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Foliage Feeders in Temperate and Boreal Forests

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Introduction

Insect consumers of tree foliage comprise one of the most abundant and diverse feeding guilds in forest ecosystems. Known as folivores, this guild is integral to the structure and functioning of forests. Folivores influence vital ecosystem processes in forests, including nutrient turnover, competition among plants, and stand structure. In addition, these insects are critical sources of food for many invertebrate and vertebrate predators. In this article, we will address foliage-feeding insects that affect trees in temperate and boreal forests. In these ecosystems, an estimated 10–30% of the total leaf area is annually removed by leaf-chewing forest insects. In some forest types, defoliating insects strongly influence productivity and the long-term dynamics of the ecosystem. Foliage-feeding insect species have little effect on tree health in most years. During outbreaks of some insect defoliators, however, the entire canopy can be consumed, sometimes for several years in succession. While outbreaks may cause significant economic harm by accelerating tree mortality, reducing productivity and increasing fire risk, they may also play an important long-term role in maintaining healthy forests.

Diversity

In this section, we focus on folivores with chewing mouthparts, which represent the vast majority of

insects feeding on the leaves of hardwood trees (deciduous angiosperms) and the needles of conifers (gymnosperms). The forest defoliator guild is comprised of insects from several different orders. The greatest diversity of species is found within the order Lepidoptera. Nearly all larval Lepidoptera are herbivorous whereas the adults may imbibe fluids such as nectar or, as in many economically important species, may not feed at all. The sawflies (Symphyta), a relatively primitive group of Hymenoptera, are also important foliage feeders. Like the Lepidoptera, larval sawflies are herbivorous while adults generally do not feed. In addition to sawflies, leaf-cutting ants (family Formicidae) are another group of Hymenoptera that feed on foliage. While not important or diverse in temperate regions, leaf-cutter ants are the dominant herbivore in many tropical forests. Among the beetles (order Coleoptera), the diversity of leaf-feeders is richest in the large families Chrysomelidae and Curculionidae. Both adults and larvae in these families feed on foliage. Several other insect orders also contain species that can function as forest defoliators. These include grasshoppers, crickets, and walking-sticks from the order Orthoptera, and several families of flies (order Diptera). Other guilds of tree-feeding insects, such as sap-feeders and shoot borers, can also cause defoliation but will be described in other articles (see **Entomology: Defoliators; Sapsuckers**).

Feeding Ecology

Folivores with chewing mouthparts can be partitioned based on their general feeding type. Three types are generally recognized: free-feeding, shelter-feeding, and leaf-mining. Insects that free-feed consume leaf tissue openly. Species utilizing this type of feeding may consume all parts of the leaf (many caterpillars, sawflies, and orthopterans) or may avoid veins and other structural tissue (shot-hole, window-feeding, or skeletonizing). Skeletonizing is characteristic of chrysomelid beetles as well as some caterpillars and sawflies. Because free-feeding species are exposed to predators as they forage, many have adaptations, that may reduce their risk of mortality from these natural enemies. These include high mobility, nocturnal feeding, cryptic coloration, sequestration of toxins, physical defenses such as urticating or stinging hairs, or stereotyped defensive behaviors like regurgitation, head flicking, or dropping immediately to the ground upon sensing danger.

Another common feeding strategy is shelter-feeding. Shelter-feeding species may enclose and feed on foliage within a silk structure, or may use silk to roll leaves or to tie leaves or needles together. Enclosures

are often used by gregarious species including fall webworm (*Hyphantria cunea*) and ugly-nest caterpillar (*Archips cerasivorana*). Many solitary species of Lepidoptera, as well as some sawflies, create tubes or shelters by leaf-rolling or tying. These structures provide a concealed place for the larva to rest and feed. Leaf-rollers and leaf-tiers tend to have lower mobility than free-feeders and fewer species have evolved physical or chemical defenses. Instead they rely on reduced visibility to escape natural enemies. Some species have evolved behaviors thought to lower the risk of detection by parasitoids that rely on chemical signals to find their hosts. For example, a number of lepidopteran leaf-rollers eject their frass (feces) from the feeding tube, often for considerable distances, which reduces the scent profile of the caterpillar.

