicating dominance. + indicates a successful or 'compatible' interaction resulting in disease and – an unsuccessful outcome to pathogen infection.

Source: Burdon 1987 and Sorci *et al.* 1997.

(Hutcheson 1998). Characterising the mechanisms of resistance to insects also takes into account their host finding, feeding and reproductive behaviour. Mammalian herbivores on the other hand are often generalists and for those that browse on trees and other woody plants, the deterrent effect of preformed secondary chemicals is often more important than the nutritional content in determining food choice. In contrast to pathogens, induced resistance to mammals is relatively uncommon (Rousi 1990; Bryant and Raffa 1995).

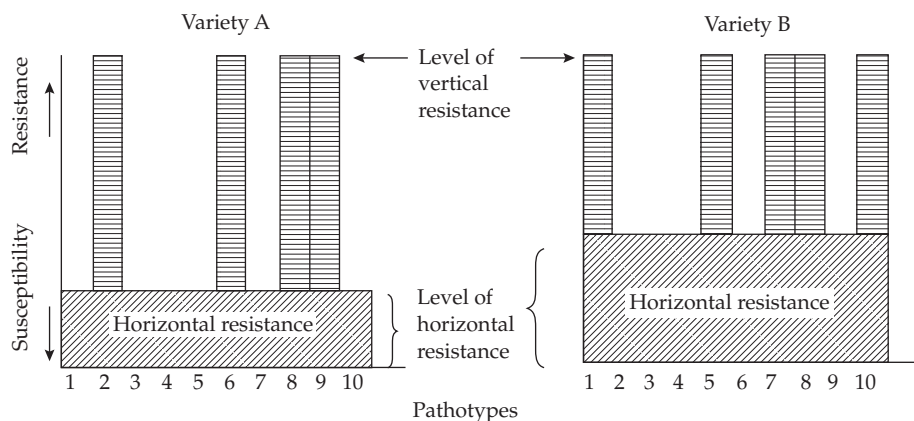
### 5.3 Genetics of resistance

The nature of the genetic control of resistance traits has an important bearing on how resistance can be

identified in the field or exploited in pest management. Resistance traits controlled by 'major' genes are inherited in a simple Mendelian fashion and plants can be classified as either resistant or susceptible. Other terms for major gene resistance include race-specific or *vertical* resistance. Often, however, resistance is polygenic, resulting from the action of many genes each of which makes a relatively small contribution to resistance. As a consequence, there is an underlying continuous distribution of phenotypes that vary from susceptible to resistant, that is, individuals show degrees of resistance (Falconer and Mackay 1996). Polygenic resistance is sometimes referred to as partial, durable, or *horizontal* resistance. The concepts of vertical and horizontal resistance were developed by Van der Plank in relation to plant resistance to pathogens. A hypothetical example of their relative importance in the resistance of two plant varieties to different fungal pathotypes is illustrated in Fig. 5.3.

#### 5.3.1 Major gene resistance

Resistance traits controlled by major genes are particularly important against pathogens and are characterised by the occurrence of only two types of individual within a population—resistant or susceptible. The inheritance of such traits can be studied by straightforward Mendelian genetics.



**Figure 5.3** Schematic relationship between *vertical* or major gene resistance and quantitative or *horizontal* resistance in two plant varieties to 10 fungal pathotypes (from Agrios 1988, after Van der Plank 1984).

Recognition that the plant has been invaded is important in resistance to plant pathogens. In host-pathogen interactions involving gene-for-gene interactions, the outcome of pathogen attack needs to be interpreted in the context of a dominant gene for resistance (R) in the host matched by a corresponding dominant gene for avirulence (V) in a diploid pathogen (Flor 1956, 1971; de Wit 1992). The protein products of avirulence genes are recognised by resistant plants and a defensive reaction is induced. This induced reaction is called a hypersensitive response and results in the rapid death of a few cells around the infection site causing a small lesion. When diploid pathogens are homozygous for virulence (vv) or hosts homozygous for susceptibility (rr), plants are susceptible and disease follows pathogen attack. The outcome for a single locus gene-for-gene interaction is shown in Table 5.1.

Such interactions can produce high levels of resistance, but are intrinsically unstable because the strong selection pressure on the pathogen can result in the appearance of new pathotypes and the breakdown of resistance. One of the best examples of gene-for-gene interactions in forest trees is that of resistance in white pines to white pine blister rust, *Cronartium ribicola* (Devey *et al.* 1995; Kinloch and Dupper 2002).

### 5.3.2 Polygenic resistance

One of the characteristics of polygenically inherited resistance to pests and pathogens is that there are degrees of resistance in the population. The level of resistance expressed by an individual-its phenotype ( $P$ ), is typically determined by the combined effect of the genes that an individual happens to possess-its genotype ( $G$ ) and the environment ( $E$ ) in which it is growing so that:  $P = G + E$ . The genetic contribution to the expression of polygenic resistance can be assessed by exploiting the resemblance between relatives that is characteristic of the expression of polygenically inherited traits, detailed discussion of which can be found in Zobel and Talbert (1984), Falconer and Mackay (1996) and Williams *et al.* (2002).

The simple model above can be applied to a population of individual trees and used to describe the

variation in the population so that:  $V_P = V_G + V_E$ . The phenotypic variation ( $V_P$ ) is the total variation between the individual members of the population, genetic variation ( $V_G$ ) is the variance of genotypic values and environmental variation ( $V_E$ ) is the variance of the deviation between phenotypic and genotypic values caused by environment, that is, all the non-genetic factors. The extent to which the phenotype of an individual is determined by the genotype, that is, the importance of genes in influencing the trait under consideration, is called the *broad-sense heritability* and is equivalent to ( $V_G/V_P$ ). However, genotypic variance ( $V_G$ ) is itself composed of two elements, the *additive* and *non-additive* genetic variance ( $V_G = V_A + V_{NA}$ ), and the distinction is an important practical one. The additive variance ( $V_A$ ) results from the combined effects of alleles at all loci influencing the trait and represents that portion of the genetic variance that is passed on from parents to offspring. Non-additive genetic variance ( $V_{NA}$ ) results from the effects of interaction of alleles either at a specific locus or at different loci and is a reflection of the unique combination of genes possessed by an individual. A more useful measure of heritability, and one that is easier to calculate, is an estimate of the contribution from genes with additive effects and this is called *narrow-sense heritability*, or often just heritability. For historical reasons, it is denoted as  $h^2$  and represents the 'usable' part of genetic variation estimated as the additive genetic variance as a proportion of phenotypic variance ( $V_A/V_P$ ).

There are a number of ways of estimating heritability. A common one involves measurements made only on offspring in half-sib progeny trials in which individuals are obtained from seed collected from a single female tree that has been open-pollinated so that the unknown male component represents a random sample from the population. Half-sib trials effectively measure the average performance of the progeny of a mother tree when crossed with many other males from the population and is therefore a reflection of the additive genetic variance. The variance components due to genetic and environmental effects can be estimated using analysis of variance and an example for a quantitative resistance trait in spruce is shown in Box 5.1.

### Box 5.1 Estimating narrow-sense heritability

Maternal half-sib families are the offspring of the same mother tree that has been open-pollinated and so the half-sibs have  $\frac{1}{4}$  of the additive genetic variance in common. In an analysis of variance (ANOVAR), the phenotypic variance can be partitioned into family groupings to provide a measure of the resemblance between relatives—the additive genetic variance  $V_A$ . Narrow sense heritability,  $h^2 = V_A/V_p$ . For a balanced experiment, the variance components for each source of variation in an analysis of a Sitka spruce progeny trial for a quantitative defensive trait are given in the table.

Because the calculation of heritability involves phenotypic values, it is characteristic of a particular population at a particular site. In this example, the trial was not replicated at different sites and so may disguise genotype  $\times$  environment interaction in which the relative expression of the trait varies between environments. Heritability may therefore be overestimated.

Key references: Wright (1976); Zobel and Talbert (1984); Falconer and MacKay (1996); Williams *et al.* (2002).

ANOVAR table for concentration of lignified stone cells in bark in a half-sib Sitka spruce progeny trial. Estimates of single-tree and family heritability ( $h^2$ ) based on Zobel and Talbert (1984) from Wainhouse and Ashburner 1996

Source of variation	df	ms	Expected ms (MS1-3)
Replicates (blocks)	4	6.991	
Families (progeny)	10	10.073	MS3
Fam x Rep	40	3.211	MS2
Trees within plots	495	2.243	MS1
Single tree heritability		0.22	
Family heritability		0.68	

$$h^2(\text{single tree}) = \frac{4\sigma_f^2}{\sigma_w^2 + \sigma_f^2 + \sigma_{fr}^2} \quad h^2(\text{family}) = \frac{\sigma_f^2}{(\sigma_w^2/TR) + (\sigma_{fr}^2/R) + \sigma_f^2}$$

Variance components were calculated as:  $\sigma_f^2 = \text{family} = (MS3 - MS2)/TR$ ;  $\sigma_{fr}^2 = \text{family} \times \text{replicates} = (MS2 - MS1)/T$  and  $\sigma_w^2 = \text{trees within plots} = MS1$ . R (replicates) = 5, T (trees within plots) = 10.

## 5.4 Resistance mechanisms

Mechanisms of resistance to insects are usually described in terms of their detrimental effects either by influencing their behaviour (*antixenosis*) or affecting survival and development (*antibiosis*) and in terms of the attributes of plants that enable them to tolerate attack (*tolerance*) (Painter 1951, 1958; Kogan and Ortman 1978). Finding and accepting host plants are complex behavioural responses and so antixenosis is a resistance trait that has no significance for plant pathogens. Volatile secondary chemicals released from plants can influence both orientation and landing by insects whereas host

acceptance may depend on properties of the plant surface or the presence of feeding or oviposition stimulants or deterrents (Bernays and Chapman 1994). The release of volatile chemicals can be greatly increased from wounded trees or those already undergoing attack and can convey information about the location or suitability of the host (Nordlander 1991; Ross *et al.* 1995; Jactel *et al.* 1996a). Antibiosis resistance traits can be effective against most kinds of organism, can be physical as well as chemical, and include traits that are induced in response to attack as well as those that are preformed. In practice, antibiosis can be difficult to distinguish from

antixenosis. Secondary chemicals that deter browsing by mammals, for example, are often also toxic to them. One of the best illustrations of the different effects of secondary chemicals is that of the complex triterpenoid, azadirachtin, present in the Neem tree. It is not only an antifeedant, but also has the properties of an insect growth regulator and sterilant (Mordue (Luntz) and Blackwell 1993; Bryant and Raffa 1995; Simmonds and Blaney 1996). Tolerance is a mechanism of resistance that can act against most organisms and is expressed by a reduced impact on the plant for a given level of pest attack.

To simplify the discussion and to avoid undue emphasis on the mechanism of resistance in relation to the biological attributes of pests and pathogens, resistance will be described here in general terms in relation to *performed* and *induced* resistance and *tolerance*. Their relative contribution to overall resistance depends, among other things, on the particular part of the tree that is attacked, the nature of the pest and the frequency and intensity of attack. The way in which different resistance mechanisms combine or interact to determine the overall level of resistance in trees is discussed under the topic of *integrated resistance*.

Although there are many similarities in the defensive attributes of leaves, bark and wood, there are nevertheless distinctive features of performed or induced defences that reflect to an extent the form and function of different parts of the tree. Leaf development is characterised by rapid early growth followed by a sink-source transition and then eventual senescence. In deciduous trees, leaves may be relatively short-lived but the mature leaves of many conifers can be retained for several years, becoming increasingly important for storing carbohydrates as their contribution to photosynthesis declines. While leaves can be fairly readily replaced following defoliation, the integrity of bark is vital to the functioning of the tree and significant loss is likely to be fatal. Bark increases in thickness with age and many species acquire a thick outer rhytidome that provides considerable physical protection in older trees. Bark is also well protected by both performed and induced defences and by elaborate wound repair mechanisms. Wood is protected by the outer covering of bark but also has performed and induced defences although, as trees

mature, an essentially non-living heartwood may form that lacks induced responses to attack. Some of the more important resistance mechanisms within trees are highlighted in the following sections.

### 5.4.1 Performed resistance

#### *Leaves*

Spiny leaves appear to be predominantly a defence against vertebrate herbivores (Cooper and Owen-Smith 1986; Myers and Bazely 1991; Grubb 1992). Physical characteristics of leaves such as their toughness, or whether the surface is smooth and shiny or covered in hairs, can also influence insect movement, feeding or oviposition (Gange 1995; Brennan *et al.* 2001; Brennan and Weinbaum 2001). Feeding by both insect and vertebrate herbivores, however, can be deterred by the high concentrations of secondary chemicals that are typically found in leaves. Terpenoids are an example of a diverse class of secondary chemicals that are very widely distributed in plants including leaves. In eucalypts, terpenoids are secreted in specialised oil glands in the leaf mesophyll (Carr and Carr 1970) and in conifers, resin is often stored in resin ducts (Wu and Hu 1997). The volatile monoterpene component of resin acts as a solvent for the diterpene resin acids and resin flows freely from wounds or sites of insect attack when ducts are severed. Diterpene resin acids can be powerful deterrents, protecting the juvenile foliage of some conifer species (Ikeda *et al.* 1977; Ohigashi *et al.* 1981). Phenolic chemicals also feature prominently in the defence of leaves and in willows, phenolic glycosides occur at high concentration. Both the amount and composition of different glycosides determine feeding patterns of willow leaf beetles and they are toxic or deterrent to non-specialist herbivores (Tahvanainen *et al.* 1985; Denno *et al.* 1990; Ikonen *et al.* 2001). The defensive characteristics of leaves can change markedly during a single growing season. In young birch leaves for example, galotannins and flavanoid glycosides are important in defence, but as leaves mature, galotannin concentration decreases while that of proanthocyanidins increases and older leaves are also tougher than younger ones (Kause *et al.* 1999).

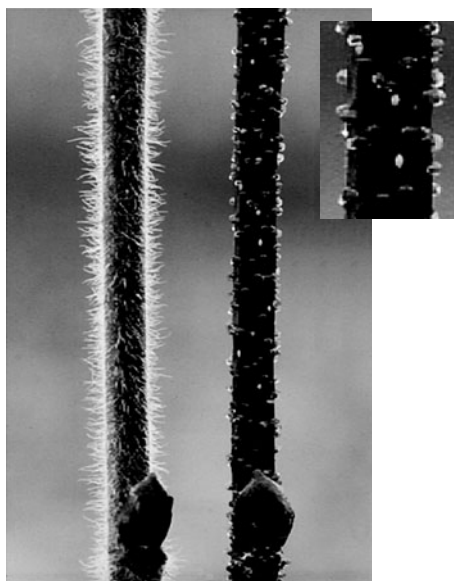
### Bark and wood

There are many similarities in defensive traits in bark and wood and the mechanisms are broadly similar in angiosperms and gymnosperms. The outer periderm of bark or the rhytidome when present, not only provides protection against the environment but also forms a 'neutral' defence of the phloem and the underlying vascular cambium. Thick outer bark, as well as thorns and spines, deters feeding by mammalian herbivores and most pathogens cannot penetrate this outer layer. Pathogens can often gain entry, however, following mechanical wounding or feeding damage and some insects that feed on bark may act as vectors of pathogenic organisms. Polyphenolics and terpenes also occur in high concentrations in bark and in spruce, for example, stilbene glycosides are important antifungal phenolic chemicals (Toscano Underwood and Pearce 1991*a,b*). The resin system in the bark and xylem of conifers is one of the most intensively studied preformed resistance traits because of its importance in resistance to bark beetles and associated fungi (Box 5.2). Resin-like substances also occur in other species. For example, bark on the juvenile stems of several birch species in boreal forests are particularly well defended against browsing mammals such as hares and

moose due to the powerful deterrent chemicals that are secreted by epithelial glands and accumulate as resin drops on the surface of the bark. The resin contains among other chemicals, the triterpene papyriferic acid (Reichardt *et al.* 1984; Taipale *et al.* 1994; Julkunen-Tiitto *et al.* 1996) (Fig. 5.4).

Because bark restricts the access of pests and pathogens to the underlying woody tissues, defences in bark and wood can be considered as an integrated system for the protection of the stem. These defensive mechanisms are characterised by both chemical and structural barriers to invading organisms, a detailed account of which is given by Blanchette and Biggs (1992) and Pearce (1996).

Relatively few insects exploit wood in the living tree. Wood has a very low nitrogen content and wood-boring insects are characterised by relatively long life-cycles and often by dependence on associations with fungi (Cowling and Merrill 1966; Mattson 1980; Danks 1992). The high moisture content of sapwood is inimical to most microorganisms and also to wood-boring insects such as cerambycids and siricid woodwasps and these insects typically attack trees that are drought stressed. Resin occurs in the ducts in the sapwood of some conifers and resin-like chemicals are also found in some hardwood species. Kino for example, is polyphenolic in



**Figure 5.4** Hairy and resinous stems of different individuals from one family of juvenile silver birch. Inset—close-up of resin droplets. Resin is secreted by epithelial glands and contains mainly triterpenoids while epithelial hairs contain phenolic chemicals. Hairs and resin drops can deter feeding by mammalian herbivores (from Rousi 1990).

nature and occurs in eucalyptus species (Hillis 1984). Wood, especially heartwood, contains high concentrations of secondary chemicals which are an important defence against wood-decay fungi (Fig. 5.1). In Scots pine, individual trees that are more resistant to heartwood decay contain higher concentrations of total phenolics (Harju *et al.* 2003). In living trees, however, sapwood is usually more resistant to pathogens because of its capacity for an induced response to attack.

### 5.4.2 Induced resistance

#### *Leaves*

Induced resistance to defoliation has been particularly well studied in birch, which in north-western Europe is periodically defoliated by the autumnal moth, *Epirrita autumnata* (Hartley and Lawton 1991; Neuvonen and Haukioja 1991). Induced effects of defoliation appear to be non-specific and have been observed in a number of insect-plant systems (Karban and Baldwin 1997). Induced effects in the leaves typically include a decrease in nutritional quality (nitrogen and carbohydrates), an increase in secondary chemical concentration and often also an increase in toughness. Induced responses are classified according to how quickly they develop (Haukioja 1990). Rapidly induced responses (RIR) occur within the same season, affecting partially damaged leaves and in some cases nearby undamaged ones. Where the response to damage is delayed (DIR) the time lag involved has the potential to influence the population dynamics of insect defoliators (Underwood 1999; Underwood and Rausher 2002).

Leaves also respond to attack by fungal pathogens but in contrast to insect-induced responses, the reaction can be much more specific. The hypersensitive response (HR), for example, is induced in response to attack by pathogenic fungi that have gene-for-gene interactions with their host (e.g. Table 5.1). The response involves rapid and localised death of a limited number of affected cells at the infection site in response to invasion by a pathogen containing genes for avirulence. The HR is in marked contrast to other reactions to fungal invasion that have the aim of protecting cells by forming barriers of lignin or suberin or by the

synthesis at the site of infection of phytoalexins, low molecular weight secondary chemicals with specific antimicrobial activity (Gottstein and Gross 1992; Goodman and Novacky 1994; Kuć 1995; Hammerschmidt 1999). Hypersensitive-type reactions to insects have been described, notably for species such as gall midges that form intimate associations with their host (Fernandes 1990, 1998; Fernandes and Negreiros 2001; Ollerstam *et al.* 2002). However, in the absence of information about the genetic basis of the interaction, such responses are difficult to distinguish from the spectrum of generalised necrotic reactions to invasion that, although relatively localised, often spread beyond the affected area.

#### *Bark and wood*

Repair mechanisms in bark, mediated through the induced formation of wound or necrophylactic periderm, are probably universal in woody plants. Periderm restoration is non-specific and stimulated by mechanical damage or injury by a range of pests and pathogens (Fig. 5.5). This response to wounding has the effect of localising infection by microorganisms or isolating the area of sustained feeding by the sessile stages of insects such as adelgids and scale insects. Deep wounds are closed by callus, formed from parenchyma cells of xylem and phloem, followed by differentiation of new cambium and formation of new xylem and phloem. The rate of callus formation or the integrity of structural barriers within bark has been shown to vary between resistant and susceptible genotypes in eucalypts, conifers and poplar (French and Hart 1978; Bucciarelli *et al.* 1999; van Zyl and Wingfield 1999).

Wounding in conifer bark is often associated with the synthesis of 'secondary' resin and its incorporation within a necrotic lesion. This reaction is sometimes referred to as a 'hypersensitive' response. However, gene-for-gene interactions do not appear to be involved and the term 'dynamic wound response' is a less confusing description (Miller *et al.* 1986; Wainhouse *et al.* 1997). It is essentially a non-specific defence response that is commonly observed in different conifer species in response to attack by bark beetles and associated fungi (Box 5.2).

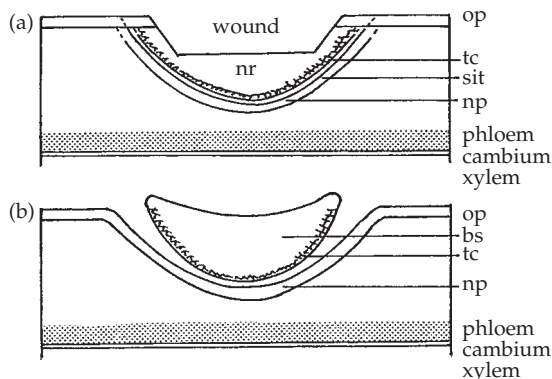
A number of induced responses have been observed in sapwood. Spread of decay fungi can be limited by 'compartmentalisation' which involves modification of cells within the wood to form a series of barriers that enclose and contain the

infected region. Barriers are often associated with increases in anti-fungal chemicals. Vascular wilt pathogens of hardwood trees move within vessels and can rapidly colonise the conductive xylem. Tyloses are induced cellular outgrowths that can block infected vessels and reduce spread of these specialised pathogens (Fink 1999).

In some conifers, wounding of bark can induce the formation of 'traumatic' resin ducts when new xylem is formed (Ito 1998; Nagy *et al.* 2000) (Fig. 5.6).

#### Whole tree responses

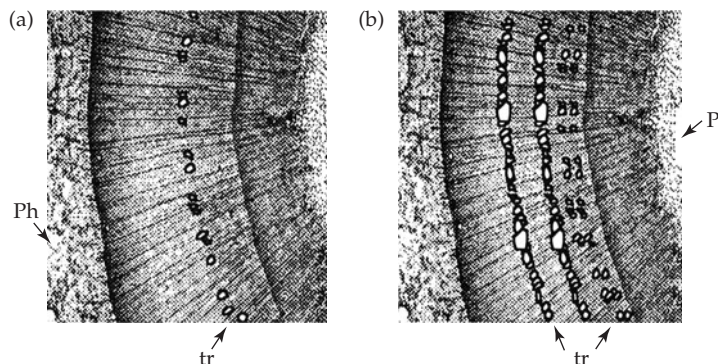
As well as a localised induced response to pest or pathogen attack, in some cases a more widespread response is induced, increasing resistance of the whole plant to future attack. This systemic acquired resistance (SAR) which is induced in response to some systemic signal has not been widely studied in trees (Ryals *et al.* 1996; Schneider *et al.* 1996; Sticher *et al.* 1997). It is known to be a generalised response in which plants become not only more resistant to subsequent invasion by the same pathogen but also to different pathogens for a more or less extended period and it can even be induced by some chemicals (Kessmann *et al.* 1994). The generalised nature of the response suggests that it might eventually be possible to induce resistance to highly virulent and damaging pathogens, at least in high value trees (Sutherland *et al.* 1995, Percival 2001). A localised form of acquired or induced resistance has been demonstrated in Norway spruce (Christiansen *et al.* 1999; Krokene *et al.* 1999; Krokene *et al.* 2001) and radiata pine (Bonello *et al.* 2001) following fungal inoculation.



**Figure 5.5** Non-specific periderm restoration in Sitka spruce bark.

This complex process consists of the formation of an impervious ligno-suberized barrier zone under the wound surface followed by formation of the wound periderm consisting of a phellogen or cork cambium producing an outer phellem or cork whose cells become impregnated with suberin, and an inner phellogen or living parenchyma. (a) Necrotic tissue (*nr*) forms under the wound which has penetrated the outer periderm (*op*). The wound area and underlying *nr* become walled off from healthy bark by parenchyma with thickened cell walls (*tc*) and deposition of lignin-like material. Internal to the *tc* layer, suberin is deposited in cell walls to form a suberized impervious tissue (*sit*). As well as forming an impermeable barrier, suberin is highly resistant to degradation by microorganisms. Wound periderm (*np*) differentiates adjacent to the *sit*. (b) The *np* eventually merges with the *op* and the *nr* is shed as a bark scale (*bs*) (from Woodward and Pearce 1988).

Key references: Blanchette and Biggs (1992); Woodward (1992); Woodward and Pocock (1996); Spanos *et al.* (1999).



**Figure 5.6** Formation of induced 'traumatic' resin ducts within the xylem shown in cross sections of a 2-year-old leader of white spruce attacked by *Pissodes strobi*. The intensity of response is proportional to the density of attack measured by the number of egg punctures on a leader and for a given attack density is higher in resistant trees. Effects of a low (a) and high (b) attack density are shown; Ph = phloem, P = pith, tr = traumatic resin ducts (from Alfaro *et al.* 1996a).

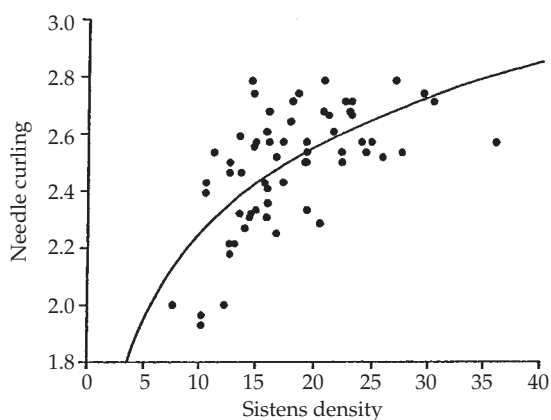


### 5.4.3 Tolerance

Tolerance in plants results in a reduced impact for a given level of attack and so effectively raises the damage threshold (Stowe *et al.* 2000). Tree species can vary in their ability to tolerate attack by particular pests, perhaps reflecting coevolved relationships with particular species. When Norway spruce are attacked by the green spruce aphid, *Elatobium abietinum*, fewer needles are lost for a given infestation density than in Sitka spruce which is an exotic host of North American origin (Skov and Wallendorf 2000; Straw and Green 2001). Intraspecific variation in tolerance can also be important, however. Fir trees infested by the silver fir adelgid, *Adelges nordmanniana*, develop characteristic curled needles but the response of different trees to a given level of attack can vary, suggesting different degrees of tolerance (Fig. 5.7).

### 5.4.4 Integrated resistance

Trees possess many generalised resistance mechanisms and some that are highly specific. For many pests, resistance in the field is likely to depend on the action of more than one mechanism. These may simply operate in sequence but may act synergistically so that, for example, preformed and induced mechanisms form an integrated response to attack. One of the best examples is the expression of resist-



**Figure 5.7** The effect of different densities of *Adelges nordmanniana* feeding on the shoots of Nordmann fir on the extent of curling of current needles (scored 0–5). The data illustrate family means from different provenances. Variation in tolerance is suggested by the fact that for similar low infestation densities there is considerable variation in the extent of needle curling. Family mean heritability for this trait was estimated at 0.57–0.67 (from Nielsen *et al.* 2002).

ance of conifers to bark beetles and associated pathogenic fungi (Box 5.2).

### 5.4.5 Environmental effects

For agricultural crops, cultural uniformity is the norm, but trees often grow on a range of sites that can vary in altitude, rainfall, or fertility, for example. In trees therefore, the influence of environmental factors on the expression of polygenically controlled resistance traits is much more important than in other crops. The effect of site fertility on the expression of resistance provides a good example, because fertilisation is sometimes used as part of normal forest management to enhance establishment and growth of trees (Section 4.2.2). The generalised relationship between tree growth and production of defensive secondary chemicals is illustrated in Fig. 5.2. For sites with moderate levels of nutrient availability, fertilisation is likely to decrease resistance, not only because the concentration of secondary chemicals is predicted to decline, but because fertilisation is likely to increase the nitrogen concentration and therefore nutritional quality for insects. This effect has been demonstrated in silver birch trees. Resistance of silver birch to feeding by the autumnal moth, *E. autumnata*, is influenced by the concentration of condensed tannins in leaves and this decreases when trees are fertilised (Fig. 5.13). In general, the relative importance of changes in the concentration of secondary chemicals and nitrogen on resistance is likely to depend on the part of the tree on which insects feed as well as their sensitivity to the nutritional quality of their food (Section 4.2.2).

Environmental effects on resistance expression can be quite important and need to be taken into account when measuring resistance in the field. This is usually done by making assessments over a range of different sites as described in the next section.

## 5.5 Measuring resistance

Natural variation in levels of pest and pathogen attack can provide important clues about the occurrence of resistance, especially where trees remain unattacked from year to year. But trees may escape attack by chance or remain relatively unaffected at low pest population density. During outbreaks,

### Box 5.2 Resistance of conifers to bark beetles and associated fungi

Most bark beetles that feed and breed in temperate conifers only utilise the bark of moribund, windblown or felled trees. Most species of economic significance also utilise moribund material but, importantly, can breed in living trees which have highly effective preformed and induced resistance mechanisms. During outbreaks, tree resistance is 'overwhelmed' by a pheromone-mediated 'mass-attack', which can occur over several days. Successful exploitation of living trees is aided in many species by their association with pathogenic fungi. The outcome of attack in different conifer-bark beetle interactions is influenced by a number of factors including beetle 'aggressiveness', fungal pathogenicity, and the 'vigour' of trees determined in part by site and environmental factors. Outbreaks are often triggered by environmental events such as windblow that increases the availability of moribund breeding material or prolonged drought that can reduce the effectiveness of preformed defences such as resin flow. At high population density, outbreaks can be self-sustaining as beetles aggregate on and kill normally resistant trees. A very few bark beetle species (in the genus *Dendroctonus*) are 'solitary' and individual females successfully initiate breeding galleries in living trees without mass-attack. Trees often survive a small number of attacks by these species.

**Preformed defences**—Resin, contained mostly within resin ducts or resin 'blisters', is the main preformed defence in conifers. Conifer species differ in the extent and complexity of the duct system and therefore in the amount of resin flow during attack and this is in part a reflection of the relative importance of preformed or induced defences in the different species. Pines and to a lesser extent spruces have an interconnected network of resin ducts that contain large amounts of preformed resin. True firs (*Abies*) store relatively small amounts of preformed resin in small resin 'blisters' but produce a lot of resin in response to wounding. Larch and Douglas fir are intermediate between these two extremes.

Resin is released when 'pioneer' beetles tunnel into bark and attempt to initiate a gallery. Resin flow has a dose-dependent physical effect on beetles, which may be expelled from galleries at high flow rates. Individual monoterpenes in resin may be toxic to beetles but on exposure to the air, monoterpenes

evaporate and resin acids solidify and seal the wound and may trap attacking beetles (Fig. 5.8). Physical defence in the form of stone cells provides an additional barrier to gallery formation in some conifers and can increase the effectiveness of induced responses to fungal pathogens (Fig. 5.9).

**Induced defences**—Pathogenic blue-stain fungi carried by the beetles induce a non-specific dynamic wound response (DWR) (Fig. 5.10). In a successful response, fungi are trapped within a necrotic lesion which contains high concentrations of induced 'secondary' resin and phenolic chemicals. Formation of secondary resin can increase the total terpene concentration of phloem to approx. 100 times that of preformed levels. Secondary resin may also contain higher proportions of monoterpenes that are more toxic to fungi and bark beetles and some phytoalexins may also be formed. Induced resinosis may be enhanced by formation of 'traumatic' resin ducts formed in the sapwood. Necrotic and resin-soaked areas of bark are eventually isolated by the underlying formation of wound or necrophylactic periderm (Fig. 5.5).

**Dynamics of attack and defence**—Successful colonisation of a tree depends on a dynamic interaction between bark beetles, fungi and preformed and induced defences in the tree. The threshold density above which pheromone-mediated beetle attack is likely to succeed (Fig. 5.11) will be influenced by the level of preformed defence, the pathogenicity of associated fungi and the strength of the induced response. Drought and other environmental factors can reduce preformed resin flow. The DWR is energy-demanding and is influenced by tree 'vigour' and the amount of induced resin formed per lesion is reduced at high attack density (Fig. 5.12). Fungi that are not contained by the DWR penetrate the sapwood and interrupt normal water relations of the tree (Fig. 5.11 inset), further reducing the tree's capacity for induced resinosis, and sapwood is quickly colonised by the fungus. Preformed and induced defences are part of an integrated response to attack rather than separate defences acting in sequence.

Key references: Paine and Baker (1993), Lorio *et al.* (1995), Kytö *et al.* (1996a), Paine *et al.* (1997), Wainhouse *et al.* (1997), Wu and Hu (1997), Franceschi *et al.* (1998), Lombardero *et al.* (2000), Lieutier (2002), Strom *et al.* (2002).

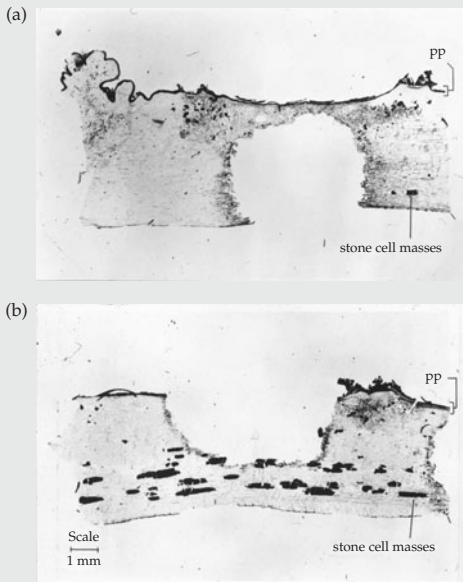
Box 5.2 Continued



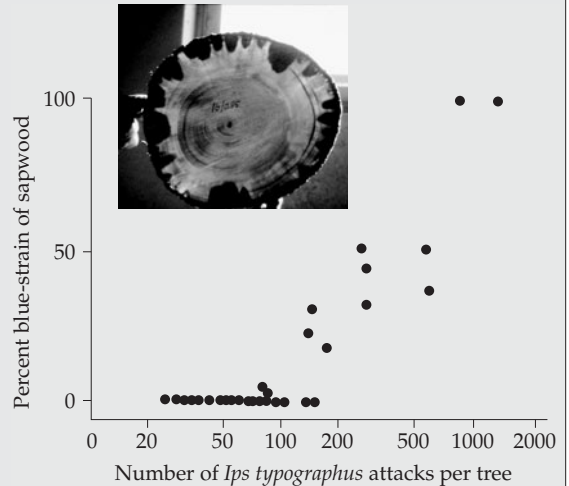
**Figure 5.8** Lodgepole pine undergoing mass-attack by *Dendroctonus ponderosae*, showing flow of preformed resin at sites of beetle entry. Inset-resin flow may prevent beetle establishment and can entrap and kill them. The resin solidifies as monoterpenes evaporate and this effectively seals the wound (from Phillips and Croteau 1999).



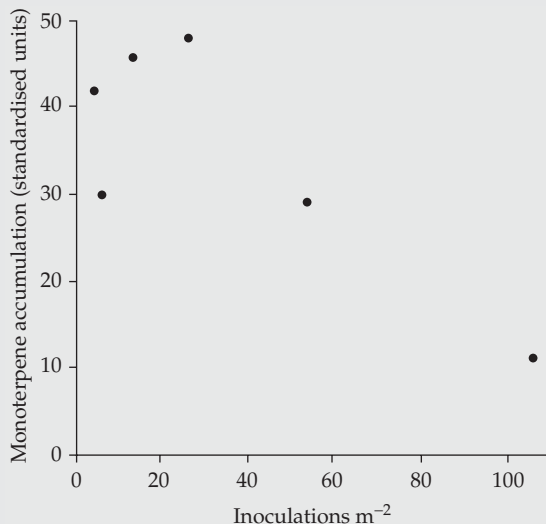
**Figure 5.10** A dynamic wound response to attack by *Ips typographus* and associated pathogenic fungi within the bark of Norway spruce (from Christiansen *et al.* 1987).



**Figure 5.9** Tunnels formed by *Dendroctonus micans* in spruce bark. (a) normal tunnel in unligified bark. (b) incomplete tunnel in bark in which the inner bark and cambium is physically defended by preformed lignified stone cell masses (from Wainhouse *et al.* 1990).



Box 5.2 Continued



**Figure 5.12** Monoterpene accumulation in lesions formed during the dynamic wound response in lodgepole pine bark. Trees were inoculated with *Ceratozystis clavigera*, a pathogenic fungus associated with *Dendroctonus ponderosae*. The localised induced response of secondary resin formation decreased with increasing inoculation density (data from Raffa 1991).

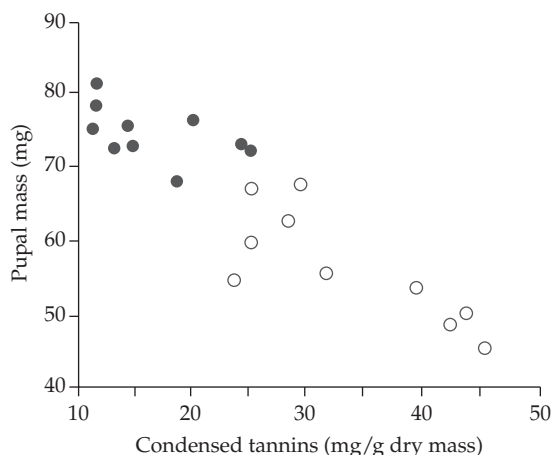
highly resistant trees may be identified but potentially useful levels of partial resistance can be obscured. Choosing an appropriate discriminating assay is therefore important in detecting resistance. The choice depends on a number of factors including characteristics of the pest, the nature of the damage, and how much is known about the under-

lying resistance mechanisms and the nature of their genetic control. A hypothetical example, illustrated in Table 5.2, shows how the underlying genetic mechanism and variation in both host and

**Table 5.2** The influence of *vertical* (major gene) and *horizontal* (polygenic) resistance traits and variation in host and pathogen populations on detection of resistance

Pathogen	Host		
	A	B	C
<i>(a) Major gene resistance</i>			
A	+	-	-
B	-	+	-
Γ	-	-	+
<i>(b) Polygenic resistance</i>			
α	4	3	2
β	3	2	1
γ	2	1	0

Note: (a) When major gene resistance is expressed, each pathogen 'culture' can only successfully attack a specific host 'cultivar' so that the resistance ranking of the host, based on presence or absence of disease, depends specifically on the pathogen naturally present in the field or used in bioassay. (b) When polygenic resistance is expressed, disease development (or insect abundance or damage) must be scaled, for example, 0 (low) - 4 (severe). All pathogens cause some disease but variation in pathogen aggressiveness is evident. The host rankings are constant regardless of pathogen culture used but cultivar C is most resistant (from Fleming and Person 1982 after Robinson 1973).



**Figure 5.13** The concentration of condensed tannins in leaves of 10 clones of silver birch transplants at an experimental site in Finland. There was natural variation among the clones in the concentration of condensed tannins but concentrations were lower in plants receiving NPK fertiliser (●) than in unfertilised plants (○). The pupal mass of larvae of *Epirrita autumnata* feeding on the leaves was related to tannin concentration (from Mutikainen *et al.* 2000).

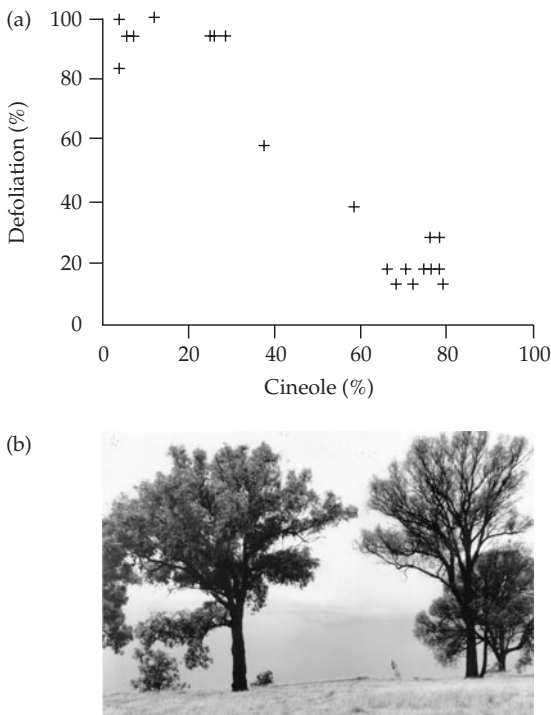
pathogen populations influences the detection of resistance. Although formulated in terms of pathogens and cultivars, the principles apply more generally to 'biotic' damage on trees.

For polygenic resistance, methods of field assessment may be based on pest abundance or symptoms of attack, or on characteristics of trees that are either correlated with resistance or are attributes of the resistance mechanism itself. A basic assumption in measuring pest abundance or damage is that on average, the degree of infestation reflects underlying variation in resistance. Floyd *et al.* (1994) and Raymond (1995) scored the amount of leaf damage to detect differences in resistance of provenances of eucalyptus, and Johnson (2002) used foliage colour and extent of needle retention to determine heritability of tolerance of Douglas fir to Swiss needle cast,

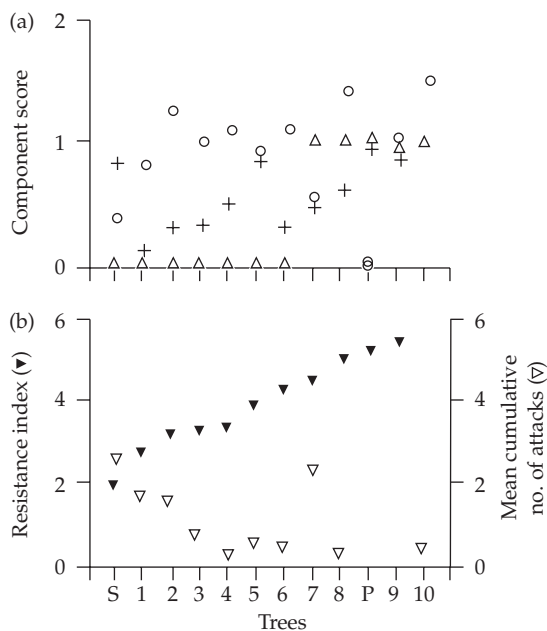
*Phaeocryptopus gaumannii*. Simple host traits that are correlated with resistance but which are not part of the resistance mechanism itself can also be used, allowing resistant trees to be identified in the absence of pest attack. In slash pine, resistance to fusiform rust caused by *Cronartium quercuum*, is associated with a high proportion of  $\beta$ -phellandrene in cortical monoterpenes although it is no more toxic to the fungus than the other main components of resin (Michelozzi *et al.* 1990). Similarly in some eucalypts, the cineole content is related to the extent of defoliation by Christmas beetles, *Anoplognathus* spp., and so can be used to identify the more resistant trees (Fig. 5.14).

In practice, resistance is likely to depend on more than one trait as is clearly demonstrated in trees attacked by white pine weevil, *Pissodes strobi*. This weevil oviposits in feeding punctures in bark on the upper part of leading shoots produced in the previous year. Larvae mine downwards in the phloem and when galleries merge, a characteristic 'feeding ring' is formed, resulting in the death of the shoot. In white spruce, few adults emerge when leaders have <60 egg punctures, emphasising the dynamic interaction between resistance and intensity of attack. Potential resistance traits include the deterrent effect of resin acids, the effect of resin flow on survival of eggs and larvae and the formation of 'traumatic' resin ducts in response to feeding and oviposition. Chemical factors in the bark have also been found to inhibit reproductive development in female weevils. Individually, these resistance traits are an unreliable guide to selecting resistant trees because when single traits are scored, no pattern is observed in relation to resistant and susceptible trees. However, a multicomponent index is of much more value and could be used to select parent trees for use in a breeding programme and to screen progeny (Fig. 5.15).

When trying to quantify resistance, results from controlled laboratory or greenhouse experiments are often highly repeatable but may not reflect levels of resistance expressed in the field. On the other hand in field trials, trees may be exposed to uncontrolled variation in natural levels of attack and pests and pathogens may themselves vary from place to place. Artificial inoculation studies in the field can reduce these sources of variation and may be appropriate in



**Figure 5.14** (a) Relationship between defoliation by *Anoplognathus* spp., and relative cineole content in the terpenoid oil extracted from foliage of the eucalypt, red ironbark. Similar relationships occur in other eucalyptus species. (b) Trees of red ironbark growing in New South Wales, Australia. The tree defoliated by *Anoplognathus* spp. has a low concentration of cineole. Terpenoids are significantly intercorrelated and no direct effect of cineole on defoliation levels is assumed (from Edwards *et al.* 1993).



**Figure 5.15** A multicomponent index for assessing resistance of Sitka spruce to *Pissodes strobi*. (a) A number of individual resistance traits have been identified including bark thickness (+), feeding deterrence ( $\Delta$ ) and total cortical resin acids ( $\circ$ ) but scores for these traits produced no consistent pattern for a Sitka spruce provenance (P), ten clones (1–10) and trees identified as susceptible (S) and were not related to the number of attacks on trees. (b) The cumulative number of natural attacks by weevils ( $\nabla$ ) in relation to a multicomponent index of resistance ( $\blacktriangledown$ ). This complex index was based on scores for seven traits related to the sequential process of host location, host acceptance, and progeny survival. The index score tends to be higher in 'resistant' trees (from Tomlin and Borden 1997).

Key references: Alfaro *et al.* (1996b, 1997), King *et al.* (1997), Lewis *et al.* (1999), Sahota *et al.* (2001).

small-scale trials. However, to detect variation in average levels of polygenic resistance between or within species in large-scale screening programmes, assessment of variation in levels of natural attack is the only practical method. Replicated trials should be established on a representative range of sites so that the significance of genotype  $\times$  environment interactions can be determined and assessed over more than one season.

An example of a large-scale trial to assess variation in susceptibility of Scots pine varieties to insect pests is illustrated in Table 5.3. In this study, trees from England and central Europe were most susceptible to all insect species except the eastern pine

shoot borer, *Eucosma gloriola*, which caused most damage on pines from southern Europe and Eurasia. Differences in phenology and growth between northern and southern varieties of Scots pine could have affected attack rates by some of the pests, indicating the care needed in interpreting results of such trials.

There are usually logistical constraints on planting large-scale trials but it may often be possible to use existing silvicultural trials of different species or provenances, or trials established to test the progeny from tree improvement programmes.

## 5.6 Tree resistance and pest management

In specialist short-rotation forestry crops such as poplars and willows, major gene resistance to some pathogens is important. Although very high levels of resistance are obtained, selection for biotypes able to develop on resistant plants is usually intense. For most tree species, resistance that is polygenically controlled is likely to provide the most durable resistance to pests and pathogens and is given most emphasis in this chapter. Partial resistance is of particular practical importance in forestry because, compared to agricultural crops, trees can tolerate higher levels of damage without significant economic impact. Utilising resistance obviously depends on the existence of heritable variation in resistance traits. The heritability of secondary chemicals or more generalised resistance traits as well as resistance to specific pests and pathogens has been estimated in a number of tree species, some examples of which are given in Table 5.4.

Exploiting natural variation in resistance through selection of appropriate provenances or by clonal propagation, for example, is one of the most common ways of incorporating resistance into pest management programmes. Selection for naturally occurring inter- and intra-specific variation in resistance is currently more effective than trying to increase resistance through selective breeding. Breeding is impracticable for resistance traits that are only expressed in mature trees unless resistance is highly correlated with other traits expressed in juvenile trees. For some major pests and pathogens

**Table 5.3** Relative susceptibility of varieties of Scots pine to four insect species in a replicated trial subject to natural infestation levels in north-central USA

Variety of <i>Pinus sylvestris</i>	<i>Hylobius radialis</i> mortality (%)	<i>Neodiprion sertifer</i> attack (%)	<i>Eucosma gloriola</i> <sup>a</sup>		<i>Dioryctria zimmermanni</i>	
			M	H	attack (%)	mortality (%)
			attack (%)	attack (%)		
Scandinavia and Scotland						
<i>lapponica</i>	14	0	5	50	15	7
<i>septentrionalis</i>	38	2	21	87	38	18
<i>rigensis</i>	45	6	31	90	47	22
<i>scotia</i>	18	6	41	100	57	26
Russia						
<i>mongolica</i>	30	1	19	83	55	29
<i>uralensis</i>	40	3	19	82	61	31
England and Central Europe						
<i>polonica</i>	67	19	37	88	62	25
<i>hercynica</i>	43	20	41	89	57	22
<i>carpatica</i>	53	19	41	86	62	26
<i>haguensis</i>	65	26	38	85	74	35
<i>pannonica</i>	45	20	47	93	62	19
'East Anglia'	55	26	36	79	75	37
Southern Europe and Eurasia						
<i>iberica</i>	17	11	58	96	33	3
<i>aquitania</i>	12	10	49	96	29	7
<i>subillyrica</i>	11	12	56	97	48	7
<i>illyrica</i>	10	19	44	93	43	9
<i>modopaea</i>	19	9	53	97	41	6
<i>armena</i>	12	7	51	97	29	3

<sup>a</sup> Figures for years of moderate (M) and high (H) attack.

Note: *Hylobius radialis* tunnels in the bark of young trees, *Neodiprion sertifer* defoliates young and old trees, *Eucosma gloriola* mines terminal and other shoots and *Dioryctria zimmermanni* mines bark on shoots and stem (from Speight and Wainhouse 1989, data from Wright and Wilson 1972, Steiner 1974 and Wright *et al.* 1975). Further evidence of geographical variation in resistance of Scots pine to pests and pathogens is discussed by Stephan (1991), Hansson (1998), and Quencez and Bastien (2001).

that attack young trees, breeding to increase intra-specific resistance may be the best way of managing them in the long term.

### 5.6.1 Exploiting natural variation in resistance

#### *Inter-specific variation and hybridisation*

In the management of forests, local experience of the relative susceptibility of different tree species may be used to increase planting of more resistant

species. In eastern Scotland, Scots pine is susceptible to outbreaks of the pine looper, *Bupalus piniaria*, particularly on dry sandy sites. Although large-scale outbreaks are relatively infrequent, defoliation not only causes growth loss but also increases susceptibility to pine shoot beetle, *Tomicus piniperda*. Outbreaks of this secondary bark beetle can kill trees previously defoliated by *B. piniaria* (Bevan 1974; Straw 1996). On susceptible sites therefore, Scots pine is gradually being replaced by

**Table 5.4** Some estimates of heritability of secondary chemicals and of resistance traits in trees

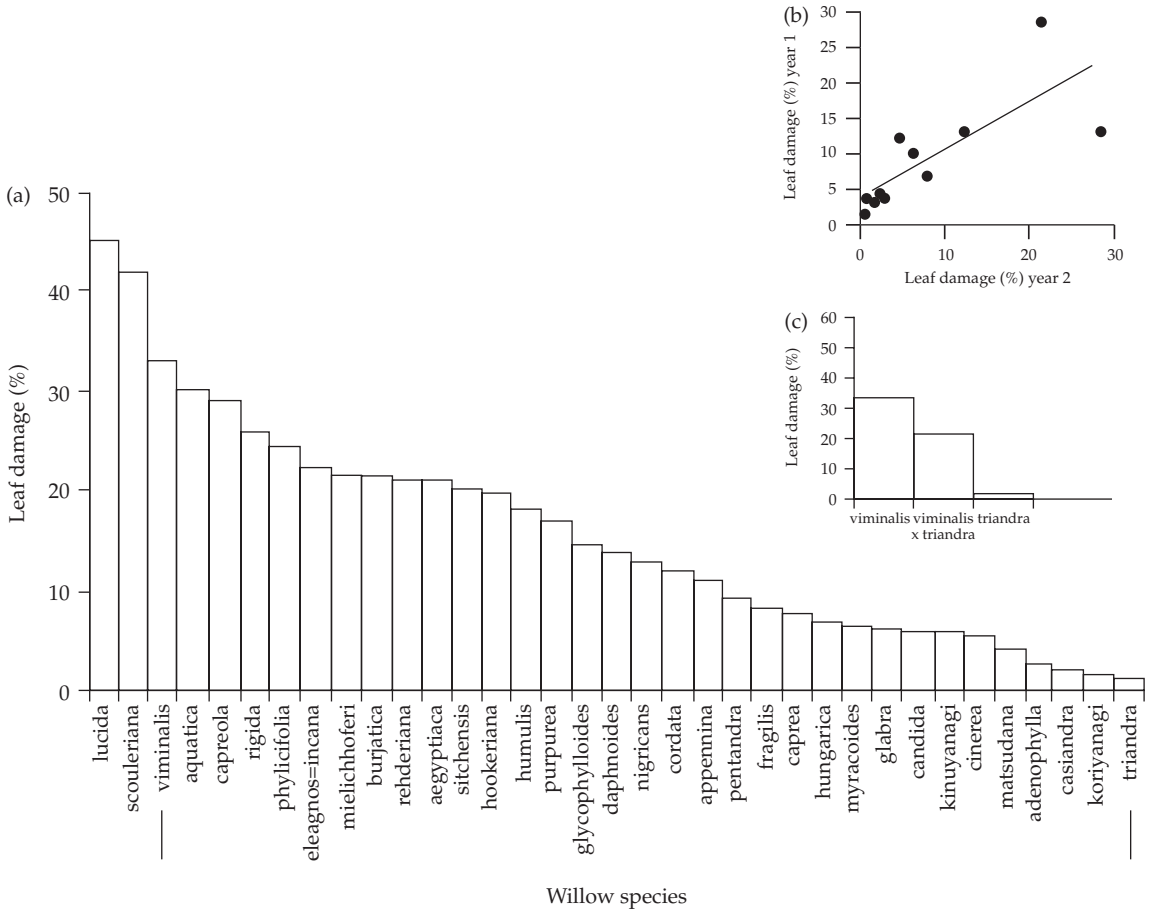
	Tree	Location or trait	Narrow sense			Broad sense	Reference
			Individual	Family	Provenance		
<b>Secondary chemical</b>							
Phenolic glycoside concentration	Willow	Leaves				0.24–0.41	Nichols-Orians <i>et al.</i> (1993)
Monoterpene composition	Radiata pine	Twig cortex				0.71–0.98	Burdon <i>et al.</i> (1992)
Taxanes	Pacific Yew	Needles		0.12–0.69			Wheeler <i>et al.</i> (1995)
Lignified stone cells	Sitka spruce	Stem bark	0.22	0.68	0.79–0.88		Wainhouse and Ashburner (1996)
<b>Defensive trait</b>							
Resistance to decay	Scots pine	Heartwood	0.02				Harju <i>et al.</i> (2001)
	Siberian larch	Heartwood				0.39	Venäläinen <i>et al.</i> (2001)
Resin canal frequency	Lodgepole pine	Needles		0.25–0.31		0.69	White and Nilsson (1984)
<b>Resistance trait</b>							
<i>Pissodes strobi</i>	Interior spruce	Leader attack	0.39	0.70			King <i>et al.</i> (1997)
<i>Elatobium abietinum</i>	Sitka spruce	Defoliation		0.72			Jensen <i>et al.</i> (1997)
<i>Phoracantha semipunctata</i>	Eucalyptus	Stem attack		0.19			Soria and Borralho (1997)
<i>Chrysophtharta bimaculata</i>	Eucalyptus	Defoliation		0.13–0.48			Raymond (1995)
<i>Endocronartium harknessii</i>	Lodgepole pine	Galling severity	0.13–0.43	0.20–0.54			Yang <i>et al.</i> (1998)
<i>Heterobasidion annosum</i>	Norway spruce	Lesion length in bark or fungal growth in sapwood				0.27–0.35	Swedjemark <i>et al.</i> (1997)
<i>Odocoileus hemionus columbianus</i>	Douglas fir	Winter browsing		0.73			Silen <i>et al.</i> (1986)

the less susceptible Corsican pine when existing stands reach the end of their normal rotation. For some tree species, the ways in which site or environmental factors influence resistance expression have been identified and so can be used as a basis for species selection. For example, species of eucalyptus that are most tolerant of drought in their native Australia are more resistant than others to the cerambycid, *Phoracantha semipunctata*, when planted in California (Hanks *et al.* 1995, 1999).

Among willow species, a number of large-scale trials have shown that there is considerable inter-specific variation in susceptibility to pests and

pathogens. For chrysomelid beetles, feeding preferences are influenced by the quantitative and qualitative variation between willow species in phenolic glycosides (Fig. 5.16). The resistance of hybrids between different willow species tends to be intermediate between that of the two parents. Natural hybridisation between closely related tree species increases the genetic variation within tree populations and natural hybrid zones may be useful sources of variation in resistance. In North American boreal forests, several species pairs are known to hybridise naturally, including white and yellow birch, balsam and subalpine fir, jack and lodgepole





**Figure 5.16** (a) Interspecific variation in willows (*Salix* spp.) in the extent of summer feeding damage by chrysomelid beetles (*Phratora* spp.) in the UK. (b) Consistency of ranking for clones assessed in consecutive years points to the absence of delayed induced responses to defoliation. (c) Hybrids tend to be intermediate in susceptibility between the two parents suggesting additive genetic control (from Hodkinson *et al.* 1998).

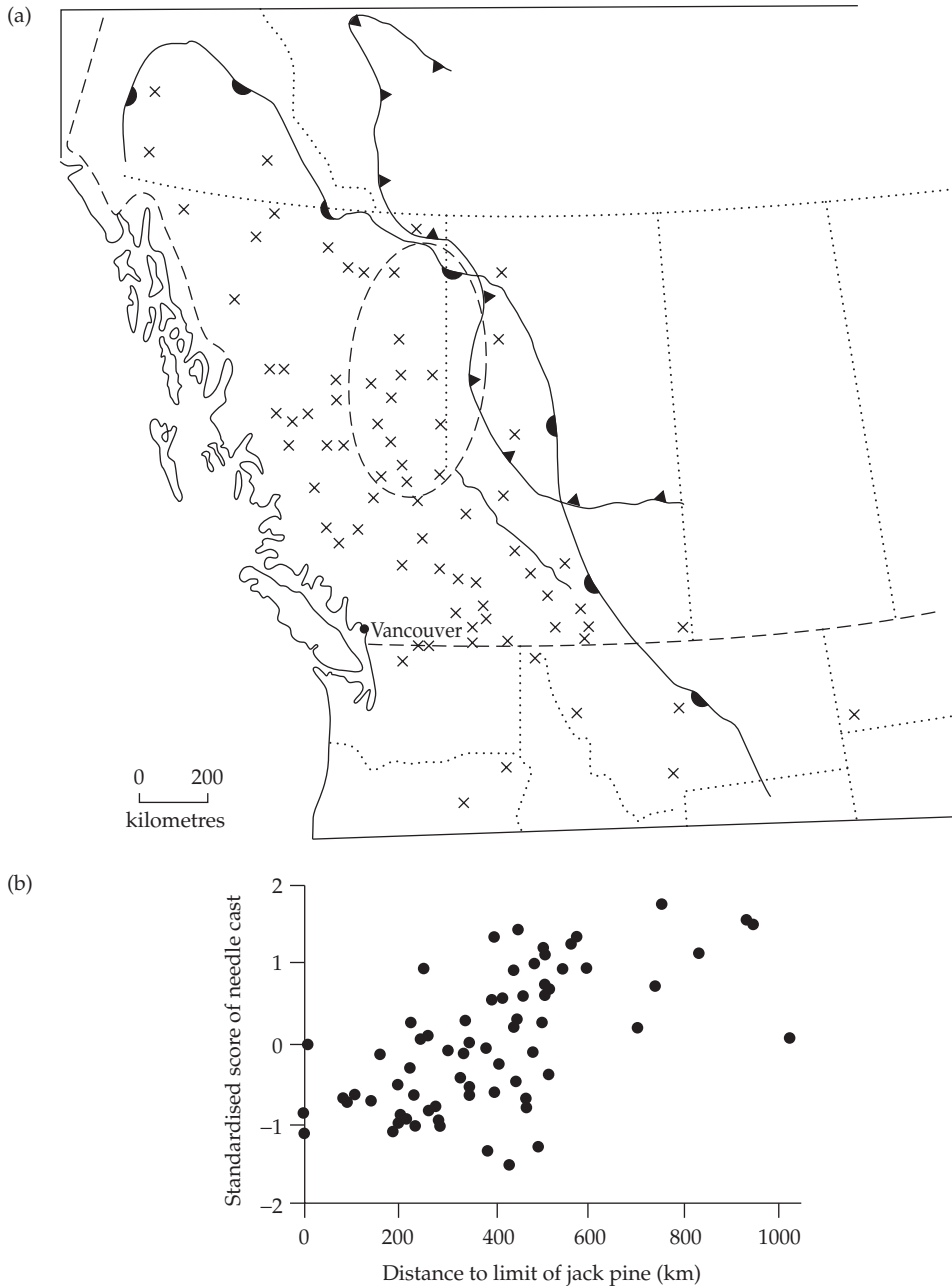
pine, and white and Sitka spruce (Gordon 1996). Where the distribution of these species pairs overlaps, resistance genes may be transferred from one species to another through introgression. Introgression is the process by which genes from one species become incorporated into the gene pool of another as a result of hybridisation and repeated backcrossing of the hybrid and its progeny to one or other of the parents (Zobel and Talbert 1984). A naturally occurring example is shown for lodgepole and jack pine in western Canada where resistance to needle cast disease caused by *Lophodermella concolor*, present in jack pine populations, has been transferred to lodgepole pine in the zone of introgression (Fig. 5.17).

#### Intra-specific variation

Provenance differences in resistance are usually most obvious in species with a wide geographical distribution. Scots pine is a well-known example (Table 5.3) but geographic variation in resistance to pests and pathogens has been observed in many different tree species (Table 5.5). Where tree species have a large and contiguous distribution, there can often be clinal variation in resistance (Fig. 5.18).

#### Individual trees

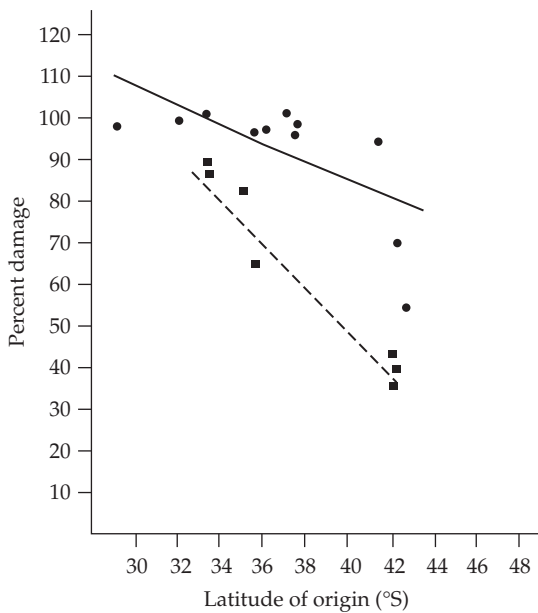
Individual tree variation in resistance provides the raw material for breeding programmes aimed at



**Figure 5.17** (a) The natural introgression zone of interior lodgepole pine (eastern limit  $\blacktriangle$ ) and jack pine (western limit  $\blacktriangle$ ) in western Canada. A large number of wind-pollinated families, collected from different provenances of lodgepole pine (x), were planted at a single location in British Columbia and tested for resistance to several pests and pathogens. (b) Resistance of lodgepole pine to needle cast disease caused by *Lophodermella concolor* was higher and more stable as provenance location approached the limit of jack pine distribution. Resistance genes for this disease appear to have been acquired from jack pine by introgression. Resistance to two other fungal diseases and one insect (Sequoia pitch moth, *Synanthedon sequoiae*) also increased in the zone of introgression. The most resistant provenances occur in the area approximately enclosed by the dotted line on the map (a) (from Wu *et al.* (1996) and Wu and Ying 1998).

**Table 5.5** Some examples of provenance variation in resistance to pests and pathogens

Tree species	Insect	Pathogen	Reference
Mahogany	<i>Hypsipyla grandella</i>		Newton <i>et al.</i> (1999)
Black locust	<i>Odontota dorsalis</i>		Zheng <i>et al.</i> (2003)
Blue gum	<i>Mnesampela privata</i>		Farrow <i>et al.</i> (1994)
	<i>Phylacteophaga froggatti</i>		
	<i>Anoplognathus</i> spp.		Floyd <i>et al.</i> (2002)
Aleppo pine	<i>Matsucoccus josephi</i>		Mendel (1998)
Lodgepole pine		<i>Endocronartium harknessii</i>	Yang <i>et al.</i> (1997)
	<i>Panolis flammea</i>		Leather (1985)
Radiata pine		<i>Dothistroma pini</i>	Ades and Simpson (1991)



**Figure 5.18** Damage caused by the eucalyptus snout beetle, *Gonipterus scutellatus*, to different Australian seed origins of two eucalyptus species, white gum (●) and mountain gum (■), planted in Lesotho, South Africa (from Richardson and Meakins 1986).

increasing the frequency of genes for resistance within tree populations. But this individual tree variation can sometimes be exploited directly by vegetative propagation, establishing clonal lines from naturally occurring resistant individuals for use in small-scale plantings. The specialised use of clonal trees has a long history but recent commercial exploitation of clonal plants in forestry is most commonly associated with broadleaved trees such as poplars and eucalypts. However, conifer clones are becoming increasingly important,

particularly through vegetative propagation from the limited supplies of seedling material available from elite specific crosses in advanced tree improvement programmes (Leakey 1987; Ritchie 1991; Sonesson 2001).

The nature of the genetic control of resistance influences how vulnerable clones are likely to be to resistance breaking. Clonal lines based on major gene resistance have been used particularly in poplars for resistance to pathogens (Newcombe 1996). Such clones have a high risk of failure because of the intense selection pressure on pathogen populations (Fig. 5.19). The risk of this can be reduced by increasing the number of genetically distinct clones used and by appropriate planting designs as discussed in Chapters 1 and 4.

Variation in resistance of poplar clones to insect pests has been reported in a number of different studies. Resistance to insect and vertebrate herbivores is most likely to be polygenic and therefore resistance of selected clones is likely to be durable (James and Newcombe 2000; Singh and Pandey 2002). The use of such clones has the advantage that non-additive as well as additive genetic variation in resistance is utilised. In Finland, naturally occurring birch trees of superior form and growth are selected for micropropagation and use in plantation forestry (Rousi *et al.* 1997). Different clones have been found to vary in resistance to mammalian herbivores, largely due to differences in the occurrence of resin droplets on the bark surface (Fig. 5.4). This trait could be used as a basis for clone selection to increase resistance to browsing (Jia *et al.* 1997). Use of clonal plants has also been tried experimentally to combat the soil-borne pathogen, *Phytophthora*



**Figure 5.19** Poplar growing in a clonal plantation. The clone on the right has been affected by the rust, *Melampsora larici-populina*.

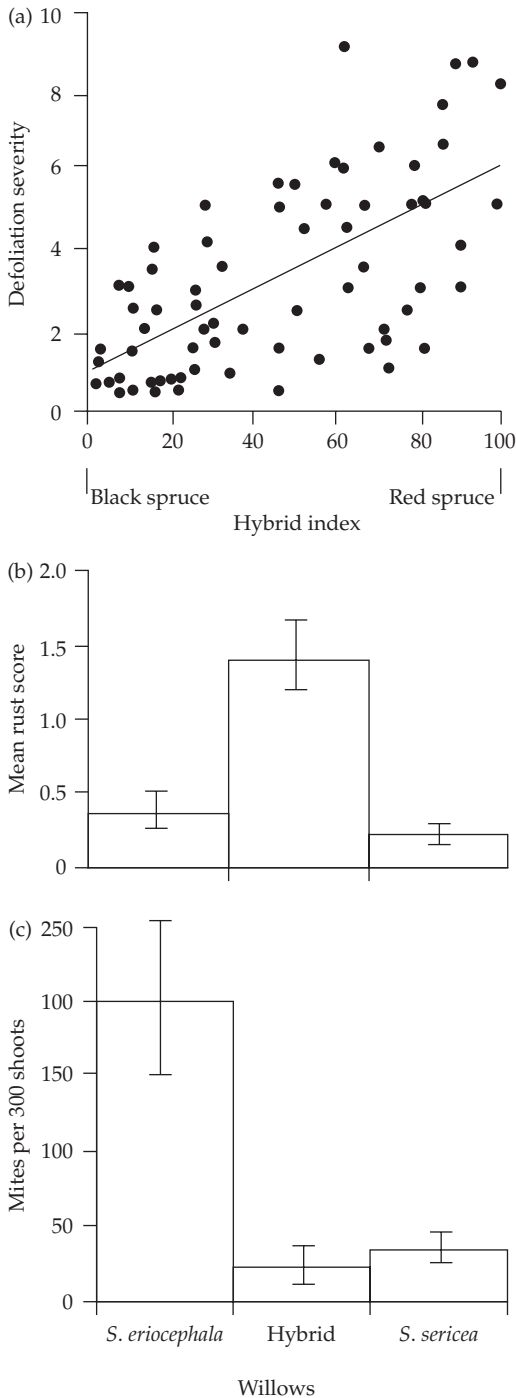
*cinnamomi*. This fungus causes high levels of mortality in the jarrah forests of Western Australia. Some trees survive attack and by screening their half-sib progeny for resistance, clonal lines have been obtained by micropropagation from resistant individuals within families. These were planted out in experimental trials on previously infected sites (Hüberli *et al.* 2002). Given that the life span of this tree is 500–1000 years, further monitoring of the durability of resistance expression is clearly needed!

### 5.6.2 Breeding for resistance

Some of the plant breeding strategies developed for the genetic improvement of highly domesticated annual crops are not appropriate for trees (Moreno-González and Cubero 1993, Panda and Khush 1995). This is largely because many tree species are naturally outcrossing, have high levels of genetic variability and usually have a relatively long juvenile period. In addition, polygenically controlled traits for resistance or other useful properties may only be expressed in older trees. For most tree species, the traditional breeding strategy for the improvement of silviculturally desirable traits is through recurrent selection and similar methods can be used to increase the frequency of resistance genes in a population. Using traditional tree breeding methods to increase resistance to particular pests or diseases is only likely to be undertaken for the most important pest or disease problems because such programmes are time consuming and

expensive (Heybroek 2000). Alternative breeding strategies such as hybridisation may however, be appropriate for some tree species. Interspecific hybrids can occur naturally where the distribution of related species overlaps and introgression can result in the transfer of genes for resistance from one species to another (Fig. 5.17). Several possible outcomes of hybridisation on resistance to pests and pathogens have been proposed depending largely on the nature of genetic control of resistance traits (Strauss 1994; Fritz *et al.* 1994, 1999). For polygenic traits, hybrids are usually intermediate in resistance between the two parents (Fig. 5.20(a), see also Fig. 5.16(c)) although sometimes they may be more susceptible than either parent (Fig. 5.20(b)). Where resistance of hybrids is similar to that of just one of the parents, Mendelian inheritance is implied (Fig. 5.20(c)).

