5

Tropical Forest Pests: Ecology, Biology and Impact

5.1 Introduction

Almost every part of a tree can serve as food for insects, and some of the more common groups associated with damage to leaves, shoots, flowers, buds, fruit, twigs, branches, stem and roots are shown in Fig. 5.1. Generally, the species of importance for forestry are contained in the Orders Phasmatodea (stick insects), Orthoptera (grasshoppers, crickets), Hemiptera (plant bugs, leafhoppers, scale insects, aphids, mealybugs), Coleoptera (beetles), Isoptera (termites), Hymenoptera (sawflies, ants, wasps, bees), Lepidoptera (butterflies, moths), Diptera (flies) and Thysanoptera (thrips). Feeding habits vary greatly, not only between but also within pest groupings. Some folivores are generalist feeders with a wide range of tree hosts (e.g. the Asian gypsy moth, *Lymantria dispar*, has over 600 recorded hosts, both conifers and hardwoods), while others are restricted to a single genus and sometimes species (the branchlet mining scolytine, Hylurdrectonus araucariae, in Papua New Guinea has been recorded only from Araucaria cunninghamii). Some insect species use several different tree parts as food sources during their life cycle (e.g. the larvae of some <mark>longicorn beetles tunnel</mark> in branches and stems and the adults feed on nectar); other insects such as leaf gall formers restrict their activities to a single tree part.

The impact of insect feeding on a tree is largely a function of the value of the affected part or parts for tree productivity or survival.

The value of older or mature leaves differs markedly from that of expanding or young leaves, which generally have ligher photosynthetic efficiencies (see Chapter 4), and ring-barking of the stem cambium by an insect is more important than heartwood tunnelling. However, economic impact is not always linked with tree fitness and, in the case of some stem borers, has more to do with the market quality of the wood product. As emphasized in earlier chapters, the vast majority of insects encountered in tropical forests are entirely benign and only very few achieve tree pest status. In this chapter, we examine the biology, ecology and impact of some of the more important pest species from around the tropics, the examples being chosen to reflect a range of feeding types, host trees and forest situations. The assigning of a pest species to a particular feeding guild (Table 5.1) is on the basis of the principal damage it causes, although some species could easily have been listed under more than one guild.

5.2 **Defoliation**

Defoliators are insects that feed on leaf tissue, their activities resulting in complete or partial



Fig. 5.1. A schematic tree showing the parts affected by various types of pest (from Jones and Elliot, 1986).

destruction of leaves. This feeding group also includes leaf-mining insects, which feed within the leaf just below the upper or lower surface, leaf tiers and leaf rollers, which make shelters from leaves and graze these from within, and leaf skeletonizers, which eat the leaf tissue between the network of leaf veins.

Defoliation by insects reduces the tree's rate of photosynthesis and transpiration. Effects vary considerably, depending on severity,

Table 5.1. L	ist of some o	f the more im	portant insec	ct pest specie	s in the tropic	s, categorized a	locording
to their feed	ing habits. Sp	ecies marked	l with an aste	erisk are disc	ussed in detai	l in this chapter.	

Feeding habit and insect order	Insect family	Scientific name	Principal host (genus)	Countries with reported damage
Defoliating Leaf chewing				
Coleoptera	Chrysomelidae	* <i>Paropsis</i> spp. * <i>Paropsisterna</i> spp.	Eucalyptus, Acacia Eucalyptus, Corymbia, Melaleuca	Australia Australia
	Curculionidae	*Gonipterus scutellatus	Eucalyptus	Australia, Africa, South America, California
	_	Hypomeces squamosus	Many	South and South-east Asia
		<i>Myllocerus</i> spp.	Acacia	
	Scarabaeidae	<i>^Anomala</i> spp.	Many	Asia, China, India
Hymenoptera	Formicidae	(Neo)alprion spp. *Atta/Acromyrmex spp.	Pinus Many	Southern USA, Central and South America
	Pergidae _	*Perga affinis	Eucalyptus	Australia
Lepidoptera	Arctiidae	Eupseudosoma spp.	Eucalyptus	South America
	Geometridae	Buzura suppressaria	Eucalyptus	China
	Hyblaeidae	*Thyrinteina arnobia * <mark>Hyblaea puera</mark>	Eucalyptus Tectona	Brazil, Venezuela India and South-, east Asia, South America
	Lasiocampidae	*Dendrolimus punctatus	Pinus	China, Vietnam, Thailand
	Lymantriidae	Lymantria ninayi	Pinus	Papua New Guinea
	Noctuidae	Spodoptera litura	Many	India, South-east Asia, Australia, Oceania
	Notodontidae	Nystalea nyseus	Eucalyptus	Brazil
	Pieridae	<i>Eurema</i> spp.	Acacia, Falcataria, Cassia	Africa, South-east Asia, Australia, Oceania
	Psychiaae	*Pteroma plagiophleps	Acacia, Falcataria, Cassia	India, South-east Asia
Phasmatodea	Phasmidae	*Ctenomorphodes tessulatus	Eucalyptus	Australia
Leaf mining				
Hymenoptera	Pergidae	Phylacteophaga eucalypti	Eucalyptus	Australia
Lepidoptera	Gracilliaridae	*Acrocercops spp.	Shorea, Swietenia, Tectona	India, Australia
	Incurvariidae	Perthida glyphopa	Eucalyptus	Australia
Leaf skeletonizing	l			
Coleoptera	Chrysomelidae	*Craspedonta leayana	Gmelina	India, Bangladesh, Myanmar
Lepidoptera	Noctuidae	Uraba lugens	Eucalyptus	Australia Continued

Feeding habit and insect order	Insect family	Scientific name	Principal host (genus)	Countries with reported damage
	Pyralidae	Eutectona machaeralis	Tectona	India, South-east Asia
Lepidoptera	Pyralidae	Lamprosema lateritialis	Afrormosia, Pericopsis	Nigeria, Ghana, West Africa
	Tortricidae	*Strepsicrates rothia	Eucalyptus	Africa, South and South-east Asia
	Yponomeutidae	Atteva fabriciella	Ailanthus	India
Sap feeding				
Hemiptera	Adelgidae	*Pineus pini boerneri	Pinus	Australia, Africa, America
	Aphididae	*Cinara cupressi cupressivora	Cupressus	Africa, South America
		Eulachnus rileyi	Pinus	Africa, Venezuela, Argentina
	Coccidae	*Ceroplastes spp.	Acacia, Melia, Cedrela, Toona, Pinus	Africa, Australia, India, South-east Asia
	o	Eriococcus spp.	Eucalyptus	Australia
	Coreidae	*Amblypelta cocophaga	Eucalyptus, Campnosperma	Solomon Islands
	Diaspididae	Aonidiella spp.	Azadirachta, Dalbergia, Swietenia, Melia	Africa, India, South-east Asia
		*Aulacaspis marina	Rhizophora	Indonesia
	Margarodidae	Conifericoccus spp.	Agathis	Australia
	Miridae	*Helopeltis spp.	Anacardium, Azadirachta, Eucalyptus	Africa, India, China, Indonesia
		<i>Lygus</i> spp.	Pinus	Southern USA, Mexico
	Pseudococcidae	*Nipaecoccus	Casuarina, Dalbergia	Africa, India
	Psyllidae	Cardiaspina spp.	Eucalyptus	Australia
		^Giycaspis brimblecombei	Eucalyptus	North America, South America, Hawaii, Mauritius
		*Heteropsylla cubana	Leucaena	Pantropical
	Thaumastocoridae	*Thaumastocoris peregrinus	Eucalyptus	South Africa, South America, Australia
	Tingidae	*Tingis beesoni	Gmelina	India, Myanmar, Thailand
Bark and wood f	feeding			
External chewing				
Coleoptera	Cerambycidae Curculionidae	Penthea pardalis Plagiophloeus	Acacia Toona	Australia India, South-east
Lepidoptera	Indarbelidae	iongiciavis *Indarbela quadrinotata	Many	Asia India, Bangladesh, Pakistan, South-east Asia
Bark boring	Apobiidae	Ernobius mallia	Pipus	Australia
Coleoptera	Anophuae	Ernobius mollis	riilus	Australia

Continued

Feeding habit and insect order	Insect family	Scientific name	Principal host (genus)	Countries with reported damage
	Curculionidae Scolvtinae	*Hylastes angustatus	Pinus	Southern Africa
Cambium and su	rface sanwood boring	*lps spp. Tomicus piniperda	Pinus Pinus	Pantropical China, Hong Kong
Coleoptera	Buprestidae	* <i>Agrilus</i> spp.	Eucalyptus	Philippines, Papua New Guinea, Africa, Indonesia
	Cerambycidae	Diadoxus spp. *Phoracantha semipunctata	Callitris Eucalyptus	Australia Africa, Australia, America
Isoptera	Curculionidae Termitidae	*Xystrocera festiva Aesiotes notabilis Macrotermes spp.	Falcataria, Acacia Araucaria, Pinus Many	Indonesia, Malaysia Australia Africa, China, South-east Asia
		Odontotermes spp.	Many	India, Africa, South-east Asia
Sapwood and he	artwood boring			
Coleoptera	Bostrychidae	<i>Apate</i> spp. <i>Sinoxylon</i> spp.	Many Shorea, Acacia, Eucalyptus	Africa Africa, India, South-east Asia
	Cerambycidae	Anoplophora spp.	Casuarina, Acacia, Eucalyptus	Taiwan, South-east Asia
		*Aristobia horridula	Dalbergia, Pterocarpus	India, Nepal, Thailand
		Batocera spp. *Celosterna scabrator	Mangifera, Ficus Acacia, Cassia, Prosopis, Tectonis, Fucalvotus	Pantropical India, Thailand
		*Hoplocerambyx spinicornis	Shorea	India
	Curculionidae	Eurhamphus fasciculatus	Araucaria	Australia
	Curculionidae/ Platypodinae	*Platypus spp.	Many	Pantropical
	Curculionidae/ Scolytinae	<i>Xyleborus</i> spp.	Many	Pantropical
		*Xylosandrus crassiusculus	Many	Asia, North and Central America, South Pacific, Australia
Hymenoptera	Siricidae	*Sirex noctilio	Pinus	Australia, South America, South Africa
Isoptera	Mastotermitidae	Mastotermes darwiniensis	Many	Australia
	Rhinotermitidae	*Coptotermes spp.	Many	Pantropical
Lepidoptera	Cossidae	*Chilecomadia valdiviana	Eucalyptus	Chile, Argentina
		*Coryphodema tristis	Eucalyptus	South Africa
	Hanialidae	*Xyleutes ceramica	Gmelina, Tectona	India, South-east Asia
	періациае	Endocina unduiller	Ginelina, Eucalyptus	Continued

Table 5.1. Continued.

Feeding habit and insect order	Insect family	Scientific name	Principal host (genus)	Countries with reported damage
Shoot boring Coleoptera	Curculionidae/ Scolvtinae	*Hylurdrectonus araucariae	Araucaria	Papua New Guinea
Lepidoptera	Pyralidae	* <i>Dioryctria</i> spp.	Pinus	Central America, India, China, South-east Asia
		*Hypsipyla robusta/ grandella	Toona, Swietenia, Cedrela, Khaya, Chukrasia	Pantropical
	Tortricidae	Rhyacionia spp.	Pinus	South America, South-east Asia
Fruit and seed b	oring			
Coleoptera	Bruchidae	*Bruchidius spp.	Acacia	Africa
Hymenoptera	Torymidae	* <i>Megastigmus</i> spp.	Cupressus, Juniperus, Eucalyptus	Africa, Australia, India, China, Thailand, Mexico
Lepidoptera	Pyralidae	Dioryctria spp.	Many	America, South-east Asia
		<i>Hypsipyla</i> spp.	Many	Australia, India, Central and South America
Gall forming				
Diptera	Agromyzidae	*Fergusonina spp.	Eucalyptus	Australia, Philippines, India
Hemiptera	Eriococcidae	Apiomorpha spp.	Eucalyptus	Australia
	Psyllidae	*Phytolyma spp.	Milicia	Africa
Hymenoptera	Eulophidae	*Leptocybe invasa	Eucalyptus	Atrica, Asia, Mediterranean, North and South America
		*Ophelimus maskelli	Eucalyptus	Mediterranean, North Africa
		*Quadrastichus erythrinae	Erythrina	Africa, Asia, South Pacific, Florida
Root feeding				
Coleoptera	Scarabaeidae	Anomala spp.	Cassia, Pinus	India, China
		Holotrichia spp.	Cassia, Shorea, Tectona	Australia, South-east Asia
		*Lepidiota spp.	Araucaria, Acacia, Eucalyptus	Australia, China, South-east Asia
Isoptera	Rhinotermitidae	Coptotermes spp.	Many	India, South-east Asia
	Termitidae	<i>Macrotermes</i> spp. <i>Microtermes</i> spp. <i>Odontotermes</i> spp.	Gmelina, Eucalyptus Tectona, Eucalyptus Hevea, Pinus	Africa, South-east Asia Africa, South-east Asia Africa, South-east Asia
Stem and branch	h cutters			
Coleoptera	Cerambycidae	*Strongylurus decoratus	Araucaria	Australia
Orthoptera	Acrididae	Valanga nigricomis	Hevea, Swietenia, Tectona	India, South-east Asia
	Gryllidae	*Brachytrupes spp.	Eucalyptus, Pinus, Cupressus, Tectona	India, Africa, South-east Asia

Table 5.1. Continued.

age of leaves eaten, position in the canopy, time of year the defoliation occurs, the site and current stresses on the tree (Elliott et al., 1998). For example, small folivore (i.e. leaffeeding) populations can cause disproportionately large foliage losses by feeding on vegetative buds or unexpanded foliage (Schowalter et al., 1986). Sunlit leaves have higher photosynthetic rates than shaded leaves, regardless of age, and insects feeding on these will affect the host more severely than similar damage to shaded leaves. Trees that are damaged or stressed are less able to cope with the effects of severe defoliation than are vigorous trees. Light (i.e. less than 20%) defoliation normally has no or very little effect on the tree, but moderate (25-50%) and severe (more than 50%) defoliation reduces growth rates, can affect wood properties (shortens fibre length) and can predispose trees to attack by other organisms (Elliott et al., 1998). Defoliation in consecutive years is more damaging than a single severe defoliation, and some species of evergreen conifers can be killed by one complete defoliation if this occurs before bud formation. Site and weather factors interact with defoliation episodes to determine the overall impact on the host tree.

In the sections which follow, examples are given of the various types of insect defoliators, with information on their life history, ecology and pest importance.

5.2.1 Leaf chewing

Paropsisterna spp. and Paropsis spp. (Coleoptera: Chrysomelidae)

More than 3000 species of chrysomelid beetle are found in Australia, most of which are never likely to achieve pest status (Waterson and Urquhart, 1995). Damage by these insects in extensively managed native forests generally has been tolerated by forest managers, but with the increasing establishment of fast-growing eucalypt plantations in several states, chrysomelid leaf beetles have become recognized as one of the most serious insect problems associated with these plantations (Nahrung and Allen, 2003). Paropsines cause not only significant losses to eucalypt plantations in Australia, where the beetles and trees are native, but also where the beetles have been introduced accidentally to eucalypt growing regions in countries such as South Africa and New Zealand (Nahrung, 2006).

Some of the more common pests belong to the genera Paropsisterna and Paropsis, sometimes called tortoise or 'paropsine' beetles, and share generally similar life cycles. As outlined by Elliott et al. (1998), in subtropical and temperate regions the adults overwinter under bark, in crevices or in leaf litter and emerge in early spring to feed on newly expanding foliage, leaving characteristic 'scalloped' damage on the leaf margins. Eggs are laid either singly or in batches on newly expanding leaves or shoots, each species having a particular ovipositional behaviour and site for the eggs. The larvae (Plate 14) of many species consume their egg cases before beginning to feed on the leaf. Species which lay eggs in batches feed colonially and, as the young larvae reach the later instars, they usually move to several feeding sites in the crown of the host plant, feeding singly or in small groups. The larvae of some species feed singly for the entire larval stage. There are usually four larval instars, which are completed in 3-4 weeks, and the larvae then drop to the ground, where they pupate in the litter or soil. Adults emerge in 7–10 days, and in the warmer regions there may be five or more generations per year with adults and/or larvae present on the trees for 8–9 months each year.

In Australia, most studies of the impact of chrysomelid leaf beetles have been carried out in temperate regions. In Tasmania, 1-year-old *Eucalyptus regnans* attacked by Ps. bimaculata lost 45.6% and 52.1% of their potential height and basal area increment, respectively, over a 2-year period compared to trees protected by an insecticide treatment (Elliott et al., 1993) (Fig. 5.2). Modelling the impact of defoliation by Ps. *bimaculata* on the growth of *E. regnans* showed that typical defoliation regimes could reduce growth over a 15-year rotation by up to 40% (Candy et al., 1992). In tropical and subtropical eucalypt plantations, Ps. cloelia is becoming an increasingly important pest

500 400 400 Protected Attacked 200 Dec Mar May Aug Dec Feb Jun 1989 19901990 1990 1990 19911991

Fig. 5.2. Mean height growth (± SE) of protected and attacked 1-year-old *Eucalyptus regnans*, Florentine Valley, Tasmania (from Elliott *et al.*, 1993).

(Carnegie et al., 2005). In an outbreak of Ps. cloelia in E. grandis plantations in north coastal New South Wales in 1972–1974, it was estimated that up to 60-70% of the potential annual height increment of the trees could be lost, and more than half the trees died in the following 2 years (Carne and Taylor, 1978). Further north, in Queensland, the relatively recent expansion of hardwood plantations has resulted in the emergence of new pest species and Nahrung (2006) collected at least 17 paropsine species from plantations of *E. cloeziana* and *E. dunnii*, about one-third of which have not been associated previously with eucalypt plantations. The most abundant of these pest species were P. atomaria, P. charybdis and Ps. cloelia.

A wide range of natural enemies of paropsine beetles has been recorded, including parasitic wasps and flies and predatory ladybird beetles and bugs. Cumulative mortalities of *Ps. bimaculata* populations resulting from attack by natural enemies can reach up to 97% by the end of the larval stage (de Little *et al.*, 1990) and up to 90% for *P. atomaria* (Tanton and Khan, 1978b).

Gonipterus scutellatus (Gyllenhal) (Coleoptera: Curculionidae)

The eucalyptus weevil or eucalyptus snout beetle, *Gonipterus scutellatus*, (Plate 15) is

a native of Australia, where it is usually a relatively minor pest in eucalypt forests and plantations, although occasionally it causes economically significant damage. However, it has spread to several other countries, where it has caused severe damage to eucalypt plantations. It was first recorded outside Australia in about 1890 in New Zealand (Withers, 2001) and was discovered in South Africa in 1916 (Mally, 1924). It spread rapidly throughout Africa to Lesotho, Malawi, Kenya, Mauritius, Mozambique, Zimbabwe, Uganda and Malagassy and has been reported from Spain, Italy, Portugal, France, Argentina, Brazil, Chile, Uruguay and California (Richardson and Meakins, 1986; Rosado-Neto, 1993; Cowles and Downer, 1995; Lanfranco and Dungey, 2001; CABI/EPPO, 2010).

Adults lay small yellow eggs on the foliage in black pods, with three to eight eggs in a pod. The eggs hatch in 3–4 weeks and the larvae emerge on the underside of the leaf by chewing through the bottom of the pod and the leaf. All the larvae emerge through one hole and begin feeding immediately on the surface of the leaf, leaving characteristic tracks where the upper surface of the leaf tissue has been removed. There are four larval instars lasting a total of 5-7 weeks. When mature, the larvae drop to the soil and form pupal chambers just below the surface, from which adults emerge after a few weeks. The adults are strong fliers and live for 2-3 months, during which period they lay eggs several times. In Australia, there are usually two generations per year with a life cycle of 10-16 weeks, but there is considerable variation in the countries where the insect now occurs. This depends largely on the incidence of cold weather inducing hibernation and on rainfall inducing flushes of young foliage, which provides the essential diet (Browne, 1968). The larvae feed mostly on the upper crown, where they skim the epidermis of the young leaves, while adults feed all over the tree, devouring the leaves from their edges. In addition, both stages eat the young, soft shoots of some species (Richardson and Meakins, 1986) and continued infestation can produce stag-headed or stunted trees. The impact of defoliation

by the weevil on tree height growth is illustrated in Fig. 5.3.

In South Africa, the arrival of *G. scutellatus* led to the cessation of planting of several commercially important eucalypt species, including *E. viminalis*, which had been favoured up until that time. Similarly, in other countries, the beetle caused economic losses in existing plantations and limited the choice of species for future plantings. An Australian wasp parasitoid of *Gonipterus* eggs, *Anaphes nitens*, was introduced into South Africa and several other countries and gave effective control at altitudes up to 1200 m, but was much less effective at higher altitudes where some major plantations of susceptible species occurred (Govender and Wingfield, 2005).

Corymbia Anomala spp. (Coleoptera: Scarabaeidae)

The genus *Anomala* is common throughout Asia, and in India alone there are more than 200 species (Beeson, 1941). The adult beetles of many species are defoliators of forest trees, while the soil-dwelling larvae or 'white grubs' are sometimes pests of nursery stock. Typically in India, beetles swarm at dusk in



Fig. 5.3. The effect of attack by snout beetle on the height growth of very susceptible and very resistant *Eucalyptus viminalis* (from Richardson and Meakins, 1986).

May–July, the earliest activity occurring after the first showers of the monsoon season. Pairing and egg laying take place throughout this period. Eggs are laid singly at night in soil at a depth of 5–8 cm, and one female may lay 30 eggs. The larva tunnels through the soil, eating the fine roots of plants and decaying vegetable matter, and completes its development in about 9 months. Pupation takes place in the shelter of the larval skin and may last a month. The immature beetle remains in the soil until suitable climatic conditions stimulate emergence and flight. The generation is usually annual.

In China, the principal species in tropical regions is A. cupripes, which defoliates young plantations of Corymbia brassiana, E. camaldulensis, E. citriodora and E. exserta in Guangxi and Gunagdong Provinces. Its pest status has increased considerably with the rapid expansion of the plantation estate in the south (Wylie, 1992). In Hong Kong, swarms of adults sometimes occur in nurseries and plantations during the summer, occasionally causing serious injury to seedlings of Pinus massoniana and to the foliage of young stands of C. citriodora, C. grandis and E. maculata (Browne, 1968). In the subtropical Chinese provinces of Fujian and Jiangxi, A. antiqua is a pest of Paulownia, adults consuming a mean of 882 mm² of Paulownia leaves a day (Tong and Fang, 1989).

Reported natural enemies of this insect are carabid beetles, ring-legged earwigs and the entomogenous fungus, *Metarhizium anisopliae*. Several *Anomala* species are pests in forest nurseries in Bangladesh (Baksha, 1990).

> Atta spp. and Acromyrmex spp. (Hymenoptera: Formicidae)

Leaf-cutting ants are the largest species group of the fungus-growing ants in the tribe Attini and effectively consist of two genera, *Atta* (Plates 16 and 17) and *Acromyrmex* (Ramos *et al.*, 2008). They are sometimes known as parasol ants because of their habit of cutting leaves into more or less circular pieces, which they hold above their heads as they carry them back to the nest. The group is restricted to the New World, *Atta* being found in 23 countries and Acromyrmex in 25 countries from the USA in the north, through Central America and the West Indies down to Uruguav in South America (Cherrett and Peregrine, 1976). They are among the most prevalent herbivores of the Neotropics, consuming far more vegetation than any other group of animals with comparable taxonomic diversity (Vieira-Neto and Vasconcelos, 2010). The ants are pests of agriculture, horticulture. rangelands and forestry. They have been reported attacking 15 different forest tree crops, including pines, teak and eucalypts, in some 16 countries and their rated importance for forestry in these countries is shown in Table 5.2.

Atta and *Acromyrmex* are social insects which live in large underground nests, where they cultivate fungal gardens on a substrate

Table 5.2. Importance of leaf-cutting antsas forestry pests (updated from Cherrett andPeregrine, 1976).

Country (in order of forestry importance, most northerly part)

USA	***
Mexico	*
Belize	***
Honduras	***
El Salvador	***
Nicaragua	****
Costa Rica	***
Panama	*
Columbia	**
Venezuela	**
Trinidad and Tobago	****
Surinam	****
French Guiana	****
Brazil	****
Ecuador	***
Peru	***
Bolivia	**
Paraguay	**
Argentina	****
Uruguay	****

Notes: ***** Major importance, one of the five worst insect pests in the country; ****considerable importance, one of the 20 worst insect pests; ***moderately important pests causing sporadic economic damage; **minor pests, infrequently producing significant damage; *unimportant, only recorded on one or two occasions as doing any damage. of harvested leaves, this fungus forming their principal diet. While the fungus provides ants with nutrients and enzymes, the ants. in turn, supply the fungus with a variety of substrates and stimulate symbiotic fungal growth (Marsaro et al., 2004). Following mass mating flights at the start of the rainy season, the founding queen (mated female) will begin to dig the nest. She will usually bring with her spores of the fungus garden from her original nest site for incorporation into this new nest and will then find a suitable place to lay her eggs. She fertilizes the spores with her own waste, to aid in development of food to feed to the larvae. The queen will continue to raise her first brood until these workers are mature enough to assist her with more eggs and the rest of the colony. Colony growth is slow in the beginning, then proceeds rapidly and reaches maturity in about 5 years.

