chestnut leafminer described above is one example. Others include white marked tussock moth (*Orgyia thyellina*) in Auckland, New Zealand which was the subject of an intensive and successful eradication campaign involving repeated aerial application of the microbial control agent *Bacillus thuringiensis*. The authorities in Auckland are currently grappling with an outbreak of painted apple moth (*Teia anartoides*), a pest from Australia. Prevention of international movement of defoliators is an important task for national and regional Plant Protection Organizations and, internationally, legislation is already in place to raise awareness and to prohibit or manage the main pathways for movement of these pests in trade. In particular, international movement of plants is controlled very carefully, which tends to reduce the likelihood of egg or larval stages of defoliators being transported. However, life stages that could survive transit are not always associated directly with plants, making it extremely difficult to both inspect and to legislate against such incursions. For example, gypsy moth egg masses can be found on virtually any substrate, including the undersides of vehicles, etc., thus making inspection a very onerous task. Detailed pest risk analysis helps to identify the high-risk pathways and can aid risk management protocols, but it is also important that pioneer populations of a new pest are detected early and, where appropriate, action taken to eradicate or manage the problem. Unfortunately, it is often the case that by the time a population of an exotic pest is discovered it is already well established, thus making eradication a difficult prospect. However, the eradication of white marked tussock moth in New Zealand does indicate that a concerted campaign carried out in a determined manner can be successful.

Conclusion

In conclusion, insect defoliators can compromise tree growth and even lead to tree mortality. However, in relation to total diversity of insects on trees, heavy defoliations tend to be the exceptions and are often caused by a single pest species, thus pointing to the possibility of developing monitoring and management regimes for detection and for direct or indirect action. Effects can be serious when volume increment is an important component, for example in the growing of a commercial crop of trees. When trees are not grown for direct commercial reasons, their relatively high tolerance to attack means that occasional episodes of defoliation, although temporarily impairing visual and amenity values, do not significantly affect the long-term contributions of trees to the landscape (**Figure 1**).

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects. **Health and Protection**: Integrated Pest Management Practices; Integrated Pest Management Principles. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

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Sapsuckers

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Introduction

Insects of the order Hemiptera have mouthparts specialized for piercing and sucking, and within the suborder Homoptera of this order two groups, the Auchenorhyncha and Sternorhyncha, specifically feed on plants. As their general name implies these insects feed on the sap of plants. This can be the sap of individual mesophyll or palisade cells of leaves or the translocating elements of plants, in particular phloem. In feeding on phloem sap not only have these insects access to a more continuous supply of food but they can inject disease-causing organisms and saliva containing physiologically active chemicals, which are then translocated throughout a plant. In addition by telescoping generations aphids have overcome the developmental constraint and for their size achieved prodigious rates of increase. As a consequence aphids often become very abundant and so in addition to any indirect damage they can be extremely damaging because of the nutrient drain they impose on plants. That is, many phloem feeders in particular are such serious pests of trees that they threaten their survival, e.g., the scale insects *Carulaspis minima* and *Lepidosaphes newsteadi* attacking Bermuda cedar on Bermuda and *Orthezia insignis* attacking the native gumwood on St Helena. However, as they often do not apparently affect the leaf area or distort the leaves the damage goes largely unnoticed. The damage done by those sapsuckers that feed on mesophyll and palisade cells is often very conspicuous but possibly less damaging to the plant than that inflicted by the phloem feeders.

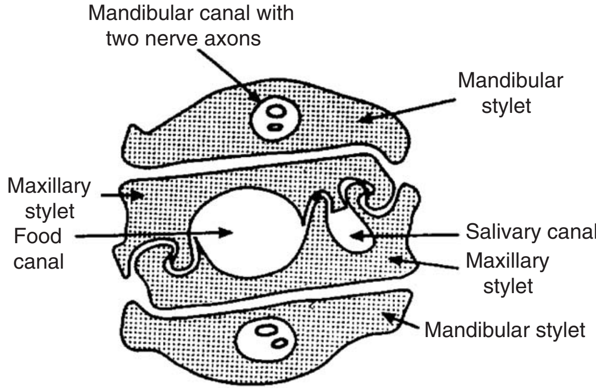

Figure 1 Diagram of a transverse section through the stylet bundle of an aphid. Reproduced with permission of Kluwer Academic Publishers from Dixon AFG (1998) *Aphid Ecology*, 2nd edn. London: Chapman & Hall.