Hybridisation can be used artificially to incorporate resistance genes into a tree population. In the Pacific North West (PNW) of North America, for example, inter-specific hybrids of the native black cottonwood with either eastern cottonwood from eastern North America, Japanese poplar from Asia, or black poplar from Europe have introduced some resistance genes effective against pathogens native to the PNW (Newcombe 1998). The inter-specific hybrids that are used commercially in forestry, are mainly of eucalypts, poplars and acacias, although some hybrids have been developed for conifers such as larch, spruce and pine (Dungey 2001; Gwaze 2001). Hybrids may be developed for purely silvicultural reasons rather than for their resistance



**Figure 5.20** Some effects of inter-specific hybridisation on expression of resistance to insects and fungi. (a) defoliation of red and black spruce and their hybrids by *Choristoneura fumiferana*. Hybridisation and introgression produces a range of phenotypes

qualities but one possible consequence of this is that there may be unintended adverse effects on resistance. In temperate regions worldwide, blue gum is an important plantation tree because it is fast growing with high wood density. In Tasmania, the frost sensitivity of the tree prevents planting above about 400 m. Inter-specific hybrids may allow growth of high quality timber in areas where environmental conditions may not be optimal for the desirable parent species. However, hybridisation with frost-tolerant species has been found to increase susceptibility to browsing by marsupial herbivores (Scott *et al.* 2002).

Tree breeding programmes to achieve incremental improvement in polygenically controlled traits such as stem straightness or growth rate have been developed for many commercially important tree species (Zobel and Talbert 1984; Fletcher 1992; Eldridge *et al.* 1993; Lee 1994). Traditional intra-specific tree improvement programmes are based on methods of recurrent selection starting from an initial population of trees with desirable traits collected from natural sources or plantations. The population is subjected to cycles of mating and reselection based on performance of their progeny, with each cycle taking several years. During this process, trees that are deformed or damaged by pest or pathogen attack are likely to be excluded and so in normal tree improvement programmes to increase form or growth rate, the general level of resistance may well be increased. The breeding cycles adopted in such programmes serve as a model for increasing resistance to specific pests and pathogens by increasing the frequency of genes controlling particular polygenic resistance traits within the population.

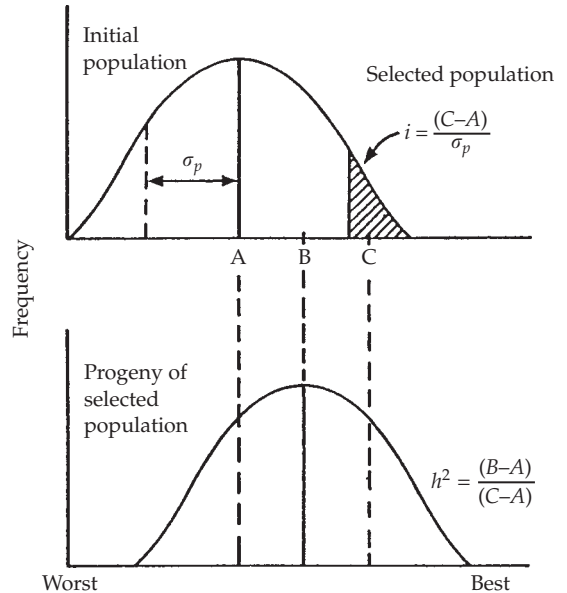
Before initiating resistance breeding programmes, it is important to select appropriate

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whose resistance is intermediate between parent trees indicating additive genetic variance. (b) Rust caused by *Melampsora* spp. on willows (*Salix eriocephala*, *S. sericea*) and their hybrids. Hybrids are presumed to be more susceptible because hybridisation disrupts the coadapted gene complexes that are present in the parent species. (c) Leaf galling by the mite, *Aculops tetanothrix* on the same two willow species. In this case, resistance of the hybrid corresponds to that of one parent, implying Mendelian inheritance (from Fritz *et al.* 1994, Manley and Fowler 1969, and Roche and Fritz 1998).

provenances or seed sources so that individuals for inclusion in the base population have the highest available natural levels of resistance. The next level of selection is to identify the phenotypically 'best' seed stands for the trait under selection. Within the stands, an initial population of phenotypically selected trees is chosen as parent trees from which seed is collected. Site can have an important influence on the phenotype so it is important to select stands from a number of different sites within the range of the provenance of interest. The base population should be large enough to avoid inbreeding depression in the more advanced stages of a breeding programme. Seed collected from these open-pollinated parent trees, together with an appropriate 'unimproved' control, can be formally tested in trials established on a range of different sites to determine the additive genetic variation for the selected trait. Parents of the best progenies are selected to give a breeding population of perhaps 200 or so trees which can be established as grafts from the parent tree in seed orchards and allowed to intermate. The genetic gains expected from the breeding cycle depend on the intensity of selection and the heritability of the trait as illustrated in Fig 5.21. Further selection and reselection can be made among the progeny and some of the outstanding individuals mated in controlled pollinations.

Tree breeding through recurrent selection depends on using selection methods that reliably reflect phenotypic expression of the desirable trait so that trees and their progeny can be easily ranked. Individuals must be assessed at an appropriate stage in development and for those traits that are only expressed in older trees, this process can take some years. The process of selection could be considerably simplified and shortened, however, by the use of molecular markers that identify the presence of genes controlling resistance traits (Yencho *et al.* 2000). Molecular markers, which can be used for major gene and polygenically controlled resistance, enable marker-aided selection in which plants with desirable traits are identified genotypically rather than phenotypically. This allows progeny to be screened at an early age and without the need for bioassay. The process of identifying markers is complex, however, and less

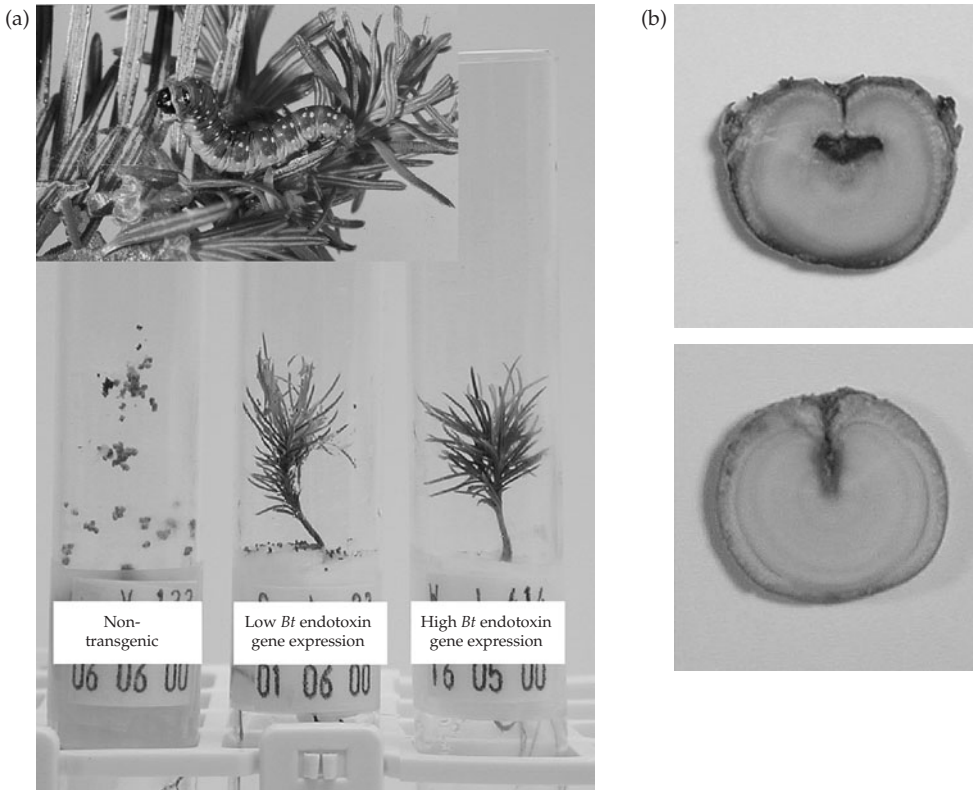


**Figure 5.21** Genetic gain from recurrent selection of a tree population in a breeding programme. A is the mean of the initial population for the trait under consideration which is assumed to be normally distributed, C the mean of the selected population and B the mean of the progeny of this population. Expected genetic gain =  $B - A = i h^2 \sigma_p$  where  $i$  is the intensity of selection in units of standard deviation of the trait,  $h^2$  is the narrow-sense heritability and  $\sigma_p$  is the phenotypic standard deviation of the trait, that is, a measure of its variability within the particular population (from Carson and Carson 1989).

developed for trees than for agricultural crops. Some of the factors affecting the application of this technology to trees are discussed by Strauss *et al.* (1992). Molecular markers have been used to identify polygenic disease resistance (Van Buijtenen 2002) and major genes for disease resistance in poplars (Cervera *et al.* 1996) and for resistance to green spruce aphid, *Elatobium abietinum* (Skov and Wellendorf 2000).

## 5.7 Genetic modification

The 'engineering' of novel genes into plants to express 'resistance' to insect pests has been developed largely in relation to agricultural plants but the potential for genetic modification (GM) of trees has also been explored (Strauss *et al.* 1991; Mullin



**Figure 5.22** Demonstration of the potential of genetic modification of trees to protect against pest and pathogen attack. (a) Expression of a *Bacillus thuringiensis cry* gene in genetically modified white spruce plantlets protects them against *Choristoneura fumiferana* (inset). (b) Expression of a gene encoding an antimicrobial protein in poplar reduces spread of a bacterial canker. The control stem section is shown on the top (from Peña and Séguin 2001).

and Bertrand 1998). For resistance to insect pests, transforming plants to express foreign insecticidal proteins has been dominated by studies on *cry* genes from *Bacillus thuringiensis* (*Bt*) (Section 7.1.1). When suitably modified and engineered into plants, a *cry* gene results in production of the toxic protein that kills susceptible insects feeding on them. The resistance expressed is therefore comparable to major gene or *vertical* resistance. The possibility of genetic modification of a plant's natural defences by altering expression of secondary chemicals that contribute to polygenic resistance has also been considered. Given that secondary chemicals are usually the product of several genes and involve complex synthetic pathways, engineering

effective *horizontal* resistance is likely to pose formidable technical challenges (Chilton 1997; McCaskill and Croteau 1998). Genetic modification of plants for expression of resistance to pathogens is much less developed than that for insects. Recent interest has centred on expression of anti-microbial peptides that have been identified from many different kinds of organism and on identifying and manipulating antifungal proteins in plants (Salmeron and Vernooij 1998; Séguin 1999).

The potential of GM to increase resistance to pests and pathogens has been demonstrated in a number of tree species (Fig. 5.22). But the practical exploitation of the technology, moving from plantlet to planted forest, depends on addressing important

questions related to stability of expression in long-lived trees and to the scale of forestry. Poplars have been most frequently transformed to express *Bt* genes for resistance to insect pests (Robison *et al.* 1994; Strauss *et al.* 2001a). Poplars are readily propagated and often grown in intensively managed plantations (Fig. 5.23). Trials in China with *Bt*-transformed black poplar have shown not only the high levels of resistance to defoliators that can be achieved but the protective effect on untransformed trees present in the same plot as a result of the reduction in insect population densities (Fig. 5.24).

Planting trees modified to express *Bt* toxins has several advantages over the using *Bt* as a microbial insecticide (Section 7.2.1). Perhaps the most obvious is that plant parts that are inaccessible to spray are protected and there are no direct non-target effects. An additional advantage is that it is no longer necessary to monitor insect populations to determine the need for, or timing of sprays. There are some disadvantages, however. In particular, the continuous expression of the toxin throughout the season, the more or less uniform exposure of the whole population and high mortality rates increases selection pressure for *Bt* resistance to develop in the insect population. Sustainable use of GM trees will, therefore, depend on appropriate resistance management strategies including provision of 'refuges' of untransformed trees allowing

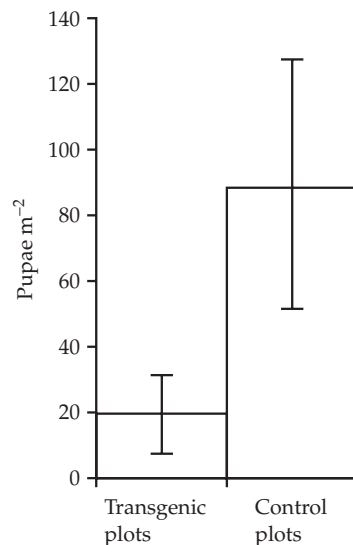


**Figure 5.23** Poplar plantation in Oregon, USA. Poplars are fast growing and often intensively managed and are potential candidates for genetic transformation to increase pest resistance (from Strauss *et al.* 2001b).

some susceptible individuals to survive, engineering trees to express more than one type of toxin or use of a mixture of trees that express different toxins (Roush 1997; Gould 1998). There are also environmental concerns about the release of genetically modified trees, reflected in the banning of GM trees in Forest Stewardship Council certified forests (Strauss *et al.* 2001b, c). Of particular concern is the risk of horizontal gene transfer to wild populations through introgression or other mechanisms. These issues are discussed by Burdon (1999), Sharma and Ortiz (2000), Strauss *et al.* (2001a) and Letourneau and Burrows (2002).

## 5.8 Resistance management

Strategies for reducing the likelihood that pests and pathogens will adapt to resistant plants are similar to those outlined for minimising adaptation of



**Figure 5.24** Combined pupal density of two defoliators, *Apocheima cinerarius* and *Orthosia incerta*, in plots of genetically modified (GM) or untransformed black poplar in Xinjiang Uygur, China. Trees were about 4 years old and around 75% of them were transformed to express *Bt* in the experimental plots. Population densities of defoliators in plots containing GM trees were below the critical density for insecticidal control of around 36 pupa m<sup>-2</sup> whereas densities in control plots were much higher. Untransformed trees in the experimental plots provide refuges for insects, a planting strategy that is likely to reduce the risk of resistance developing in the insect population (from Hu *et al.* 2001).



pests to chemical and microbial insecticides (Denholm and Rowland 1992; Tabashnik 1994; Barclay 1997; Gould 1998). The general aim is to reduce the selection pressure on pest populations by providing 'refuges' of some susceptible hosts interplanted with the resistant ones. Provided that plantations are not isolated, the immigration of

pests from outside the area planted with resistant trees will further reduce the risk of resistance breaking. Where clonal lines are used as in some specialised crops such as willow and poplars used in short-rotation forestry, selection pressure on pathogens may be reduced by using clonal mixtures or mixtures of monoclonal blocks (Fig. 4.5).

# Biological control

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In biological control, natural enemies are used in different ways to reduce pest population density. Most definitions of biological control emphasise the importance of both reduction in pest abundance and maintenance of the population at low densities, ideally below an established economic threshold of damage (Kidd and Jervis 1997). In forestry, damage thresholds are much less commonly used than in high value agricultural systems (Sections 9.1 and 9.3). This is because forests are often managed over long rotations, have a relatively low value per unit area and because they usually have a greater tolerance of sublethal pest damage. One practical consequence of this is that in forests, biological control that is considered to be only partially successful can still make an important contribution to management within the wider context of Integrated Pest Management (Chapter 9).

Biological control (biocontrol) can be divided into two broad strategies—*augmentation and conservation* and '*classical*' *biocontrol*—which are characterised principally by the origin of natural enemies and the way in which they are used. Methods of augmentation and conservation are concerned principally with management or manipulation to enhance the effectiveness of natural enemies already present in the environment. Classical biocontrol on the other hand, involves the importation and establishment of non-native natural enemies, most commonly against 'exotic' pests that have invaded a new region, usually as a result of accidental introduction.

Most of the examples given in this chapter refer to the biocontrol of insect pests using predatory insects, parasitoids, or disease-causing pathogens. These natural enemies interact with prey and host populations in different ways and this obviously affects whether they are likely to be effective agents

of biocontrol and how they are utilised in practice. A detailed discussion of the characteristics of different kinds of natural enemy can be found in Bellows and Fisher (1999).

Vertebrates can be highly effective predators. Small mammals, for example, prey on overwintering stages of insect pests in the soil and birds may feed on larval stages of defoliators and can cause significant mortality especially in low density populations (Parry *et al.* 1997). These generalist predators however have a limited capacity to respond to rapid and widespread changes in the density of their prey. They are widely considered to be unsuitable candidates for introduction in classical biocontrol and within native habitats, are not easy to manipulate in augmentation and conservation. Most predatory insects (within Coleoptera, Diptera, Hemiptera, Hymenoptera, Neuroptera and Odonata) are also considered unsuitable for introduction because they feed on a wide range of prey and so could have detrimental effects on non-target organisms. Those predators that are more specific in their choice of prey may be suitable for release in biocontrol programmes, an example of which is outlined in Box 9.4. Generalist predators are however, often important in the population dynamics of native pests and so may be amenable to augmentation and conservation (Hawkins *et al.* 1999). Parasitoids (within Diptera and Hymenoptera) whose host range is limited to the target pest or its close relatives pose the least risk to non-target insects in the new environment. Host-specific parasitoids are therefore considered to be particularly suitable candidates for classical biocontrol. Insect diseases caused by microorganisms can cause spectacular epizootics resulting in the collapse of pest outbreaks. Viruses, for example, have sometimes been accidentally

introduced during biocontrol programmes, one of the best examples of which is the highly effective control of the European spruce sawfly, *Gilpinia hercyniae*, in Canada (Bird and Elgee 1957). In general however, pathogenic organisms are not considered suitable candidates for introduction and release because many of them have a wide host range and often only affect populations once outbreak densities have been reached. They have however, been successfully used as microbial insecticides as described in the following chapter.

For some tree pathogens, one of the more promising approaches for biocontrol is the use of transmissible hypovirulence resulting from infection by naturally occurring viruses. 'Hypovirulent' strains of pathogenic fungi may have a reduced ability to sporulate, tend to be slow growing and are usually less able to infect healthy trees. An example of the naturally occurring biological control of a plant pathogen through hypovirulence is that of the chestnut blight fungus, *Cryphonectria parasitica*, which causes cankers on European and other species of chestnut (Heiniger and Rigling 1994; Fulbright 1999). Hypovirulence was first observed in Italy and attributed to an RNA virus transmitted cytoplasmically between vegetatively compatible strains of the pathogen. In contrast to insect pests, classical biocontrol has not in general been adopted for control of plant pathogens (Scott 1995). However, a rare example of this technique is the introduction of hypovirulent strains of *C. parasitica* to eastern United States in an unsuccessful attempt to combat the introduced pathogen that was killing the susceptible American chestnut (Liu *et al.* 2002). The potential of viruses in biocontrol of fungi is discussed by Nuss (1992), Brasier (2000b) and Anagnostakis (2001). The use of fungal competitors for the control of tree pathogens is discussed in Chapter 7.

## 6.1 Augmentation and conservation

The aim of augmentation and conservation is to increase the effectiveness of natural enemies where they are locally absent or are ineffective for other reasons or where satisfactory long-term suppression of pests has not occurred following classical biocontrol. Methods of augmentation and conservation may be employed on a relatively local scale,

and unlike classical biocontrol, may provide opportunities for commercial development such as breeding natural enemies for inundative release. Although most attention is focused on manipulation of native natural enemies, previously introduced exotic species may also be considered where they have only a limited impact on their host or where they disperse relatively slowly. For example, control of the spruce bark beetle, *Dendroctonus micans*, by the introduced specific predator *Rhizophagus grandis*, is augmented by releases of the predator in newly discovered infestations during annual surveys at the expanding edge of the bark beetle distribution in the United Kingdom (Box 9.5).

There are two main methods of augmentation. The 'local' transfer and inoculative release of a relatively small numbers of individuals and the inundative release of a much larger number into the pest population. Local transfer involves the collection of a few individuals and their release at a new location. Transfers are typically done early in the season with the expectation that the progeny of the released natural enemies will have the main impact on the pest population. Inundative methods in contrast are used to achieve an 'immediate' but unsustainable reduction in density. The use of 'microbial' insecticides such as *Bacillus thuringiensis* (*Bt*) (Section 7.2.1) is similar in some ways to inundative release of natural enemies.

There are several examples of the local transfer of natural enemies to control forest pests but the level of control achieved can be difficult to assess. In Europe, there have been a number of attempts to establish native wood ants of the *Formica rufa* group in areas where they were absent or not abundant. These ants are voracious predators and can reduce the density of larvae of defoliating Lepidoptera. Evidence of their impact is sometimes seen by the presence of 'green islands' of undefoliated trees around nests during periods of high insect abundance. They have a number of desirable attributes as natural enemies, including the ability to respond to prey density and to utilise alternative food sources when prey are scarce (Way and Khoo 1992). In managed forests however, it has proved difficult to maintain the necessary density and uniform distribution of nests for effective protection of the forest (Greathead 1976).

Insect pathogens have been considered for local transfer to try and increase the frequency and extent of epizootics. Diseases can be important causes of mortality in insect populations but their occurrence during pest outbreaks can be unpredictable and they usually take some time to build up and cause high mortality so that populations collapse only after there has been some damage to trees. The early inoculative establishment of disease organisms in pest populations could therefore be a way of increasing their effectiveness. This 'inoculative' technique is particularly appropriate for pathogens that cannot be readily bred or mass-produced. An experimental example of the introduction of an insect

pathogen into populations of gypsy moth, *Lymantria dispar*, is discussed in Box 6.1.

Inundative release of natural enemies is technically more involved than inoculative methods used in augmentation, and potentially much more expensive. It is necessary to use natural enemies that can be readily mass-produced and to monitor the host population to ensure optimum timing of releases. Control of the European woodwasp, *Sirex noctilio*, in Australia although often discussed as an example of classical biocontrol, also has some characteristics of inundative augmentation because it involves the breeding of nematodes and their injection into trees in outbreak areas to assist rapid

### Box 6.1 Inoculative release of a fungal pathogen of gypsy moth, *Lymantria dispar*

Fungi have been used successfully to control pests of crops in protected cultivation. But in the forest environment, their temperature-dependent growth rate and requirement for wet conditions for spore germination would seem to limit their usefulness. It may nevertheless be possible to augment populations already present in the forest. An illustrative example of how this might be done is provided by *Entomophaga maimaiga*, an exotic fungal pathogen of *L. dispar* in the United States. This example also serves to highlight some of the strengths and weaknesses of fungi as agents of biocontrol (Section 7.1.4).

Introduced to North America in the 1860s, *L. dispar* is a serious defoliator of hardwood trees and causes additional problems in densely populated areas because larvae have urticating hairs capable of causing allergic reactions in some people. It is now widely distributed in north-eastern states and is spreading south and westwards. *E. maimaiga* is an obligate pathogen that causes extensive natural epizootics in *L. dispar* populations in Japan. The origin of the fungus in the United States is 'mysterious' but it caused outbreaks of disease throughout much of the north-eastern distribution of *L. dispar* during the early 1990s. It may be a more virulent descendant of the original fungus introduced to an area near Boston from Japan early in the last century. Alternatively it may be a virulent strain accidentally introduced more recently.

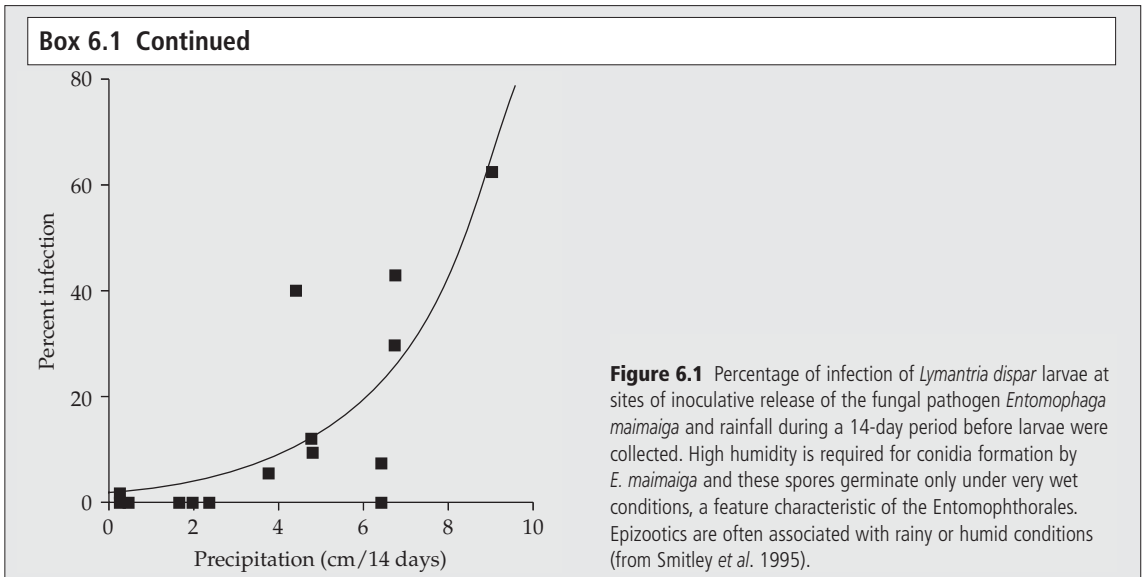
Early instars are infected by overwintering resting spores present in cadavers and as a reservoir in the soil. Young infected larvae produce large numbers of a second spore type, conidia, that disseminate infection through the population. The fungus is specific to *L. dispar* in the natural environment partly because of larval aggregation behaviour during the infection cycle and the

tendency of older larvae to hide near soil or in bark crevices.

In order to assess the potential for initiating epizootics and for preventing defoliation of oaks, experimental scale inoculative releases were made in 1991–2 in a population near the leading edge of *L. dispar* expansion in Maryland, Pennsylvania, Virginia and West Virginia, and in a disjunct population in Michigan in a region where *L. dispar* was well established. The fungus was introduced into *L. dispar* populations by transferring small amounts of soil collected from around trees in areas affected by natural epizootics in other states. The soil, which contained many resting spores, was moved with appropriate safeguards to avoid inadvertent movement of insect or plant pathogens.

Transfer was most effective when it coincided with *L. dispar* egg hatch. However, the amount of disease at the different sites was often related to the occurrence of rainfall (Fig. 6.1) and was enhanced by watering of the transferred soil. High levels of disease could occur in low as well as high density populations of *L. dispar*, usually 1–3 years after transfer of soil. In most of these studies, control plots were also affected either by natural *E. maimaiga* or by the extremely rapid spread of the induced epizootic. The effectiveness of the introductions could however, be judged by the gradients of infection that occurred over several hundred metres from release sites in the first year. There was circumstantial evidence that the fungus contributed to *L. dispar* population decline although further research is needed for a better understanding of the critical factors in pathogenicity and development of epizootics.

Key references: Weseloh and Andreadis (1992), Hajek *et al.* (1995b, 1996), Hajek and Webb (1999), Smitley *et al.* (1995), Webb *et al.* (1999).



spread and ultimate control of the woodwasp populations (Box 9.6). Inundative releases of insect parasitoids, in agriculture as well as forestry, have most frequently utilised the egg parasitoid *Trichogramma* spp. (Newton 1993). An example of experimental inundative releases against the eastern spruce budworm, *Choristoneura fumiferana*, and some of the factors influencing effectiveness in the field are discussed in Box 6.2.

Conservation of natural enemies has received a lot of attention in the agricultural literature where intensive management, frequent disruption of the environment, and use of insecticides can limit the effectiveness of natural enemies (Barbosa 1998; Gurr *et al.* 2000). Forests are much less 'disturbed' than agricultural crops and so forest management is not expected to be so detrimental to natural enemies. However, some forestry practices such as establishment of plantation monocultures may reduce the availability of non-prey food resources such as nectar or pollen (Section 1.2). The importance of these foods has been shown experimentally and providing artificial carbohydrate resources can increase the fecundity and longevity of parasitoids (Mathews and Stephen 1997; Cappuccino *et al.* 1999; Thompson 1999). The information needed to enhance non-host food sources for conservation of particular natural enemies is however, usually lacking. In practice, it is difficult to demonstrate the effects of manipulating the abundance of natural food sources on specific pests in the forest but an often quoted example is

that of the European pine shoot moth, *Rhyacionia buoliana*, and its parasitoid *Orgilus obscurator*. Wild carrot and other flowers increase longevity and fecundity of the parasitoid and when present in pine plantations, appear to result in an increase in levels of parasitism of the shoot moth (Syme 1977, 1981). This suggests that there may be some potential benefits from increasing natural carbohydrate sources such as flowers through appropriate management, but further studies on the practicability and benefits of this are needed.

Insecticides are used relatively infrequently in forestry but may occasionally be applied over large areas of semi-natural forest habitat. An important method of conserving natural enemies in treated forests is to ensure that appropriate toxicity testing allows the selection of products with minimum adverse effects on natural enemies and to time insecticide applications to reduce contact with them (Nowak *et al.* 2001b). The use of *Bt* instead of chemical insecticides avoids direct mortality of natural enemies, and indirect mortality through death of parasitised hosts may often be reduced because parasitised larvae eat less than healthy ones and so are less likely to pick up a lethal dose (Nealis and van Frankenhuyzen 1990).

## 6.2 Classical biological control

Classical biocontrol is used almost exclusively against 'exotic' pests and in contrast to the more

local effects of augmentation, is intended to be self-sustaining often over large areas. Control of native pests by introduced natural enemies is also sometimes considered despite increased risks to non-target insects (Section 6.2.2) (Mills and R  ther 1990; Mills 1993). Natural enemies for possible introduction are usually selected from the community associated with the pest in its native range. These natural enemies are assumed to be important in helping to maintain the pest at relatively low densities and in fact some of the most successful programmes have been targeted against insects that are not regarded as serious pests in the region of origin (Mills 1990*b*).

Forests are often assumed to be a favourable habitat for classical biocontrol because they are

relatively 'stable', lacking the regular disturbance associated with agricultural crops. Given that pest damage can occur over extensive and often inaccessible areas of semi-natural forest where more direct methods of control may be difficult or impracticable, there are obvious benefits to self-sustaining biocontrol in forest pest management. But is there evidence that it is likely to be more successful in forests than in other habitats or crop systems? Historical records of biocontrol operations held in databases such as BIOCAT by the International Institute of Biological Control (Greathead and Greathead 1992), can be used to show the kinds of cultivation systems and kinds of pests where classical biocontrol has been most successfully used (Fig. 6.5).

### Box 6.2 Inundative release of an egg parasitoid of spruce budworm, *Choristoneura fumiferana*

*Choristoneura fumiferana*, is an eruptive pest native to North America feeding mainly on balsam fir and spruces. Adults are active in mid-summer when females deposit egg-masses on needles. First instars are dispersed by wind and the second instars overwinter in a hibernaculum. In spring, larvae feed mainly on expanding buds and subsequently on new foliage. Later on, twigs are tied together with silk to form a small nest within which feeding is completed, usually by early July. Young adults can migrate and when flying at night above the forest canopy may be displaced long distances downwind.

Extensive insecticidal control campaigns in the 1950s and 1960s resulted in >2 million ha of forest being sprayed in some years. The possibility of biological control through inundative release of *Trichogramma* egg parasitoids was investigated in Ontario, Canada in the 1980s. The native multivoltine chalcidoid *Trichogramma minutum* is the most important egg parasitoid in budworm populations, but parasitism is typically <15% and not significant in natural control. By breeding and releasing large numbers of parasitoids during the approximately 3-week period of budworm oviposition, the aim is to increase levels of parasitism significantly and to reduce larval populations. Parasitoid strain differences are known to occur and it is important to select ones well adapted to the local host.

Mass rearing, which is an expensive part of the process, is often most conveniently done on a factitious host—Angoumois grain moth, *Sitotroga cerealella*, in this study. The generation time of *T. minutum* is around 2 weeks so initial population size is important in

preventing genetic change in the many cycles of laboratory breeding. Rearing conditions can also influence, among other things, parasitoid sex ratio, fecundity, and longevity.

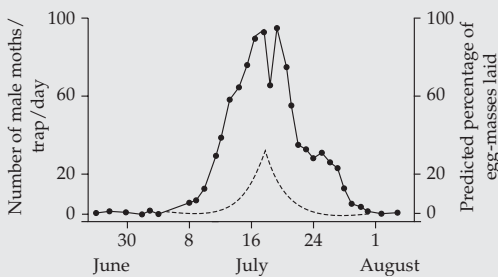
In contrast to classical biocontrol, there are many technical aspects to breeding and inundative release. *T. minutum* has limited searching ability, only lives for a few days depending on the availability of honeydew and nectar food sources, and budworm eggs are only acceptable for a 3–6-day period following oviposition. Breeding and releases need to be carefully synchronised and releases appropriately timed to budworm oviposition. The budworm oviposition period can be predicted from male trap catches and a phenology model (Fig. 6.2). *Trichogramma* species are highly polyphagous so timing of releases is also important to minimise attack on non-target species. The parasitoid release rate has a big influence on percentage of parasitism (Fig. 6.3) and more than one release may be necessary for optimal control.

The impact of releases can be determined by assessing levels of parasitism of both 'sentinel' and naturally occurring egg-masses (Fig. 6.4). The optimum release strategy increased parasitism of host eggs by 14–83% and reduced larval populations in the year following release by 42–82%.

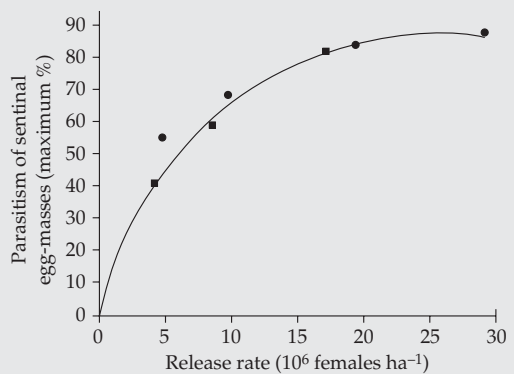
Although there are questions over commercial viability, these detailed field studies showed that inundative release of *Trichogramma* has considerable potential for the control of *C. fumiferana*.

Key references: Lawrence *et al.* (1985), Smith *et al.* (1987, 1990).

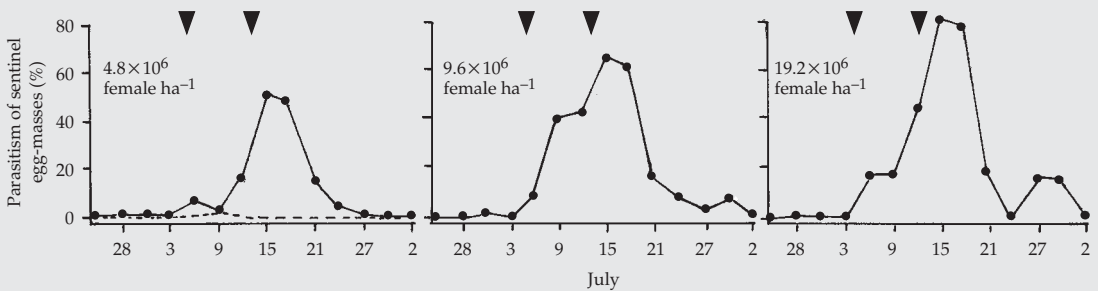
Box 6.2 Continued



**Figure 6.2** Catches of male *Choristoneura fumiferana* in pheromone-baited traps at a site in Ontario, Canada (●) and the timing of oviposition predicted from a phenology model (-----) (Règnière 1983) that predicts moth emergence from percentage of larvae  $\geq$  fifth instar on a given sampling date. Prediction allows time to programme parasitoid emergence (from Smith *et al.* 1987).



**Figure 6.3** The effect of release rate of *Trichogramma minutum* on parasitism of sentinel egg-masses of *Choristoneura fumiferana* placed in balsam fir and spruce trees in 1985 (■) and 1986 (●) in Ontario, Canada (from Smith *et al.* 1990).

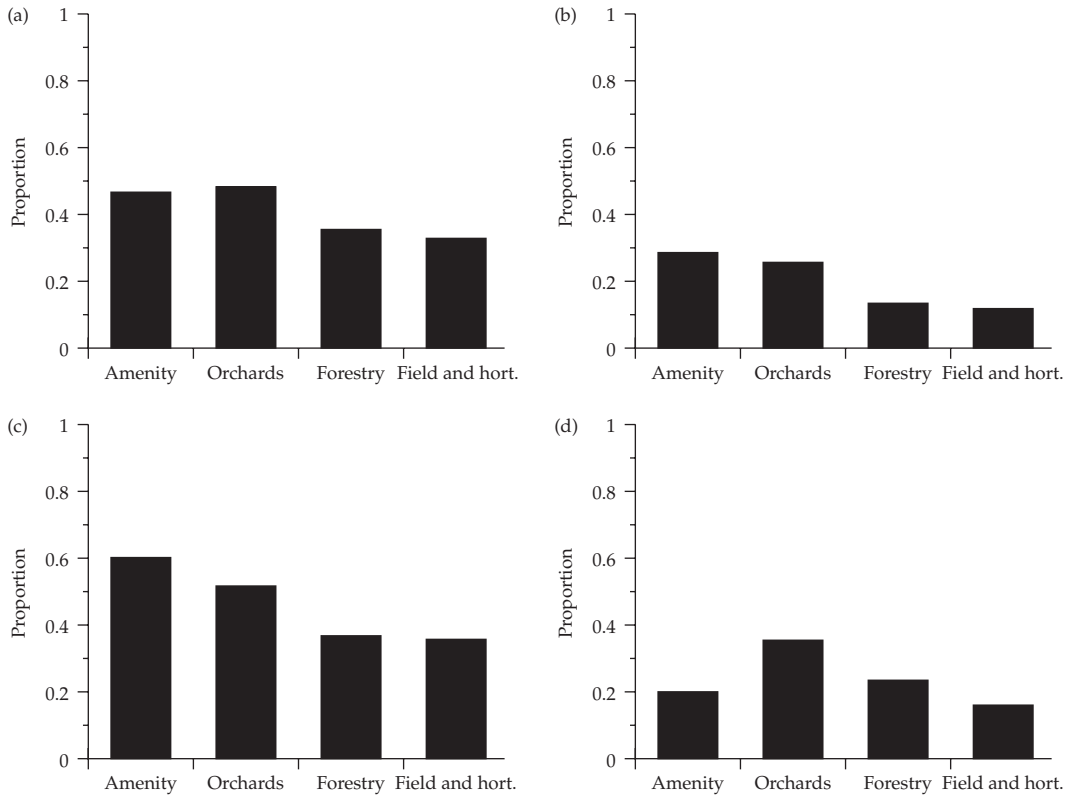


**Figure 6.4** Parasitism of sentinel egg-masses of *Choristoneura fumiferana* (—) following two releases of *Trichogramma minutum* at a site in Ontario, Canada in 1986. Results of three parasitoid release rates and a control (-----) are illustrated. The optimum release strategy, which was a compromise between impact on the population and cost, was two releases (▼) of 12–16 million females  $ha^{-1}$  made 1 week apart during the early part of the budworm oviposition period. Parasitism by the progeny of the first releases of *T. minutum* is evident at the end of July (from Smith *et al.* 1990).

These records suggest that biocontrol in forests is no more successful than in some agricultural systems and less so than that in orchards. The reasons for this are not clear but might be a reflection of the relative importance of ‘bottom-up’ forces in the dynamics of forest insects, that is, the quantity and quality of food resources as opposed to the ‘top-down’ action of natural enemies (Kidd and Jervis 1997). Most forests do however, have a distinct advantage over agricultural and horticultural crops in the application of biocontrol because they can sustain higher levels of pest damage without

significant economic loss and so may derive greater benefit from programmes that are only partially successful.

Only about a quarter of natural enemies released in classical biocontrol in different cropping systems establish successfully and of these, less than half give some level of control (Waage and Mills 1992). But the success rate varies considerably between different orders of insects and is much higher for Homoptera (Table 6.1). In fact the relatively high proportion of successes observed in orchards partly reflects particularly effective operations against



**Figure 6.5** Success of classical biological control in different plant cultivation systems. Data held in the BIOCAT database were analysed to determine relative success in establishment and some level of control for those introductions where the outcome was known. (a) Establishments as a proportion of introductions, (b) successes as a proportion of introductions. (c) successes as a proportion of establishments and (d) proportion of successes resulting in complete control. Amenity refers to gardens, parks etc. (from Kidd and Jarvis 1997 and Jarvis personal communication).

**Table 6.1** Relative success of classical biological control against different orders of insects

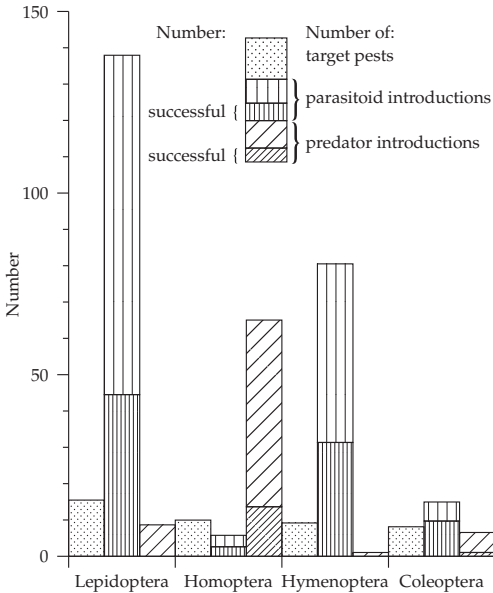
Insect order	Success (%)
Homoptera	66
Lepidoptera	18
Coleoptera	7
Diptera	5
Hymenoptera	1
Heteroptera	1
others	2

Sources: Waage and Mills (1992); Greathead (1995).

scale insects. These relatively sedentary pests feed on fairly exposed positions on plants and so are particularly susceptible to attack by natural enemies (Gross 1991; Hawkins 1994).

The major pests of forests vary in their suitability as targets for biocontrol and this is reflected in the frequency with which it has been used in different insect orders (Fig. 6.6). Coleoptera have been less frequent targets of biocontrol. This is partly a reflection of the fact that bark beetles are among the most important forest pests but their population dynamics is strongly influenced by the availability of susceptible breeding material. In addition, pheromone-mediated mass-attack of living trees can lead to eruptive population dynamics in which natural enemies are relatively unimportant (Section 3.2). So although bark beetles have many natural enemies, there have been few attempts at biological control of these important pests (Mills 1983; Miller *et al.* 1987). In Homoptera, releases have been dominated by predators, reflecting their relative importance in population





**Figure 6.6** The use of parasitoids and predators in classical biocontrol against forest insect pests. Introductions were classified as successful if some degree of control was achieved (data from Dahlsten and Mills 1999 after Greathead and Greathead 1992).

dynamics. For example, conifer-feeding adelgids lack parasitoids so that choice is restricted to predators of these insects. Some coccinellids are important predators of adelgids and may be relatively specific, making them potential candidates for introduction (Mills 1990b; Lu and Montgomery 2001). Classical biocontrol has been most frequently targeted against Lepidoptera and in this order and in the Hymenoptera, biocontrol attempts have been dominated by releases of parasitoids. Forest defoliators support a highly diverse parasitoid fauna with a high level of specialisation within the parasitoid guild (Mills 1990a). For these pests, an important consideration is how to select the most effective natural enemies from the many species that may be available. The considerable logistic, financial and regulatory support needed for the selection, introduction and release of natural enemies in classical biocontrol means that it is most effectively conducted through government institutions or international biocontrol organisations (Dahlsten and Mills 1999; Perkins and Garcia 1999).

### 6.2.1 Theory and practice in selection and release of natural enemies

Many of the factors that influence the successful establishment and invasion of new habitats by alien pests (Section 2.2) can also influence the establishment of natural enemies released to control them. As a result, even though natural enemies may be carefully selected for traits that fit them to the new environment and are released under favourable conditions where prey is abundant, they can still fail to become established. The dynamic interaction between natural enemy and prey in the new environment is also inherently unpredictable, emphasising the essentially empirical nature of biocontrol. An important aim of current research therefore is to develop methods for increasing the relatively low success rate of biocontrol. Improvements in the selection of natural enemies using some easily measurable life-history traits, such as host stage attacked, development rate and adult longevity, might form the basis of predictive models of biocontrol (Waage and Mills 1992). Previous success is one of the most useful general guides to selection of effective natural enemies. But lessons can be learned from failures where the cause can be identified. The most commonly cited reasons for failure included climate, lack of alternative hosts and the wrong strain of parasitoid (Stiling 1990, 1993). These examples suggest ways in which success could be improved in subsequent releases although in general, specific causes of failure are often difficult to determine.

In selecting natural enemies for release in classical biocontrol, the aim is not to reconstruct the complete natural enemy community associated with the pest in its native habitat, but to choose one or a few natural enemies that have a high level of host specificity and which appear to have the best chance of success (Myers *et al.* 1989; Waage 1990). Biocontrol therefore differs from natural control because specialist natural enemies, usually parasitoids, are released in an exotic location where the natural enemy complex associated with the pest is likely to be highly simplified. In native habitats on the other hand, predation by generalist species often appears to be more important in natural control. These differences illustrate what has been

referred to as the ‘unnatural nature’ of biological control (Hawkins *et al.* 1999). The selection of appropriate natural enemies is however, just the beginning of a sequence of activities that provide the overall framework for the implementation of classical biocontrol (Table 6.2). This framework has been developed since the first astonishingly successful attempt at biological control in the modern era with the release, over 100 years ago, of the Australian vedalia beetle, *Rodolia cardinalis*, against the cottony cushion scale, *Icerya purchasi*, in Californian citrus orchards (Caltagirone and Doult 1989).

The sequence of activities outlined in Table 6.2, and considered in more detail in the following sections, is designed to optimise the chances of finding and evaluating candidate natural enemies while minimising the risk of unintended ecological effects.

*Evaluation of pest in target region*

Study of the pest in the target region should ensure that it has been correctly identified and should also help to locate the likely area of origin. Possible pathways through which pests entered the region may then be identified, allowing plant quarantine measures to be reviewed and strengthened where necessary. Information on the impact and spread of the pest and possible effects of natural enemies native to the target region may be of value in selecting appropriate natural enemies for introduction.

*Exploration in pest area of origin*

The natural enemies normally associated with a pest will be influenced by a number of factors including the particular location within a possibly extensive range. Natural enemy communities tend to be more diverse in the centre of distribution of

**Table 6.2** The main activities involved in the location and selection of natural enemies that provide the overall framework for the implementation of classical biocontrol

Activity	Key information and some selection criteria
<i>Evaluation of pest in target region</i>	Taxonomic identity Likely area of origin Ecology in exotic location Associated natural enemies
<i>Exploration in pest area of origin</i>	Composition of natural enemy community Degree of specialization Impact on pest
<i>Selection of appropriate biocontrol agent</i>	Theory and evidence from past releases Pre-introductory studies  <i>Reductionist</i> <i>Holistic</i> Searching efficiency              ‘Fit’ to pest ecology Seasonal synchrony              Collection in outbreak/non-outbreak areas Numerical response              Complementary action Development time
<i>Quarantine and rearing</i>	Ease of rearing Elimination of hyperparasitoids and pathogens
<i>Release</i>	Number of species, individuals and release sites Genetic variation
<i>Evaluation and monitoring</i>	Natural enemy establishment Impact on pest Pest population monitoring Impact on non-target organisms

Sources: Ehler (1990), Waage (1990), Waage and Mills (1992), van Driesche and Bellows (1993), Kidd and Jervis (1996), Mills (2000).

the insect host and of the tree species with which it is normally associated. For example, the European distribution of larch is centred on the Alps and in this region, the larch budmoth, *Zeiraphera diniana*, which defoliates larch and other conifers, is attacked by a greater range of parasitoids with higher levels of parasitism than occur in populations in Czechoslovakia and Scotland (Table 6.3).

The degree of specialisation of particular natural enemies can be determined from a search of the literature although in general, host ranges are poorly documented with relatively little information on the number of hosts utilised by particular species (Memmot and Godfray 1993; Shaw 1994). Screening tests to assess the host range of candidate natural enemies are therefore particularly important and

would normally include species closely related to the target pest (Sands 1997). Screening should also be done where possible in the field as well as the laboratory. Laboratory testing of host range effectively measures 'physiological' rather than 'ecological' host range, especially when no-choice tests are conducted. The predatory beetle, *Rhizophagus grandis*, feeds on a wide range of prey in the laboratory, but in the field, the response of the adults to kairomones of its bark beetle prey gives it a high degree of specificity (Box 9.5). The ecological host range measured in the field is likely to be much less extensive although 'ecological opportunity' as a result of new encounters in a novel environment can increase the risk of host range expansion (Louda *et al.* 2003). A good example of host range

**Table 6.3** Some of the parasitoids reared from *Zeiraphera diniana* and variation in apparent percentage of parasitism (i.e. the percentage of hosts killed by parasitoids estimated by rearing a sample of hosts) at several sites within the alpine region of Europe, and in Scotland and Czechoslovakia where the budmoths feed on different host trees

Parasitoid complex	Alps larch							C'slovakia spruce	Scotland pine	
	1	2	3	4	5	6	7	1	1	2
<b>Larval parasitoids</b>										
Ichneumonidae										
<i>Campoletis varians</i>	0	0	0.2	0.2	0	0	0	0	0	0
<i>Campoplex faunus</i>	0	0	0.4	0.4	0	0	0	0.1	0	0
<i>Campoplex rufinator</i>	0	0	0	0	0	0	0	<0.1	0	0
<i>Enytus montanus</i>	0	0.5	1.1	12.5	13.2	2.9	2.0	0	0	0
<i>Enytus apostatus</i>	0	0	0	0	0	0	0	0	0.6	0
<i>Nythobia dinianator</i>	0	0	0	0	0	0	0.3	0.2	0	0
Braconidae										
<i>Charmon extensor</i>	0	0.2	0	0	0	0	0.1	0	0	0
<b>Larval-pupal parasitoid</b>										
Ichneumonidae										
<i>Triclistus podagricus</i>	3.4	0	0	1.0	11.4	1.5	0.4	14.5	0.9	0
<b>Late larval endoparasitoids</b>										
Tachinidae										
<i>Actia maksymovi</i>	1.1	0.5	0	0	0	0	2.5	0	0	0
<i>Elodia morio</i>	0	0	0	0.4	0	0	16.0	1.0	0	0
<i>Lyphia dubia</i>	16.6	2.3	7.0	0.9	0	22.6	0	0	0	0
<i>Nemorilla maculosa</i>	0	0.5	3.5	11.3	0.1	0	2.5	0	0	0
<i>Platymya mitis</i>	0	0	0	0.1	0	0	0.1	0	0	0
<b>Larval-cocoon parasitoid</b>										
Ichneumonidae										
<i>Phytodietus griseanae</i>	6.2	1.6	1.5	19.4	35.1	47.6	4.9	2.7	32.5	28.6

Note: Collections of 275–2448 larval hosts at each site were made between 1982 and 1986.

Source: Data from Mills (1993).

testing is provided by studies of the fungal pathogen, *Entomophaga maimaiga*, which causes epizootics in larval populations of the gypsy moth, *Lymantria dispar* (Box 6.1). In laboratory tests of a number of species of Lepidoptera, about 30% of them became infected whereas in the field, the ability of the fungus to cause disease appeared to be very much more restricted (Hajek *et al.* 1995a, 2000). While the more liberal laboratory estimates of host range provide an inbuilt 'safety factor', there is a danger that reliance on such tests may exclude effective and 'safe' natural enemies from biocontrol programmes.

The importance of particular species within the natural enemy community is often determined by their relative abundance and apparent impact on the host population but interactions between natural enemies can sometimes obscure these relationships. In a programme of biocontrol of the pine shoot moth, *Rhyacionia buoliana*, in Canada, four of the most abundant parasitoids were introduced from Europe between 1928 and 1967. Subsequent studies showed that some of those introduced were cleptoparasitoids, attacking shoot moth larvae already parasitised by *Orgilus obscurator* (Table 6.4). This braconid was most effective for biocontrol but in Canada, *Temelucha interruptor* can cause up to 50% mortality of this parasitoid, reducing its effectiveness in the field.

**Table 6.4** Parasitism of *Rhyacionia buoliana* in northern Germany

Larval parasitoid species	Hosts attacked (%) Dissection	Apparent parasitism (%) Emergence
<i>Lypha dubia</i> <sup>a</sup>	7	23
<i>Orgilus obscurator</i> <sup>b</sup>	37	5
<i>Pristomerus vulnerator</i> <sup>c</sup>	19	4
<i>Sinophorus rufifemur</i> <sup>c</sup>	7	5
<i>Temelucha interruptor</i> <sup>c</sup>	25	21

Notes: <sup>a</sup> Tachinidae. <sup>b</sup> Braconidae. <sup>c</sup> Ichneumonidae.

Dissection of host larvae to determine the percentage of hosts attacked by each parasitoid (marginal attack rate) revealed that the braconid *O. obscurator* was more effective than other species in locating and attacking hosts. However, assessing parasitism at emergence (apparent parasitism) showed that three ichneumonid species were facultative cleptoparasitoids that preferentially attacked host larvae already parasitised by *O. obscurator*.

Source: Waage and Mills (1992) and references therein.

A detailed understanding of the ecology of natural enemies is clearly important for the identification of possible deleterious interactions between natural enemies and for assessing the risk to non-target species in the release areas.

Details of the techniques used to assess the impact of natural enemies on insect populations are reviewed by Kidd and Jervis (1996) and Mills (1997). There are obvious logistic constraints on the number of parasitoids that can be collected to assess potential biocontrol agents so that systematic pre-introductory studies of the whole community of natural enemies is rarely if ever possible. Experience and judgement often play an important part in narrowing down the selection to one or a few promising candidates (Waage 1990). Long-term population studies are often ruled out because of the urgent need to restrict spread and prevent damage by newly discovered pests. Where such studies have been done, they illustrate the difficulties of accurately predicting the impact of natural enemies on the pest in an exotic habitat (Box 6.4.)

#### *Selection of appropriate biocontrol agent*

The criteria for selecting specific biocontrol agents have been categorised as 'reductionist' and 'holistic' although in practice, both approaches to selection can help in the identification of potential biocontrol agents (Waage 1990). Reductionist criteria are strongly influenced by characteristics, largely identified in predator-prey models, that reflect the ability of natural enemies to respond to changes in host abundance, to reduce pest population density, and to maintain it at low and stable levels. Important characteristics include searching efficiency, aggregation in areas of high host density, and fecundity. In practice however, these traits can be difficult to measure in the field and tend to be considered in isolation, whereas it is the interaction between these and other factors that determine the effectiveness of natural enemies in real ecological settings.

In an holistic approach to selection, the choice of species is influenced by their relationship to other natural enemies that may already be present in the target region or to those which are intended for release at the same time. In multiple releases, it is obviously important to minimise competitive

**Table 6.5** Parasitoids associated with low or high population densities of their hosts among important defoliators of forest trees

Host	Parasitoid		Reference
	Low host density	High host density	
<i>Operophtera brumata</i>	<i>Agrypon flaveolatum</i>	<i>Cyzenis albicans</i>	Embree (1966)
<i>Zeiraphera diniana</i>	<i>Sympeisis punctifrons</i>	<i>Phytodietus griseanae</i>	Delucchi (1982)
<i>Choristoneura fumiferana</i>	<i>Synetaeris tenuifemur</i>	<i>Apanteles fumiferanae</i>	Miller and Renault (1976)
<i>Neodiprion sertifer</i>	<i>Lophyproplectus luteator</i>	<i>Lamachus eques</i>	Pschorn-Walcher (1973)
<i>Neodiprion swainei</i>	Larval parasitoids	Cocoon parasitoids	Price (1973)

Source: Mills (1990a).

interaction between species as shown by the example in Table 6.4. In low density populations, natural enemies may be relatively rare and difficult to collect but they may be important in maintaining the pest at endemic levels (Pschorn-Walcher 1977). These natural enemies can therefore complement the action of those that are more abundant during pest outbreaks and which may be important in population reduction. Parasitoids characteristic of high and low density populations of some Lepidoptera and sawflies are shown in Table 6.5.

#### *Quarantine and rearing*

Natural enemies must be laboratory reared to ensure sufficient numbers for release, to eliminate hyperparasitoids and pathogens, and also to ensure synchrony with the pest population in the target region prior to release (Fisher and Andrés 1999). Ease of rearing can therefore impose practical constraints on the selection of natural enemies. When rearing natural enemies, is important that the starting population is large enough to avoid problems of limited genetic variability and that inadvertent selection in the laboratory does not alter natural enemy performance as discussed by Hopper *et al.* (1993). Couillien and Grégoire (1994) used take-off capacity as an index of quality of the predator *R. grandis*, prior to release for control of the spruce bark beetle, *Dendroctonus micans*, in France.

#### *Release*

A long-running debate in biocontrol theory and practice concerns the number of species that should be released (Myers *et al.* 1989). Releasing a small

number of species in multiple introductions avoids the problem of trying to select the 'best' agent for single release while still being relatively efficient in terms of collection, quarantine, culturing and release (Waage and Mills 1992). The release of several different 'strains' of a natural enemy collected from different geographical populations in order to increase genetic diversity does not appear to increase the chances of success (Clarke and Walter 1995).

The actual number of individuals released into the field will depend on a number of factors including the success of the breeding programme and the effectiveness of host-finding mechanisms in the natural enemies. Releasing too few individuals however, can reduce establishment success because mate location is less likely in low density populations, driving the population to extinction through the so called 'Allee effect' and in addition, small numbers limit genetic variability in the population (Allee 1931; Hopper and Roush 1993; Hopper *et al.* 1993).

#### *Evaluation and monitoring*

In obviously successful programmes, there may be little incentive or funding for follow-up studies. As a result, assessing the impact of released natural enemies is often limited in scope and does not usually include effects on non-target species. Post-release studies of selected non-targets would help in the early detection of adverse effects and so prevent further releases of the same natural enemies in other areas. Partial success in biocontrol can be difficult to quantify but detailed evaluation may

provide information that will be useful in the selection and release of different species.

### 6.2.2 Risk and regulation

The release and establishment of exotic natural enemies is an irreversible process and so an important aim of the selection procedures outlined in the previous sections is to minimise the risk of effects on non-target populations. Taken as a whole, biological control has a good safety record. But increasing understanding of the complex dynamic interactions between and within trophic levels, and wider

concerns about the environment and biodiversity, has brought the issue of the possible risks involved in biocontrol under closer scrutiny. Ironically, the notable successes in biocontrol and the perception that it is environmentally benign has made risk assessment more urgent because of the possibility that it will be more widely used in countries with little experience of its application. Continuing widespread acceptance of classical biocontrol as a method uniquely suited to combat alien pests depends on avoiding catastrophic unintended effects on the environment and on non-target organisms. The question of risk has been the subject

#### Box 6.3 Larch casebearer, *Coleophora laricella*

This European moth was first recorded in Massachusetts in eastern United States in the 1880s but spread westwards from there, appearing in Idaho in the late 1950s. This was followed by rapid spread through the larch of the intermountain regions of eastern Washington, Oregon, and northern Idaho. In the western regions, adults emerge in early summer and females oviposit in June–July. Young larvae mine within the larch needles but the second to third instars, which are too big to remain inside needles, construct a protective case of pieces of needle epidermis connected by silk. The third instars overwinter on twigs and in the spring, the fourth and final instar feeds on newly expanding needles. Successive defoliation caused by spring feeding larvae can have a significant impact on the growth of trees and some trees may be killed.

In the 1930s, both the US and Canadian governments independently imported several parasitoids from Europe for release against the eastern population, with apparent success following from the establishment of two of these, *Agathis pumila* and *Chrysocharis laricinellae*. In an attempt to repeat this success *A. pumila* was introduced into Idaho in 1960 and subsequently to other regions. This braconid attacks the needle mining first and second instars and has one generation per year (Fig. 6.7). The eulophid *C. laricinellae* was released some years later along with other species. In contrast to *A. pumila*, this parasitoid is not host-specific, attacks casebearing rather than needle mining stages and has 2–3 generations per year.

Typically, following release of parasitoids, levels of parasitism in casebearer populations remained relatively low for several years before gradually increasing. Because *A. pumila* disperses more slowly than its host, more rapid spread was promoted in some areas by field breeding of

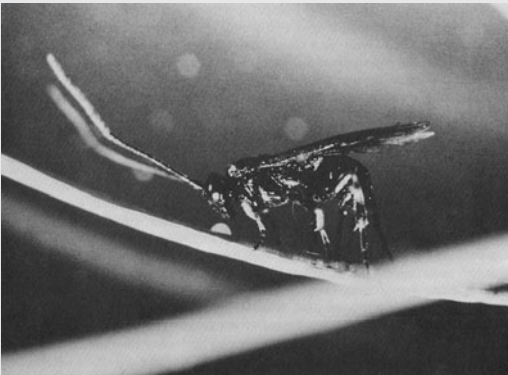
the parasitoid and release at many different sites (Fig. 6.8). Decline of casebearer populations appeared to be due largely to parasitism by *A. pumila*.

It was difficult to maintain control plots in this study so the main estimate of parasitoid impact was made in 'before' and 'after' assessments. Results from a number of study sites were combined and the effects of progressive spread of the parasitoid allowed for by synchronising populations into a 'before' and 'after' period depending on the levels of parasitism (Fig. 6.9). After a 5 year period of increasing parasitism, mean levels of parasitism fluctuated around 40–60% with pest density reduced to 1–2 per 100 buds. In northern Idaho, the impact of casebearer outbreaks and the subsequent success of biocontrol was reflected in the growth of larch close to the site of the initial discovery of the pest in the late 1950s (Fig. 6.10).

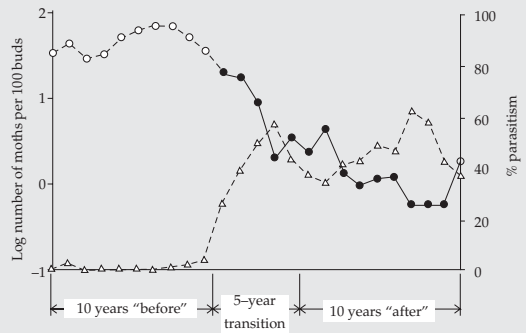
The actual mechanism of biocontrol is uncertain. Although delayed density-dependent responses to casebearer populations have been observed at some sites, in many others *A. pumila* appears not to respond in this way. Dense populations of larch casebearer are not utilised effectively by the braconid and the defoliator seems ultimately to be food-limited. *Agathis pumila* is however extremely effective at finding larvae in low density populations where most of them appear to be parasitised. Because *Coleophora laricella* is not an eruptive pest, natural enemies seem able to maintain it at low population density. There was no evidence of the competitive replacement of *A. pumila* by *C. laricinellae* which, like the more than thirty native parasitoids that attack larch casebearer, appear to be relatively unimportant in its population dynamics.

Key references: Long (1988, 1990), Ryan *et al.* (1987), Ryan (1990, 1997).

Box 6.3 Continued



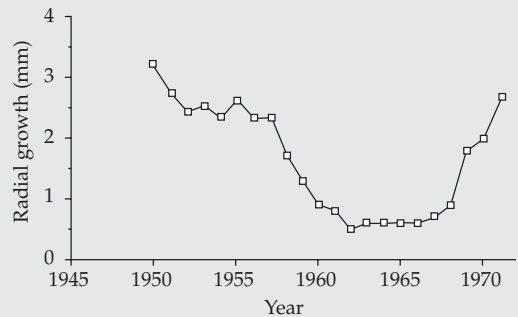
**Figure 6.7** *Agathis pumila* ovipositing through the epidermis of a larch needle into a young needle-mining larva of *Coleophora laricella* (from Long 1988).



**Figure 6.9** Mean density of *Coleophora laricella* before (○) and after (●) parasitism by *Agathis pumila* (△) in 13 long-term research plots in Oregon and Washington, USA between 1972 and 1995. The 'before' period corresponds to parasitism levels of <10% (from Ryan 1997).



**Figure 6.8** Cloth cages enclosing larch trees infested with *Coleophora laricella*. *Agathis pumila* was released into the cages and branches bearing parasitised larvae subsequently transferred to other locations in Idaho and Montana, USA, to promote spread of the parasitoid (from Ryan *et al.* 1987).



**Figure 6.10** Radial growth of larch trees in part of northern Idaho affected by *Coleophora laricella* defoliation. Growth declined in the late 1950s following discovery of casebearer populations while that of non-host trees in the area did not. Parasitism by *Agathis pumila*, first released around 1960, reached 67% by 1968. Growth increased following decline of *C. laricella* populations (from Long 1988).

of a number of reviews which should be consulted for detailed discussion of the subject (Louda *et al.* 2003 and references therein).

The principal risk of classical biocontrol is that released natural enemies may attack non-target

organisms either through host switching (attacking more common hosts), extension of the host range (attacking new species as well as the main host), or possibly by host shifting (attacking a new preferred host). Hawkins and Marino (1997) provided

evidence for such effects in a study of exotic parasitoids released in North America. They found that about 16% of over 300 parasitoids released had been recorded from native species. However measuring the impact on, rather than the utilisation of non-target organisms in native communities is much more difficult. Strong circumstantial evidence for such effects comes from studies on native silk moths which are in decline in north-eastern North America. The generalist tachinid fly, *Compsilura coccinata*, which is of European origin,

has been released against different introduced Lepidoptera over a period spanning 80 years. The main target of releases was the gypsy moth, *L. dispar*, and the brown-tail moth, *Euproctis chrysorrhoea*. It was inevitable that there would be some utilisation of non-target hosts by this parasitoid following establishment because *L. dispar* has only one generation per year whereas *C. coccinata* has three to four. The scale of impact was demonstrated when experimental populations of silkmoth larvae, exposed in the natural environment, suffered high

#### Box 6.4 Winter moth, *Operophtera brumata*

This polyphagous defoliator is well known as the subject of a detailed study of population dynamics on oak trees in Wytham wood in Oxfordshire, England. In western Europe, populations are cyclic with a period of approximately 9–10 years, with peaks coincident in different countries (Fig. 6.11). No long-term census data are available from oak forests in eastern Canada where this insect was first introduced but in apple orchards in Nova Scotia, there is some evidence of a 7–8-year cycle that is not in synchrony with the cycles of European populations.

In Europe, adults emerge from the soil in November–December. The flightless females climb the trunks of nearby trees and release a sex pheromone to attract males. Eggs are deposited in the tree canopy in crevices of bark and lichen and after overwintering hatch in the spring, usually in synchrony with bud burst. Larval development is completed by early summer when larvae spin down from trees on silk and pupate in the soil.

In the study of *O. brumata* in Wytham Wood, density-dependent predation of pupae in the soil by generalist predators (carabid and staphylinid beetles) proved to be an important factor in population dynamics. Parasitoids, including those subsequently introduced into Canada, appeared to be relatively unimportant, typically accounting for less than 10% of mortality. In the successful biocontrol programme in Canada, several parasitoid species rather than generalist predators were released, including the tachinid fly, *Cyzenis albicans*, and the ichneumonid, *Agrypon flaveolatum* which were commonly found during collections in Germany and France (Table 6.6). These parasitoids attack older larvae and kill the pupal stage in the soil. *C. albicans* has the ability to concentrate attacks on oaks damaged by the feeding activity of *O. brumata*

larvae. Although the mechanisms of biocontrol are not fully understood, subsequent research has revealed the dynamic interactions that have contributed to control in Nova Scotia and British Columbia and allowed comparison with the dynamics of natural populations from Europe.

Following release of parasitoids in outbreak areas, *O. brumata* populations usually declined after 4–5 years, the delay corresponding to the time taken for parasitism to exceed 30%. Parasitism typically rose to 70–80% and parasitoids were probably the main cause of population decline although native generalist predators also caused high levels of mortality. In some populations, parasitism and predation appeared to act synergistically.

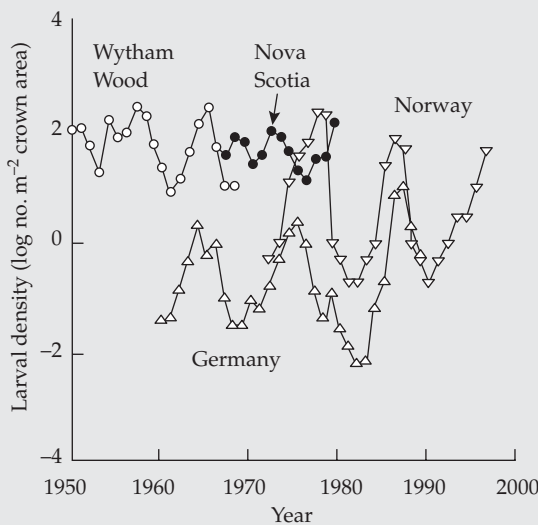
The parasitoids seem to have been effective in biocontrol by adding mortality to *O. brumata* populations. Density-dependent predation, which often exceeds 90% of unparasitised pupae, appears to be the main factor regulating populations once they have been reduced to relatively low densities by the introduced parasitoids. Predators attack some parasitised pupae but prefer unparasitised ones and so their action complements that of parasitoids. Parasitised pupae remain in the soil for an extended period, after emergence of healthy ones, and may benefit predators by increasing prey availability during winter and early spring.

Winter moth populations on oaks in Canada reflect two important aspects of biocontrol, the suppression of outbreaks and the maintenance of populations at low density. This was achieved by two introduced parasitoids, whose relative importance varied in different parts of the country, and by native generalist predators.

Key references: Embree (1991), Hunter *et al.* (1997), Roland and Embree (1995), Roland (1998), Varley and Gradwell (1968).



## Box 6.4 Continued



**Figure 6.11** Cyclic changes in abundance of *Operophtera brumata* in England, Norway, Germany and Nova Scotia (from Roland 1998).

**Table 6.6** Releases of *Cyzenis albicans* and *Agrypion flaveolatum* for biological control of *Operophtera brumata* in Canada

Parasitoid	Main area of collection	Period of releases	Total release area (km <sup>2</sup> )	Number of sites	Mean adults per site
Nova Scotia					
<i>C. albicans</i>	France/Germany	1954–65	10 000	16	1860
<i>A. flaveolatum</i>	France/Germany	1956–62	6000	9	330
British Columbia					
<i>C. albicans</i>	Nova Scotia	1979–81	500	25	240
<i>A. flaveolatum</i>	Nova Scotia	1979–81	500	33	145

Source: Data from Roland and Embree (1995).

levels of mortality caused by *C. coccinata*. This generalist parasitoid seems likely to be a major contributor to the decline of silkworm populations in North America (Boettner *et al.* 2000).