Species of *Atta* characteristically build and maintain physically defined foraging trails, which may extend 250 m or more in length (San Juan, 2005). They also use trail pheromones. When a worker ant finds forage, she will straddle the piece and cut only that portion which is equal to her leg span. She will rotate and shear the leaf with her mandibles and then carry the disc-shaped portion back to the nest, where other workers process the leaf matter and add it to the garden, which is fertilized with faecal droplets. Undigested or decaying parts of the garden are tossed aside or removed from the garden area as debris. As is usual with social insects, tasks are shared among colony members. The smallest workers tend to remain in the nest and serve as gardeners and nursemaids. The medium-sized workers forage, while others maintain the compost heap or deepen and expand the nest. Soldiers fight off other ants, guard the nest and may also control the 'traffic' in a busy working colony to ensure the proper disposal of forage. A nest may cover 600 m² and may be more than 6 m deep, containing hundreds of fungus gardens and millions of workers: a colony of A. sexdens may contain up to 8 million workers (San Juan, 2005). The nest architecture is complex and adapted to ensure temperature control of the fungus garden.

The impact of leaf-cutter ants on forests is dependent on a range of factors, but the degree of ecosystem disturbance is of great importance. For example, Jaffe and Vilela (1989) found relatively low nest densities of A. cephalotes in primary rainforest ecosystems in the Orinoco-Amazon basin, namely 0.045 nests/ha. They attributed this to a need of A. cephalotes colonies for a certain degree of sunshine (or light) on their nest heaps. The number of clearings in the forest was proposed to be the limiting factor for colonization of new forest sites by this species. Elsewhere, higher nest densities of Atta have been reported in more disturbed forests, with up to 30 nests/ha found in Pinus plantations in the south-western savannahs in Venezuela (Jaffe, 1986) and nearly 300 nests/ ha in 16-year-old eucalypt plantations in Brazil (Oliveira et al., 1998). Human intervention clearly increases Atta nest densities in affected ecosystems. Urbas et al. (2007) demonstrated edge effects on foraging and herbivory of A. cephalodes in a large remnant of the Atlantic forest in north-east Brazil. Equally-sized A. cephalodes colonies located at the forest edge removed about twice as much leaf area from their foraging grounds than interior colonies (14.3 versus 7.8%/ colony/year). This greater colony-level impact in the forest edge zone was a consequence of markedly reduced foraging areas (0.9 versus 2.3 ha/colony/year) and moderately lower leaf area index in this habitat, whereas harvest rates were the same. The reduction of the foraging area was attributed to the greater abundance of palatable pioneer plants. The release from natural enemies may also be a contributing factor (Almeida et al., 2008). Some species of *Acromyrmex*, such as A. landolti balzani, forage without trails, a behaviour that may be explained by their dependence on ephemeral or homogeneously dispersed resources, which makes main trails unnecessary (Poderoso et al., 2009).

Numerous studies have assessed the rates of leaf fragment input into various leaf-cutting ant nests and some of these are summarized in Lugo *et al.* (1973). Leaf input for *A. cephalotes* ranged from 10.9 g/h for a nest in Guiana to 290 g/h for a nest in Costa Rica. The efficiency of leaf transport to the nest has been estimated at 50-70% (i.e. many leaves are dropped along the way); so herbivory may be much higher than leaf input figures suggest (Lugo et al., 1973; Fowler and Robinson, 1979). Leaf-cutting ants are pests of Pinus spp. in several countries; for example, in Venezuela, A. laevigata causes economic damage to young P. caribaea plantations at densities of 5 nests/ha (Hernandez and Jaffe, 1995), A. cephalotes and A. sexdens attack P. caribaea seedlings in Costa Rica (Ford, 1978) and A. insularis attacks several Pinus species in Cuba (Tsankov, 1977). In Brazil, Atta and Acromyrmex attack A. angustifolia (Schoenherr, 1991) and are the most severe pests in that country's more than 6 Mha of Eucalyptus plantations (Marsaro et al., 2004). Zanetti et al. (2000, 2003) found that leaf-cutting by Atta spp. in eucalypt plantations reduced wood production, E. camaldulensis, C. citriodora and E. tereticornis being more affected than E. cloeziana and E. urophylla (Fig. 5.4). A. sexdens is a pest of rubber trees (Hevea spp.) in nurseries, sometimes affecting more than 70% of trees (Calil and Soares, 1987). In Costa Rica, a species of Atta reduced growth of Acacia mangium by 50% in trials (Glover and Heuveldop, 1985).

Natural enemies of leaf-cutting ants include nematodes, mites, ant-decapitating phorid flies, birds and armadillos, as well as other ants such as *Nomamyrmex* army ants (Erthal and Tonhasca, 2000; Powell and Clark, 2004; San Juan, 2005; Guillade and Folgarait, 2011).

Perga affinis Kirby (Hymenoptera: Pergidae)

Sawflies (Plate 18) are common pests of woodland and urban trees in many parts of the world and are one of the more dramatic groups of eucalypt-defoliating insects in Australia (Jordan *et al.*, 2002). Some have the potential to become serious pests in eucalypt plantations. The steelblue sawfly, *Perga affinis*, which has several subspecies, occurs widely throughout Australia and feeds principally on *Eucalyptus* spp.

Adults emerge in the autumn from pupation sites in the soil beneath previously infested trees (Fig. 5.5). They do not feed and only live long enough (about a week) to find



Fig. 5.4. Average wood production for *Eucalyptus* spp. (m³/ha) as function of plantation age (months) considering stands without leaf-cutting ant nests, plots with similar density of nests of the area studied (16.8/ha) and plots with density of nests similar to level of economic damage. Municipality of João Pinheiro, State of Minas Gerais, Brazil from 1991 to 1996 (from Zanetti *et al.*, 2003).



Fig. 5.5. Typical life cycle of Perga spp. (from Kent, 1995).

a host tree and lay eggs. Females lay about 65 eggs per batch, inserted by the saw-like ovipositor at regular spacing along the midrib of the leaf, and these hatch in approximately 30 days. Larvae congregate on the leaf surface in a rosette pattern, with their heads facing outwards. They move out and feed on the leaf margins at night, re-forming clusters before dawn (Elliott *et al.*, 1998).

As the larvae grow, usually by about the third instar, they no longer congregate in rosettes on leaves but cluster during the day in large masses surrounding branches and tree boles. When searching for foliage, larvae tend to move upwards and outwards, so the feeding by the older larvae occurs on the terminal shoots first. The tree therefore gets defoliated from the top down. Colonies of larvae from different egg batches can amalgamate and form very large masses. Larvae communicate with each other by vibrational signals, the most likely function of which is to maintain group cohesiveness and coordinate movement (Fletcher, 2007). A heavily infested tree can become completely defoliated, at which time the entire colony moves down the tree and across the ground to a nearby tree. There are six larval instars and when the larvae are fully grown, they leave the trees and burrow into the litter and soil beneath the tree, constructing leathery cocoons which are connected in a compact mass. In the cocoon, the larva moults to a prepupa, which lasts through the summer, when pupation occurs and adults emerge shortly after. The prepupal stage is usually completed during one summer, but some individuals may remain a prepupa for up to 4 years.

Egg mortality results mostly from desiccation and disease, with some eggs being eaten by birds. Larval colonies moving along the ground to other trees can suffer high mortality if nearby trees are more than 10 m away and larvae get caught on the ground during the hottest part of the day. Cocoons of *P. affinis* are parasitized by wasps and flies.

Carne (1969) suggested that changes in the physical environment influencing abundance were common across large areas. Good spring rains soften the soil surface, allowing larvae easy entry for cocoon formation, and also result in good foliage production, which provides favourable ovipositional sites for females in the autumn. Drv winters cause the soil to harden, causing high mortality of larvae attempting to enter the soil to pupate. Hot, dry summers cause desiccation of pupae in the soil (Elliott et al., 1998). Most defoliation by P. affinis occurs in late winter and early spring and, at this time of the year, it has least impact on tree growth and health. Trees therefore often survive repeated defoliation in successive years. A single defoliation probably has minimal impact on tree health (Carne, 1969). However, studies by Jordan et al. (2002) of *P. affinis* ssp. *insularis* attack in E. globulus plantations in north-western Tasmania demonstrated that sawfly damage caused slow growth and increased mortality of trees. Mild and severe sawfly damage resulted in 16% and 31% reduction in the basal area of surviving trees, respectively, and the effect was consistent across races and families.

Thyrinteina arnobia (Stoll) (Lepidoptera: Geometridae)

Among the Lepidoptera which defoliate *Eucalyptus* spp. plantations in Brazil, *Thyrinteina arnobia* is regarded as the most important because of its consistent damage and increasing adaptation to this exotic host (Filho *et al.*, 2010). The species occurs widely in Central and South America, from El Salvador down to Uruguay. It has numerous native hosts, including many Myrtaceae, and attacks 13 species of *Eucalyptus*, the principal being *E. grandis* and *E. saligna*.

The female lays her eggs (average 752) on thin branches and these hatch in about 10 days. First instar larvae disperse by direct movement or are carried on the wind by silk threads. There are six larval instars lasting 35–40 days. As is typical of the Geometridae, larvae at rest adopt an erect position, held by the abdominal prolegs, mimicking tree branches. Pupating caterpillars construct a rudimentary cocoon that is fastened by silk lines to eucalypt leaves or to low-lying vegetation. Pupation lasts 4–10 days. Adults emerge from the cocoons at night and are short-lived: about 4 days for males and 7 days for females. Mating and oviposition occur at night.

Caterpillars can be very destructive, especially to new plantations. Initial damage is to the lower part of the crown and attack proceeds upwards to the top of the tree. Outbreaks of this pest are usually not noticed until the larvae are in their fifth instar, when defoliation is rapid (Anjos et al., 1987). Patterns of defoliation vary; in some instances, outbreaks appear to start on the margins of plantations and progress towards the centre, and in other cases they start in the centre and move outwards in a circle, leaving large 'clearings' of defoliated trees. Adults are present throughout the year, but numbers are lowest from October to December. All recorded outbreaks have occurred during the period January– September.

Plantations aged 6 months to 20 years have been attacked. It is suggested by Anjos *et al.* (1987) that new plantations are attacked only when there are older trees nearby that have a resident population of *T. arnobia*. Berti Filho (1974) provides estimates of the average leaf area consumed by an individual caterpillar in each instar I–VI (Fig. 5.6). According to calculations by Mendes Filho (1981; cited in Anjos *et al.*, 1987), it would take 663 caterpillars to defoliate completely a 10-year-old *E. saligna* of 18 cm diameter at breast height (DBH), 4976 caterpillars for a 21 cm DBH tree and 11,610 caterpillars for



Fig. 5.6. Leaf area consumed by individual larvae of *Thyrinteina arnobia* in different instars (from Berti Filho, 1974).

a 24 cm DBH tree. Early instar caterpillars tend to feed on the leaf surface, but later instars consume the whole leaf. Studies by Oda and Berti Filho (1978) of T. arnobia defoliation in 2.5- to 3.5-year-old plantations of E. saligna showed volume losses 1 year after the event of 25.6 m3/ha for trees that had been defoliated completely and 8.3 m³/ ha for trees which had been 50% defoliated. In percentage terms, this represents volume losses of 40.4% and 13.2%, respectively. Estimated impacts for some recorded outbreaks are summarized in Table 5.3. In addition to loss of growth increment, defoliation by T. arnobia can also result in tree mortality. There is considerable variation among eucalypt species in their resistance to attack by the pest; E. grandis and E. saligna are highly susceptible, while *E. camaldulensis* has been rated as highly resistant (Oliveira et al., 1984; Lemos et al., 1999; Filho et al., 2010). Most reports of damage to eucalypt plantations by T. arnobia have been from Brazil, but Marturano and Vergara (1997) recorded that in 1996 this insect caused defoliation on 320 ha of eucalypt plantations aged 2.5 to 3.5 years in eastern Venezuela.

T. arnobia has many natural enemies, including parasitic tachinid and sarcophagid flies, ichneumonid, chalcidid, eulophid and pteromalid wasps and predatory pentatomid bugs, carabid and cicindelid beetles and birds (see, for example, Grosman *et al.*, 2005; Pereira *et al.*, 2008). Mortality rates of more than 80% have been recorded in the immature stages (Batista-Pereira *et al.*, 1995).

Hyblaea puera Cramer (Lepidoptera: Hyblaeidae)

The teak defoliator *Hyblaea puera* is one of the best known of the lepidopterous defoliators in the tropics, both because of the value of the principal tree on which it feeds and because of its pantropical distribution. Its range extends from the southern USA through the West Indies and Central America into South America as far south as Paraguay, through southern and East Africa, India, China, throughout South-east Asia to Australia and the Pacific. It is now believed that *H. puera* is not a single species but rather a species

Year	Localities	Area defoliated (ha)	Losses in yield in the next year ^a (stere) ^b
1948	Bauru	600	4,814
1949	Rio Claro	200	1,608
1961	Barra Bonita	200	1,608
1967	Cel. Fabriciano	448	2,401
1973	Ribeirao Preto	4,500	36,180
1973	Itu	827	6,649
1973	Sao Miguel Arcanjo	1,800	14,472
1973	Itupeva	10	81
1973	Itapetininga	200	1,608
1973	Suzano	200	1,608
1974	Ribeirao Preto	600	4,824
1975	Paulinia	200	1,608
1975	Cataguases	200	1,072
1981	Presidente Olegario e Joao Pinheiro	15,000	80,400
Total		24,985	158,933

Table 5.3. Losses associated with known outbreaks of *Thyrinteina arnobia* in eucalypt plantations in Brazil (from Anjos *et al.*, 1987).

Notes: ^aBased on defoliation levels of 50% in half the area and 100% in the other half and calculated according to Oda and Berti Filho (1978); ^bstere = a unit of volume equal to 1 m³.

complex (CABI, 2005). The life history, hosts, population dynamics and impacts of the insect are summarized by Nair (2007). Aside from teak, *Tectona grandis*, it has numerous dicotyledonous hosts, most of which are of minor importance for forestry. It is believed that during non-outbreak periods the insect thrives on hosts other than teak, but there are few data available on the periods of infestation or population levels on these hosts (Nair, 2007).

The moths shelter by day but are active fliers at night and can migrate considerable distances during outbreaks. Eggs are laid singly on leaves, particularly on young, tender foliage, and a female may lay up to 1000 eggs (Beeson, 1941). Early instars feed on the leaf surface, causing skeletonized patches. The third instar cuts out a circular or rectangular flap at the edge of the leaf and folds it over flat, fastening it with silk so as to form a shelter. It skeletonizes older leaves and totally consumes newly formed leaves. Instars IV and V also fold leaves to form shelters and totally consume tissue between the larger side veins to leave bare 'ribs'. Moulting takes place in the leaf folds. The mature fifth instar

larva also pupates on the leaf in a triangular fold or, if the crown is stripped, on undergrowth or in soil litter. The life cycle of *H. puera* from egg to the emergence of the adult varies from 14 to 47 days, depending on climatic conditions, and there can be up to 14 complete generations/year. The climate of the locality, particularly rainfall, is one of the main determinants of seasonal abundance (Loganathan and David, 1999). The population density is usually lowest in the season of mature foliage and leaf fall. In southern India, the insect is most abundant in April to early June, while in the north it is abundant in late July to September (Beeson, 1941). Diameter growth of teak generally stops between the beginning of October and mid-November, and defoliation at this time of year has little effect on the current annual increment but may affect future height growth and quality if buds are killed. The frequency of severe defoliation is high in stands aged 11–45 years and is at its maximum in stands 21–30 years old. Nair (1988) estimated that, during outbreaks, a 30 ha teak plantation might have over 450 m larvae.

Nair *et al.* (1985, 1996) studied the impact of defoliation by *H. puera* (Plate 19) over the period 1978–1982 in young teak plantations at Kerala, India. They found that the insect caused very significant loss of increment, 44% of the potential growth volume remaining unrealized because of its attack. On a per hectare basis, unprotected trees had a mean annual increment of 3.7 m^3 /ha and protected trees 6.7 m^3 /ha. Projections suggested that protected plantations could yield the same volume of wood in 26 years as unprotected plantations would do in 60 years.

In Bangladesh, defoliation of teak by *H. puera* is a regular annual feature, although epidemic outbreaks such as occur in India are rare (Baksha, 1990). The insect is of importance in Sri Lanka (Tilakaratna, 1991), Myanmar (Beeson, 1941), Thailand (Hutacharern, 1990), Malaysia (Abood *et al.*, 2008), China (Chen and Wu, 1984) and Indonesia (Intari, 1978). In the Solomon Islands, it is mainly a pest of nursery stock (Bigger, 1980, 1988). Outbreaks have also been recorded on species of Avicennia, Bruguiera and Rhizophora mangroves in Asia (Palot and Radhakrishnan, 2004), the Caribbean (Saur et al., 1999) and South America (Mehlig and Menezes, 2005). On Brazil's Amazon coast, for example, defoliation of Avicennia germinans by H. puera occurs every 2 years. A 4-year study by Fernandes et al. (2009) showed that leaf loss averaged 13% in the first and third years. They concluded that the conversion of A. germinans leaves into frass by the defoliator favoured nutrient cycling in the mangrove itself and provided a nutrient supply for neighbouring aquatic systems over a short period of time.

Natural enemies of *H. puera* include parasitic wasps (Chalcididae, Ichneumonidae, Braconidae and Eulophidae) and flies (Tachinidae), and predatory pentatomid bugs, mantids and carabid beetles (Mukhtar *et al.*, 1985; Sudheendrakumar, 1986; Nair, 2007). Birds are also common predators of this insect. In teak plantations in Kerala, India, Zacharias and Mohandas (1990) have recorded 48 species of birds feeding on *H. puera*, and in Papua New Guinea, the insect is a significant food resource for several bird species in teak plantations (Bell, 1979).

Dendrolimus punctatus Walker (Lepidoptera: Lasiocampidae)

Pine caterpillars belonging to the genus *Dendrolimus* (Plate 20) have long been recognized as serious pests of pine forests in China and recorded outbreaks date back to 1530 (Peng, 1989). Each year about 3 Mha of forest are infested, resulting in a growth increment loss of 5 mm³ (Peng, 1989). *D. punctatus* is the most widespread and destructive species (Zhang *et al.*, 2003), occurring in 13 provinces, including 3 in the tropical south of the country. It is also an important pest in Vietnam and Taiwan (Billings, 1991). Its main host is *P. massoniana*, but it has been recorded from several other *Pinus* species.

Each female moth lays an average of 300-400 eggs, with a possible maximum of 800, in groups on the foliage of the host. Newly hatched caterpillars disperse by 'ballooning' (blown in the wind on silk threads). The larvae feed openly and voraciously on the needles, and there are usually six instars. Mature larvae spin cocoons, in which they pupate, on branches or needles of the host tree or on adjacent vegetation. Adult emergence from the cocoon occurs at dusk and mating and oviposition take place at night. The moths are strong fliers and can migrate up to 20 km.

In the hot and dry regions of Guangxi and Guangdong Provinces in south China, there are three to four generations per year and two to three in warm, humid Hunan (Xue, 1983). In Vietnam, D. punctatus has three to five generations a year, and population densities of up to 700 larvae per branch have been recorded (Bassus, 1974). Severe defoliation may result in loss of growth and resin production, and sometimes in tree mortality. Studies in China by Ge et al. (1988) showed that after almost 100% defoliation of Pinus spp., nearly 25% of trees died and the volume growth of surviving trees was reduced to 31% of normal. Badly affected trees took 3 years to recover. Root rot infection of plantation *P. elliottii* in southern China has been linked to defoliation by *D. punctatus* (Liu and Liang, 1993). In general, outbreaks of the pest seem to be fairly erratic, and hence hard to predict (Zhang et al., 2008), though in some

localities outbreaks appear every 3–5 years or so (Li, 2007). Billings (1991) recorded that in Vietnam in 1987, 56,500 ha had been affected by the moth larvae, with 33,500 ha suffering from severe defoliation. Young trees may be defoliated completely, and even die as a result. Those between 7 and 15 years old are most commonly attacked.

Biotic agents (parasitoids and entomogenous fungi) have dominated integrated pest management strategies used against this insect in China since the 1970s (Li, 2007) (see also Chapter 10). Xu et al. (2006) list 58 species of parasitic wasps and 20 species of tachinid flies. Trichogramma wasps, particularly *T. dendrolimi*, which parasitize eggs of D. punctatus, have been widely employed and reportedly are effective (Wu et al., 1988). The number of parasitoids required for suppression varies with the age of the stand, the density of the trees and the density of the egg masses but, in general, 1,050,000/ha are required (Hsiao, 1981). There are many other natural enemies, one of the main in Hunan being the ichneumonid wasp parasitoid Casinaria nigripes Gravenhorst, which attacks first to fourth instar larvae. Ma *et al.* (1989) showed that rates of parasitism by *C. nigripes* in forests were influenced by stand type and growing conditions, with the greatest parasitism in mixed stands, followed by closed pure stands and then sparse stands. Ants are the most important predators in Vietnam and China and can regulate populations of the pest effectively (Bassus, 1974; Hsiao, 1981).

Pteroma plagiophleps Hampson (Lepidoptera: Psychidae)

Up until the late 1970s, the bagworm, *Pteroma plagiophleps*, was known only as a minor defoliator of tamarind, *Tamarindus indica*, in India and Sri Lanka. In 1977, it caused extensive defoliation to a young plantation of *Falcataria moluccana* at Kerala (Nair *et al.*, 1981) and since that time has become an important tree pest in several countries in South and South-east Asia (Nair, 2007).

P. plagiophleps belongs to a family of moths whose larvae construct individual

bag-like shelters made of host material and silk, within which the larva remains concealed and only the head and thorax protrude when feeding (Plate 21). The adult male is a normal winged moth but the female is wingless, with a poorly developed body. The female does not leave the bag but mates from inside, and her eggs also mature and hatch there. Each female usually produces 100-200 offspring, which emerge from the bag and disperse on silken threads. They settle on leaves and construct the protective bag, which they carry about with them, enlarging it as they grow. Pupation takes place in the bags hung from the branches. The generation time of P. plagiophleps is about 10-11 weeks (Nair and Mathew, 1992).

While up to five generations a year have been observed in the field, outbreaks leading to heavy defoliation generally occur only once or twice a year, usually in small patches in plantations (Plate 22). Studies by Nair and Mathew (1988, 1992) in a 20 ha plantation of F. moluccana showed that repeated defoliation over 2.5 years caused the death of 22% of trees and moderate to severe damage to 17%. Heavy infestations affecting a large number of trees have been recorded for *F. moluccana*, *Delonix regia* and E. tereticornis. In the case of E. tereticornis at least, there is evidence to suggest that such infestation is related to host stress. In the last couple of decades, the insect gradually has extended its host range and importance as a forest pest (Pillai and Gopi, 1990a; Howlader, 1992), attacking plantations of A. nilotica and even mangroves, Rhizophora mucronata (Santhakumaran et al., 1995). The latter record indicated the hardiness of P. plagiophleps, since it was feeding on saplings which became submerged during high tides and on taller mangroves which regularly received salt spray. In Indonesia also, P. pla*giophleps* is a sporadic pest, with severe defoliation occurring in some endemic patches of F. moluccana in Sumatra (Nair, 2007).

Natural enemies appear to play a decisive role in regulating the populations of *P. plagiophleps* larvae, and 18 species of parasitoids, all hymenopterans, are known (Nair, 2007). A 25–38% reduction in populations of this pest has been recorded on some occasions, due mainly to parasitism by ichneumonid and chalcidid wasps (Mathew, 1989).

Ctenomorphodes tessulatus (Gray) (Phasmatodea: Phasmatidae)

The tesselated phasmatid *Ctenomorphodes tessulatus* occurs in coastal areas of Queensland and New South Wales in eastern Australia. It is a pest of native hardwood forests and has a wide range of hosts, mostly in the family Myrtaceae (Elliott *et al.*, 1998).

The adult insect reaches approximately 120 mm in length, the male being winged and the female wingless. Females lay eggs that drop to the forest floor from the canopy and become incorporated into the litter. The eggs hatch in late August and early September and the nymphs ascend nearby trees to feed on foliage. They pass through six instars and adults begin to appear during December. There is usually one generation per year, 2- or 3-year cycles occurring only rarely in most populations. Adults live for up to a year.

All known outbreaks of this insect are from native forests and there are no records from plantations. Outbreaks in southern Queensland over the period 1974–1976 resulted in widespread defoliation and tree death, particularly of *E. tereticornis* (Wylie *et al.*, 1993). Trees bordering road corridors and on pastoral or farm land were most seriously damaged.

Several wasp parasitoids have been reared from eggs of *C. tessulatus*, notably species of Myrmecomimesis and Loboscelidia (Heather, 1965). There also appears to be high mortality among eggs, caused by pathogens. Nymphs are probably preved upon by birds, since these have been observed feeding on other phasmatids. In the case of one outbreak in northern New South Wales, forest fires had regularly burned over the area in the years preceding this event. Hadlington and Hoschke (1959) conjectured that fires in the spring and early summer would not affect the nymphs which had entered the tree canopies but would kill the egg parasites, which did not emerge from the eggs until December-February. It is possible that the reduction in

egg parasitoid numbers due to early season fires could allow *C. tessulatus* populations to build up. However, in one outbreak area, nymphs and adults disappeared prematurely, indicating that at least one other major regulating factor was operating.