Mode of Feeding and Nitrogen Metabolism

As indicated above the mouthparts of the Hemiptera are adapted for piercing and sucking rather than chewing. The mandibles and maxillae are modified to form slender bristlelike stylets, which rest in the grooved labium. Both pairs of stylets are hollow and capable of limited protrusion and retraction by means of muscles. In the coccids and psyllids the stylets may be extremely long and greatly exceed the length of the insect, being looped and coiled upon themselves within its body. The mandibular and maxillary stylets together form a needlelike structure. Cross-sections through the stylets reveal that the maxillary stylets have two parallel channels on their inner aspects and are interlocked. The approximation of the two stylets results in the formation of two extremely fine tubes. The dorsal one functions as a food canal and the finer ventral one as a salivary duct (**Figure 1**).

Of the two groups of Homoptera that specifically feed on plants it is the Sternorhyncha that have specialized on feeding on phloem elements of plants and produce large quantities of honeydew (**Figure 2**), which is often the first indication of their presence. The reason for the abundance of honeydew is that phloem sap is rich in sugars but contains relatively little amino-nitrogen. To overcome this problem the insects process very large quantities of phloem sap removing most of the amino-nitrogen and excreting the sugars as honeydew. Because phloem sap is rich in simple sugars it creates an osmotic problem for the insects, which is overcome by converting the simple sugars into complex sugars, which effectively reduces the osmolality of the phloem sap as it passes through the insect. In addition, these insects are very effective at assimilating and utilizing the low levels of amino-nitrogen in their food. First, they are able to process rapidly relatively large volumes of phloem sap and so fuel their total requirements for amino-nitrogen. Second, they generally have symbiotic bacteria in bacteriosomes within their haemocoel, which increase the efficiency of their nitrogen metabolism by converting the nonessential amino acids in phloem sap into the essential amino acids the insects need to sustain their growth. In addition the symbionts may also recycle some of the insect's nitrogenous waste. In this way the aphids in particular are able to sustain a prodigious rate of growth on what is a very poor quality diet. That is, they are able to process quickly very large quantities of phloem sap and upgrade the quality of the amino-nitrogen component of their diet.

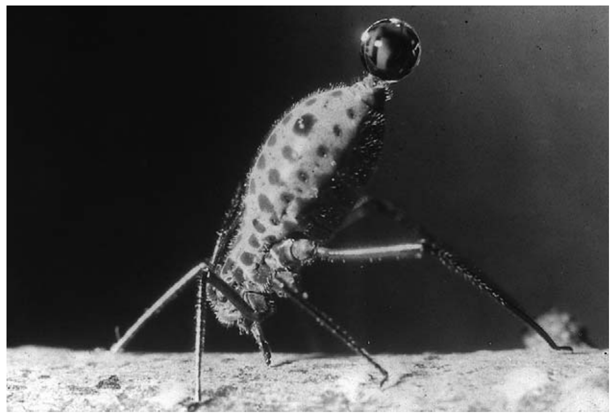

Figure 2 A giant willow aphid excreting a droplet of honeydew. In this case the aphid has its stylets inserted into a large willow twig.

Regional Distribution and Abundance

Correlation between the number of species of plants in an area is much better with the number of species of the least host-specific sapsuckers, the aleyrodids and coccids, than with the most specific, aphids and psyllids. In temperate regions sapsuckers, in particular aphids, are often an important and central component of the insect fauna of the canopies of trees. However, associated with the increase in plant diversity as one approaches the tropics is a decrease in aphid diversity, the reverse of what is seen in many other groups of animals and plants. This has been attributed to the lack of a marked seasonality in the growth of plants in the tropics or to a constraint imposed by the high host specificity and short period of time aphids can spend off their host plants searching for hosts. Although there are many species of plants in the tropics, all potential hosts of aphids, few of these plants are abundant enough to sustain a specific aphid. That is, for aphids to be able to survive its host plant has to be relatively abundant. However, other sapsuckers are more diverse, some considerably so, in the tropics. For example, there are 1000 species of Auchenorhyncha in the Panama Canal Zone, whereas there are only 350 species in the whole of Britain.

Ecology

Sapsuckers feeding on the leaves of trees that make up the forest canopy live in 'one of the least explored zones on land.' Obtaining estimates of the abundance of sapsuckers in the canopies of trees, which in the tropics can be very tall, presents considerable technical difficulties. Fogging the canopy with pesticides is often used to obtain such estimates but the accuracy of such estimates depends on the ease with which the insects are dislodged and whether they are likely to be intercepted by other leaves in falling through the canopy. Cranes have also been used to access the canopy and the estimates so obtained are likely to be more realistic and are only limited by the area that can be sampled from the crane.

