HERBIVORY IN FORESTED ECOSYSTEMS

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INTRODUCTION

Forest canopies support a complex assemblage of herbivores that are usually inconspicuous except when population outbreaks of one or more species produce noticeable defoliation or other signs of herbivore activity. Little is known about the ecological impacts of herbivores during non-outbreak phases (52, 109, 137, 141). Foliage consumption during non-outbreak periods has been measured as 5–15% of leaf area production in temperate forests (109), but the techniques used may underestimate actual herbivory (88). Foliage loss may reach 100% of foliage production during herbivore population outbreaks (33, 89, 168).

In the last five years there has been an explosion of information on both the process of herbivory and the nature of insect/plant relationships. Recent compendia include volumes by Ahmad (2), Bell & Carde (10), Crawley (34), Denno & McClure (37), Edwards & Wratten (42), Hedin (65), Rosenthal & Janzen (130), and Strong et al (147). Ecological chemistry has been a fundamental organizing theme for many of these works. As recently as 1960, Hairston et al (57) based their "green world" hypothesis on the premise that all green foliage was equally available to herbivores. "Secondary" metabolites were considered to be metabolic by-products with no known function. The emergence of ecological chemistry can be traced from Fraenkel's (49) concept of plant chemical defense to Feeny's (46) classic study of plant regulation of winter moth (*Operophtera brumata* L.) populations. More recently, the induc-

tion of plant defenses by herbivore feeding has been recognized (63, 128, 131, 139), along with the possibility that plants communicate herbivore pressure, which results in induction of defenses in spatially distinct unattacked plants (8, 128; but see 47, 98).

Ecosystem-level studies have provided a complementary approach to investigation of herbivory and insect/plant interactions. These studies suggest that the evolutionary "arms race" may not be strictly negative. Dyer & Bokhari (40), McNaughton (97), and Owen & Wiegert (111) noted that nominal levels of herbivory could stimulate or optimize plant growth. Several investigators have proposed that herbivory might act as a homeostatic mechanism at the ecosystem level, regulating primary production (26, 56, 94, 135). Schowalter (134) suggested that differential herbivory resulting from biochemical interaction is the driving force behind ecosystem succession and nutrient cycling processes.

In this review, we primarily consider the activities of foliage-consuming (folivorous) and sap-feeding insects. Wood-feeding insects that attack living trees are considered only when their activity affects ecological processes at the community or ecosystem levels. Fruit/seed predators and pollinators are not reviewed. Our purpose is to integrate the biochemical and ecosystem views of herbivory, emphasizing factors that influence herbivory in forest ecosystems and the consequences of herbivory at the tree and ecosystem levels of resolution.

FACTORS INFLUENCING HERBIVORY IN FORESTED ECOSYSTEMS

Herbivory is a function of the size or biomass of herbivore populations and is influenced by factors affecting the natality, mortality, and dispersal of such populations. Major factors include abiotic variables, plant biochemistry, physical defenses, nutrients, predation and parasitism, and forest structure.

Abiotic Factors

Abiotic factors can influence herbivory directly through effects on insect feeding and survival and indirectly through effects on host susceptibility. Weather, soil conditions, and industrial pollutants are major controlling factors in modern forests.

In general, insect activity increases with temperature, although temperature extremes are often lethal or reduce fertility (85, 150, 154). Moist conditions favor hemlock looper [*Lambdina fiscellaria* (Guenee)] populations (51), but spruce budworm [*Choristoneura fumiferana* (Clemens)] populations increase during dry periods (9). Moisture may influence populations of predators and parasites, especially bacterial and viral pathogens (150). Heavy precipitation or high winds can dislodge and kill exposed folivores (51, 85).

Many adult Homoptera, Lepidoptera, and Hymenoptera fly weakly. Dispersal by small insects occurs primarily as drift on wind currents (39, 51, 92, 132, 143). Small Homoptera can remain airborne for considerable distances (95), whereas larvae of many lepidopteran species remain airborne by means of silk balloons or specialized setae (54, 81, 92).