Leaf-mining represents another type of folivory. Insects that mine leaves or needles are usually small and dorsoventrally compressed, an adaptation for feeding between the upper and lower layers of the leaf epidermis. Leaf-mining requires a more intimate association with the host plant and specific behaviors may be required to avoid host defensive responses such as leaf-shedding, withdrawal of nutrients, or increased concentrations of secondary chemicals. These behaviors can be critical as many leaf-miners utilize only a single leaf over their lifespan and cannot mitigate unfavorable conditions by moving. Several families of Lepidoptera, sawflies (Tenthredinidae), the dipteran families Agromyzidae and Anthomyiidae, and the beetle families Chrysomelidae, Buprestidae, and Curculionidae have all adopted this life-history strategy. Folivores may utilize one feeding method when small, while switching to another feeding strategy in later larval stages. For example, spruce budworm (*Choristoneura fumiferana*) larvae may mine needles in the early larval stages, but utilize a needle-tying feeding strategy as they become larger.

Population Dynamics

The population dynamics of forest-defoliating insects have long been of particular interest to ecologists. The vast majority of this research has focused on a relatively small group of species characterized by explosive changes in population density known as outbreaks. This bias is primarily due to the spectacular nature of outbreaks and the potential of these species to cause economic harm. Because factors important in the dynamics of outbreak species may not necessarily be the same for the vast majority of leaf-feeding forest insects that never outbreak, we must be cautious in generalizing from studies of

outbreak species. In outbreaking species, populations increase from virtually undetectable levels to densities that defoliate entire forests, often in only a few generations. While outbreaks occur at irregular intervals in some species, there are a fascinating subset of species whose populations rise and fall at regular intervals, known as cycles. A number of our most economically damaging species fit this profile.

Life-History Traits

Several studies have attempted to assess whether or not outbreaks are a property of particular life-history attributes found in some forest insects. Among Lepidoptera, for example, gregariousness, flightlessness, egg-clustering, low host plant specificity, and nonfeeding adults are all found in greater frequency in species known to have outbreaks. However, there does not appear to be either a single trait or a suite of overarching traits that are uniformly associated with species that outbreak. All of the above traits can be found in species which do not outbreak. In addition, species such as the forest tent caterpillar (*Malacosoma disstria*), larch budmoth (*Zieraphera diniana*), autumnal moth (*Epirrita autumnata*), budworms (*Choristoneura* spp.), and gypsy moth (*Lymantria dispar*) outbreak in only portions of their ranges, suggesting that alone, life-history characteristics are insufficient to explain outbreak dynamics.

Population Regulation

Regardless of whether a species is prone to outbreak or not, there are three forces that influence the density and dynamics of populations: (1) top-down, driven by organisms in trophic (feeding) levels above the folivore; (2) bottom-up, the influence of species in trophic levels below the folivore; and (3) horizontal, competitive interactions with other herbivores. The relative importance of these factors is likely species-specific. Historically, top-down and bottom-up factors were considered separately, but there is increasing recognition that they function in tandem to influence population dynamics. Communities of leaf-feeding insects were also thought not to be structured by competition, a view that is less tenable when indirect competitive interactions such as those mediated through changes in host plant quality or through shared natural enemies are considered.

Top-down regulation of herbivorous insect populations is driven by a suite of organisms collectively called 'natural enemies.' Natural enemies of forest insects include invertebrate and vertebrate predators, parasitoids, and pathogens. Important invertebrate predators include pentatomid bugs (Hemiptera), ants and wasps (Hymenoptera), spiders (Arachnida), and

carabid beetles (Coleoptera). Insectivorous birds and small mammals such as mice and shrews are examples of important groups of vertebrate predators. Foliage-feeding insects are susceptible to many pathogenic organisms, including viruses, bacteria, fungi, and protozoans. In addition, they are attacked by a staggering diversity of parasitoids. The vast majority of parasitoids are found within two superfamilies of Hymenoptera, the Ichneumonoidea and Chalcidoidea, and a large and diverse family of Diptera, the Tachinidae. In general, the larvae of parasitoids develop within or sometimes on the body of a host species. Parasitoids often possess remarkable adaptations for locating hosts and for circumventing the immune system of their insect victims. Once the developing parasitoid completes larval development, the host is usually killed.

