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Defoliators

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Introduction

The dictionary definition of a defoliator is 'an insect that strips the leaves from plants.' This serves as a useful broad statement of both the nature of the biotic agent and of its overall impact on its primary target resource on trees. Its effects on tree growth and structure are manifested through removal of photosynthetic and transpiration tissues from trees, thus compromising the ability of the tree to grow, respire, control moisture loss, etc. Defoliation, therefore, is rightly regarded as detrimental to the plant but the severity of effects depends very much on both the timing and nature of defoliation. In the brief description in this article, defoliation is taken to mean the damage or removal of leaves by direct feeding, rather than the indirect defoliation that can occur from damage to other parts of the plant leading to browning of leaves and indirect loss.

Defoliating Species

Leaf feeders are found in a number of insect orders, particularly in the moths (Lepidoptera) (**Figure 1**), sawflies (Hymenoptera), grasshoppers (Orthoptera), and beetles (Coleoptera). Some feed on tree foliage exclusively in the larval stage, while others can include adult only or both adult and larval feeding. In all cases, however, timing of insect activity to coincide with the most suitable stage of leaf development and tree growth is critical. Some species, such as the winter moth (*Operophtera brumata*) overwinter as an egg and require close synchrony between egg hatch and bud burst to ensure maximum survival of the newly hatched larvae as they feed on the expanding leaves. It is fascinating to note, as an example of the potential effects of climate change, that oak bud burst in the southern part of Great Britain has advanced by an average of 20 days during the final 50 years of the twentieth century. This might be thought to give the tree an advantage in that bud burst could be too early for the young winter moth larvae. However, showing the high adaptability of many insect species, winter moth egg hatch has also advanced by around 20 days, thus retaining synchronization with its primary host tree. By contrast, a new association between winter moth and the exotic Sitka spruce (*Picea stichensis*) has not retained synchronization because bud burst in this tree species is not so dependent on temperature.

Figure 1 A larval teak defoliator moth.

Impacts

As a general rule, suitability of leaves for feeding by the most vulnerable life stages of an insect is a strong determinant of the degree of defoliation and, ultimately of breeding success by the insect. Broadleaved tree species tend to tolerate episodes of defoliation without a high risk of tree mortality. This is mainly because the trees tend to be able to refoliate during the growing season and will develop adequate buds for shoot extension in the following year. This is not to say that the effects on tree growth are negligible. Attacks by teak defoliator moth (*Hyblaea puera*) during the early stages of development of teak trees (*Tectona grandis*) can result in up to 44% loss of growth increment during the first 9 years and up to 13% loss of total volume over the rotation of the crop. Losses of up to 30% in stem growth have also been recorded for defoliators of temperate broadleaved trees (e.g., 7–13% loss of beech growth arising from 90% defoliation by pale tussock moth (*Dasychira pudibunda*) in continental Europe).

The degree of tolerance to defoliation by conifers depends on whether either or both current and older foliage is consumed. Although known to have a significant effect on growth increment, European pine sawfly (*Neodiprion sertifer*) does not kill pine trees because it feeds exclusively on older foliage. By contrast, pine beauty moth (*Panolis flammea*) feeds on both young foliage and, later, on older foliage and can completely defoliate trees leading to heavy mortality. Similar specialization in feeding sites is apparent in the major lepidopterous pests of conifer forests in North America so that, for example, although spruce budworm (*Choristoneura fumiferana*) is regarded as highly damaging and occasionally renders trees vulnerable to mortality from actions of other biotic and abiotic factors, it does not lead directly to tree mortality, unless there are several consecutive years of heavy defoliation. This arises from larval feeding specialization on expanding young foliage in the spring which, although damaging, still allows the plant to photosynthesize through older foliage and to develop buds for the following year.

Management Approaches

The above examples illustrate the diversity of feeding habits for those defoliators that totally consume leaves or needles. This external feeding habit means that they can be vulnerable to natural enemies and to direct intervention in management programs. Thus, use of chemical or, particularly, microbial control agents can be contemplated when the economic or environmental case requires intervention. Integrated pest management approaches to control of defoliator populations are discussed elsewhere in this volume (*see* **Health and Protection**: Integrated Pest Management Practices. **Tree Breeding, Practices**: Biological Improvement of Wood Properties). Other defoliators have more cryptic habits, including leaf mining where larval feeding takes place entirely within the leaf, leaving the outer surfaces intact. An interesting example in this category is the horse chestnut leafminer (*Cameraria ohridella*) which was only described for the first time in 1985 in Macedonia. This micromoth has, from a slow start, now spread across most of Western Europe and is giving rise to heavy cosmetic damage and premature leaf fall in urban horse chestnut (*Aesculus hippocastanum*) trees. The rapid spread of the moth from its original restricted range has been attributed to human movement, particularly of leaves accidentally falling onto vehicles and being carried long distances before emergence of the next generation of moths. It was found for the first time in Britain in 2002 in the Wimbledon area of London. By mid 2003 it had spread to Kingston and Oxford and is likely to colonize horse chestnut trees in most towns in the south of England and possibly elsewhere in Britain. At this stage there are no effective longer-term control measures, although collection and burning of fallen leaves in the autumn is known to reduce populations significantly.

Defoliators and Biodiversity

Defoliators are, therefore, significant biotic agents affecting tree health and growth and can even lead to tree mortality. Fortunately, the number of species resulting in these extreme impacts on trees is relatively rare. Indeed, it is a fortunate ecological fact that trees support a wide range of defoliators without showing undue signs of ill health and thus act as a valuable resource for enhancing invertebrate biodiversity at both local and landscape scales. In general, broadleaved trees with wide distributions tend to support more species than conifers or broadleaved tree species with restricted distributions. This has been well studied in Britain and it is known that oak (*Quercus* spp.) and willow (*Salix* spp.) support the greatest biodiversities of insects. Some of these, such as winter moth and oak leaf roller moth (*Tortrix viridana*) on oak occasionally reach damaging population densities, but these subside under the actions of natural enemies and resource limitation without causing tree mortality.

International Movements and Pest Risk Analysis

Greater diversity of defoliators on trees also tends to be accompanied by greater diversity of natural enemies, again contributing to the maintenance of a balance between resource utilization, in terms of leaves consumed, and effects on tree growth and health. This natural balance will have evolved over very long time periods and can be compromised through the introduction of exotic elements into the ecosystem. These can be in the form of exotic host trees or of exotic defoliator species or a combination of the two. Pine beauty moth is a good example of the former category. This species of moth is innocuous on Scots pine (*Pinus sylvestris*) in Britain but became a lethal pest when North American lodgepole pine (*P. contorta*) was planted in the north of Scotland from the 1960s. International movement of insect pests is increasing with the expansion and increased speed of global trade and there have been a number of instances of defoliators establishing and causing damage in new geographical locations. The horse 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