Patterns of forest defoliation by the spruce budworm, the gypsy moth (*Lymantria dispar* L.), and perhaps the forest tent caterpillar (*Malacosoma disstria* Hubner) depend in part on concentration of dispersing moths in zones of wind convergence (28, 51, 92). Adult moths aggregate in warm air above thermal inversions (132). These moth swarms are transported by frontal systems and deposited in convergence zones. Larval dispersal occurs at lower altitudes, where transporting winds are often interrupted by ridgetops (92). Defoliation by these species thus tends to be concentrated along parallel ridges and convergence zones.

Weather-delayed budbreak relative to initiation of insect activity contributes to host choice and mortality of folivores (35, 83, 106, 147). Weather also influences nutrient requirements of plants and plant modules as well as availability of nutrients for plant uptake and resource allocation (93, 159). Changes in plant requirements and resource allocation affect attractiveness, acceptability, and suitability for folivores (21, 48, 126, 134, 135, 145, 151, 153, 157, 167; see the section below on Nutrients).

Soil fertility, texture, drainage, and composition influence plant susceptibility to herbivory by the elongate hemlock scale (*Fiorina externa* Ferris) (95), the Douglas-fir tussock moth [*Orgyia pseudotsugata* (McD.)] (146), and the gypsy moth (22). Atmospheric emissions of fluorides, sulfur, and ozone affect patterns of folivory in forests directly by influencing folivore survival and indirectly by influencing host susceptibility (3, 71).

Chemical Defenses

Detailed information on plant chemical defenses is available in several review volumes (58, 130) and in reviews on specific classes of compounds such as phenolics (86) and tannins (12, 169). Constitutive defenses, which are ever-present defensive chemicals permanently suffusing plant tissues, can be distinguished from inducible or facultative defenses, which are produced by the action of herbivory only as they are needed.

Chemical defenses are of two types: nitrogenous and nonnitrogenous. Nitrogen-containing constitutive defenses include nonprotein amino acids, cyanogenic glycosides, glucosinolates, alkaloids, and lectins. The production of these relatively expensive chemical defenses is closely related to plant nutrition, since they require a potentially limiting nutrient (93, 102, 151) for their construction.

Nonnitrogenous defenses are of two major types: products of the terpenoid pathway, and tannins and related compounds of the phenolic pathway. Ter-

penoid defenses include mono-, di-, tri-, and sesquiterpene derivatives, cardiac glycosides, saponins, and phytohormones, and are formed by the condensation of five-carbon isoprene units produced from mevalonic acid.

Tannins and phenolics have long been assumed to play a major role in chemical defense of many forest trees against herbivores. Used in the treatment of leather, extracts of plant tannins were known to precipitate and cross-link proteins and inhibit or destroy enzyme catalysts in vitro. Feeny (46) discovered that winter moth larvae feeding on oak leaves in the spring abruptly cease feeding in mid-June and turn to other trees, despite no obvious changes in nutritional content of the leaves. He hypothesized that a concomitant sharp increase in leaf tannins complexed the leaf proteins in vivo, lowering nutritional value.

Phenolic content of foliage, as measured by precipitation of nondietary proteins such as hemoglobin, collagen, bovine serum albumin (BSA), and beta-glucosidase, is widely used as a general index of leaf palatability (90). Martin & Martin (90) measured several common tannins and reported poor correlation among many of these assays. They suggested that the use of an abundant leaf protein, RuBPC, might be a more ecologically relevant approach. Three species of oaks had sufficient tannins to precipitate at pH 6.1 all of the RuBPC in their foliage.

Berenbaum (11) compared midgut pH in larval Lepidoptera and found that folivores specializing on trees had significantly higher midgut pH than species feeding on herbs and forbs, an adaptation that may interfere with the protein-complexing ability of the tannin in tree foliage. Bernays (12) reported that diets containing tannins had little effect on the development of *Locusta* despite its relatively low gut pH, implying that tannins may not be primarily defensive in function. Zucker (169) suggested that the enormous structural diversity of tannins might imply a stereospecificity of action, with tannins having specific "gene-for-gene" inhibitory functions. Metabolically expensive, tannins would not be unnecessarily diverse in structure if they are general in function. Adapted herbivores might rely on alternative enzyme systems for digestion.