The relative importance of natural enemies varies among folivores and may also vary within a species in different parts of its range, or at different population densities. For example, in the gypsy moth, vertebrate predation on pupae and large larvae by white-footed mice is important at low population densities whereas a nuclear polyhedrosis virus (NPV), a pathogen, dominates mortality in many outbreak populations. In other species, such as tent caterpillars and budworms, specialist parasitoids may play an integral role in the cyclical rise and fall of population densities.

For leaf-feeding insects, the host plant is the primary bottom-up factor influencing their populations. Trees are not passive recipients of herbivory. Indeed, millions of years of evolution have led to numerous physical and biochemical traits that confer some degree of resistance to folivores. Concentrations of primary compounds important to insects such as water and nitrogen, secondary compounds such as tannins and terpenoids, and physical properties such as toughness vary among leaves on an individual tree, among trees, and across entire forested landscapes. Foliage quality for herbivores also changes seasonally and is generally highest in the spring. As current-year needles or new leaves fully expand, the concentration of indigestible fiber and lignin increases. New growth on conifers is of much higher quality for many foliage-feeding insects than needles retained on the tree from previous years. Thus, folivorous insects encounter great temporal and spatial variation in the quality of leaves on which they feed. To counter this, insects have evolved detoxification mechanisms, feeding behaviors, and/or restrict their feeding to specific times of the season such as early spring.

Trees may respond actively or passively to insect feeding or may simply be tolerant to some level of leaf loss. Active responses occur rapidly following da-

mage and these wounding responses often involve the production of compounds such as proteinase inhibitors or polyphenol oxidases that deter feeding or reduce the nutritional value of the leaf to subsequent herbivores. Such responses can be site-specific or can be rapidly propagated throughout the plant. The production of these compounds may involve complex biochemical signaling pathways that are only just beginning to be understood.

Trees also exhibit passive responses that result in deterioration of the nutritional value of a leaf following defoliation. While not as rapid as the wounding responses above, these effects may last for a year or more. Water and nitrogen are often reduced in damaged leaves or in trees that were severely defoliated in the previous year. In addition, levels of some carbon-based secondary compounds such as tannins may be elevated in the same trees. The combination of lower concentrations of primary nutrients and higher concentrations of secondary compounds may reduce the performance of folivorous insects on these trees. These long-term responses can reduce insect fecundity and growth for several years. These effects have been well documented for autumnal moth on mountain birch, forest tent caterpillar on aspen, and black-marked spear moth (*Rheumaptera hastata*) on paper birch.

Phenology is the seasonal timing of specific growth, developmental, and reproductive processes. In trees, the phenology of budbreak, flowering, or leaf drop, is recognized as being critical in determining the density of some foliage-feeding insect populations. For example, jack pine budworm (*Choristoneura pinus*) larvae survive by feeding in pollen cones in the spring until new needles, their preferred food, begin to expand. Many other spring-feeding folivores must time their hatch to coincide with budbreak, when primary nutrients such as water and nitrogen are high, many secondary compounds are low, and physical properties such as toughness are at their seasonal minima. Hatching earlier than budbreak may lead to starvation, whereas hatching late may lead to lowered fecundity, longer development times, and higher mortality.

Intra- and interspecific differences among trees in phenology and phytochemistry can shape foliage-feeding insect communities in both time and space. For example, the population density of folivores feeding on white and black oaks varies across the landscape with greater diversity and abundance on trees with lower tannin levels. Similarly, the phenology of individual trees can determine the density of a number of different folivores including winter moth (*Opheroptera brumata*) on oak and large aspen tortrix (*Choristoneura conflictana*) on aspen. For

both species, trees whose buds break in synchrony with the emergence of larvae in spring support higher populations than trees that leaf out prior to larval emergence or after it has already occurred. Slow growth of insects stemming from poor phenological synchrony with the host tree may lead to increased mortality from parasitoids or predators if the insect remains in a vulnerable stage for longer periods of time, as has been shown for tent caterpillars and autumnal moth. Even extreme generalist folivores like gypsy moth have a hierarchy of preferences for different tree species, based primarily on phenology and phytochemistry.