5.2.2 Leaf mining

A large number of insect species 'mine' or feed on tissue between the upper and lower surface of leaves. Most species are in the order Lepidoptera, but some species of Coleoptera, Diptera and Hymenoptera also mine leaves (Elliott *et al.*, 1998). The shape of some mines is characteristic of the species that constructs them and is therefore useful in identification. Because of the restricted size of their habitat, leaf miners are small and their larvae are grub-like and usually flattened dorsoventrally.

Acrocercops spp. (Lepidoptera: Gracillaridae)

The genus *Acrocercops* is a large one, occurring in both tropical and temperate regions around the world. In Australia, where there are more than 100 species, at least 11 species of these leaf miners attack *Acacia*, *Angophora* and *Eucalyptus* (New, 1976; Elliott *et al.*, 1998). The mines are generally of the 'blotch' type, being wide as well as long, and appearing as a blister on the leaf surface. Larvae of most species develop from egg to pupa within a few weeks, with the adults emerging a few weeks later, suggesting that several generations per year are possible.

A. plebeia is a species which attacks several Acacia spp. in subtropical Queensland. Adult moths lay eggs on the phyllode surface, usually one per phyllode and near the midrib, giving the larvae maximum choice in mining direction (New, 1976). On hatching, larvae immediately enter the epidermis of the phyllode. There are five larval instars, with a total development time of 14–25 days. The first two instars make a long, narrow and sinuous mine and the remaining instars make a blotch mine (Plate 23). At maturity, the final instar larvae cease feeding and empty the gut. A circular flap is then cut through the phyllode cuticle and the larva emerges to spin a cocoon either on the phyllode surface, on the bark or (more rarely) drops to the ground and pupates in the litter.

In India, there is also a large number of Acrocercops spp. which mine the leaves of forest trees (Beeson, 1941). Yadav and Rizvi (1994) record this group as major pests of wasteland plantations of Syzygium cumini, and Acrocercops sp. near telestris is an important pest of cinnamon (Singh et al., 1978). A. gemoniella mines the leaves of nursery stock of the milk tree, Manilkara hexandra, damaging up to 20% of leaves in some nurseries in central India (Jhala et al., 1988). In the USA, a gracillariid leaf miner, believed to be a species of Acrocercops, has shown potential for the biological control of Melaleuca quinquinerva, an Australian tree which has become a pest in the Everglades of Florida (Burrows et al., 1996).

5.2.3 Leaf skeletonizing

Skeletonizers strip away leaf tissue, leaving a network of veins, or a leaf 'skeleton'. The very early instars of many species of moth cause this type of damage, but some species are specialist skeletonizers for a considerable part of their larval life.

Craspedonta leayana (Latreille) (Coleoptera: Chrysomelidae)

This chrysomelid, formerly known as *Calopepla leayana*, is an important defoliator in plantations of *Gmelina arborea*, a fast-growing timber species, in India, Bangladesh and Myanmar (Baksha, 1997; Singh *et al.*, 2006). It has also been recorded from Thailand.

The adults aestivate and hibernate in bark crevices, clumps of grass, soil litter and other sheltered places for about 8 months in a year and become active when the new leaves begin to expand (Browne, 1968). They cut large circular holes in the leaf and also eat the young buds and shoots. Eggs are laid in clusters, either on the underside of the leaf or on the shoots inside a frothy secretion, which hardens to form an 'ootheca'. One female is capable of laying as many as 18 oothecae, each of which may contain up to 100 eggs (Ahmed and Sen-Sarma, 1983, 1990). After about a week, larvae emerge and begin feeding on the lower surface of leaves or on shoots, making discoloured, irregularly shaped feeding patches. There are five larval instars and it is the fourth and fifth instars. which cause complete skeletonization, leaving only the midrib and main veins. The larvae of *C. leavana* have an interesting defence mechanism. The excrement, instead of being discarded, is extruded in long, fine, black filaments, often twice the length of the body, which are formed into bunches and attached at the anal end. When disturbed, the larvae of all instars flick these filaments up and down in a defensive action. Pupation occurs on the leaves. There are usually three generations a year, the first two taking about 46 and 43 days, respectively, and the hibernating generation taking about 239 days (Ahmed and Sen-Sarma, 1990).

Defoliation of *G. arborea* is first noticeable at the beginning of the rains, usually in April or May, and may continue until October. A heavy attack causes the leading shoots of young trees to dry up, and the trees remain leafless for about 4 months of the growing season and eventually become bushy. Two or more consecutive complete defoliations will kill trees (Beeson, 1941). There are no other recorded hosts for *C. leayana* (Nair, 2007).

Chalcidid wasps, *Brachymeria* spp., particularly *B. excarinata*, have been recorded as pupal parasites of *C. leayana* (Mohandas, 1986; Singh *et al.*, 2006) and a eulophid wasp, *Tetrastichus* sp., is an egg parasitoid (Baksha, 1997). Factors such as temperature, rainfall and the quality and quantity of food are important contributors to seasonal fluctuations of this insect. In Assam, India, Kumar *et al.* (2010) found that temperature was the principal component influencing populations of *C. leayana*.

5.2.4 Leaf tying/rolling

Larvae in several moth groups construct shelters for protection against predators such as birds, the simplest of these constructions being a webbing-together or rolling of leaves. The larvae feed on foliage contained within the shelter. This habit is common among species of Tortricidae and Pyralidae.

Strepsicrates rothia Meyrick (Lepidoptera: Tortricidae)

This insect is widely distributed in the tropics of the eastern hemisphere, being recorded in Ghana, Nigeria, Mauritius, India, Pakistan, Sri Lanka, Taiwan and Malaysia. It is associated principally with the foliage of *Eucalyptus*, but also occurs on other dicotyledonous trees such as guava and mango (Beeson, 1941; Browne, 1968).

The larva of Strepsicrates Species rolls a single *Eucalyptus* leaf, forming a shelter in which it feeds and rests (Plate 24). When the leaf turns brown and withers as a result of the feeding, the larva crawls out to a fresh leaf to repeat the process. Pupation takes place in the rolled-up leaf. The life cycle is completed in 3–4 weeks, the egg stage lasting 3–4 days, larval development 10–21 days and pupal stage 5–8 days (Chey, 1996; Wagner *et al.*, 2008). The adult lives for only a few days in captivity.

According to Chey (1996), Strepsicrates rothia is the most serious defoliator of E. deglupta in Sabah. Damage to the shoots of young trees can be severe, and in nurseries infestation levels of 20% have been recorded in Sabah (Chey, 1996) and of more than 50% in Ghana (Wagner et al., 2008). In Ghana, *E. tereticornis* is the most preferred host species, with E. alba, E. cadamba and *C. citriodora* preferred in descending order. Wagner et al. (2008) noted that the rate of infestation of S. rothia in a forest nursery at Yenku was about twofold more on shaded beds than on unshaded beds. Infestation is not confined to seedlings, and Chey (1996) states that trees above 10 years of age in plantations are also attacked. In Sabah, a braconid wasp, Ascogaster sp., parasitizes S. rothia.

5.3 Sap Feeding

Sap-feeding insects suck liquid or semi-liquid material from succulent parts of the host plant, which can be leaves, stems, roots, fruit, flowers or even seed (Elliott *et al.*, 1998). Most are true bugs (Hemiptera), but thrips (Thysanoptera) can feed in a similar fashion, except that penetration is relatively shallow.

Sap feeders affect tree vitality by extracting sap required for normal functioning of the plant, such as shoot extension and leaf expansion. This results in stunting, distortion or wilting, depending on the size of the pest population, the insect species involved, the location of the feeding site and the season of attack (Elliott et al., 1998). As well, some species, such as certain lerp (protective case)-making psyllids and mirid bugs, can inject a toxic saliva into their hosts, causing necrosis of plant tissue. Sap feeders excrete a clear, sugary liquid (honeydew), which can coat the surfaces of leaves and stems and on which grows sooty mould fungi. Where large populations of insects are present, as with aphids and coccids, the blackening of the plant surface by the mould can cause reduced photosynthetic efficiency and the loss of host vigour.

Feeding by sap-sucking insects provides access for pathogenic fungi into plants, and aphids, mirids and cicadellids are particularly important in the transmission of viruses. Cicadas damage their host physically during oviposition, slitting the bark of stems, while thrips and other sap feeders may cause gall formation.

The known world fauna of aphids (Aphidoidea) consists of 4401 species placed in 493 genera, of which 1758 species in 270 genera spend all or part of their life feeding on trees (Blackman and Eastop, 1994). Aphids are predominantly a northern temperate group, with remarkably few species in the tropics. In contrast, psyllids, which have similar ecology and host relations to aphids, are very common in the tropics. Blackman and Eastop (1994) believe that aphids have failed to diversify in the tropics because of one particular primitive feature of aphid biology, their cyclical parthenogenesis (i.e. a life cycle consisting of one generation of sexual morphs and several generations in which only parthenogenetic females are produced). Aphids moving into the tropics lose the sexual phase of their life cycle, and in so doing, lose the potential to evolve and diversify. Despite this, several

aphid species which have become established in the tropics have flourished and are now a problem.

Pineus pini (Macquart), Pineus boerneri Annand (Hemiptera: Adelgidae)

Pine woolly adelgids, *Pineus* spp., are native to the temperate zones of the northern hemisphere and feed on conifers. Nymphs and adults suck plant juices from needles, shoots or stems of pine and cause shoot deformity and loss of height growth. Excess plant juice excreted by adelgids as honeydew is a favourable medium for growth of black sooty moulds on foliage and stems (Diekmann et al., 2002). Two species in particular, *P. pini* and P. boerneri, have become serious pests where they have been introduced accidentally into several tropical and subtropical countries in the southern hemisphere during afforestation programmes using *Pinus* spp. Both species have a confused taxonomy. P. pini (Plate 25), which is native to Europe and introduced into North America. Australia and New Zealand, has sometimes been referred to in the literature as P. laevis and guite often mistaken for P. boerneri, which is of East Asian origin (Blackman and Eastop, 1994). P. boerneri has been recorded under the name of *P. laevis* in Australia. New Zealand and Hawaii, as P. havrylenkoi in South America and as *P. pini* in East Africa (Day *et al.*, 2003). The introduction of P. boerneri into Africa is believed to have been via pine scions imported into Zimbabwe and Kenya from Australia in 1968 (Odera, 1974), and genetic analysis by Blackman et al. (1995) has confirmed an Australian link. Since then, P. boerneri has spread to a further six countries in eastern and southern Africa, mostly by the movement of infested nursery stock (Zwolinski, 1989), and also infests Pinus plantations in Brazil (Oliveira et al., 2008).

Adelgids are related closely to aphids and occur only on conifers. In Europe and North America, they have complicated life histories which may involve a primary and a secondary host belonging to two different genera (Zondag, 1977). However, in most areas where they have been introduced, they are restricted to *Pinus* spp. In Africa, for example, P. boerneri has a host range of over 50 species of exotic Pinus (Chilima and Leather, 2001). Pine woolly adelgids have both winged and apterous adults. The wingless females reproduce parthenogenetically, but there is some doubt about the ability of the winged forms to reproduce (Odera, 1974). The young, or 'crawlers', which hatch from the eggs move about on the foliage, find a suitable spot to insert their mouthparts and start sucking sap. Some crawlers are dispersed by wind. The insect moults several times before it reaches adulthood, which usually takes only a few weeks. The generations overlap and several generations are produced in a year.

Various studies have shown that population fluctuations of P. boerneri are related to rainfall, but the results are sometimes contradictory. For example, in Kenya, Mailu et al. (1980) found that there was a marked decrease in numbers during periods of heavy rainfall and a significant increase during dry weather, whereas in Hawaii, Culliney et al. (1988) found the reverse. In Kenya, the heavy rainfall caused high mortality early in the life cycle by washing eggs and crawlers off the host tree. In Hawaii, high population densities during periods of increased rainfall were attributed to the higher nutrient value of trees at such times, which favoured increased survival of the insects. Trees under stress are likely to be infested by *P. boerneri* more heavily than are unstressed trees (Madoffe and Austara, 1993).

In the early stages of infestation, or on lightly infested trees, colonies of the adelgid occur under scales of the bud base, on shoots at the base of a needle fascicle, or on needles inside a fascicle (Zwolinski, 1989). Later, the infestation spreads to the new growth and down to the bark of thicker branches and the stem. The insects produce waxy white threads, which form a dense woolly cover over the colonies and give infested parts of the tree a greyish appearance. Chlorosis of foliage, shoot dieback, malformation and, in severe cases, death of trees can result from heavy infestations of P. pini (Plate 26). In Kenya, Odera (1974) reported 20% mortality in some study plots, and Mailu et al. (1978) found that severe stunting of needles caused

by adelgid feeding could result in loss of half the tree yield. In South Africa, Zwolinski *et al.* (1988) reported a 23% decrease in seed production of *P. pinaster* due to this insect. Studies of the impact of *P. boerneri* on the growth of *P. patula* seedlings in Tanzania showed that infested seedlings had 12.2% less diameter growth and 14.1% less height growth than uninfested seedlings in a 24-week period (Madoffe and Austara, 1990).

P. boerneri has numerous natural enemies and some of these have been used in biological control programmes in several countries (Day *et al.*, 2003). In Hawaii, populations of the adelgid have been regulated below economically significant levels by a fly, *Leucopsis obscum* (Culliney *et al.*, 1988). In Kenya and Zimbabwe, coccinellids *Exochomus* spp. are important predators of *P. boerneri*, although Mailu *et al.* (1980) record only 12% reduction in populations of the pest due to these and other predators.

Cinara cupressivora Watson & Voegtlin, *Cinara cupressi* (Buckton) (Hemiptera: Aphididae)

Cypress aphids belong to the genus Cinara, whose members are commonly known as giant conifer aphids (Diekmann et al., 2002). There are about 200 described species of Cinara; approximately 150 of these are from North America, 20 from Japan and the oriental region and 30 of European or Mediterranean origin (Blackman and Eastop, 1994). They infest twigs and branches and sometimes roots of conifers, causing dieback and tree mortality (Ciesla, 1991a,b). As is the case for P. pini, the taxonomy of the species previously referred to as the cypress aphid, *C. cupressi*, is confused and it now appears to be part of a species complex (Watson et al., 1999). The species causing tree damage in Africa is actually C. (Cupressobium) cupressivora (Plate 27). In their native habitat, these aphids generally are not considered major forest pests, but C. cupressivora has had severe economic and social impact in eastern and southern Africa following its accidental introduction there in the 1980s, presumably on infested planting stock, and C. cupressi is an important pest in South America.

The native range of *C. cupressivora* is most likely the region from eastern Greece to just south of the Caspian Sea (Watson et al., 1999). It is now widely distributed throughout eastern, central and southern Africa, the margins of western Europe, countries bordering the Mediterranean Sea, the Middle East, Yemen, Mauritius and Colombia (Dav et al., 2003). It was first discovered in Africa in Malawi in 1986, and subsequently in Tanzania, Kenya, Burundi, Rwanda, Uganda, Zimbabwe and Zaire. It attacks a wide range of exotic and indigenous trees in Africa, including Callitris, Cupressus, Cupressocyparis, Juniperus, Thuja and Widdringtonia (Malawi's national tree), but is particularly severe on the widely planted Cupressus lusitanica (Plate 28).

As outlined by Ciesla (1991a), the life cycle of the cypress aphid is complex. During the summer months, only females are present and reproduce parthenogenetically, giving birth to live young. There are two forms of adults, winged and wingless. In temperate climates, as cool weather approaches, both males and females are found and eggs are produced instead of live nymphs. The eggs are laid in rough areas on twigs and foliage, where they overwinter. In warm climates, parthenogenetic reproduction continues throughout the year. Several generations are produced annually and the lifespan of a single generation is about 25 days. Adults and immature insects are found in clusters of up to 80 individuals on the branches of host trees, where they suck the plant sap. Their saliva is toxic to some trees and can cause branch dieback and tree mortality, especially when large numbers of aphids are present. Dieback usually occurs from the inner crown outward and from the lower crown upward. These insects also produce large amounts of honeydew that covers branches and foliage and on which sooty mould grows, interfering with photosynthesis. Damage appears to be more severe in the dry season.

C. lusitanica, a highly favoured plantation and agroforestry species in Africa, is extremely sensitive to feeding by *C. cupressivora*. In addition to the loss of timber, tree mortality caused by the aphid has increased the fire hazard in many rural areas, particularly where cypress hedges have been planted around homes (Ciesla, 1991a). Damage assessments by Symonds et al. (1994) in a stand of 65-year-old C. lusitanica in Kenva revealed a tree mortality of 12%. In Malawi, the estimate of financial losses on the standing crop by 1990 was over US\$3 m (Odera, 1991, cited in Obiri, 1994). Murphy (1996) estimates that in southern and eastern Africa until 1990, the value of cypress trees killed by C. cupressivora totalled £27.5 m sterling, and there was a loss in annual growth increment (including that from already dead trees) of £9.1 m sterling/year. In Argentina and Chile, C. cupressi affects forests of Austrocedrus chilensis, causing defoliation and tree mortality (El Mujtar *et al.*, 2009; Montalva *et al.*, 2010).

Conifer aphids are attacked by a range of predators that include ladybirds, syrphid flies, lacewings and bugs, but they are far less specific than the corresponding predators of adelgids and have a less significant impact on individual prey species (Mills, 1990). Also, in contrast to the adelgids, parasitoids are a very important part of the natural enemy complex, particularly braconid wasps such as Pauesia spp. P. juniperorum was released as a biocontrol agent against C. cupressivora in Kenya and Malawi in 1994 and is now widespread in these countries. Releases of this parasitoid were also made in Uganda in 1995 and more recently in Chile (Day et al., 2003; Montalva et al., 2010). There is a wide range of tolerance among species of Cupressaceae to attack by cypress aphid, which indicates that resistance breeding may offer a viable, long-term solution to the aphid problem (Day *et al.*, 2003).

Ceroplastes spp. (Hemiptera: Coccidae)

The genus *Ceroplastes* occurs widely throughout the tropics and contains many species which feed off forest trees. Few are serious pests, but when they do occur in large infestations they can reduce tree vigour seriously and even cause mortality (O'Dowd *et al.*, 2003).

One of the more important species is *C. rubens*, commonly known as the pink wax scale or red wax scale (Plate 29). It occurs throughout the Australian and

Oriental regions and also parts of Africa. Smith (1974) provides a description of its life history and habits. The adult female can lay from 600 to 700 eggs, which are deposited in a cavity beneath the body of the scale. The first instar nymphs or crawlers emerge from beneath the parent scale and spread out over the tree. These generally settle on the midrib of leaves, on needles and on young twigs, and begin feeding through long tubular mouthparts inserted into the plant tissue. There are three nymphal instars and the final moult to the adult takes place after about 10–12 weeks, by which time the soft-bodied scale is protected by a globular covering of pink wax. Adults reach maturity in 4-6 months. In Papua New Guinea, Merrifield and Howcroft (1975) reported severe attack of P. caribaea by C. rubens, heavily infested trees being characterized by sparse crowns, considerable darkening of foliage by a dense covering of sooty moulds and reduced height increment. There was evidence of clonal differences in the severity of attack. C. rubens is also a sporadic pest of P. taeda and P. caribaea in Queensland, Australia (Elliott et al., 1998).

The Florida wax scale, *C. floridensis*, is a pest of ornamental trees and shrubs in several countries, but occasionally causes damage in forest plantations. An outbreak in P. caribaea plantations in tropical Queensland affected 30% of the planted area and was expected to cause reduced growth increment and a decline in tree vigour. The sooty mould interferes with photosynthesis, and sap feeding can cause death of needles and twigs (Elliott et al., 1998). Other Ceroplastes of occasional importance are C. grandis in Brazil, *C. ceriferus* in the oriental region and C. destructor in Africa, Papua New Guinea and Australia (Browne, 1968; Iede and Machado, 1989; Wakgari, 2001).

A range of mortality factors have been reported for these insects which, in the early stages, includes failure to emerge from beneath the mother scale, crowding, desiccation and unsuccessful settling on hosts due to dislodging by wind and rain. Entomogenous fungi and natural enemies such as lacewings, ladybirds and eulophid wasps are also important; in South Africa, for example, more than 21 hymenopteran parasitoids of C. destructor have been recorded (Wakgari, 2001). Numerous studies have demonstrated that honevdew-producing scale insects benefit from the presence of ant attendants (Abbott and Green, 2007). In Japan, Itioka and Inoue (1996) showed that ant attendance on C. rubens restricted the ovipositional ability of the encyrtid parasitoid Anicetus beneficus and reduced its effectiveness as a control agent of *C. rubens*. On Christmas Island, an Australian Territory in the Indian Ocean, C. ceriferus and C. destructor are among nine species of scale insects occurring in outbreak densities over hundreds of hectares of rainforest, where they cause canopy dieback and tree death (O'Dowd et al., 2003). These outbreaks are being sustained by high densities of the invasive yellow crazy ant, Anoplolepis gracilipes. The ants assist the scales by removing honeydew, which prevents asphyxiation, 'nannying' of the mobile crawler stage and protection against natural enemies. In return, the scale insects provide A. gracilipes with an abundant source of carbohydrate in the form of honevdew, which fuels their high population densities (Abbott and Green, 2007). The exclusion of ants from plots in affected rainforests on Christmas Island caused a 100% decline in the densities of scale insects in tree canopies in 12 months (Abbott and Green, 2007).

Amblypelta cocophaga China (Hemiptera: Coreidae)

This insect is a major pest of *E. deglupta* and *Campnosperma brevipetiolata* plantations in the Solomon Islands in the Pacific and a minor pest of several forest tree species, including candlenut, *Canarium indicum* (Bigger, 1988; Ipute 1996). It is also an important pest of agricultural crops such as coconut, cassava and cocoa. Both adults and nymphs feed on young shoots, injecting toxic saliva that results in wilting and dieback of the shoot. The leading shoot is chosen in preference to side branches and when this is killed, the tree responds by putting up several new leaders from below the damaged area. These, in turn, may be

attacked and, in extreme cases, the tree becomes very bushy and flat-topped. The new shoots put out at the top of the bush provide abundant food for *A. cocophaga* to flourish, and so the condition is perpetuated (Bigger, 1985).

The genus *Amblypelta* extends from Indonesia to Australia, New Caledonia and Vanuatu, but has the greatest concentration of species in the Solomon Islands, where at least 18 species and subspecies have been recorded (Bigger, 1988).

As described by Bigger (1988), eggs are laid singly, either on a leaf or the stem of the plant. Hatching takes place after 8 days. There are five nymphal instars occupying a total of 33 days. The feeding damage done by the adult insect to E. deglupta is often not particularly severe because the insect is mobile and moves from tree to tree, not staying in one place for very long. Nymphs, being flightless, are of necessity less mobile and so their concentrated feeding is more likely to lead to dieback. Damage is most severe in the first 12 months after planting. In trial plots established to examine the effects of clearing of inter-row growth on incidence of A. cocophaga, no difference was found between cleared and uncleared plots, and an estimated 37–41% of the potential stand was rendered useless for future timber production due to damage by this pest (Bigger, 1985).

With *C. brevipetiolata*, damage by A. cocophaga usually starts when the tree is about 1 m tall and is at an end by the time the tree is 3–4 m tall (about 18 months after planting). Feeding takes place mostly on the lower parts of the leaf midribs and leaf petioles and also on young shoots, resulting in multi-stemming. Cankers often develop at the feeding sites on badly damaged trees and these persist as stem swellings on older trees. Extensive pipe rotting is associated with these swellings. Thomson (2006) mentions that plantations of Agathis macrophylla (Pacific kauri) in the Solomon Islands are affected by this pest, but the severity of damage is not stated.

Ants are known to be predators of *A. cocophaga*, particularly *A. longipes*, *Oecophylla smaragdina* and *Wasmannia auropunctata* (Way and Khoo, 1992).

Aulacaspis marina Takagi and Williams (Hemiptera: Diaspididae)

Mangrove forests are being depleted rapidly and degraded in many countries, and in the past few decades there has been an upsurge in mangrove plantings to restore these forests (Ozaki et al., 1999). The impact of insects on mangroves generally has been considered of minor importance compared to their impact on other types of forests, but it is now clear that this has been strongly underestimated (Cannicci et al., 2008). One emerging pest is the scale insect Aulacaspis marina, which has caused significant mortality of *R. mucronata* saplings in Indonesia. Sucking by these insects on the leaves of the host plant causes chlorosis of the leaf, browning and leaf fall. Newly expanded leaves are attacked by crawlers within a generation span of the insect and successive defoliation results in death of the plant after four generations of the pest.

Female scales lay about 140 eggs, which hatch in approximately 7 days. Newly hatched crawlers remain under the scale for a few days before dispersing to the leaves or stems of the infested trees. Densities of more than 200 mature females per leaf have been recorded. Generation time varies from 34 to 42 days and the insect has nine to ten generations a year (Ozaki *et al.*, 1999).

On the Indonesian island of Bali, where 150 ha of abandoned shrimp ponds had been reforested with three mangrove species (R. apiculata, R. mucronata and B. gymnorrhiza), A. marina killed 70% of R. mucronata saplings in the most heavily infested plantation within 5 months of the initial infestation (Nakamura, 1995, cited in Ozaki et al., 1999). Studies by Ozaki et al. (1999) showed that the other two species of mangrove were equally susceptible but were not heavily infested because their saplings, which were not as tall as *R. mucronata* at the site, were periodically completely submerged in seawater. Periodic spraying of seawater has been suggested as an effective way to reduce damage by A. marina. At present, serious damage by A. marina has only been reported from Bali. However, the species is also distributed in the Philippines and Malaysia, suggesting

that it may become more injurious to mangrove plantations in the broader regions as the numbers of similar reforestation programmes increase.