Surfactants in the gut fluid may further interfere with protein-complexing ability. Martin & Martin (91) reported that *Manduca sexta* gut fluid that was adjusted to pH 6.5 took more tannic acid to precipitate RuBPC than aqueous buffer at the same pH; consequently they suggested that tannins should no longer be referred to as digestibility-reducing substances.

Recent evidence indicates that foliar phenolic compounds may actually be nutritious to some herbivores (13). Schopf et al (133) reported that phenolic compounds in spruce needles can be metabolized by sawfly (*Gilpinia hercyniae* Htg.) larvae to satisfy nutritional requirements.

Facultative or inducible defenses are mobilized in response to herbivore feeding. If induction takes place rapidly and affects the herbivore causing the

damage but only weakly affects later herbivory, then the induced defense tends to stabilize the herbivore population (60, 62, 128). If the effect is stronger later than initially, the induced response is a destabilizing agent, which causes time lags in herbivore numerical response (61).

Patterns of herbivory may be expected to reflect the scale and speed of the induced response. Edwards & Wratten (43) suggested that leaves of many trees in August exhibit an "overdispersion" of grazing initiations and that the arrangement of holes appears close to regularity. Local inducement of a "halo" around feeding sites may force the next grazing initiation some minimum distance away. Defenses induced in entire leaves (63, 64), branches (131, 139), or whole trees (8, 128) serve to disperse grazing over larger scales (79, 84, 107). Since movement makes insects more conspicuous to predators and parasites, within-plant variation in deterrence increases risks to herbivores that must move to feed (68, 119, 138, 150, 162).

Some folivores have behavioral techniques to prevent the inducement of chemical defenses in foliage. Although tough, low-nutrient vascular tissue is ordinarily avoided by folivores, midrib nipping (67), or cutting of nearly complete leaf disks from leaf blades (23), isolates portions of leaf blade from the vascular system, preventing accumulation of induced defenses. Gregarious feeding, practiced by many forest folivores, and mass attack, seen in boring beetles, are behavioral techniques that prevent or overcome facultative defenses.

Physical Defenses

Physical defenses of trees include characteristics of the leaf surface and margins. Waxes, cutin, and suberin make the surface slippery and camouflage taste, whereas structural components such as calcium, cellulose, and lignins increase leaf toughness (87). Incorporation of silica and oxalate crystals lowers palatability physically, whereas gums, resins, pectins, and milky sap are sticky and may contain chemical defenses (e.g. 96). The presence of trichomes of many types, which may themselves contain specific deterrent compounds, physically deters herbivores from chewing leaves (87). Recurved trichomes pierce phytophagous larvae at intersegmental membranes and immobilize them, eventually causing death (55, 116).

Premature abscission of leaves is a potent induced physical defense against sedentary herbivores (1, 25, 75, 144). Leaves containing mining folivores are more likely to be abscised by the tree than are miner-free leaves (5, 45, 110, 120, 121). Leaves of cottonwood (*Populus*) with one *Pemphigus* aphid gall were five times more likely to drop prematurely than those with no galls; with three or more galls, there was a twenty-fold increase in the probability of abscission (164).

Nutrients

Nutrient deficiency causes high juvenile mortality among phytophagous insects (159); quality is as important as quantity of food (24, 145, 153, 167). Within-season changes in foliage quality limit insect populations in the canopy (46). At Coweeta Hydrologic Laboratory, North Carolina, herbivore biomass was significantly correlated with K and Ca concentrations in foliage, but not with N or P concentrations (D. A. Crossley, Jr. unpublished). Mattson (1980) concluded that foliar nitrogen concentration was positively correlated with herbivory, and that low nitrogen concentrations in foliage limited insect populations. Forest stands under stress from drought, crowding, or disease may derive some protection from herbivores by producing less nutritious foliage despite reduced investment in feeding deterrents (15, 32, 103, 105, 123). Low nitrogen availability in foliage, however, may lead to increased ingestion, which is often correlated with low rates of assimilation (145). Seastedt & Crossley (140) evaluated the "animal starvation hypothesis," which postulates that low Na levels in plant tissues represent a defensive strategy, but concluded that low Na levels might actually stimulate consumption.