The risk of non-target effects can be minimised by limiting introductions to species with very restricted host ranges and which do not appear to show switches in host preference. These include specialist arthropod predators such as Coccinellidae, predatory mites, insect parasitoids, certain specialised parasitic nematodes, and some pathogenic microorganisms (Greathead 1995). It is also important to minimise the risk of 'private' introductions

and this can be most readily done by appropriate regulation (Simberloff and Stiling 1996; Samways 1997; Waage 1997). The recently published FAO code of conduct provides international guidelines on the introduction of exotic natural enemies. The code is observed through collaboration between governments, international organisations, research institutes, traders, users, environmental groups, and by periodic review and updating by FAO. The objective is to facilitate the safe importation of exotic organisms for research and field releases for biological control. This is done by setting international standards in biocontrol procedures and

clearly outlining the shared responsibilities of all participants so as to minimise the risk of adverse effects. Many of the concerns about exotic pests outlined in Chapter 2 such as, their identity, spread, and possible movement between countries also apply to exotic natural enemies and so it is appropriate that National Plant Protection Organisations are increasingly involved in the regulation of introductions for biocontrol. The main areas of responsibility for those involved in biological control, and codified by FAO are outlined in Table 6.7. To a large extent, the level of acceptable risk must be determined by the importing country and set both in the socioeconomic context and the risks associated with alternative control strategies.

### 6.2.3 Case studies in classical biological control

Two of the best examples of classical biocontrol of forest pests that emphasise both its unpredictability

and the value of detailed and extended retrospective studies are provided by larch casebearer, *Coleophora laricella*, in the United States (Box 6.3) and winter moth, *Operophtera brumata*, in Canada (Box 6.4).

## 6.3 Economic aspects

In general, classical biological control programmes conducted in one or only a few areas and achieving long-term control do not attract commercial interest and are usually publicly funded (Greathead 1995). The economic and environmental benefits of successful biocontrol are potentially very large, with savings in control and associated operations accruing year by year. In addition, successful programmes developed in one region can provide the basis for control of the same pest introduced into a new region, allowing savings in some of the research and development costs (Greathead 1995). Two examples of such 'added value' are the control of the European woodwasp,

**Table 6.7** The FAO code of conduct for the import and release of exotic biological control agents defines the responsibilities of the various participants

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#### Authorities Prior to import

##### Importing country

- legislative and regulatory issues especially in relation to species identification and the evaluation and documentation of risk
- identify and liaise with participants and authorities in both neighbouring and exporting countries and disseminate information
- evaluate dossiers on target pest and proposed biocontrol agent

##### Exporting country

- comply with regulations of importing country as well as code on export

#### Upon import

- ensure transfer to, and where necessary culture in, quarantine facilities

#### Before and upon release

- appropriate pre-release Pest Risk Analysis
- full documentation e.g. identity, origin, voucher specimens

#### Importer Prior to import

- dossier on associated natural enemies of target pest to include accurate identification and information on ecology, host specificity and their own natural enemies
- risk assessment including non-target organisms and the environment

#### After import and release

- ensure use of trained personnel
- public availability of information on safety etc.
- notification of problems and corrective action where necessary

#### Exporter Prior to export

- comply with FAO and other regulations and provide documentation in relation to, among other things, safety of biopesticides and other agents, labelling and packaging
- 

Note: The main areas of responsibility are outlined but for a full listing and discussion, see FAO (1996a,b, 1997) and Kairo *et al.* (2003).

*Sirex noctilio*, with nematodes in South America using methods developed in Australia (Box 9.6), and the control of the eucalyptus snout beetle, *Gonipterus scutellatus*, on eucalypts in several regions of the world using the egg parasitoid, *Anaphes nitens* (Hanks *et al.* 2000).

Estimating the actual economic benefits of biocontrol is difficult because both direct and indirect effects are likely to be involved and some success may be only partial. Indirect environmental benefits such as avoiding insecticide use or improving the quality of the environment are difficult to quantify although Pickett *et al.* (1996) were able to devise a way of estimating the aesthetic benefit of biocontrol of the ash whitefly, *Siphoninus phillyreae*,

in an 'urban' forest in California. Where economic appraisals have been done, they tend to indicate highly favourable benefit : cost ratios (Table 6.8).

**Table 6.8** Estimated benefit: cost ratios for biocontrol of some forest pests

Pest	Country	Benefit : cost ratio	Reference
<i>Operophtera brumata</i>	Canada	15 : 1	Hill and Greathead (2000)
<i>Gilpinia hercyniae</i>	Canada	19 : 1	Hill and Greathead (2000)
<i>Sirex noctilio</i>	Australia	2 : 1	Hill and Greathead (2000)
<i>Sirex noctilio</i>	Australia	69 : 1	Cullen and Whitten (1995)

Note: In cost-benefit analysis, all studies used a 10% discount rate but the period of discounting varied from 14 to 40 years.

# Microbial control

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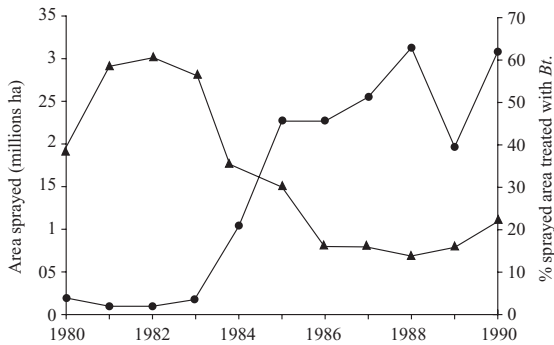
Microorganisms that cause disease in insect herbivores are sometimes considered within the context of biological control and they can in principle be used in broadly similar ways to predators and parasitoids. So, for example, introduced exotic diseases could be used to control introduced pests in a classical biocontrol strategy and native ones used for inoculative or inundative releases or conserved through appropriate management. In practice, microorganisms have only rarely been used in classical biocontrol but one notable success followed the accidental introduction of a virus disease against the European spruce sawfly, *Gilpinia hercyniae*, in North America. The sawfly had become well established in Canada and the United States by the early 1900s. Parasitoids from Sweden were introduced during the 1930s as part of a biocontrol programme and some of them appear to have been contaminated by a nucleopolyhedrovirus (NPV). The virus became established in the sawfly population and was spectacularly successful in controlling this introduced pest (Balch and Bird 1944; Cunningham and Entwistle 1981). Two more recent examples of classical biocontrol are the use of the fungus *Entomophaga maimaiga* against the gypsy moth, *Lymantria dispar*, in eastern United States (Box 6.1) and the nematode *Beddingia* (= *Deladenus*) *siricidicola* to control *Sirex noctilio* in Australasia (Box 9.6).

Inoculative releases and conservation could be of value in pest management for those native pathogens that are self-sustaining within the pest population and which can persist in the environment (Fuxa 1998). But not all microorganisms cause natural epizootics and often not enough is known about their ecology to manipulate the habitat or modify forest management practices so

as to enhance natural levels of pathogen-induced mortality. Inundative releases on the other hand, dominate the practical application of microorganisms. They are in effect used as microbial pesticides where the main aim is to achieve a high kill relatively quickly, so high pathogenicity is more important than an ability to replicate and spread within the population. The formulation and application of microorganisms as microbial insecticides are sufficiently distinctive from the use of natural enemies in biological control to warrant separate consideration. Although most of the discussion in this chapter focuses on the control of insect pests, important examples of the control of fungal pathogens of trees by other fungi are also briefly considered.

The main organisms identified with microbial control of insects are predominantly the bacterium, *Bacillus thuringiensis* (*Bt*), NPVs, entomopathogenic fungi and nematodes. Nematodes are usually considered together with microorganisms in part because the host is killed not by the nematode itself but by a specific bacterium associated with it. These very different kinds of microorganisms vary in the way they infect the host, the extent of mortality they cause in populations and their natural distribution and abundance. They also have different host ranges, varying from highly specific viruses to entomopathogenic fungi, some of which have a very wide host range. These distinctive ecological characteristics largely determine the way in which microorganisms are or could be used in practice.

In forestry there is often no clearly defined economic damage threshold. The amount and timing of damage reduction during pest outbreaks is therefore often less critical than that in high



**Figure 7.1** Total area sprayed against *Choristoneura fumiferana* in Canada (▲). In the early 1980s, this control was mostly with the insecticides fenitrothion or aminocarb. Since then, the area sprayed annually has declined but the proportion treated with *Bt* (●) has increased considerably (from Cunningham and van Frankenhuyzen 1991).

value agricultural crops. In the control of some defoliators, for example, the broad aim may simply be to prevent >50% defoliation (van Frankenhuyzen *et al.* 2000a). Forests are also in general less sensitive to the higher levels of unpredictability in the level of control associated with the use of microbial insecticides. Yet despite these favourable characteristics, microorganisms have made only a small overall contribution to the management of forest pests. This arises partly from limitations of the organisms themselves such as their sensitivity to environmental conditions (UV light, humidity and temperature) or their particular host range. But economic factors are also important, often illustrated by reference to the 'microbial control paradox' (Federici 1999a). This arises because the advantages that microbial agents have over chemical insecticides such as their relatively narrow spectrum of activity and limited residual effects, restrict commercial exploitation within a market where development costs are high relative to likely sales. That market is currently dominated by *Bt*. The increasing use and effectiveness of *Bt* in replacing chemical insecticides to control major forest defoliators in North America is largely due to research and development effort in Canada (Fig. 7.1). This effort followed on from the first aerial trials in 1960 against black-headed budworm,

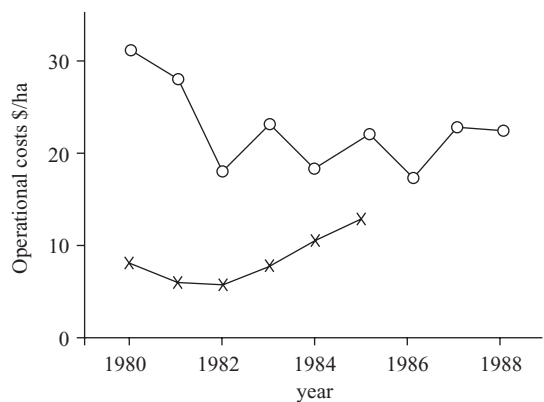
*Acleris gloverana*, in British Columbia and spruce budworm, *Choristoneura fumiferana*, in New Brunswick (Cunningham and van Frankenhuyzen 1991). The history of the development of *Bt* as a microbial insecticide is discussed by Beegle and Yamamoto (1992).

The success of *Bt* was not due to any natural superiority over chemical insecticides but to a combination of biological, economic and sociopolitical factors. In a climate of increasing restrictions on the use of chemical insecticides, *Bt* is perceived as safe, is relatively easy to culture *in vitro*, can be used against more than one pest within susceptible groups and there are no undue restrictions on registration. Cost-effectiveness is also a key element and this has gradually increased as shown by comparison of the relative costs of *Bt* and insecticides in Quebec (Fig. 7.2).

## 7.1 Characteristics and ecology of microbial agents

### 7.1.1 *Bacillus thuringiensis*

*Bacillus thuringiensis* (*Bt*) is a Gram-positive, rod-shaped bacterium that has a worldwide distribution and yet, despite this widespread occurrence, *Bt* does not appear to cause natural epizootics in forest insect populations. The bacterium has been



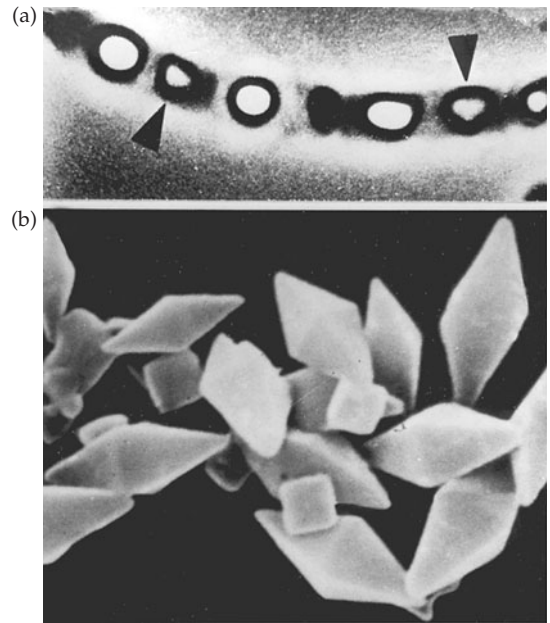
**Figure 7.2** Relative costs of applying chemical insecticide (x) and *Bt* (o) in Quebec, Canada during a period of rapid development of *Bt* as a microbial insecticide and increasing restrictions on the use of chemicals (data from van Frankenhuyzen 1990).

found to occur naturally on the leaves of both deciduous and conifer trees but the principal reservoir is in the soil (Smith and Couche 1991; Damgaard 2000). Its role in the ecology of soil biota is not well understood but much more is known about *Bt* as a facultative pathogen. The ecology and characteristics of *Bt* have been thoroughly reviewed (Entwistle *et al.* 1993a; van Frankenhuyzen 1993; Federici 1999a,b; Hall and Menn 1999; Charles *et al.* 2000).

A key feature of the relatively simple life cycle is that, when conditions no longer support vegetative growth, the bacterium forms a dormant spore stage that can remain viable during periods of environmental stress. During sporulation, a parasporal body is formed that typically consists of 'Cry' proteins. These proteins belong predominantly to a class of proteinaceous crystal toxins called  $\delta$ -endotoxins and are released into the environment together with the spores when the bacterial cell wall breaks down (Fig. 7.3). When the Cry protein is ingested by a susceptible insect larva, the toxins are activated by enzymes within the alkaline conditions of the insect gut and they then bind to and cause lysis of midgut cells. Affected larvae stop feeding and those that have ingested a lethal dose die after several days.

*Bacillus thuringiensis* is in fact a complex of many different subspecies and strains. Different pathotypes of the  $\delta$ -endotoxin determine activity against different insect groups as well as the spectrum of activity within them. Activity is difficult to predict from detailed knowledge of the Cry proteins present, but broad categories of insecticidal activity are recognised based on the size and pathotype of the proteins (Federici 1999b). Most isolates are toxic to Lepidoptera (Cry 1 and 2) but some have been identified that are active against Coleoptera (Cry 3) and Diptera (Cry 4). The formation of Cry proteins is controlled by *cry* genes located mainly on large plasmids, many of which have been identified (Crickmore 2000). Some of these genes have been cloned and engineered not only into *Bt* itself, to alter its pathogenicity, but also into plants where expression of the *cry* gene reduces feeding by insect pests (Jenkins 1999).

For control of forest Lepidoptera, *B. thuringiensis* subsp. *kurstaki*, in particular the HD-1 isolate (named after the discoverer, Howard Dulmage), is



**Figure 7.3** (a) Sporulating cells of *Bacillus thuringiensis* subsp. *kurstaki* (*Bt*) observed under phase-contrast light microscopy to reveal the parasporal bodies (arrows) that contain the insecticidal proteins. (b) The parasporal body of the HD-1 isolate highly enlarged by scanning electron microscopy. The bipyramidal crystal contains CryIA proteins a, b, and c and the cuboidal crystals the single protein CryIIA. Crystals make up approximately 25% of the dry weight of sporulating *Bt* (from Federici and Maddox 1996).

the most important and is used almost exclusively in control programmes (Dulmage 1970). This highly active strain has a relatively broad spectrum of activity against Lepidoptera that arises from the fact that there are four Cry proteins in the parasporal body (Fig. 7.3). Other components of the parasporal body affect the toxicity of the proteins in the HD-1 strain and the spore itself synergises the action of the Cry proteins and so is included in some commercial formulations of *Bt*. An important advantage in the commercial development of *Bt* is that it can be readily mass-produced *in vitro* (Couch 2000).

### 7.1.2 Viruses

Viruses belonging to several different families are known to infect insects but the Baculoviridae exclusively infect arthropods. The family comprises two

genera, the nucleopolyhedrovirus (NPV) and granulovirus. From the point of view of microbial control, NPVs are by far the most important group. The biological characteristics of viruses and their potential as microbial insecticides have been exhaustively reviewed (Cunningham 1995; Hunter-Fujita *et al.* 1998; Federici 1999c; Hall and Menn 1999; Moscardi 1999).

Nucleopolyhedroviruses are DNA viruses with rod-shaped virions enclosed within polyhedra. These polyhedra or occlusion bodies are made of protein crystals and under certain circumstances allow the virus to survive in the external environment for extended periods. Their hosts are predominantly larvae of Lepidoptera and Hymenoptera (sawflies). Most viruses have a relatively narrow host range and some, such as those infecting Lymantriidae are host specific (Cory and Myers 2003). In Lepidoptera, polyhedra that are ingested by larvae dissolve in the midgut, releasing the virus particles that initially invade the mid-gut cells and replicate in the nuclei before invading susceptible tissues in other parts of the body. New occlusion bodies are released into the environment by the breakdown of the infected larva after death (Fig. 7.4). In sawfly larvae however, infection is largely confined to the mid-gut epithelium. One consequence of this is that virus can be passed into the environment before larvae are killed, usually in faeces but also during defensive regurgitation to deter natural enemies.

Unlike *Bt*, viruses are able to cause natural epizootics that can result in the collapse of outbreaks.

Although many species of Lepidoptera and Hymenoptera can be infected by viruses, epizootics are however relatively infrequent in their populations. Epizootics are most commonly observed in the families Lymantriidae (*Lymantria* spp., *Orgyia* spp.), Lasiocampidae (*Malacosoma* spp.), and Diprionidae (*Neodiprion* spp.) and in these species, spraying populations with virus may have the best chance of controlling populations through initiation of epizootics. The initiation of epizootics is in part due to the ability of viruses to cause secondary infection and to spread through the population of a single generation ('horizontal' transmission) and for transmission to occur from adults to their offspring, that is, from generation to generation ('vertical' transmission). Spread within and between populations can occur in a number of ways, but depends on the ability of the virus to persist in the environment, in particular on plant surfaces and in the soil. Larvae of some Lepidoptera like the gypsy moth, *Lymantria dispar*, can disperse on silken threads in early instars, contributing to virus spread at an early stage. Virus can also be spread over large distances by birds which can excrete it in their faeces after feeding on diseased larvae (Entwistle *et al.* 1993b). Invertebrate natural enemies and adult sawflies can also be contaminated and so contribute to virus spread. Horizontal spread through the population can be particularly rapid in sawflies, especially in species where larvae feed gregariously, because virus contamination of foliage by infected larvae occurs much earlier than in populations of Lepidoptera. Rainfall can be an



**Figure 7.4** Larva of *Panolis flammea* killed by NPV. Polyhedral inclusion bodies are released when the larval integument ruptures. (Photo by H.F. Evans).

important abiotic cause of spread by washing virus on to leaves in the lower canopy and eventually into the soil. Soil is therefore an important reservoir for virus and in this protected environment, it can persist for several years (Thompson *et al.* 1981). Vertical transmission can occur through contamination of eggs although its relative importance varies for different species (Myers *et al.* 2000; Cory 2003).

All microorganisms are sensitive to environmental conditions and viruses are no exception. Viruses are particularly vulnerable to UV light and can be deactivated in a few hours to several days depending on the degree of sun exposed. In the architecturally complex forest environment however, survival of NPV can be higher in shaded parts of the tree canopy (Killick and Warden 1991).

There are currently two main disadvantages of virus as a microbial insecticides. Because host mortality depends on virus replication within the host, there is usually a delay between application and larval mortality, although this varies for particular hosts and viruses. In general however, speed of kill is influenced by the initial dose and temperature. The commercial preparation, Gypcheck, for example, kills larvae of *L. dispar* in 10–14 days compared to 3–5 days after application of *Bt* (Podgwaite 1999). A second disadvantage is the current high cost of *in vivo* production, a method that is restricted to those forest pests that can be reared continuously in the laboratory.

### 7.1.3 Nematodes

There are many families of nematodes that contain entomopathogenic species but only the rhabditid nematodes in the families Heterorhabditidae and Steinernematidae and the tylenchid nematode *Beddingia siricidicola* are currently of practical significance. Heterorhabditidae and Steinernematidae are obligate pathogens and many species and strains of these nematodes have been isolated from soils worldwide. They are able to parasitise a wide range of soil inhabiting insects when tested under laboratory conditions (Peters 1996). Their 'ecological' host range is however, likely to be much more restricted, being constrained by their limited dispersal ability and local availability of hosts. There is nevertheless, considerable variation in virulence

within nematode species and it is usual to specify the particular isolate or strain when working with nematodes (Barbercheck and Millar 2000). Selection of the optimal strain for target pests can therefore be an important part of the effective practical use of nematodes. Detailed discussion of the characteristics and ecology of entomopathogenic nematodes and their use or potential for microbial control can be found in Kaya and Gaugler (1993) Ehlers (1996), Grewal and Georgis (1999) and Koppenhöfer (2000).

Rhabditid nematodes have a relatively simple life cycle that has two important characteristics—the occurrence of a free-living non-feeding third stage larva in the soil referred to as an infective juvenile (IJ) or dauer larva (Fig. 7.5) and an association with highly specific symbiotic bacteria.

Different species of soil-inhabiting nematodes have different strategies for locating hosts (Lewis *et al.* 1992). Some rely on host movement and adopt a sit-and-wait or 'ambush' strategy and often occur near the soil surface. More active species have a search or 'cruiser' strategy and by moving throughout the soil profile can be effective in locating less mobile hosts. Juvenile stages of the nematode usually



**Figure 7.5** Infective juvenile or dauer larva of *Steinernema carpocapsae* (photo by U. Kölzer).



enter the insect body through the spiracles and other natural openings. Once inside the host, symbiotic bacteria carried within the gut are released, killing the insect through septicaemia usually within 2–4 days. The proliferating bacterial cells and degenerating host tissues provide food for the developing nematodes which reproduce within the host. As the food supply declines, IJs are again formed and are released back into the soil when the insect dies. Like other microorganisms, nematodes are relatively well protected in the soil environment but nevertheless are susceptible to environmental conditions. For example, IJs tend to be relatively ineffective at low temperatures (<10–15°C).

Nematodes do not appear to cause natural epizootics but mortality can be quite high in some cases. In some sawflies (*Cephalcia* spp.), for example, natural mortalities of up to 25% have been reported (Peters 1996). The general impact of nematodes on insect populations is however, largely unknown.

The simple life cycle of most entomopathogenic nematodes and their wide host range greatly facilitates their mass production and commercialisation (Grewal and Georgis 1999; Koppenhöfer 2000).

#### 7.1.4 Fungi

Many different kinds of fungi can kill insects, but most entomopathogenic fungi occur within two of the major divisions of true fungi, the Deuteromycotina and the Zygomycotina. The Deuteromycotina is an artificial grouping of fungi which are unable to reproduce sexually and are known as Fungi Imperfecti. Fungi in this group have affinities with the Ascomycotina and in some cases are thought to be fungi that have lost the capacity for sexual reproduction (Inglis *et al.* 2001). The Fungi Imperfecti includes entomopathogenic species such as, *Beauveria* spp., *Metarhizium* spp., and *Verticillium* spp. The Zygomycotina contains species such as *Entomophaga* spp. and *Entomophthora* spp. within the order Entomophthorales. A detailed discussion of the ecology of these fungal pathogens can be found in Hajek (1997) and in Butt *et al.* (2001).

Unlike most other microorganisms, entomopathogenic fungi usually initiate infection by penetrating the insect cuticle directly so that even insects

with sucking mouthparts such as aphids and scale insects that are not susceptible to *Bt* or viruses can be infected. Once inside the insect, vegetative growth in the haemocoel may be facilitated by the production of toxins and after death of the host, spores are produced for liberation into the environment. In the Fungi Imperfecti, these asexually produced spores known as conidia, are passively released from cadavers and can spread to a limited extent, infecting new hosts by contact. Survival during unfavourable conditions is mainly within mummified cadavers or as conidia but facultative pathogens are also able to grow as saprotrophs in the soil. Spores produced by fungi in the Entomophthorales can be actively ejected and this aids effective dispersal by the wind. These fungi can also form a distinctive sexual resting spore within the insect cadaver and this is the principal means of surviving adverse conditions as well as providing a reservoir in the soil that is important for vertical transmission.

Fungi usually have a much wider host range than other entomopathogenic microorganisms, but strains can vary in virulence and some may have relatively narrow host ranges. In general, the host range of deuteromycete entomopathogens is wider than that of the Entomophthorales and they can be grown *in vitro* much more readily (Federici and Maddox 1996). As with other microorganisms there is a difference between the physiological and ecological host range as discussed in Section 6.2.1 for *Entomophaga maimaiga*, a fungal pathogen of *L. dispar*.

Pathogenic fungi can sometimes cause natural epizootics that decimate populations of forest insects and these have been recorded in aphids and in several families of Lepidoptera (Pell *et al.* 2001). Epizootics are particularly associated with the Entomophthorales which tend to infect foliar feeding insects. Relatively little is known about the initiation and development of epizootics but attributes of entomopathogenic fungi that are important from an applied perspective are their pathogenicity (qualitative ability to cause disease), virulence (quantitative aspects of disease in populations), and persistence in the environment (Inglis *et al.* 2001). Entomopathogenic fungi are known to be sensitive to and often dependent on environmental conditions when released into the environment. For

example, they are sensitive to UV light but generally tolerant of a wide range of temperatures. Germination of spores may however, require the presence of free water and the spread of epizootics is generally inhibited by dry conditions.

Fungi have been used both experimentally and operationally to control other fungi. Applied as microbial fungicides they have been used most commonly to competitively exclude pathogenic fungi (Section 7.2.3).

## 7.2 Experimental and operational use

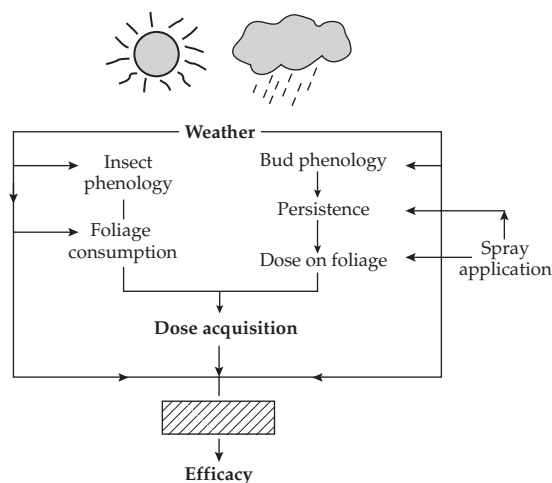
### 7.2.1 *Bacillus thuringiensis* and viruses

Microbial insecticides for control of defoliating Lepidoptera such as those based on *Bt* or NPVs can be sprayed with conventional equipment used for chemical insecticides (Mathews 1992; Picot and Kristmanson 1997). The special factors that need to be taken into account in spraying microbial insecticides such as their particulate nature, dose-response characteristics and estimation of field dose are discussed in detail in Hunter-Fujita *et al.* (1998) and Lacey and Kaya (2000). Effective application depends on delivering the correct dose to the right place at the right time and this requires information on pest phenology and some knowledge of how spray is distributed within the tree crown. Timing is especially important because *Bt* and NPVs have limited residual activity and no contact toxicity and can therefore act only if ingested by larvae. In general, younger smaller larvae are more susceptible and the lethal dose increases much more rapidly with increasing larval size than it does for chemical insecticides. Timing is also important in targeting larvae of those species that feed in protected positions such as within developing buds or needles or within silken tents. Timing spray operations for relatively large forest areas can be difficult because variation in topography and tree species composition can result in locally different rates of both larval and tree development (Cadogan and Scharbach 1993). Monitoring target populations for egg hatch or trees for bud flushing can help to ensure correct timing of spray operations.

Important factors that have contributed to the successful commercial development of *Bt* include

the discovery of the highly active HD-1 strain, and improvements in predictability in operational use. An increase in the predictability of formulations followed the development of international standards for product potency based on the number of international units per product (BIU = billion international units) determined in standardised bioassays (van Frankenhuyzen 1993; Skovmand *et al.* 2000). Although sprays are usually highly effective when targeted against susceptible instars, *Bt* still shows unresolved variation in field efficacy (Cooke and Régnière 1999). The search for a solution to this problem has helped to identify the range of interacting factors that influence effectiveness of spray programmes (Fig. 7.6).

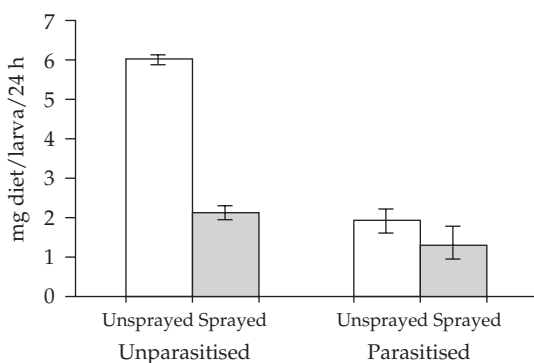
The availability of high potency formulations, which can be used in undiluted form, have allowed the more widespread use of ultra-low volume (ULV) controlled droplet application methods that were first used in forestry for chemical control of the pine beauty moth, *Panolis flammea*, in Scotland (Holden and Bevan 1979). These formulations are efficient to use because a high proportion of droplets produced, which are usually  $<10\ \mu\text{m}$ , impact onto the target surface and because spray



**Figure 7.6** Factors that can interact to determine the probability of larvae of *Choristoneura fumiferana* ingesting a lethal dose of *Bacillus thuringiensis* following aerial application. They include spray droplet deposition and persistence, larval feeding and development rates, phenological synchrony between insects and foliage, and weather (from Fleming and van Frankenhuyzen 1992). A similar scheme has been developed for viruses (Evans 2000).

volumes and handling time are significantly reduced in comparison to conventional spraying (van Frankenhuyzen 1993). However, small droplets can be less effective in killing larvae, especially those in later instars. One of the effects of *Bt* is to paralyse the insect gut with the result that larvae stop feeding. In ULV spraying, many small droplets must be ingested for larvae to acquire a lethal dose so that if they stop feeding, only a sublethal dose is ingested and they can recover over several days (Fig.7.7). The size and distribution of spray droplets and the concentration of *Bt* in them are therefore important determinants of dose acquisition. The interaction between droplet size and density of deposition for second to fourth instar gypsy moth, *Lymantria dispar*, is shown in Fig 7.8. The ineffectiveness of the 100  $\mu\text{m}$  droplets in killing fourth instars at any of the densities used, illustrates both the importance of targeting small larvae and the difficulty of getting sufficiently high concentrations in small droplets. In spraying operations, there is therefore an interaction between the potency of the formulation, the size of droplets giving optimum impaction on foliage and the number of droplets that need to be ingested to acquire a lethal dose.

Slowing the rate at which biological activity declines is important in increasing the effectiveness of microbial insecticides. In exposed parts of the canopy, microbial insecticides are rapidly inactivated



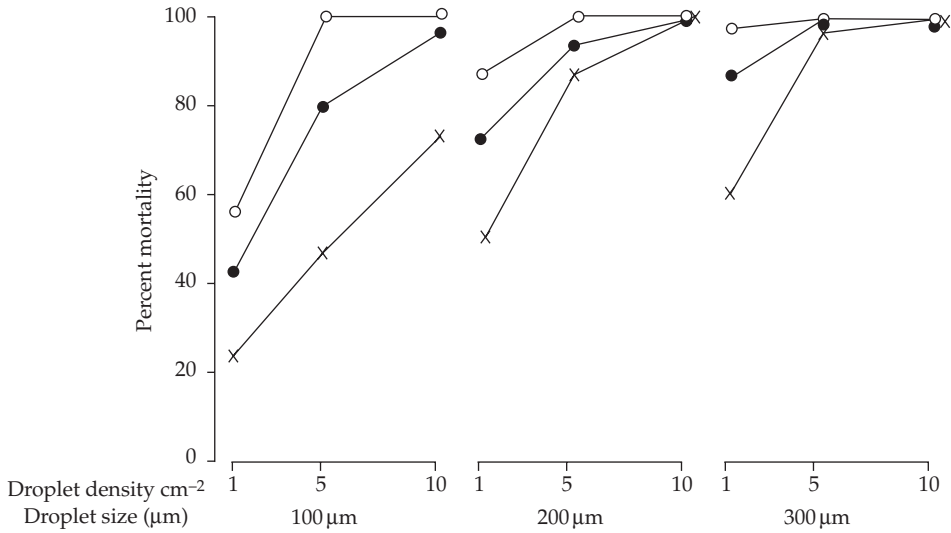
**Figure 7.7** The amount of *Bt*-free artificial diet consumed by larvae of *Choristoneura fumiferana* collected from balsam fir sprayed with *Bt* or left unsprayed. For larvae that had not been parasitised by braconids, those from sprayed plots that had acquired a sublethal dose of *Bt* consumed only about a third as much diet as larvae from unsprayed plots. Parasitised larvae consumed much less diet overall and were not affected by the spray (from van Frankenhuyzen *et al.* 2000b).

by UV light and they can also be washed off by rain (Fig. 7.9). The half-life of deposits on plant surfaces can be considerably extended by appropriate formulation with a range of additives such as protectants against UV light, antioxidants, and stickers that increase retention on foliage (Burgess and Jones 1998).

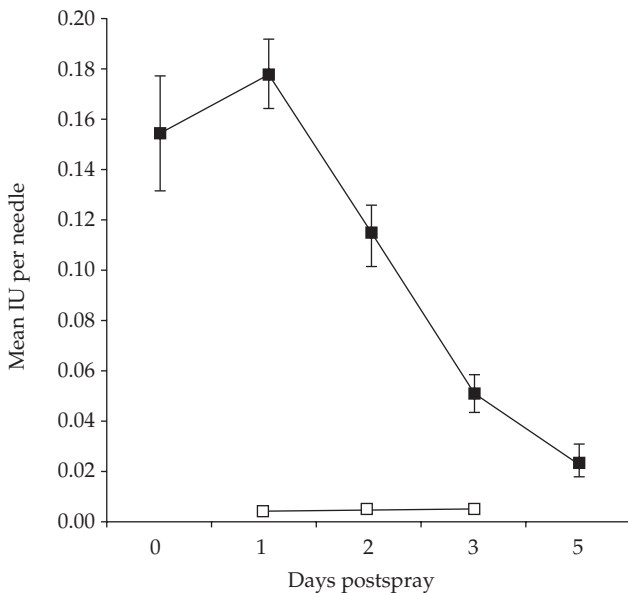
The main advantages of NPVs over *Bt* as microbial insecticides are that they are highly specific, generally lacking direct non-target effects (Cory 2003). Viruses can spread out rapidly from the point of introduction and can also be vertically transmitted. However, viruses are relatively slow to kill and although the rate of feeding may be reduced after spraying, it is not inhibited to the extent of larvae affected by *Bt* so that further defoliation occurs. Another limitation, which is one of the most important barriers to their wider use, is their relative lack of commercial availability largely because of the high cost of *in vivo* production. The most widely used viral insecticide in forestry is that against the European pine sawfly, *Neodiprion sertifer* (Cunningham and Entwistle 1981), but operational scale applications are sometimes used against Lepidoptera. Douglas fir tussock moth, *Orgyia pseudotsugata*, is an important defoliator of Douglas fir and true firs in western North America. Outbreaks tend to be cyclic and are often terminated naturally by a virus epizootic but only after significant damage has been caused. The registered virus (Table 7.3) is produced on contract by the USDA Forest Service and sprayed only to prevent significant defoliation (Brookes *et al.* 1978; Martignoni 1999). Sufficient virus is kept in store to control anticipated future large-scale outbreaks. Other examples of the use of virus in large-scale trials are given by Cunningham (1995), Federici (1999c) and Moscardi (1999).

## 7.2.2 Nematodes

In general, the use of nematodes in forestry is very limited. However, recent successes in the horticultural industry in the commercialisation of nematode formulations for control of the black vine weevil, *Otiorhynchus sulcatus*, and sciarid flies may facilitate their use for control of forest pests (Klein 1990; Richardson 1996; Kakouli-Duarte *et al.* 1997). Particularly suitable targets include species that spend at least part of their life cycle in soil where



**Figure 7.8** Percentage of mortality of different instars of *Lymantria dispar* larvae when exposed for 6 days to droplets of a *Bacillus thuringiensis* formulation sprayed onto foliage to achieve different mean droplet sizes and density. The experimental droplet size and densities are within the range expected in the tree canopy following application at a rate of  $4.7 \text{ l ha}^{-1}$  using  $12.5 \text{ BIU l}^{-1}$  (Dubois *et al.* 1993). Larvae that survived treatment lost weight and consumed 2–6 times less foliage than untreated larvae. Second instars (○), third instars (●), fourth instars (×) (data from Maczuga and Mierzejewski 1995).



**Figure 7.9** Persistence of a formulation of *Bacillus thuringiensis* sprayed onto foliage of balsam fir. Loss of activity was largely attributed to wash-off by rain, a typical cause of short half-life under Canadian boreal conditions. Sprayed (■), unsprayed (□) (from van Frankenhuyzen *et al.* 2000b).

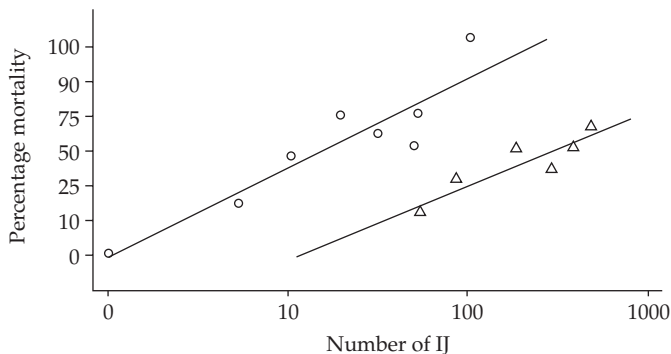
nematodes are protected to a greater or lesser extent from UV light, desiccation and high temperature. Some trials of soil sprays have been made against the larch sawfly, *Cephalcia lariciphila* (Georgis and Hague 1988), the spruce budmoth, *Zeiraphera canadensis* (Cunningham and van Frankenhuyzen 1991), and both larvae and adults of *Hylobius* spp. weevils (Burman *et al.* 1979; Pye and Pye 1985; Eidt *et al.* 1995a,b). Adult pine weevils, *Hylobius abietis*, are damaging pests of temperate conifer forestry, feeding on seedling trees used to replant areas after clearfelling. The larvae spend 1–3 years feeding on the bark of root-stumps of trees left in the ground after clearfelling and so are a particularly suitable target for nematodes. Trial applications of the nematode *Steinernema carpocapsae* have demonstrated their potential to significantly reduce emergence of adult weevils from treated stumps (Burman *et al.* 1979). Nematodes can be applied directly to the soil surface using commercially available spray equipment but targeting and timing are often important to kill the most susceptible stages because dispersal and persistence of infective juveniles (IJ) is limited and the hosts relatively immobile.

The potential of nematodes for control of aerial stages of insects in cryptic locations has also been demonstrated experimentally. In a trial in eastern Canada, *S. carpocapsae* incorporated into a commercial formulation of *Bt* was sprayed at high volume onto young trees infested by larvae of *Z. canadensis*. The budworm larvae feed on developing needles beneath the budcap of new shoots and so are not affected by the *Bt* formulation which simply acted as

a convenient carrier. The active nematodes however, were able to locate the feeding larvae and reduce budmoth populations by 82% (Eidt and Dunphy 1991). Larvae that tunnel in the xylem of trees can also be suitable targets for nematodes. In northern China, the carpenterworm, *Holocerus insularis*, is an important pest of shade trees such as ash and willow in urban areas and of Chinese hawthorn in agricultural areas. Larvae initially feed in the bark of their host tree before tunnelling into the xylem. Within the xylem, several larvae of more than one generation can occur within interconnecting tunnels and can kill 15-year-old trees in 3–5 years. Sponges impregnated with IJ of *S. carpocapsae* and used to block all visible tunnels were found to be a highly effective method of control. Nematode treatment killed 96% of larvae over 40 days in contrast to a mortality rate of 76% over 10 days achieved by using chemical insecticides (Yang *et al.* 1993). The possibility of using similar techniques to control the Asian longhorn beetle, *Anoplophora glabripennis*, in North America have also been considered (Solter *et al.* 2001). Experimental trials with different nematode species against this introduced pest demonstrated that *Heterorhabditis marelatus* was most effective, largely as a result of its active host-searching strategy (Fig. 7.10). This illustrates the importance of selecting appropriate species when using nematodes in microbial control.

### 7.2.3 Fungi

The formulation and application of entomopathogenic fungi, mainly in relation to agricultural and



**Figure 7.10** Mortality of different instars of *Anoplophora glabripennis* when exposed to infective juveniles (IJ) of *Heterorhabditis marelatus*. The lethal dose ( $LD_{50}$ ) was estimated to be 19 IJs for second to third instar cerambycid larvae (○) and 347 IJs for fourth to fifth instars (△) (from Solter *et al.* 2001).

horticultural pests, are discussed by Goettel *et al.* (2000) and Wraight *et al.* (2001). The sensitivity of fungi to environmental conditions, resulting in part from their temperature-dependent growth rate and requirement for wet conditions for spore germination, would seem to limit their usefulness as microbial insecticides in the forest environment. There is however one apparently successful example of the large-scale use of entomopathogenic fungi in forestry. In China, *Beauveria bassiana* has been applied from the air in extensive control programmes against pine defoliators (*Dendrolimus* spp.) (Inglis *et al.* 2001). There have also been some notable successes in the use of fungi as microbial 'fungicides' applied to control plant pathogenic fungi. One of the best examples is the use of *Phlebiopsis* (= *Peniophora*) *gigantea* to prevent colonisation of freshly cut conifer stumps by the root- and butt-rot pathogen, *Heterobasidion annosum* (Rishbeth 1963; Holdenrieder and Greig 1998). *H. annosum*, now recognised as three separate species, has a wide distribution in Eurasia and North America. In Britain as elsewhere, it is principally a pathogen of managed forests, causing most economic damage to pines, spruces and firs (Woodward *et al.* 1998) (Fig. 7.11). Inundative application of a suspension of spores of *P. gigantea* to stumps immediately after felling is highly effective at excluding *H. annosum*. Both these basidiomycete fungi are primary colonisers of new stump surfaces, but the weakly pathogenic *P. gigantea* is able to out-compete *H. annosum* and effectively prevents it from colonising stumps

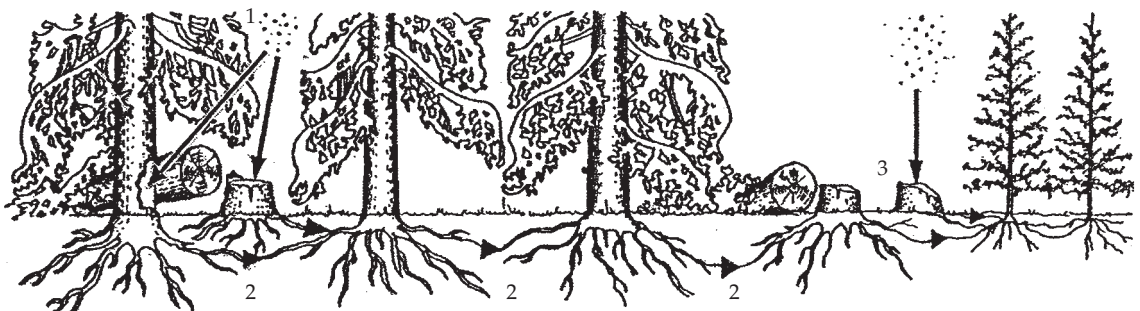
and then infecting standing trees. In the United Kingdom, this biological stump treatment is applied as part of the harvesting process, and ingenious methods of application through the cutting head of mechanical harvesters have been developed (Holdenrieder and Greig 1998).

Similar techniques of competitive exclusion have been proposed for control of other fungi. They include the treatment of logs with unpigmented strains of blue-stain fungi to prevent discolouration and degradation of timber by widely distributed pigmented species of blue-stain fungi (Behrendt *et al.* 1995) and treatment of stem wounds with antagonistic fungi to prevent establishment of wound pathogens (Zimmermann *et al.* 1995).

## 7.3 Registration and environmental impact

### 7.3.1 Registration and commercial availability

Microbial insecticides are considered to be much less harmful to the environment and to non-target organisms than chemical insecticides. This is partly because they are naturally occurring, usually lack persistence in the environment and are generally much more specific in their mode of action. These attributes are reflected in the regulatory environment for *Bt* and viruses which is less stringent and consequently less expensive than that for chemical insecticides. Even so the requirements



**Figure 7.11** The establishment and spread of the basidiomycete pathogen *Heterobasidion annosum*, in managed conifer forests. Where there are local sources of inoculum, basidiospores commonly occur in the air microflora and can be deposited on tree wounds or freshly cut stumps or logs following thinning (1) or clearfelling (3). Infection can be transferred to surrounding living trees after thinning or to trees of the next rotation after clearfelling via root contacts (2). The risk of infection is higher on some sites, for example, where soil pH is high (from Stenlid and Redfern 1998).

for registration of microbial insecticides vary considerably between countries. Within the European Union, for example, there is currently no harmonised approach to registration. Proposed data requirements for the approval of new active ingredients for inclusion in plant protection products are outlined in Table 7.1. Further testing and documentation would be needed for the particular formulations intended for use in the field. Requirements for registration continue to evolve in response to new kinds of products that are increasingly being developed such as those based on exotic species or produced through genetic modification.

Regulatory issues relating to genetically modified organisms are discussed by Whitten (1995) and Hunter-Fujita *et al.* (1998). Some examples of commercially available microbial insecticides based on *Bt* and NPVs are given in Tables 7.2 and 7.3.

Nematodes are regarded as particularly safe for release into the environment and this is reflected in the limited regulation of their commercialisation and use (Ehlers 1996; Ehlers and Hokkanen 1996; Richardson 1996). For example, in Great Britain and several other countries, indigenous nematodes that have not been subject to genetic modification do

not have to be registered as microbial insecticides. Introduction of non-indigenous species however, is much more closely regulated (Bedding *et al.* 1996; Rizvi *et al.* 1996).

### 7.3.2 Non-target effects in the environment

Viruses, nematodes and other kinds of microorganism vary in their host range and in their ability to persist and spread in the environment and initiate epizootics. This variation influences the perceived risk to non-targets when they are used in control programmes. Entomopathogens may have both direct and indirect effects on non-targets and methods for evaluating them are discussed by Hajek and Goettel (2000). In complex forest habitats, indirect effects may be particularly important because forests may well contain rare or endangered species (Lacey and Siegel 2000).

The main effect of NPVs on non-targets is likely to be indirect because of their restricted host range. Indirect effects occur, for example, when parasitised larvae are killed before the next generation of parasitoids emerge. Some strains of *Bt* on the other hand, have a relatively broad spectrum of

**Table 7.1** Data collection and documentation relating to inclusion of microorganisms (excluding nematodes) as active ingredients of biopesticides that have been proposed as a basis for harmonising registration within the EU

Data requirements	Example information
Identity of the organism	Collection and culture reference number Tests and criteria for identification
Biological properties of the organism	Host-specificity and non-target effects Relationship to plant or animal pathogens
Further information on the organism	Field of use envisaged Method of production
Analytical methods	Methods to show microbiological purity Methods to determine viable and non-viable residues
Toxicological, pathogenicity, and infectivity studies	Oral, inhalation, and skin toxicity
Residues in or on treated products, food, and feed	Likelihood of multiplication in the crop
Fate and behaviour in the environment	Persistence in the air, water, and soil
Ecotoxicological studies	Acute toxicity to honey bees and other non-targets
Labelling	Indication of danger

Notes: Some examples of the information required are given but see Neale and Newton for further details (from Neale and Newton 1999). The current situation for different countries is outlined in Hunter-Fujita *et al.* (1998), Sexsmith (1998), McClintock (1999), and Libman and MacIntosh (2000).

activity and a number of studies have demonstrated direct effects on Lepidoptera after spraying operations particularly on those species closely related to the target pest (Miller 1990, 2000). These direct effects can be reduced to some extent by careful timing of sprays because differences in phenology mean that susceptible instars of target and non-target species do not usually coincide precisely. Most effects of *Bt* sprays do seem to be transitory however, especially in comparison to those following use of synthetic insecticides. Even so, in highly diverse forest ecosystems, especially where rare species are known to be present, the effects of potent *Bt* formulations should be monitored. Natural enemies are not generally affected directly by *Bt* sprays but as for viruses, indirect effects occur when parasitised hosts are killed. In spraying

operations against some defoliating Lepidoptera, the impact on parasitoids may in fact be less than expected because parasitised larvae have a higher probability of survival. Larvae of spruce budworm, *Choristoneura fumiferana*, that are parasitised by *Apanteles fumiferanae* eat less than unparasitised ones. They are therefore less likely to acquire a lethal dose after spraying operations and as a result the effects of *Bt* and natural enemies on the pest population can be additive (Nealis *et al.* 1992) (Fig. 7.7). Additive effects may also occur if sublethally affected larvae are more vulnerable to parasitism. For example, the slow development of larvae of the gypsy moth, *Lymantria dispar*, sublethally affected by *Bt*, makes them more vulnerable to attack by the parasitoid, *Cotesia melanoscelus*, that specialises in attacking young larvae and this results in increased parasitoid population levels (Weseloh *et al.* 1983).

Nematodes are generalist pathogens of insects and so there would appear to be a significant risk of non-target effects (Ehlers and Peters 1995; Bathon 1996; Barbercheck and Millar 2000). The ability of entomopathogenic nematodes to kill many insect species has been shown in laboratory tests, but as opportunists their host range is likely to be much more limited in their natural environment. When nematodes are applied to soil, above ground insects are unlikely to be affected because the nematodes are rapidly deactivated by environmental factors, in particular by UV light. What happens in the very complex soil environment itself is more difficult to study, but it is known that even after inundative releases, nematodes are lost from the soil at a rapid rate and have limited capacity for dispersal. In general therefore, it seems likely that any non-target effects following application of nematodes would be of short duration.

Fungi, unlike nematodes, can cause epizootics. High levels of fungal inoculum can therefore occur naturally in the environment so where local isolates are released, control programmes mimic natural events. Entomopathogenic fungi can have indirect effects on parasitoids as observed for *Bt* and viruses but they can also infect adult predators and parasitoids. The significance of these direct effects on populations of natural enemies have not however, been widely studied (Hajek 1997). General aspects of non-target effects following release of fungi are

**Table 7.2** Examples of commercially available formulations based on *Bacillus thuringiensis* subsp. *kurstaki* for control of forest Lepidoptera

Product ®	Potency (BIU l <sup>-1</sup> )
Dipel	8.4–25.4
Foray	12.7–20.0
Thuricide	12.7
Condor <sup>a</sup>	

<sup>a</sup> Manipulated through non-recombinant genetic methods to improve potency.

Sources: van Frankenhuyzen (1993), Federici (1999b), and van Frankenhuyzen *et al.* (2000a). Several products used in eastern Europe of unknown commercial availability are listed by Glowacka (1996).

**Table 7.3** Examples of NPV formulations registered as microbial insecticides for control of forest Lepidoptera and sawflies

Pest	Product
<i>Neodiprion sertifer</i>	Neoscheck-S Sertifervirus
<i>Neodiprion lecontei</i>	Lecontivirus
<i>Lymantria dispar</i>	Gypcheck Disparvirus
<i>Orgyia pseudotsugata</i>	TM BioControl-1

Sources: Federici (1999a), and Podgwaite (1999).



considered by Moore and Prior (1993) and Goettel *et al.* (2001).

The risks associated with the release of genetically modified microorganisms have been discussed by Crook and Winstanley (1995), Richards *et al.* (1998), Cory (2000) and Tappeser *et al.* (2002). The main concerns relate to unexpected effects on virulence or host range, possible intra- and inter-specific transfer of genetic information (e.g. conjugation in *Bt* or recombination events in viruses) or more rapid development of resistance to strains with enhanced pathogenicity.

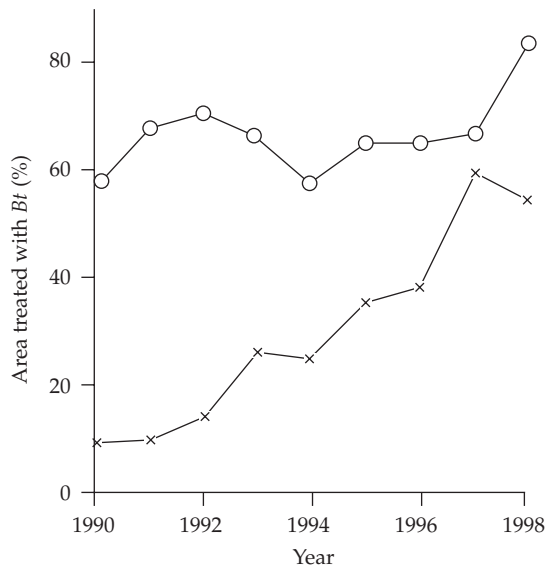
#### 7.4 Developments in the use of microbial control

The relatively high cost of commercial production is an important factor limiting the wider use of microbial insecticides, especially for viruses which are currently produced *in vivo*. Improvements in the cost-effective large-scale *in vitro* production of microorganisms would therefore, make a significant contribution to the wider use of microorganisms in pest management. For most microorganisms, improvements in field efficacy are most likely to come from the discovery of new strains or species that differ in pathogenicity or in their tolerance of non-optimal environmental conditions (Kaya and Gaugler 1993; Waage 1995; Barbercheck and Millar 2000; Hajek *et al.* 2000). For nematodes there is also potential for the application of classic breeding techniques to improve traits such as host finding and UV tolerance (Burnell and Dowds 1996). For *Bt* and viruses, genetic manipulation has the potential to increase pathogenicity or host range. Strains of *Bt*, for example, have been engineered to express new *cry* genes and so alter their spectrum of activity or to increase the number of copies of a gene already present so that more toxin is produced than would occur naturally (Baum *et al.* 1998, Sanchis 2000) (Table 7.2).

Detailed ecological and behavioural studies may help to identify causes of variation in efficacy in the field. For example, the effectiveness of *Bt* and viruses can be influenced by the host plants on which larvae are feeding so that efficacy could be affected by stand composition. In *Bt*, the host plant effect seems to be caused by tannins which can reduce toxicity by complexing with the dissolved

protein crystal in the larval gut. In experiments with the formulation 'Thuricide', *Bt* was found to be 2–5 times less effective against larvae of the gypsy moth, *Lymantria dispar*, feeding on oaks than those feeding on aspen and therefore a more detailed understanding of the mechanism of inhibition could lead to improved formulations (Appel and Schultz 1994).

*Bacillus thuringiensis* is being increasingly used for control of forest defoliators (Fig. 7.12). Improvements in formulation that increase retention time on treated foliage and improve residual toxicity, together with increases in pathogenicity of natural or modified strains raise concerns about possible development of resistance. Although it is much less likely to develop than resistance to chemical insecticides, insect pests do have the potential to develop at least some level of resistance to most microbial organisms if they are applied frequently enough to exert selection pressure on the target population (Shelton and Roush 2000). Resistance to *Bt* in the field has been reported in one agricultural pest and other



**Figure 7.12** The operational use of *Bacillus thuringiensis* to control forest defoliators in the USA and Europe expressed as a percentage of the total area sprayed. In the USA, populations of *Lymantria dispar* and *Choristoneura occidentalis* were sprayed on a total area of 2.6 million ha from 1990–8 (○). In Europe, 6.8 million ha were sprayed to control *Thaumetopoea pityocampa*, *L. monacha*, *L. dispar*, *Dendrolimus* sp., *Bupalus piniaria*, *Panolis flammea*, *Tortrix viridana*, and *Operophtera brumata* (×) (data from van Frankenhuyzen 2000).

species clearly have similar potential (Ferré and Van Rie 2002). In forestry *Bt* is used most commonly for control of the spruce budworm, *Choristoneura fumiferana* and *L. dispar*. In these insects, natural variation in susceptibility within and between populations is known to exist, suggesting the possibility that resistance could evolve in treated populations (Rossiter *et al.* 1990; van Frankenhuyzen *et al.* 1995). The development of resistance to chemical insecticides has been widely studied and methods of managing it are applicable to microbial insecticides (Denholm and Rowland 1992; Tabashnik 1994; Gould 1998; Shelton and Roush 2000). A number of strategies for reducing resistance development have been proposed of which the provision of untreated refuges is probably the most reliable. The effectiveness of other techniques such as the use of doses high enough to kill a high proportion of individuals that are heterozygous for resistance or the rotation of different *Bt* toxins must be considered in relation to several important factors. These include the initial frequency of resistance alleles, whether resistance is dominant or recessive, the stability of resistance (i.e. the rate at which resistance declines in

the absence of selection), and the extent of immigration of susceptible individuals.

As agents for microbial control of forest pests, viruses have so far shown more promise in theory than in practice. However, they could become more important if significant resistance to *Bt* were to develop in forest defoliators. Viruses have a number of desirable attributes such as their high degree of specificity and their ability to spread within and between generations. But they are currently expensive to produce and tend to be slow acting, so that significant defoliation often occurs after spraying. One way of increasing the speed of kill is to engineer the virus using recombinant DNA technology to express foreign proteins toxic to insects (Bonning and Hammock 1996; Treacy 1999). However, a formidable amount of testing would be necessary to establish that modified viruses do not pose a threat to non-target organisms. In general, viruses modified to express insect toxins are likely to be less competitive than the wild-type because they kill larvae more quickly and so much less virus would be produced and released to the environment when the larvae die.

# Semiochemicals

Signalling chemicals, known as semiochemicals, transmit information within or between species and play an important role in many aspects of insect behaviour including finding and accepting host plants and locating mates. Research on semiochemicals and their role in the ecology and behaviour of insect pests has provided novel and potentially very powerful techniques for the management of insect populations. Much of this research has been on pheromones, semiochemicals that transmit information between individuals of the same species. They include the sex pheromones of Lepidoptera and sawflies and the aggregation pheromones of scolytid bark beetles.

Sex pheromones emitted by females of Lepidoptera and sawflies serve to attract males for mating. In Lepidoptera, many of the pheromones are based on straight chain hydrocarbons with an alcohol, aldehyde or acetate ester functional group and are commonly synthesised by the females from fatty acids. In most cases the complete pheromonal message is conveyed by a blend of two or more chemicals which comprise a species-specific pheromone. Different pheromone components are distinguished by variation in the length of the carbon chain, the type of functional group and isomeric form (Franke and Schultz 1999; Tillman *et al.* 1999). The same basic pheromone blend may however be used by different sympatric species and, when this occurs, cross-attraction between them is avoided through differences in the release rate, the relative composition of a multicomponent pheromone or because females 'call' at different times of the day (Tamaki 1985).

Much less is known about sawfly pheromones. In several diprionid species, sex pheromones have been identified as particular isomeric forms of esters of the alcohol diprionol (3,7-dimethyl-2-pentadecanol).

However, diprionol can exist in eight optical isomeric forms some of which may be synergistic or inhibitory to the main attractive isomer so that a high level of chemical purity is required for trials of these pheromones. Studies have consequently been limited (Anderbrant 1993; Anderbrant *et al.* 1995).

The pheromones of scolytid bark beetles that mediate aggregation on the host also serve to bring the sexes together because the sex that attacks first may initially attract the opposite sex (Borden 1985). For 'secondary' bark beetles that breed largely in moribund host material such as fallen trees or branches, sexual attraction may be the primary function of the pheromone. Late arriving beetles, however, can simply exploit the pheromone released to aggregate on suitable host material located by beetles that arrive first. For 'aggressive' bark beetles that can attack living trees, pheromones attractive to both males and females are essential for coordinating an aggregated or 'mass-attack', as host resistance would normally repel attack by one or a few beetles. An essential feature of mass-attack is that a critical or threshold number of beetles is required to overcome host resistance, usually by reaching a threshold density of inoculation points of symbiotic fungi that aid in killing the host tree (Box 5.2). The amount of bark available for utilisation by the beetles is finite however, so if too many beetles become established, intraspecific competition has the potential to reduce reproductive success (Anderbrant *et al.* 1985; Berryman *et al.* 1985). In fact the aggregation pheromone that mediates the complex process of attack and conquest of a tree typically has several chemical constituents which, either independently or in combination, contribute both to the initiation and to the termination of attack by affecting the behaviour of beetles in different

ways. Understanding how aggregation pheromones influence different aspects of bark beetle behaviour has led to new ways of manipulating populations for management and control.

During the early stages of mass-attack, 'pioneer' beetles release attractive chemicals that result in more beetles orientating towards and landing on the tree, an aggregation response that for some species may be synergised by host monoterpenes (Miller and Borden 1990; Erbilgin and Raffa 2000). Monoterpenes therefore function as kairomones, that is, chemicals that mediate communication between different species by inducing a response that benefits the receiver of the 'message'. As colonisation of the tree proceeds, the aggregation response can be 'masked' or inhibited by other pheromones that can divert attack to less heavily colonised parts of the tree and eventually cause attack to switch to other trees nearby. These inhibitory chemicals can function as straightforward antiaggregation pheromones or they may be 'multifunctional' in that they are attractive at low but repellent at high concentrations (Borden 1997).

The pheromone components of different species of bark beetle that utilise the same host trees may also have an antiaggregation effect and so can play a role in reducing interspecific competition (Miller *et al.* 1995; Borden 1997).

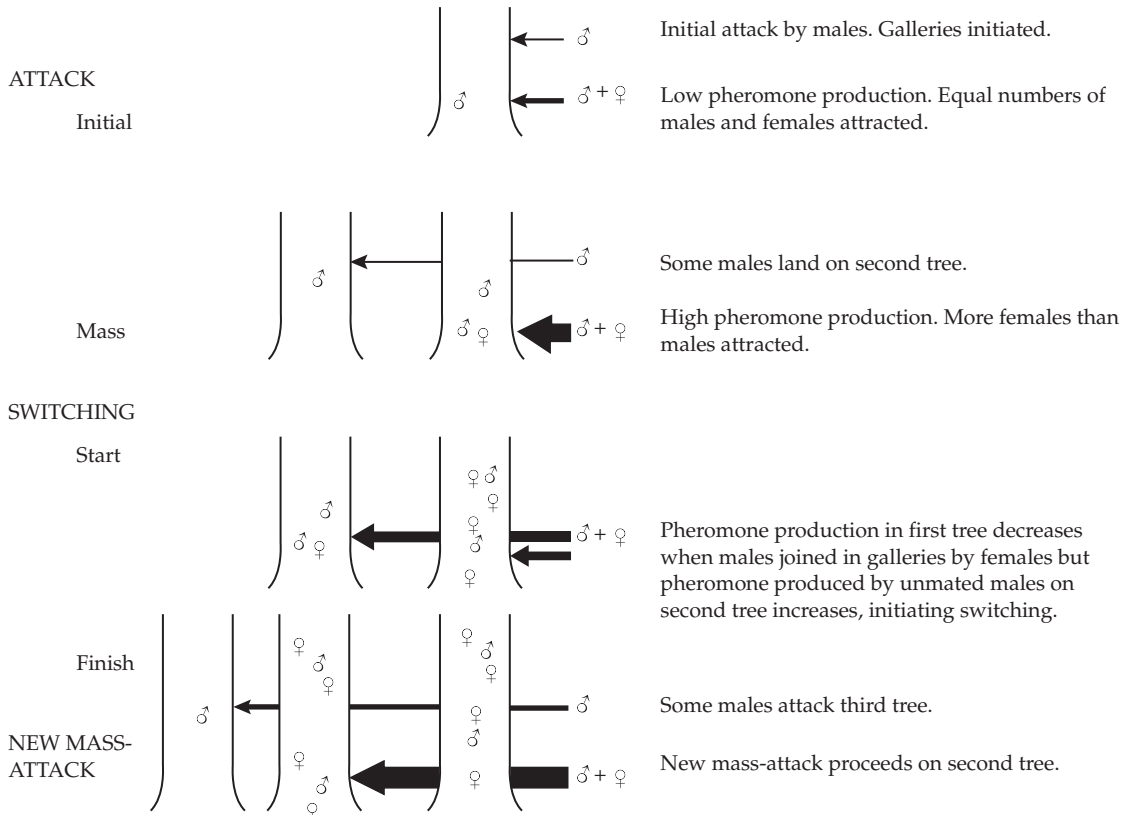
The different chemical constituents of aggregation pheromones may be synthesised by the beetles themselves, or they may be of host plant origin, being either simply sequestered for use by the beetles or modified by them to produce new active chemicals (Seybold *et al.* 2000). As well as conveying information as kairomones, monoterpenes can also provide the chemical basis for several different bark beetle pheromones. Some of the main semiochemicals identified from *Ips* and *Dendroctonus* species are listed in Table 8.1. Within each genus, the multicomponent aggregation pheromone of different species is formed from a particular subset of these chemicals. The behavioural response of different species to the same chemical can vary however, and in species with a wide geographic range there may even be regionally specific responses to particular pheromone blends

**Table 8.1** Some of the main semiochemicals involved in the multicomponent aggregation pheromones of some *Ips* and *Dendroctonus* bark beetles

Semiochemical	Origin	Role identified in different species
<i>Dendroctonus</i>		
Frontalin	<i>De novo</i> biosynthesis	Aggregation–antiaggregation–multifunctional
exo-Brevicommin	<i>De novo</i> biosynthesis	Aggregation–multifunctional
endo-Brevicommin	<i>De novo</i> biosynthesis	Aggregation–antiaggregation
trans-Verbenol	Monoterpene	Aggregation–multifunctional
Seudenol	Unknown	Aggregation
Verbenone	Monoterpene	Antiaggregation–multifunctional
Methylcyclohexenone	Unknown	Antiaggregation–multifunctional
<i>Ips</i>		
cis-Verbenol	Monoterpene	Aggregation
Methylbutenol	Hemiterpene	Aggregation
Ipsdienol	Monoterpene/ <i>de novo</i> biosynthesis	Aggregation–antiaggregation–multifunctional
Ipsenol	Monoterpene/ <i>de novo</i> biosynthesis	Aggregation–antiaggregation
Verbenone	Monoterpene/microorganisms	Antiaggregation

*Notes:* Most of the semiochemicals are ultimately derived from monoterpenes of host tree origin but some are synthesised *de novo* by the bark beetles. Not all chemicals are utilised by all species within a genus but many share similar chemicals. In different species however, they can influence behaviour in different ways. In some cases, the behavioural response may depend on the isomeric form of the chemical. Host kairomones may also synergise attraction for some species.

*Sources:* Borden (1985, 1997, personal communication), Miller *et al.* (1991), Byers (1995), Tillman *et al.* (1999), Seybold *et al.* (2000).



**Figure 8.1** Pheromone-mediated mass-attack by *Ips typographus*. *Male-produced pheromone components*—The main components are 2-methyl-3-buten-2-ol (*mb*) produced independently of the tree and *cis*-verbenol (*cv*) dependent on  $\alpha$ -pinene in the tree. Ipsdienol and ipsenol are produced when egg-laying females are present and verbenone is produced by some associated microorganisms. *Behavioural responses*—The two main components (*mb*+*cv*) are needed for attraction but *mb* is important in close-range landing behaviour. In high concentrations of pheromone, males are less likely than females to land near the source. Attraction is inhibited by concentrations of ipsdienol and ipsenol higher than *cv* and by verbenone.

Sources: Schlyter and Anderbrant 1989, Byers 1989; modified from Schlyter and Anderbrant 1989.

(Byers 1995; Borden *et al.* 1996). Detailed experimental studies are therefore needed to characterise multicomponent pheromones before they can be used in pest management programmes.

Semiochemicals may be released by one or both sexes and the concentration and relative composition of the multicomponent pheromone, the 'bouquet' dispersing from the tree, is influenced by the sex ratio as well as the overall density of beetles on the tree. An example of the way in which a pheromone-mediated mass-attack develops is illustrated for the spruce bark beetle, *Ips typographus*, in Fig. 8.1.

The practical application of pheromones is dominated by their use in traps to detect or monitor pest

populations (Section 3.4.2), but they have also been used more directly in management and control. Examples discussed in this chapter include the application of the sex pheromones of Lepidoptera to areas of forest to disrupt mating, the use of scolytid aggregation pheromones in traps for mass-trapping to reduce the density of local populations and the use of aggregation and antiaggregation pheromones to manipulate the behaviour of bark beetle populations in the forest.

The natural enemies of bark beetles, Lepidoptera and sawflies may respond to their pheromones, using them as kairomones to signal the presence of prey (Rutledge 1996; Hilker *et al.* 2000; Erbilgin and

Raffa 2001). When pheromones are used in pest management and control, it is important therefore to consider possible effects on the wider insect community.

## 8.1 Mating-disruption

In mating-disruption, the sex pheromone of the target pest is dispersed throughout the treated area. The aim is to reduce significantly the success of males in locating and mating with 'calling' females against the background of competing pheromone sources. Both theoretical studies and practical experience have helped to identify the kinds of pests for which mating-disruption is likely to be most effective and to define the kinds of conditions under which it is most likely to be successful (Barclay and Judd 1995). To disrupt mating and initiate a decline in population size in the next generation, the concentration of pheromone must remain sufficiently high in the right part of the habitat and the incidence of chance encounters between males and females must be relatively low. The method is therefore most appropriate when used at low population densities. Another important caveat is that populations should be relatively isolated with no nearby sources of already mated females that can disperse into the treated area and so species with flightless females such as the gypsy moth, *Lymantria dispar*, are particularly promising candidates for control by mating-disruption.

When sex pheromone is dispersed throughout treated forest areas, a number of possible mechanisms, reviewed by Cardé and Minks (1995) and Sanders (1997), may operate in preventing males locating calling females. In essence, mating-disruption treatments disrupt upwind flight of males responding to calling females. The principal mechanisms are likely to be adaptation and habituation of males to the pheromone that is being continuously released from the artificial sources, together with false trail following toward sources of synthetic pheromone that outcompete the female-produced pheromone that is only released during a limited 'calling' period. In the vicinity of the pheromone source however, males search for calling females and may use visual cues to locate them. The efficiency of close-range orientation and the influence of population density on the frequency of chance encounters will therefore have an important

influence on the effectiveness of mating-disruption (Charlton and Cardé 1990).