Ants are important predators of *A. marina* in natural mangrove forests, as demonstrated by Ozaki *et al.* (2000) in Bali. On ant-excluded saplings, 90% of artificially introduced female scales survived a 3-day experiment, while only 22% survived on plants foraged by the ants *Monomorium floricola* and *Paratrechina* sp. (Fig. 5.7).

Helopeltis spp. (Hemiptera: Miridae)

Plant bugs of the genus Helopeltis, sometimes called mosquito bugs, are serious pests of cultivated plants in the Old World tropics, particularly of major cash crops such as tea, cocoa, cinchona, cashew and pepper (Stonedahl, 1991) (Fig. 5.8). There are 40 known species distributed from West Africa to Papua New Guinea and northern Australia. They have been regarded generally as only minor pests of forest trees, occasional damage being reported to Swietenia, Terminalia, Cinnamomum and Melia. However, in more recent years, Wylie et al. (1998) have recorded severe damage to young eucalypt and acacia plantations in Indonesia, and there have been similar instances in other countries.



Fig. 5.7. Survival of female *Aulacaspis marina* (mean \pm SE) on ant-excluded and ant-present seedlings of *Rhizophora mucronata* introduced into five stands (A–E) in natural forests (from Ozaki *et al.*, 2000).

Fig. 5.8. Adult female of Helopeltis theivora (from Stonedahl, 1991).

As with many other tropical Miridae, Helopeltis spp. exhibit a more or less continuous cycle of generations throughout the year (Stonedahl, 1991). Eggs are embedded in plant tissue singly or in small groups, often on new shoots. Hatching takes place after 6–11 days and there are five nymphal instars taking from 9 to 54 days to complete, depending on species and climatic conditions. Adults may live for up to 30 days. In forest crops, nymphs and adults feed on the leaves and stems of new shoots. Damage first appears as a necrotic area or lesion around the point of entry of the stylets into the plant tissue and progresses to wilt and dieback of the shoot. A single late-instar nymph of *H*. theivora can make as many as 80 feeding lesions during a 24-h period (Das, 1984, cited in Stonedahl, 1991). In heavily infested young eucalypt plantations in Sumatra, feeding by H. bradyi and H. fasciaticollis resulted in 'bushing' and stunting of the trees (Plate 30). Attack of new growth in the following year left trees with a 'pompom' appearance (Wylie et al., 1998). Rahardjo (1992) reported that the loss due to attack by *Helopeltis* spp. on eucalypt plantations in north Sumatra was 11 m³/ha. On A. mangium in central Sumatra, feeding by H. theivora caused distortion of shoots and retardation of growth (Wylie et al., 1998). In south India, widespread and severe shoot dieback of neem trees, A. indica, due to feeding by H. antonii has become an annual event (Pillai and Gopi, 1990b) and is a limiting factor for the cultivation of neem in some parts (Annamalai et al., 1996). Leaf loss of up to 95% has been recorded, as well as heavy seedling mortalities in forest nurseries. In the Congo, the adaptation of the native *H. schoutendeni* to planted *Eucalyptus* spp. has been a relatively recent development. In 1994, out of 90 host plants inventoried for Helopeltis, no Eucalyptus species was mentioned (Diabangouya and Gillon, 2001). Since then, severe attacks have been reported for eucalypts, particularly for clones of E. urophylla.

Population levels of the various Helopeltis spp. in different countries fluctuate throughout the year, but in some cases a build-up in numbers is synchronized with the emergence of new foliage following the cessation of the monsoon rains (Stonedahl, 1991). There are suggestions that the insects do not do well under conditions of heavy rain, high winds or low relative humidity. In West Bengal, Ghosh (1993) found that incidence of mosquito bug was higher where cashew and E. tereticornis had been intercropped than where cashew was grown alone and inferred that the eucalypts created an environment favourable for rapid multiplication of the pest.

A wide range of natural enemies of Helopeltis spp. has been recorded, including scelionid and mymarid wasp parasitoids of eggs, braconid wasp parasitoids of nymphs and predatory reduviid bugs and ants. In most instances, however, these natural enemies cannot maintain populations of the pests below economic thresholds (Stonedahl, 1991). Several studies in horticultural crop systems have demonstrated



the potential for the tree ant, *O. smaragdina*, to reduce damage by *Helopeltis* spp. significantly, but its painful bite makes it unacceptable to plantation workers (Way and Khoo, 1991; Stonedahl *et al.*, 1995).

Nipaecoccus viridis (Newstead) (Hemiptera: Pseudococcidae)

The mealybug *Nipaecoccus viridis*, often referred to erroneously in the literature as *N. vastator*, is an important tropical and subtropical insect pest of many food, forage, fibre and ornamental crops. It has been recorded in 54 countries from Africa and the Middle East, throughout Asia to Australia and the Pacific, and from 96 species of plants (Sharaf and Meyerdirk, 1987; CABI/ EPPO, 2005). Its tree hosts include *A. arabica, Albizia lebbek, F. moluccana, Dalbergia sisso* and *Casuarina equisetifolia*.

This mealybug has been reported reproducing both sexually and parthenogenetically. In the sexual type of reproduction, the adult female lays an average of 667 eggs in an ovisac secreted a few days prior to oviposition (Sharaf and Meyerdirk, 1987). Eggs are laid in batches, gradually causing an increase in the size of the ovisac until it attains a hemispherical shape, from which the common name 'spherical mealybug' is derived. The female dies soon after oviposition, which lasts from 21 to 37 days, and by this time her empty body becomes raised to a vertical position, being anchored to the plant by means of stylets. Eggs hatch in about 10 days. First instar nymphs emerge from the ovisac and search for a suitable spot to begin feeding, preferably near the mother. Males have five instars, while the females have four, development being completed in 19-20 days. The mealybug reproduces continuously throughout the year and there are multiple, overlapping generations.

N. viridis may feed on the host's branches, twigs, shoots, leaves, flower buds, fruit and roots, causing curling and stunting of terminal growth, abortion of flowers, yellowing of leaves and dropping of fruit. In severe infestations, wilting and dieback occur (Sharaf and Meyerdirk, 1987). As well, the insects secrete large amounts of honeydew on which sooty moulds grow, interfering with photosynthesis.

The spherical mealybug is subject to heavy natural mortality induced by unfavourable weather conditions and natural enemies. High humidities have an adverse effect on the hatching of eggs and high temperatures may kill all stages. The insect may feed on different parts of the same host plant in different seasons, partly in response to changing climatic conditions. For example, populations are usually low in winter, but in spring they develop rapidly on the growing buds and on the underside of new leaves. In summer, most of the mealybugs on the exposed parts of the tree perish, and only those in the lower and protected parts remain. In autumn, the surviving insects resume their activities and invade new growth. Over 77 different natural enemies of N. viridis have been recorded, comprising 54 hymenopterous parasites, 14 coleopteran predators, seven dipteran predators and two neuropteran predators. Only 13 of these species are considered highly effective against the pest, and several have been used in biocontrol programmes. For example, in Hawaii, the encyrtid wasp Anagyrus dactylopii, which was introduced from Hong Kong, has maintained the pest at very low levels. In Guam, natural enemies are also very effective, although Nechols and Seibert (1985) found that the presence of ants decreased the performance of these agents against N. viridis.

Glycaspis brimblecombei Moore (Hemiptera: Psyllidae)

The red gum lerp psyllid, *Glycaspis brimblecombei*, is an important pest in several parts of the world, where it feeds on *Eucalyptus* species, especially red gums *E. camaldulensis* and *E. tereticornis*. Sap sucking by adults and nymphs results in early leaf drop, loss of tree vigour and premature death of some highly susceptible species. *G. brimblecombei* is native to Australia and was first detected outside this country in 1998 in California, USA (Brennan *et al.*, 1999). It was found in Baja California, Mexico, in 2000, where it spread rapidly to 21 other states. It was detected subsequently

in Florida, Hawaii and Mauritius in 2001, Chile in 2002, Brazil in 2003, Argentina in 2005, Ecuador in 2006, Europe (Spain and Portugal) and Venezuela in 2007 and Peru in 2008 (Halbert *et al.*, 2003; Sookar *et al.*, 2003; Diodato and Venturini, 2007; Santana and Burckhardt, 2007; Burckhardt *et al.*, 2008; Rosales *et al.*, 2008; Valente and Hodkinson, 2009; Huerta *et al.*, 2010).

Female psyllids lay their eggs singly or in scattered groups on succulent leaves and young shoots, and the nymphs and adults feed by sucking plant phloem sap through their straw-like mouthparts. Red gum lerp psyllid nymphs form a cover or 'lerp' which is a small, white, hemispherical cap composed of solidified honeydew and wax (Plate 31). Lerps on leaves can be up to 3 mm in diameter and 2 mm tall and resemble an armoured scale. Nymphs enlarge their lerp as they grow, or they move and form a new covering. The vellow or brownish nymphs resemble a wingless aphid and spend most of their time covered beneath a lerp. Adults live openly on foliage and do not live under lerp covers (Plate 32). All life stages can occur on both new and mature foliage. The life cycle ranges from several weeks to several months, depending on temperature; in Australia, there are two to four generations each year.

High populations of psyllids secrete copious amounts of honeydew on which grows a black sooty mould, affecting leaf photosynthesis and fouling surfaces beneath affected trees. Extensive defoliation weakens trees and can increase tree susceptibility to damage from other insects and diseases, leading to dieback and tree mortality. Halbert et al. (2003) list 22 hosts for G. brimblecombei. In southern California, thousands of mature E. camaldulensis were killed within 2-3 years by uncontrolled populations of red gum lerp psyllid. The removal costs for these dead trees are estimated at millions of dollars (Hoddle, 2010). In Mauritius, Eucalyptus is the main melliferous plant and, if severely damaged, may result in a setback to honey production (Sookar *et al.*, 2003).

Likely pathways for dissemination are plants for planting or cut foliage of *Eucalyptus* from countries where *G. brimblecombei* occurs. Long-range dispersal by air transport may be involved, as evidenced in Chile where the red gum lerp psyllid was first detected on *E. camaldulensis* in 2001 in the neighbourhood of the International Airport of Santiago (Huerta *et al.*, 2010).

Classical biological control of *G. brimblecombei* by the Australian encyrtid wasp *Psyllaephagus bliteus* has been implemented in several countries (Daane *et al.*, 2005).

Heteropsylla cubana Crawford (Hemiptera: Psyllidae)

While several psylloid species have spread from their natural range to other parts of the world, few have done so as rapidly or as spectacularly as *Heteropsylla cubana* (Geiger and Gutierrez, 2000; FAO, 2007) (Plate 33). This insect is a serious pest of the widely planted, multi-purpose tree *Leucaena leucocephala*, used as a source of fodder, fuelwood, shade for agricultural crops, reforestation and timber in many countries.

The leucaena psyllid is indigenous to tropical America, where its original range extended from Cuba and Mexico to Argentina (Showler, 1995). It was reported from Florida in late 1983 and the first populations established outside of the Neotropics were found on Hawaii in April 1984. The chronology of its spread is documented by several authors (e.g. Mitchell and Waterhouse, 1986; Muddiman *et al.*, 1992; Napompeth, 1994; Nair, 2007) and is summarized as follows:

•	Late 1983	Florida
•	April 1984	Hawaii
•	February 1985	Western Samoa and
		Cebu, Philippines
•	March 1985	Mariana Islands
•	June 1985	Cook Islands, Fiji
		and Niue
•	July 1985	Tonga, Vanuatu and
		Caroline Islands
•	October 1985	New Caledonia,
		throughout the
		Philippines and
		American Samoa
•	December 1985	Solomon Islands
		and Taiwan
•	March 1986	Java, Indonesia and
		Papua New Guinea

•	April 1986	Australia
•	May 1986	Christmas Island
•	June 1986	Sumatra, Bali,
		Flores, Sulawesi and
		eastern islands
		of Indonesia
•	September 1986	Thailand
•	1986	Malaysia, China,
		Singapore, Japan,
		Myanmar, Vietnam,
		Cambodia, Laos
•	1987	Sri Lanka,
		Bangladesh
•	1988	Andaman and
		Nicobar Islands,
		India
•	1989	Nepal
•	1991	Mauritius and
		Reunion
•	1992	Tanzania, Kenya,
		Uganda, Burundi,
		Sierra Leone
•	1993	Ethiopia,
		Mozambique
•	1994	Sudan, Zimbabwe,
		Zambia, Malawi

The mechanisms by which H. cubana dispersed so quickly over such great distances were uncertain. Many psyllids form part of the aerial plankton, and this accounts for some of the range extension (Muddiman et al., 1992). However, it has also been suggested that the spread was facilitated by transportation in or on aircraft. There are several reported instances of introduced psyllid pests being first detected on plants in the vicinity of airports. H. cubana lay eggs on young, unopened leucaena leaves, the eggs being attached to the leaf surface by a stalk. After 2–3 days, nymphs hatch and begin feeding. There are five nymphal instars lasting approximately 9 days. Females begin laying eggs within a few days of becoming adults, and a female may lay about 400 eggs in her lifetime. The total life cycle is about 14 days. Both nymphs and adults feed on foliage, causing leaflets to turn yellow, curl and wilt. Massive populations can cause shoot necrosis, defoliation and death of the tree (Showler, 1995). The deposition of honeydew encourages the growth of sooty moulds, which can interfere

with the development of adjacent leucaena leaflets.

Leucaena psyllid damage and population trends vary from location to location. Populations generally build up in the wetter months when the trees are growing vigorously, but the effects of their feeding are most severe at the beginning of the dry season when leaf growth slows and psyllid numbers are already high (NFTA, 1990). Populations may fall to very low levels during extended hot, dry periods. In Australia, Bray and Woodroffe (1988) reported a rapid build-up of adults, from almost none to large numbers within 3-4 days after rain. The insects presumably were attracted to new growth on the plants, which was stimulated by the rain. Psyllid damage is often severe when juvenile foliage development is rapid, as on hedges managed for green manure or fodder (NFTA, 1990).

The economic and social impact of H. cubana worldwide has been considerable. L. leucocephala was widely regarded and promoted as a 'wonder tree' and many countries had extensive plantings of this species. For example, in Indonesia, 1.2 Mha of leucaena were planted in Java as part of the productive taungya agroforestry system for establishing teak plantations (Showler, 1995). In Bali, it shades 12,000 ha of vanilla. and on Irian Jaya, oil palm and cocoa. In the Philippines, Thailand, Australia and Indonesia, the first year of infestation caused an estimated US\$525m in damages, with US\$316m in Indonesia alone (Geiger et al., 1995). Such damages included not only the direct loss of leucaena as a cash crop for fuelwood, fodder and timber but also decline in crop yields and death of crops where leucaena was used as shade, decline in small farm livestock production and loss of exports of livestock and agricultural produce. Small farmers experienced considerable reduction of income as a result of the psyllid damage; for example, in the Philippines the net monthly income generated from leucaena plantings declined from 1046 pesos in 1984 to 489 pesos in 1987 (Showler, 1995). Another consequence of the psyllid problem in some developing countries has been a loss of confidence in external recommendations, which in turn

has affected progress towards larger goals such as reforestation (Geiger *et al.*, 1995).

Classical biological control has been employed against *H. cubana*, the two main agents being the coccinellid predator Curinus *coeruleus* and the encyrtid wasp parasitoid Psyllaephagus yaseeni. The predator has been introduced into several countries and has had partial success in Hawaii and Indonesia. but has failed to establish in many seasonal dry areas and is a poor disperser (Geiger and Gutierrez, 2000). The parasitoid has been released in Hawaii, Indonesia and Thailand. It established and dispersed quite readily, having reached Malaysia and the Philippines without human intervention. Geiger et al. (1995) report a long-term trend in damage caused by *H. cubana*, this being generally heavy in the first 2 years of infestation, then gradually weakening in duration and severity. This has been attributed to biological control efforts.

Thaumastocoris peregrinus Carpintero and Dellape (Hemiptera: Thaumastocoridae)

Thaumastocoris peregrinus, commonly referred to as the winter bronzing bug or bronze bug, is an emerging pest of *Eucalyptus* in native and non-native regions of the southern hemisphere (Nadel et al., 2009). This sap-sucking insect feeds on eucalypt leaves, causing death of the leaves and leaf drop, resulting in loss of growth increment, dieback and sometimes tree death. In its native Australia, it was virtually unknown until 2001, when severe outbreaks occurred in Sydney's urban forest (Noack and Rose, 2007). It was reported from South Africa in 2003 and in Argentina in 2005. In the initial reports of these outbreaks, T. peregrinus was identified incorrectly as T. australicus (Carpintero and Dellape, 2006). Since 2003, populations of the pest have grown explosively in South Africa and it has attained an almost ubiquitous distribution over several regions on 26 Eucalyptus species (Nadel et al., 2009). T. peregrinus reached Zimbabwe in 2007 and Malawi in 2008 and it was recorded as established in Uruguay and Brazil in 2008 (Carpintero and Dellape, 2006; Martinez and Bianchi, 2010; Wilcken et al., 2010).

Thaumastocoris are gregarious insects, with adults and nymphs occurring on the same leaf. Adults live for an average of 16 days and each female will produce about 60 eggs (Noack and Rose, 2007). The eggs are laid in black capsules on the leaves, often in a cluster that can be seen as a large black mark on the leaf (Button, 2007). Eggs hatch in 4-8 days and the total nymphal time is 17-25 days. Typical symptoms of infestation include initial reddening of the canopy leaves, a condition sometimes referred to as 'winter bronzing', although this can occur throughout the year (Plate 34). Subsequently, the foliage changes to a reddish-vellow or vellow-brown colour, and loss of leaves associated with heavy infestations leads to severe canopy thinning and sometimes branch dieback or tree mortality (Nadel et al., 2009).

T. peregrinus has a wide host range, infesting at least 30 *Eucalyptus* species and hybrids. In South Africa, all commercially grown *Eucalyptus* are susceptible to attack, and the pest has been reported from seven eucalypt species in South America (Nadel *et al.*, 2009). In Australia, the insect has become a pest of tropical and subtropical plantations in Queensland and New South Wales, affecting species of *Corymbia* as well as *Eucalyptus*.

Nadal *et al.* (2009) used DNA bar-coding to investigate the source and patterns of *T. peregrinus* invasions in South Africa and South America and concluded that Sydney was the most likely origin of both these introductions. Extreme long-range dispersal by air travel is thought to be the main mechanism for spread. This hypothesis is supported by information from Brazil, where, in the state of Sao Paulo, the bronze bug was first found in *Eucalyptus* trees adjacent to two international airports in the metropolitan region of Sao Paulo city (Wilcken *et al.*, 2010). The insect may also hitchhike on the clothes of travellers or be dispersed by wind.

Tingis beesoni Drake (Hemiptera: Tingidae)

The lace bug *T. beesoni*, recorded only from India, Thailand and Myanmar, is a serious pest of *G. arborea* in those countries, causing defoliation and dieback in young plantations (Mathew, 1986; Kamnerdratana, 1987; Harsh et al., 1992; Nair, 2007) (Fig. 5.9).

The life history of the insect is described by Mathur (1979). Eggs are laid over a period of 4-5 days in small batches; they are inserted into the tissue of the tender shoot in a vertical row. They hatch in 2-6 days and the nymphs congregate on the lower surfaces of the foliage and suck sap at the base of the lamina or in the axils of leaves. A feeding cluster may comprise as many as 60 nymphs. There are five nymphal instars taking from 9 to 30 days to complete, depending on the season. Adults are quite active in summer and move about on the under-surface of leaves and new shoots for feeding. They disperse to other plants, but their flight is limited. There are seven generations a year, with considerable overlap. At the onset of cool weather, the adults of the last generation lay



Fig. 5.9. Adult of *Tingis beesoni* (from Mathur, 1979).

their eggs under bark, where they hibernate, hatching the following spring.

Feeding by nymphs and adults causes leaves to become blotched-brown near the base. They wither and fall and the shoots become dry. Eventually, the shoots die back, retarding tree growth. During one outbreak in a 10 ha plantation of 1-year-old trees in India, 67% of the plants were infested, 21% suffering total defoliation and dieback of the terminal shoot (Nair and Mathew, 1988). A study by Harsh et al. (1992) of top dieback and mortality in a G. arborea provenance trial in Madhya Pradesh, India, showed that the problem was caused by T. beesoni in combination with the fungus Hendersonula toruloidea. Meshram and Tiwari (2003) recorded an 80% incidence of top dving in one plantation of G. arborea in Madhya Pradesh and noted that trees aged 2-3 years were more susceptible to this insect. Feeding by the lace bugs in the wet season provided conditions favouring the infection of damaged plants by the canker-causing *H. toruloidea*. The fungus was capable of invading and killing plants within a year.

5.4 Bark and Wood Feeding

Bark- and wood-feeding forest insects are contained in four main orders: Coleoptera (bark beetles, ambrosia beetles, longicorn beetles, bostrychid beetles, scarab beetles, weevils), Hymenoptera (wood wasps), Isoptera (termites) and Lepidoptera (wood moths). Usually, the larval stages cause most of the damage to the wood and bark. Only in the Coleoptera do the adults of some species (e.g. pinhole borers) tunnel extensively in the wood or feed externally on bark (e.g. some scarab beetles).

The effects of bark- and wood-boring insects on their hosts vary depending on the condition of the tree when attacked, the particular tissue attacked and the activity of associated agencies such as symbiotic fungi, bacteria and predators (Elliott *et al.*, 1998). An obvious effect is structural weakness in stems and branches resulting from extensive tunnelling. This may be exacerbated by the activities of predators excavating for larvae in the tree, as is the case with yellowtailed black cockatoos (Calyptorhynchus funereus) predating larvae of the giant wood moth, Endoxyla cinerea, in eucalypts in Australia (Wylie and Peters, 1993). Tunnelling by larvae of longicorn and jewel beetles in stems and branches may interrupt the tree's conductive processes and sometimes results in ring-barking and death of affected parts. Some borers, such as ambrosia beetles, cause damage that is not immediately apparent until timber is cut from the tree. Termites such as species of Odontotermes and Macrotermes are common and important agents of tree mortality in young plantations throughout the tropics. However, in Australia, termites cause most damage by feeding in the heartwood of trees, causing significant losses in wood volume and downgrading potential sawlog into lower value pulpwood. Several important wood- and bark-feeding insects have very close associations with other organisms such as fungi, with these organisms forming an essential part of the life history of the pest. An example is the sirex wasp and its symbiotic fungus Amylostereum areolatum, which not only provides food for the larvae but also contributes to death of the host tree.

The physiological condition of host trees has a major influence on the type of insect borers which attack them and the ability to withstand this attack. For example, drought-stressed trees can be very susceptible to sirex and *Ips* bark beetles, particularly if other factors such as overstocking aggravate these effects. Many borers, such as ambrosia beetles, are attracted to damaged trees.

5.4.1 External chewing

Indarbela quadrinotata Walker (Lepidoptera: Indarbelidae)

The bark-eating caterpillar, *I. quadrinotata*, which occurs throughout Asia, is a polyphagous pest infesting many fruit trees, street trees and important forest trees such

as teak, *T. grandis*, mahogany, *Swietenia* spp., *G. arborea* and species of *Acacia*, *Casuarina*, *Syzygium* and *Terminalia* (Beeson, 1941; Garg and Tomar, 2008; Patel and Patel, 2008). Damage has been reported from India, Pakistan, Bangladesh, Myanmar and Malaysia.

The adult female may lay up to 2000 eggs, which she places in groups of about 15-25 on the bark of the stem or branches of the host. The eggs hatch in 9–11 days. Each larva bores a short tunnel downwards into the wood and shelters there during the day, coming out at night to feed on the outer surface of the bark. Broad irregular patches are excavated in the bark and these areas are roofed in with silk mixed with excrement and fragments of bark. A single larva can damage a considerable area of bark (Plate 35), and in a heavy infestation most of the outer bark of the stem may be destroyed (Beeson, 1941; Browne, 1968). The larval period lasts about 10 months in India and Bangladesh, pupation takes place in the shelter tunnel and moths emerge after 21-31 days. In Myanmar, there are two generations a year.

Feeding by this caterpillar can result in loss of growth increment and, with heavy infestations, girdling and mortality (Sasidharan et al., 2010). The shelter tunnels bored into the sapwood allow the entry of fungi and other organisms and degrade the wood. Zia-ud-Din (1954) also suggests that heavy damage may prevent flowering of some trees. In India, I. quadrinotata has been reported as a moderately serious pest of A. senegal and A. tortilis in the Thar desert (Vir and Parihar, 1993). These tree species are the major component of plantation forestry programmes related to wasteland development, sand dune stabilization, fuelwood and fodder in this arid region. In Tamil Nadu, India, C. equisetifolia is a major species used for coastal afforestation and agroforestry and plays a crucial role in the rural economy. Of 40 species of insect associated with *C. equisetifolia* in that state, I. quadrinotata is the most economically important pest (Sasidharan and Varma, 2008). Meshram et al. (2001) rate I. quadrinotata as a major pest of *G. arborea* in India. Baksha (1991) reported a 70% incidence of the pest in a 4-year-old plantation of F. moluccana

near Chittagong, Bangladesh. *Populus* spp., widely used in farm forestry programmes in Pakistan and India, are also commonly attacked by *I. quadrinotata* (Veer and Chandra, 1984; Gul and Chaudhry, 1992).

Natural enemies of the bark-eating caterpillar include braconid and eulophid wasp parasitoids, ant predators and the entomopathogenic fungus *Beauveria bassiana* (Gul and Chaudhry, 1992).