Such samples show that ants can dominate the biomass of the arboreal fauna of tropical lowland forests. Since ants are largely regarded as predominantly predacious, this pattern challenges the usually accepted pattern of energy flow, in which the biomass of predators should only constitute a proportion of their prey. This has led authors to hypothesize that the availability of homopteran (Coccidae and Membracidae) honeydew provides a key resource for ants. As in temperate regions the homoptera on a particular tree are mostly monopolized by a single ant colony.

In summary, the few data that are available tend to indicate that there are more species of sapsucker in the tropics but they are less abundant than aphids such as the lime or sycamore aphids in temperate regions (**Table 1**). However, until projects with similar objectives and using similar methodologies are undertaken in the tropics and temperate regions these conclusions need to be treated with caution.

Direct Effects of Sapsucker Infestation

As phloem sap contains high concentrations of sugar and very little amino-nitrogen aphids have to process very large quantities of sap in order to obtain sufficient amino-nitrogen to sustain their very high rates of growth. In the case of the giant willow aphid (*Tuberolachnus salignus*), a single aphid consumes the photosynthetic product of 5–20 cm^2 of leaf per day. The annual energy drain imposed on a 14-m tall lime tree by a natural population of the lime aphid (*Eucallipterus tiliae*) is considerable (**Figure 3**). During the course of a year, the population turns over its own standing crop 482 times, or 3.4 times day^{-1}. This is considerably greater than that achieved by oribatid soil mites (38 times $year^{-1}$) and grasshopper populations (10 times $year^{-1}$). Thus although the lime aphid is not particularly effective at utilizing its energy intake, it turns over energy at a massive rate, much of which falls to the ground as honeydew. The annual production of honeydew by the lime aphid is equivalent in energy terms to 0.8 of

Table 1 Estimates of the standing crops of sapsuckers on trees in tropical and temperate forests

Forest	*Country*	*Method of sampling*	*Standing crop/unit weight or area of leaf*		*Reference*
			Number	*Weight*	
Tropical	Panama	Direct	3.4 m^{-2}		Basset (2001)
Tropical	Panama	Direct	3.5–11.8 m^{-2}	5.7–20 mg m^{-2}	Wolda (1979)
Tropical	Puerto Rica	Direct	6–500 kg^{-1}		Schowalter and Ganio (1999)
Temperate	UK	Direct	**Sycamore aphid**		Author's data
			115–742 m^{-2}	85–520 mg m^{-2}	
			508–7364 kg^{-1}	374 mg–5.15 g kg^{-1}	
			Lime aphid		
			150–801 m^{-2}	27.5–143 mg m^{-2}	
			955–7864 kg^{-1}	175 mg–1.39 g kg^{-1}	

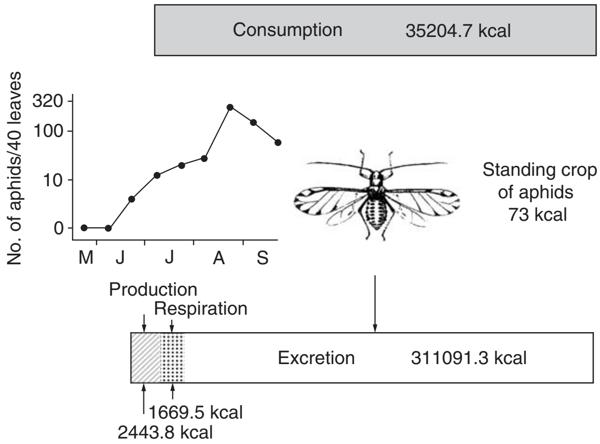

Figure 3 The annual consumption, production, respiration, and excretion, and average standing crop of a population of lime aphids on a 14-m tree, expressed in terms of energy. Inset is a graph of the lime aphid population trend for which this energy budget was computed.

that locked up in the leaves at leaf fall. In the case of the sycamore (*Acer pseudoplatanus*) it is on average equal to the energy in the leaves at leaf fall.

In the presence of the wood ant (*Formica rufa*) the energy drain imposed on sycamore can change dramatically. This ant preys on the sycamore aphid and tends another aphid found on sycamore, *Periphyllus testudinaceus*. In the absence of the ant the sycamore aphid removes approximately three times as much sap from trees than in its presence, whereas the ant-tended species removes 50 times more sap from ant-foraged trees than from unforaged trees. However, the ant-tended aphid on average only removes one-fifth of that removed by the sycamore aphid each year.