Mating-disruption has been used with considerable success in agriculture (Cardé and Minks 1995). For forest pests however, it is still largely an experimental technique. Its effectiveness and suitability for operational use has been demonstrated for isolated populations of some defoliating Lepidoptera such as *L. dispar*, which has flightless females, and various shoot moths, *Rhyacionia* spp., and coneworms, *Dioryctria* spp. (Leonhardt *et al.* 1996; DeBarr *et al.* 2000). Shoot moths and coneworms cause significant economic damage at relatively low population density especially in high value crops such as seed orchards of genetically improved trees and so are ideal targets for mating-disruption. Sawflies are also potential targets, but the methodology is much less developed than for Lepidoptera and so far has been tried only on a small experimental scale. This is partly a reflection of the difficulties of synthesising the highly pure form of the pheromone needed (Anderbrant *et al.* 1995; Anderbrant 1999). An additional factor is that in many sawflies unfertilised eggs produce males so that effects on population density in the year immediately following treatment are likely to be small (Martini *et al.* 2002).

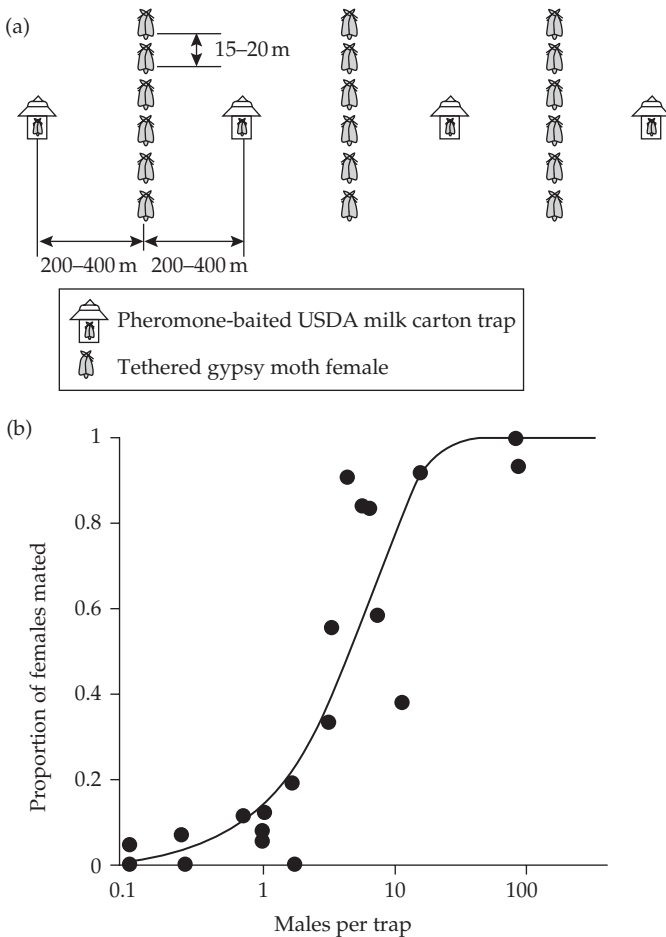
Extensive field experiments against a number of different Lepidoptera have been used to answer certain key questions concerning formulation, dose per unit area, spatial distribution within the forest, pheromone release rate and impact of treatments on mating success and so provide the basis for the development of operational methods. The following experimental trials of mating-disruption against *L. dispar* illustrate this approach and demonstrate the levels of population reduction that may be achieved.

### 8.1.1 Development of operational programmes for mating-disruption

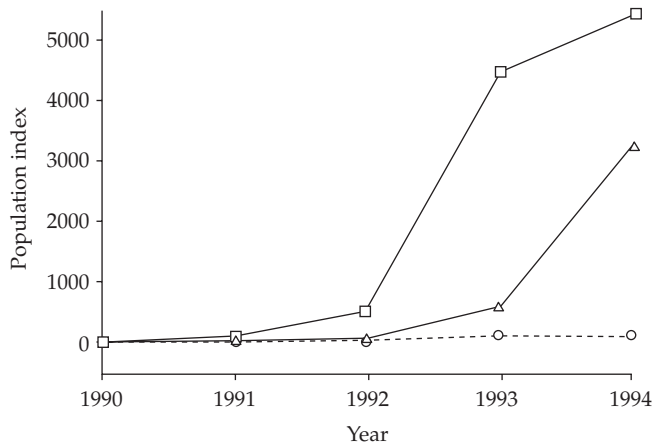
The critical concentration of pheromones and the optimal distribution of pheromone dispensers within the habitat necessary to achieve mating-disruption in particular species are usually not known. Thus the effectiveness of different pheromone treatments needs to be determined experimentally. Sex pheromones have been formulated in a number of different ways that influence not only their release

rate but also how and where they are applied (Sanders 1997). Dispersible formulations of microcapsules or beads release very small amounts of pheromone for a limited period but have the advantage that they can be applied from the air in conventional spray equipment and tend to provide a fairly uniform distribution. 'Female equivalent' formulations consisting of plastic chips, flakes or fibres release amounts of pheromone that approximate the emission rate of calling females over a relatively extended period. Unlike microencapsulated formulations, they can provide many individual competing pheromone sources but need modified sprayers for application. Reservoir formulations of tape or ropes have high potential release rates over an extended period but need to be deployed manually and so tend to be distributed close to the ground.

Assessing the effectiveness of different pheromone treatments depends on appropriate quantification, either directly or indirectly, of both disruption of mating and subsequent population decline. One direct method is to use tethered, sentinel, females in treated and untreated plots and then to dissect them so as to determine whether mating has occurred. It may also be possible to collect egg-masses laid after application of pheromone treatments to determine the proportion that have been laid by mated females (Leonhardt *et al.* 1996). Where indirect methods are used, such as the reduction in male captures in pheromone-baited traps within treated areas, it is necessary to demonstrate that the inability of male moths to find traps is equivalent to an inability to find females (Fig. 8.2).



**Figure 8.2** (a) Tethered female *Lymantria dispar* used in mating-disruption trials to determine the relationship between mating success and reduction in male captures in pheromone traps. Females were tethered using thread tied to the base of the forewing and attached to the bole of a tree. In experimental plots three rows of females were used, each separated from pheromone traps by at least 200 m. Females, which 'call' for up to 3 days, were dissected to determine mating success. (b) The proportion of female *L. dispar* mated in a low density population in relation to captures of males in pheromone-baited traps based on trials in 2 years together with a fitted model of mating probability. The relationship is influenced by such factors as trap type, pheromone source and population density (from Sharov *et al.* 1995).



**Figure 8.3** The effect of mating-disruption on populations of *Lymantria dispar* in isolated oakwoods at the southern leading edge of the moth's expanding range in Virginia, USA. Population index was the sum of the means of three measures of population—the number of immature stages and the number of fertile egg-masses per 100 burlap bands on host trees and the number of fertile egg-masses per hectare. Disparlure, the synthetic sex-pheromone of *L. dispar*, was applied aerially in plastic laminate flakes with a single application of 75 g ha<sup>-1</sup> each year (○) or two 75 g applications applied in 1990 only (△). Control (□) (from Leonhardt *et al.* 1996).

Leonhardt *et al.* (1996) combined several different measures of efficacy of mating-disruption to derive a 'population index' that allowed assessment of the effects of treatment over several seasons, demonstrating that local populations of *L. dispar* could be suppressed for 3–4 years following treatment (Fig. 8.3).

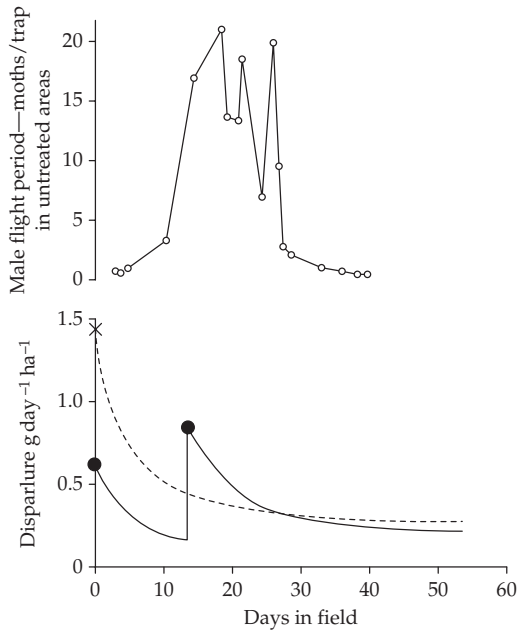
A number of factors have been observed to influence the degree of mating-disruption in experimental trials. In *L. dispar*, mating success of females decreases with increasing pheromone dose per hectare. At higher doses however, the decrease in mating success is relatively small for large increases in dose so that it may not be cost-effective to use high doses (Webb *et al.* 1990). The efficacy of mating-disruption treatments is also influenced by the spatial distribution of pheromone treatments within the habitat, the optimal distribution depending on the location of the majority of calling females. When plastic 'flake' formulations are applied from the air, some flakes can penetrate the canopy to be deposited on understorey vegetation or even on the ground but when sticking agents are added to ensure retention throughout the canopy, the success of mating in wild females can be considerably reduced (Thorpe *et al.* 2000). The release rate for a given formulation and the rate at which it decreases over time influence both the concentration of pheromone during mating-disruption and the number of applications necessary during the male flight period of *L. dispar*. Thorpe *et al.* (1999) compared a single application of plastic laminated flakes that released about 30% of the commercially available pheromone, Disparlure, during the 6 week flight period with two applications of polymethacrylate

beads that lost around 75% over the same period (Fig. 8.4). The effectiveness of treatments was assessed by their ability to reduce catches of males in pheromone-baited traps, to reduced mating success and, importantly, to reduce populations in the following year (Table 8.2). Both pheromone treatments appeared to be equally effective, not only reducing trap catches and mating success but also reducing populations in the following year. The fact that similar levels of mating-disruption were achieved by the two treatments suggests that neither exact timing of the application immediately before male flight, nor the release rate characteristics of the formulation are critical for successful mating-disruption in *L. dispar*. Release rate would in any case be affected by changes in temperature and wind movement during the course of the flight season. However, it is necessary to define a dose that is sufficiently high to disrupt mating while minimizing the use of expensive pheromones.

## 8.2 Mass-trapping

In mass-trapping, the aim is to reduce the pest population size by capturing adults in highly attractive pheromone-baited traps. The sex pheromones of Lepidoptera could in principle be used for mass-trapping and, since only males are trapped, the effect would be like that of mating-disruption because it would increase the proportion of unmated females and so reduce the population in the next generation. However bark beetles have been much more frequent targets for mass-trapping, in part because both sexes are attracted to aggregation





**Figure 8.4** Experimental release of Disparlure to disrupt mating of *Lymantria dispar* in an outbreak in isolated oakwoods in Virginia, USA. The seasonal timing of treatments, applied in 1993, was related to the male flight period which is shown for the untreated plots (○). In treated plots, Disparlure, applied aerially, was released from a single application of plastic laminate flakes (50 g a.i. ha<sup>-1</sup>) (x) or two applications of polymethacrylate beads (15 g a.i. ha<sup>-1</sup> each) (●). The predicted change in release rate is shown for the two treatments. Effects on gypsy moth populations are illustrated in Table 8.2 (from Thorpe *et al.* 1999).

**Table 8.2** The influence of mating-disruption treatments, illustrated in Fig. 8.4., on populations of *Lymantria dispar*

Treatment	Males per trap		Mating (%)		Life stages per 100 burlap bands		Egg-masses ha <sup>-1</sup>	
	1993	1994	1993	1994	1993	1994	1993	1994
Control	196.8	401.6	28.4	—	49.6	226.1	68.7	156.7
Beads	3.4	106.9	0	—	27.8	20.8	10.8	26.7
Flakes	1.3	37.5	0.2	—	34.1	27.5	16.6	34.3

*Notes:* Treatments were applied in 1993. Within experimental plots, the ability of males to locate females was assessed from captures in pheromone-baited milk carton traps and mating success determined by placing virgin females in mating stations. Effects on population density and growth were determined from surveys of egg-masses and by counting life stages under burlap bands placed on trees.

*Source:* Thorpe *et al.* (1999).

pheromones. Both experimental and operational programmes of mass-trapping have been developed and there have also been some theoretical studies to identify those factors most likely to contribute to successful control (Stenseth 1989; Byers 1993). The benefits of mass-trapping may be quantified in terms of reduced dispersal, reduced damage to timber, or reduced reproductive success depending on the characteristics of the target species and where trapping is actually done.

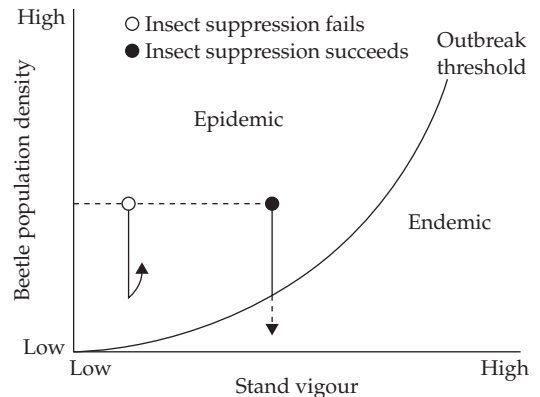
At ports, trapping exotic bark beetles that have been imported in infested timber is aimed at pre-

venting or reducing dispersal to surrounding forest areas. Following detection in monitoring traps or plant health inspections that identify infested timber, intensive trapping may be carried out around the sources of infestation. The rapid deployment of pheromone-baited traps depends on prior knowledge of the species likely to be imported and obviously also on the availability of appropriate pheromone lures. Ports are often isolated from suitable beetle breeding sites and so reducing dispersal from them is likely to reduce the probability of successful establishment of exotic species.

Ambrosia beetles are important pests of both conifer and hardwood timber, boring into wood of felled trees and timber and producing characteristic 'pinhole' galleries that are darkly stained by their symbiotic fungi (Dowding 1984; McLean 1985). High levels of damage can occur in timber processing areas where wood is stored and trapping ambrosia beetles can be of economic benefit by reducing attack and degrade of felled timber as discussed in Box 8.1.

For aggressive bark beetles that can attack living trees within the forest, the use of mass-trapping is logistically much more difficult and not practicable for extensive outbreaks in remote forest areas with poor infrastructure. Its effectiveness against these species is also more difficult to quantify than against ambrosia beetles in timber processing areas, in part because of the complex dynamics of outbreaks and the high dispersal capacity of many species. At endemic beetle population density, conifers are normally resistant to attack and beetles breed in relatively scarce moribund, windbroken or fallen branch material. Outbreaks may be precipitated when the availability of such material increases following disturbance of the forest by for example, windblow, drought or even lightning strikes on individual trees (Coulson *et al.* 1999b; Powers *et al.* 1999). As population density rises, standing trees may be colonised during pheromone mediated mass-attack. Colonisation is most likely to be successful when trees are overmature or when unfavourable environmental factors such as high temperature and low rainfall cause drought stress in trees, reducing their resistance to attack (Box 5.2). This dynamic interaction between bark beetle population density and tree resistance can be expressed in terms of an outbreak threshold density required to overcome host resistance (Fig. 8.5). At high population densities, outbreaks can become self-sustaining and spread rapidly over large areas of forest. In theory therefore, it should be possible to reduce the local population density below the outbreak threshold, precipitating the collapse of an outbreak.

While the conceptual model illustrated in Fig. 8.5 is useful for mass-trapping of aggressive bark beetle species, in practice the outbreak threshold for the stand as a whole, and therefore the degree of



**Figure 8.5** The theoretical outbreak threshold for bark beetles in relation to 'stand vigour'. In mass-trapping, or other direct control measures, the aim is to suppress self-sustaining outbreaks by reducing population density below the threshold. This is difficult to achieve when stand vigour is low or when large amounts of windblown material are available for breeding (after Berryman 1978, from Speight and Wainhouse 1989).

population reduction required, is generally not known. Nor is the extent to which local population 'suppression' affects the progress of an outbreak because the effect of trapping might be offset by immigration (Weslien and Lindelöw 1989; Duelli *et al.* 1997). The extent of beetle movement will therefore be an important factor determining the scale of area-wide or landscape-level trapping programmes. Some of the factors identified as important in the planning and execution of a mass-trapping programme are given in Table 8.3, and an operational programme against the spruce bark beetle, *Ips typographus*, during outbreaks in southern Norway and Sweden is summarised in Box 8.2.

### 8.2.1 Development of operational programmes for mass-trapping

Mass-trapping with pheromone traps in bark beetle outbreaks is, in a number of respects, similar to the traditional management technique of using trap trees. The idea of using trap trees was first developed in the eighteenth century as a response to outbreaks of *Ips typographus* in spruce forests in central Europe and from the mid-nineteenth century their use became standard practice, together with the application of 'clean silviculture' to reduce

availability of bark beetle breeding material (Vité 1989). Trees are usually made attractive to bark beetles by felling or girdling them, although herbicides have sometimes been applied to standing trees (O'Callaghan *et al.* 1980). Attaching pheromone lures to trees considerably enhances their attractiveness. In one comparative study, pheromone-baited trap trees caught up to 3.5 times more *I. typographus* than pheromone-baited traps (Fig. 8.6). Beetles may be more responsive to pheromone lures when attached to trees than when placed in traps because an 'appropriate' silhouette and natural host kairomone may complement the

lure. However, the superiority of pheromone-baited trap trees does not appear to hold for all bark beetle species. For Douglas fir beetle, *Dendroctonus pseudotsugae*, for example, traps are much more effective than trees. One of the main reasons for this is that as trees become colonised, antiaggregation pheromones are produced, deterring later arriving beetles (Laidlaw *et al.* 2003). For different bark beetle species therefore, the optimum trapping method may need to be determined experimentally.

Both trap trees and traps have the disadvantage that within stands they can initiate 'spillover' attack by attracting and concentrating beetles within the forest, making it necessary to monitor surrounding trees to prevent the formation of new outbreak foci. Trap trees are also labour intensive and careful monitoring is necessary to ensure that they are removed before becoming fully colonised to prevent beetle reemergence or completion of brood development. Spraying the trunk with insecticide can prevent beetle breeding and so reduce the need for regular surveillance. Particular advantages of using traps are that captured beetles cannot breed or reemerge and that traps can be located where they are likely to be most effective. For mass-attacking bark beetles therefore, traps should normally be placed *outside* the stand, such as on areas where previously infested trees have been clear-felled.

Traps and lures for mass-trapping should ideally be designed to maximise trap catches but the response of insects to traps can be complex and

**Table 8.3** Key aspects of mass-trapping programmes against aggressive bark beetles

### Mass-trapping programmes

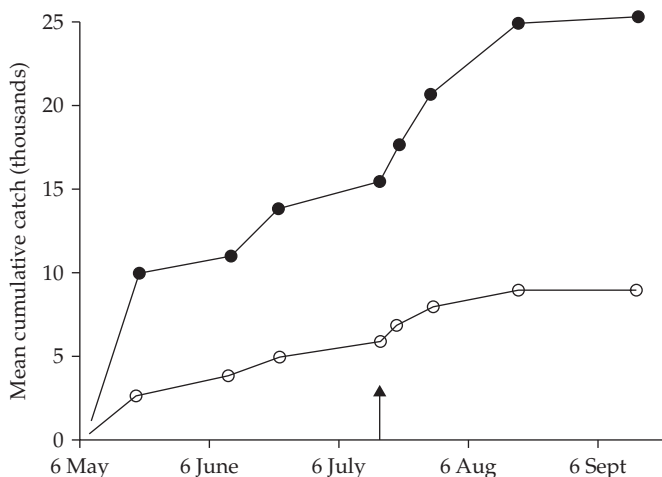
#### Pre-requisites

- Pheromone has been fully identified
- Synthetic pheromone components, suitably formulated, are commercially available
- An efficient trap is commercially available
- Main factors affecting trap catch in the field have been identified
- Area-wide campaign economically feasible
- Some damage can be tolerated

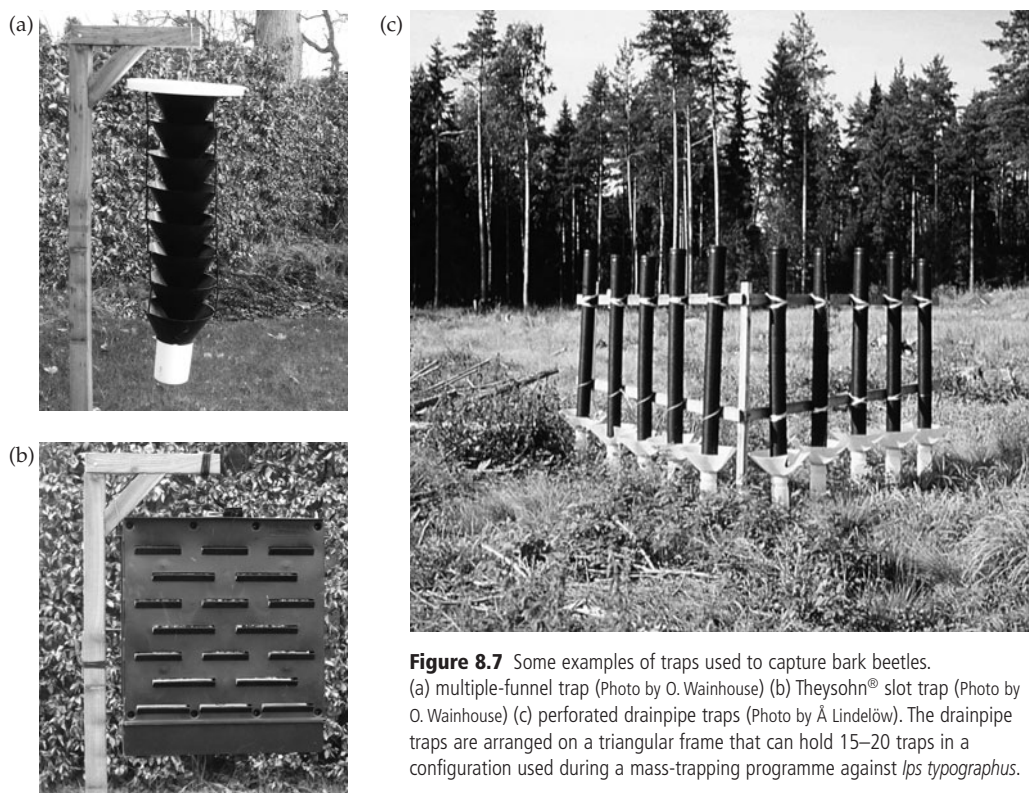
#### Protocol

- Initiate trapping in the early stages of the outbreak
- Avoid trapping (1) in or near unaffected stands during outbreaks  
(2) in vulnerable stands already attacked
- Trap in affected stands clearfelled in the previous season

Sources: Bakke (1989), Eidmann (1983), Weslien (1992a).



**Figure 8.6** Captures of *Ips typographus* at trap trees (●) and in slot traps (○), both of which were baited with aggregation pheromone dispensers. Several trees, which were insecticide treated, were paired with traps and the pheromone lure alternated between trap and tree when collections were made. Catches reflect the 'catching power' of a tree or single trap and were not adjusted for differences in trapping area. The greater increase in catch on the tree when lures were changed in mid-July reflected the higher pheromone loss rate from lures that had been exposed on the tree trunk compared to ones enclosed in the trap (from Raty *et al.* 1995).



**Figure 8.7** Some examples of traps used to capture bark beetles. (a) multiple-funnel trap (Photo by O. Wainhouse) (b) Theysohn® slot trap (Photo by O. Wainhouse) (c) perforated drainpipe traps (Photo by Å Lindelöw). The drainpipe traps are arranged on a triangular frame that can hold 15–20 traps in a configuration used during a mass-trapping programme against *Ips typographus*.

often poorly understood so this is difficult to achieve in practice (Muirhead-Thomson 1991). As a result, traps are often a compromise between 'designed' characteristics and the cost and ease of handling which are particularly important when considering logistics of large-scale trapping programmes. For bark beetle traps (Fig. 8.7), designed features include a strong silhouette, large trapping

area and ease of entry so as to maximise close range orientation and landing, and the capture of attracted beetles (McLean *et al.* 1987; Strom *et al.* 2001).

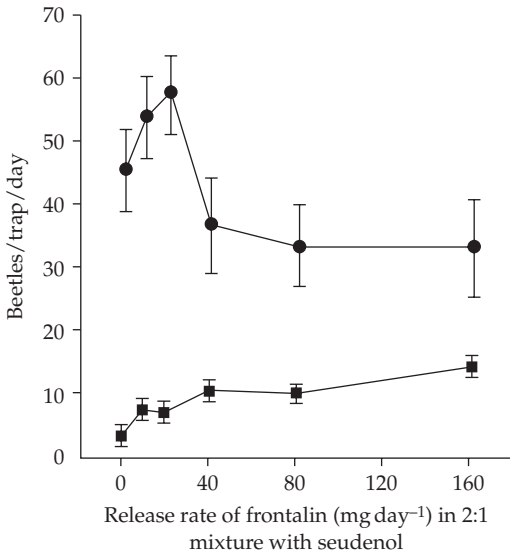
In a comparison between different types of trap, multiple-funnel traps were found to be much more effective than slot traps for trapping *D. pseudotsugae*, and being collapsible, they are easier to transport and deploy at trapping sites (Table 8.4).

**Table 8.4** Captures of *Dendroctonus pseudotsugae* and the clerid predator *Thanasimus undatulus* in 16-unit multiple-funnel traps and slot traps within a single forested area in Oregon, USA

Trap type	Number per trap		Number per 10 cm <sup>2</sup> trap surface		Male bark beetles (%)
	Bark beetle	Predator	Bark beetle	Predator	
Multiple-funnel	6803 ± 1427	92 ± 18	10.3 ± 2	0.14 ± 0.03	88.8
Slot	2748 ± 516	35 ± 11	6.9 ± 1	0.09 ± 0.03	89.0

Notes: Traps were baited with frontalinal and seudenol releasing respectively 5 and 2.5 mg day<sup>-1</sup> under standardised conditions and were deployed for approximately 2 months.

Source: Ross and Daterman (1998).



**Figure 8.8** The effect of the release rate of aggregation pheromones of *Dendroctonus pseudotsugae* on catches of the bark beetle (●) and an associated clerid predator *Thanasimus undatulus* (■) in multiple-funnel traps. The seudanol release rate was half that of frontalinalin. Catches of the predator increased with release rate. Most bark beetles were caught at a frontalinalin : seudanol release rate of 20 : 10 mg day<sup>-1</sup>. At higher release rates, threshold concentrations further from the trap may stimulate landing on other objects. The percentage of male bark beetles trapped increased from 62% to 92% as release rate increased (from Ross and Daterman 1998).

Although these traps also caught more clerid predators, the ratio of bark beetles to predators caught was similar for the two trap types.

The composition and release rate of the pheromone lure have an important influence on the capture not only of bark beetles but also of their natural enemies. The approach to the trap, landing and trap entry can all be affected and the different components of the pheromone blend may interact with trap type to determine the number of beetles caught (Borden *et al.* 1982). In a study of the effect of pheromone release rate on capture of *D. pseudotsugae* and one of its predators, catches of the bark beetle were found to increase at first but then to decrease as the release rate went up (Fig. 8.8). The capture rate of predators on the other hand increased steadily with the release rate. The effect on bark beetle captures, also observed in other species including *I. typographus*, could be due to the occurrence of threshold concentrations of pheromone at some distance from traps, possibly resulting in landing and initiation of attack on nearby trees. Manipulating lure composition and release rate can help to minimise the impact of trapping programmes on natural enemies (Aukema *et al.* 2000). Physical exclusion of natural enemies from traps or provision of escape routes can also reduce the catch of natural enemies relative to that of bark beetles (Ross and Daterman 1998).

## 8.2.2 Case studies in mass-trapping

Two of the best examples of mass-trapping programmes on an operational-scale are those of ambrosia beetles in timber processing areas (Box 8.1) and *I. typographus* (Box 8.2). For mass-trapping of ambrosia beetles, the relationship between the number of beetles trapped and the reduction in damage to timber resulting from gallery construction by beetles and fungal staining of wood is likely to be relatively straightforward. For mass-attacking bark beetles, the effects of reducing population density are difficult to predict because tree mortality depends on a dynamic interaction between the number of attacking beetles and tree resistance, and intraspecific competition can be an important cause of beetle mortality. The number of beetles trapped therefore, cannot readily be equated to the number of trees 'saved' (Stenseth 1989). Some examples of estimating impact are given in Box 8.2.

## 8.3 Population manipulation

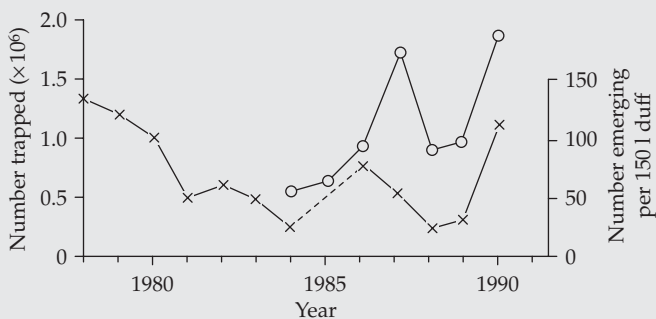
Some of the most important bark beetle pests are natural candidates for manipulation of populations. This is largely because their multicomponent pheromones include several active chemicals which have been identified and whose roles in different

### Box 8.1 Mass-trapping of *Trypodendron lineatum* in timber processing areas

Ambrosia beetles cause degrade of the timber when beetles excavate egg galleries in xylem of logs which become darkly stained by associated fungi. In a log sorting area on Vancouver Island, Canada, where logs are held prior to distribution to sawmills, populations of the ambrosia beetle, *T. lineatum*, can build up and cause significant economic damage. Beetles may enter the storage area in infested logs and can breed in these and in other logs held in store for an extended period, with a resulting build-up of populations overwintering in the surrounding forest margin. Mass-trapping was used in an operational-scale trial to reduce beetle populations and damage to logs. During a sustained period of trapping

(Fig. 8.9), millions of beetles were caught in multiple-funnel traps baited with the synthetic aggregation pheromone lineatin. Although in this study there was no direct evidence of a relationship between beetle population size and damage, degrade losses at sawmills declined significantly, apparently as a result of management of both timber supply and storage at the sorting areas, as well as mass-trapping. Assuming that trapped beetles would have successfully attacked and degraded logs, the benefit/cost ratio was estimated to exceed 5 to 1.

Key references: McLean (1985), Lindgren (1990), Lindgren and Fraser (1994).



**Figure 8.9** Total number of *Trypodendron lineatum* caught in multiple-funnel traps in a 15.5 ha log sorting area ( $\odot$ ) and number of beetles emerging from overwintering sites in the surrounding conifer forest margin ( $\times$ ). Prior to the sustained trapping effort, beetle populations were reduced by management of harvesting date and the amount of timber in storage in order to avoid beetle attack or emergence (from Lindgren and Fraser 1994).

phases of the attack behaviour have been described. Two contrasting strategies of manipulating bark beetle behaviour have been used in operational-scale trials—aggregation pheromones to contain and concentrate bark beetle attack in stands and antiaggregation pheromones to inhibit mass-attack on individual trees. In contrast to pheromones used in mass-trapping, pheromones used to manipulate populations are usually deployed *within* stands.

#### 8.3.1 Aggregation pheromones

Deployment of aggregation pheromones to contain beetles within specific areas of the forest can be a useful means of managing both spatial and temporal aspects of the silvicultural control of bark beetle infestations. Pheromone lures attached to trees can concentrate attack within already infested stands that are scheduled for harvesting. This method was used during outbreaks of the spruce bark beetle,

*Ips typographus*, in Sweden, with lures transferred from stand to stand as part of a rolling programme of clearfelling (Eidmann 1983). A similar technique of concentration and containment of infestations in localised areas within a stand has also been shown to have potential in the management of several bark beetle species where individually affected trees cannot be removed quickly in silvicultural operations (Shore *et al.* 1990; Borden 1992; Stock *et al.* 1994; Greenwood and Borden 2000). For managing small infestations of the mountain pine beetle, *Dendroctonus ponderosae*, baited transects are established throughout the affected area by attaching pheromone lures to the largest lodgepole pine at 50 m intervals along transects 50 m apart (Fig. 8.13). Emerging beetles are induced to attack baited trees within the infested area and so reduce the likelihood of the outbreak expanding. For univoltine populations, this allows up to 10 months for sanitation felling and the removal of infested trees.

### Box 8.2 Mass-trapping of *Ips typographus* in Scandinavia

Mass-trapping of the spruce bark beetle, *I. typographus*, in Norway and Sweden during outbreaks that persisted through most of the 1970s still provides one of the best examples of a large operational programme, with retrospective analysis of its impact.

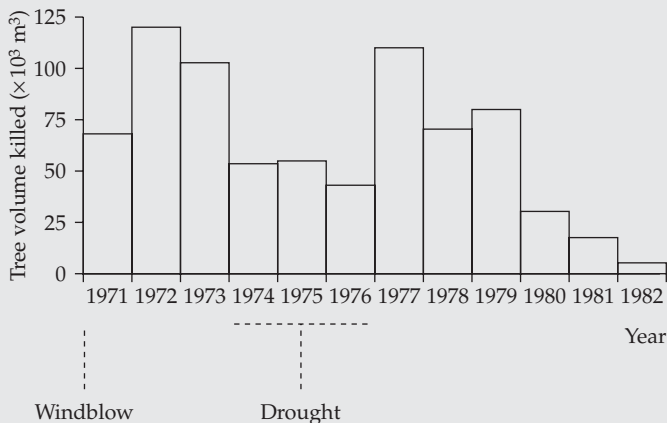
The bark beetle usually has one generation per year in Fennoscandia. Flight of overwintering beetles starts in May when trees are attacked, with a possible weather-influenced second flight of beetles that reemerge 2–4 weeks later. The seasonal trapping period for the bark beetle is therefore relatively short.

The outbreak was initiated by a combination of windblow and drought that coincided with a period when beetle populations were already high and many spruce forests mature or overmature (Fig. 8.10). In Norway, traditional methods of control before 1978 included felling thousands of trap trees in April for removal from the forest in June and locating and removing naturally infested trees. Pheromone-baited drainpipe traps (Fig. 8.7) were used from 1979, with about 600 000 deployed in 1979 and 1980, declining to 100 000 in 1982. In heavily infested areas, 20–30 traps were used per hectare after clearfelling to trap overwintering beetles and to reduce dispersal. Fewer traps

were used in less severely affected areas. Captures in monitoring traps (Fig. 8.11) allowed estimates of the total number caught and indicated that  $2.9 \times 10^9$  and  $4.5 \times 10^9$  beetles were trapped in 1979 and 1980, respectively.

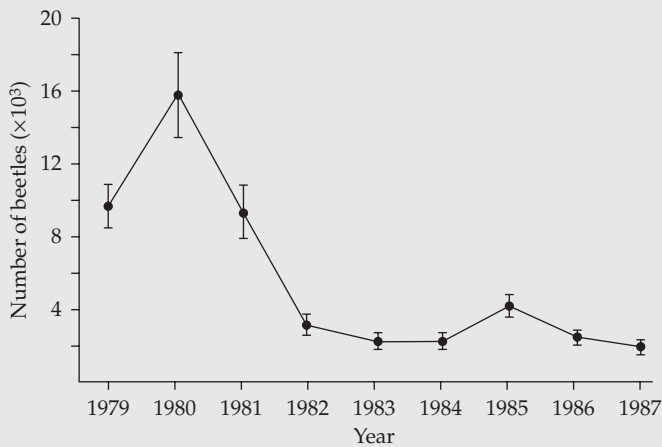
In the worst affected province of southern Sweden, both pheromone-baited standing trap-trees and drainpipe traps were used to trap beetles from 1978–81. The number of beetles colonising both baited and unbaited trees was proportional to size of the trees, with 7300 beetles colonising the 'average' tree (d.b.h. 24 cm). This allowed the numbers caught in traps to be related to an approximate estimate of population size based on the number of trees killed (Table 8.5) and suggests a capture rate of around 30%. The effect of capture rate on the growth rate of populations with different net reproductive rates (daughters per female) (Fig. 8.12), suggests that in the initial phase of an outbreak, population growth rate can be significantly reduced by the observed capture rate of ~30% although populations continue to increase. In declining populations, trapping has relatively little effect.

Key references: Bakke (1982, 1983, 1989), Eidmann (1983), Weslien (1992).



**Figure 8.10** Impact of an outbreak of *Ips typographus* in southern Norway. The initial outbreak was triggered by windblow in 1969 that affected around 4 million trees. The outbreak epicentre was initially concentrated around areas of windblow but the outbreak subsequently spread into surrounding spruce stands. Control measures included the use of trap trees and summer clearfelling of infested stands. From 1974–6, severe summer drought directly killed several million trees and affected the growth and resistance of trees over a wide area, resulting in a new outbreak (from Bakke 1983).

## Box 8.2 Continued



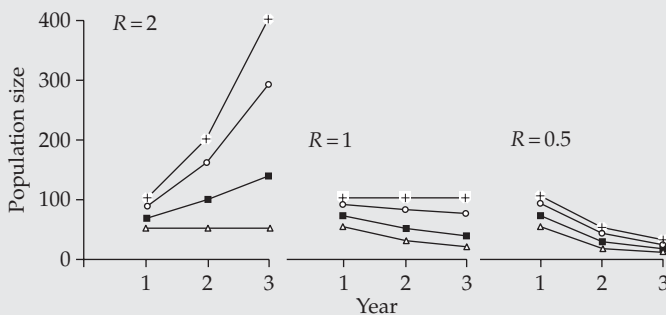
**Figure 8.11** Mean catch in 3000 designated monitoring traps initially established within the mass-trapping programme in Norway against *Ips typographus*. Pheromone-baited drainpipe traps were located on areas that had been clearfelled the previous winter (from Bakke 1989).

**Table 8.5** Estimated number of *Ips typographus* in pheromone traps and in trees attacked and killed by the bark beetle in the province of Värmland in southern Sweden

Year	Trees killed (thousands)	Attacking beetles (millions)	Trapped beetles (millions)	Capture rate (%)
1979	750	5500	1340	20
1980	510	3700	1960	34
1981	180	1300	550	30
Total	1440	10 500	3850	27

Note: Capture rate was estimated from numbers in traps as a proportion of the total population in trees and traps.

Source: Weslien (1992a).



**Figure 8.12** The effect of capture rate on *Ips typographus* population trends with different constant net reproductive rates ( $R$ ).  $R$ -values approximate to those found during the initial phase of attack ( $R = 2$ ), the declining phase of an outbreak ( $R = 0.5$ ), and an intermediate stage ( $R = 1.0$ ). +, No trapping; O, 10%; ■, 30%; and △, 50% capture rate (from Weslien 1992a).

### 8.3.2 Antiaggregation pheromones

Antiaggregation pheromones play an important role in helping to divert bark beetles to neighbouring trees as the tree under attack becomes fully

colonised. At different stages of the attack and at different distances from the tree, the absolute concentration of antiaggregation pheromone and the ratio of aggregation to antiaggregation pheromone



will vary but exactly how this affects beetle behaviour is not known. In *D. ponderosae*, the antiaggregation pheromone verbenone is produced by females, but inhibits the aggregation response of both sexes. The amount of verbenone relative to *trans*-verbenol and *exo*-brevicommin changes as a mass-attack progresses and the antiaggregation effect is strongest when the amount of verbenone released greatly exceeds that of the attractive components, as occurs on fully colonised trees (Miller *et al.* 1995). When antiaggregation pheromones are used in practice, their effectiveness is initially judged by their ability to depress catches in traps baited with the normal aggregation pheromone. Ultimately however, efficacy is determined by a reduction in attack on trees or stands as a whole. For several bark beetle species, verbenone has been found to be broadly dose-dependent in its effects (Fig. 8.14).

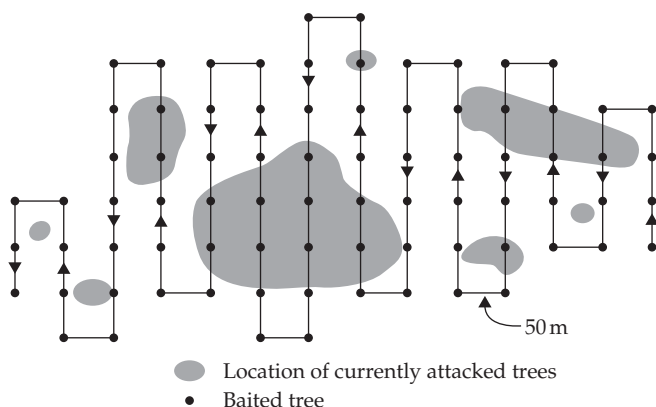
Verbenone inhibits attraction in several *Dendroctonus* spp. (Bertram and Paine 1994) and has been used to prevent growth of spot infestations of southern pine beetle, *D. frontalis*, in the extensive pine forests of southern United States. Outbreaks of this species often start around lightning-struck trees and then enlarge in a characteristic way, with dead or dying trees behind an expanding front of newly infested trees. Suppression of these infestations is important not only to minimise local losses but also to prevent spots coalescing to form large uncontrolled outbreaks. Typical management operations consist of felling infested trees which may either be left in the forest, removed or burnt, or on

rare occasions treated with insecticide. Management of spot infestations however, can be difficult in remote or wilderness areas, where there may be constraints on silvicultural operations. Verbenone has been shown to be of value in disrupting the active front of spot infestations especially when used in conjunction with felling (Payne *et al.* 1992; Clarke *et al.* 1999) (Fig. 8.15).

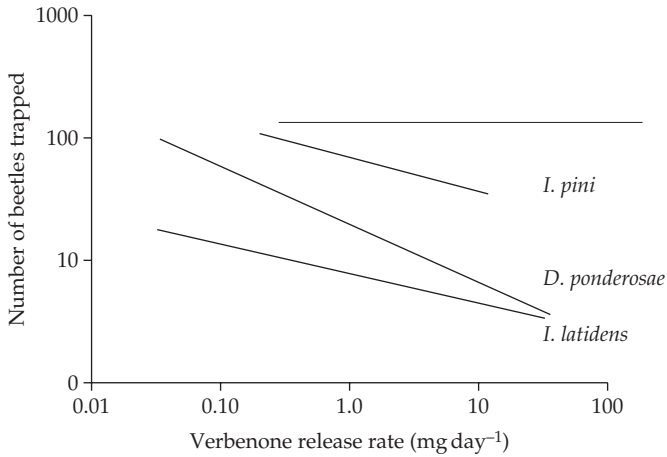
Operational-scale trials in which felling to suppress spot infestations was compared with verbenone treatment used alone or in combination with felling have shown how antiaggregation pheromones can be used in bark beetle management (Table 8.6). In the verbenone-only treatment, controlled-release dispensers were attached to all newly attacked trees as well as to uninfested trees in a buffer zone around the expanding spot front. In the verbenone plus felling treatment, dispensers were attached only to uninfested trees in the buffer zone and all currently infested trees were felled (Fig. 8.15). In these trials, both of the verbenone treatments were more effective than felling alone.

An economic comparison was made between verbenone treatment and the commonly used method of felling both infested trees and uninfested trees in a buffer zone and leaving them on site ('cut and leave'). This showed that the additional costs of the verbenone treatment were largely offset by the value of the uninfested buffer trees that did not need to be felled when using verbenone.

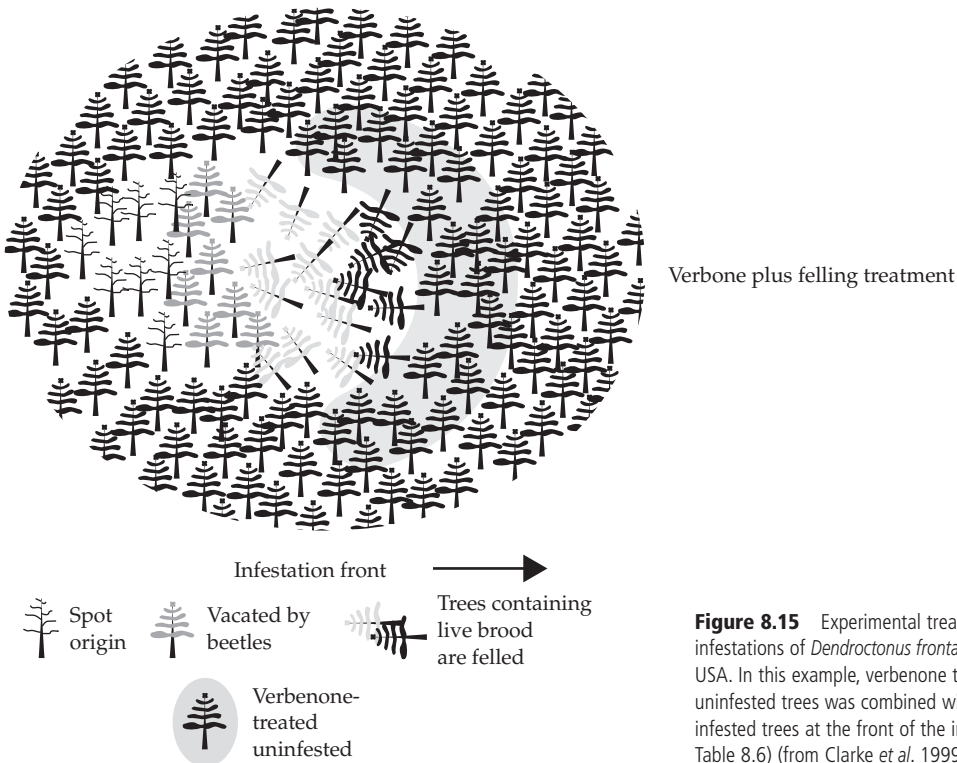
Antiaggregation pheromones have also been used to provide temporary protection of vulnerable



**Figure 8.13** A proposed arrangement of baited trees for containment of an infestation of *Dendroctonus ponderosae* in a lodgepole pine stand. Baiting trees with pheromone lures containing *trans*-verbenol, *exo*-brevicommin and the host tree monoterpene myrcene will induce emerging overwintered beetles to attack trees within the infested area, preventing spread of the outbreak. This method is now used operationally in western North America (from Borden 1992).



**Figure 8.14** The influence of different release rates of the antiaggregation pheromone verbenone on catches of the sympatric bark beetles *Dendroctonus ponderosae*, *Ips pini* and *I. latidens* in lodgepole pine forests in British Columbia, Canada. Increasing concentrations of verbenone released together with the relevant aggregation pheromones in multiple-funnel traps significantly depressed capture of beetles in the traps (data points have been omitted for clarity). The aggregation pheromones used were: *D. ponderosae*—*exo*-brevicomin, *cis*- and *trans*-verbenol and host kairomone myrcene; *I. pini*—*ipsdienol*; *I. latidens*—*ipsenol* (from Miller *et al.* 1995).



**Figure 8.15** Experimental treatment of spot infestations of *Dendroctonus frontalis* in south-eastern USA. In this example, verbenone treatment of uninfested trees was combined with felling currently infested trees at the front of the infestation (see Table 8.6) (from Clarke *et al.* 1999).

trees. The Douglas fir beetle, *D. pseudotsugae*, normally breeds in windblown or recently felled trees but may attack standing trees if populations build up. The antiaggregation pheromone 3-methyl-2-cyclohexenone (MCH) has been tested for its ability to inhibit attack on fallen trees and so

prevent an increase in population density. Douglas fir trees were felled to simulate windblown trees. Attack densities on unprotected trees were then compared with those on trees protected by MCH or MCH in combination with a nearby pheromone trap to attract and capture beetles repelled from

**Table 8.6** The effect of verbenone and felling treatments on the mean number of trees attacked or killed in spot infestations of *Dendroctonus frontalis* in pine forests in south-eastern USA

Treatment	Trees killed per day		Reduction in tree mortality(%)
	Pre-treatment	Post-treatment	
Verbenone plus felling	2.1	0.3	86
Verbenone-only	1.5	0.4	73
Felling-only	1.1	0.7	36
Control	1.8	1.8	0

Note: Polyethylene controlled-release dispensers were attached to trees at a height of 4 m and released verbenone over 40–50 days (i.e. exceeding one beetle generation). The number of dispensers used was related to tree size and to the number of infested trees in the spot. Approximately double the number of dispensers was used in the verbenone only treatment.

Source: Clarke *et al.* (1999).

**Table 8.7** Attack densities of *Dendroctonus pseudotsugae* on felled Douglas fir trees

Treatment	Galleries initiated per 0.1 m <sup>2</sup>	Brood production per tree	
		Curve 1	Curve 2
Control	5.8	6960	24 360
Trap-only	4.1	4920	20 910
MCH	0.4	4800	4800
MCH + trap	0.2	3000	3300

Note: Some trees were treated with the antiaggregation pheromone MCH by placing several dispensers along the bole, each releasing approximately 3 mg per 24 h. A multiple-funnel trap baited with the aggregation pheromone frontalin and seudenol and the host kairomone  $\alpha$ -pinene was placed next to some of the treated and untreated trees. Two published density dependent relationships between attack density and offspring per attack (curves 1 and 2) were used to estimate the effect of treatments on brood production per tree. For this bark beetle, antiaggregation pheromone treatment needed to reduce attack densities to <1 per 0.1 m<sup>2</sup> to achieve significant population reduction in the next generation.

Source: Lindgren *et al.* (1988).

treated trees in a 'push-pull' tactic (Table 8.7) (Borden 1997; Pickett *et al.* 1997).

Although the MCH treatment proved to be highly effective, it did not completely prevent attack and this finding is particularly significant for *D. pseudotsugae* because reproductive success is highly density dependent, even in susceptible felled trees. Reducing attack density by antiaggregation pheromone treatment could therefore actually increase the number of surviving offspring per

attacking beetle as a result of reduced competition. It is important therefore to determine whether anti-aggregation pheromone treatments can reduce attack enough to prevent significant population increase in the following generation. When antiaggregation pheromones are used to protect standing trees against aggressive bark beetle species, it may only be necessary to reduce attack density to below the critical threshold needed to overcome tree resistance.

A further refinement to the use of antiaggregation pheromones could include their release together with non-host volatiles. A range of volatile chemicals extracted from the bark of broadleaved trees has been shown to reduce the aggregation response of bark beetles (Borden *et al.* 2003; Zhang 2003).

A potential problem with antiaggregation pheromones is that, in the absence of supplementary aggregation lures, beetles are not trapped or killed so that treatments could simply divert attack onto surrounding trees with little overall reduction in the number of trees attacked within a stand. This is most likely to occur when beetle population density is high because there are abundant natural sources of aggregation pheromone as pioneer beetles initiate mass-attack. Beetles dispersing further afield may initiate new spot infestations or, perhaps more likely, contribute to the growth of existing infestations. This raises the question of the appropriate spatial scale of pest management tactics. In a study of management of spot infestations of

*D. frontalis*, Cronin *et al.* (1999) marked beetles and found that around 10% of beetles from untreated infestations colonised other spots up to 0.5 km away but this increased fourfold when spot infestations were treated by 'cut and leave' showing that local management can affect the movement of pests at relatively large spatial scales. Application of antiaggregation pheromone could exacerbate this problem although combining treatments with the use of pheromone-baited traps as in the case of the MCH treatments of *D. pseudotsugae* (Table 8.7), may help to reduce dispersal. The question of area-wide pest management is discussed further in Chapter 9.

#### **8.4 Registration and commercial availability of semiochemicals**

For the purposes of registration, pheromones, together with microbial pesticides and transgenic plant pesticides are usually classified as biological pesticides as distinct from chemical pesticides. Registration requirements in the United States and Europe are similar and are discussed by McClintock (1999), Neale and Newton (1999) and OECD (2001). The data requirements for

registration of pheromones are much less stringent than those for chemical insecticides, reflecting the fact that pheromones are classified as naturally occurring, non-toxic in their mode of action and with a narrow range of activity. It is necessary to establish that synthetic pheromones are substantially similar to the naturally occurring chemicals; data are also required on toxicity to mammals and non-target organisms in the environment. For some specific kinds of use, such as when only deployed in traps, pheromones may be exempt from regulation.

Effective operational use of pheromones depends to a large extent on the commercial availability of pheromone appropriately formulated to give the required release rate over an extended period. For mating-disruption of gypsy moth, *Lymantria dispar*, a plastic laminate flake formulation, Disparlure II, is the only one which is currently registered with the US Environmental Protection Agency (EPA) and commercially available (Thorpe *et al.* 2000). Other behaviour modifying chemicals registered by the EPA include the antiaggregation pheromones 3-methyl-2-cyclohexenone (MCH) and verbenone, and the volatile phenylpropanoid, 4-allylanisole, an inhibitory chemical present in pines and other conifers (McClintock 1999, [www.epa.gov](http://www.epa.gov)).

# Integrated pest management

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Integrated Pest Management (IPM) was originally developed as a response to the overuse of chemicals for the control of insect pests in agriculture and it came into common practice in the early 1970s. Since then the concept has been broadened to encompass later developments in pest management and control and to reflect the increasing importance, particularly in forestry, of wider aspects of environmental management and sustainability. Kogan (1998) gives a modern definition, emphasising the importance of IPM as a mechanism for selecting and using pest control tactics either singly or as part of a coordinated management strategy. Where appropriate, IPM should be based on cost-benefit analysis, taking into account the impact on society and the environment as well as the needs of producers. The overall emphasis of IPM is therefore on the management rather than the control of pests (Waters and Stark 1980).

Insecticides are much less widely used in forestry than in agriculture. They are used most commonly to protect plants during nursery production and may be applied to young transplants during forest establishment. Insecticide spraying of older trees is more likely to be done in high yielding, intensively managed plantations or in seed orchards than in managed forests. Nevertheless, extensive aerial spraying programmes to control pest outbreaks on mature trees are sometimes necessary. One of the best known examples is that of spruce budworm, *Choristoneura fumiferana*, in North America (Fig. 7.1). Allard (1998) gives some examples of large-scale programmes involving international collaboration to control pests that are likely to have a significant impact on national forestry programmes. The large scale of most forests, their low value per unit area and, in temperate regions at least, the often long rotation times are important logistical and economic constraints on expensive

direct control with chemical or microbial insecticides. An additional factor limiting insecticide use in forests is simply that many important forest pests have life-history characteristics or population dynamics traits that make them unsuitable targets for insecticides. For example, bark beetles that attack living trees often have eruptive population dynamics and are protected within the bark for much of their life-cycle. Similarly, leaf miners and shoot borers are difficult to target with insecticides. Clearly, an important aim of IPM in forestry, as in agriculture, is to minimise insecticide use especially in environmentally sensitive areas, in urban environments and in multiple-use forests where uses for amenity and recreation are important. But in managing forest pests, there is much more emphasis on integrating management techniques appropriate to the nature of the pests and the objectives of forest management. It is important to recognise, however, that such 'non-chemical' methods of pest management may themselves have unintended non-target effects. For example, the removal of moribund trees and other potential 'deadwood' from forests to prevent them being utilised by bark beetles has a significant effect on populations of those specialist insects and fungi that exploit this scarce resource but which have limited capacity for dispersal. In the management of forest pests and pathogens therefore, selection of the appropriate combination of methods outlined in the previous chapters should be used, based on an assessment not only of economic necessity but also of the possible environmental consequences of their application.

## 9.1 The economics of control

In agriculture, an assessment of potential losses in yield or 'quality' of produce as a result of pest

attack is particularly important and this is commonly used as a basis for decision-making in IPM. By emphasising the link between losses caused by pests and the need for and costs of control, IPM has played a key role in reducing insecticide input. For agricultural crops, determining economic damage thresholds is usually straightforward because the areas at risk are relatively small and there is often a simple relationship between pest abundance and loss. In forests, however, rotation times are usually measured in decades rather than months and this complicates an assessment of economic impact. In addition, many forests are publicly owned and maximising productivity is not always the primary objective of management. In forestry therefore, an economic assessment of pest impact as a component of IPM is usually much less developed than in agriculture. In the following sections, examples are given of how the impact of forest pests is measured and used either to assess the cost-effectiveness of management or as a decision rule for application of control measures.

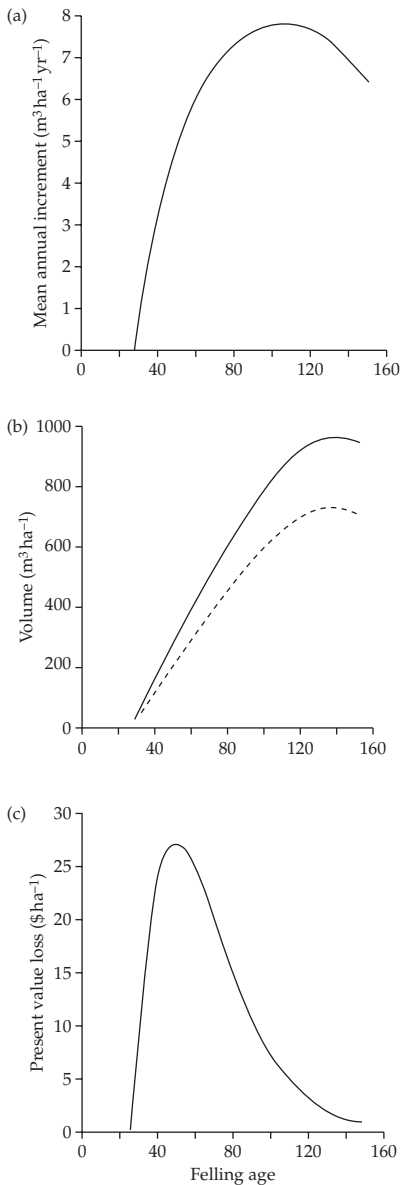
### 9.1.1 Measuring the economic effects of pest damage

From a strictly economic point of view, expenditure on control should not exceed the increase in eventual income resulting from the prevention of pest damage. When estimating the economic impact of damage to trees, and how much should be spent to prevent it, it is necessary to make allowance for the often long rotation times of trees. This is because the 'real' cost of expenditure on control is the current cost projected to rotation age, taking into account interest that could otherwise have been earned on the money spent. In fact, to compare current costs and future revenues on an equal basis, including additional revenue obtained as a result of control, income is usually discounted to present value rather than projected forwards to rotation age. This is usually done at a fixed rate of interest following standard forestry and economic practice (Price 1989; Fox *et al.* 1997).

The dynamics of stand growth and the effects of discounting on volume loss as a result of pest attack can be illustrated by a hypothetical example. Over a rotation, a stand increases in volume determined

by the growth rate of the trees. The average rate of growth of the stand varies over time and as trees mature, tends to slow down. The point at which this occurs for different tree species has an important influence on the time of felling, that is, the rotation length. The growth rate of a stand is normally expressed as the mean annual increment (MAI) in cubic metres per hectare per year (Fig. 9.1(a)). Rotation length can be determined in a number of ways but is often taken to be the time of maximum MAI which, in the example illustrated, is around 105 years. The growth of a stand of a given species on a particular site and under a particular forest management regime can be predicted by appropriate mensurational models. This predicted growth provides the basis of production forecasting in forestry. The growth function in Fig. 9.1(b) illustrates the increase in volume of a stand and the effect of a pest attack that causes a 25% volume loss at harvest. This loss could occur either through mortality of some individual trees within the stand or through sublethal effects causing growth loss. The value of the timber at felling and the estimated loss in value as a result of pest attack is usually determined from long-term average timber prices. The present value of that loss depends on felling age, that is, the period over which discounting occurs (Fig. 9.1(c)). This relationship shows that not only is there an upper limit to cost-effective expenditure on control, but that in this example, the present value of losses becomes much less significant as the stand approaches its rotation age. An example of the use of stand growth predictions and estimated yield losses in economic decisions in IPM is given in Box 9.1.

Mortality and growth loss are the dominant economic impacts of most forest pests and pathogens, although loss of quality can be important especially for those pests that affect the stems of high value trees. Quantifying impact helps to determine not only the level at which economic losses outweigh the costs of control but also how losses are likely to affect future timber supply, allowing forward planning of harvesting schedules. Although preventing yield loss is a major objective of pest management, other effects on forests and forest ecosystems can be important and can influence management decisions. For example, outbreaks can



**Figure 9.1** (a) A hypothetical mean annual increment (MAI) of a managed forest stand. A common method of determining rotation age is the point of maximum MAI, which in this example is approximately 105 years. (b) An example of a growth function showing the increase in volume of a forest stand without pest damage (—(yield)) and with pest damage assumed to result in a 25% loss (---(harvest)). (c) The present value (PV) of volume loss based on the growth function illustrated (Fig. 9.1(b)) assuming treatment was applied at establishment and to prevent volume loss.  $PV = (1/1 + r)^n \times P \times (\text{yield}_n - \text{harvest}_n)$ , where  $r = 0.05$  (i.e. 5% interest rate),  $P = \text{value of wood at felling } (\$5 \text{ m}^{-3})$  and  $n = \text{the number of years of discounting}$  (from Fox *et al.* 1997).

affect the structure and species composition of forests, influence nutrient cycling or affect people in urban environments. Some introduced pests that turn out to cause relatively little damage to trees may nevertheless have a significant effect on exports to countries that have phytosanitary measures directed against these pests. Making an economic assessment of these different kinds of impact and the cost-effectiveness of management is often impracticable and in many cases impossible. Some examples of pest impacts, their measurement and their economic significance are given below.

### 9.1.2 Impact on forests and forest ecosystems

#### *Growth loss and mortality*

Loss in basal area or volume growth is most commonly associated with defoliation. Defoliators therefore provide the main examples in this section. But attack by a range of pests can disrupt the normal growth of trees and examples include stem-colonising adelgids or scale insects and shoot-boring insects that occur within the tree crown. Insects that feed on terminal buds and shoots not only affect height growth but can also deform the main stem, resulting in a significant reduction in stem quality in mature trees. Loss of buds can sometimes induce dieback of one or more internodes, further affecting height growth. In some tree species, the effects of pest attack on height growth may be as important as those on radial growth (Van Sickle *et al.* 1983; Austarå *et al.* 1987; Väisänen *et al.* 1992; Carroll *et al.* 1993; Hall *et al.* 1993).

The effect that defoliators have on tree growth is influenced by a range of factors including the relative importance of carbohydrate stores in stems and roots as opposed to leaves, seasonal timing of defoliation and the age class of leaves on which they feed. Many broadleaved species are able to reflush following defoliation, especially when they are attacked early in the year, and this can reduce the overall impact of defoliation on growth. Conifers generally lack the ability to reflush in the same season and when completely defoliated, important stores of carbohydrates in the older age-class needles are lost. The impact of this on growth can be severe and in some conifers may leave them unable to survive the dormant season especially in regions

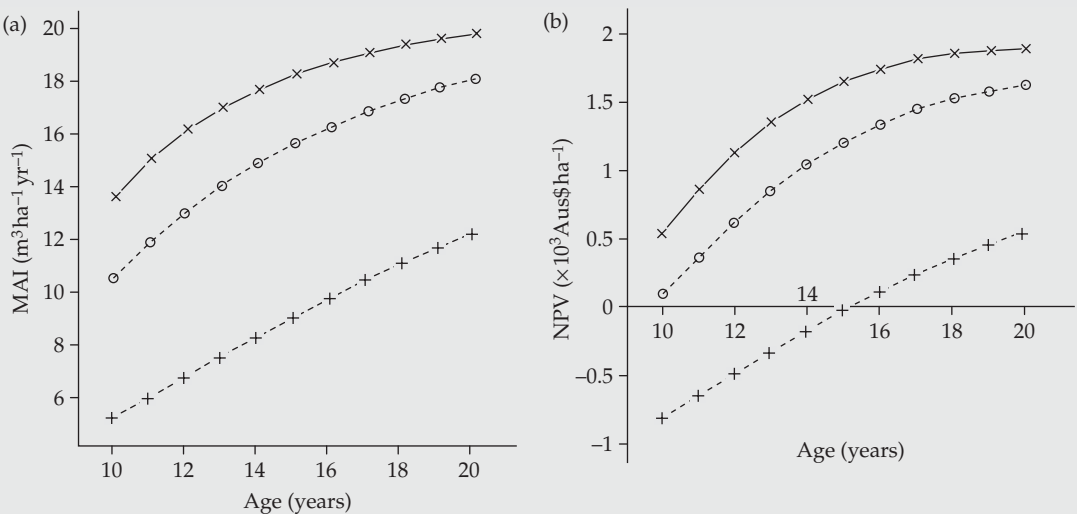
**Box 9.1 Tasmanian eucalyptus leaf beetle, *Chrysophtharta bimaculata***

This chrysomelid beetle, which is native to Tasmania, is economically the most important pest of eucalypt plantations of both native and introduced species. Larvae can cause high levels of defoliation but feeding by adults later in the season can also cause significant leaf damage. Defoliation and growth loss are linearly related and the effect of larval and adult feeding on young *Eucalyptus regnans* has been estimated using artificial defoliation applied to mimic natural attack. Data on the impact of defoliation have been used together with a single-tree growth model to estimate stand growth (Fig. 9.2(a)) and net present value (Fig. 9.2(b)) under different levels of attack by *C. bimaculata*. Although tree mortality can only occur after complete defoliation in consecutive growing seasons, the main economic impact is through growth loss and this can be prevented by direct control with insecticides.

There is a linear relationship between the number of egg batches or small larvae on shoots and the amount of defoliation, allowing prediction of levels of defoliation likely to cause economic losses. Monitoring is therefore an important part of IPM of this pest. In plantations at risk, egg or larval populations are regularly assessed during the summer period (mid-November–February).

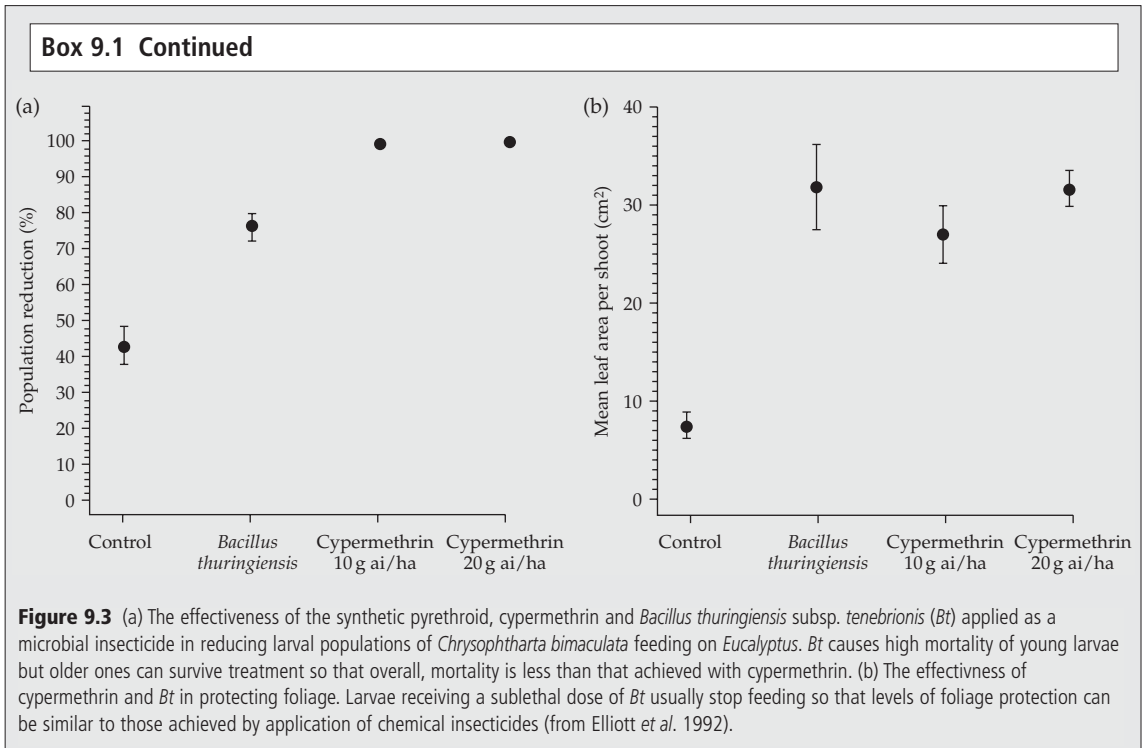
Studies on the ecology of *C. bimaculata* have shown that predatory beetles are an important cause of mortality of young larvae and can keep populations below the economic threshold. Most food consumption by larvae occurs in the third-fourth instar. Therefore where direct control with insecticides is necessary, and where populations are synchronous, insecticide can be applied after the main impact of predators on young larvae but before significant defoliation has occurred. Chemical insecticides are highly effective in direct control, killing both larvae and adults though some natural enemies are also killed. A microbial insecticide based on *Bacillus thuringiensis* subsp. *tenebrionis* (*Bt*) that is active against Coleoptera, is less effective in killing larvae (Fig. 9.3(a)). However, larvae that acquire a sublethal dose stop feeding so that overall levels of foliage protection are similar to those achieved with chemical insecticides (Fig. 9.3(b)). Although *Bt* does not affect adult beetles, which continue feeding, it has minimal effects on natural enemies and so has potential as a relatively safe replacement for chemical insecticides.

Key references: De Little *et al.* (1990), Candy *et al.* (1992), Elliot *et al.* (1992, 1993), Greener and Candy (1994), Elek and Beveridge (1999).



**Figure 9.2** (a) Mean annual increment (MAI) of young stands of *Eucalyptus regnans* in a simulation study of the effect of defoliation by *Chrysophtharta bimaculata*. In control stands (X), trees were ‘protected’ from defoliation with insecticides at 3, 5 and 7 years old, on the assumption that monitoring as part of IPM indicated likely damage in those years. Unprotected trees were attacked in years 3, 5 and 7 either by a ‘light’ defoliation by larvae equivalent to removal of 63% dry weight of new foliage (O) or light defoliation plus removal of refoliating shoots (+) that simulated repeated browsing by adult beetles. (b) Net present value (NPV), using a 6% discount rate, estimated for stand treatments in (a). NPV is the current (i.e. discounted) value of revenues minus costs. The simulation study illustrates the significant economic impact of continued adult feeding as well as providing an approximate guide to the likely economic impact of defoliation and the benefit of direct control as part of an IPM programme (from Candy *et al.* 1992).





where the growing season is short. For many defoliators the general relationship between growth loss and amount of defoliation is linear (Kulman 1971) (Fig. 9.4). The relationship between defoliation and mortality, however, is typically non-linear (Fig. 9.5). Very high levels of defoliation, especially if repeated in consecutive years, can often result in tree mortality. In some cases, trees can recover even from high levels of defoliation but may have increased susceptibility to attack by secondary pests or by pathogens which may kill them (Hadley and Veblen 1993; Wargo 1996; Alfaro *et al.* 1999; Cedervind *et al.* 2003).