In addition to the direct influences mentioned above, trees may indirectly influence the population dynamics of folivores. Alterations to relationships between a herbivore and its natural enemies mediated by the host tree are known as tritrophic interactions. For example, leaves damaged by feeding folivores may release volatile chemicals that predators or parasitoids can use as cues to locate the herbivore. There are both intraspecific and interspecific differences in the type and strength of volatiles released by trees, contributing to variability in the susceptibility of folivores to predators and parasitoids. Tree chemistry can also alter the susceptibility of folivores to pathogens. Gypsy moth larvae are less likely to succumb to NPV when feeding on oaks which are rich in hydrolyzable tannins than when feeding on other species with lower concentrations such as aspen. In some, but not all studies, increases in tannins following defoliation of oaks reduce susceptibility of gypsy moth to NPV.

Another indirect influence of trees on herbivore populations can occur through so-called 'maternal effects' where the foliage quality experienced by the parental generation can have significant effects on the performance of their offspring. The influence of the environmental quality experienced by the parental generation on offspring is well documented for many organisms, including some foliage-feeding insects. An example is the change in yolk provisioning of gypsy moth eggs after the parental generation has experienced defoliation-induced declines in tree quality. While these effects have been documented in some studies of gypsy moth, they were not evident in several other folivores and their importance in population dynamics continues to be debated.

Population Cycles

A fractious debate in ecology during the mid-twentieth century focused on the relative role of density-dependent and density-independent factors in population dynamics. Density-dependent factors

have effects that are a function of the size of a population. Such factors can act immediately or with a lag time or delay in the response. It is now generally accepted that cycles can only occur if a density-dependent process has sufficient lag time. Any process that functions in a delayed density-dependent manner can drive population cycles. Mathematical models have suggested that natural enemies, maternal effects, and host plant quality can all cause population cycles, although it has proved difficult to show whether or not any one density-dependent factor is critical to population cycling.

A long-standing hypothesis for explaining forest insect outbreaks was that periods of favorable climate allow populations to increase. This was thought to occur because the herbivore population grows faster than its natural enemies during favorable periods or because plant quality changes in a way that is advantageous to the herbivore, either through reduced defenses or increases in nutritive value. Although it is possible that periods of favorable weather could be driving the dynamics of species which outbreak at irregular intervals, weather patterns are too random (stochastic) to be responsible for the regular cycles that characterize the dynamics of many important defoliators.

Forest insects such as jack pine and spruce budworms, forest tent caterpillar, larch budmoth, and large aspen tortrix are prone to region-wide, synchronous outbreaks, some spanning distances of several hundred kilometers or more. The Moran effect, originally used to describe the synchronization of lynx populations across large regions of Canada, may offer an explanation for the remarkable degree of synchrony among these widespread populations. It postulates that an extrinsic factor such as weather may act to synchronize populations across a region so that they fluctuate in unison. In this case, the cycling of individual insect populations is driven by intrinsic density-dependent factors, but is brought into regional synchrony through Moran-effect processes.

Some have also proposed that dispersal among populations could also be responsible for synchronization. Certainly, large dispersals of adults from outbreak populations have been documented for conifer-feeding budworms. However, while dispersal among populations may account for synchrony over a small scale, the outbreak areas that are affected greatly exceed the dispersal capabilities of individual insects. In addition species such as Douglas-fir tussock moth (*Orygia pseudotsugata*), spring canker worm (*Paleacrita vernata*), and gypsy moth also exhibit strong regional synchrony despite very poor dispersal abilities.

Impacts of Foliage-Feeding Insects on Trees

Effects of insect defoliation on tree health vary considerably depending on the species of tree, how much foliage is consumed, and the general health or vigor of the tree. In addition, the timing of the defoliation and the age or location of the affected foliage can also influence the severity of impact.