Aphid-infested sycamore saplings clearly grow markedly less than uninfested saplings. Although aphids do not affect the number of leaves borne by lime (*Tilia* spp.), oak (*Quercus* spp.), or sycamore, sycamore produces smaller leaves, which contain more nitrogen, when heavily infested in spring. However, the leaf area equivalent to the energy removed by sycamore aphids only accounts for a small proportion of the observed diminution in leaf area. If the drain imposed is expressed in terms of nitrogen rather than energy then aphids again remove far less nitrogen than expected from the reduced size of the leaves. This implies that the effect aphids have on tree growth is not a direct consequence of the energy and/or nutrient drain. Other factors, e.g., the saliva aphids inject into plants, contain physiologically active components that might also adversely affect tree growth.

The width of the annual rings of sycamore is positively correlated with the average size of the leaves, and negatively with the numbers of aphids on the tree throughout a year. This is possibly associated with the fact that each annual ring is composed of two types of vessel, which make up the spring and summer wood. The springwood is mainly laid down when the leaves are developing in spring, whereas the summerwood is mainly laid down after the leaves stop growing. In the absence of aphids some sycamore trees could produce as much as 280% more stem wood. Lime and oak aphids hatch later, relative to the time of bud burst of their host trees, than the sycamore aphid, and as a consequence rarely become abundant before the leaves are fully grown. This is reflected in the fact that the aphids on these trees do not affect the aboveground growth in girth and stem length of their respective hosts. However, infested saplings of lime and oak often weigh less at the end of a year than they did at the start, mainly due to a reduction in the mass of their roots.

Aphid infestation causes early leaf fall in all three species and, in oak and sycamore, results in the leaves becoming a darker green. In oak this is a consequence of a 25% increase in the quantity of both chlorophyll A and B. Associated with this is an increase in dry matter production per unit area of leaf, which in sycamore can be 1.7 times greater in infested than in uninfested saplings. Following years of heavy aphid infestations lime and sycamore break their buds later than usual, and in the case of lime the leaves are smaller and a darker green, and have a net production 1.6 times greater than the leaves of previously uninfested saplings.

Indirect Effects of Sapsucker Infestation

As indicated above, aphids produce large quantities of honeydew, which contains a high percentage of the trisaccharide sugar melezitose. Much of this honeydew reaches ground level, which can result in there being as much as 10 g of sugar per 100 g of soil. This has led to the proposal that trees release surplus sugars by enlisting the help of aphids. This sugar is utilized by free-living nitrogen-fixing bacteria in the soil, which increase in number beneath aphid-infested trees and make more nitrogen available to these trees. Melezitose, or a particular mixture of sugars characteristic of honeydew, is thought to have an optimal affect on nitrogen fixation. The aphids are seen as a necessary ‘part’ of a tree, releasing surplus sugars that promote a better supply of nitrogen.

The addition of the four sugars commonly found in honeydew – fructose, glucose, melezitose, and sucrose – to soil at rates equivalent to those found beneath lime trees infested with aphids causes an increase in the abundance of bacteria in woodland soils. In the laboratory fructose is more effective at promoting nitrogen fixation than melezitose. However, as a single sugar was used rather than a mixture this result does not refute the original hypothesis. In a more rigorous test of the mutualism hypothesis, in which alder aphids (*Pterocallis alni*) were removed from red alder (*Alnus rubra*) by spraying with malathion, aphid infestation resulted in a decrease in ammonification and nitrification in the soil, and a decrease in aboveground primary production. Although this does not rule out the possibility that melezitose may stimulate nitrogen fixation by soil bacteria, nevertheless, contrary to the prediction of the hypothesis, nitrogen availability in the soil is markedly reduced by large quantities of aphid honeydew and there is no positive effect on tree growth.

Much of the honeydew excreted by aphids feeding on the leaves and needles of trees falls on to the upper surface of other leaves where it promotes the growth of sooty molds. In some years these sooty molds blacken the upper surface of the leaves. On pecan (*Carya illinoensis*) these molds can reduce light penetration and photosynthesis by factors of from 25% to 98%. In addition, the darkening of the leaf surface can result in an increase in leaf temperature of 4°C. Epiphytic microorganisms, which include the sooty molds, are one of the most abundant groups of organisms. In areas where there is a lot of industrial pollution rich in nitrogen the limiting resource for epiphytic microorganisms is energy. Increasing the availability of energy in forest canopies in such areas results in a dramatic increase in the abundance of microorganisms (bacteria, yeasts, and filamentous fungi) of two to three orders of magnitude on the needles and leaves of aphid-infested trees. In addition to the changes in abundance there are also changes in species composition, more so on the leaves of beech (*Fagus sylvaticus*) than on oak, probably due to differences in the surface micromorphology of the leaves. In nonpolluted areas the nitrogen and sugar in honeydew are sufficient to stimulate an abundant growth of microorganisms when aphids are abundant on sycamore.