5.4.2 Bark boring

Hylastes angustatus (Herbst) (Coleoptera: Curculionidae: Scolytinae)

The pine bark beetle, *Hylastes angustatus*, of European and southern Russian origin, is thought to have been introduced accidentally into South Africa on fresh pine logs (Bevan and Jones, 1971; Govender and Wingfield, 2005). It was found originally in the southern Cape Province, but now occurs wherever *Pinus* spp. are grown commercially in South Africa, as well as in Swaziland and Zambia. Although it is not considered a pest in the winter rainfall areas in the south, it is a serious, though sporadic, pest in summer rainfall regions, causing damage to seedlings of the economically important *P. patula* (Erasmus and Chown, 1994).

As described by Bevan and Jones (1971), there are two distinct phases in the life cycle of *H. angustatus*, a breeding phase and a feeding phase. The former is that period from sexually mature adult, through egg and larva, to young virgin unemerged imago, when the insect is confined to the chosen breeding site. In this phase, the insect is 'secondary', attacking only damaged, dying or dead material such as logs and stumps, and is generally of no direct economic importance. The feeding phase is the period between the emergence of the virgin adult from its breeding site and its eventual arrival at another breeding site when sexually mature. During this time, the beetle feeds on young green bark, this being necessary for proper maturation of the gonads. In this phase, the insect is 'primary', attacking healthy living plants, and its damage is significant.

After feeding, the female enters the bark, excavates a nuptial chamber and is

then joined by the male. Following copulation, she constructs a straight gallery about 7 cm long and lays eggs at intervals along both sides of it. Larvae hatch and bore meandering galleries outwards from the mother gallery, and eventually pupate at the end of their tunnel. The duration of the life cycle from egg to egg is about 48 days (Webb, 1974), and there are four to five generations a year in the Transvaal area (Tribe, 1990).

Maturation feeding by *H. angustatus* under bark on roots and root collars of pine seedlings can result in girdling and death of seedlings, which are most vulnerable up to 1 year after planting. Mortalities of up to 52% have been recorded in young P. patula plantations in Transvaal (Toit, 1975). The generally accepted loss rate is 15%, above which replacement is necessary. Because *H. angustatus* feeds beneath the bark and mainly below ground, the beetles have already departed by the time the damage is first noticed (Tribe, 1990). The presence of harvesting residues (slash) has been found to impact negatively on the early survival of tree seedlings because this favours build-up of H. angustatus, but the practice of slash burning promotes losses due to the fungus *Rhizina undulata*, which requires a heat stimulus for the onset of pathogenicity (Wingfield and Swart, 1994). The discontinuation of slash burning has necessitated the implementation of chemical control for *H. angustatus* in summer rainfall areas of South Africa (Allan et al., 2000).

Various natural enemies of *Hylastes* have been recorded, but these have been considered of little use in commercial plantations.

Ips spp. (Coleoptera: Curculionidae Scolytinae)

The genus *Ips* contains more than 60 species (Wood, 1982) and is one of the best-known groups of bark beetles, with a worldwide distribution. Several species occur in the tropics and subtropics, and some of these are important pests of *Pinus* spp. They can attack living trees, freshly felled logs and unbarked pine slash (Hanula *et al.*, 2002).

The attack is generally initiated by the adult male, which tunnels into the inner

bark/cambial region where the nuptial chamber is carved out. The male produces a pheromone which attracts the females and other males to the log or tree. A male may be joined by up to seven females and mating takes place in the nuptial chamber. Each female bores a tunnel away from this chamber and deposits eggs in niches along the sides. The frass which is produced is pushed back along the tunnel by the female and cleared out through the entrance hole by the male. On hatching, the larvae tunnel in the inner bark. At high densities, the larval tunnels overlap and the phloem is converted into a layer of frass. The larval period may vary from a few weeks to a few months, depending on temperature, and at the end of this period, larvae form a cell at the end of their gallery and pupate. The new adults feed on the inner bark before emerging through exit holes similar to that by which their parents entered.

Ips species carry out 'feeding' and 'breeding' attacks when colonizing the bark of green to semi-green dead pine material or that of apparently healthy trees. In feeding attacks, the inner bark and outer sapwood surface is etched by large numbers of male and female adults in the period prior to reproduction and, as a consequence, the bark peels off. Breeding attacks are made by virgin male and female beetles and/or by fertilized females when entering the inner bark and constructing characteristic gallery systems for breeding (Neumann, 1987).

Different species of *Ips* may show preference for infesting different parts of the host plant. For example, in Jamaica, *I. calligraphus* showed preference for the older, thick-barked regions of the trunk and the larger branches, while *I. grandicollis* preferred the thinnerbarked regions of the trunk and smaller branches (Garraway, 1986). Bark thickness also influences certain parasitoids of *Ips*, those species that oviposit through the bark being limited to areas of bark that are no thicker than their ovipositors are long (Riley and Goyer, 1988).

Commonly, *Ips* are secondary pests, colonizing recently cut logs, pine slash and physiologically unhealthy trees. However, sometimes they can assume a primary role,

causing tree mortality, particularly when populations are very high. The propensity of *Ips* to attack living trees varies with species; *I. calligraphus* is regarded as one of the most aggressive species (Yates, 1972). In Australia, I. grandicollis (Plates 36 and 37) has sometimes caused extensive, although localized, tree death, particularly when trees were stressed by drought or damaged by fire and lightning (Neumann, 1987; Elliott et al., 1998). Following fires in south-east Oueensland in 1994, which affected over 8000 ha of P. elliottii, P. taeda and P. caribaea plantations, *I. grandicollis* attacked fire-damaged trees after 6 weeks and was a significant pest in most areas after 10 weeks (Wylie et al., 1999) (Fig. 5.10). Sap staining, caused by fungi (principally Ophiostoma ips) carried by the beetle, became significant in attacked stems at the completion of the insect's life cycle (about 4 weeks in summer) (Plate 71). This attack necessitated rapid salvage of the timber and its storage under water spray (Plate 109). The losses caused by I. grandicollis and sap stain following these fires were estimated at several million Australian dollars, most of this being in privately owned plantations where salvage was delayed for several months.

Garraway (1986) cited two instances of large-scale attack in pine plantations in Jamaica by I. calligraphus and I. grandicollis; the first was on fire-ravaged *P. caribaea* in 1979 and the other on a mixed plantation of Pinus spp. which had been exposed to flooding and landslides, followed by several months of intense drought in 1980. In the latter case, 22% of the pines were lost over a 6-month period. In the Philippines, Lapis (1985a) reported occasional large-scale mortality of *P. kesiya* in northern Luzon due to I. calligraphus, and this species was the principal mortality agent in the deaths of thousands of drought-affected *P. occidentalis* in the Dominican Republic in 1986–1987 (Haack et al., 1990). In Honduras, primary attack of P. oocarpa by I. cribricollis has been reported and it has been found frequently attacking apparently healthy pines in association with other Ips species (Lanier, 1987). In southern USA, three species of *Ips* engraver beetles (I. avulsus, I. grandicollis and I. calligraphus)



Fig. 5.10. Progress of *Ips grandicollis* attack with time in five plots in fire-damaged pine plantations in Queensland, Australia (from Wylie *et al.*, 1999).

are responsible for documented annual losses of approximately US\$6.6m to pine forests (Riley and Goyer, 1988).

Predators and parasitoids are important factors in the regulation of *Ips* spp. bark beetles. In southern USA, Riley and Goyer (1986) found 27 species of insect predators and 10 species of parasitoids associated with *Ips* broods in *P. taeda* and *P. elliottii*, which decreased brood survival by 30.8%. Biological control has been used to reduce populations of *I. grandicollis* in Australia, the torymid wasp parasitoid *Roptrocerus xylophagorum* now being widely established and the braconid wasp *Dendrosoter sulcatus* also being established in the subtropics (Elliott *et al.*, 1998).

5.4.3 Cambium and surface sapwood boring

Agrilus spp. (Coleoptera: Buprestidae)

Agrilus is a cosmopolitan genus containing well over 1000 species. Most of these are of little or no economic importance, but a few species in Africa, Asia and the Pacific are serious pests in forest plantations, causing growth loss, stunting and tree mortality.

The biologies of the main pest species in Papua New Guinea and the Philippines are very similar. Generally, the eggs are laid singly in cracks or crevices in the bark, or under bark flakes, on the lower stem of the host tree. The eggs hatch in about 2 weeks and the larvae burrow directly into the bark down to the wood surface, where they feed on the tissues of inner bark and outer wood (Braza, 1988a). In the course of their feeding and development, the larvae construct frassfilled zigzag tunnels, sometimes more than 2 m long and extending down to the roots. When mature, larvae tunnel into the wood, constructing a chamber, where they pupate. Adults emerge a few weeks later and tunnel to the surface, cutting a 'D'-shaped hole in the bark. The length of the life cycle varies with species of Agrilus and the type and condition of the host. In Papua New Guinea, A. opulentus completes its life cycle in small-diameter felled trees in 6–7 weeks. In trees with a larger diameter trunk, the life history may take up to three times longer, while in standing, living trees the life history takes at least 9 months to 1 year (Roberts, 1987). Young adults must feed before they can mate and before the females can lay eggs. They usually feed on the new foliage of their preferred host trees.

On thin-barked trees, the zigzag tunnelling of the larvae is clearly visible in the form of raised welts on the bark, giving rise to the names 'zigzag' or 'varicose' borers for these insects (Plate 38). These welts are the result of callus tissue overgrowing old tunnels and are usually not visible where larvae are active.

In Papua New Guinea, the two trees most widely grown in forest plantations in the wet lowlands, E. deglupta and Terminalia brassii, are attacked by A. opulentus and A. viridissimus, respectively. Attack is often heaviest on trees which are stressed; for example, E. deglupta growing on badly drained soils and T. brassii on soils which dry out rapidly (Roberts, 1987). Infested trees show loss of annual increment, and small and suppressed trees are girdled and killed. Estimated growth losses in E. deglupta plantations at Madang due to A. opulentus totalled US\$2.5m over the 10-year rotation (Mercer, 1990). In the Philippines, E. deglupta plantations (Papua New Guinea provenance) in Mindanao have been severely attacked by A. sexsignatus, with up to 63% mortality. Numerous studies have shown that the Papua New Guinea provenance of *E. deglupta* is most susceptible to attack by Agrilus spp., while the native Philippines E. deglupta is more resistant (Braza, 1987, 1988a).

In the Sudan, after a long drought during 1979–1984, gum production by *A. senegal* and *A. seyal* decreased and this was attributed in part to attack by jewel beetles, including species of *Agrilus* (Jamal, 1994). In Pakistan, *A. dalbergiae* has caused yellowing and death of unhealthy *D. sissoo* trees in amenity plantings (Sheikh and Aleem, 1983), and in Indonesia, *A. kalshoveni* caused large-scale mortality of scattered trees of all sizes of *Actinophora fragrans* (Kalshoven, 1953; Nair, 2007).

Four hymenopterous parasitoids have been recorded for *A. sexsignatus* in the Philippines, with parasitism rates for eggs and larvae of up to 57% (Braza, 1989; Noyes, 1990). In Papua New Guinea, Mercer (1990) suggests the use of the ant *A. longipes* as a biocontrol agent for *A. opulentus* in *E. deglupta* plantations.

Phoracantha semipunctata (Fabricius) (Coleoptera: Cerambycidae)

This Australian insect (Plate 39) is now established in many regions of the world

(Europe, Africa, the Middle East, North and South America and New Zealand), having been present in South Africa and Argentina since the early 1900s (CABI/EPPO, 2007b). In some places, it is a serious pest of planted eucalypts, attacking and killing young trees (Loyttyniemi, 1991; Hanks *et al.*, 1995a, 2001), but in Australia it is regarded as only a minor pest attacking damaged, severely stressed or newly felled trees.

As described by Elliott et al. (1998) for Phoracantha semipunctata in Australia, females lay batches of 10-100 eggs in crevices in the bark of dead, dying or stressed trees, in freshly cut logs or in branches down to a diameter of about 150 mm. Dry material is not attacked. The eggs hatch in 10-14 days and larvae tunnel in the inner bark/cambial/outer sapwood region for 4-6 months, making wide galleries, sometimes 1-2 m long, that are tightly packed with frass. When fully fed, the larvae bore deeply into the heartwood and pupate. The pupal period lasts about 10 days. Adults may be found during all months of the year, and generations overlap considerably. Adults can live for more than 90 days (Paine et al., 1995). The length of the life cycle throughout the range of the insect varies with climate and season, and can take from 2 months in the hot tropics up to 1 year in cooler regions.

P. semipunctata occurs widely in Africa from the south through Angola, Malawi, Mozambique, Zambia and Zimbabwe to Morocco and the Canary Islands in the north. In Zambia, where it was first recorded in 1968, severe outbreaks of the insect in eucalypt plantations (mainly *E. grandis*) started at the beginning of the 1970s and tree mortality has reached up to 40% of stocking during a rotation period (Loyttyniemi, 1991). At the beginning of the 1980s, up to 67% of the total area of eucalypt plantations in the country was regarded as severely infested (Selander and Bubula, 1983).

Numerous studies have shown that drought is one of the main factors predisposing trees to attack by *P. semipunctata*. This can be exacerbated by factors such as site and silviculture. For example, in Zambia, Ivory (1977) found that tree mortality associated with attack by this longicorn in eucalypt plantations was highest for trees on soils with a high sand content (Fig. 5.11). Delayed thinning, poor sanitation and damage by termites and fire have also been implicated in attack and mortality (Loyttyniemi, 1991). In Chile, P. semipunctata is only considered a hazardous species in the arid and semi-arid regions (Lanfranco and Dungey, 2001). There is considerable variation among eucalypt species in resistance to attack by *P. semipunctata*. In California, Hanks et al. (1995b) found that species that were resistant to attack were those that were most tolerant of drought in Australia. Bark moisture content may play a critical role in resistance, the insect being able to colonize trees where this is reduced (Hanks et al., 1991). Water stress has a major influence on the survival and growth of the larvae, as demonstrated by Caldeira et al. (2002) in Portugal. E. globulus trees subjected to water stress during 2 consecutive years were compared with rainfed and irrigated trees. Larvae of *P. semipunctata* were introduced artificially into the bark of trees of both treatments. Larval mortality was found to be lower and weight gain was higher in water-stressed trees than in rainfed trees, and there was no larval survival in irrigated trees.

Studies of the insect on logs of *E. grandis* in Malawi (Plate 40) showed that most



Fig. 5.11. Relationship between attack by *Phoracantha semipunctata* and sand content of soil in Zambia (from Ivory, 1977).

mortality occurred in the larval stage, and the major mortality factor was intraspecific competition. Severe overcrowding led to a reduction in population density from one generation to the next. Overcrowding also led to a reduction in beetle size and to a shift in the sex ratio in favour of males, which being smaller than the females were more likely to complete their development in crowded conditions (Powell, 1982). This effect could reduce the breeding potential of the next generation greatly. Hanks et al. (2005) showed that optimal development conditions for *P. semipunctata* larvae, in terms of larval performance and adult body size, were available in large, aged host logs having low densities of larvae.

Numerous predators and parasitoids attack P. semipunctata in Australia and several of these have been used in biocontrol programmes in other countries. One of the earliest attempts was the introduction of Megalyra fasciipennis into South Africa in 1910. In 1993, parasitism of the cerambycid by this insect frequently reached 50% (Moore, 1993). Three other Australian parasitoids of *P. semipunctata*, an encyrtid and two braconids, are now established in South Africa where an indigenous pteromalid wasp, Oxysychus genualis, has also been recorded (Prinsloo, 2004). The egg parasitoid Avetianella longoi was released in California in 1993 and Hanks et al. (1996) reported high rates of parasitism (up to 91% of all eggs in some instances). This, coupled with the wasp's strong powers of dispersal and efficient location of host eggs, suggests that it may have an important impact on P. semipunctata in California, but see Chapter 10.

In southern California, *P. recurva* appears to be replacing *P. semipunctata* rapidly in their shared habitat, for reasons that are not yet clear (Bybee *et al.*, 2004a,b), and there is a similar report of this from Argentina (Di-Iorio, 2004).

> *Xystrocera festiva* (Coleoptera: Cerambycidae)

F. moluccana (formerly known as *Paraserianthes falcataria*, *A. falcata*, *A. falcataria* and *A. moluccana*) is a fast-growing leguminous tree, native to Indonesia, Papua New Guinea and the Solomon Islands, which is widely planted in the humid tropics for pulpwood, matchsticks, plywood, lightweight packing materials and community forestry (Nair, 2007). One of the principal pests of this species is the cerambycid borer *Xystrocera festiva*, whose larvae tunnel in the stems of living trees, often causing tree mortality.

Nair (2007) provides a comprehensive pest profile of the insect, drawing on studies by Suharti et al. (1994), Hardi et al. (1996), Matsumoto and Irianto (1998) and Kasno and Husaeni (2002). Adults are nocturnal and live for only 5–10 days. Eggs are deposited in clusters of over 100, in one or two batches, preferably in crevices on the stem or branch stubs, generally 3-4 m above ground. The average number of eggs laid per female is estimated at 170. Newly hatched larvae bore into the inner bark and as the larvae grow, they feed on the outer sapwood, making irregular downward galleries packed with frass. The larvae remain gregarious, which is unusual in cerambycids. Symptoms of infestation are exudation of a brownish liquid through the bark and the expulsion of a powdery frass. The larval development is completed in about 4 months and each larva bores an oval tunnel upward in the sapwood, in which it pupates. The insect has overlapping generations, with all developmental stages present at any one time.

Infestation by *X. festiva* usually begins when the trees are 2–3 years old and the infestation increases with age. Larval tunnelling can reduce growth rate and timber quality, and heavy infestation can result in ring-barking and death of the tree. The insect is a major pest of *F. moluccana* in Indonesia and Malaysia and also occurs in Myanmar. It is a minor pest of several other tree species, including *Acacia* spp.

A related species, *X. globosa*, is also a pest of *F. moluccana* but, unlike *X. festiva*, larvae are not gregarious and tunnel individually (Matsumoto *et al.*, 2000).

An encyrtid egg parasitoid of *X. festiva*, *Anagyrus* sp., has been released in biological control trials in East Java, which has given promising results.

5.4.4 Sapwood and heartwood boring

Aristobia horridula (Hope) (Coleoptera: Cerambycidae)

This insect (Plate 41) was first recorded damaging forest trees (D. paniculata and D. volubilis) in India in the 1930s (Beeson and Bhatia, 1939), but it was not until the last decade or so that it emerged as a serious pest of forest plantations in Thailand, Nepal and India (Hutacharern and Panva, 1996; Dhakal et al., 2005; Nair, 2007). In Thailand, it is regarded as the most important stem borer of Pterocarpus macrocarpus and it also causes serious damage to P. indicus and D. cochinchinensis (Hutacharern and Panya, 1996). Both P. macrocarpus and D. cochinchinensis are high-value timber species. In India and Nepal, it infests D. sissoo, also an important and widely planted tree in South Asia.

Eggs are laid singly in the bark of the host tree, in a crescent-shaped incision made by the adult female, and hatch in 8–10 days. Newly hatched larvae bore extensively in the sapwood and then into the heartwood, where pupation occurs in a chamber plugged by wood slivers (Hutacharern and Panya, 1996). Larval galleries may be up to 70 cm long and are packed with frass (Nair, 2007). In smaller trees, larval tunnelling may extend down to the root (Hutacharern and Panya, 1996). Swelling of the bark, resin exudation and extruded frass are visible symptoms of infestation, and emerging adults cut circular exit holes in the bark. The life cycle is annual. Adult beetles are active during the day and feed on the bark of young branches, sometimes causing girdling and death of small branches (Hutacharern and Panya, 1996). Larval tunnelling in the stems and branches of trees not only degrades the wood but also weakens the trees, making them prone to wind damage, and may cause the death of young trees (Hutacharern, 1995).

The incidence of infestation by *A. horridula* can be high. In Thailand, Hutacharern and Panya (1996) reported infestation levels of 83% of trees in a 16-year-old plantation of *P. macrocarpus*, 33% of trees in an 8-year-old plantation of the same species and 25% in an 8-year-old plantation of D. cochinchinensis. Also in Thailand, they reported that 100% of trees in a 10-year-old roadside planting of *P. indicus* were infested. In India, incidence of *A. horridula* in *D. sissoo* plantations in West Bengal ranged from 10 to 90%, the older age classes being affected most seriously. It was suggested that the pest had migrated from nearby native forests in which D. sissoo was a component into the monoculture plantations (Mishra et al., 1985). Dhakal et al. (2005) reported severe damage by A. horridula in sissoo seedling seed orchards in Nepal 2 years after planting. Of a total of 6720 trees planted in 1996, 67% were dead in 2002 and only 19 trees showed no symptoms of infestation.

Two other species of Aristobia are known to cause damage to forest plantations in Asia. In the Mekong Delta of south-western Vietnam, A. approximator girdled and killed about 4000 ha (half the estate) of E. camaldulensis and E. tereticornis plantations (Wylie and Floyd, 1998). The attack was believed to be stress related and associated with the acid sulfate soils on which the trees were planted (Kawabe and Ito, 2003). In India, A. octofasciculata bores in the small branches and stem of saplings of Santalam album, causing dieback and mortality (Remadevi and Muthukrishnan, 1998). Tunnelling extends into the heartwood, allowing entry of termites and decay fungi. This combination of agents leads to hollowing-out of the sandalwood heartwood, resulting in an overall loss in volume/weight of almost 20% and a financial loss of US\$3000/t (Remadevi and Muthukrishnan, 1998).

Celosterna scabrator Fabricius (Coleoptera: Cerambycidae)

Celosterna scabrator, commonly known as the Babul borer because of its attacks on acacias such as *A. arabica* and *A. nilotica* in India, is also a pest of other tree species in that country, for example, teak, *Casuarina* spp., *Eucalyptus* spp., *Shorea robusta* and *Prosopis* spp. (Nair, 2007). It also infests *Dipterocarpus alatus* in Thailand (Gotoh, 1994).

The eggs are laid in the bark of young trees with a minimum basal girth of 5 cm and a maximum of 23 cm. According to Beeson (1941), above this dimension the bark is too hard for the insertion of the egg and too dry for the larva to hatch. Females may lay about 40 eggs over a period of several weeks, usually one egg to a stem, and these hatch in 2-3 weeks. The larva bores downwards, hollowing out the main root and keeping its tunnel clean by means of a frass ejection hole just above ground level (Browne, 1968). Tunnels may be up to 60 cm long. The larval period lasts about 9 or 10 months and pupation takes place in the host, lasting about 15–17 days. The beetle emerges by cutting a circular hole in the bark, usually below ground level. The beetles may live 80 days and are also destructive, feeding mainly at night on the bark of young living shoots.

Feeding by the larvae causes cessation of growth and sometimes death of the plant above ground. Incidence of attack of up to 80% has been recorded where trees are growing on unsuitable sites. An endemic pest in scrub and open-thorn forests, it has become of major importance in clear-felled areas replanted with eucalypts. Attack of Eucalyptus spp. in plantations in India is common (Ralph, 1985; Sivaramakrishnan, 1986), and Sen-Sarma and Thakur (1983) regard it as a 'key pest' in several states. *C. scabrator* was believed to be responsible for up to 14% mortality of Prosopis cineraria, an important agroforestry tree species, in the arid Thar desert in the north of India (Jain, 1996). Further south, in Karnataka, outbreaks have occurred in 1-year-old plantations of *E. tereticornis* and *A. nilotica*, sometimes with high mortalities (Sivaramakrishnan, 1986; Ralph, 1990). Feeding by the adults can result in girdling and breakage of the main stem and branches (Shivayogeshwara et al., 1988). In Thailand, attack rates in 5- to 8-year-old stands of *D. alatus* ranged from 33 to 59%, resulting in loss of growth, lowering of timber quality and some tree death (Gotoh, 1994). Few natural enemies of this insect have been recorded.

Hoplocerambyx spinicornis Newman (Coleoptera: Cerambycidae)

Known as the sal borer, *Hoplocerambyx* spinicornis is the most notorious forest pest

of India because of its periodic outbreaks, during which millions of sal trees (*S. robusta*) are killed (Nair, 2007). Besides India, its distribution includes Afghanistan, Pakistan, Nepal, Bangladesh, Myanmar, Thailand, Indonesia and the Philippines.

A detailed pest profile of this insect is provided by Nair (2007), who summarizes studies dating back to the early 1900s. The female beetle lays her eggs on cuts or holes in the bark of sal trees, normally choosing trees that are freshly dead or highly weakened by various causes. However, during outbreaks even healthy trees are attacked. Each female will lay 100-300 eggs over a lifespan of about 1 month. The newly hatched larvae feed under the bark initially, then in the sapwood and finally bore into the heartwood. A large sal tree may support the development of about 300 beetles, although more than 1000 eggs may be laid on the tree. Coarse dust is thrown out of holes in the bark of infested trees and accumulates at the base of the tree. When larval development is completed, the larva constructs a chamber in the heartwood with an adult exit hole, and turns into a prepupa, then pupa and adult. The adult beetle remains quiescent until it emerges with the onset of rainfall. The length of the life cycle is 1 year.