The amount of growth loss for a given level of defoliation, and the intensity and frequency of defoliation necessary to kill trees, depends on the characteristics of particular pest–tree interactions. These aspects of the vulnerability of trees are often affected by site or stand factors and these can be an important component of the assessment of risk (Section 3.3). Quantifying growth loss and relating it to pest abundance depends on establishing a relationship between pest population size and injury, and between injury and economic damage. The distinction between injury such as defoliation, which

has a negative effect on the normal functioning of the tree, and damage in the narrow economic sense, such as yield loss, is important when calculating economic injury levels (EIL) (Box 9.3). The nature of the injury will obviously depend on the life-history characteristics of pests and pathogens but different types of injury can result in similar kinds of economic damage such as, for example, growth loss.

Methods for quantifying tree growth from measurements on annual rings were developed by Duff and Nolan (1953). Annual rings provide a record of the growth of individual trees at a particular site, preserving their response to, among other things, climatic variation and pest infestations. Their measurement is now a standard technique for assessing growth loss following pest attack. Growth rings also allow reconstruction of the timing and, to some extent, the impact of past outbreaks (Fig. 3.2), bearing in mind that such retrospective studies cannot account for losses that result from tree mortality.

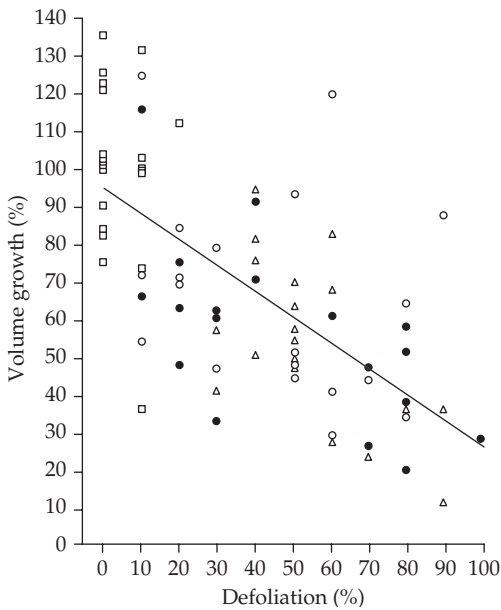
The most accurate and unbiased assessments of pest impact on growth are achieved by using insecticide-treated controls and experimentally manipulating plots of trees to achieve different levels of defoliation or other injury. Artificial defoliation

can sometimes provide useful information on growth loss, provided there is evidence that the effects are broadly equivalent to insect-caused defoliation. Methods of dating and measuring rings, and of cross-dating to detect missing ones, are discussed

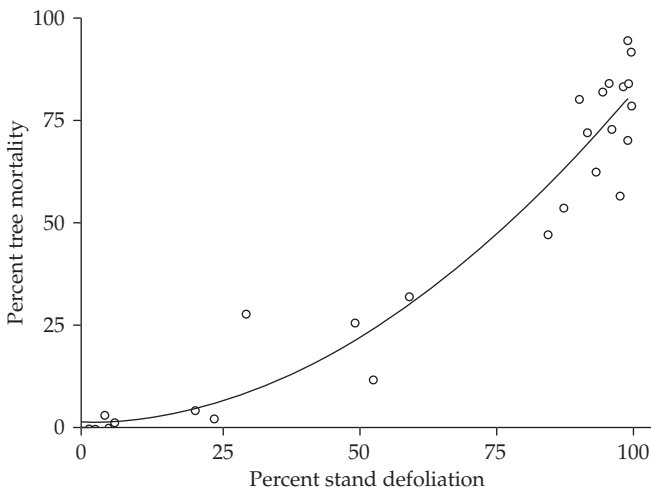
by Fritts (1976), Thomson and Van Sickle (1980), Phipps (1985) and Fritts and Swetnam (1989).

Simple measurements of growth can be made from increment cores, usually taken at breast height (~1.3 m), thus avoiding the need to fell trees. The extent to which measurements from increment cores reflect changes in tree growth depends on how the width of annual growth rings varies along the length of the stem and how this is modified by the effects of defoliation. For some pest-tree interactions, the effects of defoliation on stem radial growth are greater in the crown of trees than at other positions along the stem (Gross 1992). If there is significant variation in growth reduction along the stem, the much more time consuming method of whole stem analysis is needed to provide an accurate assessment of losses. In whole stem analysis, growth ring measurements are made on cross-sections taken at intervals along the stem after trees have been felled. Appropriate models are then used for calculating the volume of stem sections (Thomson and Van Sickle 1980; Fayle *et al.* 1983; Alfaro *et al.* 1985; Gross 1992).

Loss of growth resulting from pest attack is usually measured by comparing the period of depressed growth with that in the absence of attack, using suitable controls to allow for environmental or other influences on the trees. This is usually done in one of two ways. For individual trees, growth during the period of attack and subsequent recovery phase is compared with periods of 'normal' growth before and after attack (Thomson and



**Figure 9.4** The volume growth of dominant and codominant trees in stands of jack pine in Canada in relation to defoliation by *Choristoneura pinus pinus*, in the upper crown of trees. Growth is expressed as a percentage of average annual volume increment for the preinfestation period. Symbols represent different stands (from Gross 1992).

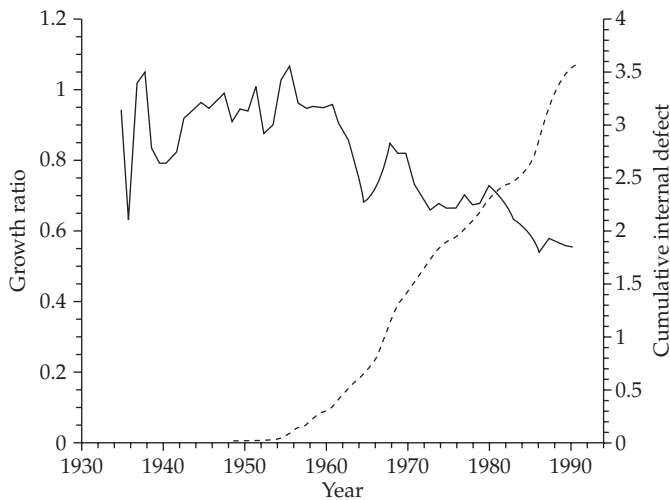


**Figure 9.5** The relationship between maximum percent defoliation by *Lambdina fuscicollis lugubrosa* and mortality in stands of mixed conifers in British Columbia, Canada. Trees were usually killed only when defoliation was severe or repeated in consecutive years. Mortality was higher in subdominant and suppressed trees than in dominant and codominant ones (from Alfaro *et al.* 1999).

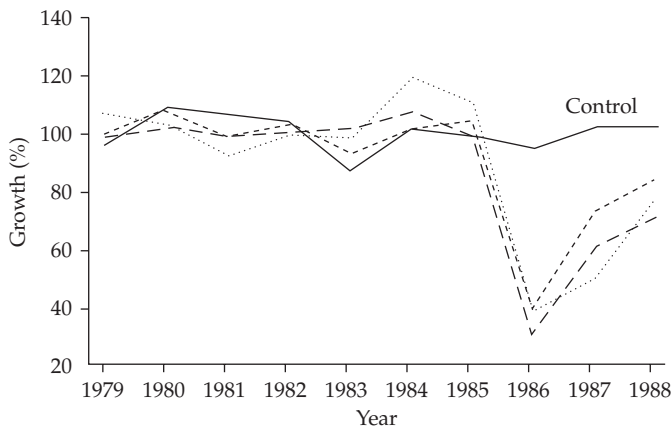
Van Sickle 1980; Alfaro *et al.* 1982, 1985; Van Sickle *et al.* 1983; Straw 1996). This method is not applicable where attacks are frequent or prolonged because chronic infestation prevents trees from achieving their growth potential on the site (Morrow and LaMarche 1978) (Fig. 9.6). Where chronic attack on individual trees is evident, growth loss can be estimated by comparison with similar unattacked trees in the same or nearby stands (Fig. 9.7). However, such trees will not be unbiased controls if they are affected by the reduced growth of their attacked neighbours or if their freedom from attack is not independent of growth-related factors such as vigour or timing of leaf flush.

When measuring the response of trees to defoliation, there is sometimes a delayed effect of defoliation on growth. To some extent, this is influenced by the seasonal timing of attack and the pattern of allocation of carbohydrate and other resources within affected trees (Kulman 1971; Alfaro and Sheppard 1991; Gross 1992; Straw 1996). Trees can sometimes compensate for the effects of moderate defoliation by internal reallocation of resources, by the buffering effect of carbohydrate stores and sometimes by increases in the photosynthetic rate of remaining foliage (Whitham *et al.* 1991; Trumble *et al.* 1993).

The size or age of trees, and whether they are dominant, subdominant or suppressed within the



**Figure 9.6** The effect of the stem colonising *Cryptococcus fagisuga* and associated infection by *Nectria coccinea* (beech bark disease) on radial growth of American beech in New Hampshire, USA. Chronic infestation by this introduced scale insect is evident from stem cross-sections showing darkened areas of xylem (internal defects) caused by local death of cambium due to fungal lesions (----). Growth was expressed as a ratio of that of similar uninfected trees (—). In severely infected trees, growth had been declining since they first became infected in the mid-1950s (from Gavin and Peart 1993).



**Figure 9.7** An example of the impact of defoliation by *Choristoneura pinus pinus* on growth of jack pine in Ontario, Canada, determined by whole stem analysis of a sample of dominant and codominant trees. Growth in one control and three defoliated stands was expressed as a percentage of the expected growth based on the mean annual volume increment for the 5-year pre-infestation period (1979–83). Intense defoliation occurred in 1985. Expressing proportional growth for each tree removes some effects due to variation in tree size (from Gross 1992).

stand, can affect their responses to a given level of defoliation as well as their ability to recover from attack. This may need to be taken into account when selecting trees for measuring effects at the level of the stand. Another complicating factor in estimating stand level effects is that compensatory growth can occur particularly by unattacked neighbouring trees that are able to respond to reduced competition.

If outbreaks kill trees, estimation of losses is more straightforward than when the main effect is a reduction in final yield. When young plantation trees are affected, losses include the costs of establishment and the relatively small effect on length of the rotation. If the establishment of plantations is affected, prophylactic insecticide treatment may be required or where protection from mammalian herbivores is needed, physical protection in the form of fencing may be essential for successful establishment (Gill 1992*a,b,c*). Mortality caused part way through a rotation is much more serious however. This is because significant expenditure on establishment and management has already been incurred but the trees may not be in their most productive period of growth and thus have little value. Outbreaks late in the rotation, such as those caused by bark beetles, have the greatest potential for economic loss although mature trees usually have significant salvage value. The practicability of salvage operations will depend on the size of the area affected and other logistic considerations. Where only some of the trees in a stand are killed, the effect may be equivalent to a silvicultural thinning, inducing a growth response in surviving trees that can compensate to some extent for the loss.

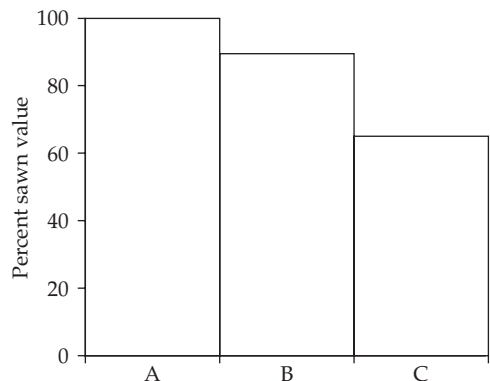
#### *Effects on timber quality and on seed loss in seed orchards*

When leading shoots are destroyed by pest attack, not only is height growth affected, but the resulting stem deformities can significantly affect timber quality in mature trees (Turgeon 1992; Väisänen *et al.* 1992). Mahogany is a highly desirable tropical hardwood but its value is dependent on high quality undeformed stems. Mahogany shoot borers, *Hypsipyla* spp., often kill the leading shoot, producing forked or otherwise deformed trees of little value and their attacks severely restrict the commercial

production of mahogany in conventional plantations (Newton *et al.* 1993). Mammalian herbivores can also affect the quality of timber by stripping the bark from the stems during winter browsing. This can result in extensive fungal staining of the timber and the initiation of decay (Gill 1992*c*).

Once trees have been harvested, the timber can still be vulnerable to pest attack and such post-harvest degrade can have significant economic impact. Ambrosia beetles that commonly attack logs in timber storage and processing areas can penetrate 8–9 cm into the sapwood of conifer logs and the often darkly stained adult galleries ('pinholes') as well as the larval galleries can significantly reduce timber values. Losses occur not only as a result of a reduction in value of the timber with pinholes but also as a result of changes to the sawing pattern necessary to minimise the amount of prepared timber with insect damage (Fig. 9.8). Similar problems can arise with timber affected by decay such as that caused by *Heterobasidion annosum* which affects the lower, most valuable part of the tree (Pratt 1979).

In seed orchards, specialist seed feeding insects can cause significant loss of seed. Seed orchards



**Figure 9.8** Losses in timber value resulting from attack by ambrosia beetles (*Trypodendron lineatum*, *Gnathotrichus sulcatus*) on western hemlock logs in Canadian sawmills. The theoretical maximum value (A) was estimated by a 'simulated' optimum cut of a log to obtain best timber value. In practice, changes to the automated optimum cut were made to remove the worst affected outer sapwood. The resulting timber, if uninfested, would have reduced value (B) representing deviation from optimum cut but there would also be additional losses due to extra handling time. Typically, some pinholes would remain in some timber after the modified cut, further reducing value (C) (from Orbay *et al.* 1994).

may be established with trees that are the product of expensive long-term breeding programmes. In these cases, seed pests can jeopardise the utilisation of genetic gains achieved by these programmes (Hodge *et al.* 1997). For these reasons, seed orchards are often managed much more intensively than normal stands.

#### *Home and export markets*

Where pest outbreaks cannot be effectively controlled or where control is not economically justified, it may be necessary to estimate projected losses and adjust forecasts of future timber supply. Even relatively low levels of attack when repeated periodically may require an extended rotation to achieve projected growth based on yield class (Straw 2002). Significant adjustments to future harvesting levels are most likely to be needed for pests that damage forests over extensive areas and where control is impracticable or only partially successful (Thomson and Alfaro 1990; Erdle and MacLean 1999; MacLean *et al.* 2002). One of the best examples of this approach to determining sustainable harvest levels is that of the spruce budworm, *C. fumiferana*, in eastern Canada, which is discussed in the section on Decision Support Systems (Fig. 9.11).

When exotic pests have become established, their impact may need to be assessed both in terms of yield loss in affected forests and possible effects on exports to areas from which the pest is absent. Pests which attack timber are most likely to have an effect on the export market. Timber may be prohibited or require costly treatments such as kiln drying before export to pest-free regions.

Assessment of both these impacts can be used to inform decisions on whether to attempt eradication of introduced pests (Section 2.5.2). Because exotic pests can be especially damaging, internal quarantine or other measures are often used to contain the pest and reduce spread where eradication is not possible. It is difficult and often impossible to get accurate estimates of the economic effectiveness of such measures but some attempts have been made (Box 9.5 and 9.7).

#### *People and the urban environment*

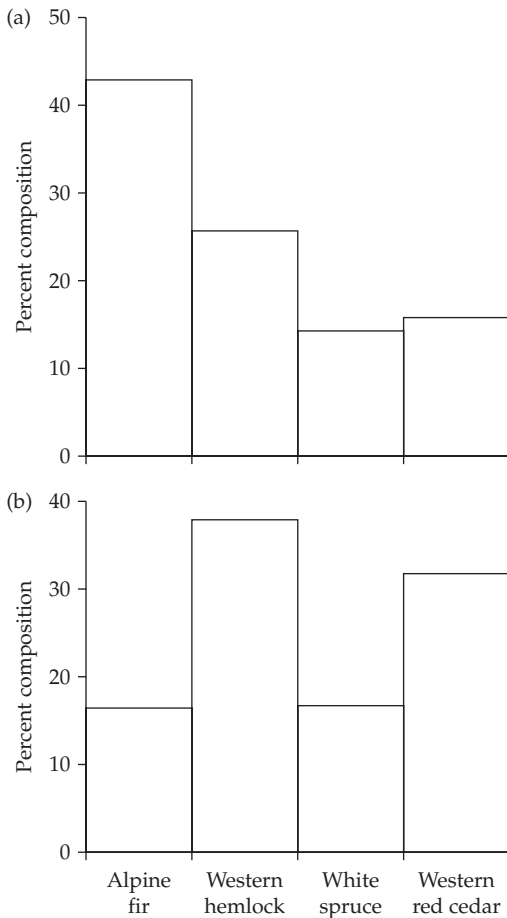
Pests such as gypsy moth, *Lymantria dispar*, and brown tail moth, *Euproctis chryorrhoea*, have larvae

with irritant hairs that cause allergic reactions in some people. Such pests can affect recreational and residential values (Table 9.3) and may warrant direct control. Defoliators also affect the shade value of trees in areas with high summer temperatures. Wood-boring insects such as Asian longhorn, *Anoplophora glabripennis*, can affect the stability of trees in urban areas, increasing the risk to people and property from falling trees or branches during stormy weather (Nowak *et al.* 2001). A similar introduced pest, the eucalyptus longhorn borer, *Phoracantha semipunctata*, attacks and can kill eucalypts that are important trees in the urban landscape of California, USA. Management of this pest includes avoiding injury to the trees, planting with species better adapted to the local climate (Section 5.6.1), sanitation felling and destruction of infested logs, together with biocontrol with an introduced parasitic wasp (Paine *et al.* 1995).

#### *Stand composition and ecosystem effects*

Some exotic pests and pathogens are so damaging to native tree species that they can cause significant changes in forest composition within a relatively short time and in some cases, their impacts may extend to a regional scale (Castello *et al.* 1995). One of the best known examples is that of the chestnut blight, *Cryphonectria parasitica*. Following introduction to eastern North America, this devastating pathogen killed most of the mature American chestnut, reducing a once commercially important tree species to a minor component of the understorey of the mixed hardwood forests (Griffen 2000). In Western Europe, Dutch elm disease, caused by *Ophiostoma novo-ulmi*, which is transmitted by scolytid bark beetles, has killed millions of elm trees and permanently altered rural landscapes (Box 2.2).

On a more local scale, pests and pathogens can influence species composition by killing susceptible species in mixed-species stands (Fig. 9.9). In oak-dominated stands in eastern United States, defoliation by *L. dispar* can lead to mortality of oaks that dominate the upper canopy, allowing slower growing shade tolerant species to occupy dominant positions within the canopy (Fajvan and Wood 1996). Sometimes, the death of susceptible species can increase the abundance of that species within



**Figure 9.9** In British Columbia, Canada, outbreaks of the defoliator *Lambdina fuscicornis lugubrosa* cause mortality in mixed conifer stands after 2–4 years defoliation. (a) In the study area, pre-outbreak stands were dominated by alpine fir. The primary host of this insect is western hemlock but significantly more alpine fir were killed in defoliated stands (b) resulting in a significant difference in pre- and post-outbreak species composition of forests (from Alfaro *et al.* 1999).

stands. In north-eastern USA, beech bark disease caused by the sequential action of an introduced scale insect, *Cryptococcus fagisuga*, and the pathogen, *Nectria coccinea*, kills susceptible American beech in mixed hardwood stands but subsequent development of root suckers can result in dense thickets of beech trees (Houston 1994).

In some cases, changes in species composition may actually increase susceptibility to other pests. In western USA, the mountain pine beetle,

*Dendroctonus ponderosae*, causes significant mortality in stands dominated by overmature lodgepole pine. The resulting regeneration of shade-tolerant true firs and spruce is likely to result in forests that will ultimately be more susceptible to western spruce budworm, *Choristoneura occidentalis* (Wilson *et al.* 1998).

Other more general effects of herbivory on forest ecosystems may arise through their effects on nutrient recycling (Schowalter *et al.* 1986, 1991). The leaf litter and frass from the activities of defoliators and honeydew secreted by aphids can influence the nitrogen cycle and so have the potential to affect plant growth. However, effects on soil nutrient levels appear to be complex and at least partly dependent on soil fertility, activity of microorganisms and other site characteristics (Stadler and Michalzik 1999; Christensen *et al.* 2002; Lovett *et al.* 2002).

## 9.2 Decision support and expert systems

Management decisions in IPM often depend on utilising information from many different sources. Relevant information may include an assessment of the risk associated with particular stands, results from local pest monitoring and the relationship between the severity of attack and yield loss. This information may not always be readily available and this can constrain the development and integration of IPM methods. Much potentially useful information may therefore be unutilised and sometimes valuable expertise can be lost through movements of personnel. The development of a decision support system (DSS) can be of considerable value in 'capturing' and organising diverse sources of information, facilitating and increasing the flow of information to forest managers.

A DSS can be defined as 'an interactive computer-based system designed to help decision-makers utilise data, narrative information, and models to solve unstructured problems' (Coulson and Saunders 1987). For unstructured problems, which are generally complex, the full range of possible solutions is unknown. The ability of DSSs to deal with qualitative information is important because both 'facts' and 'experience' can aid decision-making. The emphasis is therefore on decision support because the judgement

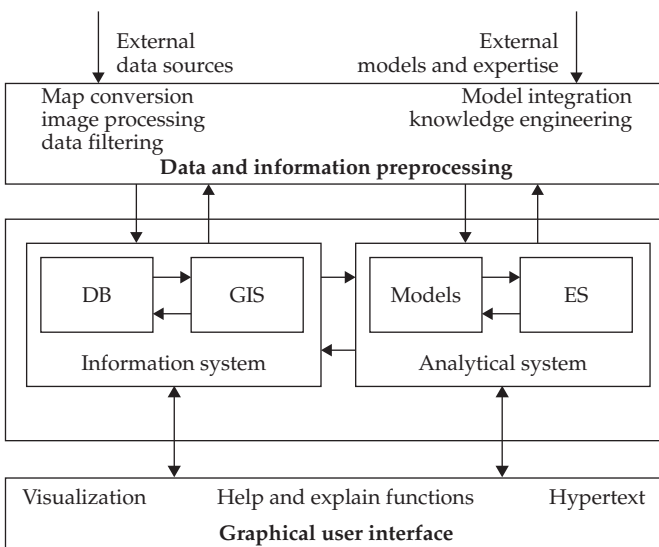
of the manager or user is still important, particularly where the decision has socio-political as well as economic or environmental aspects.

A DSS can be relatively simple and based, for example, around a single main component such as a risk-rating system together with methods for reducing risk. The DSS for management of the spruce beetle, *Dendroctonus rufipennis*, (SBexpert) is an example of such a system (Reynolds *et al.* 1994). More complex DSSs may incorporate a number of different subsystems and can be used at different levels (Fig. 9.10). A database (DB), for example, could contain information on stand composition, management history and history of pest attack and, based on previous experience, could be used to inform judgements on future stand management. Expert systems (ES) are knowledge-based and can be defined as 'computer programs that emulate the decision-making logic that human experts use when solving a particular problem' (Heong 1990). Within a clearly defined area such as diagnosis or systematics, they allow the solution of problems using expert knowledge that would normally take years of training and experience to acquire and they are therefore a valuable aid in decision-making (Stone *et al.* 1986; Väkevä and Saarenmaa 1992; Thomson and Van Sickle 1996). An expert subsystem within a DSS can also be used as part of the

user interface, making the more complicated aspects of DSS such as mathematical models more accessible. Geographic information systems (GIS) as sub-components are particularly useful where IPM has a landscape scale perspective such as in control of eruptive pests. The incorporation of models into DSSs can allow managers to examine the effects of alternative management strategies within the limitations of the accuracy of data or models and the unpredictability of natural systems. An example of this is given in Box 9.2.

When developing a DSS, it is important that the needs of the manager or decision-maker are understood and that the problem has therefore been clearly defined (Knight and Mumford 1994). This not only ensures that the right kind of information is available in sufficient detail but it can also help to focus research on areas where more information is needed.

Decision support systems do however, have some disadvantages that may have affected their wider development. For example, they require considerable effort and technical infrastructure to develop and there is a continuing need for maintenance and upgrading. Detailed analysis of the structure and operation of expert and DSSs can be found in Turban (1993) and Rauscher (1995). Several DSSs for forest pest management are available either as illustrative prototypes or as systems under



**Figure 9.10** An example of the organisation and level of integration of a decision support-system that contains a number of subsystems including databases (DB), geographical information systems (GIS), quantitative numerical models and qualitative, rule-based expert systems (ES) (from Fedra 1995).

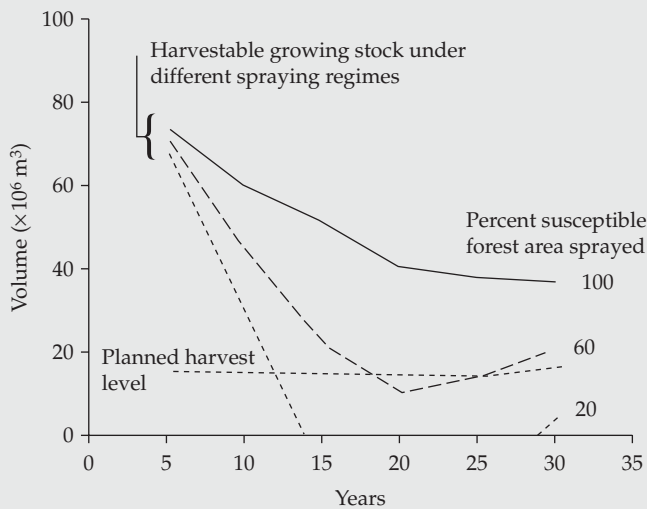
**Box 9.2 Spruce Budworm Decision Support System—determining impact on timber supply**

The spruce budworm, *C. fumiferana*, is the most important forest pest in Canada and is responsible for almost half of the timber volume lost to insects and pathogens. It is also one of the few forest pests for which both stand dynamics models and detailed impact data are available. Outbreaks of this pest usually last for 10–12 years and can result in repeated defoliation of current foliage of balsam fir and spruce, causing growth loss and eventually tree mortality.

Within the Spruce Budworm Decision Support System (SB-DSS), a stand growth model allows the effects of outbreak intensity and alternative management actions on stand development and timber supply to be determined. The areas affected by outbreaks are so large that it is neither feasible nor desirable to spray all of them during outbreaks. Methods for risk-rating of stands are used to predict where and when stands are likely to be defoliated.

The significance of tree mortality for a given region depends on how much timber supply exceeds demand. During outbreaks, the main choices for stand management are—no action, application of *Bt* or chemical insecticides, or salvage harvesting. In New Brunswick, targeted use of chemical and microbial insecticides is necessary to maintain planned harvesting levels. Potential losses during a severe outbreak were estimated using the SB-DSS which showed that at least 60% of susceptible forests would need to be protected to maintain current harvest levels (Fig. 9.11). Spraying with chemical or microbial insecticides is initiated in monitored stands only after at least 2 years of moderate to severe defoliation and is aimed at reducing defoliation of balsam fir in the year of treatment to 40%.

Key references: MacLean *et al.* (1996), Erdle and MacLean (1999), MacLean *et al.* (2002).



**Figure 9.11** The effect of a severe outbreak of *Choristoneura fumiferana* on timber supply in forests of New Brunswick, Canada. A simulated budworm outbreak cycle of about 30 years resulted in defoliation of current-year foliage during the first 10 years corresponding to 70, 90, 100, 100, 100, 90, 80, 80, 70 and 40% followed by 20 years of zero to light defoliation. Using the Spruce Budworm decision support system, losses in volume were estimated for different degrees of forest protection with chemical or microbial insecticides. Maintaining planned harvesting levels in budworm affected areas requires harvesting of some stands earlier than planned, depleting the harvestable growing stock. During severe outbreaks, at least 60% of the susceptible forest area would need to be sprayed to maintain current harvesting levels (from MacLean *et al.* 2002).

progressive development. In addition to the SB-DSS (Box 9.2), examples include jack pine budworm, *Choristoneura pinus pinus* (Loh *et al.* 1991) and spruce

beetle, *D. rufipennis* (Reynolds *et al.* 1994). Magarey *et al.* (2002) discuss the application of DSSs to the management of plant diseases in general.



### 9.3 IPM in practice

An assessment of the economic or environmental impact of pests and pathogens is an important aspect of IPM even though this can be difficult to quantify. Use of an economic injury level (EIL), developed largely for agricultural crops, can help to focus attention on the factors that are important in determining the relationship between pest population size and damage to trees. Strictly speaking, the EIL is a *damage* level and is defined as the lowest pest population density that will cause economic damage. When used in conjunction with a critical density (CD)—the density at which control measures should be initiated to prevent the pest population from reaching the EIL—the economic injury level can provide the basis for decision-making in IPM. The level at which the CD is set is usually based on judgement and experience and will depend, for example, on the rate at which the population is likely to increase towards the EIL and how quickly control operations can be initiated. The concepts of EIL and CD, originally developed for insect populations, are

not easily applied to pathogens. This is largely because it is difficult to estimate their abundance and often significant damage occurs before symptoms are visible (Jacobsen 1997). The EIL can be of practical value in assessing the cost-effectiveness of control actions against insect pests of intensively managed short-rotation energy or biomass crops, where assessing the short-term benefits of control is more straightforward (Box 9.3).

Integrated pest management programmes vary in complexity and sophistication. Management of some pests may be dominated by one method of control, influenced by key characteristics of their life history and their economic significance. Examples include programmes based on mating-disruption or on population monitoring and where necessary, treatment with microbial insecticides. The development of more sophisticated programmes requires much more information about population ecology and host interactions and for many pests this is often lacking, especially in developing countries (Wagner *et al.* 1991; Speight and Wylie 2001). In

#### Box 9.3 Economic injury level (EIL)

Control of *Chrysomela scripta*, a chrysomelid beetle defoliating short-rotation poplar plantations in North America, provides an example of the determination of the EIL which is defined as  $EIL = \frac{C}{V/DK}$ , where  $C$  is the cost of pest management per production unit of market value ( $V$ ),  $I$  represents injury units per pest,  $D$  the amount of damage per injury unit and  $K$  is the proportional reduction in pest attack by applied control.

The economic impact of first and third generation larvae is limited by the action of natural enemies and abiotic factors but defoliation by second generation larvae causes significant damage that can be prevented by direct control with insecticides. For second generation larvae on 2-year-old hybrid poplars, the EIL ranged from 0.2–0.9 egg-masses per actively growing terminal and was determined as follows:

Insecticide control ( $C$ ) was costed at \$25–30 for each hectare of 2622 trees and market value ( $V$ ) at \$0.02 (biomass fuel) to \$0.07 kg<sup>-1</sup> (pulp). The relationship between egg-mass density and defoliation (Fig. 9.12) was used to determine injury units per pest ( $I$ ). The damage per injury unit ( $D$ ) was determined from artificial defoliation experiments on actively growing terminals (Fig. 9.13). Insecticidal control of the beetle approached 100% effectiveness so that  $K$ , the proportional reduction in pest attack, was given a value of 1. EIL is calculated in

four steps:

1. Determine the 'gain threshold' corresponding to the yield needed to offset pest management costs =  $\frac{C}{V}$  kg ha<sup>-1</sup>. This ranged from 357–1500 kg ha<sup>-1</sup>.

2. Express gain threshold as equivalent percent biomass loss necessary for control costs to be

offset =  $\left( \frac{C \div V}{\text{projected biomass kg ha}^{-1}} \right) \times 100$ . With a projected

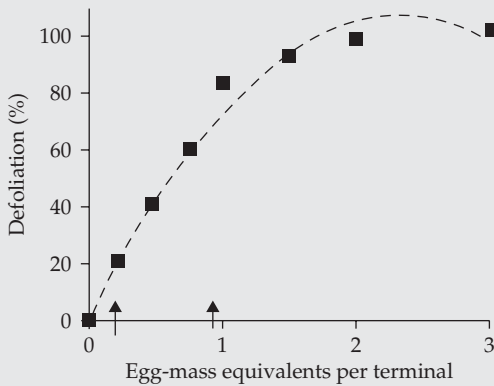
biomass of 5525 kg ha<sup>-1</sup> (from yield per tree at zero defoliation level  $\times$  trees per hectare) this gives percentage biomass loss equivalent to the gain threshold and ranges from 6.5–27.2%.

3. Determine percentage defoliation necessary to give this equivalent biomass loss (Fig. 9.13) = 22–69%.

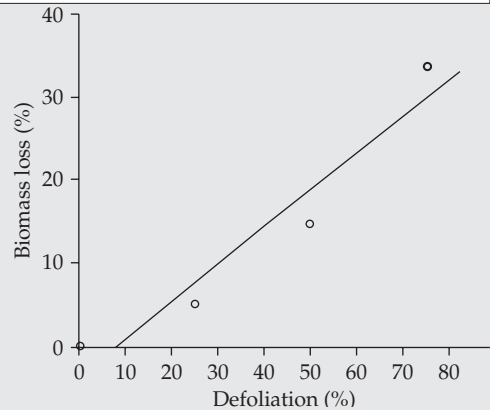
4. EIL is the number of egg-masses per actively growing terminal that would cause the necessary level of defoliation, that is, 0.2–0.9 (Fig. 9.12).

Market value ( $V$ ) is clearly important for setting limits to expenditure on management and for most forests is relatively low. How much damage or yield loss ( $D$ ) results from a given injury level is poorly understood for many forest pests causing sublethal damage.

Key references: Pedigo *et al.* (1986), Reichenbacher *et al.* (1996), Fang and Hart (2000), Fang *et al.* (2002).

**Box 9.3 Continued**


**Figure 9.12** The relationship between density of second generation egg-masses of *Chrysomela scripta* and defoliation of apical growth of young hybrid poplar saplings in Iowa, USA. Egg-masses contained approximately 42 eggs. The economic injury level was 0.2–0.9 egg-mass equivalents per terminal (↑) (from Fang and Hart 2000).



**Figure 9.13** The effect of artificial defoliation on percentage above-ground biomass loss of young hybrid poplar saplings. The timing and method of defoliation simulated natural damage predominantly by second generation larvae of *Chrysomela scripta* (data from Reichenbacher *et al.* 1996).

some cases, it may be possible to adapt existing IPM programmes developed for the same pest in another region or even those used for related pests. This approach is particularly useful in the management of exotic pests where little information is available on population dynamics or impact in the

region of introduction. In practice therefore, the development of IPM programmes requires an adaptive and flexible approach, selecting and combining methods based on existing information and experience, and improving techniques through continuing research. An example of combining and

**Box 9.4 The pine shoot beetle, *Tomicus piniperda*, as an exotic pest in North America**

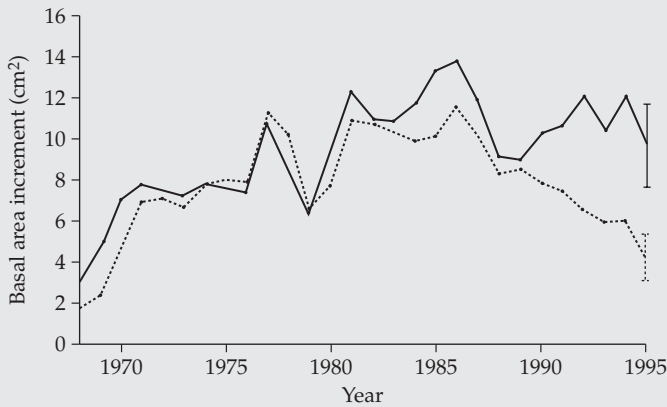
The way in which well-known methods for managing bark beetle populations can be effectively combined to minimise damage by pests is illustrated by an IPM programme developed for the pine shoot beetle, *T. piniperda*, following its introduction to the United States. Native to Europe and Asia, this bark beetle only breeds in highly stressed or moribund trees or more commonly in trees after felling. Adult beetles tunnel in the shoots of the crown of living trees during maturation feeding and this can have a significant impact on growth (Fig. 9.14.; see also Fig. 4.14). It is largely a secondary pest whose numbers can increase significantly following windblow or defoliation of trees by other pests. In north-central and north-eastern United States, this bark beetle has become an important pest of pines including valuable pine Christmas trees. Although in managed Christmas tree plantations, relatively little aesthetic damage is caused, there is a premium on

pest-free trees for export to uninfested areas. Part of the management strategy, therefore, is to reduce spread by only allowing trees certified free of beetle attack to be exported from the restricted areas covered by the Federal and State quarantines.

Several insecticides were shown to be effective but did not give 100% control or persist for an entire season. A combination of cultural and chemical controls designed to reduce infestation levels was widely tested among commercial growers (Table 9.1). Methods included destruction of potential breeding material, use of trap-logs which were destroyed before brood emergence and application of insecticide to control adults that were beginning maturation feeding.

Key references: Långström and Hellqvist (1990, 1993), Czokajlo *et al.* (1997), Haack *et al.* (1997b), McCullough and Sadof (1998).

## Box 9.4 Continued



**Figure 9.14** The effect of crown shoot maturation feeding by *Tomicus piniperda* on growth of Scots pine in New York State, USA. Mean basal area increment was determined from increment cores taken from trees that suffered 'moderate' (—) or 'severe' (-----) loss of lateral shoots. Attack by this introduced pest began around 1989 (from Czokajlo *et al.* 1997).

**Table 9.1** Percentage of Scots pine ( $\pm$ SE) with shoot damage cause by *Tomicus piniperda* in Christmas tree fields in Indiana, USA

Combinations of cultural and chemical control in an integrated management programme	Percent damage in autumn survey	Live adults per 1000 inspected trees
None	37.2 $\pm$ 1.1	159.7 $\pm$ 65.3
Sanitation; trap logs not properly destroyed	19.6 $\pm$ 10.2	69.3 $\pm$ 41.7
Sanitation	12.4 $\pm$ 1.3	32.5 $\pm$ 21.1
Sanitation + trap logs	5.4 $\pm$ 1.5	5.4 $\pm$ 1.5
Sanitation + foliar spray	3.2 $\pm$ 2.6	3.2 $\pm$ 2.6
Sanitation + trap logs + foliar spray	3.6 $\pm$ 0.4	0.9 $\pm$ 0.9

*Note:* Recommended cultural and chemical controls were adopted to different degrees by growers.

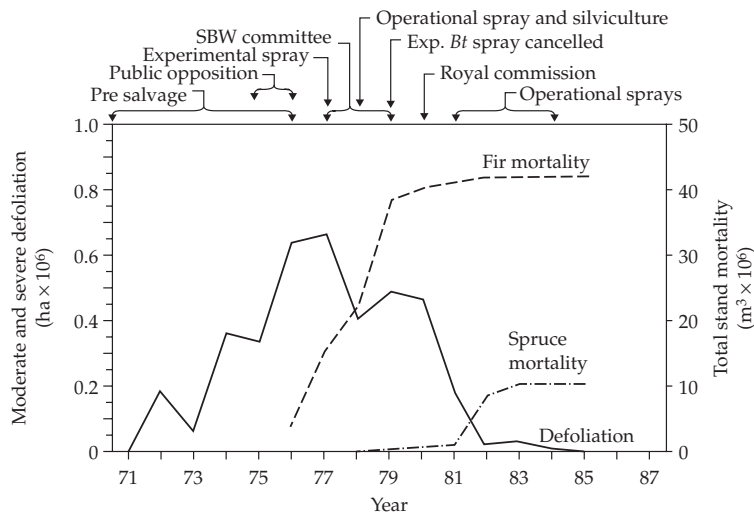
*Source:* McCullough and Sadof (1998).

developing established methods for the management of an introduced pest is given in Box 9.4.

The most comprehensive and sophisticated IPM programmes are aimed at 'key' pests that cause significant economic damage, often over very large areas and they are likely to have government involvement through national forest services (e.g. Bakke 1991). Government support is especially important where improvements in infrastructure are needed to allow access to remote or isolated areas, where there is a need for a coordinated response over forests of multiple ownership or where regulations are needed to impose internal quarantines. Government involvement is also likely to be needed when providing the public with information, especially when large-scale operations such as aerial spraying are planned, and also where targeted research effort is needed such as in the rapid isolation and identification of pheromones (e.g. Box 2.1).

Contingency planning is as important for IPM as it is in relation to plant health and the introduction of exotic pests (Section 2.5). Contingency plans allow strategies for management to be developed in advance (Shepherd 1994). Hudak (1991) gives an interesting example of the need for pre-planning in relation to public consultation when considering aerial spraying operations against the spruce budworm, *Choristoneura fumiferana* (Fig. 9.15).

Three examples of IPM programmes are discussed in the following Boxes. In all three examples, an attempt has been made to assess the cost-effectiveness of the programmes. Management of the spruce bark beetle, *Dendroctonus micans*, in the United Kingdom developed in stages as a response to the accidental introduction of this pest from mainland Europe. Unlike other economically important bark beetles, *D. micans* is not an eruptive pest but can damage and sometimes kill standing



**Figure 9.15** Moderate-severe defoliation by *Choristoneura fumiferana* and tree mortality during an outbreak in the largely publicly owned forests of Newfoundland, Canada. The forest management and public response at different stages of the outbreak are shown. This sequence of events resulted in considerable delay in implementing the programme so that effective control operations were only conducted during the declining phase of the outbreak. As a result, there was widespread tree mortality (from Hudak 1991).

trees when its populations are relatively low. If it became widely established, it would therefore impose a significant burden on the management of the highly productive plantations of the exotic Sitka spruce in the mild maritime climate of western Britain (Box 9.5).

The second example concerns the management of the European woodwasp, *Sirex noctilio*, during outbreaks in Australia in the 1980s. Methods for the biocontrol of *S. noctilio* with nematodes were developed in a classic study following the first experimental releases in Tasmania in 1970. In formulating the approach to management of more recent outbreaks, the original methods were adapted and incorporated into a comprehensive IPM programme (Box 9.6).

The final example describes the implementation of a programme to reduce the rate of spread of the gypsy moth, *Lymantria dispar*, in North America (Box 9.7). Key features of the programme were the development of the methodology in a series of pilot studies and the extensive use of the Internet to coordinate this large-scale programme.

## 9.4 Future developments in pest management

Forests are increasingly being managed for recreation and amenity as well as for commercial production.

This applies not just to natural or semi-natural forests but also to plantations which harbour a surprisingly diverse range of species (Chey *et al.* 1997, 1998). The requirements of management for conservation and biodiversity need therefore to be taken into account in the planning and execution of IPM programmes.

### 9.4.1 Certification, conservation and multiple-use forests

The emergence of forest and forest product certification schemes in the 1990s has focused attention on the environmental impact of forest management, including that of pest management. The catalyst for the emergence of such schemes was the 'Rio Earth Summit' (United Nations World Commission on Environment and Development 1987) and several schemes are now administered by environmental non-government organisations (Kneeshaw *et al.* 2000; Mihajlovich 2001). One of the best known is the Forest Stewardship Council (FSC) ([www.fsoax.org](http://www.fsoax.org)) and its guiding principles for best forestry practice include the promotion of non-chemical methods of pest management. Although minimising insecticide usage has always been an important part of IPM, for some countries reducing pesticide use in forests in order to achieve certification will require significant changes to pest management practices (Govender 2002).

Managing commercial forests for multiple objectives as varied as recreation, groundwater management or the enhancement of biodiversity, as well as wood production is likely to be difficult

to achieve. Conflicts are likely to arise where, for example, management for biodiversity increases the likelihood of pest outbreaks. When moribund trees are left in forests as a resource for rare or

### Box 9.5 The spruce bark beetle, *Dendroctonus micans*, in Britain

Widely distributed in Eurasia, the spread of this 'solitary' bark beetle in western Europe has been associated with the development of outbreaks in newly colonised areas, often resulting in significant mortality. *D. micans* does not kill trees through pheromone-mediated mass-attack but single females establish galleries in the bark of living trees so that significant damage can occur at relatively low population density. Eggs are laid *en-masse* and after hatching, larvae respond to an aggregation pheromone and feed communally on fresh bark. The life-cycle often takes more than 1 year. Trees usually survive one or two attacks, even though larval galleries can be large, but successive attacks are often fatal. The long life-cycle and the presence of effective defences within the bark of some trees results in relatively slow population build-up. However, a combination of sib-mating within galleries and solitary attack behaviour means that single females can establish viable populations, a factor that contributes to the significant risk of national and international spread.

*Dendroctonus micans* was first accidentally introduced to Wales and the English border region in the early 1970s. Following discovery of its presence in 1982, the main priorities were to minimise further spread through internal quarantine, to determine the extent of infestation by systematic survey and to reduce population densities by sanitation felling and destruction of infested bark. Timber movement was prohibited from a legally defined outbreak region, the *D. micans* Control Area (DMCA, Fig. 9.16), unless it had been processed in designated sawmills and certified pest-free before movement to other parts of the United Kingdom. Sanitation felling was subsequently restricted to a 'buffer' or peripheral area (PA) on the eastern border of the DMCA. With a limited pest distribution and effective internal quarantine in place, EU plant health legislation allows the designation of uninfested parts of the country as a *D. micans* protected zone (DMPZ) so that quarantine restrictions on imports can be maintained (Fig. 9.16).

The PA was repositioned several times reflecting spread of the beetle at 2–5 km year<sup>-1</sup> and was increasingly costly to maintain. Techniques of investment appraisal were used

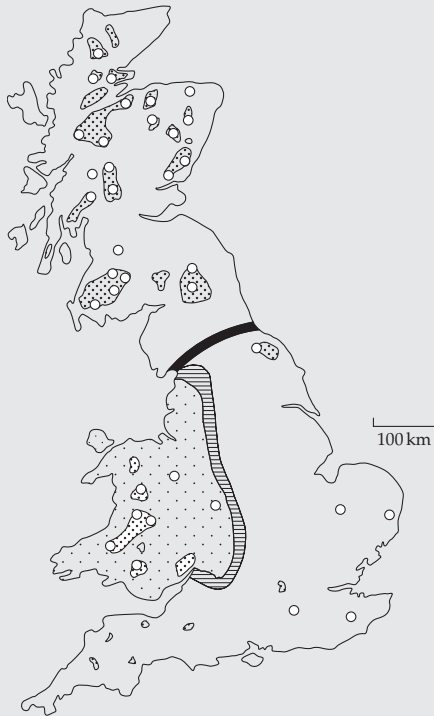
to cost three alternative options—maintain the current DMCA, abandon internal quarantine arrangements or reduce the length of the PA from 514 to 214 km by establishing a new one to the south of the major spruce growing areas in northern England and Scotland (Fig. 9.16). Making a number of alternative assumptions relating to rates of spread and tree mortality, the current practice, estimated to cost £54 500 per year (net present value of £860 000 over 50 years) proved to be the most cost-effective option under the range of assumptions made.

Along with the internal quarantine and sanitation measures, a classical biological control programme was developed, based on earlier studies in Belgium and France. These studies indicated that the specific predatory beetle, *Rhizophagus grandis*, was effective in locating and destroying *D. micans* larvae within galleries. Adult predators find attacked trees by responding to the odour of larval frass and both adults and their larvae feed on the immature stages of the bark beetle. The programme was based on the 'inoculative' release of relatively small numbers of laboratory-reared predators—50 pairs at sites with over 100 attacked trees, with smaller pro-rata releases with fewer attacked trees. This method quickly established the predator over a wide area where it occurs in 60–80% of galleries. The long generation time of the bark beetle, typically 15–18 months, low population density after sanitation felling and effective host-finding by the predator have all contributed to the success of the biocontrol programme.

The IPM programme has kept the main spruce growing areas of the United Kingdom outside Wales free of this introduced pest for over 20 years. A new introduction into southern England, discovered in the early 1990s, together with evidence of recent long-range dispersal from existing infestations is likely to require further modification of the IPM programme.

Key references: Grégoire (1988), Wainhouse *et al.* (1991), Evans and Fielding (1994), Wainhouse and Ashburner (1996), Fielding and Evans (1997), O'Neill and Evans (1999).

## Box 9.5 Continued



**Figure 9.16** Protection of major spruce growing areas (▨) in Great Britain by management of the spread of an introduced pest by internal quarantine, sanitation felling, and classical biocontrol. Within the *Dendroctonus micans* control area (DMCA) (▤), timber movement was restricted and bark beetle populations are suppressed initially by sanitation felling and then by release of the predator *Rhizophagus grandis*. Later on, annual surveys followed by sanitation felling and natural enemy release were restricted to a peripheral area (PA) (▨). International quarantine measures remained in force as a consequence of the designation of a *Dendroctonus micans* protected zone (DMPZ) within the European Union. This includes all areas of Britain outside the DMCA and can be maintained provided that regular surveys of permanent sample points (○) demonstrate the continued absence of the bark beetle from the DMPZ. An economic appraisal showed that maintaining the existing PA was more cost-effective than relocating it south of the main spruce growing areas in northern Britain (▬) or removing all controls. The discovery of a newly introduced population in southern England and the recent northwards extension of the existing infestation is however, likely to change current management practices (from O'Neill and Evans 1999).

specialised organisms, there can be an increased risk of damage by bark beetles and possibly by pathogenic fungi. For example, in the pine forests of southern United States, the red-cockaded woodpecker, *Picoides borealis*, is an endangered species. It is usually rare in commercial forests but the abundance of these birds can be increased by leaving mature trees infected with the heartwood infecting fungus, *Phellinus pini*, within stands. These trees are preferred by the birds for cavity excavation but such trees are vulnerable to attack by southern pine beetle, *Dendroctonus frontalis*, and so can serve as foci for infestation (Coulson *et al.* 1999a).

To avoid the problem of conflicts in management of multiple-use forests, it has been argued in Canada that the landscape should be zoned to achieve a balance between intensively managed plantations for commercial timber production, multiple-use areas and strictly protected wilderness areas (Binkley 1997). One obvious disadvantage of this approach is that in unmanaged wilderness areas, uncontrolled outbreaks of pests such as bark

beetles could develop and spread to neighbouring managed forests. In the much more densely populated European countries with limited land area, there is relatively little scope for segregated land use and here there is more emphasis on multiple-use management (Koch and Skovsgaard 1999). In less densely populated small countries such as New Zealand, the situation is intermediate between these two extremes. Much of the indigenous southern beech forest has been lost following European settlement and exotic conifer plantations have been established to ensure adequate timber supply. This has effectively zoned the landscape into commercial forests and the largely state-owned non-commercial native forest types. Whether, in the long term, survival of the relatively small and fragmented areas of native forest will depend on some form of sustainable management is a matter of continuing debate (Perley 2000; Whyte 2000). Another area of considerable debate is the extent to which projected climate change could influence the distribution and abundance of pests and pathogens and pose new challenges for pest management.

### 9.4.2 Climate change

Over the next 100 years or so, an increase in global average temperature and changes in rainfall pattern are predicted to occur largely in response to anthropogenically-caused increases in atmospheric CO<sub>2</sub> (Houghton *et al.* 2001, www.ipcc.ch). The main prediction from climate models, based on projected increases in greenhouse gasses are that over this period, average temperatures will rise by

1.4–5.8°C, accompanied by changes in rainfall pattern and increased climatic variability including the occurrence of more extreme weather. However, there is considerable uncertainty over the extent and variability of climate change on a regional scale. These general predictions have stimulated applied ecologists to examine the possible consequences of climate change for the distribution and abundance of pests and pathogens and on the

#### Box 9.6 The European woodwasp, *Sirex noctilio*, in the 'Green Triangle' of southern Australia.

Accidentally introduced into New Zealand in the early 1900s, this woodwasp spread to Tasmania in the early 1950s and to mainland Australia about a decade later. The idea of using nematodes for biocontrol developed from the observation in New Zealand that some outbreaks of *S. noctilio* collapsed naturally due to parasitism by the neotylenchid nematode, *Beddingia siricidicola*, which must have been introduced along with its host. The nematode life-cycle is unusual (Fig. 9.17). In particular, the free-living fungus-feeding or mycetophagous stage allows the nematode to be cultured more easily and to survive in the environment in the absence of its host. The parasitic stage of the nematode is effectively dispersed by sublethally affected female woodwasps.

The basic procedures for breeding and releasing nematodes were developed in Australia in the 1970s and subsequently used in an IPM programme in the Green Triangle of southern Australia. This is an area of up to 100 000 ha of radiata pine plantations affected by an outbreak of *S. noctilio* that had killed around 1 million trees by the start of the control programme in 1987. The objectives were to inoculate 20% of the *S. noctilio*-infested trees throughout the infested area, salvage some of the remaining infested trees, target thinning operations in stands with high levels of mortality to reduce tree susceptibility and to release parasitoid natural enemies.

Aerial and ground surveys were used to identify affected areas in which *S. noctilio*-infested trees were felled and delimbed prior to inoculation during the winter period. Using a specially designed hammer, nematodes formulated in gelatin foam, were inoculated at many points along the bole using around a 1000 nematodes per inoculation hole. Around 147 000 trees were inoculated throughout the area and the outbreak was brought under control. The programme was cost-effective (Table 9.2) and its success attributed in part to the large scale of the inoculation programme which evidently counteracted reduced

effectiveness of the nematode. Nematode parasitism, which had been close to 100% in the original Tasmanian programme, had dropped to around 25%. This was traced to the effects of continuous subculturing of the free-living form which over a period of 20 years had selected a strain that rarely formed the parasitic stage. The nematode was re-isolated from the original release area in Tasmania and found to have high levels of pathogenicity. This strain was of Hungarian origin and had been selected on the basis that when it was inoculated into trees, emerging *S. noctilio* were highly parasitised but could nevertheless fly further and lay more eggs than those parasitised with other strains and so it was more effectively dispersed.

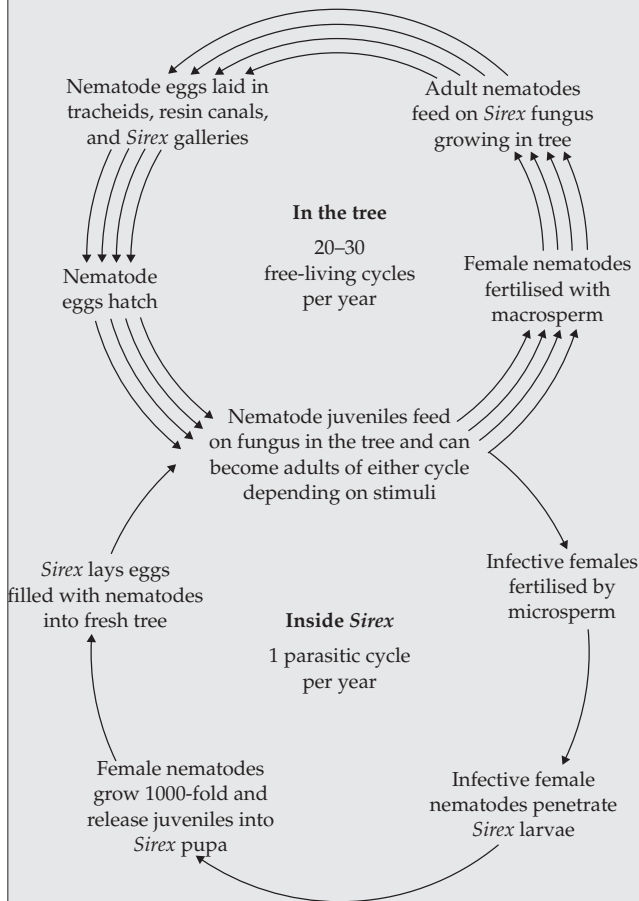
Early detection of outbreaks is important in minimising losses but locating and inoculating *Sirex*-infested trees over large areas when infestation levels are low is time consuming and expensive. Under these circumstances, inoculating trap trees at intervals along the edge of the forest can be much more cost-effective. Trap trees are created by injecting herbicide in the spring to predispose them to attack by *S. noctilio*, after which they are felled in late autumn and inoculated with nematodes. Trap trees may also be used for early detection and monitoring in areas at risk of attack.

As part of the IPM programme, there was also widespread release of the ichneumonid, *Megarhyssa nortoni*, but its impact on pest population dynamics in the presence of the nematode is largely unknown.

In the Green Triangle and subsequently in other countries to which *S. noctilio* has been introduced, knowledge and experience accumulated through many years of R&D has been utilised to implement IPM programmes adapted to the characteristics of outbreaks in different regions.

Key references: Zondag (1969), Neumann *et al.* (1982), Haugen (1990), Haugen and Underdown (1990), Bedding (1993).

Box 9.6 Continued



**Figure 9.17** The complicated bicyclic life cycle of *Beddingia siricidicola*, a nematode parasite of *Sirex noctilio*. Parasitised female *S. noctilio* lay nematode-infected eggs and introduce a symbiotic fungus *Amylostereum areolatum* and toxic mucus into pines in which uninfected females also lay eggs. Within the tree (upper cycle) nematodes go through many free-living cycles, feeding on the fungus as it grows and allowing millions of nematodes to spread to all parts of the tree. Fungal growth and consequent local drying of the wood stimulates hatching of uninfected *S. noctilio* eggs and tunnelling larvae feed on the fungus which has spread throughout the tree following its death. The microenvironment around woodwasp larvae stimulates transformation of juvenile nematodes to adult females of the parasitic form (lower cycle) which, after mating, burrow into the larvae. Juveniles released by the adult female nematodes migrate to the reproductive organs following pupation and emerging female woodwasps transport the nematodes to other trees (from Bedding 1993).

**Table 9.2** Costs (A\$) of the nematode inoculation programme against *Sirex noctilio* in the Green Triangle of southern Australia in 1987

	Cost
Survey	31 000
Tree marking and felling	442 000
Inoculation	618 000
Nematode production and supplies	75 000
Administration etc.	172 000
Total	1 338 000

Notes: During this year alone, the value of trees killed by *S. noctilio* was estimated to be at least Aus \$5–6 million. Within Australian pine plantations as a whole, *S. noctilio* could cause losses of Aus \$1–4 billion over a 30 year rotation.

Source: Data from Haugen and Underdown (1990) and Bedding (1993).



damage they cause (Coakley *et al.* 1999; Ayres and Lombardero 2000; Harrington *et al.* 2001). Both direct and indirect effects on pests, their host plants and natural enemies have been described but relatively few generalisations have emerged. Broad predictions of the effects of climate change in northern forest ecosystems indicate the range of possible effects (Table 9.4).

For insect pests, simple responses to rising average temperatures include an increase in the

number of generations per year, effects on overwintering survival or extension of the range into areas that were previously unsuitable. These responses will be strongly influenced by life-history characteristics. For example, insects that overwinter in diapause are likely to respond to less extreme winter minimum temperatures differently from those insects that remain active when conditions allow. In the summer, pests with short generation times such as aphids should benefit

### Box 9.7 Slowing the spread of *Lymantria dispar* in North America

In north-eastern North America, *L. dispar* is expanding its range to the south and west. In colonised areas, the main impacts are the effect of defoliation on growth and mortality of hardwood trees, and the effect of larvae, which have urticating hairs, on recreational and residential values. The rate of spread is influenced by a number of factors and has changed over time (Fig. 2.3). Natural spread by dispersing larvae is relatively slow, but 'jump-spread' by human-aided transport of egg-masses significantly increases the overall rate of range expansion. Currently, the moth occupies less than 30% of potentially suitable forest habitat and is projected to continue expanding its range for at least 100 years. Once areas have been colonised, the need for management and control is likely to continue indefinitely. There is a persuasive case for reducing the rate of colonisation of new areas if this can be done cost-effectively.

The 'slow-the-spread' strategy was developed in several pilot study areas and is now operated in a 100 km wide transition zone along the expanding population front extending from Wisconsin to North Carolina. Approximately 80 000 pheromone-baited traps are used in grids over an

area of about 22 million ha, with individual traps placed at intervals of 2 km (Fig. 9.18(a)). When males are captured, traps are placed locally at 0.5 km intervals so that the area requiring treatment can be defined. In areas targeted for treatment (which is applied in the year following detection) controlled-release pheromone dispensers may be aerially applied for mating-disruption (Section 8.1). The technique is ideally suited for low density populations that typically occur in the transition zone. Alternatively, larger populations may be sprayed with *Bacillus thuringiensis* (Section 7.2.1) or with insecticide (Fig. 9.18(b)). Coordination over such a large programme was made possible by automated data processing and availability of distribution maps via the Internet. The programme is expected to slow the rate of spread of *L. dispar* by half (Fig. 9.19). The economic impact of *L. dispar* has been estimated not only for timber loss but also for effects on residential and recreational areas and provides the basis for an assessment of the cost-effectiveness of the programme (Table 9.3).

Key references: Elkinton and Liebhold (1990), Leuschner *et al.* (1996), Sharov and Liebhold (1998), Sharov *et al.* (1998, 1999, 2002), [www.ento.sts.edu/STS](http://www.ento.sts.edu/STS).

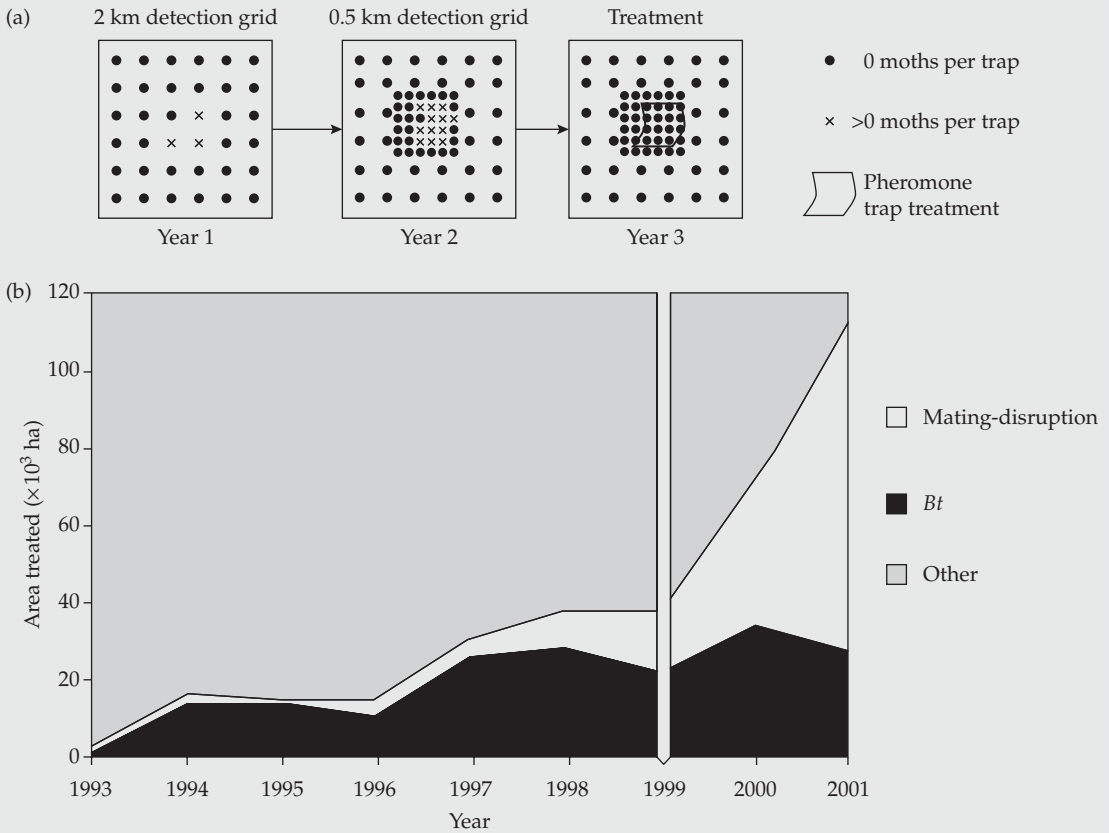
**Table 9.3** Estimated costs (US\$ millions present value) over 25 years of the impact of *Lymantria dispar* spreading at different rates to the south and west of the generally infested zone in north-eastern USA

Impact	Rate of spread (miles year <sup>-1</sup> )		
	2.5	7.5	12.5
Management	32	93	159
Timber	66	174	268
Recreation	47	143	242
Residential	650	1821	3131
Total	795	2230	3799

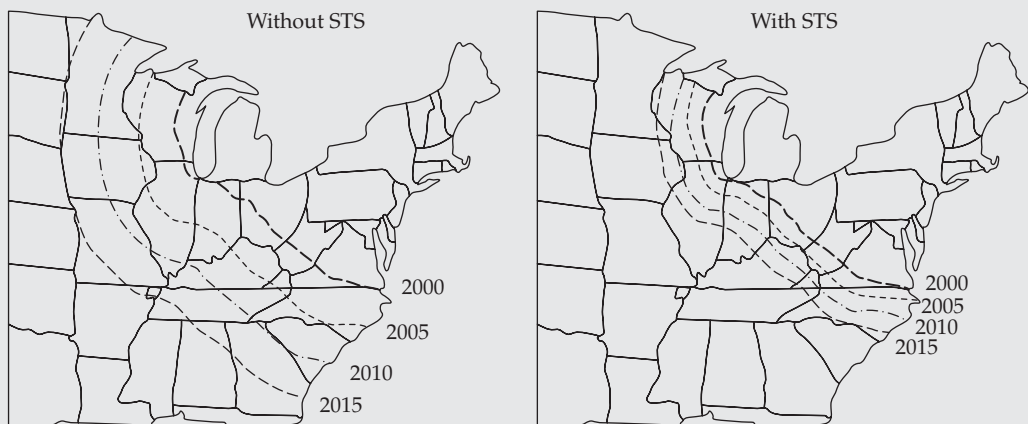
*Notes:* The higher rate of spread approximates to the average rate estimated for 1966–1990 (Liebhold *et al.* 1992) and estimated benefits of 'slowing the spread' to the lower rates can be obtained by subtraction.

*Sources:* Leuschner *et al.* (1996); see Sharov *et al.* (1998) for an alternative analysis.

Box 9.7 Continued



**Figure 9.18** Pheromone detection surveys and treatment of infested areas in the ‘slow-the-spread’ (STS) campaign against *Lymantria dispar* in north-eastern North America. (a) Pheromone traps are deployed in a 2 km grid to detect moths in a transition zone where the moth is expanding its range to the south and west. When some moths are caught, traps are deployed every 0.5 km to define the local infested area which is then treated by mating-disruption, Bt or insecticides. (b) Treatment of infested areas during the development phase and following the adoption of the STS strategy as part of a national programme in 1999 (from Sharov *et al.* 2002).



**Figure 9.19** Predicted spread of *Lymantria dispar* with and without the STS campaign (from Sharov *et al.* 2002).

more from increasing temperatures than root-feeding insects with semi-voltine development. More complex effects are also likely. For example, differences in response of host trees and insects to changes in temperature could affect phenological synchrony as well as interactions with natural enemies but effects are difficult to predict other than in very general terms.

Where temperature or other environmental variables have a key influence on pest distribution or population dynamics, specific predictions may be possible. Projections of the effect of climate warming on the pine sawfly, *Neodiprion sertifer*, one of the most important defoliators of Scots pine in northern Europe, suggests that warmer winters

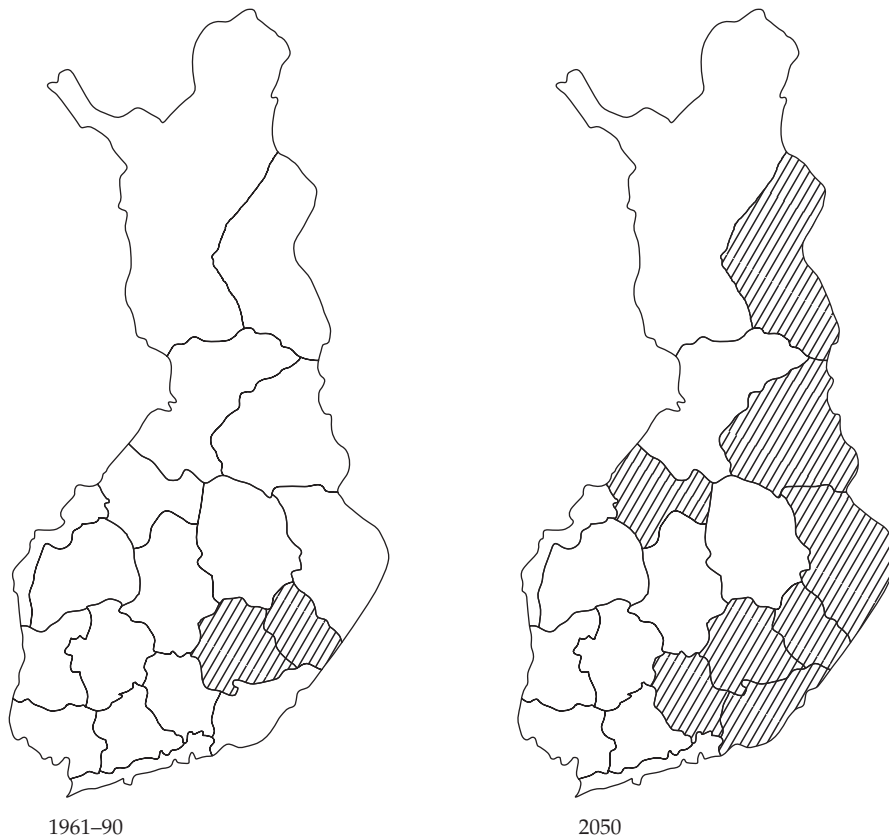
will reduce overwintering egg mortality in cold northern regions. In Finland, most outbreaks occur in southern areas but the frequency of outbreaks in eastern and northern Finland is predicted to increase in a warming climate (Fig. 9.20). One of the more general predictions of climate change relates to alterations to the range of insect pests. In temperate regions of the northern hemisphere, ranges are likely to extend northwards and to increase in elevation but predictions can vary even for similar kinds of pests. In southern United States, the northern limit of the southern pine beetle, *D. frontalis* is determined by lethal winter temperatures so that an increase in the minimum annual temperature is predicted to result in a

**Table 9.4** The main projected short-medium term effects of climate change on boreal forests and associated vertebrate and insect herbivores

Climate	Herbivore	Trees
<b>Southern Fennoscandia</b>		
Higher winter temperature	Increased overwintering survival of pine sawfly and winter moth	Increased herbivory of pine and birch, reducing survival and growth
Loss of permanent snow cover	Increased survival of moose and roe deer; decreased survival of voles	Increased winter browsing; differential browsing favours increase in spruce abundance
<b>Northern Fennoscandia</b>		
Higher winter and summer temperatures	Increased overwintering survival of pine sawflies and both autumn moth and its predators	Higher summer temperatures significantly increase growth of spruce, pine, and birch; increased herbivory on pine; increased abundance of spruce and birch; reduced abundance of pine
Increased snow cover	Reduced survival of moose and reindeer	Reduced winter browsing favours increased abundance of broadleaved trees
<b>Interior Alaska</b>		
Higher winter and summer temperatures	Increased frequency of bark beetle outbreaks on spruce	Small increases in tree growth; increased fire frequency in warm and relatively dry summers increases proportion of early successional birch and aspen forests

Notes: Likely changes in temperature and precipitation patterns were based on the current consensus, and effects on herbivores based on published observations of the influence of geographical and year to year variation in climate. In general, greater increases in precipitation in coastal Scandinavia than interior Alaska and eastern Siberia were projected.