Less well understood are the effects of these microorganisms on throughfall chemistry, which is important because it determines the input of nutrients and ions into forest soils. For example, in June when aphids are most abundant on Sitka spruce (*Picea sitchensis*), the concentration of dissolved organic carbon (DOC) in throughfall collected beneath infested spruce trees is high and declines with the subsequent decline in aphid numbers. There is a very high correlation between DOC concentrations in throughfall and aphid abundance. The concentration of dissolved organic nitrogen (DON) in throughfall increases after the aphid population peaks and starts to decline in abundance. Concentrations of inorganic nitrogen are lower in throughfall collected beneath spruce heavily infested with aphids compared with uninfested trees but it becomes similar as the aphid numbers decline.

Field experiments show that following a high input of DOC from the canopy there is an increase in the DOC concentration in forest soil solutions, which is slightly delayed and longer-lasting than the aboveground aphid infestation. Similarly, there is an increase in the concentrations of DON and NO_3-N in the forest floor solution beneath aphid-infested trees. Laboratory experiments, in which simulated artificial honeydew is applied to cores of forest soil, reveal that low to medium inputs of honeydew increase base respiration within 1 h and cause a decline in NH_4-N fluxes. Large inputs of honeydew increased the immobilization of both NH_4-N and NO_3-N and slightly reduced DON fluxes. The DOC fluxes increase considerably but decline to base level within 72 h of applying the honeydew. That is, inorganic carbon from aphids in throughfall affects the mineralization, mobilization, and transport of organic matter in forest soils.

In conclusion, we are only just beginning to record the species and abundance of sapsuckers present in the canopy of forests, especially in the tropics. Nevertheless, they appear to be more species-diverse in this habitat in the tropics than in temperate regions but in terms of total biomass they are possibly more abundant in the temperate regions.

In temperate regions sapsuckers, in particular aphids, greatly reduce the growth of trees, whereas their honeydew encourages the growth/activity of epiphytic and soil microorganisms. This is in addition to their being an abundant source of food for insectivorous birds and the hosts and prey of various insect parasitoids and predators. That is, in spite of being relatively inconspicuous, sapsuckers possibly have a 'keystone' role in determining the community structure of temperate forests.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

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Bark Beetles

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Bark beetles are small, dark, cylindrical beetles, usually less than 7 mm long. As their name implies, they are usually associated with woody plants. Despite their small size and modest appearance, they have an intriguing assemblage of feeding and breeding habits, some of which result in significant economic losses to forest and agricultural industries. This article reviews the taxonomy, life cycle, host–plant interactions, and ecosystem consequences of bark beetles, concluding with management options.

Taxonomy

Bark beetles have commonly been considered a family, Scolytidae, but recent taxonomy places them as a subfamily, Scolytinae, within the weevil family Curculionidae. Major characteristics that are shared with weevils include elbowed, clubbed antennae, larvae that feed within plant tissues, and the loss of the development of legs in larvae (**Figure 1**). The Scolytinae and closely related Platypodinae differ from typical weevils in their oviposition behavior: adults bore deeply into plant tissues to oviposit, while typical weevils use their elongated rostrum to create egg niches from the surface of the plant. Many of the Scolytinae do not actually breed in bark, as discussed below, but the common name 'bark beetle' is applied to this whole taxonomic group.

Bark beetles comprise approximately 6000 species, found worldwide. Their origin was in the Cretaceous, with an early association with the ancient conifer *Araucaria* distributed across Gondwana. Subsequent diversification into tribes and subtribes has occurred in North America, South America, Eurasia, and Africa. About 30% of extant genera are temperate in distribution.

Life Cycle

Upon arrival at a host plant, adults quickly begin to burrow into the plant to breed. Several species are known to histolyze their wing muscles upon arriving at breeding habitat. The sex that initiates a breeding site, the pioneer sex, differs among species. In many species, the beetle initially constructs a nuptial chamber where mating will occur (**Figure 2**). Many species emit pheromones at this stage that attract the opposite sex but also others of the same sex. When both sexes are attracted, the pheromones are called aggregation pheromones, and they result in a rapid colonization of the surrounding plant tissues. Such aggregation is a notable feature of bark beetles. Many pheromones are derived from precursors in the plant tissues, especially defensive compounds such as monoterpenes. However, the same pheromones can sometimes be synthesized *de novo*, or be produced by associated microbes. The link between plant defenses and pheromones means that pheromones can indicate the state of the tree to other beetles, which is especially important for those beetle species that