Extensive galleries in the sapwood made by several larvae cause partial or complete girdling of the tree, leading to its death (Nair, 2007). Outflow of resin from the infested tree traps many young larvae but mass attacks during epidemics kill even vigorous trees. Both the main trunk and crown branches are infested. Nair (2007) presents a chronology of *H. spinicornis* outbreaks spanning the period 1897–2000. One of the most severe was the 1923 outbreak in Madhya Pradesh, which persisted over a 5-year period killing about 7 m sal trees. Another in the same state in 1994-2000 killed more than 3m trees over an area of 500,000 ha. No clear pattern is evident in the timing of the outbreaks. Trapping programmes carried out by the State Forest Department using sal logs yielded a peak of 32.59 m beetles in 1998 before the population declined. The timber of the heavily infested trees is riddled with tunnels and rendered

useless, causing enormous economic loss. The circumstances under which outbreaks develop are not understood fully, but they often occur in dense over-mature stands where conditions favour rapid build-up of populations of the insect. Any stress factor which compromises the tree's ability to produce the defensive resin flow may trigger an outbreak.

An elaterid beetle, Alaus sordidus, is a predator of H. spinicornis, and during an epidemic, up to 10–15% of vacant sal borer pupal chambers were found to be occupied by A. sordidus.

Platypus spp. (Coleoptera: Curculionidae)

All *Platypus* spp. are ambrosia beetles, so named because they feed on 'ambrosia fungus', which grows on the walls of their tunnels (Alfaro *et al.*, 2007). They do not feed on the wood itself. *Platypus* species construct galleries in 'green' (unseasoned) wood, either in living trees or in logs and freshly sawn timber. These galleries are usually more extensive in the sapwood, but they can extend deep into the heartwood.

The male beetle generally initiates the attack and is joined by the female. After mating, the female takes over boring of the tunnel, while the male merely removes and ejects the bore dust. Fungal spores are carried into the tunnel by the beetles, either trapped in the hairs on their body surface, in special structures (mycangia), or in their gut. The spores germinate and fungal spores grow on the walls of the tunnel, providing food for the adults and larvae, meeting most if not all of their nutrient requirements (Elliott et al., 1998). The ambrosia fungus discolours the tunnel wall and this dark staining may extend along the grain around the gallery or hole, a condition commonly referred to as 'pencil streak'. Tunnels may extend well into the wood and may be branched or unbranched, depending on the species of borer. Fully mature larvae usually make short side tunnels in which they pupate. New adults emerge by means of the parent tunnels. The length of the life cycle varies with species and with climatic conditions, and can range from 4 weeks to 12 months.

Species of *Platypus* are to be found throughout the world's tropics. Mostly, they are pests of logs and freshly sawn timber, but some attack damaged or unhealthy standing trees, and in a few cases, apparently healthy trees. In Sabah, Malaysia, widespread infestation by an unidentified species of *Platypus* occurred in provenance trials of A. crassicarpa aged 1–4 years (Thapa, 1991). Up to 80% of trees were infested, some with almost 300 holes in the lower stem. Despite this, there was no outward symptom of any deleterious effect on the trees. However, associated with the attack, a black stain developed in the sapwood region all along the bole length due to bacterial infection. Testing of the stained wood for suitability in papermaking showed that more bleaching agent than usual was required, but the quality of the paper was in no way affected. Chey (1996) records P. pseudocupulatus from the same host in Sabah and P. solidus attacking E. grandis. Similar attacks have been noted on eucalypts and acacias in several other countries in Southeast Asia (Wylie et al., 1998).

In Fiji, mahogany trees, Swietenia macrophylla, are attacked by P. gerstaeckeri. Although the insects are unable to complete their life development in living trees, beetles being killed by gum exudation produced by the mahogany, the short galleries that they attempt to form are sufficient to reduce the quality of the timber when the trees are cut down (Roberts, 1977). Trees less than 5 years old are generally not attacked. In plantations, attack generally is related to some forest operation such as thinning, pruning, cleaning, or the removal of sample trees. Site is also important, and the incidence of attack is highest where drainage is bad and soils are poor.

P. hintzi, which is widely distributed in Africa south of the Sahara, may attack healthy trees during periods of temporarily decreased vigour, especially during the dry season (Browne, 1968). In Nigeria, such attacks have occurred on *C. equisetifolia* and *Eucalyptus* spp. and rarely result in successful breeding, but cause degradation of the timber. In South America, *Megaplatypus mutatus*, often referred to in the literature as *P. mutatus* or *P. sulcatus*, is a serious problem in commercial plantations of a number of broadleaf tree species. It is native to tropical and subtropical areas of South America and occurs in Argentina, Bolivia, Brazil, French Guiana, Paraguay, Peru, Uruguay and Venezuela. It attacks only living, standing trees and its hosts include Acacia, Casuarina, Cedrela and *Eucalyptus*, but it is particularly damaging to poplars, Populus deltoides, in Argentina (Alfaro et al., 2007). Tunnelling by M. mutatus degrades the lumber and weakens the tree stems, which often then break during windstorms. Infestation by *M. mutatus* has been recorded in an experimental plantation of brazilwood, *Caesalpinia echinata*, in Brazil. Although the infestation was low level, it is nevertheless of concern because C. echinata is at risk of extinction due to exploitation and deforestation, and the wood of this species is highly valued for the manufacture of violin bows (Girardi et al., 2006).

Platypodidae have numerous predators, both of adult beetles outside the nest and of brood within the tunnels.

Xylosandrus crassiusculus (Coleoptera: Curculionidae Scolytinae)

Xylosandrus crassiusculus, commonly referred to as the Asian ambrosia beetle or granulate ambrosia beetle, is a highly polyphagous pest of tree and shrub species, including many economically important horticultural crops and forest trees. Unlike other ambrosia beetles which normally attack only stressed, damaged or 'unthrifty' plants, *X. crassiusculus* is apparently able to attack healthy plants. Infested plants can show wilting, branch dieback, shoot breakage and general decline. Newly planted seedlings are often attacked at the root collar and the resulting girdling can stunt or kill the young tree (EPPO, 2010).

As its name implies, the Asian ambrosia beetle, *X. crassiusculus*, is considered to originate in tropical and subtropical Asia and to have been spread to equatorial Africa hundreds of years ago by early traders. More recently, it has been introduced into the Americas (detected in the USA in the 1970s and in Costa Rica and Panama in the 1990s) and has been reported from several countries in the Pacific, such as New Caledonia, Papua New Guinea, Samoa, Fiji, Hawaii and Australia.

As described by Atkinson et al. (2005), females bore into twigs, branches or small trunks of susceptible woody plants, where they excavate a system of tunnels in the wood or pith, introduce an ectosymbiotic fungus (Ambrosiella sp.) and produce a brood. Like other ambrosia beetles, they feed on the introduced fungus and not on the wood and pith of their hosts. When boring galleries, frass is pushed out in the form of a compact, 'toothpick-like' cylinder, which may reach 3–4 cm in length before it breaks off (Plate 42). Eggs, larvae and pupae (Plate 43) are found together in the tunnel system excavated by the female and there are no individual egg niches, larval tunnels or pupal chambers. The insect breeds in host material from 2 to 30 cm in diameter, although small branches and stems are most commonly attacked. Attacks may occur on apparently healthy, stressed or freshly cut host material. Attacks on living plants usually are near ground level on saplings or at bark wounds on older trees. Females remain with their brood until maturity. Males are rare, reduced in size, flightless and presumably haploid. Females mate with their brother(s) before emerging to attack a new host (Atkinson et al., 2005). In the tropics, breeding is continuous throughout the year, with overlapping generations (EPPO, 2010).

Schedl (1962) listed 124 hosts of X. crassiusculus, mostly tropical, in 46 families. The insect has been observed to kill nursery seedlings of mahogany, S. macrophylla, in Fiji (ACIAR, 2010), and in Pakistan three important tree species, T. grandis, D. sissoo and *E. camaldulensis*, are listed as hosts (Khuhro et al., 2005). In Ghana, tree mortality due to this pest has been reported in Aucoumea klaineana and Khava ivorensis plantations. In south India, X. crassiusculus has been implicated in the death of silver oak (Grevillea robusta), one of the most common shade trees grown in almost all the coffee zones (Sreedharan et al., 1991). It has caused death of saplings and seedlings of several hardwood species in the southern USA (Horn and Horn, 2006).

Sirex noctilio (Hymenoptera: Siricidae)

The sirex wood wasp, Sirex noctilio (Plate 44), is not considered an important pest in its native range in Eurasia and northern Africa, to the extent that many European texts on forest entomology do not discuss it (Ciesla, 2003). However, it is a significant pest of Pinus spp., where it has established in the southern hemisphere threatening approximately 8 Mha of pine plantations (Bedding and Iede, 2005) (Fig. 5.12). The female wasp oviposits eggs into stressed or suppressed trees, along with a phytotoxic mucus and a wood decay fungus (A. areolatum) carried by the wasps. Trees drilled by S. noctilio soon die, due to a combination of the mucus and the fungus. Carnegie et al. (2006) chronicle the spread of the pest and predict its potential distribution. It was first reported in the southern hemisphere in New Zealand in the early 1900s infesting P. radiata plantations and was detected in Tasmania in southern Australia in 1952, from whence it spread northwards in that country over the next 50 years to reach subtropical New South Wales and, very recently, Queensland. It was detected in Uruguay in South America in 1980, in north-eastern Argentina in 1985, southern Brazil in 1988 and Chile in 2001. It was found in the Western Cape of South Africa in 1994 and spread slowly east to KwaZulu-Natal, where it caused extensive damage to *P. patula* plantations. In 2005, an established population was found in the USA (Hoebeke et al., 2005). Carnegie et al. (2006) predicted its spread to southern China, parts of Central America and most of the countries along eastern, mid-western and northern Africa.

As described by Ciesla (2003), the female wasp inserts her ovipositor through the bark of the tree into the sapwood and lays eggs singly. Each female may lay between 20 and 500 eggs, which hatch in about 9 days. During oviposition, a symbiotic fungus, *A. areolatum*, is introduced along with a phytotoxic mucus. The mucus changes the water relations within the tree, creating conditions which are ideal for the growth and spread of the fungus. The fungus rots and dries the wood, providing a suitable



Fig. 5.12. Detection of *Sirex noctilio* in the southern hemisphere. Countries are indicated as: Ar = Argentina; Au = Australia; Br = Brazil; Ch = Chile; NZ = New Zealand; SA = South Africa; Ur = Uruguay. The numbers after the letters indicate the date that *S. noctilio* was first detected in those countries (from Hurley *et al.*, 2007).

environment, nutrients and enzymes for the developing insect larvae, which tunnel in the decayed wood (Plate 45). When feeding is complete, the larvae enter a prepupal stage, then a pupal stage. Pupation lasts 16–21 days and when the female emerges from the pupal skin, she takes up fungal spores and stores them in her abdomen. Adult sirex bore their way out of infested trees and leave a characteristic round exit hole. Males emerge before the females and may outnumber females by 20 to 1. The adults do not feed and live instead on stored fat. Adult lifespan can be 12 days, but a female that has deposited all her eggs may live just 3–4 days. Adults are strong fliers, capable of travelling several kilometres in search of suitable host trees. The dispersal rate in Australia is 30-40 km/year (Carnegie et al., 2006) and in South Africa 48 km/year (Tribe and Cillie, 2004). Typically, suppressed trees are attacked first, but as sirex populations increase, they are capable of attacking and killing more vigorous trees. The first indication of infestation is the appearance of resin droplets and oviposition scars on the bark. Foliage wilts and turns from green to yellow to reddish brown. Perfectly round exit holes appear when the new generation of adult insects emerge. S. noctilio can complete a generation in as little as 10 months (Ciesla, 2003).

S. noctilio affects a wide range of Pinus species, *P. radiata*, *P. taeda* and *P. patula* being particularly susceptible (Carnegie et al., 2006). The impact of the pest, where it has established, has varied from minimal to devastating in some areas. In Australia, integrated pest management aims to restrict losses to less than 2% per annum, but there has been the occasional severe outbreak. One example is the outbreak which occurred in the Green Triangle area of southern Australia between 1987 and 1989, when more than 5 m trees with a rovalty value of AUS\$10–12 m were killed (Haugen et al., 1990). In South America, tree mortality has been over 60% in some stands in Argentina and as high as 70% in some stands in Uruguay (Hurley et al., 2007). In Brazil, 350,000 ha of pine plantations are infested and an estimated US\$6.6 m would be lost each year if an integrated pest management programme were not in place (Bedding and Iede, 2005). In South Africa, infestation in some compartments has reached 35% but the overall mean is about 6%, with a total estimated value of damage being R300 m per annum (Hurley et al., 2007).

Integrated pest management for S. noctilio involves a combination of silvicultural measures and biological control. Susceptible plantations are generally 10–25 years old and unthinned stands are more susceptible than thinned stands. Trees under stress (e.g. drought conditions) or injured (e.g. by wind, fire or during logging) appear more likely to be attacked. Therefore, a major preventative measure is to increase stand vigour by thinning (Neumann et al., 1987). The parasitic nematode *Beddingia* (formerly *Deladenus*) siricidicola is the primary biocontrol agent for the pest. This nematode is able to breed in vast numbers throughout the tree while feeding on the fungus A. areolatum; then, it enters the wasp larva and begins reproduction when its host pupates. Nematode juveniles sterilize the adult female S. noctilio by entering all her eggs. When nematode-infected wasps emerge and attack other trees, they transmit packets of nematodes instead of fertile eggs. Infection levels can approach 100% and lead to a collapse in the pest population (Haugen et al., 1990). Several species of parasitic wasps have been

released for biocontrol, of which the most successful have been *Ibalia leucospoides*, *Megarhyssa nortoni* and *Rhyssa persuasoria*. In combination, these species usually do not kill more than 40% of an *S. noctilio* population and are therefore not considered sufficient to control the pest on their own.

Hurley et al. (2007) review the success of control programmes in the southern hemisphere and conclude that the results have been variable. In New Zealand, S. noctilio is no longer considered a major threat and an active control programme is not considered necessary. In Australia, infestations are mostly below 1%, although an active control programme remains in place. The pest is still considered a major pest in South America, where biological control has been successful in some areas but less so in others. In South Africa, infestations remain low in the Western Cape but are above 30% in some areas of KwaZulu-Natal and the Eastern Cape, and they are increasing in these provinces. The performance of the nematode in summer rainfall areas of South Africa has been poor, for reasons currently unknown (Hurley et al., 2008).

Coptotermes spp. (Isoptera: Rhinotermitidae)

Coptotermes is a large genus with numerous representatives in the tropics and many species which are injurious to trees. Among the best known are *C. formosanus* and *C. curvignathus* (Plate 46) in Asia, *C. elisae* and *C. obiratus* in Papua New Guinea, *C. acinaciformis* in Australia, *C. amanii* and *C. truncatus* in Africa and *C. niger* and *C. testaceus* in Central and South America.

Like most subterranean termites, they are generally ground dwelling or require contact with the soil or some constant source of water. Nests may be in dead timber, logs and old tree stumps, mounds or in the trunks of living or dead trees. Nest material usually consists of a mixture of termite excrement and earth glued together with salivary secretions. Colonies can be very large, in excess of 1.25 m individuals (Krishna and Weesner, 1970). As with other termites, within each colony are several types or castes which are specialized to perform different tasks. The main three castes are workers (nest and gallery construction, nurturing, food gathering), soldiers (defence) and reproductives (primary king and queen and winged forms which disperse to establish new colonies).

Foraging from the nest takes place via underground tunnels or, sometimes, under covered runways of digested wood and soil particles built above ground. These galleries may be up to 50 m long and, in the case of one colony of *C. formosanus* in the southern USA, cover an area of more than 0.5 ha. Cellulose obtained from plant material is the basic food requirement and termites digest this with the aid of microorganisms in their gut.

Many *Coptotermes* species are destructive pests of timber in service, but some attack living trees as well, causing death of young plantings and hollowing out the centre of older trees (Plates 47 and 48). Some species gain entry through diseased or damaged roots, or through scars or wounds on the lower stem. With others, such as C. curvignathus, attack can be primary, independent of decay or wounds, and entry may be made through the roots or above ground. When a tree is attacked above ground level, its stem is encased in a thick crust of earth, the bark is eaten away and the termites penetrate to the heartwood, which is hollowed out and often filled with woodcarton combs (Browne, 1968). Infested trees are frequently wind-thrown.

C. elisae has caused considerable mortality among plantations of A. cunninghamii and A. hunsteinii in submontane areas of Papua New Guinea (Gray and Buchter, 1969). In some compartments, incidence of infestation was about 7% and nearly all attacked trees died. Groups of up to 20 dying trees were common, each group representing the foraging of one colony from a central nest. A novel method of control was employed in new plantation areas, colonies being destroyed by means of explosives. In established plantations, the primary queens were removed from the main termitarium by excavation. In lowland Papua New Guinea, *C. obiratus* frequently destroys

the bark and sapwood of very young teak trees, causing death.

In Africa, *C. amanii* damages plantation trees in several countries, hollowing out pipes in mature trees and killing young trees. It has the habit of forming 'budded nests' by isolation of subsidiary nests, containing supplementary reproductives, from the original colony (Krishna and Weesner, 1970). *C. sjostedti* is a general pest of living trees throughout West Africa (Wagner *et al.*, 2008) and *C. truncatus* is considered to be the most destructive termite in the Seychelles, killing plantation trees such as *Corymbia (Eucalyptus) citriodora*.

The Formosan termite, C. formosanus, originally from Taiwan, is a 'tramp' species which has been widely spread by international trade. It now occurs not only in Japan and China but also on various Pacific Islands, including Hawaii, south-eastern USA, Sri Lanka and South Africa. It is able to construct and, if conditions are sufficiently damp, maintain aboveground nests in enclosed spaces without requiring ground connection. It is this characteristic that enables *C. formosanus* to occur in large, viable colonies on board ships or in containers. In Hawaii, it has been recorded from 48 host plants, and in southern China, it caused about 8% mortality in young plantations of E. excerta (Wylie and Brown, 1992). Also in southern China, an investigation showed that about 16% of 'ancient and valuable trees' was damaged by termites in Guangzhou and Coptotermes spp. were responsible for nearly 96% of that damage (Liu, 1997). In southern states of the USA, Formosan subterranean termites routinely attack standing live trees and can cause extensive damage, resulting in the weakening of the tree to the point of failure (Brown et al., 2007). The rubber termite, C. curvignathus, is most notorious as a pest of *Hevea brasiliensis* (Pong, 1974), but attacks a wide range of other trees including A. mangium in plantations in Sumatra (Wylie et al., 1998) and in Malaysia (Intachat and Kirton, 1997; Kirton and Cheng, 2007). Studies by Kirton *et al.* (1999) in A. mangium plantations in Peninsular Malaysia showed that while C. curvignathus was capable of primary attack, its entry

into the wood was often facilitated by large pruning wounds, abscission scars resulting from natural pruning and damage by insect bark borers. In Malaysia, infestation of living trees appears to be most frequent on low-lying, moist sites (Browne, 1968). Flooding, however, curtails foraging activity (Sajap, 1999).

In Australia, C. acinaciformis, now believed to be a species complex, is responsible for greater economic losses, in the aggregate, than all the other species of Australian termites combined (Krishna and Weesner, 1970). This is due not only to its extensive range and to the severe nature of its attack, but also to its extraordinary success in adapting to urban conditions. It causes severe damage to forest trees in at least six genera, including 25 species of eucalypt, hollowing out large pipes in the stems. Various studies have shown that the majority of trees (66–89%) in the eucalypt savannahs of tropical northern Australia have hollow cores or pipes attributable to termite activity, mainly by C. acinaciformis, and the effect of such damage on tree growth and survival has been examined by Werner and Prior (2007). They found that growth and survival of eucalypts increased with tree diameter and decreased with pipe ratio (Fig. 5.13). Contrary to the suggestion that tree hollows are an adaptive trait whereby trees benefit by the release of nutrients, in north Australian eucalypt savannahs the net effect of termite piping on individual tree growth and survival was negative.

C. niger occurs in the Caribbean, Central America and northern South America, where it attacks forest trees such as *G. arborea*, *S. macrophylla* and especially *P. caribaea* (Krishna and Weesner, 1970). It forages freely on the bark of living trees and is thought to be a vector of a nematode-related disease of palms. The heartwood termite, *C. testaceus*, is a pest of *Eucalyptus* spp. in plantations in Brazil, attacking trees 2-yearsold or older, destroying their inner portion and leaving the trees hollow (Junqueira *et al.*, 2008).

Ants are the most important natural enemies of this group. When disturbed, soldiers defend themselves by exuding a milk-like latex from a pore, the fontanelle, on the front



Fig. 5.13. Survival (proportion) of (a) eucalypts and of (b) pantropics in northern Australia savannah woodland following termite attack: modelled values of survival as a function of tree dbh, for a range of pipe ratios. Few pantropics had a pipe ration > 0.2 and there were none > 0.4. No eucalypts < 20 cm dbh had a pipe ratio > 0.6 (from Werner and Prior, 2007).

of the head and this compound is applied to the adversary when the soldier strikes.

Chilecomadia valdiviana (Philippi) (Lepidoptera: Cossidae)

Chilecomadia valdiviana, variously known as the quince borer, carpenterworm or butterworm, is an emerging pest of *Eucalyptus* spp. plantations in Chile (Lanfranco and Dungey, 2001). It is native to both Chile and Argentina and typically is associated with *Salix chilensis* and native forest tree species such as *Nothofagus* spp. As well, it infests commercial fruit trees and ornamental species such as *Ulmus glabra* (Angulo and Olivares, 1991). It is widely distributed in Chile, from Atacama in the dry northern tropics to Aisen in the most southerly region (Tierra del Fuego).

The insect infests live trees from 4 cm DBH and larger, with attacks occurring in all portions of the bole. Tree stress is not a prerequisite for attack. As described by Kliejunas et al. (2001), attacks on the host trees begin in the spring. The female lays eggs in groups of 30–50 at branch axils or in natural bark crevices. Each female is capable of laving up to 200 eggs. The newly hatched larvae feed gregariously beneath the bark near the point of oviposition. Their feeding produces a sap flow on the bark that is an ideal substrate for the development of sooty mould fungi. Trees with multiple attacks are easily recognized from a distance by the darker colour of the bole resulting from the sooty mould. Towards the end of summer, the larvae leave the phloem and begin boring deeply into the heartwood. At this stage, they feed individually, boring longitudinal galleries up to 27 cm in length and 1 cm in diameter. They produce large quantities of frass, which is expelled from the gallery and accumulates at the base of the tree. Larvae may grow to 50 mm in length and pupation takes place in the gallery. The adult female may have a wingspan of 48-60 mm and a body length of 30–40 mm; males are slightly smaller. The life cycle can take from 1 to 3 years to complete, depending on both the host species and climatic conditions (Lanfranco and Dungey, 2001). C. valdiviana often infests the same tree, suggesting a slow rate of spread (Boreham, 2006).

The insect first came to prominence in 1992 when it was detected infesting *E. nitens* in localized areas in the eighth and ninth regions of Chile, where the majority of the eucalypt plantations are situated. Since then, it has been found associated with *E. gunnii*, *E. camaldulensis* and *E. delegatensis* and there are concerns that the insect could create future serious wood quality problems for the industry.

C. valdiviana does not kill the tree but lowers wood quality through the formation of multiple galleries at all levels along the trunk. Fungi are known to colonize larval galleries, causing both staining and rot. This in turn can weaken the trees and cause stem breakage in strong winds. There are no foliar symptoms of larval presence.

Interestingly, tens of millions of larvae of *C. valdiviana* and another species of *Chilecomadia*, *C. morrie*, are sold as fishing bait and reptile food in the USA and Europe (Thomas, 1995; Iriarte *et al.*, 1997).

Plant protection agencies in the USA and Australia rate *C. valdiviana* as a potential quarantine risk (Tkacz, 2001; Lawson, 2007).

> Coryphodema tristis (Drury) (Lepidoptera: Cossidae)

As with the Chilean carpenterworm, C. valdiviana, discussed above, the South African quince borer, Coryphodema tristis, is another example of a native insect developing a new and very damaging host association with Eucalyptus plantations. C. tristis is widely distributed throughout South Africa and is well known as an economically important pest on many fruit trees, including quince, grapevines, apples and sugar pears (Gebeyehu et al., 2005; Boreham, 2006). It also feeds on a wide range of native and exotic trees, including species in the families Ulmaceae, Vitaceae, Rosaceae, Scrophulariaceae, Myoporaceae, Malvaceae and Combretaceae, to which can now be added Myrtaceae.

As described by Gebeyehu *et al.* (2005), the moth lays its eggs (from 104 to 316 per female) on the bark of the main stem or branches, and soon after hatching the early instar larvae begin to feed on the cambium. As they grow, they tunnel into the sapwood and heartwood, making extensive galleries and pushing frass to the outside of the stems, which makes their presence easy to detect (Plates 49 and 50). Fully-grown larvae range in size from 2 to 4 cm, depending on the size of the stems on which they have fed. The insect takes 2 years to complete its life cycle, approximately 18 months of this being spent in the larval stage. Pupation occurs in the tree and pupae cut holes to the exterior, from which their cases are left protruding after moth emergence. The adults do not feed and live for about 6 days.

Serious damage caused by C. tristis on E. nitens was first noticed in 2004 in Mpumalanga province, which lies in the high altitude, summer rainfall area of the Highveld of South Africa. There are approximately 25,000 ha of *E. nitens* plantations established in this region. In September 2004, a survey conducted in about 3000 ha of these plantations in 95 compartments showed infestation levels of up to 77% in some compartments, with an area weighted mean infestation of 9.6% for the entire survey area (Boreham, 2006). Infested trees ranged in age from 8 to 13 years. Infestations occurred in both high and low productivity sites and were not restricted to stressed trees. No other *Eucalyptus* species in adjacent compartments was affected.