Source: Data from Niemelä *et al.* (2001).



**Figure 9.20** Predicted effects of winter warming caused by climate change on the risk of outbreaks of *Neodiprion sertifer* in Finland. Forest areas particularly susceptible to damage occur mainly on dry infertile mineral soils but egg mortality due to cold winters (critical value for egg mortality,  $-36^{\circ}\text{C}$ ) appears to be important in restricting the geographic distribution of outbreaks. Forest regions with  $\geq 10\%$  of municipalities having outbreaks each year (////) in the period 1961–90 and those predicted for 2050 following a projected rise of  $+3.6^{\circ}\text{C}$  in mean winter temperature. Predictions suggest a significantly increased risk of outbreaks in eastern and northern Finland, with the proviso that while very low winter temperatures may prevent outbreaks, higher temperatures may not be the only factor contributing to them (from Virtanen *et al.* 1996).

northward extension of the range into existing pine forests (Ungerer *et al.* 1999; Williams and Liebhold 2002). For mountain pine beetle, *D. ponderosae*, on the other hand, outbreak areas are predicted to decline in extent and to move towards higher elevation in western United States (Williams and Liebhold 2002). But in western Canada, the bark beetle is predicted to become more widespread, extending its range to the north and east, and possibly coming into contact with jack pine for the first time (Carroll *et al.* 2003).

For plant pathogens, temperature increases are also likely to affect their geographic range but changes in rainfall pattern will probably have the

most important effects (Coakley *et al.* 1999). Many pathogens are widely distributed but disease severity can vary within the range in relation to climate which may act directly on the pathogen or indirectly by affecting host resistance (Coakley *et al.* 1999; Lonsdale and Gibbs 2002). The pathogen *Phytophthora cinnamomi*, which causes root- and stem-based diseases on a wide range of broadleaved and coniferous trees, is widely distributed in Australasia, North America and Europe. In cool temperate parts of Europe, disease is sporadic but in the warm-temperate climate of southern Europe, the fungus is associated with decline of oaks (Brasier 1992). The fungus is most pathogenic at

25–30°C and the range in which pathogenic activity of the fungus occurs is predicted to extend northwards with global warming (Brasier and Scott 1994).

In the short term, one of the most important effects of climate change for pest management is likely to be an increase in the threat of introduction of exotic pests and pathogens that are able to survive in regions that were previously inhospitable or at least suboptimal. Models such as CLIMEX can be used to predict the likely 'favourableness' of climate for specific pests, an example of which is given in Fig. 2.5.

Changes in weather patterns such as summer temperatures, the amount or seasonal timing of rainfall or an increase in the frequency or severity of

storms (Mearns *et al.* 1997) could increase damage by pests influenced by host 'stress' or able to breed in windblown trees. 'Decline' syndromes caused by a complex of biotic and abiotic factors may also be exacerbated by changes in temperature and rainfall patterns (Manion and Lachance 1992). The natural distribution of tree species is likely to be altered relatively slowly under climate change (Peters R.L. 1990). But for plantation species, forest managers may need to select species or provenances that are better adapted to changing conditions to reduce the risk of increased susceptibility to pests and pathogens as a result of stress-related effects on growth and vigour.

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# References

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- Ades, P. K. and Simpson, J. A. (1991). Variation in susceptibility to *Dothistroma* needle blight among provenances of *Pinus radiata* var. *radiata*. *Silvae Genetica*, **40**, 6–13.
- Agrios, G. N. (1988). *Plant pathology*, 3rd edn. Academic Press, San Diego.
- Alfaro, R. I. and Sheppard, R. F. (1991). Tree-ring growth of interior Douglas-fir after one year's defoliation by Douglas-fir tussock moth. *Forest Science*, **37**, 959–964.
- Alfaro, R. I., Van Sickle, G. A., Thomson, A. J., and Wegwitz, E. (1982). Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas fir stand in British Columbia. *Canadian Journal of Forest Research*, **12**, 780–787.
- Alfaro, R. I., Thomson, A. J., and Van Sickle, G. A. (1985). Quantification of Douglas-fir growth losses caused by western spruce budworm defoliation using stem analysis. *Canadian Journal of Forest Research*, **15**, 5–9.
- Alfaro, R. I., Kiss, G. K., and Yanchuk, A. (1996a). Variation in the induced resin response of white spruce, *Picea glauca*, to attack by *Pissodes strobi*. *Canadian Journal of Forest Research*, **26**, 967–972.
- Alfaro, R. I., He, F., Kiss, G., King, J., and Yanchuk, A. (1996b). Resistance of white spruce to white pine weevil: development of a resistance index. *Forest Ecology and Management*, **81**, 51–62.
- Alfaro, R. I., He, F. L., Tomlin, E., and Kiss, G. (1997). White spruce resistance to white pine weevil related to bark resin canal density. *Canadian Journal of Botany*, **75**, 568–573.
- Alfaro, R. I., Taylor, S., Brown, G., and Wegwitz, E. (1999). Tree mortality caused by the western hemlock looper in landscapes of central British Columbia. *Forest Ecology and Management*, **124**, 285–291.
- Alfaro, R. I., Taylor, S., Brown, R. G., and Clowater, J. S. (2001). Susceptibility of northern British Columbia forests to spruce budworm defoliation. *Forest Ecology and Management*, **145**, 181–190.
- Allard, G. (1998). Integrated pest management for forests and trees, a review of FAO's activities. *Forestry Chronicle*, **74**, 541–543.
- Allee, W. C. (1931). *Animal aggregations*. University of Chicago Press, Chicago.
- Allen, D. C., Abrahamson, L. P., Eggen, D. A., Lanier, G. N., Swier, S. R., Kelley, R. S., and Auger, M. (1986). Monitoring spruce budworm (Lepidoptera: Tortricidae) populations with pheromone-baited traps. *Environmental Entomology*, **15**, 152–165.
- Amman, G. D. (1985). A test of lodgepole pine hazard rating methods for mountain pine beetle infestation in southeastern Idaho. In *The role of the host in the population dynamics of forest insects*. (ed. L. Safranik), pp. 186–200. Proceedings of the IUFRO conference, Banff, Canada. Canadian Forest Service, Pacific Forest Research Centre, Victoria BC.
- Amman, G. D., McGregor, M. D., Schmitz, R. F., and Oakes, R. D. (1988). Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Canadian Journal of Forest Research*, **18**, 688–695.
- Anagnostakis, S. L. (2001). American chestnut sprout survival with biological control of the chestnut-blight fungus population. *Forest Ecology and Management*, **152**, 225–233.
- Anderbrant, O. (1993). Pheromone biology of sawflies. In *Sawfly life history adaptations to woody plants* (eds. M. R. Wagner and K. F. Raffa), pp. 119–154. Academic Press, Inc. San Diego.
- Anderbrant, O. (1999). Sawflies and seed wasps. In *Pheromones of non-lepidopteran insects associated with agricultural plants* (eds. J. Hardie and A. K. Minks), pp. 199–226. CABI Publishing, Wallingford.
- Anderbrant, O., Schlyter, F., and Birgersson, G. (1985). Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, **45**, 89–98.
- Anderbrant, O., Löfqvist, J., Högberg, H.-E., and Hedenström, E. (1995). Development of mating disruption for control of pine sawfly populations. *Entomologia Experimentalis et Applicata*, **74**, 83–90.
- Anderson, L., Carlson, C. E., and Wakimoto, R. H. (1987). Forest fire frequency and western spruce budworm outbreaks in western Montana. *Forest Ecology and Management*, **22**, 251–260.

- Andow, D. A. (1991). Vegetational diversity and arthropod population response. *Annual Review of Entomology*, **36**, 561–586.
- Anon. (1985). *Insects of eastern forests*. USDA Forest Service Miscellaneous Publication No. 1426, Washington, DC.
- Anon. (1993a). Guidelines on pest risk analysis. No. 1. Check-list of information required for pest risk analysis (PRA). *Bulletin OEPP/EPPO Bulletin*, **23**, 191–198.
- Anon. (1993b). Guidelines on pest risk analysis. No. 2. Pest risk analysis to decide immediate action to be taken on interception of a pest in an EPPO country. *Bulletin OEPP/EPPO Bulletin*, **23**, 199–202.
- Anon. (1997). Guidelines on pest risk analysis. No. 3. Pest risk assessment scheme. *Bulletin OEPP/EPPO Bulletin*, **27**, 281–305.
- Anon. (1999). 100 years ago. *Nature*, **399**, 309.
- Anon. (2001). Pest risk analysis. Pest risk management scheme. *Bulletin OEPP/EPPO Bulletin*, **31**, 15–28.
- Appel, H. M. and Schultz, J. C. (1994). Oak tannins reduce effectiveness of Thuringide (*Bacillus thuringiensis*) in the gypsy moth (Lepidoptera: Lymantriidae). *Journal of Economic Entomology*, **87**, 1736–742.
- Armour, H., Straw, N., and Day, K. (2003). Interactions between growth, herbivory and long-term foliar dynamics of Scots pine. *Trees*, **17**, 70–80.
- Attiwill, P. M. (1994). The disturbance of forest ecosystems: the ecological basis for conservation management. *Forest Ecology and Management*, **63**, 247–300.
- Aukema, B. H., Dahlsten, D. L., and Raffa, K. F. (2000). Exploiting behavioral disparities among predators and prey to selectively remove pests: maximising the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology*, **29**, 651–660.
- Austarå, Ø., Orlund, A., Svendsrud, A., and Veidahl, A. (1987). Growth loss and economic consequences following two years defoliation of *Pinus sylvestris* by the pine sawfly *Neodiprion sertifer* in West-Norway. *Scandinavian Journal of Forest Research*, **2**, 111–119.
- Ayres, M. P. and Lombardero, M. J. (2000). Assessing the consequences of climate change for forest herbivores and pathogens. *Science of the Total Environment*, **262**, 263–286.
- Baker, F. A. (1993). Classification and regression tree analysis for assessing hazard of pine mortality caused by *Heterobasidion annosum*. *Plant Disease*, **77**, 136–139.
- Bakke, A. (1982). The utilisation of aggregation pheromone for the control of the spruce bark beetle. In *Insect pheromone technology: chemistry and application* (eds. B. A. Leonhardt and M. Beroza), ACS Symposium Series No. 190, pp. 219–229. American Chemical Society, Washington.
- Bakke, A. (1983). Host tree and bark beetle interaction during a mass outbreak of *Ips typographus* in Norway. *Zeitschrift für angewandte Entomologie*, **96**, 118–125.
- Bakke, A. (1989). The recent *Ips typographus* outbreak in Norway—experiences from a control program. *Holarctic Ecology*, **12**, 515–519.
- Bakke, A. (1991). Socioeconomic aspects of an integrated-pest-management program in Norway. *Forest Ecology and Management*, **39**, 299–303.
- Bakke, A. (1992). Monitoring bark beetle populations: effects of temperature. *Journal of Applied Entomology*, **114**, 208–211.
- Balch, R. E. and Bird, F. T. (1944). A disease of the European spruce sawfly, *Gilpinia hercyniae* [Htg.] and its place in natural control. *Scientific Agriculture*, **25**, 65–80.
- Baltensweiler, W. (1993). Why the larch bud-moth cycle collapsed in the subalpine larch-Cembra pine forests in the year 1990 for the 1st time since 1850. *Oecologia*, **94**, 62–66.
- Barbercheck, M. E. and Millar, L. C. (2000). Environmental impacts of entomopathogenic nematodes used for biological control in soil. In *Nontarget effects of biological control* (eds. P. A. Follett and J. J. Duan), pp. 287–308. Kluwer Academic Publishers, Boston.
- Barbosa, P. (ed.) (1998). *Conservation biological control*. Academic Press, San Diego.
- Barclay, H. J. (1997). Assessing natural selection in white pine weevils (*Pissodes strobi* Peck) (Coleoptera: Curculionidae) for overcoming resistance in trees: an evolutionary model. *Canadian Entomologist*, **129**, 1105–1120.
- Barclay, H. J. and Judd, G. J. R. (1995). Models for mating disruption by means of pheromone for insect pest control. *Researches on Population Ecology*, **37**, 239–247.
- Bathon, H. (1996). Impact of entomopathogenic nematodes on non-target hosts. *Biocontrol Science and Technology*, **6**, 421–434.
- Battisti, A. (1994). Voltinism and diapause in the spruce web-spinning sawfly *Cephalcia arvensis*. *Entomologia Experimentalis et Applicata*, **70**, 105–113.
- Bauce, E. (1996). One and two years impact of commercial thinning on spruce budworm feeding ecology and host tree foliage production and chemistry. *Forestry Chronicle*, **72**, 393–398.
- Baum, J. A., Johnson, T. B., and Carlton, B. C. (1998). *Bacillus thuringiensis*: natural and recombinant bioinsecticide products. In *Methods in biotechnology, vol 5: Biopesticides: use and delivery* (eds. F. R. Hall and J. J. Menn), pp. 189–209. Humana Press Inc., Totowa, N.J.
- Bedding, R. A. (1993). Biological control of *Sirex noctilio* using the nematode *Deladenus siricidicola*. In *Nematodes and the biological control of insect pests*, (eds. R. Bedding, R. Akhurst, and H. Kaya), pp. 11–20. CSIRO, Australia.

- Bedding, R. A., Tyler, S., and Rochester, N. (1996). Legislation on the introduction of exotic entomopathogenic nematodes into Australia and New Zealand. *Biocontrol Science and Technology*, **6**, 465–475.
- Beegle, C. C. and Yamamoto, T. (1992). History of *Bacillus thuringiensis* Berliner research and development. *Canadian Entomology*, **124**, 587–616.
- Begon, M., Harper, J. L., and Townsend, C. R. (1996). *Ecology individuals, populations and communities*. 3rd edition. Blackwell Science, Oxford.
- Behrendt, C. J., Blanchette, R. A., and Farrell, R. L. (1995). An integrated approach, using biological and chemical control, to prevent blue stain in pine logs. *Canadian Journal of Botany*, **73**, 613–619.
- Bellows, T. S. and Fisher, T. W. (1999). *Handbook of biological control principles and applications of biological control*. Academic Press, San Diego.
- Benz, B. J., Amman, G. D., and Logan, J. A. (1993). A critical assessment of risk classification systems for the mountain pine beetle. *Forest Ecology and Management*, **61**, 349–366.
- Bergeron, Y., Leduc, A., Morin, H., and Joyal, C. (1995). Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research*, **25**, 1375–1384.
- Berisford, C. W. (1988). The nantucket pine tip moth. In *Dynamics of forest insect populations patterns, causes, implications* (ed. A. A. Berryman), pp. 141–161. Plenum Press, New York.
- Bernays, E. A. and Chapman, R. F. (1994). *Host-plant selection by phytophagous insects*. Chapman & Hall, New York.
- Berryman, A. A. (1978). A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest management. In *Theory and practice of mountain pine beetle management in lodgepole pine forests* (eds. A. A. Berryman, G. D. Amman, and R. W. Stark), pp. 98–105. University of Idaho, Moscow, Idaho.
- Berryman, A. A. (1987). The theory and classification of outbreaks. In *Insect outbreaks* (eds. P. Barbosa and J. C. Schultz), pp. 3–30. Academic Press, Inc. San Diego.
- Berryman, A. A. (1996). What causes population cycles of forest Lepidoptera? *TREE*, **11**, 28–32.
- Berryman, A. A. (1999). *Principles of population dynamics and their application*. Stanley Thornes (Publishers) Ltd. Cheltenham.
- Berryman, A. A. and Stark, R. W. (1985). Assessing the risk of forest insect outbreaks. *Zeitschrift für angewandte Entomologie*, **99**, 199–208.
- Berryman, A. A., Denis, B., Raffa, K., and Stenseth, N. C. (1985). Evolution of optimal group attack with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology*, **66**, 898–903.
- Bertram, S. L. and Paine, T. D. (1994). Influence of aggregation inhibitors (verbenone and ipsdienol) on landing and attack behavior of *Dendroctonus brevicomis* (Coleoptera: Scolytidae). *Journal of Chemical Ecology*, **20**, 1617–1629.
- Bevan, D. (1974). Control of forest insects: there is a porpoise close behind us. In *Biology of pest and disease control* (eds. D. Price Jones and M. E. Solomon), pp. 302–312. Blackwell Scientific Publications, Oxford.
- Bhowmick, A. K. and Vaishampayan, S. M. (1986). Observations on the activity of teak defoliator *Hyblaea puera* Cramer on teak (*Tectona grandis*) influenced by the movement of monsoon. *Journal of Tropical Forestry*, **2**, 27–35.
- Binkley, C. S. (1997). Preserving nature through intensive plantation forestry: The case for forestland allocation with illustrations from British Columbia. *Forestry Chronicle*, **73**, 553–559.
- Binns, M. R. and Nyrop, J. P. (1992). Sampling insect populations for the purpose of IPM decision making. *Annual Review of Entomology*, **37**, 427–453.
- Binns, M. R., Nyrop, J. P., and van der Werf, W. (2000). *Sampling and monitoring in crop protection*. The theoretical basis for developing practical decision guides. CABI Publishing.
- Bird, F. T. and Elgee, D. E. (1957). A virus disease and introduced parasites as factors controlling the European spruce sawfly *Diprion hercyniae* (Htg.) in central New Brunswick. *Canadian Entomologist*, **89**, 371–378.
- Bishir, J. and Roberds, J. (1995). Analysis of failure time in clonally propagated plant populations. *Mathematical Biosciences*, **125**, 109–125.
- Björklund, N., Nordlander, G., and Bylund, H. (2003). Host-plant acceptance on mineral soil and humus by the pine weevil *Hylobius abietis* (L.). *Agricultural and Forest Entomology*, **5**, 61–65.
- Björkman, C., Larsson, S., and Gref, R. (1991). Effects of nitrogen fertilization on pine needle chemistry and sawfly performance. *Oecologia*, **86**, 202–209.
- Blanchette, R. A. and Biggs, A. R. (1992). *Defense mechanisms of woody plants against fungi*. Springer-Verlag, Berlin.
- Boettner, G. H., Elkinton, J. S., and Boettner, C. J. (2000). Effects of a biological control introduction on three non-target native species of saturniid moths. *Conservation Biology*, **14**, 1798–1806.
- Bonello, P., Gordon, T. R., and Storer, A. J. (2001). Systemic induced resistance in Monterey pine. *Forest Pathology*, **31**, 99–106.
- Bonning, B. C. and Hammock, B. D. (1996). Development of recombinant baculoviruses for insect control. *Annual Review of Entomology*, **41**, 191–210.



- Booth, T. H., Jovanovic, T., and New, M. (2002). A new world climatic mapping programme to assist species selection. *Forest Ecology and Management*, **163**, 111–117.
- Borden, J. H. (1985). Aggregation pheromones. In *Insect physiology biochemistry and pharmacology volume 9 behaviour* (eds. G. A. Kerkut and L. I. Gilbert), pp. 257–285. Pergamon Press, Oxford.
- Borden, J. H. (1992). Two tree baiting tactics for the management of bark beetles with semiochemicals. *Journal of Applied Entomology*, **114**, 201–207.
- Borden, J. H. (1997). Disruption of semiochemical-mediated aggregation in bark beetles. In *Insect pheromone research new directions* (eds. R.T. Cardé and A. K. Minks), pp. 421–438. Chapman and Hall, New York.
- Borden, J. H., King, C. J., Lindgren, S., Chong, L., Gray, D. R., Oehlschlager, A. C., Slessor, K. N., and Pierce, H. D. Jr. (1982). Variation in response of *Trypodendron lineatum* from two continents to semiochemicals and trap form. *Environmental Entomology*, **11**, 403–408.
- Borden, J. H., Gries, G., Chong, L. J., Werner, R. A., Holsten, E. H., Wieser, H., Dixon, E. A., and Cerezke, H. F. (1996). Regionally-specific bioactivity of two new pheromones for *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae). *Journal of Applied Entomology*, **120**, 321–326.
- Borden, J. H., Chong, L. J., Earle, T. J., and Huber, D. P. W. (2003). Protection of lodgepole pine from attack by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) using high doses of verbenone in combination with nonhost bark volatiles. *Forestry Chronicle*, **79**, 685–691.
- Bradley, T. and Tueller, P. (2001). Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe Basin. *Forest Ecology and Management*, **142**, 205–214.
- Brändle, M. and Brandl, R. (2002). Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology*, **70**, 491–504.
- Brasier, C. M. (1990). China and the origins of Dutch elm disease: an appraisal. *Plant Pathology*, **39**, 5–16.
- Brasier, C. M. (1992). Oak mortality in Iberia. *Nature*, **360**, 539.
- Brasier, C. M. (1995). Episodic selection as a force in fungal microevolution with special reference to clonal speciation and hybrid introgression. *Canadian Journal of Botany*, **73**, 1213–1221.
- Brasier, C. M. (1996). New horizons in Dutch elm disease control. In *Report on Forest Research, 1996*, pp. 20–28. HMSO, London.
- Brasier, C. M. (2000a). Intercontinental spread and continuing evolution of the Dutch elm disease pathogens. In *The elms: breeding, conservation and disease management* (ed. C. P. Dunn), pp. 61–72. Kluwer Academic Publishers, Boston.
- Brasier, C. M. (2000b). Viruses as biological control agents of the Dutch elm disease fungus *Ophiostoma novo-ulmi*. In *The elms: breeding, conservation, and disease management* (ed. C. P. Dunn), pp. 201–212. Kluwer Academic Publishers, Boston.
- Brasier, C. M. (2001). Rapid evolution of introduced plant pathogens via interspecific hybridisation. *BioScience*, **51**, 123–133.
- Brasier, C. M. and Kirk, S. A. (2001). Designation of the EAN and NAN races of *Ophiostoma novo-ulmi* as subspecies. *Mycological Research*, **105**, 547–554.
- Brasier, C. M. and Scott, J. K. (1994). European oak declines and global warming: a theoretical assessment with special reference to the activity of *Phytophthora cinnamomi*. *OEPP/EPPO Bulletin*, **24**, 221–232.
- Brasier, C. M., Cooke, D., and Duncan, J. M. (1999). Origin of a new *Phytophthora* pathogen through interspecific hybridization. *Proceedings of the National Academy of Sciences*, **96**, 5878–5883.
- Breiman, L., Friedman, J. H., Olshen, R. A., and Stone, C. J. (1984). *Classification and regression trees*. Wadsworth, Inc., Belmont, CA.
- Brennan, E. B. and Weinbaum, S. A. (2001). Effect of epicuticular wax on adhesion of psyllids to glaucous juvenile and glossy adult leaves of *Eucalyptus globulus* Labillardière. *Australian Journal of Entomology*, **40**, 270–277.
- Brennan, E. B., Hrusa, G. F., Weinbaum, S. A., and Levison Jr., W. (2001). Resistance of *Eucalyptus* species to *Glycaspis brimblecombei* (Homoptera: Psyllidae) in the San Francisco bay area. *Pan-Pacific Entomologist*, **77**, 249–253.
- Brookes, M. H., Stark, R. W., and Campbell, R. W. (1978). *The Douglas-fir tussock moth: a synthesis*. U.S. Forest Service Technical Bulletin 1585 USDA, Washington, DC.
- Bryant, J. P. and Raffa, K. F. (1995). Chemical antiherbivore defence. In *Plant stems: physiology and functional morphology* (ed. B. L. Gartner), pp. 365–381. Academic Press, Inc. San Diego.
- Bucciarelli, B., Ostry, M. E., Fulcher, R. G., and Anderson, N. A. (1999). Histochemical and microspectrophotometric analyses of early wound responses of resistant and susceptible *Populus tremuloides* inoculated with *Entoleuca mammata* (= *Hypoxylon mammatum*). *Canadian Journal of Botany*, **77**, 548–555.
- Bulman, L. S. (1992). Forest quarantine risk of cargo imported into New Zealand. *New Zealand Journal of Forest Science*, **22**, 32–38.
- Bulman, L. S. (1998). Quarantine risk posed to forestry by full container loads, and efficiency of FCL door inspections. *New Zealand Journal of Forest Science*, **28**, 335–346.
- Bulman, L. S., Kimberley, M. O., and Gadgil, P. D. (1999). Estimation of the efficiency of pest detection surveys. *New Zealand Journal of Forestry Science*, **29**, 102–115.

- Bunce, H. W. F. and McLean, J. A. (1990). Hurricane Gilbert's impact on the natural forests and *Pinus caribaea* plantations of Jamaica. *Commonwealth Forestry Review*, **69**, 147–155.
- Burdon, J. J. (1987). *Diseases and plant population biology*. Cambridge University Press, Cambridge.
- Burdon, R. D. (1999). Risk-management issues for genetically engineered forest trees. *New Zealand Journal of Forest Science*, **29**, 375–390.
- Burdon, R. D., Gaskin, R. E., Low, C. B., and Zabkiewicz, J. A. (1992). Clonal repeatability of monoterpene composition of cortical oleoresin of *Pinus radiata*. *New Zealand Journal of Forest Science*, **22**, 299–305.
- Burges, H. D. and Jones, K. A. (1998). Formulation of bacteria, viruses, and protozoa to control insects. In *Formulation of microbial biopesticides* (ed. H. D. Burges), pp. 34–127. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Burgess, T. and Wingfield, M. J. (2002). Quarantine is important in restricting the spread of exotic seed-borne tree pathogens in the southern hemisphere. *International Forestry Review*, **4**, 56–65.
- Burman, M., Pye, A. E., and Nöjd, N. O. (1979). Preliminary field trials of the nematode *Neoapectana carpocapsae* against larvae of the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). *Annales Entomologici Fennici*, **45**, 88.
- Burnell, A. M. and Dowds, B. C. A. (1996). The genetic improvement of entomopathogenic nematodes and their symbiont bacteria: Phenotypic targets, genetic limitations and an assessment of possible hazards. *Biocontrol Science and Technology*, **6**, 435–447.
- Burrill, E. A., Worrall, J. J., Wargo, P. M., and Stehman, S. V. (1999). Effects of defoliation and cutting in eastern oak forests on *Armillaria* spp. and a competitor, *Megacollybia platyphylla*. *Canadian Journal of Forest Research*, **29**, 347–355.
- Butt, T. M., Jackson, C., and Magan, N. (eds.) (2001). *Fungi as biocontrol agents progress, problems and potential*. CABI publishing, Wallingford.
- Byers, J. A. (1989). Behavioural mechanisms involved in reducing competition in bark beetles. *Holarctic Ecology*, **12**, 466–476.
- Byers, J. A. (1993). Simulation and equation models of insect population control by pheromone-baited traps. *Journal of Chemical Ecology*, **19**, 1939–1956.
- Byers, J. A. (1995). Host-tree chemistry affecting colonisation in bark beetles. In *Chemical ecology of insects 2*, (eds. R. T. Cardé and W. J. Bell), pp. 154–213. Chapman and Hall, New York.
- Cadogan, B. L. and Scharbach, R. D. (1993). Efficacy of Foray 48B (*Bacillus thuringiensis* Berliner) applications against the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), timed for phenological development of balsam fir and black spruce. *Canadian Entomologist*, **125**, 479–488.
- Caltagirone, L. E. and Doult, R. L. (1989). The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology*, **34**, 1–16.
- Campbell, F. T. (2001). The science of risk assessment for phytosanitary regulation and the impact of changing trade regulations. *BioScience*, **51**, 148–153.
- Candau, J.-N., Fleming, R. A., and Hopkin, A. (1998). Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. *Canadian Journal of Forest Research*, **28**, 1733–1741.
- Candy, S. G., Elliott, H. J., Bashford, R., and Greener, A. (1992). Modelling the impact of defoliation by the leaf beetle, *Chrysophtharta bimaculata* (Coleoptera: Chrysomelidae), on height growth of *Eucalyptus regnans*. *Forest Ecology and Management*, **54**, 69–87.
- Cappuccino, N., Houle, M.-J., and Stein, J. (1999). The influence of understorey nectar resources on parasitism of the spruce budworm *Choristoneura fumiferana* in the field. *Agricultural and Forest Entomology*, **1**, 33–36.
- Cardé, R. T. and Minks, A. K. (1995). Control of moth pests by mating disruption: Successes and constraints. *Annual Review of Entomology*, **40**, 559–585.
- Carlyle, J. C. (1995). Nutrient management in a *Pinus radiata* plantation after thinning: the effect of thinning and residues on nutrient distribution, mineral nitrogen fluxes, and extractable phosphorus. *Canadian Journal of Forest Research*, **25**, 1278–1291.
- Carr, D. J. and Carr, S. G. M. (1970). Oil glands and ducts in *Eucalyptus* L'Hérit. II Development and structure of oil glands in the embryo. *Australian Journal of Botany*, **18**, 191–212.
- Carroll, A. L., Lawlor, M. F., and Quiring, D. T. (1993). Influence of feeding by *Zeiraphera canadensis*, the spruce bud moth, on stem-wood growth of young white spruce. *Forest Ecology and Management*, **58**, 41–49.
- Carroll, A. L., Taylor, S. W., and Régnière, J. (2003). Climate change and range expansion by the mountain pine beetle: tomorrow's problem or today's reality. In *Climate change in the western and northern forests of Canada: impacts and adaptations*, Canadian climate impacts and adaptations research network (in press).
- Carson, S. D. and Carson, M. J. (1989). Breeding for resistance in forest trees—a quantitative genetic approach. *Annual Review of Phytopathology*, **27**, 373–395.
- Carter, G. A., Seal, M. R., and Haley, T. (1998). Airborne detection of southern pine beetle damage using key

- spectral bands. *Canadian Journal of Forest Research*, **28**, 1040–1045.
- Carter, P. C. S. (1989). Risk assessment and pest detection surveys for exotic pests and diseases which threaten commercial forestry in New Zealand. *New Zealand Journal of Forestry Science*, **19**, 353–374.
- Castello, J. D., Leopold, D. J., and Smallidge, P. J. (1995). Pathogens, patterns, and processes in forest ecosystems. *BioScience*, **45**, 16–24.
- Cedervind, J., Pettersson, M., and Långström, B. (2003). Attack dynamics of the pine shoot beetle, *Tomicus piniperda* (Col.; Scolytinae) in Scots pine stands defoliated by *Bupalus piniaria* (Lep.; Geometridae). *Agricultural and Forest Entomology*, **5**, 253–261.
- Cervera, M. T., Gusmão, J., Steenackers, M., Peleman, J., Storme, V., Vanden Broeck, A., Van Montagu, M., and Boerjan, W. (1996). Identification of AFLP molecular markers for resistance against *Melampsora larici-populina* in *Populus*. *Theoretical and Applied Genetics*, **93**, 733–737.
- Chaisurisri, K. and El-Kassaby, Y. A. (1994). Genetic diversity in a seed production population vs. natural populations of Sitka spruce. *Biodiversity and Conservation*, **3**, 512–523.
- Charles, J.-F., Delécluse, A., and Nielsen-Le Roux, C. (eds.) (2000). *Entomopathogenic bacteria: from laboratory to field application*. Kluwer Academic Publishers, Dordrecht.
- Charlton, R. E. and Cardé, R. T. (1990). Orientation of male gypsy moths, *Lymantria dispar* (L.), to pheromone sources: The role of olfactory and visual cues. *Journal of Insect Behaviour*, **3**, 443–469.
- Chey, V. K., Holloway, J. D., and Speight, M. R. (1997). Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371–385.
- Chey, V. K., Holloway, J. D., Hamblen, C., and Speight, M. R. (1998). Canopy knockdown of arthropods in exotic plantations and natural forests in Sabah, north-east Borneo, using insecticidal mist-blowing. *Bulletin of Entomological Research*, **88**, 15–24.
- Chilton, S. (1997). Genetic engineering of plant secondary metabolism for insect protection. In *Advances in insect control: The role of transgenic plants* (eds. N. Carozzi and M. Koziel), pp. 237–269. Taylor & Francis.
- Chou, C. K. S. (1991). Perspectives of disease threat in large-scale *Pinus radiata* monoculture—the New Zealand experience. *European Journal of Forest Pathology*, **21**, 71–81.
- Christiansen, E. (1985). *Ips/Ceratocystis*—infection of Norway spruce: what is a deadly dosage? *Zeitschrift für angewandte Entomologie*, **99**, 6–11.
- Christiansen, E. and Fjone, G. (1993). Pruning enhances the susceptibility of *Picea abies* to infection by the bark beetle-transmitted blue-stain fungus, *Ophiostoma polonicum*. *Scandinavian Journal of Forest Research*, **8**, 235–245.
- Christiansen, E., Krokene, P., Berryman, A. A., Franceschi, V. R., Krekling, T., Lieutier, F., Lönneborg, A., and Solheim, H. (1999). Mechanical injury and fungal infection induce acquired resistance in Norway spruce. *Plant Physiology*, **19**, 399–403.
- Christenson, L. M., Lovett, G. M., Mitchell, M. J., and Groffman, P. M. (2002). The fate of nitrogen in gypsy moth frass deposited to an oak forest floor. *Oecologia*, **131**, 444–452.
- Christiansen, E., Waring, R. H., and Berryman, A. A. (1987). Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management*, **22**, 89–106.
- Ciesla, W. M. (1993). Recent introductions of forest insects and their effects: a global overview. *FAO Plant Protection Bulletin*, **41**, 3–13.
- Ciesla, W. M. (2003). European woodwasp a potential threat to North America's conifer forests. *Journal of Forestry*, **101**, 18–23.
- Claridge, M. F. and Wilson, M. R. (1982). Insect herbivore guilds and species-area relationships: leafminers on British trees. *Ecological Entomology*, **7**, 19–30.
- Clarke, A. R. and Walter, G. H. (1995). "Strains" and the classical biological control of insect pests. *Canadian Journal of Zoology*, **73**, 1777–1790.
- Clarke, S. R., Salom, S. M., Billings, R. F., Berisford, C. W., Upton, W. W., McClellan, Q. C., and Dalusky, M. J. (1999). A scentsible approach to controlling southern pine beetles—Two new tactics using verbenone. *Journal of Forestry*, **97**, 26–31.
- Coakley, S. M., Scherm, H., and Chakraborty, S. (1999). Climate change and plant disease management. *Annual Review of Phytopathology*, **37**, 399–426.
- Cohen, S. D., Chang, L. W., Griffin, R. L., and Orr, R. L. (1995). Plant pest risk information system (PPRIS) for USDA-APHIS: design of a functional prototype. *Bulletin OEPP/EPPO Bulletin*, **25**, 637–650.
- Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209–233.
- Coley, P. D., Bryant, J. P., and Chapin III, F. S. (1985). Resource availability and plant antiherbivore defence. *Science*, **230**, 895–899.
- Connor, E. F., Faeth, S. H., Simberloff, D., and Opler, P. A. (1980). Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology*, **5**, 205–211.
- Conway, B. E., Leefers, L. A., and McCullough, D. G. (1999). Yield and financial losses associated with a jack pine budworm outbreak in Michigan and the

- implications for management. *Canadian Journal of Forest Research*, **29**, 382–392.
- Cooke, B. J. and Régnière, J. (1999). Predictability and measurability of *Bacillus thuringiensis* efficacy against spruce budworm (Lepidoptera: Tortricidae). *Environmental Entomology*, **28**, 711–721.
- Cooper, S. M. and Owen-Smith, N. (1986). Effects of spinescence on large mammalian herbivores. *Oecologia*, **68**, 446–445.
- Cory, J. S. (2000). Assessing the risks of releasing genetically modified virus insecticides: progress to date. *Crop Protection*, **19**, 779–785.
- Cory, J. S. (2003). Ecological impacts of virus insecticides: host range and non-target organisms. In *Environmental Impacts of Microbial Insecticides* (eds. H. Hokkanen and A. Hajek), pp. 73–91. Bios.
- Cory, J. S. and Myers, J. H. (2003). The ecology and evolution of insect baculoviruses. *Annual Review of Ecology and Systematics*, **39**, 239–272.
- Couch, T. L. (2000). Industrial fermentation and formulation of entomopathogenic bacteria. In *Entomopathogenic bacteria: from laboratory to field application* (eds. J.-F. Charles, A. Delécluse, and C. Nielsen-Le Roux), pp. 297–316. Kluwer Academic Publishers, Dordrecht.
- Couillien, D. and Gregoire, J. C. (1994). Take-off capacity as a criterion for quality control in mass-produced predators, *Rhizophagus grandis* (Col: Rhizophagidae) for the biocontrol of bark beetles, *Dendroctonus micans* (Col: Scolytidae). *Entomophaga*, **39**, 385–395.
- Coulson, R. N. and Sanders, M. C. (1987). Computer-assisted decision-making as applied to entomology. *Annual Review of Entomology*, **32**, 415–437.
- Coulson, R. N., Guzman, M. D., Skordinski, K., Fitzgerald, J. W., Conner, R. N., Rudolph, D. C., Oliveria, F. L., Wunneburger, D. F., and Pulley, P. E. (1999a). Forest landscapes. Their effect on the interaction of the southern pine beetle and the red-cockaded woodpecker. *Journal of Forestry*, **97**, 4–11.
- Coulson, R. N., McFadden, B. A., Pulley, P. E., Lovelady, C. N., Fitzgerald, J. W., and Jack, S. B. (1999b). Heterogeneity of forest landscapes and the distribution and abundance of southern pine beetle. *Forest Ecology and Management*, **114**, 471–485.
- Coutinho, T. A., Wingfield, M. J., Alfenas, A. C., and Crous, P. W. (1998). Eucalyptus rust: a disease with the potential for serious international implications. *Plant Disease*, **82**, 819–825.
- Coutts, M. P. and Grace, J. (eds.) (1995). *Wind and trees*. Cambridge University Press, Cambridge.
- Cowling, E. B. and Merrill, W. (1966). Nitrogen in wood and its role in wood deterioration. *Canadian Journal of Botany*, **44**, 1539–1534.
- Crawley, M. J. (1989). Chance and timing in biological invasions. In *Biological invasions: a global perspective*, (eds. J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmének, and M. Williamson), pp. 407–423. John Wiley & Sons, Chichester.
- Crickmore, N. (2000). The diversity of *Bacillus thuringiensis*  $\delta$ -endotoxins. In *Entomopathogenic bacteria: from laboratory to field application* (eds. J.-F. Charles, A. Delécluse, and C. Nielsen-Le Roux), pp. 65–79. Kluwer Academic Publishers, Dordrecht.
- Critchfield, W. B., and Little, E. L. (1966). Geographic distribution of pines of the world. Miscellaneous Publication, USDA No. 991.
- Cronin, J. T., Turchin, P., Hayes, J. L., and Steiner, C. A. (1999). Area-wide efficacy of a localized forest pest management practice. *Environmental Entomology*, **28**, 496–504.
- Crook, G. W., Vézina, P. E., and Hardy, Y. (1979). Susceptibility of balsam fir to spruce budworm defoliation as affected by thinning. *Canadian Journal of Forest Research*, **9**, 428–435.
- Crook, N. E. and Winstanley, D. (1995). Benefits and risks of using genetically engineered baculoviruses as insecticides. In *Biological control: benefits and risks*, (eds. H. M. T. Hokkanen and J. M. Lynch), pp. 223–230. Cambridge University Press, Cambridge.
- Cullen, J. M. and Whitten, M. J. (1995). Economics of classical biological control: a research perspective. In *Biological control: benefits and risks* (eds. H. M. T. Hokkanen and J. M. Lynch), pp. 270–276. Cambridge University Press, Cambridge.
- Cunningham, J. C. (1995). Baculoviruses as microbial insecticides. In *Novel approaches to integrated pest management* (ed. R. Reuveni), pp. 261–292. Lewis Publishers, Boca Raton.
- Cunningham, J. C. and Entwistle, P. F. (1981). Control of sawflies by baculovirus. In *Microbial control of pest and plant diseases* (ed. H. D. Burges), pp. 379–407. Academic Press, London.
- Cunningham, J. C., and van Frankenhuyzen, K. (1991). Microbial insecticides in forestry. *The Forestry Chronicle*, **67**, 473–480.
- Czokajlo, D., Wink, R. A., Warren, J. C., and Teale, S. A. (1997). Growth reduction of Scots pine, *Pinus sylvestris*, caused by the larger pine shoot beetle, *Tomicus piniperda* (Coleoptera, Scolytidae), in New York State. *Canadian Journal of Forest Research*, **27**, 1394–1397.
- Dahlsten, D. L. and Mills, N. J. (1999). Biological control of forest insects. In *Handbook of biological control principles and applications of biological control* (eds. T. S. Bellows and T. W. Fisher), pp. 761–788. Academic Press, San Diego.
- Dahlsten, D. L., Garcia, R., and Lorraine, H. (eds.) (1989). *Eradication of exotic pests analysis with case histories*. Yale University Press, New Haven.

- Damgaard, P. H. (2000). Natural occurrence and dispersal of *Bacillus thuringiensis* in the environment. In *Entomopathogenic bacteria: from laboratory to field application* (eds. J.-F. Charles, A. Delécluse, and C. Nielsen-Le Roux), pp. 23–40. Kluwer Academic Publishers, Dordrecht.
- Danks, H. V. (1987). *Insect dormancy: An ecological perspective*. Biological survey of Canada (terrestrial arthropods), Monograph series No. 1, Ottawa, Ontario.
- Danks, H. V. (1992). Long life cycles in insects. *Canadian Entomologist*, **124**, 167–187.
- De Little, D. W., Elliott, H. J., Madden, J. L., and Bashford, R. (1990). Stage specific mortality in two field populations of immature *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae). *Journal (of the) Australian Entomological Society*, **22**, 15–18.
- de Wit, P. J. G. M. (1992). Molecular characterization of gene-for-gene systems in plant-fungus interactions and the application of avirulence genes in control of plant pathogens. *Annual Review of Phytopathology*, **30**, 391–418.
- DeBarr, G. L., Hanula, J. L., Niwa, C. G., and Nord, J. C. (2000). Synthetic pheromones disrupt *Dioryctria* spp. moths in a loblolly pine seed orchard. *Canadian Entomologist*, **132**, 345–351.
- Delucchi, V. (1982). Parasitoids and hyperparasitoids of *Zeiraphera diniana* (Lep. Tortricidae) and their role in population control in outbreak areas. *Entomophaga*, **27**, 77–92.
- Denholm, I. and Rowland, M. W. (1992). Tactics for managing pesticide resistance in arthropods: Theory and practice. *Annual Review of Entomology*, **37**, 91–112.
- Denno, R. F., Larsson, S., and Olmstead, K. L. (1990). Role of enemy-free space and plant quality in host-plant selection by willow beetles. *Ecology*, **71**, 124–137.
- Desprez-Loustau, M.-L., and Wagner, K. (1997) Influence of silvicultural practices on twisting rust infection and damage in maritime pine, as related to growth. *Forest Ecology and Management*, **98**, 135–147.
- Devey, M. E., Delfino-Mix, A., Kinloch, Jr., B. B., and Neale, D. B. (1995). Random amplified polymorphic DNA markers tightly linked to a gene for resistance to white pine blister rust in sugar pine. *Proceedings of the National Academy of Science (Check name)*, **92**, 2066–2070.
- Dicke, M. and Loon, J. A. van. (2000). Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis et Applicata*, **97**, 237–249.
- Dickinson, R. B. B., Haggis, M. J., and Rainey, R. C. (1983). Spruce budworm moth flight and storms: case study of a cold front system. *Journal of Climate and Applied Meteorology*, **22**, 278–286.
- Dickinson, R. B. B., Haggis, M. J., Rainey, R. C., and Burns, L. M. D. (1986). Spruce budworm moth flight and storms: further studies using aircraft and radar. *Journal of Climate and Applied Meteorology*, **25**, 1600–1608.
- Dobson, A. P. and May, R. M. (1986). Patterns of invasion by pathogens and parasites. In *Ecology of biological invasions of North America and Hawaii* (eds. H. A. Mooney and J. A. Drake), pp. 58–76. Springer Verlag, New York.
- Dowding, P. (1984). The evolution of insect-fungus relationships in the primary invasion of forest timber. In *Invertebrate microbial interactions. British Mycological Society Symposium 6* (eds. J. M. Anderson, A. D. M. Rayner, and D. W. H. Walton), pp. 135–153. Cambridge University Press, Cambridge.
- Dreistadt, S. H. and Weber, D. C. (1989). Gypsy moth in the northeast and great lakes states. In *Eradication of exotic pests analysis with case histories*, pp. 229–256 (eds. D. L. Dahlsten, R. Garcia and H. Lorraine). Yale University Press, New Haven.
- Dubois, N. R., Reardon, R., and Mierzejewski, K. (1993). Field efficacy and deposit analysis of *Bacillus thuringiensis*, Foray 48B, against gypsy moth (Lepidoptera: Lymantriidae). *Journal of Economic Entomology*, **86**, 26–33.
- Duelli, P., Zahradnik, P., Knizek, M., and Kalinova, B. (1997). Migration in spruce bark beetles (*Ips typographus* L.) and the efficiency of pheromone traps. *Journal of Applied Entomology*, **121**, 297–303.
- Duff, G. H. and Nolan, N. J. (1953). Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa* Ait. *Canadian Journal of Botany*, **31**, 471–513.
- Dulmage, H. T. (1970). Insecticidal activity of HD-1, a new isolate of *Bacillus thuringiensis* var. *alesti*. *Journal of Invertebrate Pathology*, **15**, 232–239.
- Dungey, H. S. (2001). Pine hybrids—a review of their use performance and genetics. *Forest Ecology and Management*, **148**, 243–258.
- Dupont, A., Bélanger, L., and Bousquet, J. (1991). Relationships between balsam fir vulnerability to spruce budworm and ecological site conditions of fir stands in central Quebec. *Canadian Journal of Forest Research*, **21**, 1752–1759.
- Dwinell, L. D. (1997). The pinewood nematode: regulation and mitigation. *Annual Review of Entomology*, **35**, 153–166.
- Edwards, P. B., Wanjura, W. J., and Brown, W. V. (1993). Selective herbivory by Christmas beetles in response to intraspecific variation in *Eucalyptus* terpenoids. *Oecologia*, **95**, 551–557.
- Edwards, P. J. (1989). Insect herbivory and plant defence theory. In *Towards a more exact ecology* (eds. P. J. Grubb and J. B. Whittaker), pp. 275–297. Blackwell Scientific Publications, Oxford.

- Edwards, P. J. (1992). Resistance and defence: the role of secondary plant substances. In *Pests and pathogens plant responses to foliar attack* (ed. P. G. Ayres), pp. 69–84. Bios Scientific Publishers Ltd. Oxford.
- Ehler, L. E. (1990) Introduction strategies in biological control of insects. In *Critical issues in biological control* (eds. M. Mackauer, L. E. Ehler, and J. Roland), pp. 111–134. Intercept, Andover.
- Ehlers, R. U. (1996) Current and future use of nematodes in biocontrol: Practice and commercial aspects with regard to regulatory policy issues. *Biocontrol Science and Technology*, **6**, 303–316.
- Ehlers, R.-U. and Peters, A. (1995). Entomopathogenic nematodes in biological control: feasibility, perspectives and possible risks. In *Biological control: benefits and risks* (eds. H. M. T. Hokkanen and J. M. Lynch), pp. 119–136, Cambridge University Press, Cambridge.
- Ehlers, R. U. and Hokkanen, H. M. T. (1996). Insect biocontrol with non-endemic entomopathogenic nematodes (*Steinernema* and *Heterorhabditis* spp): Conclusions and recommendations of a combined OECD and COST Workshop on Scientific and Regulatory Policy Issues. *Biocontrol Science and Technology*, **6**, 295–302.
- Ehrlich, P. R. and Raven, P. H. (1964). Butterflies and plants: a study in coevolution. *Evolution*, **18**, 586–608.
- Eichhorn, O. and Pausch, K.-L. (1986). Untersuchungen über die Fichtengespinstblattwespen *Cephalcia* spp. Panz. (Hym., Pamphiliidae). I. Zur Problematik des Generationszyklus von *Cephalcia abietis* L. *Journal of Applied Entomology*, **101**, 101–111.
- Eidmann, H. H. (1983). Management of spruce bark beetle *Ips typographus* in Scandinavia using pheromones. *10th International Congress of Plant Protection*, **3**, 1042–1050.
- Eidmann, H. H. (1992). Impact of bark beetles on forests and forestry in Sweden. *Journal of Applied Entomology*, **114**, 193–200.
- Eidmann, H. H. and von Sydow, F. (1989). Stockings for protection of containerized conifer seedlings against pine weevil (*Hyllobius abietis* L.) damage. *Scandinavian Journal of Forest Research*, **4**, 537–547.
- Eidmann, H. H., Nordenhem, H., and Weslien, J. (1996). Physical protection of conifer seedlings against pine weevil feeding. *Scandinavian Journal of Forest Research*, **11**, 68–75.
- Eidt, D. C. and Dunphy, G. B. (1991). Control of spruce budmoth, *Zeiraphera canadensis* Mut., and Free., in white spruce plantations with entomopathogenic nematodes, *Steinernema* spp. *Canadian Entomologist*, **123**, 379–385.
- Eidt, D. C., Zervos, S., Pye, A. E., and Finney-Crawley, J. R. (1995a). Control of *Hyllobius congener* Dalle Torre, Shenkling, and Marshall (Coleoptera: Curculionidae) using entomopathogenic nematodes. *Canadian Entomologist*, **127**, 431–438.
- Eidt, D. C., Zervos, S., and Finney-Crawley, J. R. (1995b). Susceptibility of adults of *Hyllobius congener* Dalle Torre, Shenkling, and Marshall (Coleoptera: Curculionidae) to entomopathogenic nematodes. *Canadian Entomologist*, **127**, 439–441.
- Eldridge, K., Davidson, J., Harwood, C., and van Wyk, G. (1993). *Eucalypt domestication and breeding*. pp. 163–180. Clarendon Press, Oxford.
- Eldridge, R. H. and Simpson, J. A. (1987). Development of contingency plans for use against exotic pests and diseases of trees and timber 3. Histories of control measures against introduced pests and diseases of forests and forest products in Australia. *Australian Forestry*, **50**, 24–36.
- Elek, J. and Beveridge, N. (1999). Effect of a *Bacillus thuringiensis* subsp. *tenebrionis* insecticidal spray on the mortality, feeding, and development rates of larval Tasmanian Eucalyptus leaf beetles (Coleoptera: Chrysomelidae). *Journal of Economic Entomology*, **92**, 1062–1071.
- El-Kassaby, Y. A. and Ritland, K. (1996). Impact of selection and breeding on the genetic diversity in Douglas-fir. *Biodiversity and Conservation*, **5**, 795–813.
- Elkinton, J. S. and Liebhold, A. M. (1990). Population dynamics of gypsy moth in North America. *Annual Review of Entomology*, **35**, 571–596.
- Elliott, H. J., Bashford, R., Greener, A., and Candy, S. G. (1992). Integrated pest management of the Tasmanian Eucalyptus leaf beetle, *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae). *Forest Ecology and Management*, **53**, 29–38.
- Elliott, H. J., Bashford, R., and Greener, A. (1993). Effects of defoliation by the leaf beetle, *Chrysophtharta bimaculata*, on growth of *Eucalyptus regnans* plantations in Tasmania. *Australian Forestry*, **56**, 22–26.
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. Methuen, London.
- Embree, D. G. (1966). The role of introduced parasites in the control of the winter moth in Nova Scotia. *Canadian Entomologist*, **98**, 1159–1168.
- Embree, D. G. (1991). The winter moth *Operophtera brumata* in eastern Canada, 1962–1988. *Forest Ecology and Management*, **39**, 47–54.
- Engelmark, O., Sjöberg, K., Andersson, B., Rosvall, O., Ågren, G. I., Baker, W. L., Barklund, P., Björkman, C., Despain, D. G., Elfving, B., Ennos, R. A., Karlman, M., Knecht, M. F., Knight, D. H., Ledgard, N. J., Lindelöw, Å., Nilsson, C., Peterken, G. F., Sörlin, S., and Sykes, M. T. (2001). Ecological effects and management aspects of an exotic tree species: the case of lodgepole pine in Sweden. *Forest Ecology and Management*, **141**, 3–13.

- Entwistle, P. F., Cory, J. S., Bailey, M. J., and Higgs, S. (1993a). *Bacillus thuringiensis*, an environmental biopesticide: theory and practice. John Wiley & Sons, Chichester.
- Entwistle, P. F., Forkner, A. C., Green, B. M., and Cory, J. S. (1993b). Avian dispersal of nuclear polyhedrosis virus after induced epizootics in the pine beauty moth, *Panolis flammea* (Lepidoptera: Noctuidae). *Applied Environmental Microbiology*, **45**, 493–501.
- Erbilgin, N. and Raffa, K. F. (2000). Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromones. *Journal of Chemical Ecology*, **26**, 2527–2548.
- Erbilgin, N. and Raffa, K. F. (2001). Kairomonal range of generalist predators in specialized habitats: responses to multiple phloeophagous species emitting pheromones vs. host odors. *Entomologia Experimentalis et Applicata*, **99**, 205–210.
- Erdle, T. A. and MacLean, D. A. (1999). Stand growth model calibration for use in forest pest impact assessment. *Forestry Chronicle*, **75**, 141–152.
- Ericsson, T., Danell, Ö., and Andersson, B. (1994). Genetic variation of *Pinus contorta* var. *latifolia* breeding material in Sweden. *Canadian Journal of Forest Research*, **24**, 723–729.
- Evans, H. F. (2000). Viruses. In *Field manual of techniques in invertebrate pathology application and evaluation of pathogens for control of insects and other invertebrate pests*, (eds. L. A. Lacey and H. K. Kaya), pp. 179–208. Kluwer Academic Publishers, Dordrecht.
- Evans, H. F. and Fielding, N. J. (1994). Integrated management of *Dendroctonus micans* in the UK. *Forest Ecology and Management*, **65**, 17–30.
- Evans, H. F., McNamara, D. G., Braasch, H., Chadoeuf, J., and Magnusson, C. (1996). Pest risk analysis (PRA) for the territories of the European Union (as PRA area) on *Bursaphelenchus xylophilus* and its vectors in the genus *Monochamus*. *Bulletin OEPP/EPPO Bulletin*, **26**, 199–249.
- Evans, J. (1992). *Plantation forestry in the tropics tree planting for industrial, social, environmental, and agroforestry purposes*, 2nd edn. Clarendon Press, Oxford.
- Evans, J. (1999). Planted forests in the wet and dry tropics: their variety, nature, and significance. *New Forests*, **17**, 25–36.
- Evenden, M. L., Borden, J. H., and Van Sickle, G. A. (1995a). Predictive capabilities of a pheromone-based monitoring system for western hemlock looper (Lepidoptera: Geometridae). *Environmental Entomology*, **24**, 933–943.
- Evenden, M. L., Borden, J. H., Van Sickle, G. A., and Gries, G. (1995b). Development of a pheromone-based monitoring system for western hemlock looper (Lepidoptera: Geometridae): Effect of pheromone dose, lure age, and trap type. *Environmental Entomology*, **24**, 923–932.
- Everitt, J. H., Richerson, J. V., Karges, J., Alaniz, M. A., Davis, M. R., and Gomez, A. (1997). Detecting and mapping western pine beetle infestations with airborne videography, global positioning system and geographic information system technologies. *Southwestern Entomologist*, **22**, 293–300.
- Everitt, J. H., Escobar, D. E., Appel, D. N., Riggs, W. G., and Davis, M. R. (1999). Using airborne digital imagery for detecting oak wilt disease. *Plant Disease*, **83**, 502–505.
- Fajvan, M. A. and Wood, J. M. (1996). Stand structure and development after gypsy moth defoliation in the Appalachian Plateau. *Forest Ecology and Management*, **89**, 79–88.
- Falconer, D. S. and Mackay, T. F. C. (1996). *Introduction to quantitative genetics*, 4th edn. Longman, Harlow.
- Fang, Y. and Hart, E. R. (2000). Effect of cottonwood leaf beetle (Coleoptera: Chrysomelidae) larval population levels on *Populus* terminal damage. *Environmental Entomology*, **29**, 43–48.
- Fang, Y., Pedigo, L. P., Colletti, J. P., and Hart, E. R. (2002). Economic injury level for second-generation cottonwood leaf beetle (Coleoptera: Chrysomelidae) in two-year-old *Populus*. *Journal of Economic Entomology*, **95**, 313–316.
- FAO (1996a). Code of conduct for the import and release of exotic biological control agents, International Standards for Phytosanitary Measures (ISPM) Publication No. 3.
- FAO (1996b). Guidelines on pest risk analysis. FAO Rome, International Standards for Phytosanitary Measures (ISPM) Publication No. 2.
- FAO (1997). Code of conduct for the import and release of exotic biological control agents. *Biocontrol News and Information*, **18**, 119N–124N.
- FAO (2001). State of the world's forests. Rome, Italy.
- FAO (2002). *International standards for phytosanitary measures: guidelines for regulating wood packaging material in international trade*. Rome, Italy. Food and Agriculture Organisation of the United Nations, Publication No. 15.
- FAO (2003). *State of the world's forests*. Rome, Italy.
- Farrow, R. A., Floyd, R. B., and Neumann, F. G. (1994). Inter-provenance variation in resistance of *Eucalyptus globulus* juvenile foliage to insect feeding. *Australian Forestry*, **57**, 65–68.
- Fatzinger, C. W. and Dixon, W. N. (1996). Day-degree models for predicting levels of attack by slash pine flower thrips (Thysanoptera: Phlaeothripidae) and the phenology of female strobilus development on slash pine. *Environmental Entomology*, **25**, 727–735.
- Fayle, D. C., MacIver, D., and Bentley, C. V. (1983). Computer graphing of annual tree ring widths during measurement. *Forestry Chronicle*, **59**, 291–293.

- Federici, B. A. (1999a). A perspective on pathogens as biological control agents for insect pests. In *Handbook of biological control* (eds. T. S. Bellows and T. W. Fisher), pp. 517s–548s. Academic press, San Diego.
- Federici, B. A. (1999b). *Bacillus thuringiensis* in biological control. In *Handbook of biological control* (eds. T. S. Bellows and T. W. Fisher), pp. 575–593. Academic Press, San Diego.
- Federici, B. A. (1999c). Naturally occurring baculoviruses for insect control. In *Methods in biotechnology, vol. 5: Biopesticides: use and delivery* (eds. F. R. Hall and J. J. Menn), pp. 301–320. Humana Press Inc., Totowa, N.J.
- Federici, B. A. and Maddox, J. V. (1996). Host specificity in microbe–insect interactions insect control by bacterial, fungal, and viral pathogens. *Bioscience*, **46**, 410–421.
- Fedra, K. (1995). Decision support for natural resources management: models, GIS, and expert systems. *AI Applications*, **9**, 3–19.
- Fernandes, G. W. (1990). Hypersensitivity: A neglected plant resistance mechanism against insect herbivores. *Environmental Entomology*, **19**, 1173–1182.
- Fernandes, G. W. (1998). Hypersensitivity as a phenotypic basis of plant induced resistance against a galling insect (Diptera: Cecidomyiidae). *Environmental Entomology*, **27**, 260–267.
- Fernandes, G. W. and Negreiros, D. (2001). The occurrence and effectiveness of hypersensitive reaction against galling herbivores across host taxa. *Environmental Entomology*, **26**, 46–55.
- Ferré, J. and Van Rie, J. (2002). Biochemistry and genetics of insect resistance to *Bacillus thuringiensis*. *Annual Review of Entomology*, **47**, 501–533.
- Fettig, C. J. and Berisford, C. W. (2002). Use of historical temperature data for timing insecticide applications of the Nantucket pine tip moth (Lepidoptera: Tortricidae): evaluation of damage and volume increment efficiency. *Agricultural and Forest Entomology*, **4**, 167–171.
- Fielding, N. J. and Evans, H. F. (1997). Biological control of *Dendroctonus micans* (Scolytidae) in Great Britain. *Biocontrol News and Information*, **18**, 51N–60N.
- Fields, P. G. and White, N. D. G. (2002). Alternatives to methyl bromide treatments for stored-product quarantine insects. *Annual Review of Entomology*, **47**, 331–359.
- Fink, S. (1999). *Pathological and regenerative plant anatomy*. Gebrüder Borntraeger, Berlin.
- Fisher, T. W. and Andrés, L. A. (1999). Quarantine concepts, facilities and procedures. In *Handbook of biological control principles and applications of biological control* (eds. T. S. Bellows and T. W. Fisher), pp. 103–124. Academic Press, San Diego.
- Fleischer, S. J., Ravlin, F. W., and Reardon, R. C. (1991). Implementation of sequential sampling plans for gypsy moth (Lepidoptera, Lymantridae) egg masses in eastern hardwood forests. *Journal of Economic Entomology*, **84**, 1100–1107.
- Fleming, R. A. and Person, C. O. (1982). Consequences of polygenic determination of resistance and aggressiveness in nonspecific host parasite relationships. *Canadian Journal of Plant Pathology*, **4**, 89–96.
- Fleming, R. A. and van Frankenhuyzen, K. (1992). Forecasting the efficacy of operational *Bacillus thuringiensis* Berliner applications against spruce budworm *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), using dose ingestion data: initial models. *Canadian Entomologist*, **124**, 1101–1113.
- Fletcher, A. M. (1992). Breeding improved Sitka spruce. In *Super Sitka for the 90s, Forestry Commission Bulletin 103* (ed. D. A. Rook), pp. 11–24. HMSO, London.
- Flor, H. H. (1956). The complementary genic systems in flax and flax rust. *Advances in Genetics*, **8**, 29–54.
- Flor, H. H. (1971). Current status of the gene-for-gene concept. *Annual Review of Phytopathology*, **9**, 275–296.
- Floyd, R. B., Farrow, R. A., and Neumann, F. G. (1994). Inter- and intra-provenance variation in resistance of red gum foliage to insect feeding. *Australian Forestry*, **57**, 45–48.
- Floyd, R. B., Farrow, R. A., and Matsuki, M. (2002). Variation in insect damage and growth in *Eucalyptus globulus*. *Agricultural and Forest Entomology*, **4**, 109–115.
- Fox, G., Beke, J., Hopkin, T., and McKenney, D. (1997). A framework for the use of economic thresholds in forest pest management. *Forestry Chronicle*, **73**, 331–339.
- Fox, L. R. and Morrow, P. A. (1992). Eucalypt responses to fertilization and reduced herbivory. *Oecologia*, **89**, 214–222.
- Franceschi, V. R., Krekling, T., Berryman, A. A., and Christiansen, E. (1998). Specialized phloem parenchyma cells in Norway spruce (Pinaceae) bark are an important site of defense reactions. *American Journal of Botany*, **85**, 601–615.
- Franke, W. and Schultz, S. (1999). Pheromones. In *Comprehensive natural product chemistry Vol. 8 miscellaneous natural products including marine natural products, pheromones, plant hormones, and aspects of ecology* (ed. K. Mori), pp. 197–261. Elsevier, Amsterdam.
- French, J. R. and Hart, J. H. (1978). Variation in resistance of trembling aspen to *Hypoxylon mammatum* identified by inoculating naturally occurring clones. *Phytopathology*, **68**, 485–489.
- Fries, C. (1993). Development of planted *Pinus sylvestris* and *P. contorta* after soil preparation in a northern climate. *Scandinavian Journal of Forest Research*, **8**, 73–80.
- Fritts, H. C. (1976). *Tree rings and climate*. Academic Press, London.



- Fritts, H. C. (1991). *Reconstructing large-scale climatic patterns from tree-ring data*. University of Arizona Press, Tuscon, Arizona.
- Fritts, H. C. and Swetnam, T. W. (1989). Dendroecology: a tool for evaluating variations in past and present forest environments. *Advances in Ecological Research*, **19**, 111–188.
- Fritz, R. S., Nichols-Orians, C. M., and Brunsfeld, S. J. (1994). Interspecific hybridization of plants and resistance to herbivores: hypotheses, genetics, and variable responses in a diverse herbivore community. *Oecologia*, **97**, 106–117.
- Fritz, R. S., Moulia, C., and Newcombe, G. (1999). Resistance of hybrid plants and animals to herbivores, pathogens, and parasites. *Annual Review of Ecology and Systematics*, **30**, 565–591.
- Fulbright, D. W. (1999). Hypovirulence to control fungal pathogenesis. In *Handbook of biological control principles and applications of biological control* (eds. T. S. Bellows and T. W. Fisher), pp. 691–698. Academic Press, San Diego.
- Furuta, K. and Aloo, I. K. (1994). Between-tree distance and spread of the Sakhalin fir aphid (*Cinara todocola* Inouye) (Hom., Aphididae) within a plantation. *Journal of Applied Entomology*, **117**, 64–71.
- Fuxa, J. R. (1998). Environmental manipulation for microbial control of insects. In *Conservation biological control* (ed. P. Barbosa), pp. 255–268. Academic Press, San Diego.
- Gadgil, P. D. and Bain, J. (1999). Vulnerability of planted forests to biotic and abiotic disturbances. *New Forests*, **17**, 227–238.
- Gadgil, P. D., Bulman, L. S., Dick, M. A., and Bain, J. (2000a). Dutch elm disease in New Zealand. In *The elms: Breeding, conservation and disease management* (ed. C. P. Dunn), pp. 187–199. Kluwer Academic Publishers, Boston.
- Gadgil, P. D., Bulman, L. S., Crabtree, R., Watson, R. N., O'Neil, J. C., and Glassey, K. L. (2000b). Significance to New Zealand forestry of contaminants on the external surfaces of shipping containers. *New Zealand Journal of Forestry Science*, **30**, 341–358.
- Gange, A. C. (1995). Aphid performance in an alder (*Alnus*) hybrid zone. *Ecology*, **76**, 2074–2083.
- Gara, R. I., Millegan, D. R., and Gibson, K. E. (1999). Integrated pest management of *Ips pini* (Col., Scolytidae) populations in south-east Montana. *Journal of Applied Entomology*, **123**, 529–534.
- Gavin, D. G. and Peart, D. R. (1993). Effects of beech bark disease on the growth of American beech (*Fagus grandifolia*). *Canadian Journal of Forest Research*, **23**, 1566–1575.
- Georgis, R. and Hague, N. G. M. (1988). Field evaluation of *Steinernema feltiae* against the web-spinning larch sawfly *Cephalcia lariciphila*. *Journal of Nematology*, **20**, 317–320.
- Gershenson, J. (1994). The cost of plant chemical defense against herbivory: a biochemical perspective. In *Insect-plant interactions, Vol. V* (ed. E. A. Bernays), pp. 105–173. CRC Press, Boca Raton.
- Gibbs, J. and Evans, H. (2000). Pests and diseases. *Forest Research Annual Report and Accounts 1999–2000*, 9–15.
- Gibbs, J. N. (1978). Intercontinental epidemiology of Dutch elm disease. *Annual Review of Phytopathology*, **16**, 287–307.
- Gibbs, J. N. and Webber, J. F. (1996). Comparative experiences of emergency water storage and considerations for the future. In *Water storage of timber: experience in Britain* (eds. J. F. Webber and J. N. Gibbs), pp. 42–47. HMSO, London.
- Gibbs, J. N., Liese, W., and Pinon, J. (1984). Oak wilt for Europe? *Outlook on Agriculture*, **13**, 203–207.
- Gibbs, J. N., Greig, B. J. W., and Pratt, J. E. (2002). Fomes root rot in Thetford Forest, East Anglia: past, present and future. *Forestry*, **75**, 1917–202.
- Gibbs, N. (1996). Environmental impact assessment of aerial spraying Btk (*Bacillus thuringiensis* var. *Kurstaki*) in New Zealand to eradicate White-spotted tussock moth (*Orgyia thyellina*). New Zealand Ministry of Forestry, 68 pp.
- Gilbert, N. and Raworth, D. A. (1996). Insects and temperature—a general theory. *Canadian Entomologist*, **128**, 1–13.
- Gill, R. M. A. (1992a). A review of damage by mammals in north temperate forests: 1. Deer. *Forestry*, **65**, 145–169.
- Gill, R. M. A. (1992b). A review of damage by mammals in north temperate forests: 2. Small mammals. *Forestry*, **65**, 281–308.
- Gill, R. M. A. (1992c). A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. *Forestry*, **65**, 363–388.
- Glowacka, B. (1996). The control of the nun moth *Lymantria monacha* L. with the use of *Bacillus thuringiensis* Berl. in Poland. *IOBC (WPRS) Bulletin*, **19**, 57–60.
- Gninenko, Yu. I. and Gninenko, M. Yu. (2002). Little known lymantriids of the Russian Far East—potential for movement to other countries of the Pacific region. *Bulletin OEPP/EPPO Bulletin*, **32**, 477–480.
- Gninenko, Yu. I. and Orlinskii, A. D. (2002). *Dendrolimus sibiricus* in the coniferous forests of European Russia at the beginning of the twenty-first century. *Bulletin OEPP/EPPO Bulletin*, **32**, 481–483.
- Goettel, M. S., Inglis, G. D., and Wraight, S. P. (2000). Fungi. In *Field manual of techniques in invertebrate pathology application and evaluation of pathogens for control of insects and other invertebrate pests* (eds. L. A. Lacey and H. K. Kaya), pp. 255–282. Kluwer Academic Publishers, Dordrecht.