Hardwood and conifer trees differ greatly in their ability to tolerate severe defoliation. Healthy hardwood trees can generally recover from defoliation, even if 100% of the foliage is consumed. Most hardwood trees are able to produce a second set of leaves a few weeks after the initial foliage is lost – a process referred to as ‘reflush.’ As a rule, hardwood trees do not reflush until roughly 60% or more of the canopy has been consumed or otherwise damaged. The second set of leaves is typically smaller and less photosynthetically active than the original leaves, but they enable the tree to produce an adequate amount of energy to survive the winter and leaf out the following spring. Of course, there is a cost when a tree has to reflush. Carbohydrates and other nutrients must be utilized to form the second set of leaves, depleting the stored energy available to the tree and substantially reducing its radial growth. While healthy hardwood trees can generally reflush for 2 or 3 consecutive years, the stress eventually becomes too great. Trees that have sustained heavy defoliation for more than 2 or 3 years often succumb to secondary pests such as bark beetles, phloem-borers or root rot pathogens. These secondary pests rarely affect healthy trees but are able to take advantage of stressed trees. Hardwood trees that experience other stresses such as extended drought, wounds, or poor growing conditions are less likely to tolerate and recover from insect defoliation.

Unlike hardwood trees, conifers produce only a single set of buds in mid to late summer and cannot reflush in response to defoliation. Conifer trees that sustain complete defoliation will die and moderate to heavy defoliation increases the vulnerability of conifers to bark beetles and other secondary pests. Conifer forests killed by defoliating insects or associated secondary pests can be highly susceptible to wildfire, especially when conditions are dry. Some conifer feeders, such as jack pine budworm and yellow-headed spruce sawfly (*Pikonema alaskensis*), feed more heavily on needles at the top of the tree than in the middle or lower portion of the canopy. This can result in top-kill – a condition in which the tree survives and continues to grow radially, but the leader and upper whorls of branches die.

Because foliage-feeding insects reduce leaf area, photosynthesis is reduced during defoliation. This, in turn, leads to a decrease in the rate of radial growth. Most people are familiar with the annual rings of spring and summer wood growth that are visible in cross-sections of the trunk and branches of trees. Healthy trees produce wider rings and grow at a faster rate than unhealthy trees. When a tree loses more than about 10–20% of its canopy, less energy will be available for wood production and growth rings will be narrow. When defoliation exceeds 50–60% of the canopy, little or no radial growth will occur that year. Radial growth rates of hardwood trees may recover the following year while growth rates of conifer may only recover after 2 years or more.

Insects that feed in the spring or early summer generally have more effect on tree vigor than insects that feed later in the summer. Early in the year, young, succulent leaves or needles function as a sink for stored carbohydrates and nutrients. When young foliage is consumed by insects, the tree effectively loses that investment before the tissue begins to produce energy through photosynthesis. In contrast, defoliation in the latter part of the summer, when trees are beginning to prepare for winter dormancy, generally has little effect on tree health. Fall webworm and orange-striped oakworm (*Anisota senatoria*) typically cause less harm to trees than species like gypsy moth or forest tent caterpillar simply because they feed later in the year. Insects that feed on current-year foliage of conifers such as jack pine budworm or red-headed pine sawfly (*Neodiprion lecontei*) are generally more harmful than are insects such as European pine sawfly (*N. sertifer*) that feed primarily on needles 1 year old or more.

While severe defoliation can reduce radial growth, cause top-kill or tree death, foliage-feeding insects can also increase the overall long-term health of a forest. Suppressed or diseased trees are usually more vulnerable to mortality during outbreaks of defoliators. When these trees succumb, space, water, light, and nutrients are freed up for the healthier trees that survive the outbreak. Forest entomologists sometimes refer to this pattern as a ‘thinning from below,’ because mortality of the less vigorous trees can lead to increased rates of growth and productivity for the forest as a whole. This regulation of productivity by foliage-feeding insects is an important part of the long-term dynamics of many forest ecosystems.

See also: **Ecology:** Plant-Animal Interactions in Forest Ecosystems. **Entomology:** Bark Beetles; Defoliators; Population Dynamics of Forest Insects; Sapsuckers.

Further Reading

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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



Figure 1 A larval teak defoliator moth.

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.

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. Broad-leaved 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 broad-leaved trees (e.g., 7–13% loss of beech growth arising from 90% defoliation by pale tussock moth (*Dasychira pudibunda*) in continental Europe).