C. tristis does not cause tree mortality directly, but the open larval galleries provide potential entry points for stain and decay fungi and other pathogens (Boreham, 2006).

Xyleutes ceramica Walker (Lepidoptera: Cossidae)

The beehole borer, *Xyleutes ceramica*, is best known as a major pest of teak, *T. grandis*, in Myanmar and Thailand but attacks several tree species, particularly *G. arborea*, in other parts of Asia.

According to Beeson (1941), the adult female is short-lived and lays up to 50,000 eggs attached in strings in the crevices of bark. These hatch in 10–20 days and the young larvae are dispersed on silken threads by the wind. A larva can survive without food for up to 6 days after hatching. When it alights on the stem of a suitable host, it seeks a crevice and spins a web, under the protection of which it bores through the bark and into the sapwood, the tunnel then curving upwards and becoming vertical in the heartwood. A tunnel may reach a length of 25 cm and a diameter of 25 mm. The larva (Plate 51) feeds not on the wood but on the callus tissue that develops on the wound

around the entrance of the tunnel, or 'beehole'. A feeding chamber is excavated in the bark and outer sapwood and one or more circular holes are drilled to the outside through which frass is ejected. Larval development may take 1–2 years, after which the larva clears a free passage in its beehole, closes the exit hole with a circular disc of silk and debris, and retires to the upper end of the tunnel to pupate behind a loose wad of silk. After 2–3 weeks, the pupa wriggles down the tunnel, cuts through the disc covering the exit hole and protrudes itself halfway out of the hole to facilitate emergence of the moth (Plate 52).

On vigorously growing trees, the exit hole is soon occluded by callus. Within a few years, there is no external sign of the tunnel. Host trees may be attacked by X. ceramica throughout their life. When such a tree is felled in a thinning or at the end of the rotation, it contains the accumulated effects of attack by this insect. Attack does not retard growth appreciably or increase mortality, but seriously degrades the timber. An attack of one beehole per tree per year in any period is a very heavy incidence commercially (Beeson, 1941). The vertical distribution of beeholes in the trunk of an average tree varies progressively through its life. In young trees up to an age of 25, there is a definite preponderance of beeholes in the lower portion of the bole, but by age 60 the site of maximum beeholing is towards the top of the bole. This may be related to changes in the nutritive value of the bark as the tree ages.

No epidemics of *X. ceramica* have been recorded and population densities of adults are usually very low. Beeson (1941) stated that a population of 40 moths/ha would be regarded as a high incidence. In Peninsular Malaysia, incidence of borer attack in young plantations of *G. arborea* approached 50% at some localities (Sajap, 1989) and 10% in Indonesia (Suratmo, 1996). The insect has been recorded from *A. mangium* in the Philippines (Braza, 1993). Healthier trees have a higher incidence of attack than suppressed trees and this may be related to the superior quality and quantity of food for larvae in vigorously growing trees. Ants and birds are important predators of the beehole borer and, according to Mathew (1987), the ichneumonid parasitoid *Nemeritis tectonae* provides effective control of this insect.

5.5 Shoot Boring

Shoot- or tip-boring insects cause the most damage when they attack the apical terminal or leader of the tree, which results in irregular stem growth or multiple branching when secondary terminals take over dominance. Trees which have been subjected to repeated attack by such insects may have a stunted, bushy appearance, or at least malformed or forked boles, and their value for timber production can be reduced greatly or eliminated (Berryman, 1986). Attack on the buds and terminals of very young seedlings will often kill them, or so stunt their growth that they are overtopped by undesirable plant species. Attack on saplings often results in crooked stems, but on pole-sized and mature trees the impact is usually inconsequential because height growth is well advanced and the bole form already established. Damage is usually most severe in plantations and in natural regeneration after heavy cutting, and is often associated with particular site and stand conditions that affect the vigour and exposure of young trees (Berryman, 1986).

Hylurdrectonus araucariae Schedl (Coleoptera: Scolytidae)

This scolytid occurs only in Papua New Guinea and has just a single host, *A. cunninghamii*, commonly known as hoop pine. Whereas most bark beetles are cambial borers, *Hylurdrectonus araucariae* is unusual in that it is a branchlet miner (Gray and Lamb, 1975). The damage caused by this insect to the country's main plantations of hoop pine at Bulolo and Wau resulted in the abandonment of planting of this species there in the late 1960s.

Hoop pine branchlets consist of sharply pointed leaves or needles arranged along an axis. The nest of *H. araucariae* invariably is initiated by the female (Grav, 1974), which bores into the needles either close to their junction with the axis or directly into the axis. She is then joined by the male, and occasionally an extra male or another pair. Up to four nests may be established in one branchlet. The beetles lay their eggs inside the excavated needles, usually at the base, and these hatch in 5–15 days. The larvae and adults mine into the needles and along the branchlet shaft, consuming most of the tissue except for the epidermis and pith (Plate 53). The length of the excavation is proportional to the age of the nest, and after 100 days may extend for several centimetres. The distal portion of the infested branchlet behind the area of active excavation turns brown, dies and eventually falls off. After 1-3 years of severe attack, most branches have been infested repeatedly and there is nearly complete defoliation of all branchlets on many branches (Gray and Lamb, 1975). The larval stage lasts 10–25 days, the pupal stage 10-15 days and the immature adult possibly 2–10 days to mature and establish a new colony. Nests may contain up to 75 individuals in all stages of development and the maximum number of adults recorded in a nest is 25. The adult may live 60 days or more. The life cycle takes 5–9 weeks and there are 5–10 generations per annum.

Attack by *H. araucariae* on hoop pine is primary, nearly all trees in an outbreak area being infested regardless of condition. However, there is a definite age effect, trees aged 2.5-12 years being the most susceptible (Gray, 1976). The insect is comparatively rare in natural stands of hoop pine but has infested approximately 47.5% of major plantations at Bulolo and 91% at Wau (Grav, 1975). This circumstance was attributed to the fact that most of the plantations were of an age class susceptible to attack and that trees of similar age in natural stands had different physiochemical characteristics of foliage to those of plantation-grown hoop pine. Considerable growth loss and high tree mortality has been recorded in severely infested stands, particularly on poor sites. Most mortality was due to secondary insects, such as the weevil Vanapa oberthuri, which attacked the weakened trees. As a result of *H. araucariae* damage to hoop pine at Bulolo and Wau, the planting emphasis there switched to *A. hunsteinii*, which is resistant to attack by the beetle.

Apart from spiders, which prey on the adults when they leave the nest, no other natural enemies of *H. araucariae* have been found (Gray and Lamb, 1975).

Dioryctria spp. (Lepidoptera: Pyralidae)

Until comparatively recently, *Dioryctria* spp. (Plate 54) were best known as cone or shoot borers of conifers in Europe and North America. However, with the rapid expansion of plantations of *Pinus* spp. in Asia during the past few decades, mainly destined to provide long fibre pulp, there has been an increase in damage caused by several pests and diseases, including shoot moths in the genus Diorvctria. Severe damage to shoots and bark of young *Pinus* spp. has occurred in the Philippines, Thailand, Vietnam, Indonesia, India, Pakistan, Taiwan, southern China and Cuba (Wang et al., 1999; Nair, 2007). As well, species of Dioryctria have been reported to attack cones of *Pinus* spp. in the Central American countries of Honduras and Nicaragua (Becker, 1973), and in Florida *D. amatella*, commonly referred to as a pitch moth, is a serious pest of pine seed orchard crops in that state (Meeker, 2008).

As described by Speight and Speechly (1982), eggs are laid around the bases of needles of young shoots. The hatching larvae feed externally at first on the needle bases, spinning small silken tents which become covered in resin and frass. Some mining of the needles may also occur. The larvae may remain on the outside of the shoots for a week or more before boring in, and may reappear on the surface from time to time as they mature. Usually, larvae bore upwards at first towards the shoot tip and later down towards the basal part, the tunnelling extending for up to 30 cm (Plate 55). Pupation occurs in the shoot near the old entrance hole. The length of the life cycle varies with climatic conditions and may take from 2 to 4 months.

Attack results in dieback of leading and lateral shoots with a browning of needles and

tips, which break off easily to reveal the hollowed-out shoot. By this time, the larvae usually have already pupated and the adult moths emerged. In moderate infestations, the terminal shoot dies but laterals take over to produce a 'stag-headed' effect, with a resultant loss in form. In more serious cases where the majority of shoots are attacked, the trees become stunted and bush-like (Plate 56). Increment is reduced greatly and the trees become valueless for timber. Larvae of *Dioryctria* spp. sometimes also bore in the bark cambium and can girdle and kill young trees.

In Thailand, especially in lowland areas, several species of *Pinus*, principally *P. kesiva*, are attacked by D. sylvestrella and D. abietella (Hutacharern, 1978; Speight and Speechly, 1982). In Vietnam, D. sylvestrella attacks P. kesiya and P. caribaea, while in the Philippines heavy attacks on *P. caribaea* by D. rubella affect the viability of the plantation programme there (Lapis, 1985b). D. castanea is a major pest of P. kesiva in India and during one outbreak in a 900 ha plantation in the north-east of the country, all age groups were attacked and every tree affected (Singh et al., 1988). The most important of the Dioryctria spp. in Taiwan is D. pryeri (Yie et al., 1967), and in Pakistan it is D. abietella (Ahmad et al., 1977). Also in Pakistan, Ghani and Cheema (1973) reported severe damage by D. raoi to P. roxburghii trees in Kashmir, with up to 55% of shoots affected on some trees, resulting in stunting and malformation. Of the tropical pines planted in southern China, P. caribaea var. hondurensis is the species affected most seriously by D. alternatus, whose damage to the apex and main stem is one of the principal contributors to the generally poor stem form of this tree species in the region (Wang et al., 1999). In Yunnan Province in the south-west of China, D. rubella causes severe damage to P. kesiya var. langbianensis. In the rainy season, the damage rate is 35-40% and in the dry season 90-100% (Tong and Kong, 2010). One of the reasons given for such a high rate of infestation is the ability of the larva to attack more than one shoot. Altitude seems important in determining the severity of shoot moth attack; at altitudes over 1000 m, damage is of little significance but may be severe in

plantings below this level (Speight, 1983). Other associated factors are uniformly high all-year-round temperatures, soils low in nutrients (especially phosphorus) and the presence of older trees that are already infested.

Numerous wasp parasitoids of the egg, larval and pupal stages of several *Dioryctria* species in the tropics have been recorded (Ghani and Cheema, 1973; Belmont and Habeck, 1983; Thakur, 2000; Nair, 2007).

Hypsipyla robusta (Moore), Hypsipyla grandella (Zeller) (Lepidoptera: Pyralidae)

Hypsipyla spp. shoot borers are among the most economically important insect pests in tropical forestry, virtually preventing the cultivation of mahoganies (Swietenia spp., Khaya spp.), cedars (Cedrella spp., Toona spp.) and other valuable Meliaceae, primarily of the subfamily Swietenioideae, in their native areas (Griffiths, 2001; Opuni-Frimpong et al., 2008b; Wagner et al., 2008). H. grandella is found throughout Central and South America and also occurs on many Caribbean islands and the southern tip of Florida. The species referred to as 'H. robusta' is widely distributed throughout West and East Africa, India, Indonesia, Australia and South-east Asia (Table 5.4). It has now been shown that *H. robusta* is not one but at least three different species (Horak, 2001; Cunningham et al., 2005), which accounts for some of the differences apparent in the reported biology and behaviour of the species in various parts of its range.

Newton et al. (1993) have summarized the biology, ecology and importance of these pests. The two species appear to behave similarly, the total life cycle lasting about 1–2 months, depending on climate and food availability. In H. grandella, oviposition occurs during evening or early morning and egg eclosion occurs at night. An individual female lays 1–7 eggs at a time on one or more plants and may repeat oviposition over a period of 6 days, laying 200-300 eggs in all. In comparison, a *H. robusta* female may lay 450 eggs during a 7- to 10-day period (Griffiths, 2001). Eggs are laid singly, or occasionally in clusters of three to four, usually on shoots, stems and leaves, often in

concealed positions such as leaf axils, scars and fissures. Eggs hatch in about 3 days and the larvae move towards the new shoots, burrowing into the stem or leaf axil. The larvae (Plate 57) cover their entrance holes with a protective web containing plant particles and frass (Plate 58) and tunnel in the primary stem or branches, feeding on the pith. There are five to six larval stages lasting about 30 days. Larvae pupate in cocoons spun in the stem tunnels, or among the leaf litter and soil around the tree base. Pupation lasts about 10 days.

Larvae are also known to feed on the bark, fruit and flowers of their hosts. In Australia, larvae of H. robusta feeding on Toona ciliata fruit initially feed externally on the epidermis and later live within, and consume, the seeds and soft tissue of a single fruit before emerging and entering a new fruit (Griffiths, 2001). Neighbouring fruit are joined by a tunnel of silk and frass through which the larvae move. Feeding damage to fruit results in their premature shedding and larvae apparently circumvent this by spinning a mat of webbing across the point of abscission (Griffiths, 1997). Fully fed larvae generally exit the fruit to pupate beneath the bark of the mature trees close to the base, or among surrounding soil and leaf litter, but sometimes pupate in the hollowed-out fruit. In Nigeria, Roberts (1968) reports that while it is usual to find only one larva in each shoot, fruits of Carapa procera have vielded up to 26 larvae, and more than one larva is not uncommon in fruits of *Khaya* spp.

The adults are nocturnal, are strong fliers and able to locate their food plants over large distances by means of chemoreception. The exact nature of the attractants emitted by the plant is unknown.

The number of generations a year varies with variations in climatic conditions and availability of new shoots. In areas which are wet all year round, the insects are able to attack continuously as the young trees resprout repeatedly (Newton *et al.*, 1993). In areas with a pronounced dry season, attacks switch from shoots to fruit during the dry period when no unlignified shoots are available.

Tree species	Bangladesh	Sri Lank	a India	Philippines	Vietnam	Laos	Thailand	Malaysia	Indonesia	Papua New Guinea	Solomon Islands	Australia
Cedrela odorata		✓					✓	✓			x	✓
Cedrela lilloi							\checkmark					\checkmark
Chukrasia tabularis	\checkmark				\checkmark	\checkmark	$\checkmark\checkmark$	\checkmark				$\checkmark\checkmark$
Khaya anthotheca								\checkmark				
Khaya grandifolia								\checkmark				
Khaya ivorensis								\checkmark				
Khaya nyasica												\checkmark
Khaya senegalensis		\checkmark			\checkmark			х	\checkmark			\checkmark
Swietenia macrophylla	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	$\checkmark\checkmark$	$\checkmark\checkmark$	$\checkmark\checkmark$	\checkmark	$\checkmark\checkmark$	$\checkmark\checkmark$	
Swietenia mahagoni	\checkmark	\checkmark	\checkmark				$\checkmark\checkmark$	$\checkmark\checkmark$	\checkmark			
Toona ciliata	\checkmark	\checkmark	\checkmark			\checkmark	$\checkmark\checkmark$		\checkmark	\checkmark		$\checkmark\checkmark\checkmark$
Toona calantas				х								
Toona sinensis								\checkmark				
Toona sureni					\checkmark	\checkmark	\checkmark	$\checkmark\checkmark$	\checkmark	\checkmark		
Xylocarpus moluccensis						$\checkmark\checkmark$						

Table 5.4. *Hypsipyla robusta* damage on species of Meliaceae (subfamily Swietenioideae) grown in various Asian and Pacific countries (from Floyd and Hauxwell, 2000).

Notes: Empty cells in the table indicate that there are no records of a tree species in a country. The number of ticks indicates the severity of damage and a cross indicates no damage observed. Countries with a single tick against all species recorded for that country indicates damage has been observed but no indication of relative severity of damage.

Tunnelling by the larvae in the shoots causes shoot mortality, growth reduction, branching and poor tree form (Plate 59). Repeated attacks can result in tree death. Trees may be attacked from the nursery stage through to maturity, but attacks up to the pole stage are most critical from a silvicultural point of view. Newton et al. (1993) cite many examples of damage caused by *Hypsipyla* spp. throughout the tropics, with up to 100% of plantings affected in some cases. Plantation programmes using species of Meliaceae (subfamily Swietenioideae) have been abandoned almost completely in many countries. Despite such pest pressure, there are instances where susceptible species of Meliaceae have been grown with minimal shoot borer damage. This often involved the growing of the desired species in mixtures with other tree species. The reasons for the occasional success are not clear but have been variously suggested to relate to the effects of shade (overhead and lateral), planting density and growth rate, or interactions between these factors. Published viewpoints on this subject are often conflicting.

Many species of parasitoids, principally braconid and ichneumonid wasps, and predators of *Hypsipyla* spp. have been recorded, but these do not provide effective control either in their native country or where they have been introduced to other countries in classical biocontrol programmes (Newton *et al.*, 1993). In Australia and Malaysia, investigations into the use of weaver ants, *O. smaragdina*, as a biological control agent for *H. robusta* show some promise (Lim *et al.*, 2008).

5.6 Fruit and Seed Boring

Several different groups of insects attack the fruit, cones or seeds of forest trees. Some, such as torymid wasps, lay their eggs directly into the seed of young cones and their larvae feed within the seed; others, such as bruchid beetles, lay their eggs on the exterior of the pod or fruit and the larvae tunnel inwards to the seed, which they consume. Insect tunnelling may sometimes result in abortion of cones or fruit before the seeds have developed, or cause seed abortion (Berryman, 1986).

In plantations established for wood production, and even in natural forests, insects that feed on seeds or cones are relatively unimportant, but in seed orchards such damage is more serious and losses can be considerable (Speight and Wainhouse, 1989). In years when the cone crop is small and populations of cone and seed insects are high, the entire crop may be destroyed. Because of the expense in managing seed production areas, even a 5 or 10% loss may economically intolerable (Berryman, be 1986). Problems may also arise when natural seeding is required following logging operations, for example, where only a few select trees are left to provide seed and the insect population is high.

Bruchidius spp. (Coleoptera: Bruchidae)

Species of *Bruchidius*, commonly known as seed weevils, are numerous in the tropics, where they are pests of the seed of various plants, including some important leguminous tree species in the genera *Acacia*, *Albizia*, *Falcataria* and *Prosopis*.

According to Beeson (1941), the habits of all species are very similar. The eggs are laid normally on the skin of the pod or fruit to which they are attached by an adhesive fluid. The larva hatches in a few days and burrows directly into the fruit to the seed on which it feeds. One larva may hollow out several seeds during its development. Pupation occurs in the seed. The length of the life cycle varies considerably according to temperature, humidity and the quality of the food available. In the tropics, development may be completed in a few weeks and there may be numerous overlapping generations during a year. Because of the specificity of legume allelochemical substances, the larvae of a particular bruchid species may feed on the seed of just a single host species (Singh and Bhandari, 1988).

Leguminous trees are important in social forestry, particularly in arid lands where there is a demand for large quantities of sound seed which can be collected locally. Destruction of the seed crop by bruchids can therefore have serious consequences for rural communities in these areas (Singh and Bhandari, 1988). A. tortilis has been suggested to function as a keystone species in the arid and semi-arid regions of Africa and the Middle East but sometimes suffers from extraordinarily high infestation of seed beetles (Noumi et al., 2010a). Tunisia (Noumi et al., 2010b) recorded from 31 to 83% infestation of A. tortilis seed by B. raddianae and B. aurivillii. In Botswana, the degree of seed parasitism of A. tortilis by several Bruchi*dius* spp., principally *B. albosparsus*, B. aurivillii and B. rubicundus, ranged from 10 to 82% between trees and years (Ernst et al., 1989). Infestation rates of almost 100% have been recorded for B. spadiceus in Tanzania (Lamprey et al., 1974).

One of the reasons for the success of Acacia spp. is that they produce substantial quantities of seeds in order to overcome a range of environmental uncertainties, including the high rates of infestation by bruchid beetles (Sabiiti and Wein, 1987). Fire and grazing by large herbivores also contribute to the survival of these plants, not only by stimulating seed germination (fire, animals) and aiding dispersal (animals) but also by reducing populations of the seed beetles. Bruchid larvae are more sensitive to fire than the seed embryo, and this heat treatment leads indirectly to higher germination. Studies by Sabiiti and Wein (1987) in Uganda suggest that as fire intensities increase there will be fewer Bruchidius spp. larvae and more viable seed embryos. Lamprey et al. (1974) in Tanzania showed that fluids in the gut of animals that grazed and ingested seeds or pods of A. tortilis killed a higher proportion of bruchid larvae in the seed than seed embryos, and this contributed to higher rates of germination.

In Australia, *B. sahlbergi* was introduced from Pakistan as one of a complex of biocontrol agents for the prickly shrub *A. nilotica*, a declared noxious plant in arid sheep and cattle grazing regions in the tropical north of the country (Wilson, 1985).

Numerous hymenopteran parasitoids of *Bruchidius* spp. have been reported, but

generally their impact on populations of these pests is small (Ernst *et al.*, 1989).

Megastigmus spp. (Hymenoptera: Torymidae)

Megastigmus is an important genus of seed pests and these wasps are particularly destructive of conifer seed in Europe and North America. Worldwide, there are 51 species of *Megastigmus* which damage the seeds of conifers (Roques *et al.*, 2003) and several species which attack the seeds of eucalypts. The biology and impact of tropical species is less well known, but damage has been reported from southern China, Mexico, Thailand, Africa and Australia.

As described by Drake (1974) for *Megastigmus* on eucalypts in Australia, the insects lay their eggs in the ovules of young seeds during or just after the flowering period. After hatching, they feed off the developing embryos, often leaving the seed coat intact. Each insect consumes only the seed within which it has been deposited and therefore not all the seeds in an infested capsule are necessarily destroyed. The level of attack varies considerably, but between 20 and 50% of eucalypt capsules in localized areas can be destroyed (Drake, 1974).

In southern Mexico, M. albifrons damages seed of three species of *Pinus*, affecting up to 27% of seed (Rio Mora and Mayo-Jimenez, 1993). The wasp has an annual generation, but a small part of the population stays in diapause for 2 years, which is probably an adaptation to the irregular periodicity of seed production (Browne, 1968). In Thailand, seeds of Sesbania grandiflora are commonly infested with larvae of Megastigmus, infestation levels reaching 70% (Helium and Sullivan, 1990). Recently, a new species of Megastigmus, M. zebrinus, has been described from South Africa, associated with seed capsules of E. camaldulensis, an endemic Australian tree. The wasp presumably was introduced along with its host tree. It appears to be a true gall-maker, rather than a parasitoid of gall-forming insects, and now has adapted to the fruit of *S. cordatum*, an endemic South African myrtaceous tree (Grissell, 2006).

5.7 Gall Forming

Galls are unusual plant growths which develop as a result of abnormal cell division and/or cell enlargements following infestation of plants by organisms such as insects, mites and fungi (Elliott et al., 1998). They can occur on all plant organs, but are found most commonly on leaves, stems and buds. Insect-induced galls can be caused by species in several Orders, but the most important groups are Hymenoptera, Hemiptera and Diptera. Galls provide food and shelter for the invading insects, but the plant derives no benefit in this relationship, sustaining loss of nutrients, changes in growth architecture and structural weakening. The shape of a gall is often characteristic of a particular insect species, and in some cases there is marked sexual dimorphism, with the males producing a gall of a different shape from that produced by the females.

Galling rarely results in the death of the host tree, but severe dieback of attacked parts can occur (Cobbinah, 1986) and branches may break under the weight of galls (Currie, 1937). Photosynthetic capacity may be reduced where leaves are heavily galled and distorted (Elliott *et al.*, 1998). Some gall-making insects can have a serious impact on seed production. For example, the pteromalid gall wasp, *Trichilogaster acaciaelongifoliae*, is used as a biocontrol agent for *A. longifolia*, which has become a weed in South Africa, and on some sites has reduced seed production by 95–99% (Dennill, 1985).

Fergusonina spp. (Diptera: Agromyzidae)

Fergusonina spp. are pests of myrtaceous trees and are associated in their galls with nematodes in the genus *Fergusobia*. This is the only known mutualistic association between insects and nematodes (Davies and Giblin-Davis, 2004). Six genera in the family Myrtaceae, viz. *Corymbia, Eucalyptus, Angophora, Syzygium, Melaleuca* and *Metrosideros*, are known to be hosts of this association, with most records being from *Eucalyptus* and *Melaleuca* (Taylor and Davies, 2008). The galls may appear on stem tips, leaf buds, leaves and flower buds and are a result of the combined effect of the nematodes and fly larvae (Currie, 1937). While several species have been recorded from Asia and Papua New Guinea (Davies and Giblin-Davis (2004), they are most numerous in Australia, where they are commonly known as eucalypt flies.

Detailed studies of these flies in Australia have been carried out by Currie (1937) and are summarized by Elliott et al. (1998). In species which infest eucalypt flowers, adult flies emerge from galls in the summer. Following mating, females fly to flowers and lay eggs in the young flower buds. From 1–50 larval nematodes are laid with each egg. Many fly eggs may be laid in the same eucalypt flower bud by a single fly or several different flies. While the fly egg is developing, the immature nematodes feed on the primordia of the stamens, causing rapid proliferation of cells, which form irregular masses of cells inside the now galled bud. On hatching, the fly larvae form cavities between two contiguous cell masses and develop rapidly to the pupal stage by feeding initially on cell sap and later on ruptured plant cells. The nematodes join the fly larvae in these feeding cavities and eventually undergo parthenogenetic reproduction, with the female nematodes laying eggs beside the fly larvae. The nematodes do not harm the fly larvae.