- Goettel, M. S., Hajek, A. E., Siegel, J. P., and Evans, H. C. (2001). Safety of fungal biocontrol agents. In *Fungi as biocontrol agents progress, problems and potential* (eds. T. M. Butt, C. Jackson, and N. Magan), pp. 347–375. CABI publishing, Wallingford.
- Gömöry, D. (1992). Effect of stand origin on the genetic diversity of Norway spruce (*Picea abies* Karst.) populations. *Forest Ecology and Management*, **54**, 215–223.
- Goodman, R. N. and Novacky, A. J. (1994). *The hypersensitive reaction in plants to pathogens a resistance phenomenon*. APS Press, Minnesota.
- Gordon, A. G. (1996). The sweep of the boreal in time and space, from forest formations to genes, and implications for management. *Forestry Chronicle*, **72**, 19–30.
- Gottstein, D. and Gross, D. (1992). Phytoalexins of woody plants. *Trees*, **6**, 55–68.
- Gould, F. (1998). Sustainability of transgenic insecticidal cultivars: Integrating pest genetics and ecology. *Annual Review of Entomology*, **43**, 701–726.
- Govender, P. (2002). Management of insect pests: have the goalposts changes with certification? *Southern African Forestry Journal*, **195**, 39–45.
- Gray, B. (1972). Economic tropical entomology. *Annual Review of Entomology*, **17**, 313–353.
- Gray, D. R., Régnière, J., and Boulet, B. (2000). Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Quebec. *Forest Ecology and Management*, **127**, 217–231.
- Grayson, A. J. (ed.) (1989). *The 1987 storm: Impacts and responses*, Forestry Commission Bulletin 87. HMSO, London.
- Greathead, D. J. (ed.) (1976). *A review of biological control in western and southern Europe*. Technical communication No. 7. Commonwealth Institute of Biological Control.
- Greathead, D. J. (1995). Benefits and risks of classical biological control. In *Biological Control: benefits and risks* (eds. H. M. T. Hokkanen and J. M. Lynch), pp. 53–63. Cambridge University Press, Cambridge.
- Greathead, D. J. and Greathead, A. H. (1992). Biological control of insect pests by parasitoids and predators: the BIOCAT database. *Biocontrol News and Information*, **13**, 61N–68N.
- Greenbank, D. O., Schaefer, G. W., and Rainey, R. C. (1980). Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. *Memoirs of the Entomological Society of Canada*, **110**, 1–49.
- Greener, A. and Candy, S. G. (1994). Effect of the biotic insecticide, *Bacillus thuringiensis* and a pyrethroid on survival of predators of *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae). *Journal of the Australian Entomological Society*, **33**, 321–324.
- Greenwood, M. E. and Borden, J. H. (2000). Co-baiting for spruce beetles, *Dendroctonus rufipennis*, and western balsam bark beetles, *Dryocoetes confusus* (Coleoptera: Scolytidae). *Canadian Journal of Forest Research*, **30**, 50–58.
- Grégoire, J.-C. (1988). The greater European spruce bark beetle. In *Dynamics of forest insect populations. Patterns, causes, implications* (ed. A. A. Berryman), pp. 455–478. Plenum, New York.
- Greig, B. J. W. (1984). Management of East England pine plantations affected by *Heterobasidion annosum* root rot. *European Journal of Forest Pathology*, **14**, 393–397.
- Grewal, P. and Georgis, R. (1999). Entomopathogenic nematodes. In *Methods in biotechnology, vol 5 Biopesticides: use and delivery*, (eds. F. R. Hall and J. J. Menn), pp. 271–299. Humana Press Inc., Totowa, New Jersey.
- Griffen, G. J. (2000). Blight control and restoration of the American chestnut. *Journal of Forestry*, **98**, 22–27.
- Gross, H. L. (1992). Impact analysis for a jack pine budworm infestation in Ontario. *Canadian Journal of Forest Research*, **22**, 818–831.
- Gross, P. (1991). Influence of target pest feeding niche on success rates in classical biological control. *Environmental Entomology*, **20**, 1217–1227.
- Grubb, P. J. (1992). A positive distrust in simplicity—lessons from plant defences and from competition among plants and among animals. *Journal of Ecology*, **80**, 585–610.
- Gurr, G. M., Wratten, S. D., and Barbosa, P. (2000). Success in conservation biological control of arthropods. In *Biological control: measures of success* (eds. G. Gurr and S. Wratten), pp. 105–132. Kluwer Academic Publishers, Dordrecht.
- Gwaze, D. P. (2001). Interspecific hybrids in Zimbabwe: status review and future challenges. *South African Forestry Journal*, **192**, 85–91.
- Haack, R. A. (2001). Intercepted Scolytidae (Coleoptera) at U.S. ports of entry: 1985–2000. *Integrated Pest Management Reviews*, **6**, 253–282.
- Haack, R. A. and Poland, T. M. (2001). Evolving management strategies for a recently discovered exotic forest pest: the pine shoot beetle, *Tomicus piniperda* (Coleoptera). *Biological Invasions*, **3**, 307–322.
- Haack, R. A., Law, K. R., Mastro, V. C., Ossenbruggen, H. S., and Raimo, B. J. (1997a). New York's battle with the Asian long-horned beetle. *Journal of Forestry*, **95**, 11–15.
- Haack, R. A., Lawrence, R. K., McCullough, D. C., and Sadof, C. S. (1997b). *Tomicus piniperda* in North America: an integrated response to a new exotic scolytid. In *Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests* (eds. J.-C. Grégoire,

- A. M. Liebhold, F. M. Stephen, K. R. Day, and S. M. Salom), pp. 62–72. USDA Forest Service General Technical Report, NE 236.
- Hadley, K. S. and Veblen, T. T. (1993). Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Research*, **23**, 479–491.
- Hagner, M. and Jonsson, C. (1995). Survival after planting without soil preparation for pine and spruce seedlings protected from *Hylobius abietis* by physical and chemical shelters. *Scandinavian Journal of Forest Research*, **10**, 225–234.
- Hajek, A. E. (1997). Ecology of terrestrial fungal entomopathogens. *Advances in Microbial Ecology*, **15**, 193–249.
- Hajek, A. E. and Goettel, M. S. (2000). Guidelines for evaluating effects of entomopathogens on non-target organisms. In *Field manual of techniques in invertebrate pathology* (eds. L. A. Lacey and H. K. Kaya), pp. 847–868. Kluwer Academic Publishers, Dordrecht.
- Hajek, A. E. and Webb, R. E. (1999). Inoculative augmentation of the fungal entomopathogen *Entomophaga maimaiga* as a homeowner tactic to control gypsy moth (Lepidoptera: Lymantriidae). *Biological Control*, **14**, 11–18.
- Hajek, A. E., Butler, L., and Wheeler, M. M. (1995a). Laboratory bioassays testing the host range of the gypsy moth fungal pathogen *Entomophaga maimaiga*. *Biological Control*, **5**, 530–544.
- Hajek, A. E., Humber, R. A., and Elkinton, J. S. (1995b). Mysterious origin of *Entomophaga maimaiga* in North America. *American Entomologist*, **41**, 31–42.
- Hajek, A. E., Elkinton, J. S., and Witcosky, J. J. (1996). Introduction and spread of the fungal pathogen *Entomophaga maimaiga* (Zygomycetes: Entomophthorales) along the leading edge of gypsy moth (Lepidoptera: Lymantriidae) spread. *Environmental Entomology*, **25**, 1235–1247.
- Hajek, A. E., Butler, L., Kiebherr, J. K., and Wheeler, M. M. (2000a). Risk of infection by the fungal pathogen *Entomophaga maimaiga* among Lepidoptera on the forest floor. *Environmental Entomology*, **29**, 645–650.
- Hajek, A. E., Delalibera Jr., I., and McManus, M. L. (2000b). Introduction of exotic pathogens and documentation of their establishment and impact. In *Field manual of techniques in invertebrate pathology application and evaluation of pathogens for control of insects and other invertebrate pests* (eds. L. A. Lacey and H. K. Kaya), pp. 339–369. Kluwer Academic Publishers, Dordrecht.
- Hall, F. R. and Menn, J. J. (eds.) (1999). *Biopesticides use and delivery*. Humana Press, Totowa, New Jersey.
- Hall, R. J., Titus, S. J., and Volney, W. J. A. (1993). Estimating top-kill volumes with large-scale photos on trees defoliated by the jack pine budworm. *Canadian Journal of Forest Research*, **23**, 1337–1346.
- Hall, R. J., Volney, W. J. A., and Wang, Y. (1998). Using a geographic information system (GIS) to associate forest stand characteristics with top kill due to defoliation by jack pine budworm. *Canadian Journal of Forest Research*, **28**, 1317–1327.
- Hammerschmidt, R. (1999). Phytoalexins: what have we learned after 60 years? *Annual Review of Phytopathology*, **37**, 285–306.
- Hanks, L. M., Paine, T. D., Millar, J. G., and Hom, J. L. (1995). Variation among *Eucalyptus* species in resistance to eucalyptus longhorned borer in Southern California. *Entomologia Experimentalis et Applicata*, **74**, 185–194.
- Hanks, L. M., Paine, T. D., Millar, J. G., Campbell, C. D., and Schuch, U. K. (1999). Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). *Oecologia*, **119**, 400–407.
- Hanks, L. M., Millar, J. G., Paine, T. D., and Campbell, C. D. (2000). Classical biological control of the Australian weevil *Gonipterus scutellatus* (Coleoptera: Curculionidae) in California. *Environmental Entomology*, **29**, 369–375.
- Hansen, E. M., Bentz, B. J., and Turner, D. L. (2001). Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Canadian Entomologist*, **133**, 827–841.
- Hansson, P. (1998). Susceptibility of different provenances of *Pinus sylvestris*, *Pinus contorta* and *Picea abies* to *Gremmeniella abietina*. *European Journal of Forest Pathology*, **28**, 21–32.
- Hanula, J. L., DeBarr, G. L., Weatherby, J. C., Barber, L. R., and Berisford, C. W. (2002). Degree-day model for timing insecticide applications to control *Dioryctria amatella* (Lepidoptera: Pyralidae) in loblolly pine seed orchards. *Canadian Entomologist*, **134**, 255–268.
- Harborne, J. B. (1999). Plant chemical ecology. In *Comprehensive natural products chemistry Vol. 8 miscellaneous natural products including marine natural products, pheromones, plant hormones, and aspects of ecology* (ed. K. Mori), pp. 137–196. Elsevier, Amsterdam.
- Hard, J. S. (1985). Spruce beetles attack slowly growing spruce. *Forest Science*, **31**, 839–850.
- Harju, A. M., Venäläinen, M., Beuker, E., Velling, P., and Viitanen, H. (2001). Genetic variation in the decay resistance of Scots pine wood against brown rot fungus. *Canadian Journal of Forest Research*, **31**, 1244–1249.
- Harju, A. M., Venäläinen, M., Anttonen, S., Viitanen, H., Kainulainen, P., Saranpää, P., and Vapaavuori, E. (2003). Chemical factors affecting the brown-rot decay resistance of Scots pine heartwood. *Trees*, **17**, 263–268.

- Harrington, R., Fleming, R. A., and Woivod, I. P. (2001). Climate change impacts on insect management and conservation in temperate regions: can they be predicted? *Agricultural and Forest Entomology*, **3**, 233–240.
- Harris, M. K., and Frederiksen, R. A. (1984). Concepts and methods regarding host plant resistance to arthropods and pathogens. *Annual Review of Phytopathology*, **22**, 247–272.
- Hartley, S. E. and Lawton, J. H. (1991). Biochemical aspects and significance of the rapidly induced accumulation of phenolics in birch foliage. In *Phytochemical induction by herbivores* (eds. D. W. Tallamy and M. J. Raupp), pp. 105–132. John Wiley & Sons, Inc. New York.
- Hartmann, T. (1996). Diversity and variability of plant secondary metabolism: a mechanistic view. *Entomologia Experimentalis et Applicata*, **80**, 177–188.
- Haugen, D. A. (1990). Control procedures for *Sirex noctilio* in the Green Triangle: Review from detection to severe outbreak (1977–1987). *Australian Forestry*, **53**, 24–32.
- Haugen, D. A. and Underdown, M. G. (1990). *Sirex noctilio* control program in response to the 1987 Green Triangle outbreak. *Australian Forestry*, **53**, 33–40.
- Haukiola, E. (1990). Induction of defenses in trees. *Annual Review of Entomology*, **36**, 25–42.
- Hawkins, B. A. (1994). *Pattern and process in host–parasitoid interactions*. Cambridge University Press, Cambridge.
- Hawkins, B. A. and Marino, P. C. (1997). The colonisation of native phytophagous insects in North America by exotic parasitoids. *Oecologia*, **112**, 566–571
- Hawkins, B. A., Mills, N. J., Jervis, M. A., and Price, P. W. (1999). Is the biological control of insects a natural phenomenon? *Oikos*, **86**, 493–506.
- Heikkilä, J., Nevalainen, S., and Tokola, T. (2002). Estimating defoliation in boreal coniferous forests by combining Landsat TM, aerial photographs and field data. *Forest Ecology and Management*, **158**, 9–23.
- Heiniger, U. and Rigling, D. (1994). Biological control of chestnut blight in Europe. *Annual Review of Phytopathology*, **32**, 581–599.
- Helliwell, D. R. (1997). Dauerwald. *Forestry*, **70**, 377–379.
- Heong, K. L. (1990). Computer expert systems for improving insect pest management. *Review of Agricultural Entomology*, **78**, 1–11.
- Hermes, D. A. and Mattson, W. J. (1992). The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*, **67**, 283–335.
- Hessburg, P. F., Goheen, D. J., and Koester, H. (2001). Association of black stain root disease with roads, skid trails, and precommercial thinning in Southwest Oregon. *Western Journal of Applied Forestry*, **16**, 127–135.
- Heybroek, H. M. (2000). Notes on elm breeding and genetics. In *The elms: breeding, conservation and disease management* (ed. C. P. Dunn), pp. 249–258. Kluwer Academic Publishers, Boston.
- Hicks, C. M. (2001). Exotic pests and international trade. *Exotic forest pests online symposium*. <http://exoticpests.apsnet.org/papers/hicks.htm>
- Hicks, B. J., Barbour, D. A., Evans, H. F., Heritage, S., Leather, S. R., Milne, R., and Watt, A. D. (2001). The history and control of the pine beauty moth, *Panolis flammea* (D. & S.) (Lepidoptera: Noctuidae), in Scotland from 1976 to 2000. *Agricultural and Forest Entomology*, **3**, 161–168.
- Hilker, M., Bläske, V., Kobs, C., and Dippel, C. (2000). Kairomonal effects of sawfly sex pheromones on egg parasitoids. *Journal of Chemical Ecology*, **26**, 2591–2601.
- Hill, G. and Greathead, D. (2000). Economic evaluation in classical biological control. In *The economics of biological invasions* (eds. C. Perrings, M. Williamson, and S. Dalmazzone), pp. 208–223. Edward Elgar, Cheltenham.
- Hillis, W. E. (1984). Wood quality and utilization. In *Eucalypts for wood production*, 2nd edn. (eds. W. E. Hillis and A. G. Brown), pp. 259–289. CSIRO/Academic, Melbourne.
- Hindmarch, T. D. and Reid, M. L. (2001). Forest thinning affects reproduction in pine engravers (Coleoptera: Scolyidae) breeding in felled lodgepole pine trees. *Environmental Entomology*, **30**, 919–924.
- Hodge, G. R., Masters, C. J., Cameron, R. S., Lowe, W. J., and Weir, R. J. (1997). Seed orchard pest management the case for forest service R & D. *Journal of Forestry*, **95**, 29–32.
- Hodkinson, I. D., Flynn, D. H., and Shackel, S. C. (1998). Relative susceptibility of *Salix* clones to chrysomelid beetles: evidence from the Stott willow collection at Ness. *European Journal of Forest Pathology*, **28**, 271–279.
- Holden, A. V. and Bevan, D. (eds.) (1979). *Control of the pine beauty moth by fenitrothion in Scotland 1978*. Forestry Commission, Edinburgh.
- Holdenreider, O. and Greig, B. J. W. (1998). Biological methods of control. In *Heterobasidium annosum biology, ecology, impact and control* (eds. S. Woodward, J. Stenlid, R. Karjalainen, and A. Hüttermann), pp. 235–258. CAB International, Wallingford.
- Holmes, T. P. (1991). Price and welfare effects of catastrophic forest damage from southern pine beetle epidemics. *Forest Science*, **37**, 500–516.
- Hopkin, A. A., Greifenhagen, S., and Holland, J. (2001). Decay, stains, and beetles in ice-storm-damaged forests: A review. *Forestry Chronicle*, **77**, 605–611.
- Hopper, K. R. and Roush, R. T. (1993). Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology*, **18**, 321–331.

- Hopper, K. R., Roush, R. T., and Powell, W. (1993). Management of genetics of biological-control introductions. *Annual Review of Entomology*, **38**, 27–51.
- Hosking, G. P. (1979). Contingency plan for use against exotic forest insects introduced into New Zealand. *New Zealand Forest Service Technical Paper No. 69*, 14 pp.
- Hosking, G. (1998a). White-spotted tussock moth in New Zealand. *Antenna*, **22**, 74–76.
- Hosking, G. (1998b). White-spotted tussock moth—an aggressive eradication strategy. *Aliens*, **7**, 4–5.
- Hosking, G. P. and Gadgil, P. D. (1987). Development of contingency plans for use against exotic pests and diseases of trees and timber. 4. Forest insect and disease protection in New Zealand: an integrated approach. *Australian Forestry*, **50**, 37–39.
- Houghton, J. T., Ding, Y., Griggs, D. J., Noguier, M., van der Linden, P. J., Dai, X., Maskell, K., and Johnson, C. A. (eds.) (2001). *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge.
- Houston, D. R. (1994). Major new tree disease epidemics: beech bark disease. *Annual Review of Phytopathology*, **32**, 75–87.
- Hu, J. J., Tian, Y. C., Han, Y. F., Li, L., and Zhang, B. E. (2001). Field evaluation of insect-resistant *Populus nigra* trees. *Euphytica*, **121**, 123–127.
- Hüberli, D., Tommerup, I. C., Colquhoun, I. J., and Hardy, G. E. St J. (2002). Evaluation of resistance to *Phytophthora cinnamomi* in seed-grown trees and clonal lines of *Eucalyptus marginata* inoculated in lateral branches and roots. *Plant Pathology*, **51**, 435–442.
- Hudak, J. (1991). Integrated pest management and the eastern spruce budworm. *Forest Ecology and Management*, **39**, 313–337.
- Hunt, R. S. (1991). Operational control of white pine blister rust by removal of lower branches. *Forestry Chronicle*, **67**, 284–287.
- Hunter, A. F. (1991). Traits that distinguish outbreaking and non-outbreaking macrolepidoptera feeding on northern hardwood trees. *Oikos*, **60**, 275–282.
- Hunter, A. F. (1995). Ecology, life history, and phylogeny of outbreak and nonoutbreak species. *Population dynamics new approaches and synthesis* (eds. N. Cappuccino and P. W. Price), pp. 41–64. Academic Press, San Diego.
- Hunter, M. D., Varley, G. C., and Gradwell, G. R. (1997). Estimating the roles of top-down and bottom-up forces on insect herbivore populations: a classic study re-visited. *Proceedings of the National Academy of Sciences*, **94**, 9176–9181.
- Hunter-Fujita, F. R., Entwistle, P. F., Evans, H. F., and Crook, N. E. (1998). *Insect viruses and pest management*. John Wiley & Sons, Chichester.
- Hutcheson, S. W. (1998). Current concepts of active defense in plants. *Annual Review of Phytopathology*, **36**, 59–90.
- Ikeda, T. (1984). Integrated pest management of Japanese pine wilt disease. *European Journal of Forest Pathology*, **14**, 398–414.
- Ikeda, T., Matsamura, F., and Benjamin, D. M. (1977). Mechanism of feeding discrimination between matured and juvenile foliage by two species of pine sawflies. *Journal of Chemical Ecology*, **3**, 677–694.
- Ikin, R. (1991). Plant quarantine principles as related to international trade. *FAO Plant Protection Bulletin*, **39**, 61–64.
- Ikonen, A., Tahvanainen, J., and Roininen, H. (2001). Chlorogenic acid as an antiherbivore defence of willows against leaf beetles. *Entomologia Experimentalis et Applicata*, **99**, 47–54.
- Inglis, G. D., Goettel, M. S., Butt, T. M., and Strasser, H. (2001). Use of hyphomycetous fungi for managing insect pests. In *Fungi as biocontrol agents progress, problems and potential* (eds. T. M. Butt, C. Jackson, and N. Magan), pp. 23–69. CABI Publishing, Wallingford.
- Ito, K. (1998). Spatial extent of traumatic resin duct induction in Japanese cedar, *Cryptomeria japonica* D. Don, following feeding damage by the cryptomeria bark borer, *Semanotus japonicus* Lacordaire (Coleoptera: Cerambycidae). *Applied Entomology and Zoology*, **33**, 561–566.
- Jääskelä, M., Peltonen, M., Saarenmaa, H., and Heliövaara, K. (1997). Comparison of protection methods of pine stacks against *Tomicus piniperda*. *Silva Fennica*, **31**, 143–152.
- Jacobsen, B. J. (1997). Role of plant pathology in integrated pest management. *Annual Review of Phytopathology*, **35**, 373–391.
- Jactel, H. and Kleinhenz, M. (1997). Intensive silvicultural practices increase the risk of infestation by *Dioryctria sylvestrella* Ratz (Lepidoptera: Pyralidae), the Maritime pine stem borer. In *Integrating cultural tactics into the management of bark beetle and reforestation pests* (eds. J. C. Grégoire, A. M. Liebhold, F. M. Stephen, K. R. Day, and S. M. Salom), pp. 177–190. USDA Forest Service Northeastern Forest Experiment Station General Technical Report NE-236.
- Jactel, H., Brockerhoff, E., and Duelli, P. (in press). A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. In: *The functional significance of forest diversity* (eds. M. Scherer-Lorenzen, M. C. Körner, and E.-D. Schulze), Springer Verlag.
- Jactel, H., Kleinhenz, M., Marpeau-Bezard, A., Marion-Poll, F., Menassieu, P., and Burban, C. (1996a). Terpene

- variations in maritime pine constitutive oleoresin related to host tree selection by *Dioryctria sylvestrella* Ratz. (Lepidoptera: Pyralidae). *Journal of Chemical Ecology*, **22**, 1037–1050.
- Jactel, H., Menassieu, P., Raise, G., and Burban, C. (1996b). Sensitivity of pruned maritime pine (*Pinus pinaster* Ait) to *Dioryctria sylvestrella* Ratz. (Lep., Pyralidae) in relation to tree vigour and date of pruning. *Journal of Applied Entomology*, **120**, 153–157.
- James, R. R. and Newcombe, G. (2000). Defoliation patterns and genetics of insect resistance in cottonwoods. *Canadian Journal of Forest Research*, **30**, 85–90.
- Jardon, Y., Filion, L., and Cloutier, C. (1994). Tree-ring evidence for endemicity of the larch sawfly in North America. *Canadian Journal of Forest Research*, **24**, 742–747.
- Jenkins, J. N. (1999). Transgenic plants expressing toxins from *Bacillus thuringiensis*. In *Methods in biotechnology, vol 5: Biopesticides: use and delivery* (eds. F. R. Hall and J. J. Menn), pp. 221–232. Humana Press Inc., Totowa, N.J.
- Jensen, J. S., Harding, S., and Roulund, H. (1997). Resistance to the green spruce aphid (*Elatobium abietinum* Walker) in progenies of Sitka spruce (*Picea sitchensis* (Bong) Carr.). *Forest Ecology and Management*, **97**, 207–214.
- Jervis, M. A., Kidd, N. A. C., and Heimpel, G. E. (1996). Parasitoid adult feeding behaviour and biocontrol—a review. *Biocontrol News and Information*, **17**, 11N–26N.
- Jia, J., Niemelä, P., Rousi, M., and Härkönen, S. (1997). Selective browsing of moose (*Alces alces*) on birch (*Betula pendula*) clones. *Scandinavian Journal of Forest Research*, **12**, 33–40.
- Johnson, C. A. (1997). *Geographic information systems in ecology*. Blackwell Science Ltd., Oxford.
- Johnson, G. R. (2002). Genetic variation in tolerance of Douglas-fir to Swiss needle cast as assessed by symptom expression. *Silvae Genetica*, **51**, 80–86.
- Julkunen-Tiitto, R., Rousi, M., Bryant, J., Sorsa, S., Keinänen, M., and Sikanen, H. (1996). Chemical diversity of *Betulaceae* species: comparison of phenolics and terpenoids in northern birch stems. *Trees*, **11**, 16–22.
- Kahn, R. P. (1989). *Plant protection and quarantine. Vol. I. Biological concepts*. CRC Press Boca Raton.
- Kairo, M. T. K., Cock, M. J. W., and Quinlan, M. M. (2003). An assessment of the use of the code of conduct for the import and release of exotic biological control agents (ISPM No. 3) since its endorsement as an international standard. *Biocontrol News and Information*, **24**, 15N–27N.
- Kakouli-Duarte, T., Labuschagne, L., and Hague, N. G. M. (1997). Biological control of the black vine weevil, *Otiorynchus sulcatus* (Coleoptera Curculionidae) with entomopathogenic nematodes (Nematoda: Rhabditida). *Annals of Applied Biology*, **131**, 11–27.
- Karban, R. and Baldwin, I. T. (1997). *Induced responses to herbivory*. The University of Chicago Press, Chicago.
- Karlman, M. (2001). Risks associated with the introduction of *Pinus contorta* in northern Sweden with respect to pathogens. *Forest Ecology and Management*, **141**, 97–105.
- Karlman, M., Hansson, P., and Witzell, J. (1994). *Scleroderris* canker on lodgepole pine introduced in northern Sweden. *Canadian Journal of Forest Research*, **24**, 1948–1959.
- Kause, A., Ossipov, V., Haukioja, E., Lempa, K., Hanhimäki, S., and Ossipova, S. (1999). Multiplicity of biochemical factors determining quality of growing birch leaves. *Oecologia*, **120**, 102–112.
- Kaya, H. K. and Gaugler, R. (1993). Entomopathogenic nematodes. *Annual Review of Entomology*, **38**, 181–206.
- Kelsey, R. G. (1994). Ethanol synthesis in Douglas-fir logs felled in November, January, and March and its relationship to ambrosia beetle attack. *Canadian Journal of Forest Research*, **24**, 2096–2104.
- Kemperman, J. A. and Barnes, B. V. (1976). Clone size in American aspens. *Canadian Journal of Botany*, **54**, 2603–2607.
- Kennedy, C. E. J. and Southwood, T. R. E. (1984). The number of species of insects associated with British trees: a re-analysis. *Journal of Animal Ecology*, **53**, 455–478.
- Kennedy, G. G. and Barbour, J. D. (1992). Resistance variation in natural and managed systems. In *Plant resistance to herbivores and pathogens ecology, evolution, and genetics* (eds. R. S. Fritz and E. L. Simms), pp. 13–41. The University of Chicago Press, Chicago.
- Kerr, G. (1999a). European silver fir (*Abies alba*) in Britain: time for reassessment? *Quarterly Journal of Forestry*, **93**, 294–298.
- Kerr, G. (1999b). The use of silvicultural systems to enhance the biological diversity of plantation forests in Britain. *Forestry*, **72**, 191–205.
- Kershaw, D. J. (1989). History of forest health surveillance in New Zealand. *New Zealand Journal of Forest Science*, **19**, 375–377.
- Kessmann, H., Staub, T., Hofmann, C., Maetzke, T., Herzog, J., Ward, E., Uknes, S., and Ryals, J. (1994). Induction of systemic acquired disease resistance in plants to chemicals. *Annual Review of Phytopathology*, **32**, 439–459.
- Kidd, N. A. C., and Jervis, M. A. (1996). Population dynamics. In *Insect natural enemies practical approaches to their study and evaluation* (eds. M. Jervis and N. Kidd), pp. 293–374. Chapman and Hall, London.
- Kidd, N. A. C. and Jervis, M. A. (1997). The impact of parasitoids and predators on forest insect populations.

- In *Forests and insects* (eds. A. D. Watt, N. E. Stork, and M. D. Hunter), pp. 49–68. Chapman and Hall, London.
- Killick, H. J. and Warden, S. J. (1991). Ultraviolet penetration of pine trees and insect virus survival. *Entomophaga*, **36**, 87–94.
- King, J. N., Yanchuk, A. D., Kiss, G. K., and Alfaro, R. I. (1997). Genetic and phenotypic relationships between weevil (*Pissodes strobi*) resistance and height growth in spruce populations of British Columbia. *Canadian Journal of Forest Research*, **27**, 732–739.
- Kinloch, Jr., B. B. and Dupper, G. E. (2002). Genetic specificity in the white pine-blister rust pathosystem. *Phytopathology*, **92**, 278–280.
- Klein, M. G. (1990). Efficacy against soil-inhabiting insect pests. In *Entomopathogenic nematodes in biological control* (eds. R. Gaugler and H. K. Kaya), pp. 195–214. CRC Press, Boca Raton.
- Kneeshaw, D. D., Leduc, A., Drapeau, P., Gauthier, S., Paré, D., Carignan, R., Doucet, R., Bouthillier, L., and Messier, C. (2000). Development of integrated ecological standards of sustainable forest management at an operational scale. *Forestry Chronicle*, **76**, 481–493.
- Knight, D. H., Baker, W. L., Engelman, O., and Nilsson, C. (2001). A landscape perspective on the establishment of exotic tree plantations: lodgepole pine (*Pinus contorta*) in Sweden. *Forest Ecology and Management*, **141**, 131–142.
- Knight, J. D. and Mumford, J. D. (1994). Decision support systems in crop protection. *Outlook on Agriculture*, **23**, 282–285.
- Knipling, E. F. (1985). Sterile insect technique as a screwworm control measure: the concept and its development. *Symposium on eradication of the screw-worm from the United States and Mexico* (ed. O. H. Graham). Miscellaneous Publication of the Entomological Society of America. *Entomological Society of America*, **62**, 4–7.
- Koch, N. E. and Skovsgaard, J. P. (1999). Sustainable management of planted forests: some comparisons between Central Europe and the United States. *New Forests*, **17**, 11–22.
- Kogan, M. (1998). Integrated pest management: Historical perspectives and contemporary developments. *Annual Review of Entomology*, **43**, 243–270.
- Kogan, M. and Ortman, E. F. (1978). Antixenosis—a new term proposed to define Painter's 'nonpreference' modality of resistance. *Bulletin of the Entomological Society of America*, **24**, 175–176.
- Konrad, H., Kirisits, T., Riegler, M., Halmshlager, E., and Stauffer, C. (2002). Genetic evidence for natural hybridization between Dutch elm disease pathogens *Ophiostoma novo-ulmi* ssp. *novo-ulmi* and *O. novo-ulmi* ssp. *americana*. *Plant Pathology*, **51**, 78–84.
- Koppenhöfer, A. M. (2000). Nematodes. In *Field manual of techniques in invertebrate pathology application and evaluation of pathogens for control of insects and other invertebrate pests* (eds. L. A. Lacey and H. K. Kaya), pp. 283–301. Kluwer Academic Publishers, Dordrecht.
- Koricheva, J., Larsson, S., Haukioja, E., and Keinänen, M. (1998). Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos*, **83**, 212–226.
- Kouki, J., McCullough, D. G., and Marshall, L. D. (1997). Effects of forest stand and edge characteristics on the vulnerability of jack pine stands to jack pine budworm (*Choristoneura pinus pinus*) damage. *Canadian Journal of Forest Research*, **27**, 1765–1772.
- Krokene, P., Christiansen, E., Solheim, H., Franceschi, V. R., and Berryman, A. A. (1999). Induced resistance to pathogenic fungi in Norway spruce. *Plant Physiology*, **121**, 565–569.
- Krokene, P., Solheim, H., and Christiansen, E. (2001). Induction of disease resistance in Norway spruce (*Picea abies*) by necrotising fungi. *Plant Pathology*, **50**, 230–233.
- Kuč, J. (1995). Phytoalexins, stress metabolism, and disease resistance in plants. *Annual Review of Phytopathology*, **33**, 275–297.
- Kuittinen, H., Muona, O., Kärkkäinen, K., and Borzan, Ž. (1991). Serbian spruce, a narrow endemic, contains much genetic variation. *Canadian Journal of Forest Research*, **21**, 363–367.
- Kulman, H. M. (1971). Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology*, **16**, 289–324.
- Kuno, E. (1991). Sampling and analysis of insect populations. *Annual Review of Entomology*, **36**, 285–304.
- Kytö, M., Niemelä, P., and Annala, E. (1996a). Vitality and bark beetle resistance of fertilized Norway spruce. *Forest Ecology and Management*, **84**, 149–157.
- Kytö, M., Niemelä, P., and Larsson, S. (1996b). Insects on trees: Population and individual response to fertilization. *Oikos*, **75**, 148–159.
- Kytö, M., Niemelä, P., and Annala, E. (1998). Effects of vitality fertilization on the resin flow and vigour of Scots pine in Finland. *Forest Ecology and Management*, **102**, 121–130.
- Laarman, J. G. and Sedjo, R. A. (1992). *Global forests*. McGraw-Hill, New York.
- Lacey, L. A. and Kaya, H. K. (2000). *Field manual of techniques in invertebrate pathology application and evaluation of pathogens for control of insects and other invertebrate pests*. Kluwer Academic Publishers, Dordrecht.
- Lacey, L. A. and Siegel, J. P. (2000). Safety and ecotoxicology of entomopathogenic bacteria. In *Entomopathogenic bacteria: From laboratory to field application* (eds.

- J. F. Charles, A. Delecluse, and C. Nielsen-LeRoux), pp. 253–273. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Laidlaw, W. G., Prenzel, B. G., Reid, M. L., Fabris, S., and Wieser, H. (2003). Comparison of the efficacy of pheromone-baited traps, pheromone-baited trees, and felled trees for the control of *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Environmental Entomology*, **32**, 477–483.
- Långström, B. and Hellqvist, C. (1990). Spatial distribution of crown damage and growth losses caused by recurrent attacks of pine shoot beetles in pine stands surrounding a pulp mill in southern Sweden. *Journal of Applied Entomology*, **110**, 261–269.
- Långström, B. and Hellqvist, C. (1991). Shoot damage and growth losses following three years of *Tomicus*-attacks in Scots pine stands close to timber storage site. *Silva Fennica*, **25**, 133–145.
- Långström, B. and Hellqvist, C. (1993). Induced and spontaneous attacks by pine shoot beetles on young scots pine trees—tree mortality and beetle performance. *Journal of Applied Entomology*, **115**, 25–36.
- Lawrence, R. K., Houseweart, M. W., Jennings, D. T., Southard, S. G., and Halteman, W. A. (1985). Development rates of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) and implications for timing augmentative releases for suppression of egg populations of *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Canadian Entomologist*, **117**, 556–563.
- Leakey, R. R. B. (1987). Clonal forestry in the tropics—a review of developments, strategies and opportunities. *Commonwealth Forestry Review*, **66**, 61–75.
- Leather, S. R. (1985). Oviposition preferences in relation to larval growth rates and survival in the pine beauty moth, *Panolis flammea*. *Ecological Entomology*, **10**, 213–217.
- Leather, S. R. and Barbour, D. A. (1987). Associations between soil type, lodgepole pine (*Pinus contorta* Douglas) provenance, and the abundance of the pine beauty moth, *Panolis flammea* (D & S). *Journal of Applied Ecology*, **24**, 945–952.
- Ledgard, N. (2001). The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management*, **141**, 43–57.
- Ledig, F. T. (1992). Human impacts on genetic diversity in forest ecosystems. *Oikos*, **63**, 87–108.
- Ledig, F. T. and Smith, D. M. (1981). The influence of silvicultural practices on genetic improvement: height growth and weevil resistance in eastern white pine. *Silvae Genetica*, **30**, 31–36.
- Lee, S. J. (1994). Breeding radiata pine in New Zealand. *Scottish Forestry*, **48**, 9–15.
- Leonhardt, B. A., Mastro, V. C., Leonard, D. S., Mclane, W., Reardon, R. C., and Thorpe, K. W. (1996). Control of low-density gypsy moth (Lepidoptera: Lymantriidae) populations by mating disruption with pheromone. *Journal of Chemical Ecology*, **22**, 1255–1272.
- Lester, P. J., Rogers, D. J., Petry, R. J., Connolly, P. G., and Roberts, P. B. (2000). The lethal effects of gamma irradiation on larvae of the Huhu beetle, *Prionoplus reticularis*: a potential quarantine treatment for New Zealand export pine trees. *Entomologia Experimentalis et Applicata*, **94**, 237–242.
- Letourneau, D. K. and Burrows, B. E. (eds.) (2002). *Genetically engineered organisms assessing environmental and human health effects*. CRC Press, Boca Raton.
- Leuschner, W. A., Young, J. A., Waldon, S. A., and Ravlin, F. W. (1996). Potential benefits of slowing the gypsy moth's spread. *Southern Journal of Applied Forestry*, **20**, 65–73.
- LeVeen, E. P. (1989). Economic evaluation of eradication programs. In *Eradication of exotic pests analysis with case histories* (eds. D. L. Dahlsten, R. Garcia, and H. Lorraine), pp. 41–56. Yale University Press, New Haven.
- Lewis, E. E., Gauger, R., and Harrison, R. (1992). Entomopathogenic nematode host finding: response to host contact cues by cruise and ambush foragers. *Parasitology*, **105**, 103–107.
- Lewis, K. G., Alfaro, R. I., and Andrucko, D. (1999). Variation in *Elatobium abietinum* attack on *Picea glauca* and its relation to *Pissodes strobi* resistance. *Scandinavian Journal of Forest Research*, **14**, 334–340.
- Libman, G. N. and MacIntosh, S. C. (2000). Registration of biopesticides. In *Entomopathogenic bacteria: from laboratory to field application* (eds. J-F. Charles, A. Delécluse, and C. Nielsen-Le Roux), pp. 333–353. Kluwer Academic Publishers, Dordrecht.
- Liebholt, A. M. and Kamata, N. (2000). Are population cycles and spatial synchrony a universal characteristic of forest insect populations. *Population Ecology*, **42**, 205–209.
- Liebholt, A. M., Halverson, J. A., and Elmes, G. A. (1992). Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography*, **19**, 513–520.
- Liebholt, A. M., Rossi, R. E., and Kemp, W. P. (1993a). Geostatistics and geographic information systems in applied insect ecology. *Annual Review of Entomology*, **38**, 303–327.
- Liebholt, A. M., Simons, E. E., Sior, A., and Unger, J. D. (1993b). Forecasting defoliation caused by the gypsy moth from field measurements. *Environmental Entomology*, **22**, 26–32.
- Liebholt, A. M., Elkinton, J. S., Zhou, G., Hohn, M. E., Rossi, R. E., Boettner, G. K., Boettner, C. W., Burnham, C.,



- and Mcmanus, M. L. (1995a). Regional correlation of gypsy moth (Lepidoptera: Lymantriidae) defoliation with counts of egg masses, pupae, and male moths. *Environmental Entomology*, **24**, 193–203.
- Liebholt, A. M., MacDonald, W. L., Bergdahl, D., and Mastro, V. C. (1995b). Invasion by exotic forest pests: A threat to forest ecosystems. *Forest Science Monograph*, **30**, 1–49.
- Liese, W. and Peek, R.-D. (1984). Experiences with wet storage of conifer logs. *Dansk Skovforenings Tidsskrift*, **69**, 73–91.
- Lieutier, F. (2002). Mechanisms of resistance in conifers and bark beetle attack strategies. In *Mechanisms and deployment of resistance in trees to insects* (eds. M. R. Wagner, K. M. Clancy, F. Lieutier, and T. D. Paine), pp. 31–77. Kluwer Academic Publishers, Dordrecht.
- Lindgren, B. S. (1990). Ambrosia beetles. *Journal of Forestry*, **88**, 8–11.
- Lindgren, B. S. and Fraser, R. G. (1994). Control of ambrosia beetle damage by mass trapping at a dryland log sorting area in British Columbia. *Forestry Chronicle*, **70**, 159–163.
- Lindgren, B. S., McGregor, M. D., Oakes, R. D., and Meyer, H. E. (1988). Effect of MCH and baited Lindgren traps on Douglas-fir beetle attacks on felled trees. *Journal of Applied Entomology*, **105**, 289–294.
- Lindström, A., Hellqvist, C., Gyldberg, B., Långström, B., and Mattsson, A. (1986). Field performance of a protective collar against damage by *Hylobius abietis*. *Scandinavian Journal of Forest Research*, **1**, 3–15.
- Liu, Y.-C., Double, M. L., MacDonald, W. L., and Milgroom, M. G. (2002). Persistence of *Cryphonectria* hypoviruses after their release for biological control of chestnut blight in West Virginia forests. *Forest Pathology*, **32**, 345–356.
- Lodge, D. M. (1993). Biological invasions: lessons from ecology. *TREE*, **8**, 133–137.
- Loehle, C. (1988). Tree life history strategies: the role of defences. *Canadian Journal of Forest Research*, **18**, 209–222.
- Loh, D. K., Connor, M. D., and Janiga, P. (1991). Jack pine budworm decision support system: a prototype. *AI Applications*, **5**, 29–45.
- Lombardero, M. J., Ayres, M. P., Lorio, P. L. Jr., and Ruel, J. J. (2000). Environmental effects on constitutive and inducible resin defences of *Pinus taeda*. *Ecological Letters*, **3** 329–339.
- Long, G. E. (1988). The larch casebearer in the intermountain northwest. In *Dynamics of forest insect populations patterns, causes, implications* (ed. A. A. Berryman), pp. 233–242. Plenum Press, New York.
- Long, G. E. (1990). Modelling the dynamics of larch casebearer. In *Population dynamics of forest insects* (eds. A. D. Watt, S. R. Leather, M. D. Hunter, and N. A. C. Kidd), pp. 347–58. Intercept, Andover.
- Lonsdale, D. (1999). *Principles of tree hazard assessment and management*. The Stationery Office, London.
- Lonsdale, D. and Gibbs, J. (2002). Effects of climate change on fungal diseases of trees. In *Climate change: Impacts on UK forests* (ed. M. Broadmeadow), pp. 83–97. Forestry Commission Bulletin 125. Forestry Commission, Edinburgh.
- Lorio Jr., P. L., Stephen, F. M., and Paine, T. D. (1995). Environment and ontogeny modify loblolly pine response to induced acute water deficits and bark beetle attack. *Forest Ecology and Management*, **73**, 97–110.
- Louda, S. M., Pemberton, R. W., Johnson, M. T., and Follett, P. A. (2003). Nontarget effects—the Achilles’ heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. *Annual Review of Entomology*, **48**, 365–396.
- Lovett, G. M., Christenson, L. M., Groffman, P. M., Jones, C. G., Hart, J. E., and Mitchell, M. J. (2002). Insect defoliation and nitrogen cycling in forests. *BioScience*, **52**, 335–341.
- Lu, W. and Montgomery, M. E. (2001). Oviposition, development, and feeding of *Scymnus* (*Neopullus*) *sinuanodulus* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America*, **94**, 64–70.
- Luther, J. E., Franklin, S. E., Hudak, J., and Meades, J. P. (1997). Forecasting the susceptibility and vulnerability of balsam fir stands to insect defoliation with Landsat Thematic Mapper data. *Remote Sensing of Environment*, **59**, 77–91.
- MacLean, D. A. (1980). Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. *Forestry Chronicle*, **56**, 213–221.
- MacLean, D. A. (1996a). Forest management strategies to reduce spruce budworm damage in the Fundy Model Forest. *Forestry Chronicle*, **72**, 399–405.
- MacLean, D. A. (1996b). The role of a stand dynamics model in the spruce budworm decision support system. *Canadian Journal of Forest Research*, **26**, 1731–1741.
- MacLean, D. A. (1998). Landscape management for restructuring forest areas. In *Forest scenario modelling for ecosystem management at landscape level* (eds. G.-J. Nabuurs, T. Nuutinen, H. Bartelink, and M. Korhonen), pp. 25–45. European Forest Institute Proceedings No. 19.
- MacLean, D. A. and MacKinnon, W. E. (1996). Accuracy of aerial sketch-mapping estimates of spruce budworm defoliation in New Brunswick. *Canadian Journal of Forest Research*, **26**, 2009–2108.
- Maclean, D. A. and Mackinnon, W. E. (1997). Effects of stand and site characteristics on susceptibility and vulnerability

- of balsam fir and spruce to spruce budworm in New Brunswick. *Canadian Journal of Forest Research*, **27**, 1859–1871.
- MacLean, D. A., Beaton, K. P., Porter, K. B., MacKinnon, W. E., and Budd, M. G. (2002). Potential wood supply losses to spruce budworm in New Brunswick estimated using the Spruce Budworm Decision Support System. *Forestry Chronicle*, **78**, 739–750.
- MacLeod, A., Evans, H. F., and Baker, R. H. A. (2002). An analysis of pest risk from Asian longhorn beetle (*Anoplophora glabripennis*) to hardwood trees in the European community. *Crop Protection*, **21**, 635–645.
- Maczuga, S. A. and Mierzejewski, K. J. (1995). Droplet size and density effects of *Bacillus thuringiensis kurstaki* on gypsy moth (Lepidoptera: Lymantriidae) larvae. *Journal of Economic Entomology*, **88**, 1376–1379.
- Magarey, R. D., Travis, J. W., Russo, J. M., Seem, R. C., and Magarey, P. A. (2002). Decision support systems: quenching the thirst. *Plant Disease*, **86**, 4–14.
- Mahoney, R. L. (1978). Lodgepole pine/mountain pine beetle risk classification methods and their application. In *Theory and practice of mountain pine beetle management in lodgepole pine forests*, pp. 106–113. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, USDA Forest Service, Forest Insect and Disease Research, Washington, D.C., and the Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Mahroof, R. M., Hauxwell, C., Edirisinghe, J. P., Watt, A. D., and Newton, A. C. (2002). Effects of artificial shade on attack by the mahogany shoot borer, *Hypsipyla robusta* (Moore). *Agricultural and Forest Entomology*, **4**, 283–292.
- Malinoski, M. K. and Paine, T. D. (1988). A day-degree model to predict Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae), flights in southern California. *Environmental Entomology*, **17**, 75–79.
- Maloy, O. C. (1997). White pine blister rust control in North America: a case history. *Annual Review of Phytopathology*, **35**, 87–109.
- Mamiya, Y. (1983). Pathology of the pine wilt disease caused by *Bursaphelenchus xylophilus*. *Annual Review of Phytopathology*, **21**, 201–220.
- Manion, P. D. and Lachance, D. (eds.) (1992). *Forest decline concepts*. American Phytopathological Society, St. Paul.
- Manley, S. A. M. and Fowler, D. P. (1969). Spruce budworm defoliation in relation to introgression in red and black spruce. *Forest Science*, **15**, 365–366.
- Marchand, P. J. (1983). Sapwood area as an estimator of foliage biomass and projected leaf area for *Abies balsamea* and *Picea rubens*. *Canadian Journal of Forest Research*, **14**, 85–87.
- Margolis, H. A. and Brand, D. G. (1990). An ecophysiological basis for understanding plantation establishment. *Canadian Journal of Forest Research*, **20**, 375–390.
- Martignoni, M. E. (1999). History of TM BioControl-1: the first registered virus-based product for control of a forest insect. *American Entomologist*, **45**, 30–37.
- Martini, A., Baldassari, N., Baronio, P., Anderbrant, O., Hedenström, E., Högberg, H.-E., and Rocchetta, G. (2002). Mating disruption of the pine sawfly *Neodiprion sertifer* (Hymenoptera: Diprionidae) in isolated pine stands. *Agricultural and Forest Entomology*, **4**, 195–201.
- Mathews, G. A. (1992). *Pesticide application methods*. Longman, London.
- Mathews, P. L. and Stephen, F. M. (1997). Effect of artificial diet on longevity of adult parasitoids of *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environmental Entomology*, **26**, 961–965.
- Matsuki, M., Kay, M., Serin, J., Floyd, R., and Scott, J. K. (2001). Potential risk of accidental introduction of Asian gypsy moth (*Lymantria dispar*) to Australasia: effects of climatic conditions and suitability of native plants. *Agricultural and Forest Entomology*, **3**, 305–320.
- Mattila, U., Jalkanen, R., and Nikula, A. (2001). The effects of forest structure and site characteristics on probability of pine twisting rust damage in young Scots pine stands. *Forest Ecology and Management*, **142**, 89–97.
- Mattson, W. J. Jr. (1980). Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.
- Maun, K. and Webber, J. (1996). Changes in the properties of timber during water storage. In *Water storage of timber: experience in Britain* (eds. J. F. Webber and J. N. Gibbs), pp. 33–41. HMSO, London.
- McCaskill, D. and Croteau, R. (1998). Some caveats for bioengineering terpenoid metabolism in plants. *Trends in Biotechnology*, **16**, 349–355.
- McClintock, J. T. (1999). The federal registration process and requirements for the United States. In *Methods in biotechnology, vol. 5: Biopesticides: use and delivery* (eds. F. R. Hall and J. J. Menn), pp. 415–441. Humana Press Inc., Totowa, N.J.
- McCracken, A. R. and Dawson, W. M. (1998). Short rotation coppice willow in Northern Ireland since 1973: development of the use of mixtures in the control of foliar rust (*Melampsora* spp.). *European Journal of Forest Pathology*, **28**, 241–250.
- McCullough, D. G. and Sadof, C. S. (1998). Evaluation of an integrated management and compliance program for *Tomicus piniperda* (Coleoptera: Scolytidae) in pine Christmas tree fields. *Journal of Economic Entomology*, **91**, 785–795.

- McCullough, D. G., Marshall, L. D., Buss, L. J., and Kouki, J. (1996). Relating jack pine budworm damage to stand inventory variables in northern Michigan. *Canadian Journal of Forest Research*, **26**, 2180–2190.
- McCullough, D. G., Werner, R. A., and Neumann, D. (1998). Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology*, **43**, 107–127.
- McGregor, M. D., Amman, G. D., Schmitz, R. F., and Oakes, R. D. (1987). Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. *Canadian Journal of Forest Research*, **17**, 1234–1239.
- McKay, H. M. (1997). A review of the effect of stresses between lifting and planting on nursery stock quality and performance. *New Forests*, **13**, 369–399.
- McKey, D., Waterman, P. G., Mbi, C. N., Gartlan, J. S., and Struhsaker, T. T. (1978). Phenolic content of vegetation in two African rainforests: ecological implications. *Science*, **202**, 61–63.
- McLean, J. A. (1985). Ambrosia beetles: a multimillion dollar degrade problem of sawlogs in coastal British Columbia. *Forestry Chronicle*, **61**, 295–298.
- McLean, J. A., Bakke, A., and Niemeyer, H. (1987). An evaluation of three traps and two lures for the ambrosia beetle *Trypodendron lineatum* (Oliv.) (Coleoptera: Scolytidae) in Canada, Norway, and West Germany. *Canadian Entomologist*, **119**, 273–280.
- Mearns, L. O., Rosenzweig, C., and Goldberg, R. (1997). Mean and variance change in climatic scenarios: methods, agricultural applications, and measures of uncertainty. *Climate Change*, **35**, 367–396.
- Memmot, J. and Godfray, H. C. J. (1993). Parasitoid webs. In *Hymenoptera and biodiversity*, (eds. J. LaSalle and I. D. Gauld), pp. 217–234. CAB International Press, Wallingford.
- Mendel, Z. (1998). Biogeography of *Matsucoccus josephi* (Homoptera: Matsucoccidae) as related to host resistance in *Pinus brutia* and *Pinus halepensis*. *Canadian Journal of Forest Research*, **28**, 323–330.
- Messier, C. and Kneeshaw, D. D. (1999). Thinking and acting differently for sustainable management of the boreal forest. *Forestry Chronicle*, **75**, 929–938.
- Michelozzi, M., Squillace, A. E., and White, T. L. (1990). Monoterpene composition and fusiform rust resistance in slash pine. *Forest Science*, **36**, 470–475.
- Mihajlovich, M. (2001). Does forest certification assure sustainability?—a case study. *Forestry Chronicle*, **77**, 994–997.
- Miller, A. and Rusnock, P. (1993). The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. *Forest Ecology and Management*, **61**, 171–189.
- Miller, C. A. and Renault, T. R. (1976). Incidence of parasitoids attacking endemic spruce budworm (Lepidoptera: Tortricidae) populations in New Brunswick. *Canadian Entomologist*, **108**, 1045–1052.
- Miller, C. A., Greenbank, D. O., and Kettla, E. G. (1978). Estimated egg deposition by invading spruce budworm moths (Lepidoptera: Tortricidae). *Canadian Entomologist*, **110**, 609–615.
- Miller, D. R. and Borden, J. H. (1990).  $\beta$ -Phellandrene: Kairomone for pine engraver *Ips pini* (Say) (Coleoptera: Scolytidae). *Journal of Chemical Ecology*, **16**, 2519–2531.
- Miller, D. R., Borden, J. H., King, G. G. S., and Slessor, K. N. (1991). Ipsdienol: an aggregation pheromone for *Ips latidens* (LeConte) (Coleoptera: Scolytidae). *Journal of Chemical Ecology*, **17**, 1517–1527.
- Miller, D. R., Borden, J. H., and Lindgren, B. S. (1995). Verbenone: Dose-dependent interruption of pheromone-based attraction of three sympatric species of pine bark beetles (Coleoptera: Scolytidae). *Environmental Entomology*, **24**, 692–696.
- Miller, J. C. (1990). Field assessment of the effects of a microbial pest control agent on nontarget Lepidoptera. *American Entomologist*, **36**, 135–139.
- Miller, J. C. (2000). Monitoring the effects of *Bacillus thuringiensis kurstaki* on nontarget Lepidoptera in woodlands and forests of western Oregon. In *Nontarget effects of biological control* (eds. P. A. Follett and J. J. Duan), pp. 277–286. Kluwer Academic Publishers, Boston.
- Miller, J. T. and Knowles, F. B. (1989). Introduced forest trees in New Zealand: recognition, role and seed source. 6. The spruces. *New Zealand Forest Research Institute Bulletin No. 124*.
- Miller, M. C., Moser, J. C., McGregor, M., Grégoire, J.-C., Baisier, M., Dahlsten, D. L., and Werner, R. A. (1987). Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). *Annals of the Entomological Society of America*, **80**, 417–428.
- Miller, R. H., Whitney, H. S., and Berryman, A. A. (1986). Effects of induced translocation stress and bark beetle attack (*Dendroctonus ponderosae*) on heat pulse velocity and the dynamic wound response of lodgepole pine (*Pinus contorta* var. *latifolia*). *Canadian Journal of Botany*, **64**, 2669–2674.
- Miller, W. E. (1978). Use of prescribed burning in seed production areas to control red pine cone beetle. *Environmental Entomology*, **7**, 698–702.
- Mills, N. (2000). Biological control: the need for realistic models and experimental approaches to parasitoid introductions. In *Parasitoid population biology* (eds. M. E. Hochberg and A. R. Ives), pp. 217–234. Princeton University Press, Princeton.

- Mills, N. J. (1983). The natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. *Biocontrol News and Information*, **4**, 305–328.
- Mills, N. J. (1990a). Are parasitoids of significance in endemic populations of forest defoliators? Some experimental observations from gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae). In *Population dynamics of forest insects* (eds. A. D. Watt, S. R. Leather, M. D. Hunter, and N. A. C. Kidd), pp. 265–273. Intercept, Andover.
- Mills, N. J. (1990b). Biological control, a century of pest management. *Bulletin of Entomological Research*, **80**, 359–362.
- Mills, N. J. (1993). Observations on the parasitoid complexes of budmoths (Lepidoptera: Tortricidae) on larch in Europe. *Bulletin of Entomological Research*, **83**, 103–112.
- Mills, N. J. (1997). Techniques to evaluate the efficacy of natural enemies. In *Methods in ecological and agricultural entomology* (eds. D. R. Dent and M. P. Walton), pp. 271–291. CAB International, Wallingford.
- Mills, N. J. and Räther, M. (1990). Hemlock loopers in Canada; biology; pest status and potential for biological control. *Biocontrol News and Information*, **11**, 209–221.
- Mitchell, R. G., Waring, R. H., and Pitman, G. B. (1983). Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science*, **29**, 204–211.
- Mooney, H. A. and Drake, J. A. (1989). Biological invasions: a SCOPE program overview. In *Biological invasions: a global perspective* (eds. J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmének, and M. Williamson), pp. 491–508. John Wiley & Sons, Chichester.
- Moore, D. and Prior, C. (1993). The potential of mycoinsecticides. *Biocontrol News and Information*, **14**, 31N–40N.
- Moran, G. F., Bell, J. C., and Eldridge, K. G. (1988). The genetic structure and the conservation of the five natural populations of *Pinus radiata*. *Canadian Journal of Forest Research*, **18**, 506–514.
- Mordue (Luntz), A. J. and Blackwell, A. (1993). Azadirachtin; an update. *Journal of Insect Physiology*, **39**, 903–924.
- Moreno-González, J. and Cubero, J. I. (1993). Selection strategies and choice of breeding methods. In *Plant breeding: principles and prospects* (eds. M. D. Hayward, N. O. Bøsemark, and I. Romagosa), pp. 281–313. Chapman & Hall, London.
- Morewood, P., Gries, G., Liška, J., Kapitola, P., Häußler, D., Möller, K., and Bogenschütz, H. (2000). Towards pheromone-based monitoring of nun moth, *Lymantria monacha* (L.) (Lep., Lymantriidae) populations. *Journal of Applied Entomology*, **124**, 77–85.
- Morrell, J. J. (1995). Importation of unprocessed logs into North America: a review of pest mitigation procedures and their efficacy. *Forest Products Journal*, **45**, 41–50.
- Morrison, D. J., Pellow, K. W., Nemec, A. F. L., Norris, D. J., and Semenoff, P. (2001). Effects of selective cutting on the epidemiology of armillaria root disease in the southern interior of British Columbia. *Canadian Journal of Forest Research*, **31**, 59–70.
- Morrow, P. A. and LaMarche, V. C. (1978). Tree ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. *Science*, **201**, 1244–1246.
- Moscardi, F. (1999). Assessment of the application of baculoviruses for control of Lepidoptera. *Annual Review of Entomology*, **44**, 257–289.
- Mota, M., Braasch, H., Bravo, M. A., Penas, A. C., Burgermeister, W., Metge, K., and Sousa, E. (1999). First report of *Bursaphelenchus xylophilus*. Portugal and in Europe. *Nematology*, **1**, 727–734.
- Muhs, H. J. (1993). Policies, regulations and laws affecting clonal forestry. In *Clonal forestry. Vol 2 Conservation and application* (eds. M. R. Ahuja and W. J. Libby), pp. 215–227. Springer-Verlag, Berlin.
- Muirhead-Thomson, R. C. (1991). *Trap responses to flying insects*. Academic Press, London.
- Mullin, T. J. and Bertrand, S. (1998). Environmental release of transgenic trees in Canada—potential benefits and assessment of biosafety. *Forestry Chronicle*, **74**, 203–219.
- Mutikainen, P., Walls, M., Ovaska, J., Keinänen, M., Julkunen-Tiitto, R., and Vapaavuori, E. (2000). Herbivore resistance in *Betula pendula*: effect of fertilization, defoliation, and plant genotype. *Ecology*, **81**, 49–65.
- Myers, J. H. (1988). Can a general hypothesis explain population cycles of forest Lepidoptera? *Advances in Ecological Research*, **18**, 179–242.
- Myers, J. H. (1993). Population outbreaks in forest Lepidoptera. *American Scientist*, **81**, 241–251.
- Myers, J. H. and Bazely, D. (1991). Thorns, spines, prickles and hairs: are they stimulated by herbivory and do they deter herbivores? In *Phytochemical induction by herbivores* (eds. D. W. Tallamy and M. J. Raupp), pp. 325–344. John Wiley & Sons, Inc. New York.
- Myers, J. H., Higgins, C., and Kovacs, E. (1989). How many insect species are necessary for the biological control of insects? *Environmental Entomology*, **18**, 541–547.
- Myers, J. H., Savoie, A., and Randen, E. van (1998). Eradication and pest management. *Annual Review of Entomology*, **43**, 471–491.
- Myers, J. H., Malakar, R., and Cory, J. S. (2000). Sublethal nucleopolyhedrovirus infection effects on female pupal weight, egg mass size, and vertical transmission in gypsy moth (Lepidoptera: Lymantriidae). *Environmental Entomology*, **29**, 1268–1272.
- Nagarajan, S. and Singh, D. V. (1990). Long-distance dispersion of rust pathogens. *Annual Review of Phytopathology*, **28**, 139–153.

- Nagy, N. E., Franceschi, V. R., Solheim, H., Krekling, T., and Christiansen, E. (2000). Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): anatomy and cytochemical traits. *American Journal of Botany*, **87**, 302–313.
- Nambiar, E. K. S. (1999). Pursuit of sustainable plantation forestry. *South African Forestry Journal*, **184**, 45–62.
- Neale, M. and Newton, P. (1999). Registration/regulatory requirements in Europe. In *Methods in biotechnology, vol 5: Biopesticides: use and delivery* (eds. F. R. Hall and J. J. Menn), pp. 453–471. Humana Press Inc., Totowa, N.J.
- Nealis, V. G. and Lomic, P. V. (1994). Host-plant influence on the population ecology of the jack pine budworm, *Choristoneura pinus* (Lepidoptera: Tortricidae). *Ecological Entomology*, **19**, 367–373.
- Nealis, V. G. and van Frankenhuyzen, K. (1990). Interactions between *Bacillus thuringiensis* Berliner and *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae), a parasitoid of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Canadian Entomologist*, **122**, 585–594.
- Nealis, V. G., van Frankenhuyzen, K., and Cadogan, B. L. (1992). Conservation of spruce budworm parasitoids following application of *Bacillus thuringiensis* var. *kurstaki* Berliner. *Canadian Entomologist*, **124**, 1085–1092.
- Negrón, J. F., Wilson, J. L., and Anhold, J. A. (2000). Stand conditions associated with roundheaded pine beetle (Coleoptera: Scolytidae) infestations in Arizona and Utah. *Environmental Entomology*, **29**, 20–27.
- Neumann, F. G., Harris, J. A., Kassaby, F. Y., and Minko, G. (1982). An improved technique for early detection and control of the *Sirex* wood wasp in radiata pine plantations. *Australian Forestry*, **45**, 117–124.
- Neuvonen, S. and Haukioja, E. (1991). The effects of inducible resistance in host foliage on birch-feeding herbivores. In *Phytochemical induction by herbivores* (eds. D. W. Tallamy and M. J. Raupp), pp. 277–291. John Wiley & Sons, Inc. New York.
- Newcombe, G. (1996). The specificity of fungal pathogens of *Populus*. In *Biology of Populus and its implications for management and conservation* (eds. R. F. Stettler, H. D. Bradshaw, Jr., P. E. Heilman, and T. M. Hinckley), pp. 223–246. NRC Research Press, Ottawa.
- Newcombe, G. (1998). A review of exapted resistance to diseases of *Populus*. *European Journal of Forest Pathology*, **28**, 209–216.
- Newsom, L. D. (1978). Eradication of plant pests—con. *Bulletin of the Entomological Society of America*, **24**, 35–40.
- Newton, A. C., Baker, P., Ramnarine, S., Mesén, J. F., and Leakey, R. R. B. (1993). The mahogany shoot borer: prospects for control. *Forest Ecology and Management*, **57**, 301–328.
- Newton, A. C., Watt, A. D., Lopez, F., Cornelius, J. P., Mesén, J. F., and Corea, E. A. (1999). Genetic variation in host susceptibility to attack by the mahogany shoot borer, *Hypsipyla grandella* (Zeller). *Agricultural and Forest Entomology*, **1**, 11–18.
- Newton, P. J. (1993). Increasing the use of trichogrammatids in insect pest management: a case study from the forests of Canada. *Pesticide Science*, **37**, 381–386.
- Nichols-Orians, C. M., Fritz, R. S., and Clausen, T. P. (1993). The genetic basis for variation in the concentration of phenolic glycosides in *Salix sericea*: clonal variation and sex-based differences. *Biochemical Systematics and Ecology*, **21**, 535–542.
- Nicol, D., Armstrong, K. F., Wratten, S. D., Walsh, P. J., Straw, N. A., Cameron, C. M., Lahmann, C., and Frampton, C. M. (1998). Genetic diversity of an introduced pest, the green spruce aphid *Elatobium abietinum* (Hemiptera: Aphididae) in New Zealand and the United Kingdom. *Bulletin of Entomological Research*, **88**, 537–543.
- Nielsen, U. B., Kirkeby-Thomsen, A., and Roulund, H. (2002). Genetic variation in resistance to *Dreyfusia nordmanniana* Eckst. infestations in *Abies nordmanniana* (Stev.) Spach. *Forest Ecology and Management*, **165**, 271–283.
- Niemelä, P. and Mattson, W. J. (1996). Invasion of North American forests by European phytophagous insects: legacy of the European crucible? *BioScience*, **46**, 741–753.
- Niemelä, P., Chapin, F. S. III, Danell, K., and Bryant, J. P. (2001). Herbivory-mediated responses of selected boreal forests to climatic change. *Climatic Change*, **48**, 427–440.
- Nilssen, A. C. (1978). Development of a bark fauna in plantations of spruce (*Picea abies* (L.) Karst) in North Norway. *Astarte*, **11**, 151–169.
- Nishida, R. (2002). Sequestration of defensive substances from plants by Lepidoptera. *Annual Review of Entomology*, **47**, 57–92.
- Nordlander, G. (1991). Host finding in the pine weevil, *Hylobius abietis*: effects of conifer volatiles and added limonene. *Entomologia Experimentalis et Applicata*, **59**, 229–238.
- Nothnagle, P. J. and Schultz, J. C. (1987). What is a forest pest? In *Insect outbreaks* (eds. P. Barbosa and J. C. Schultz), pp. 59–79. Academic Press, London.
- Nowak, D. J., Pasek, J. E., Sequeira, R. A., Crane, D. E., and Mastro, V. C. (2001a). Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. *Journal of Economic Entomology*, **94**, 116–122.
- Nowak, J. T., McCravy, K. W., Fettig, C. J., and Berisford, C. W. (2001b). Susceptibility of adult hymenopteran

- parasitoids of the Nantucket pine tip moth (Lepidoptera: Tortricidae) to broad-spectrum and biorational insecticides in a laboratory study. *Journal of Economic Entomology*, **94**, 1122–1129.
- Nuss, D. L. (1992). Biological control of chestnut blight: an example of virus-mediated attenuation of fungal pathogenesis. *Microbiological Reviews*, **56**, 561–576.
- O'Callaghan, D. P., Gallagher, E. M., and Lanier, G. N. (1980). Field evaluation of pheromone-baited trap trees to control elm bark beetles, vectors and Dutch elm disease. *Environmental Entomology*, **9**, 181–185.
- O'Hehir, J. F. and Leech, J. W. (1997). Logging residue assessment by line intersect sampling. *Australian Forestry*, **60**, 196–201.
- O'Neill, M., and Evans, H. F. (1999). Cost-effectiveness analysis of options within an Integrated Crop Management regime against great spruce bark beetle, *Dendroctonus micans*, Kug. (Coleoptera: Scolytidae). *Agricultural and Forest Entomology*, **1**, 151–156.
- Obst, J. R. (1998). Special (secondary) metabolites from wood. In *Forest Products Biotechnology* (eds. A. Bruce and J. W. Palfreyman), pp. 151–165. Taylor & Francis.
- OECD (2001). Guidance for registration requirements for pheromones and other semiochemicals used for arthropod pest control. OECD Environment, Health and Safety Publications Series on Pesticides No. 12. Environment Directorate Organisation for Economic Co-operation and Development Paris 2001 ([www.oecd.org](http://www.oecd.org)).
- Ohgashi, H., Wagner, M. R., Matsumura, F., and Benjamin, D. M. (1981). Chemical basis of differential feeding behaviour of the larch sawfly, *Pristiphora erichsonii* (Hartig). *Journal of Chemical Ecology*, **7**, 599–614.
- Ollerstam, O., Rohfritsch, O., Höglund, S., and Larsson, S. (2002). A rapid hypersensitive response associated with resistance in the willow *Salix viminalis* against the gall midge *Dasineura marginemtorquens*. *Entomologia Experimentalis et Applicata*, **102**, 153–162.
- Orbay, L., Mclean, J. A., Sauder, B. J., and Cottell, P. L. (1994). Economic losses resulting from ambrosia beetle infestation of sawlogs in coastal British Columbia, Canada. *Canadian Journal of Forest Research*, **24**, 1266–1276.
- Orlinskii, A. D. (2001). Quarantine pests for forestry. *Bulletin OEPP/EPPO Bulletin*, **31**, 391–396.
- Östlund, L., Zackrisson, O., and Axelsson, A.-L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, **27**, 1198–1206.
- Paine, T. D. and Baker, F. A. (1993). Abiotic and biotic predisposition. In *Beetle-pathogen interactions in conifer forests* (eds. T. D. Schowalter and G. M. Filip), pp. 61–79. Academic Press London.
- Paine, T. D. and Millar, J. G. (2001). Insect pests of eucalypts in California: implications of managing invasive species. *Bulletin of Entomological Research*, **92**, 147–151.
- Paine, T. D., Stephen, F. M., and Mason, G. N. (1983). A risk population level. In *The role of the host in population dynamics of forest insects* (eds. L. Safranyik), pp. 210–212. Canadian Forest Service and USDA Forest Service, Banff, Alta.
- Paine, T. D., Stephen, F. M., and Taha, H. A. (1984). Conceptual model of infestation probability based on bark beetle abundance and host tree susceptibility. *Environmental Entomology*, **13**, 619–624.
- Paine, T. D., Millar, J. G., and Hanks, L. M. (1995). Integrated program protects trees from eucalyptus longhorned borer. *California Agriculture*, **49**, 34–37.
- Paine, T. D., Raffa, K. F., and Harrington, T. C. (1997). Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology*, **42**, 179–206.
- Painter, R. H. (1951). *Insect resistance in crop plants*, The Macmillan Company, New York.
- Painter, R. H. (1958). Resistance of plants to insects. *Annual Review of Entomology*, **3**, 267–290.
- Panda, N. and Khush, G. S. (1995). *Host plant resistance to insects*. CAB International, Wallingford.
- Paré, P. W. and Tumlinson, J. H. (1999). Plant volatiles as a defence against insect herbivores. *Plant Physiology*, **121**, 325–331.
- Parker, M. A. (1992). Constraints on the evolution of resistance to pests and pathogens. In *Pests and pathogens plant responses to foliar attack* (ed. P. G. Ayres), pp. 181–197. Bios Scientific Publishers Ltd. Oxford.
- Parry, D., Spence, J. R., and Volney, W. J. A. (1997). Responses of natural enemies to experimentally increased populations of the forest tent caterpillar, *Malacosoma disstria*. *Ecological Entomology*, **22**, 97–108.
- Pautasso, M., Holdenrieder, O., and Stenlid, J. (in press). Susceptibility to fungal pathogens of forests differing in tree diversity. In *The functional significance of forest diversity* (eds. M. Scherer-Lorenzen, M., C. Körner, and E.-D. Schulze), Springer Verlag.
- Payne, T. L., Billings, R. F., Berisford, C. W., Salom, S. M., Grosman, D. M., Dalusky, M. J., and Upton, W. W. (1992). Disruption of *Dendroctonus frontalis* (Col., Scolytidae) infestations with an inhibitor pheromone. *Journal of Applied Entomology*, **114**, 341–347.
- Peacock, L., Herrick, S., and Brain, P. (1999). Spatio-temporal dynamics of willow beetle (*Phratorta vulgatissima*) in short-rotation coppice willows grown as monocultures or a genetically diverse mixture. *Agricultural and Forest Entomology*, **1**, 287–296.