Male nematodes appear in the galls in the autumn and winter. When the female fly larvae are about to pupate, fertilized female nematodes enter these larvae. During the fly pupal stage, the nematodes change from free-living forms to much enlarged parasitic forms. By the time the female fly emerges, the parasitic nematodes are discharging eggs inside the fly body cavity. On hatching, the larval nematodes migrate to the ovaries, penetrate the oviduct and wait there until an egg passes down the oviduct. The nematodes then accompany the eggs into the flower bud where the fly–nematode cycle begins again (Fig. 5.14).



Fig. 5.14. Life cycles of the Fergusonina-Fergusobia association (from Davies and Giblin-Davis, 2004).

The frequency of galling of flower buds of some eucalypts by *Fergusonina* varies markedly from year to year and can be low even in the presence of abundant flower buds. Currie (1937) records that galling reduced seed production in some eucalypts and that whole branches might break under the weight of galls. A species of *Fergusonina* is a pest of *E. deglupta* in the Philippines (Braza, 1991) and F. syzygii galls flower buds of S. cumini in India (Siddiqi et al., 1986). Fergusonina is being considered as a potential biocontrol agent for the broadleaved paperbark tree, M. quinquenervia, which was introduced from Australia into Florida in the USA in the early 1900s and has since become a serious weed. It infests over 200,000 ha in the Everglades, causing extensive environmental damage (Goolsby et al., 2001). The high degree of host specificity of the Fergusonina-Fergusobia association makes it an ideal candidate for biological control (Goolsby et al., 2000).

Chalcid and braconid wasp parasitoids are the main natural enemies of *Fergusonina* spp. and are thought to exert some measure of control (Currie, 1937). Goolsby *et al.* (2000) reared 11 species of wasps from *Fergusonina* galls on *M. quinquenervia* and recorded a parasitism level of the fly larvae and pupae of greater than 60%. The two most common parasitoid species they reared were *Eurytoma* sp. and *Coelocyba* sp.

Phytolyma spp. (Hemiptera: Psyllidae)

Milicia [*Chlorophora*] is a tropical African genus of forest trees of considerable economic importance because of its natural durability and good working properties (Ofori and Cobbinah, 2007). It occurs naturally in the forest belt of West Africa, extending from Gambia to Nigeria and also in Central and East Africa. Attempts to cultivate *Milicia* spp. on a large scale have been hampered by *Phytolyma* psyllids, particularly *P. lata*, commonly known as the Iroko gallfly, which forms galls on the foliage (Nichols *et al.*, 1999; Wagner *et al.*, 2008).

Eggs are laid in rows, or scattered singly, on the buds, shoots or leaves of the host and hatch in about 5–25 days. The larva burrows into the adjacent tissues, breaking down the epidermal cells, which causes fermentation of the parenchyma. A gall is formed within 1 or 2 days, which encloses the nymph completely. The insect feeds within the gall tissue and there are five nymphal instars lasting approximately 2–3 weeks (Wagner *et al.*, 2008). The gall eventually splits open, usually at the point of original infection, to release the adult. Occasionally, the gall hardens without opening and the trapped insect dies. The total life cycle is completed in 22–45 days.

Phytolyma spp. galls disrupt the plant's translocation processes, and when they erupt to release the adults, death of the leading and lateral shoots can result (Atuahene, 1972; Cobbinah and Wagner, 1995). Terminal dieback causes growth reduction and seedling mortality in many cases. Agyeman et al. (2009) studied the impact of P. lata on seedling growth of *M. excelsa* in Ghana. They found that infested plants had lower height, stem diameter and biomass growth than uninfested plants. Mean yield losses of stem, branches and leaves of infested plants were 68.9%, 48.3% and 64%, respectively, of matched uninfested plants. Infested plants also had smaller, fewer and highly chlorotic leaves. The insects have a preference for young leaves, which not only ensures that goodquality food is available but also that they are able to complete development before leaf fall (Cobbinah, 1986). Physical properties such as cuticle thickness may enhance the preference for young leaves (Wagner et al., 2008).

Phytolyma spp. attack is more injurious in nurseries and vigorous young plantations than in natural forests and 100% failures have been reported in Ghana (Wagner *et al.*, 2008). Studies by Bosu *et al.* (2006) of survival and growth of mixed plantations of *M. excelsa* and *T. superba* 9 years after planting in Ghana indicated that shade from *T. superba* reduced psyllid galls on *M. excelsa*, though crop growth was slow.

A species of *Trichogramma* parasitizes eggs of *P. lata*, while encyrtid and eulophid wasps parasitize the nymphs. Mantids predate first instar crawlers and, to a lesser degree, exposed adults.

Leptocybe invasa (Hymenoptera: Eulophidae)

The blue gum chalcid, *Leptocybe invasa* (Plate 60), is a new pest of *Eucalyptus* that was found in the Middle East in 2000 and has since spread rapidly to most Mediterranean countries, to many countries in

Africa and, more recently, to Asia and North and South America. It is native to Australia, where it is unknown as a pest, but poses a serious threat to young *Eucalyptus* plantations, where it has become established in other countries.

The chronology of the spread of blue gum chalcid, as determined from the literature and from information provided by researchers on the pest, is summarized below (Mendel *et al.*, 2004; Doganlar, 2005; Hesami *et al.*, 2005; CABI/EPPO, 2007a; FABI, 2007; Costa *et al.*, 2008; Tang *et al.*, 2008; Wiley and Skelley, 2008; Jhala *et al.*, 2009; Nyeko *et al.*, 2009; Thu *et al.*, 2009; Botto *et al.*, 2010; Javaregowda and Prabhu, 2010). In some of the earlier records from the Mediterranean region, *L. invasa* was named erroneously as *Aprostocetus* sp. (Protasov *et al.*, 2008).

- 2000: Israel, Iran, Algeria, Italy
- 2001: India (Karnataka), Morocco, Egypt, Turkey, Jordan, Syria
- 2002: Uganda, Kenya, Ethiopia, Tamil Nadu (India), Vietnam
- 2004: Corsica (France), Spain, Greece
- 2005: Mainland France, Tanzania, Portugal
- 2006: Gujarat (India), Thailand, Southern England
- 2007: Zimbabwe, Guangxi (China), Brazil, South Africa
- 2008: Florida, Lao PDR, Hainan (China)
- 2009: Argentina
- 2010: Chile

The rapidity of spread of *L. invasa* around the world (29 countries in a period of 10 years) is akin to that of the leucaena psyllid *H. cubana*, which spread to 45 countries over a similar timespan (see earlier in this chapter). This spread has been attributed to movement of nursery stock (plants for planting) or to the cut flower trade.

L. invasa causes galls on the midribs, petioles and stems of new shoots of eucalypt trees, including coppice and nursery stock. Heavy infestations can lead to deformed leaves and shoots, a growth reduction of the tree, dieback and, in some cases, tree death.

Adult females insert their eggs in the epidermis of young leaves on both sides of

the midrib, in the petioles and in the parenchyma of twigs. Mendel et al. (2004) identified five stages of gall development on *E. camaldulensis*. The first stage begins 1–2 weeks after oviposition, with the first symptoms of cork tissue appearing at the egg insertion spot, accompanied by a change in midrib colour from green to pink. Towards the end of the stage, the galls are spherical and glossy green. In the second stage, the galls develop their typical bump shape and reach their maximum size (about 2.7 mm). In the third stage, the green colour of the gall changes to glossy pink and in the fourth stage, the gall loses its glossiness and changes to light or dark red. In the final stage, emergence holes of the wasp are noticeable (Plate 61). In Israel, the development time from oviposition to emergence was 4.5 months. Adult wasps may live 3–6 days and may feed on the flowers of their host plant. In the Middle East, two to three overlapping generations per year have been observed. A wide range of *Eucalyptus* species are hosts to this pest, including: E. botryoides, E. bridesiana, E. camaldulensis, E. dunnii, E. globulus, E. grandis, E. gunnii, E. maidenii, E. robusta, E. saligna, E. tereticornis, E. urophylla, E. viminalis and various clones and hybrids.

L. invasa attacks trees of all ages, from nursery stock to mature tree, but the damage is most severe on younger plants. Mendel *et al.* (2004) reported that in the Bet Shean Valley in Israel, where *L. invasa* had reached epidemic levels, juvenile shoots were often killed due to egg overloading. In southern states of India, more than 20,000 ha of 2-year-old eucalypt plantations had already been affected by gall formation within 5 years of first discovery of the insect there (Javaregowda and Prabhu, 2010). In Vietnam, where the plantation industry is reliant on only a few clones of *E. urophylla* and E. camaldulensis, it reportedly has devastated nurseries and young plantations (Thu et al., 2009). The wasp has been similarly problematic in *E. camaldulensis* plantations and nurseries in Thailand (Dell et al., 2008). Surveys by Nyeko et al. (2009) in Uganda across 154 stands of young (< 3-yearold) *Eucalyptus* spp. and clonal hybrids

showed that infestation by blue gum chalcid was most severe on *E. grandis* and *E. camaldulensis*, with most of the trees having galls in more than 50% of total shoots. Evaluation of growth losses caused by *L. invasa* on an *E. grandis* \times *E. urophylla* clone in Guangdong, China, showed leaf loss of greater than 90% and average loss of tree height and tree diameter of 29.2% and 30.8%, respectively (Zhao *et al.*, 2008).

Two species of eulophid wasps from Quadrastichus mendeli and Australia, Selitrichodes kryceri, which are larval parasitoids of L. invasa, have been introduced into Israel as part of a biological control programme for the pest (Kim et al., 2008). Two local species of *Megastigmus* have been found to be parasitoids of *L. invasa* in Turkey and Israel (Protasov et al., 2008) and another in Italy (Viggiani et al., 2001), but are not considered to be natural associates of L. invasa (Protasov et al., 2008). The strategies being adopted by most affected countries for dealing with the pest are the introduction of biocontrol agents and the deployment of resistant or tolerant species or clones.

Ophelimus maskelli (Hymenoptera: Eulophidae)

Ophelimus maskelli is another gall-forming pest of Eucalyptus that originated in Australia, where it is largely unknown, and has been found recently in several other countries, where it has become a problem. While O. maskelli has not yet been recorded from the tropics, it has been included in this chapter because its spread to date parallels closely that of the blue gum chalcid, L. invasa, which was first reported from Europe and the Middle East and now occurs in several tropical and subtropical countries in Africa, Asia and the Americas. Coupled with this is the striking similarity between the host ranges of O. maskelli and L. invasa.

In the Mediterranean and the Middle East, *O. maskelli* severely injures eucalypts, particularly *E. camaldulensis*, the most economically important planted hardwood species in the region (Protasov *et al.*, 2007b). As with *L. invasa*, this gall wasp was not accompanied by its principal natural enemies, which occurred in Australia, and therefore quickly reached epidemic levels. When it was first discovered in Europe, it was reported erroneously as O. eucalypti, a species known to be an invasive gall inducer on Eucalyptus in New Zealand (Withers, 2001; Protasov et al., 2007b). The first report of the insect from Europe was in Italy in 2000 and it has been recorded subsequently from Greece, Spain, France, England, Israel, Turkey, Portugal and Morocco. Protasov et al. (2007b) detail the biology and impact of the pest in the region. O. maskelli shows a clear tendency to oviposit in developed immature leaves, generally in the lower canopy, and it prefers to oviposit on an area of the leaf blade near the petiole. Each female lays an average of 109 eggs and each egg induces a gall. Gall diameter ranges from 0.9mm to 1.2 mm and there can be 11–36 galls/cm² of leaf. Under epidemic conditions, the entire upper leaf surface can be covered densely with galls (Plate 62). Heavy leaf galling can result in premature leaf drop soon after the emergence of the wasps. Both mature and voung trees can be infested. In Israel, where infested trees are close to humans, mass emergence of the spring population can cause a nuisance by forming 'clouds' of wasps (Protasov et al., 2007b). The insect produces three generations a year in Israel. Of 84 eucalypt species tested, 14 species were found to be suitable hosts: E. botryoides, E. bridgesiana, E. camaldulensis, E. cinerea, E. globulus, E. grandis, E. gunnii, E. nicholii, E. pulverulenta, E. robusta, E. rudis, E. saligna, E. tereticornis and E. viminalis (Protasov et al., 2007b).

In the Mediterranean region, *O. maskelli* shares its new habitat with *L. invasa*, and both species may infest the same leaf. *O. maskelli* develops only on the leaf blade, whereas *L. invasa* induces galls on the midrib, the petiole and newly developed twigs. This partitioning should minimize interference and competition, although preliminary data collected by Protasov *et al.* (2007b) suggest that *O. maskelli* is a better competitor and displaces *L. invasa*, or impairs its performance.

Two species of mymarid wasp, *Stethy*nium ophelimi and *S. breviovipositor*, and a eulophid wasp, *Closterocerus chamaeleon*, are parasitoids of *O. maskelli* (Huber *et al.*, 2006). *C. chamaeleon* has been released in Israel and appears to achieve effective biological control (Protasov *et al.*, 2007a). In the 16 months since its release at Bet Dagan in Israel, *C. chamaeleon* has spread some 1300 km to the city of Izmir in Turkey (Doganlar and Mendel, 2007).

Quadrastichus erythrinae (Hymenoptera: Eulophidae)

Erythrina is a widespread and diverse genus of trees with a pantropical distribution. It contains some 120 species (Mabberly, 2008), many of which have an important commercial, ecological or social value. Some are grown in tree plantations for timber or pulp, some are used as a living fence or as fodder for stock, but the principal use of Erythrina is as a shade tree for crops such as coffee and cocoa and a support tree for vines such as pepper or vanilla. Various species known as coral trees are used widely in the tropics and subtropics as street and park trees, and others are important components of native ecosystems (Rubinoff et al., 2010). Damage to *Erythrina* trees due to an invasive wasp, Q. erythrinae (Plate 63), was first documented in 2003 in Reunion, Mauritius, Singapore and Taiwan (Kim et al., 2004; Yang et al., 2004). In 2005, the insect was detected in southern China (Huang et al., 2005) and in Hawaii (Heu et al., 2005). Since then, it has been reported from India, Japan, Vietnam, Sri Lanka, Thailand, Malaysia, American Samoa, Western Samoa, Guam, Florida and Fiji (Faizal et al., 2006; Heu et al., 2006; Prathapan, 2006; Wiley and Skelly, 2006; Uechi et al., 2007; Messing et al., 2009). Q. erythrinae originates in East Africa (La Salle et al., 2009a) and is predicted to spread more widely in that continent as well as in Asia, Oceania and South America (Li et al., 2006). The predicted potential range includes tropical rainforest, tropical monsoon, subtropical monsoon and tropical savannah climates. In commenting on the rate of spread of *Q. erythrinae*, Rubinoff *et al*. (2010) note that within 2 years of its discovery, the pest was distributed across a tropical swath from Hawaii to India, a distance

of more than 12,546 km, much of it across open ocean. Long-distance dispersal is likely to be by global trade and locally by wind or transport on items such as clothing or flowers.

The erythrina gall wasp inserts eggs into young leaf and stem tissue of the tree. The larvae then develop within the plant tissue, forming galls in leaflets and petioles. As the infestation progresses, leaves curl and appear malformed, while the petioles and shoots become swollen (Plate 64). After feeding is complete, larvae pupate within the galls and the adult wasps cut exit holes through the plant gall material to emerge. Adults may live 3-10 days (Heu et al., 2006) and a single female wasp carries on average 322 eggs (Yang et al., 2004). The life cycle, egg to adult, is about 20 days (Heu et al., 2006). The species has overlapping generations and different stages of development can be found at the same time. Trees with large populations of wasps within the leaves and stems have reduced leaf growth and the plant declines in health. Severe gall wasp infestations may cause defoliation and tree death.

Studies by Messing et al. (2009) in five botanical gardens in Hawaii showed that 59 of the 71 species of *Erythrina* planted there were susceptible to Q. ervthrinae. It is in Hawaii that some of the most severe impacts of the pest have been reported. E. sandwi*censi*, known as the wiliwili tree, is endemic and a 'keystone' species in Hawaii's lowland dry forest, one of the most endangered ecosystems in the world (IUCN, 2010). It is also an important cultural and ethnobotanical resource (Doccola et al., 2009). In the first few years following the arrival of the gall wasp in 2005, mortality of E. sandwi*censi* due to the pest was estimated at 10% and the survival of the wiliwili tree was questioned, prompting a major seed-banking effort (Doccola et al., 2009). Widespread and nearly complete mortality, believed greater than 95%, was also reported in Hawaii for the Indian coral tree, *E. variegata*, a popular landscape tree, and on O'ahu alone the cost of removing dead trees exceeded US\$1m (Doccola et al., 2009). In Taiwan, where Erythrina also has great cultural importance, five species of Erythrina were affected across

the whole island, severe infestations resulting in defoliation and tree death (Yang *et al.*, 2004). The pest was reported from Sri Lanka in 2006 and at that time was confined to the plains, but there were fears that it would spread to the highlands, where *Erythrina* was the single most important shade tree of tea (Prathapan, 2006). Similar concerns are held in south India, where *Erythrina* is widely used as a live standard for trailing black pepper and vanilla (Faizal *et al.*, 2006).

A eulophid parasitoid, *Eurytoma erythrinae*, from Tanzania has been released in Hawaii as a biological agent of *Q. erythrinae* and reportedly is very effective (La Salle *et al.*, 2009b). Two other eulophid wasps from Africa, *Aprostocetus excertus* and *A. nitens*, also have potential as biocontrol agents against erythrina gall wasp (La Salle *et al.*, 2009b; Prinsloo and Kelly, 2009).

5.8 Root Feeding

A wide range of insects feed on the roots of trees, including white grubs, termites, root weevils, larvae of longicorn and buprestid beetles and root aphids. These insects generally are not a problem for established trees with well-developed and extensive root systems but they can cause serious damage in nurseries and young plantations, where the trees have small and fragile roots. The problem is sometimes intensified when soil cultivation or site preparation removes the other vegetation on the site, and root insects are then forced to feed on the roots of the planted stock (Berryman, 1986).

Among groups of root-feeding insects, termites are the most damaging in the tropics, species of *Odontotermes*, *Macrotermes*, *Microtermes* and *Coptotermes* (Plate 65) being responsible for considerable mortality of newly established plantations throughout Asia and Africa.

Lepidiota spp. (Coleoptera: Scarabaeidae)

The larvae of some species of scarab beetles, such as *Lepidiota* spp., feed on the root systems of young trees, often ring-barking and severing the stems below ground. Such insects are commonly referred to as 'white grubs' or 'curl grubs' and are important pests in nurseries and young plantations (Plate 66).

Typically, the adult female burrows into the soil to lay her eggs. Larvae live in the soil, feeding on decaying organic matter when young and, later, on plant roots. They migrate through the soil profile, burrowing deeper in very cold or very hot, dry weather and coming close to the surface in wet conditions. They pupate in the soil, often in a smooth-walled cell. New adults may remain in the soil for a period until stimulated to emerge by heavy rain. Some species feed on the leaves of trees and occasionally can cause severe damage. The life cycle of most species lasts 1–2 years.

In tropical and subtropical Queensland in Australia, the larvae of *L. trichosterna* and L. picticollis are among the most important nursery pests of hoop pine, A. cunninghamii, necessitating routine treatment of nursery beds with chemical pesticides. In young plantations of hoop pine, local losses of up to 60% have been recorded (Elliott *et al.*, 1998). Attack is usually most severe where plantations have been established on grasslands or on land previously devoted to agriculture. In 2-month-old E. exserta plantations on soft, sandy soils in southern China, Wylie and Brown (1992) record losses of up to 50% caused by *L. stigma* white grubs, often requiring a replanting of the whole area (Plate 67). This species is also reported as a pest of 1- to 2-year-old trees (Swietenia spp., T. grandis, F. moluccana, Anthocephala *cadamba*) in taungya plantations in East Java (Intari and Natawiria, 1973). The authors note that in such situations, the trees suffer more than the farm crops. In the Philippines, adults of a species of *Lepidiota* have caused almost complete defoliation of young plantations of A. auriculiformis and A. mangium in Mindanao (Wylie, 1993). L. mashona larvae are very injurious to seedlings of A. mearnsii in Zimbabwe and have been known to kill large saplings (Browne, 1968).

5.9 Stem and Branch Cutters

Several insect groups damage trees by severing stems or branches completely. In the case of some species of crickets and grasshoppers, such damage occurs mostly on nursery stock or newly planted trees. However, larvae of several species of longicorn beetle make spiral tunnels or 'cuts' across branches and stems up to 10 cm in diameter, causing them to snap off in wind or under their own weight. An example is *Hesthesis cingulata* in Australia, which severs the stems of eucalypt saplings just above ground level (Elliott *et al.*, 1998).

Strongylurus decoratus (McKeown) (Coleoptera: Cerambycidae)

This insect is common in hoop pine, *A. cunninghamii*, plantations in southern Queensland, Australia. It prunes mainly branches, but occasionally causes more severe damage, particularly to young trees, through pruning the leader.

As described in Elliott *et al.* (1998), eggs are laid singly into branches or leading shoots of hoop pine. The larva (Plate 68) tunnels in the cambial region for a time before boring longitudinally in the centre of the branch or top. Infested material may range from 1 to 10 cm in diameter. The larval stage occupies the tunnel for 39–41 weeks and pupation takes place at the end of the tunnel. Prior to pupation, the larva makes a transverse spiral tunnel or 'cut' across the stem, which creates a point of weakness where breakage can occur due to the weight of the stem or the effects of wind, leaving behind on the tree a stub which contains the insect. Sometimes, more than one larva may infest a branch and shed sections may then contain immature stages of Strongylurus decoratus. In constructing the pupation chamber, the mature larva cuts two sets of two exit holes transversely from its tunnel to the exterior, a short distance back from the pruning cut. It blocks both ends of its tunnel between the two sets of holes with plugs of wood slivers, forming a pupation chamber (Plate 69). Approximately 4 weeks after the holes are cut, the insect enters a prepupal stage, which lasts for 7–10 days, and then pupates for a further 4 weeks. The teneral adult may remain in the chamber for 1 or 2 weeks before removing a plug and

exiting through one of the holes cut previously. Egg laying commences after 1-2 weeks.

S. decoratus has affected trees ranging in age from 4 years to more than 30 years and in height from 3 to 31 m. In some cases, trees have been defoliated completely, with only branch stubs remaining, but top damage is generally of most concern. In some areas, an incidence of leader attack of between 15 and 41% has been recorded. Some of the most severe attacks have been linked with below-average site quality, usually in upper slope positions, and with tree provenance (Wylie, 1982b).

A complex of natural control agents operates against larval and pupal stages of the insect, including encyrtid and ichneumonid wasp parasitoids and tachinid flies, and a predatory clerid beetle larva. Cockatoos are important predators of pupating larvae and seem to use the exit holes cut by the larva as visual clues to the location of their prey. Incidence of cockatoo predation sometimes reaches 20%.

Brachytrupes spp. (Orthoptera: Gryllidae)

Crickets, together with grasshoppers, cutworms and white grubs, form the chief pests of young seedlings but they are rarely detected in the act of injury. *Brachytrupes* is a genus of ground-dwelling crickets, occurring in Africa and throughout Asia, which contains several species injurious to seedlings in the nursery and sowings in the open.

The main species in Asia is *B. portentosus*, which makes a deep tunnel with an opening at the ground surface that is surrounded by ejected earth (Beeson, 1941). The eggs are laid at the bottom of the tunnel and the newly hatched nymphs remain in the tunnel for a time and then disperse. Young crickets dig themselves new tunnels every few days and these become longer and more ramified as the insects grow older. The adult stage is reached in a few months and the insect then occupies the same tunnel throughout its life. There is usually one generation a year. The cricket feeds on young seedlings and low shoots, cutting them off at night and dragging the pieces into the tunnel for feeding. In India, this species has been recorded damaging several tree species in nurseries. In north Bihar, for example, it killed up to 30% of E. tereticornis and G. arborea in one season (Ali and Chaturvedi, 1996) and 8-21% of D. sissoo seedlings (Sah et al., 2007). Similarly, in the Jabalpur region of India, B. portentosus damage to roots and shoots of D. sissoo in nurseries resulted in 20-25% mortality of plants (Kalia and Lal, 1999). Beeson (1941) mentions that it attacks field plantings of Casuarina less than 60 cm high, but that taller trees escape. B. portentosus is a pest of newly planted trees in southern China, at one site damaging 40% of 3-monthold E. urophylla in a 10 ha plantation (Wylie and Brown, 1992). In a community woodlot project in north-eastern Thailand, the cricket was listed by Hutacharem and Sabhasri (1985) as one of the main pests of young E. camaldulensis.

In Zimbabwe, *B. membranaceus* is a pest of *Thuya* sp. and *E. grandis*, in some cases affecting more than 50% of plants (Taylor, 1981). This cricket occurs mainly on sandy soils, where it lives in a long, curved burrow up to 1 m in length. It cuts off seedlings, leaving just a stump, and carries them back to the burrow, where they are consumed. The insect also collects plants that have been cut off and left by cutworms and false wireworms.

In both Africa and Asia, indigenous peoples use *Brachytrupes* species as food (Fasoranti and Ajiboye, 1993; Agbidye *et al.*, 2009; Raksakantong *et al.*, 2010).