- Peacock, L., Hunter, T., Turner, H., and Brain, P. (2001). Does host genotype diversity affect the distribution of insect and disease damage in willow cropping systems? *Journal of Applied Ecology*, **38**, 1070–1081.
- Pearce, R. B. (1996). Tansley Review No. 87. Antimicrobial defences in the wood of living trees. *New Phytologist*, **132**, 203–233.
- Pedgley, D. (1982). *Windborne pests and diseases: Meteorology of airborne organisms*. Harwood, Chichester.
- Pedigo, L. P., Hutchins, S. H., and Higley, L. G. (1986). Economic injury levels in theory and practice. *Annual Review of Entomology*, **31**, 341–368.
- Pell, J. K., Eilenberg, J., Hajek, A. E., and Steinkraus, D. C. (2001). Biology, ecology and pest management potential of Entomophthorales. In *Fungi as biocontrol agents progress, problems and potential* (eds. T. M. Butt, C. Jackson, and N. Magan), pp. 71–153. CABI Publishing, Wallingford.
- Peltonen, M. (1999). Windthrows and dead-standing trees as bark beetle breeding material at forest-clearcut edge. *Scandinavian Journal of Forest Research*, **14**, 505–511.
- Peltonen, M., Heliövaara, K., and Väisänen, R. (1997). Forest insects and environmental variation in stand edges. *Silva Fennica*, **31**, 129–141.
- Peña, L. and Séguin, A. (2001). Recent advances in the genetic transformation of trees. *TRENDS on Biotechnology*, **19**, 500–506.
- Percival, G. C. (2001). Induction of systemic acquired disease resistance in plants: potential implications for disease management in urban forestry. *Journal of Arboriculture*, **27**, 181–192.
- Perkins, J. H. and Garcia, R. (1999). Social and economic factors affecting research and implementation of biological control. In *Handbook of biological control principles and applications of biological control* (eds. T. S. Bellows and T. W. Fisher), pp. 933–1009. Academic Press, San Diego.
- Perley, C. J. K. (2000). Does timberlands represent a positive vision? *International Forestry Review*, **2**, 129–136.
- Peterken, G. F. (2001). Ecological effects of introduced tree species in Britain. *Forest Ecology and Management*, **141**, 31–42.
- Peters, A. (1996). The natural host range of *Steinernema* and *Heterorhabditis* spp., and their impact on insect populations. *Biocontrol Science and Technology*, **6**, 389–402.
- Peters, B. C. (1990). Infestations of *Cryptotermes brevis* (Walker) (Isoptera:Kalotermitidae) in Queensland, Australia 1. History, detection and identification. *Australian Forestry*, **53**, 79–88.
- Peters, R. L. (1990). Effects of global warming on forests. *Forest Ecology and Management*, **35**, 13–33.
- Phillips, M. A. and Croteau, R. B. (1999). Resin-based defences in conifers. *Trends in Plant Science*, **4**, 184–190.
- Phipps, R. L. (1985). Collecting, preparing, crossdating, and measuring tree increment cores. *Water-Resources Investigations Report 85–4148*, U.S. Geological Survey.
- Pickett, C. H., Ball, J. C., Casanave, K. C., Klonsky, K. M., Jetter, K. M., Bezark, L. G., and Schoenig, S. E. (1996). Establishment of the ash whitefly parasitoid *Encarsia inaron* (Walker) and its economic benefit to ornamental street trees in California. *Biological Control*, **6**, 260–272.
- Pickett, J. A., Wadhams, L. J., and Woodcock, C. M. (1997). Developing sustainable pest control from chemical ecology. *Agriculture, Ecosystems and Environment*, **64**, 149–156.
- Picot, J. J. C. and Kristmanson, D. D. (1997). *Forestry pesticide aerial spraying. Spray droplet generation, dispersion and deposition*. Environmental science and technology library, Vol. 12, Kluwer Academic Publishers, The Netherlands.
- Pimentel, D. (1961). Species diversity and insect population outbreaks. *Annals of the Entomological Society of America*, **54**, 76–86.
- Pimentel, D. (1986). Biological invasions of plants and animals in agriculture and forestry. In *Ecology of biological invasions of North America and Hawaii* (eds. H. A. Mooney and J. A. Drake), pp. 149–162. Springer-Verlag, New York.
- Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience*, **50**, 53–65.
- Pimm, S. L. (1998). The forest fragment classic. *Nature*, **393**, 23–24.
- Plochmann, R. (1992). The forests of central Europe a changing view. *Journal of Forestry*, **90**, 12–16 and 41.
- Podgwaite, J. D. (1999). Gypcheck biological insecticide of the gypsy moth. *Journal of Forestry*, **97**, 16–19.
- Powers, H. R., Schmidt, R. A., and Snow, G. A. (1981). Current status and management of fusiform rust on southern pines. *Annual Review of Phytopathology*, **19**, 353–371.
- Powers, J. S., Sollins, P., Harmon, M. E., and Jones, J. A. (1999). Plant-pest interactions in time and space: a Douglas-fir bark beetle outbreak as a case study. *Landscape Ecology*, **14**, 105–120.
- Pratt, J. E. (1979). *Fomes annosus* butt rot of Sitka spruce. III Losses in yield and value of timber in diseased trees and stands. *Forestry*, **52**, 113–127.
- Pratt, J. E. (1998). Economic appraisal of the benefits of control treatments. In *Heterobasidium annosum* biology, ecology, impact and control (eds. S. Woodward, J. Stenlid, R. Karjalainen, and A. Hüttermann), pp. 315–331. CAB International, Wallingford.
- Price, C. (1989). *The theory and application of forest economics*. Basil Blackwell Ltd. Oxford.

- Price, P. W. (1973). Parasitoid strategies and community organisation. *Environmental Entomology*, **2**, 623–626.
- Price, P. W. (1991). The plant vigor hypothesis and herbivore attack. *Oikos*, **62**, 244–251.
- Pschorn-Walcher, H. (1973). Die Parasiten der gesellig lebenden Kiefern-Buchshornblattwespen als Beispiel für Koexistenz und Konkurrenz in multiplen Parasit-Wirt-Komplexen. *Verhanden Deutsch Zoologische Gesellschaft*, **66**, 136–145.
- Pschorn-Walcher, H. (1977). Biological control of forest insects. *Annual Review of Entomology*, **22**, 1–22.
- Putz, F. E. and Sharitz, R. R. (1991). Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, U.S.A. *Canadian Journal of Forest Research*, **21**, 1765–1770.
- Pye, A. and Pye, N. (1985). Different applications of the insect parasitic nematode *Neoaplectana carpocapsae* to control the large pine weevil, *Hylobius abietis*. *Nematologica*, **31**, 109–116.
- Quencez, C. and Bastien, C. (2001). Genetic variation within and between populations of *Pinus sylvestris* L. (Scots pine) for susceptibility to *Melampsora pinitorqua* (pine twist rust). *Heredity*, **86**, 36–44.
- Quine, C. P., Coutts, M., Gardner, B., and Pyatt, G. (1995). *Forests and wind: Management to minimise damage*. Forestry Commission Bulletin 114. HMSO, London.
- Radeloff, V. C., Mladenoff, D. J., and Boyce, M. S. (1999). Detecting jack pine budworm defoliation using spectral mixture analysis: separating effects from determinants. *Remote Sensing of Environment*, **69**, 156–169.
- Raffa, K. F. (1991). Induced defensive reactions in conifer-bark beetle systems. In *Phytochemical induction by herbivores* (eds. D. W. Tallamy and M. J. Raupp), pp. 245–276. John Wiley & Sons, Inc., New York.
- Raffa, K. F. and Berryman, A. A. (1987). Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *American Naturalist*, **129**, 234–262.
- Raty, L., Drumont, A., de Windt, N., and Grégoire, J.-C. (1995). Mass trapping of the spruce bark beetle *Ips typographus* L.: traps or trap trees? *Forest Ecology and Management*, **78**, 191–205.
- Rauscher, H. M. (1995). Natural resource decision support: theory and practice. (special issue) *AI Applications*, **9**, 1–127.
- Raymond, C. A. (1995). Genetic variation in *Eucalyptus regnans* and *Eucalyptus nitens* for levels of observed defoliation caused by the *Eucalyptus* leaf beetle, *Chrysophtharta bimaculata* Olivier, in Tasmania. *Forest Ecology and Management*, **72**, 21–29.
- Régnière, J. (1983). An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Canadian Entomologist*, **115**, 1371–1382.
- Reichardt, P. B., Bryant, J. P., Clausen, T. P., and Wieland, G. D. (1984). Defence of winter-dormant Alaska paper birch against snowshoe hares. *Oecologia*, **65**, 58–59.
- Reichenbacher, R. R., Schultz, R. C., and Hart, E. R. (1996). Artificial defoliation effect on *Populus* growth, biomass production, and total nonstructural carbohydrate concentration. *Environmental Entomology*, **25**, 632–642.
- Reynolds, K. M. and Hard, J. S. (1991). Risk and hazard of spruce beetle attack in unmanaged stands on the Kenai peninsula, Alaska, under epidemic conditions. *Forest Ecology and Management*, **43**, 137–151.
- Reynolds, K. M. and Holsten, E. H. (1994a). Classification of spruce beetle hazard in Lutz spruce (*Picea × lutzii*) stands on the Kenai Peninsula, Alaska. *Canadian Journal of Forest Research*, **24**, 1015–1021.
- Reynolds, K. M. and Holsten, E. H. (1994b). Relative importance of risk factors for spruce beetle outbreaks. *Canadian Journal of Forest Research*, **24**, 2089–2095.
- Reynolds, K. M., Holsten, E. H., and Werner, R. A. (1994). SBExpert users guide (version 1.0): a knowledge-based decision-support system for spruce beetle management. *General Technical Report PNW-GTR-345U*, Portland OR. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 72pp.
- Rhoades, D. F. (1979). Evolution of plant chemical defence against herbivores. In *Herbivores: Their interaction with secondary plant metabolites* (eds. G. A. Rosenthal and D. H. Janzen), pp. 3–54. Academic Press, New York.
- Rhoades, D. F. and Cates, R. G. (1976). Towards a general theory of plant antiherbivore chemistry. In *Biochemical interactions between plants and insects* (eds. J. W. Wallace and R. L. Mansell), pp. 168–213. Plenum Press, New York.
- Richards, A., Matthews, M., and Christian, P. (1998). Ecological considerations for the environmental impact evaluation of recombinant baculovirus insecticides. *Annual Review of Entomology*, **43**, 493–517.
- Richardson, D. M. (1998). Forestry trees as invasive aliens. *Conservation Biology*, **12**, 18–26.
- Richardson, D. M. and Higgins, S. I. (1998). Pines as invaders in the southern hemisphere. In *Ecology and biogeography of Pinus* (eds. D. M. Richardson), pp. 450–473. Cambridge University Press, Cambridge.
- Richardson, K. F. and Meakins, R. H. (1986). Inter- and intra-specific variation in the susceptibility of Eucalypts to the snout beetle *Gonipterus scutellatus* Gyll. (Coleoptera: Curculionidae). *South African Forestry Journal*, **139**, 21–31.
- Richardson, P. N. (1996). British and European legislation regulating rhabditid nematodes. *Biocontrol Science and Technology*, **6**, 449–463.
- Richens, R. H. (1983). *Elm*. Cambridge University Press, Cambridge.



- Riley, J. R. (1989). Remote sensing in entomology. *Annual Review of Entomology*, **34**, 247–271.
- Rishbeth, J. (1963). Stump protection against *Fomes annosus*. III Inoculation with *Peniophora gigantea*. *Annals of Applied Biology*, **52**, 63–77.
- Ritchie, G. A. (1991). The commercial use of conifer rooted cuttings in forestry: a world review. *New Forests*, **5**, 247–275.
- Rizvi, S. A., Hennessey, R., and Knott, D. (1996). Legislation on the introduction of exotic nematodes in the US. *Biocontrol Science and Technology*, **6**, 477–480.
- Roberds, J. H. and Bishir, J. W. (1997). Risk analyses in clonal forestry. *Canadian Journal of Forest Research*, **27**, 425–432.
- Roberds, J. H., Namkoong, G., and Skrøppa, T. (1990). Genetic analysis of risk in clonal populations of forest trees. *Theoretical and Applied Genetics*, **79**, 841–848.
- Robinson, R. A. (1973). Horizontal resistance. *Review of Plant Pathology*, **52**, 483–501.
- Robison, D. J., McCown, B. H., and Raffa, K. F. (1994). Responses of gypsy moth (Lepidoptera: Lymantriidae) and forest tent Caterpillar (Lepidoptera: Lasiocampidae) to transgenic poplar, *Populus* spp., containing a *Bacillus thuringiensis* *d*-endotoxin gene. *Environmental Entomology*, **23**, 1030–1041.
- Roche, B. M. and Fritz, R. S. (1998). Effects of host plant hybridization on resistance to willow leaf rust caused by *Melampsora* sp. *European Journal of Forest Pathology*, **28**, 259–270.
- Roland, J. (1993). Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, **93**, 25–30.
- Roland, J. (1998). The population dynamics of *Operophtera brumata* (Lepidoptera: Geometridae). In *Insect populations in theory and practice*. 19th Symposium of the Royal Entomological Society (eds. J. P. Dempster and I. F. G. McLean), pp. 309–321. Kluwer Academic Publishers, Dordrecht.
- Roland, J. and Embree, D. G. (1995). Biological control of the winter moth. *Annual Review of Entomology*, **40**, 475–492.
- Roland, J. and Kaupp, W. J. (1995). Reduced transmission of forest tent caterpillar (Lepidoptera: Lasiocampidae) nuclear polyhedrosis virus at the forest edge. *Environmental Entomology*, **24**, 1175–1178.
- Roland, J., Taylor, P., and Cooke, B. (1997). Forest structure and the spatial pattern of parasitoid attack. In *Forests and insects* (eds. A. D. Watt, N. E. Stork, and M. D., Hunter), pp. 97–106. Chapman & Hall, London.
- Rolland, C., Baltensweiler, W., and Petitcolas, V. (2001). The potential for using *Larix decidua* ring widths in reconstructions of larch budmoth (*Zeiraphera diniana*) outbreak history: dendrochronological estimates compared with insect surveys. *Trees*, **15**, 414–424.
- Rosenthal, G. A. and Berenbaum, M. R. (eds.) (1991). *Herbivores: Their interactions with secondary plant metabolites I The chemical participants*, 2nd ed. Academic Press, Inc. San Diego.
- Rosenthal, G. A. and Berenbaum, M. R. (eds.) (1992). *Herbivores: Their interactions with secondary plant metabolites II Ecological and evolutionary processes*, 2nd ed. Academic Press, Inc. San Diego.
- Ross, D. W. and Daterman, G. E. (1998). Pheromone-baited traps for *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae): Influence of selected release rates and trap designs. *Journal of Economic Entomology*, **91**, 500–506.
- Ross, D. W., Birgersson, G., Espelie, K. E., and Berisford, C. W. (1995). Monoterpene emissions and cuticular lipids of loblolly and slash pines: potential bases for oviposition preference of the nantucket pine tip moth. *Canadian Journal of Botany*, **73**, 21–25.
- Rositer, M., Yendol, W. G., and Dubois, N. R. (1990). Resistance to *Bacillus thuringiensis* in gypsy moth (Lepidoptera: Lymantriidae): genetic and environmental causes. *Journal of Economic Entomology*, **83**, 2211–2218.
- Roth, H. (1989). Concepts and recent developments in regulatory treatments. In *Plant protection and quarantine. Vol III Special topics* (ed. R. P. Kahn), pp. 117–144. CRC Press, Boca Raton.
- Roush, R. (1997). Managing resistance to transgenic crops. In *Advances in insect control: The role of transgenic plants* (eds. N. Carozzi and M. Koziel), pp. 271–294. Taylor & Francis, London.
- Rousi, M. (1990). Breeding forest trees for resistance to mammalian herbivores—a study based on European white birch. *Acta Forestalia Fennica*, **210**, 1–20.
- Rousi, M., Tahvanainen, J., and Uotila, I. (1991). A mechanism of resistance to hare browsing in winter-dormant European white birch (*Betula pendula*). *American Naturalist*, **137**, 64–82.
- Rousi, M., Tahvanainen, J., Henttonen, H., and Uotila, I. (1993). Effects of shading and fertilization on resistance of winter-dormant birch (*Betula pendula*) to voles and hares. *Ecology*, **74**, 30–38.
- Rousi, M., Tahvanainen, J., Henttonen, H., Herms, D. A., and Uotila, I. (1997). Clonal variation in susceptibility of white birches (*Betula* spp.) to mammalian and insect herbivores. *Forest Science*, **43**, 396–402.
- Roux, J., Wingfield, M. J., Bouillet, J.-P., Wingfield, B. D., and Alfenas, A. C. (2000). A serious wilt disease of *Eucalyptus* cause by *Ceratocystis fimbriata* in central Africa. *European Journal of Forest Pathology*, **30**, 175–184.
- Rowell-Rahier, M. and Pasteels, J. M. (1992). Third trophic level influences of plant allelochemicals. In

- Herbivores: Their interactions with secondary plant metabolites II Ecological and evolutionary processes*, 2nd edn (eds. G. A. Rosenthal and M. R. Berenbaum), pp. 243–277. Academic Press, Inc. San Diego.
- Ruohomäki, K., Tanhuanpää, M., and Ayres, M. P. (2000). Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. *Population Ecology*, **42**, 211–223.
- Russell, G. E. (1978). *Plant breeding for pest and disease resistance*. Butterworths, London.
- Rutledge, C. E. (1996). A survey of identified kairomones and synonyms used by insect parasitoids to locate and accept hosts. *Chemoecology*, **7**, 121–131.
- Ryall, K. L. and Smith, S. M. (2001). Bark and wood-boring beetle response in red pine (*Pinus resinosa* Ait.) plantations damaged by the 1998 ice storm: Preliminary observations. *Forestry Chronicle*, **77**, 657–660.
- Ryals, J. A., Neuenschwander, U. H., Willits, M. G., Molina, A., Steiner, H. Y., and Hunt, M. D. (1996). Systemic acquired resistance. *The Plant Cell*, **8**, 1809–1819.
- Ryan, R. B. (1990). Evaluation of biological control: introduced parasites of larch casebearer (Lepidoptera: Coleophoridae) in Oregon. *Environmental Entomology*, **19**, 1873–1881.
- Ryan, R. B. (1997). Before and after evaluation of biological control of the larch casebearer (Lepidoptera: Coleophoridae) in the Blue Mountains of Oregon and Washington, 1912–1995. *Environmental Entomology*, **26**, 703–715.
- Ryan, R. B., Tunnock, S., and Ebel, F. W. (1987). The larch casebearer in North America. *Journal of Forestry*, **85**, 33–39.
- Saaty, T. L. (1990). How to make a decision: the analytic hierarchy process. *European Journal of Operational Research*, **48**, 9–26.
- Safranyik, L., Shore, T. L., and Linton, D. A. (1999). Attack by bark beetles (Coleoptera: Scolytidae) following spacing of mature lodgepole pine (Pinaceae) stands. *Canadian Entomologist*, **131**, 671–685.
- Sahota, T. S., Manville, J. F., Hollmann, J., Leal, I., Ibaraki, A., and White, E. (2001). Resistance against *Pissodes strobi* (Coleoptera: Curculionidae) in severed leaders and in a water-soluble bark extract of *Picea sitchensis* (Pinaceae): evidence for a post ingestive mode of action. *Canadian Entomologist*, **133**, 315–323.
- Sailer, R. I. (1978). Our immigrant insect fauna. *Bulletin of the Entomological Society of America*, **24**, 3–11.
- Salmeron, J. M. and Vernooij, B. (1998). Transgenic approaches to microbial disease resistance in crop plants. *Current Opinion in Plant Biology*, **1**, 347–352.
- Samways, M. J. (1997). Classical biological control and biodiversity conservation: What risks are we prepared to accept? *Biodiversity and Conservation*, **6**, 1309–1316.
- Sanchis, V. (2000). Biotechnological improvements of *Bacillus thuringiensis* for agricultural control of insect pests: benefits and ecological implications. In *Entomopathogenic bacteria: from laboratory to field application* (eds. J-F. Charles, A. Delécluse, and C. Nielsen-Le Roux), pp. 441–459. Kluwer Academic Publishers, Dordrecht.
- Sanders, C. J. (1988). Monitoring spruce budworm population density with sex pheromone traps. *Canadian Entomologist*, **120**, 175–183.
- Sanders, C. J. (1997). Mechanisms of mating disruption in moths. In *Insect pheromone research new directions* (eds. R. T. Cardé and A. K. Minks), pp. 333–346. Chapman and Hall, New York.
- Sands, D. P. A. (1997). The ‘safety’ of biological control agents: assessing their impact on beneficial and other non-target hosts. *Memoirs of the Museum of Victoria*, **56**, 611–615.
- Santoro, A. E., Lombardero, M. J., Ayres, M. P., and Ruel, J. J. (2001). Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management*, **144**, 245–254.
- Savill, P., Evans, J., Auclair, D., and Falck, J. (1997). *Plantation silviculture in Europe*. Oxford University Press, Oxford.
- Savotikov, I. F. Smetnik, A. I., and Orlinskii, A. D. (1995). Situation of the Asian form of gypsy moth (*Lymantria dispar*) in Russia and in the world. *Bulletin OEPP/EPPO Bulletin*, **25**, 617–622.
- Schaefer, P. W. and Wallner, W. E. (1992). Asian gypsy moth (AGM) bioecology: Comparisons with North American gypsy moth and other species of *Lymantria*. In *Proc. USDA interagency gypsy moth research forum 1992* (eds. K. W. Gottschalk and M. J. Twery), pp. 42–43. USDA For. Serv. Gen. Tech. Rep. NE-170.
- Schlyter, F. and Anderbrant, O. (1989). Mass attack of trees by *Ips typographus* induced by sex-specific pheromone: a model of attack dynamics. *Holarctic Ecology*, **12**, 415–426.
- Schmid, J. M., Mata, S. A., and Schmidt, R. A. (1991). Bark temperature patterns in ponderosa pine stands and their possible effects on mountain pine beetle behaviour. *Canadian Journal of Forest Research*, **21**, 1439–1446.
- Schneider, M., Schweizer, P., Meuwly, P., and Métraux, J. P. (1996). Systemic acquired resistance in plants. *International Review of Cytology*, **168**, 303–340.
- Schowalter, T. D. and Turchin, P. (1993). Southern pine beetle infestation development: interaction between pine and hardwood basal areas. *Forest Science*, **39**, 201–210.
- Schowalter, T. D., Hargrove, W. W., and Crossley Jr., D. A. (1986). Herbivory in forested ecosystems. *Annual Review of Entomology*, **31**, 177–196.

- Schowalter, T. D., Sabin, T. E., Stafford, S. G., and Sexton, J. M. (1991). Phytophage effects on primary production, nutrient turnover, and litter decomposition of young Douglas-fir in western Oregon. *Forest Ecology and Management*, **42**, 229–243.
- Schroeder, L. M. and Lindelöw, Å. (2002). Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and Forest Entomology*, **4**, 47–56.
- Scott, J. K. (1995). Classical biological control of plant pathogens. *Advances in Plant Pathology*, Vol. 11 (eds. J. H., Andrews and I. C. Tommerup), pp. 131–146. Academic Press, London.
- Scott, S. L., McArthur, C., Potts, B. M., and Joyce, K. (2002). Possum browsing—the downside to a eucalypt hybrid developed for frost tolerance in plantation forestry. *Forest Ecology and Management*, **157**, 231–245.
- Sedjo, R. A. (2001). The role of forest plantations in the world's future timber supply. *Forestry Chronicle*, **77**, 221–225.
- Séguin, A. (1999). Transgenic trees resistant to microbial pests. *Forestry Chronicle*, **75**, 303–304.
- Sexsmith, W. (1998). Policy and regulations for registration of microbial organisms in Canada. *Phytoprotection*, **79**, 3–4.
- Seybold, S. J., Bohlmann, J., and Raffa, K. F. (2000). Biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: evolutionary perspective and synthesis. *Canadian Entomologist*, **132**, 697–753.
- Shainsky, L. J. and Rose, C. L. (1995). Effects of competition on the foliar chemistry of young Douglas-fir in monoculture and mixed stands with young red alder. *Canadian Journal of Forest Research*, **25**, 1969–1977.
- Sharma, H. C. and Ortiz, R. (2000). Transgenics, pest management, and the environment. *Current Science*, **79**, 421–437.
- Sharov, A. A. and Liebhold, A. M. (1998). Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecological Applications*, **8**, 833–845.
- Sharov, A. A., Liebhold, A. M., and Ravlin, F. W. (1995a). Prediction of gypsy moth (Lepidoptera: Lymantriidae) mating success from pheromone trap counts. *Environmental Entomology*, **24**, 1239–1244.
- Sharov, A. A., Roberts, E. A., Liebhold, A. M., and Ravlin, F. W. (1995b). Gypsy moth (Lepidoptera: Lymantriidae) spread in the central appalachians: three methods for species boundary estimation. *Environmental Entomology*, **24**, 1529–1538.
- Sharov, A. A., Liebhold, A. M., and Roberts, E. A. (1997). Methods for monitoring the spread of gypsy moth (Lepidoptera: Lymantriidae) populations in the Appalachian mountains. *Journal of Economic Entomology*, **90**, 1259–1266.
- Sharov, A. A., Liebhold, A. M., and Roberts, E. A. (1998). Optimizing the use of barrier zones to slow the spread of gypsy moth (Lepidoptera: Lymantriidae) in North America. *Journal of Economic Entomology*, **91**, 165–174.
- Sharov, A. A., Pijanowski, B. C., Liebhold, A. M., and Gage, S. H. (1999). What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility. *Agricultural and Forest Entomology*, **1**, 37–45.
- Sharov, A. A., Leonard, D., Liebhold, A. M., Roberts, E. A., and Dickerson, W. (2002). “Slow the spread” a national program to contain gypsy moth. *Journal of Forestry*, **100**, 30–35.
- Shaw, M. R. (1994). Parasitoid host ranges. in *Parasitoid community ecology* (eds. B. A. Hawkins and W. Sheehan), pp. 111–144. Oxford University Press, Oxford.
- Shelton, A. M. and Roush, R. T. (2000). Resistance to insect pathogens and strategies to manage resistance. In *Field manual of techniques in invertebrate pathology application and evaluation of pathogens for control of insects and other invertebrate pests*, (eds. L. A. Lacey and H. K. Kaya), pp. 829–845. Kluwer Academic Publishers, Dordrecht.
- Shepherd, R. F. (1994). Management strategies for forest insect defoliators in British Columbia. *Forest Ecology and Management*, **68**, 303–324.
- Shigesada, N. and Kawasaki, K. (1997). *Biological invasions: theory and practice*. Oxford University Press, Oxford.
- Shore, T. L. and Safranyic, L. (1992). Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Forestry Canada. Pacific and Yukon Region. Pacific Forestry Centre. BC-X-366 12pp.
- Shore, T. L., Hall, P. M., and Maher, T. F. (1990). Grid baiting of spruce stands with frontalinal for pre-harvest containment of the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae). *Journal of Applied Entomology*, **109**, 315–319.
- Silen, R. R., Randall, W. K., and Mandel, N. L. (1986). Estimates of genetic parameters for deer browsing of Douglas-fir. *Forest Science*, **32**, 178–184.
- Simberloff, D. and Stiling, P. (1996). Risks of species introduced for biological control. *Biological Conservation*, **78**, 185–192.
- Simmonds, M. S. J. and Blaney, W. M. (1996). Azadirachtin—advances in understanding its activity as an antifeedant. *Entomologia Experimentalis et Applicata*, **80**, 23–26.
- Simms, E. L. (1992). Costs of plant resistance to herbivory. In *Plant resistance to herbivores and pathogens* (eds. R. S. Fritz

- and E. L. Simms), pp. 392–425. The University of Chicago Press, Chicago.
- Singh, A. P. and Pandey, R. (2002). Natural resistance of *Populus deltoides* clones selection to defoliator *Clostera cupreata* (Lep., Notodontidae) in northern India: relative pupal weight as an easier criteria for accurate evaluation. *Journal of Applied Entomology*, **126**, 475–480.
- Skov, E. and Wellendorf, H. (2000). RAPD markers linked to major genes behind field resistance against the green spruce aphid *Elatobium abietinum* (Walker) in *Picea sitchensis* (Bong. (Carr.)). *Forest Genetics*, **7**, 233–246.
- Skovmand, O., Thiéry, I., and Benzon, G. (2000). Is *Bacillus thuringiensis* standardisation still possible? In *Entomopathogenic bacteria: from laboratory to field application* (eds. J-F. Charles, A. Delécluse, and C. Nielsen-Le Roux), pp. 275–295. Kluwer Academic Publishers, Dordrecht.
- Smith, R. A. and Couche, G. A. (1991). The phylloplane as a source of *Bacillus thuringiensis* variants. *Applied Environmental Microbiology*, **57**, 311–331.
- Smith, I. M., McNamara, D. G., Scott, P. R., Holderness, M., and Burger, B. (eds.) (1997). *Quarantine pests for Europe*, 2nd edn. CAB International, Oxford.
- Smith, S. M., Carrow, J. R., and Laing, J. E. (eds.) (1990). Inundative release of the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae), against forest insect pests such as the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae): the Ontario project 1982–1986. *Memoirs of the Entomological Society of Canada No. 153*.
- Smith, S. M., Hubbes, M., and Carrow, J. R. (1987). Ground releases of *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) against the spruce budworm (Lepidoptera: Tortricidae). *Canadian Entomologist*, **119**, 251–263.
- Smitley, D. R., Bauer, L. S., Hajek, A. E., Sapio, F. J., and Humber, R. A. (1995). Introduction and establishment of *Entomophaga maimaiga*, a fungal pathogen of gypsy moth (Lepidoptera: Lymantriidae) in Michigan. *Environmental Entomology*, **24**, 1685–1695.
- Solheim, H., Langström, B., and Hellqvist, C. (1993). Pathogenicity of the blue-stain fungi *Leptographium wingfieldii* and *Ophiostoma minus* to Scots pine: effect of tree pruning and inoculum density. *Canadian Journal of Forest Research*, **23**, 1438–1443.
- Solter, L. F., Keena, M., Cate, J. R., McManus, M. L., and Hank, L. M. (2001). Infectivity of four species of nematodes (Rhabditiodea: Steinernematidae, Heterorhabditidae) to the Asian Longhorn beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae). *Biocontrol Science and Technology*, **11**, 547–552.
- Sonesson, J. (2001). Ecological evaluation of clonal forestry with cutting-propagated Norway spruce. *SkogForsk Report No. 1*, 1–59.
- Sorci, G., Møller, A. P., and Boulinier, T. (1997). Genetics of host–parasite interactions. *TREE*, **12**, 196–200.
- Soria, F. and Borralho, N. M. G. (1997). The genetics of resistance to *Phoracantha semipunctata* attack in *Eucalyptus globulus* in Spain. *Silvae Genetica*, **46**, 365–369.
- South, D. B. and Zwolinski, J. B. (1997). Transplant stress index: A proposed method of quantifying planting check. *New Forests*, **13**, 315–328.
- Spanos, K. A., Pirrie, A., Woodward, S., and Xenopoulos, S. (1999). Responses in the bark of *Cupressus sempervirens* clones artificially inoculated with *Seiridium cardinale* under field conditions. *European Journal of Forest Pathology*, **29**, 135–142.
- Speight, M. R. and Wainhouse, D. (1989). *Ecology and management of forest insects*. Clarendon Press, Oxford.
- Speight, M. R. and Wylie, F. R. (2001). *Insect pests in tropical forestry*. CABI publishing, Oxford.
- Stadler, B. and Michalzik, B. (1999). The impact of spruce aphids on nutrient flows in the canopy of Norway spruce. *Agricultural and Forest Entomology*, **1**, 3–9.
- Stadler, B., Solinger, S., and Michalzik, B. (2001). Insect herbivores and the nutrient flow from the canopy to the soil in coniferous and deciduous forests. *Oecologia*, **126**, 104–113.
- Stark, R. W. (1965). Recent trends in forest entomology. *Annual Review of Entomology*, **10**, 303–324.
- Steiner, K. (1974). Genetic differences in resistance of scotch pine to eastern pineshoot borer. *The Great Lakes Entomologist*, **7**, 103–107.
- Stenlid, J. and Redfern D. B. (1998). Spread within the tree and stand. In *Heterobasidium annosum biology, ecology, impact and control* (eds. S. Woodward, J. Stenlid, R. Karjalainen, and A. Hüttermann), pp. 125–141. CAB International, Wallingford.
- Stenseth, N. C. (1989). A simple population model for bark beetles providing general guidelines for the application of aggregation and anti-aggregation pheromones. *Holarctic Ecology*, **12**, 395–407.
- Stephan, B. R. (1991). Inheritance of resistance to biotic factors. In *Genetics of Scots pine*, (eds. M. Giertych, C. Matyas), pp. 205–218. Elsevier, Amsterdam.
- Sticher, L., Mauch-Mani, B., and Métraux, J. P. (1997). Systemic acquired resistance. *Annual Review of Phytopathology*, **35**, 235–270.
- Stiling, P. (1990). Calculating the establishment rates of parasitoids in classical biological control. *American Entomologist*, **36**, 225–230.
- Stiling, P. (1993). Why do natural enemies fail in classical biological control programs? *American Entomologist*, **39**, 31–37.

- Stoakley, J. T. (1985). Outbreaks of winter moth, *Operophtera brumata* L. (Lep., Geometridae) in young plantations of Sitka spruce in Scotland. Insecticidal control and population assessment using the sex attractant pheromone. *Zeitschrift für angewandte Entomologie*, **99**, 153–160.
- Stock, A. J., Borden, J. H., and Pratt, T. L. (1994). Containment and concentration of infestations of the western balsam bark beetle, *Dryocoetes confusus* (Coleoptera: Scolytidae), using the aggregation pheromone *exo-brevicomin*. *Canadian Journal of Forest Research*, **24**, 483–492.
- Stone, N. D., Coulson, R. N., Frisbie, R. E., and Loh, D. K. (1986). Expert systems in entomology: three approaches to problem solving. *Bulletin of the ESA*, 161–166.
- Stoneman, G. L. and Whitford, K. (1995). Analysis of the concept of growth efficiency in *Eucalyptus marginata* (jarrah) in relation to thinning, fertilising and tree characteristics. *Forest Ecology and Management*, **76**, 47–53.
- Stowe, K. A., Marquis, R. J., Hochwender, C. G., and Sims, E. L. (2000). The evolution of tolerance to consumer damage. *Annual Review of Ecology and Systematics*, **31**, 565–595.
- Strauss, S. Y. (1994). Levels of herbivory and parasitism in host hybrid zones. *TREE*, **9**, 209–214.
- Strauss, S. H., Howe, G. T., and Goldfarb, B. (1991). Prospects for genetic engineering of insect resistance in forest trees. *Forest Ecology and Management*, **43**, 181–209.
- Strauss, S. H., Lande, R., and Namkoong G. (1992). Limitations of molecular-marker-aided selection in forest tree breeding. *Canadian Journal of Forest Research*, **22**, 1050–1061.
- Strauss, S. H., DiFazio, S. P., and Meilan, R. (2001a). Genetically modified poplars in context. *Forestry Chronicle*, **77**, 271–279.
- Strauss, S. H., Campbell, M. M., Pryor, S. N., Coventry, P., and Burley, J. (2001b). Plantation certification and genetic engineering FSC's ban on research is counter productive. *Journal of Forestry*, **99**, 4–7.
- Strauss, S. H., Coventry, P., Campbell, M. M., Pryor, S. N., and Burley, J. (2001c). Certification of genetically modified forest plantations. *International Forestry Review*, **3**, 87–104.
- Straw, N. A. (1996). The impact of pine looper moth, *Bupalus piniaria* L (Lepidoptera; Geometridae) on the growth of Scots pine in Tentsmuir Forest, Scotland. *Forest Ecology and Management*, **87**, 209–232.
- Straw, N. A. and Green, G. (2001). Interactions between green spruce aphid (*Elatobium abietinum* (Walker)) and Norway and Sitka spruce under high and low nutrient conditions. *Agricultural and Forest Entomology*, **3**, 263–274.
- Strom, B. L., Goyer, R. A., and Shea, P. J. (2001). Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. *Entomologia Experimentalis et Applicata*, **100**, 63–67.
- Strom, B. L., Goyer, R. A., Ingram Jr., L. L., Boyd, G. D. L., and Lott, L. H. (2002). Oleoresin characteristics of progeny of loblolly pines that escape attack by the southern pine beetle. *Forest Ecology and Management*, **158**, 169–178.
- Su, Q., MacLean, D. A., and Needham, T. D. (1996). The influence of hardwood content on balsam fir defoliation by spruce budworm. *Canadian Journal of Forest Research*, **26**, 1620–1628.
- Sun, J., DeBarr, G. L., Liu, T-X, Berisford, C. W., and Clarke, S. R. (1996). An unwelcome guest in China a pine-feeding mealybug. *Journal of Forestry*, **94**, 27–32.
- Sun, J. H., Kulhavy, D. L., and Roques, A. (2000). Effects of fertilizer and herbicide application on Nantucket pine tip moth infestation (Lep., Tortricidae). *Journal of Applied Entomology*, **124**, 191–195.
- Sutherland, M. L., Mittempergher, L., and Brasier, C. M. (1995). Control of Dutch elm disease by induced host resistance. *European Journal of Forest Pathology*, **25**, 307–318.
- Sutherst, R. W., Maywald, G. F., and Bottomley, W. (1991). From CLIMEX to PESKY, a generic expert system for pest risk assessment. *Bulletin OEPP/EPPO Bulletin*, **21**, 595–608.
- Sutherst, R. W., Maywald, G. F., Yonow, T., and Stevens, P. M. (1999). *CLIMEX: Predicting the effects of climate on plants and animals*. CSIRO Publishing, Collingwood, Australia.
- Sutton, R. F. (1993). Mounding site preparation: A review of European and North American experience. *New Forests*, **7**, 151–192.
- Sutton, W. R. J. (Wink) (1999). The need for planted forests and the example of radiata pine. *New Forests*, **17**, 95–109.
- Swedjemark, G., Stenlid, J., and Karlsson, B. (1997). Genetic variation among clones of *Picea abies* in resistance to growth of *Heterobasidion annosum*. *Silvae Genetica*, **46**, 369–374.
- Sweeney, J. D., Mclean, J. A., and Shepherd, R. F. (1990). Factors affecting catch in pheromone traps for monitoring the western spruce budworm, *Choristoneura occidentalis* Freeman. *Canadian Entomologist*, **122**, 1119–1130.
- Swetnam, T. W. and Lynch, A. M. (1993). Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*, **63**, 399–424.
- Sykes, M. T. (2001). Modelling the potential distribution and community dynamics of lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.) in Scandinavia. *Forest Ecology and Management*, **141**, 69–84.

- Syme, J. H. and Saucier, J. R. (1995). Effects of long-term storage of southern pine sawlogs under water sprinklers. *Forest Products Journal*, **45**, 47–50.
- Syme, P. D. (1977). Observations on the longevity and fecundity of *Orgilus obscurator* (Hymenoptera: Braconidae) and the effects of certain foods on longevity. *Canadian Entomologist*, **109**, 995–1000.
- Syme, P. D. (1981). *Rhyacionia buolinana* (Schiff.), European pine shoot moth (Lepidoptera: Tortricidae). In *Biological control programmes against insects and weeds in Canada, 1969–1980* (eds. J. S. Kelleher and M. A. Hulme), pp. 387–394. Commonwealth Agricultural Bureau, London.
- Tabashnik, B. E. (1994). Evolution of resistance to *Bacillus thuringiensis*. *Annual Review of Entomology*, **39**, 47–79.
- Tahvanainen, J., Julkunen-Tiitto, R., and Kettunen, J. (1985). Phenolic glycosides govern the food selection pattern of willow feeding leaf beetles. *Oecologia*, **67**, 52–56.
- Taipale, H. T., Härmälä, L., Rousi, M., and Lapinjoki, S. P. (1994). Histological and chemical comparison of triterpene and phenolic deterrent contents of juvenile shoots of *Betula* species. *Trees*, **8**, 232–236.
- Tallamy, D. W. and Raupp, M. J. (eds.) (1991). *Phytochemical induction by herbivores*. John Wiley & Sons, Inc. New York.
- Tamaki, Y. (1985). Sex pheromones. In *Insect physiology biochemistry and pharmacology volume 9 behaviour* (eds. G. A. Kerkut and L. I. Gilbert), pp. 145–191. Pergamon Press, Oxford.
- Tappeser, B., Jäger, M., and Eckelkamp, C. (2002). Survival, persistence, transfer: The fate of genetically modified microorganisms and recombinant DNA in different environments. In *Genetically engineered organisms assessing environmental and human health effects* (eds. D. K. Letourneau and B. E. Burrows), pp. 223–250. CRC Press, Boca Raton.
- Tauber, M. J., Tauber, C. A., and Masaki, S. (1986). *Seasonal adaptations of insects*. Oxford University Press, Oxford.
- Taylor, L. R. (1984). Assessing and interpreting the spatial distributions of insect populations. *Annual Review of Entomology*, **29**, 321–359.
- Taylor, S. P., Alfaro, R. I., DeLong, C., and Rankin, L. (1996). The effects of overstory shading on white pine weevil damage to white spruce and its effects on spruce growth rates. *Canadian Journal of Forest Research*, **26**, 306–312.
- Thies, W. G., Nelson, E. E., and Zabowski, D. (1994). Removal of stumps from a *Phellinus weirii* infested site and fertilization affect mortality and growth of planted Douglas-fir. *Canadian Journal of Forest Research*, **24**, 234–239.
- Thompson, C. G., Scott, D. W., and Wickman, B. E. (1981). Long term persistence of the nuclear polyhedrosis virus of the Douglas-fir tussock moth *Orgyia pseudotsugata*, (Lepidoptera: Lymantriidae) in forest soil. *Environmental Entomology*, **10**, 254.
- Thompson, J. N. (1994). *The coevolutionary process*. The University of Chicago Press. Chicago.
- Thompson, S. N. (1999). Nutrition and culture of entomophagous insects. *Annual Review of Entomology*, **44**, 561–592.
- Thomson, A. J. and Alfaro, R. I. (1990). A method to calculate yield-correction factors for the overstory component of budworm-attacked Douglas-fir. *Forest Ecology and Management*, **31**, 255–267.
- Thomson, A. J. and Van Sickle, G. A. (1980). Estimation of tree growth losses caused by pest activity. *Canadian Journal of Forest Research*, **10**, 176–182.
- Thomson, A. J. and Van Sickle, G. A. (1996). Forest insect and disease diagnosis and management using expert system-guided hypermedia. *AI applications*, **10**, 23–31.
- Thorpe, K. W., Mastro, V. C., Leonard, D. S., Leonhardt, B. A., McLane, W., Reardon, R. C., and Talley, S. E. (1999). Comparative efficacy of two controlled-release gypsy moth mating disruption formulations. *Entomologia Experimentalis et Applicata*, **90**, 267–277.
- Thorpe, K. W., Leonard, D. S., Mastro, V. C., McLane, W., Reardon, R. C., Sellers, P., Webb, R. E., and Talley, S. E. (2000). Effectiveness of gypsy moth mating disruption from aerial applications of plastic laminate flakes with and without a sticking agent. *Agricultural and Forest Entomology*, **2**, 225–231.
- Tillman, J. A., Seybold, S. J., Jurenka, R. A., and Blomquist, G. J. (1999). Insect pheromones—an overview of biosynthesis and endocrine regulation. *Insect Biochemistry and Molecular Biology*, **29** 481–514.
- Tomiczek, Ch. (2003). Der Asiatische Laubholzbockkäfer *Anoplophora glabripennis*—Befallssituation und Bekämpfungsmassnahmen in Österreich. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes, Stuttgart*, **55**, 79–80.
- Tomlin, E. S. and Borden, J. H. (1997). Multicomponent index for evaluating resistance by Sitka spruce to the white pine weevil (Coleoptera: Curculionidae). *Journal of Economic Entomology*, **90**, 704–714.
- Tømmervik, H., Høgda, K. A., and Karlsen, S. R. (2001). Using remote sensing to detect caterpillar outbreaks in mountain birch forests—a new approach. In *Nordic mountain birch ecosystems* (ed. F. E. Wielgolaski), pp. 241–249. The Parthenon Publishing Group, New York.
- Tomminen, J. and Nuorteva, M. (1992). Pinewood nematode, *Bursaphelenchus xylophilus* in commercial sawn wood and its control by kiln-heating. *Scandinavian Journal of Forest Research*, **7**, 113–120.

- Toro, J. and Gessel, S. P. (1999). Radiata pine in Chile. *New Forests*, **18**, 33–44.
- Toscano Underwood, C. D. and Pearce, R. B. (1991a) Astringin and isorhapontin distribution in Sitka spruce trees. *Phytochemistry*, **30**, 2183–2189.
- Toscano Underwood, C. D. and Pearce, R. B. (1991b) Variation in the levels of the antifungal stilbene glycosides astringin and isorhapontin in the bark of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *European Journal of Forest Pathology*, **21**, 279–289.
- Treacy, M. F. (1999). Recombinant baculoviruses. In *Methods in biotechnology, vol. 5 Biopesticides: use and delivery* (eds. F. R. Hall and J. J. Menn) pp. 321–340. Humana Press Inc., Totowa, New Jersey.
- Trumble, J. T., Kolodny-Hirsch, D. M., and Ting, I. P. (1993). Plant compensation for arthropod herbivory. *Annual Review of Entomology*, **38**, 93–119.
- Turban, E. (1993). *Decision support and expert systems: management support systems*, 3rd edn. Macmillan Publishing Company, New York.
- Turgeon, J. J. (1992). Status of research on the development of management tactics and strategies for the spruce bud moth in white spruce plantations. *Forestry Chronicle*, **68**, 614–622.
- Turgeon, J. J. and Régnière, J. (1987). Development of sampling techniques for the spruce budmoth *Zeiraphera canadensis* Mut., and Free. (Lepidoptera: Tortricidae). *Canadian Entomologist*, **119**, 239–249.
- Underwood, N. (1999). The influence of plant and herbivore characteristics on the interaction between induced resistance and herbivore population dynamics. *American Naturalist*, **153**, 282–294.
- Underwood, N. and Rausher, M. (2002). Comparing the consequences of induced and constitutive plant resistance for herbivore population dynamics. *American Naturalist*, **160**, 20–30.
- Ungerer, M. J., Ayres, M. P., and Lombardero, M. J. (1999). Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography*, **26**, 1133–1145.
- United Nation World Commission on Environment and Development (1987). *Our common future*. Oxford University Press, London.
- Väisänen, R., Heliövaara, K., and Kemppe, E. (1992). Height growth loss in Scots pine infested by the pine resin gall moth, *Retinia resinella* (Lepidoptera: Tortricidae). *Forest Ecology and Management*, **59**, 145–152.
- Vaishampayan, S. M., Verma, R., and Bhowmik, A. K. (1987). Possible migration of teak-defoliator, *Hyblaea puera* Cramer (Lepidoptera: Hyblaeidae) in relation to the movement of the south-west monsoon as indicated by light trap catches. *Indian Journal of Agricultural Sciences*, **57**, 41–46.
- Väkevä, J. and Saarenmaa, H. (1992). A rule-based expert system for the diagnosis of biotic damage on Scots pine. *Scandinavian Journal of Forest Research*, **7**, 533–546.
- Vanbergen, A. J., Raymond, B., Pearce, I. S. K., Watt, A. D., Hails, R., and Hartley, S. E. (2003). Host shifting by *Operophtera brumata* into novel environments leads to population differentiation in life-history traits. *Ecological Entomology*, **28**, 604–612.
- Van Buijtenen, J. P. (2002). Genomics and quantitative genetics. *Canadian Journal of Forest Research*, **31**, 617–622.
- van dem Bussche, G. H. (1993). Storage of timber under permanent irrigation. *South African Forestry Journal*, **164**, 59–64.
- van der Kamp, B. J. (1994). Lodgepole pine stem diseases and management of stand density in the British Columbia interior. *Forestry Chronicle*, **70**, 773–779.
- Van der Plank, J. E. (1984). *Disease resistant plants*, 2nd edn. Academic Press, Orlando.
- van Driesche, R. G. and Bellows, T. S. (1993). *Steps in classical arthropod biological control*. Entomological Society of America, Lanham, MD.
- van Frankenhuyzen, K. (1990) Development and current status of *Bacillus thuringiensis* for control of defoliating forest insects. *The Forestry Chronicle*, **66**, 498–507.
- van Frankenhuyzen, K. (1993). The challenge of *Bacillus thuringiensis*. In *Bacillus thuringiensis, an environmental biopesticide: theory and practice* (eds. P. F. Entwistle, J. S. Cory, M. J. Bailey, and S. Higgs), pp. 1–35. John Wiley & Sons, Chichester.
- van Frankenhuyzen, K. (2000). Application of *Bacillus thuringiensis* in forestry. In *Entomopathogenic bacteria: from laboratory to field application* (eds. J-F. Charles, A. Delécluse, and C. Nielsen-Le Roux), pp. 371–382. Kluwer Academic Publishers, Dordrecht.
- van Frankenhuyzen, K., Nystrom, C. W., and Tabashnik, B. E. (1995). Variation in tolerance to *Bacillus thuringiensis* among and within populations of the spruce budworm (Lepidoptera: Tortricidae) in Ontario. *Journal of Economic Entomology*, **88**, 97–105.
- van Frankenhuyzen, K., Reardon, R. C., and Dubois, N. R. (2000a). Forest defoliators. In *Field manual of techniques in invertebrate pathology application and evaluation of pathogens for control of insects and other invertebrate pests* (eds. L. A. Lacey and H. K. Kaya), pp. 527–556. Kluwer Academic Publishers, Dordrecht.
- van Frankenhuyzen, K., Nystrom, C., Dedes, J., and Seligy, V. (2000b). Mortality, feeding inhibition, and recovery of spruce budworm (Lepidoptera: Tortricidae) larvae following aerial application of a high-potency formulation of *Bacillus thuringiensis* subsp. *kurstaki*. *Canadian Entomologist*, **132**, 505–518.
- Van Sickle, G. A., Alfaro, R. I., and Thomson, A. J. (1983). Douglas-fir height growth affected by western spruce

- budworm. *Canadian Journal of Forest Research*, **13**, 445–450.
- van Zyl, L. M. and Wingfield, M. J. (1999). Wound response of *Eucalyptus* clones after inoculation with *Cryphonectria cubensis*. *European Journal of Forest Pathology*, **29**, 161–167.
- Vargas, L. G. (1990). An overview of the analytic hierarchy process and its applications. *European Journal of Operational Research*, **48**, 2–8.
- Varley, G. C. and Gradwell, G. R. (1968). Population models for the winter moth. In *Insect abundance* (ed. T. R. E. Southwood), pp. 132–142. Blackwell Scientific Publications, Oxford.
- Vasiliauskas, R. (2001). Damage to trees due to forestry operations and its pathological significance in temperate forests: a literature review. *Forestry*, **74**, 319–336.
- Venäläinen, M., Harju, A., Nikkanen, T., Paajanen, L., Velling, P., and Viitanen, H. (2001). Genetic variation in the decay resistance of Siberian larch (*Larix sibirica* Ledeb.) wood. *Holzforschung*, **55**, 1–6.
- Verbyla, D. L. (1987). Classification trees: a new discriminant tool. *Canadian Journal of Forest Research*, **17**, 1150–1152.
- Virtanen, T., Neuvonen, S., Nikula, A., Varama, M., and Niemelä, P. (1996). Climate change and the risks of *Neodiprion sertifer* outbreaks on Scots pine. *Silva Fennica*, **30**, 169–177.
- Vité, J. P. (1989). The European struggle to control *Ips typographus*—past, present and future. *Holarctic Ecology*, **12**, 520–525.
- Volney, W. J. A., Hammond, H. E. J., Maynard, D. G., MacIsaac, D. A., Mallett, K. I., Langor, D. W., Johnson, J. D., Pohl, G. R., Kishchuk, B., Gladders, B., Avery, B., Chemango, R., Hoffman, T., Chorney, M., Luchkow, S., Maximchuk, M., and Spence, J. R. (1999). A silvicultural experiment to mitigate pest damage. *Forestry Chronicle*, **75**, 461–465.
- von Broembsen, S. L. (1989). Invasions of natural ecosystems by plant pathogens. In *Biological invasions: a global perspective* (eds. J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmének, and M. Williamson), pp. 77–83. John Wiley & Sons, Chichester.
- von Sydow, F. (1997). Abundance of pine weevils (*Hylobius abietis*) and damage to conifer seedlings in relation to silvicultural practices. *Scandinavian Journal of Forest Research*, **12**, 157–167.
- von Sydow, F. and Örlander, G. (1994). The influence of shelterwood density on *Hylobius abietis* (L.) occurrence and feeding on planted conifers. *Scandinavian Journal of Forest Research*, **9**, 367–375.
- Waage, J. (1990). Ecological theory and the selection of biological control agents. In *Critical issues in biological control* (eds. M. Mackauer, L. E. Ehler, and J. Roland), pp. 135–157. Intercept, Andover.
- Waage, J. (1995). The use of exotic organisms as biopesticides: some issues. In *Biological control: benefits and risks* (eds. H. M. T. Hokkanen and J. M. Lynch), pp. 93–100. Cambridge University Press, Cambridge.
- Waage, J. (1997). Global developments in biological control and the implications for Europe. *Bulletin OEPP/EPPO*, **27**, 5–13.
- Waage, J. K. and Mills, N. J. (1992). Biological control. In *Natural enemies the population biology of predators, parasites and diseases* (ed. M. J. Crawley), pp. 412–430. Blackwell Scientific Publications, London.
- Wagner, M. R., Atuahene, S. K. N., and Cobbinah, J. R. (1991). *Forest entomology in West Tropical Africa: Forest insects in Ghana*. Kluwer Academic Publishers, Dordrecht.
- Wainhouse, D. and Ashburner, R. (1996). The influence of genetic and environmental factors on a quantitative defensive trait in spruce. *Functional Ecology*, **10**, 137–143.
- Wainhouse, D., Cross, D. J., and Howell, R. S. (1990). The role of lignin as a defence against the spruce bark beetle *Dendroctonus micans*: effects on larvae and adults. *Oecologia*, **85**, 257–265.
- Wainhouse, D., Wyatt, T., Phillips, A., Kelly, D. R., Barghian, M., Beech-Garwood, P., Cross, D., and Howell, R. S. (1991). Response of the predator *Rhizophagus grandis* to host plant derived chemicals in *Dendroctonus micans* larval frass in wind tunnel experiments (Coleoptera: Rhizophagidae, Scolytidae). *Chemoecology*, **2**, 55–63.
- Wainhouse, D., Rose, D. R., and Peace, A. J. (1997). The influence of preformed defences on the dynamic wound response in spruce bark. *Functional Ecology*, **11**, 564–572.
- Wainhouse, D., Ashburner, R., Ward, E., and Rose, J. (1998). The effect of variation in light and nitrogen on growth and defence in young Sitka spruce. *Functional Ecology*, **12**, 561–562.
- Wallenmaier, T. (1989). Wood-boring insects. In *Plant protection and quarantine. Vol II Selected pests and pathogens of quarantine significance* (ed. R. P. Kahn), pp. 99–108. CRC Press Boca Raton.
- Wargo, P. M. (1996). Consequences of environmental stress on oak: predisposition to pathogens. *Annales des Sciences Forestières*, **53**, 359–368.
- Waring, R. H. (1983). Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Research*, **13**, 327–354.



- Waring, R. H. and Pitman, G. B. (1980). *A simple model of host resistance to bark beetles*. Forest Research Laboratory Research Note 65, Oregon State University, Corvallis.
- Waring, R. H. and Pitman, G. B. (1983). Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. *Zeitschrift für angewandte Entomologie*, **96**, 265–270.
- Waring, R. H., Schroeder, P. E., and Oren, R. (1982). Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research*, **12**, 556–560.
- Warren, J. M., Allen, H. L., and Booker, F. L. (1999). Mineral nutrition, resin flow and phloem chemistry in loblolly pine. *Tree Physiology*, **19**, 655–663.
- Waters, W. E. and Stark, R. W. (1980). Forest pest management: concept and reality. *Annual Review of Entomology*, **25**, 479–509.
- Watt, A. D. (1992). Insect pest population dynamics: effects of tree species diversity. In *The ecology of mixed-species stands of trees* (eds. M. G. R. Cannell, D. C. Malcolm, and P. A. Robertson), pp. 267–275. Blackwell Scientific Publications, London.
- Way, M. J. and Khoo, K. C. (1992). Role of ants in pest management. *Annual Review of Entomology*, **37**, 479–503.
- Webb, R. E., Leonhardt, B. A., Plimmer, J. R., Tatman, K. M., Boyd, V. K., Cohen, D. L., Schwalbe, C. P., and Douglass, L. W. (1990). Effect of racemic disparlure released from grids of plastic ropes on mating success of gypsy moth (Lepidoptera: Lymantriidae) as influenced by dose and by population density. *Journal of Economic Entomology*, **83**, 910–916.
- Webb, R. E., White, G. B., Thorpe, K. W., and Talley, S. E. (1999). Quantitative analysis of a pathogen-induced premature collapse of a “leading edge” gypsy moth (Lepidoptera: Lymantriidae) population in Virginia. *Journal of Entomological Science*, **34**, 84–100.
- Webber, J. F. (2000). Insect vector behaviour and the evolution of Dutch elm disease. In *The elms: breeding, conservation and disease management* (ed. C. P. Dunn), pp. 47–60. Kluwer Academic Publishers, Boston.
- Webber, J. F. and Gibbs, J. N. (eds.) (1996). Water storage of timber: experience in Britain. *Forestry Commission Bulletin 117*. HMSO, London, xvi + 48pp.
- Weber, U. M. (1995). A dendroecological reconstruction of western spruce budworm outbreaks (*Choristoneura occidentalis*) in the front range, Colorado, from 1720 to 1986. *Trees*, **9**, 204–213.
- Weber, U. M. (1997). Dendroecological reconstruction and interpretation of larch budmoth (*Zeiraphera diniana*) outbreaks in two central alpine valleys of Switzerland from 1470–1990. *Trees*, **11**, 277–290.
- Welch, R. C. (1981) The insect fauna of *Nothofagus*. *NERC Institute of Terrestrial Ecology Annual Report 1980*, 50–53.
- Weseloh, R. M. and Andreadis, T. G. (1992). Epizootiology of the fungus *Entomophaga maimaiga*, and its impact on gypsy moth populations. *Journal of Invertebrate Pathology*, **59**, 133–141.
- Weseloh, R. M., Andreadis, T. G., Moore, R. E., Anderson, J. R., Dubois, N. R., and Lewis, F. B. (1983). Field confirmation of a mechanism causing synergism between *Bacillus thuringiensis* and the gypsy moth parasitoid, *Apanteles melanoscelus*. *Journal of Invertebrate Pathology*, **41**, 99–103.
- Weslien, J. (1992a) Effects of mass trapping on *Ips typographus* (L.) populations. *Journal of Applied Entomology*, **114**, 228–232.
- Weslien, J. (1992b). Monitoring *Ips typographus* (L.) populations and forecasting damage. *Journal of Applied Entomology*, **114**, 338–340.
- Weslien, J. and Lindelöw, Å. (1989). Trapping a local population of spruce bark beetles *Ips typographus* (L.): population size and origin of trapped beetles. *Holarctic Ecology*, **12**, 511–514.
- Weslien, J. and Lindelöw, Å. (1990). Recapture of marked spruce bark beetles (*Ips typographus*) in pheromone traps using area-wide mass trapping. *Canadian Journal of Forest Research*, **20**, 1786–1790.
- Weslien, J., Annala, E., Bakke, A., Bejer, B., Eidman, H. H., Narvestad, K., Nikula, A., and Ravn, H. P. (1989). Estimating risks for spruce bark beetle (*Ips typographus* (L.)) damage using pheromone-baited traps and trees. *Scandinavian Journal of Forest Research*, **4**, 87–98.
- Wheeler, N. C., Jech, K. S., Masters, S. A., O'Brien, C. J., Timmons, D. W., Stonecypher, R. W., and Lupkes, A. (1995). Genetic variation and parameter estimates in *Taxus brevifolia* (Pacific yew). *Canadian Journal of Forest Research*, **25**, 1913–1927.
- White, E. E. and Nilsson, J. E. (1984). Genetic variation in resin canal frequency and relationship to terpene production in foliage of *Pinus contorta*. *Silvae Genetica*, **33**, 2–3.
- White, T. C. R. (1993). *The inadequate environment nitrogen and the abundance of animals*. Springer-Verlag, Berlin.
- Whitham, T. G., Maschinski, J., Larson, K. C., and Paige, K. N. (1991). Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. In *Plant-animal interactions: evolutionary ecology in tropical and temperate regions* (eds. P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson), pp. 227–257. John Wiley & Sons, Inc., New York.
- Whitten, M. J. (1995). An international perspective for the release of genetically engineered organisms for biological control. In *Biological control: benefits and risks* (eds. H. M. T. Hokkanen and J. M. Lynch), pp. 253–260. Cambridge University Press, Cambridge.

- Whyte, A. G. D. (2000). Forestry in New Zealand undermined. *International Forestry Review*, **2**, 126–129.
- Wichmann, L. and Ravn, H. P. (2001). The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. *Forest Ecology and Management*, **148**, 31–39.
- Williams, D. W. and Liebhold, A. M. (2002). Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology*, **4**, 87–99.
- Williams, E. R., Matheson, A. C., and Harwood, C. E. (2002). *Experimental design and analysis for use in tree improvement*, 2nd edn. CSIRO Publishing, Victoria.
- Williamson, M. (1989). Mathematical models of invasion. In *Biological invasions: a global perspective* (eds. J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson), pp. 329–350. John Wiley & Sons, Chichester.
- Williamson, M. (1996). *Biological invasions*. Chapman and Hall, London.
- Wilson, J. S., Isaac, E. S., and Gara, R. I. (1998). Impacts of mountain pine beetle (*Dendroctonus ponderosae*) (Col., Scolytidae) infestation on future landscape susceptibility to the western spruce budworm (*Choristoneura occidentalis*) (Lep., Tortricidae) in north central Washington. *Journal of Applied Entomology*, **122**, 239–245.
- Wingfield, M. J., Blanchette, R. A., and Nicholls, T. H. (1984). Is the pine wood nematode an important pathogen in the United States? *Journal of Forestry*, **82**, 232–235.
- Withers, T. M. (2001). Colonization of eucalypts in New Zealand by Australian insects. *Austral Ecology*, **26**, 467–476.
- Wolda, H. (1978). Fluctuations in abundance of tropical insects. *American Naturalist*, **112**, 1017–1045.
- Wolda, H. (1983). “Long-term” stability of tropical insect populations. *Researches in Population Ecology*, suppl. 3, 112–126.
- Wolda, H. (1992). Trends in abundance of tropical forest insects. *Oecologia*, **89**, 47–52.
- Woodward, S. (1992). Responses of gymnosperm bark tissues to fungal infections. In *Defence mechanisms of woody plants against fungi* (eds. R. A. Blanchette and A. R. Biggs), pp. 62–75. Springer-Verlag, Berlin.
- Woodward, S. and Pearce, R. B. (1988). Wound-associated responses in Sitka spruce root bark challenged with *Phaeolus schweinitzii*. *Physiological and Molecular Plant Pathology*, **33**, 151–162.
- Woodward, S. and Pocock, S. (1996). Formation of the ligno-suberized barrier zone and wound periderm in four species of European broad-leaved trees. *European Journal of Forest Pathology*, **26**, 97–105.
- Woodward, S., Stenlid, J., Karjalainen, R., and Hüttermann, A. (1998). *Heterobasidium annosum biology, ecology, impact and control*. CAB International, Wallingford.
- Woollons, R. C. and Hayward, W. J. (1984). Growth losses in *Pinus radiata* stands unsprayed for *Dothistroma pini*. *New Zealand Journal of Forest Science*, **14**, 14–22.
- Wraight, S. P., Jackson, M. A., and de Kock, S. L. (2001). Production, stabilization and formulation of fungal biocontrol agents. In *Fungi as biocontrol agents progress, problems and potential* (eds. T. M. Butt, C. Jackson, and N. Magan), pp. 253–287. CABI Publishing, Wallingford.
- Wright, J. W. (1976). *Introduction to forest genetics*. Academic Press, New York.
- Wright, J. W. and Wilson, L. F. (1972). Genetic differences in scotch pine resistance to pine root collar weevil. *Michigan State University Agricultural Experiment Station Research Report 159*, 1–5.
- Wright, J. W., Wilson, L. F., and Bright, J. N. (1975). Genetic variation in resistance of scotch pine to Zimmerman pine moth. *The Great Lakes Entomologist*, **8**, 231–236.
- Wu, H. and Hu, Z.-H. (1997) Comparative anatomy of resin ducts of the Pinaceae. *Trees*, **11**, 135–143.
- Wu, H. X. and Ying, C. C. (1998). Stability of resistance to western gall rust and needle cast in lodgepole pine provenances. *Canadian Journal of Forest Research*, **28**, 439–449.
- Wu, H. X., Ying, C. C., and Muir, J. A. (1996). Effect of geographic variation and jack pine introgression on disease and insect resistance in lodgepole pine. *Canadian Journal of Forest Research*, **26**, 711–726.
- Yamane, A. (1981). The Japanese pine sawyer, *Monochamus alternatus* Hope (Coleoptera: Cerambycidae): bionomics and control. *Review of Plant Protection Research*, **14**, 7.
- Yang, H., Zhang, G., Zhang, S., and Jian, H. (1993). Biological control of tree borers (Lepidoptera: Cossidae) in China with the nematode *Steinernema carpocapsae*. In *Nematodes and the biological control of insects pests* (eds. R. Bedding, R. Akhurst, and H. Kaya).
- Yang, R.-C., Dhir, N. K., Yeh, F. C., and Hiratsuka, Y. (1997). Geographic variation in susceptibility of Alberta lodgepole pine to western gall rust. *Canadian Journal of Forest Research*, **27**, 1398–1405.
- Yang, R.-C., Dhir, N. K., and Barnhardt, L. K. (1998). Comparative assessment of genetic variation of young high-elevation lodgepole pine for height and western gall rust resistance across two sites in Alberta. *Canadian Journal of Forest Research*, **28**, 478–484.
- Yates, M. G. (1984). The biology of the oak bark beetle, *Scolytus intricatus* (Ratzeburg) (Coleoptera: Scolytidae), in southern England. *Bulletin of Entomological Research*, **74**, 569–579.

- Yencho, G. C., Cohen, M. B., and Byrne, P. F. (2000). Applications of tagging and mapping insect resistance loci in plants. *Annual Review of Entomology*, **45**, 393–422.
- Zahedi, F. (1986). The analytic hierarchy process—a survey of the method and its applications. *Interfaces*, **16**, 96–108.
- Zhang, Q.-H. (2003). Interruption of aggregation pheromone in *Ips typographus* (L.) (Col. Scolytidae) by non-host volatiles. *Agricultural and Forest Entomology*, **5**, 145–153.
- Zheng, Y., Harman, D. M., and Swartz, H. J. (2003). Resistance to locust leafminer (Coleoptera: Chrysomelidae) in black locust. *Journal of Economic Entomology*, **96**, 53–57.
- Zimmermann, M., Sieber, T. N., and Holdenrieder, O. (1995). Preliminary evaluation of *Epicoccum purpurascens* as a biocontrol agent against wound pathogens on stems of *Picea abies*. *European Journal of Forest Pathology*, **25**, 179–183.
- Zobel, B. (1993). Clonal forestry in the eucalypts. In *Clonal forestry. Vol. 2. Conservation and application* (eds. M. R. Ahuja and W. J. Libby), pp. 139–148. Springer-Verlag, Berlin.
- Zobel, B. and Talbert, J. (1984). *Applied forest tree improvement*. John Wiley and Sons, New York.
- Zobel, B. J., Van Wyk, G., and Stahl, P. (1987). *Growing exotic forests*. John Wiley and Sons, New York.
- Zondag, R. (1969). A nematode infection of *Sirex noctilio* (F.) in New Zealand. *New Zealand Journal of Science*, **12**, 732–747.
- Zsuffa, L., Senneby-Forsse, L., Weisgerber, H., and Hall, R. B. (1993). Strategies for clonal forestry with poplars, aspens, and willows. In *Clonal forestry. Vol. 2. Conservation and application* (eds. M. R. Ahuja and W. J. Libby), pp. 91–119. Springer-Verlag, Berlin.

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# Glossary of tree names

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acacia, *Acacia* spp.

Aleppo pine, *Pinus halepensis*

American beech, *Fagus grandifolia*

American chestnut, *Castanea dentata*

aspen, *Populus tremula*

balsam fir, *Abies balsamea*

birch, *Betula* spp.

black locust, *Robinia pseudoacacia*

black cottonwood, *Populus trichocarpa*

black poplar, *Populus nigra*

blue gum, *Eucalyptus globulus*

cembra pine, *Pinus cembra*

Douglas fir, *Pseudotsuga menziesii*

eastern cottonwood, *Populus deltoides*

eucalyptus, *Eucalyptus* spp.

European chestnut, *Castanea sativa*

field elm, *Ulmus minor*

fir, *Abies* spp.

interior lodgepole pine, *Pinus contorta* ssp. *latifolia*

interior spruce, complex of white spruce *Picea glauca*,  
Engelmann spruce *P. engelmannii* and their  
hybrid swarn

jack pine, *Pinus banksiana*

Japanese poplar, *Populus maximowiczii*

loblolly pine, *Pinus taeda*

lodgepole pine, *Pinus contorta*

longleaf pine, *Pinus palustris*

mahogany, *Cedrela odorata* or *Swietenia macrophylla*

mountain birch, *Betula pubescens*

mountain gum, *Eucalyptus dalrympleana*

neem, *Azadirachtin indica*

Norway spruce, *Picea abies*

Pacific Yew, *Taxus brevifolia*

ponderosa pine, *Pinus ponderosa*

poplar, *Populus* spp.

radiata pine, *Pinus radiata*

red ironbark, *Eucalyptus sideroxylon*

Scots pine, *Pinus sylvestris*

Serbian spruce, *Picea omorika*

shortleaf pine, *Pinus echinata*

Siberian larch, *Larix sibirica*

silver birch, *Betula pendula*

Sitka spruce, *Picea sitchensis*

southern beech, *Nothofagus* spp.

subalpine larch, *Larix decidua*

trembling aspen, *Populus tremuloides*

Weymouth or white pine, *Pinus strobus*

white fir, *Abies concolor*

white gum, *Eucalyptus viminalis*

white spruce, *Picea glauca*

willow, *Salix* spp.

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