However, effects of forest fertilization on herbivory are little understood and are contradictory, perhaps because few studies have included examination of plant allocation of subsidized nutrients (6, 16, 59). Tuomi et al (151) suggested that inducible responses of trees to herbivores is a by-product of mechanisms that rearrange the plant carbon/nutrient balance in response to nutrient stress. Excess carbon that cannot be diverted to growth due to nutrient stress is diverted to the production of plant defenses (64).

Predation and Parasitism

Predation and parasitism have a large effect on herbivore population sizes and therefore on herbivory in forested ecosystems (57). Pathogens, especially nuclear polyhedrosis viruses (NPV) and *Bacillus thuringiensis* (Bt), may become epizootic in dense defoliator populations, resulting in defoliator population decline (85, 150). Forest herbivores are subject to a complex array of hymenopteran, dipteran, arachnid, and vertebrate predators and parasitoids (137, 150).

Trees may "buy" protection from herbivores by encouraging residence by predators, especially ants, using sugary exudates produced by extrafloral nectaries (119, 149). Ants may become obligate occupiers (e.g. on *Cecropia*) and, in return for food and shelter, protect the tree from herbivores and encroaching vines. Ants may, however, inadvertently protect or encourage some defoliators by creating a refuge from other predators and parasites (50). The mistletoe butterfly (*Orgyris amaryllis* Hewitson), which is myrmecophilous and secretes honeydew as a larva, preferentially oviposits on ant-patrolled hosts regardless of biochemical suitability (4).

Folivores engage in a number of predator-avoidance behaviors that affect herbivory in forested ecosystems. Birds, which are major predators of lepidopterous defoliators, key on leaf damage to locate prey items (67, 68). Frequent movement from damaged areas (43) and nocturnal feeding (138) may be predator-avoidance techniques, although movement may increase likelihood of discovery by predators and parasites (138, 150). After feeding, several forest folivores clip the petiole of the damaged leaf, dropping it to the forest floor (67). Other species scallop leaf margins, producing the illusion of a smaller undamaged leaf. Damage camouflage for predator avoidance has important ramifications not only for herbivory but also for nutrient cycling effects (see the section on Effects on Nutrient Cycling, below).

Forest Structure

Forest structure determines the spatial distribution of acceptable resources and influences the efficiency of resource discovery by dispersing herbivores. Aspects of forest structure also affect host conditions, which influence survival of feeding herbivores.

Within-plant variation with respect to chemical defenses, nutrition, genetics, and other factors in time and space makes the plant appear to be a shifting mosaic of acceptability to herbivores (30, 36, 41, 152, 164). Herbivores are confronted with mosaics of vulnerability through which plant tissues may escape in time and space. Somatic mutations arising in meristematic tissue of buds propagate genetic mutations with the annual growth of the plant (152, 155, 163). Fluctuating environmental conditions can indirectly impose additional variation among modules by forcing reallocation of resources in the plant (21, 24, 53, 93, 123, 134, 151, 152, 164). As a result of this integration of genetic and environmental factors, resource acceptability to herbivores varies considerably among foliage modules, genets (i.e. all parts derived from a single zygote), and stands.

Populations of most herbivore species peak during particular stages of host development (89, 117, 135, 137, 147). Physiological changes during tree development influence the susceptibility and suitability of the host as a resource (29, 108, 124, 134, 135, 146). Tree size can influence predator foraging efficiency. Ants (*Formica obscuripes* Forel) foraging for extrafloral nectaries produced by young cherry trees attack and kill eastern tent caterpillar larvae (*Malacosoma americanum* Fabricius); as cherry trees grow, ant foraging efficiency declines, tent caterpillar survival and herbivory increase, and extrafloral nectary production ceases (149). Tree size may be associated with apparency or attractiveness to host-seeking herbivores (81, 84, 107, 108).

Stand density can influence herbivory in at least three ways. First, the distance between hosts determines the period of time that dispersing insects are exposed to between-tree mortality agents (138, 150). Host switching by gypsy

moth larvae increases as tree density increases (81). Second, the degree of canopy exposure to climatic extremes can affect folivore survival (9, 150) and foliage condition (161). Finally, the degree of competition for resources affects tree condition and patterns of resource allocation (24).

Forest composition determines the probability that dispersing folivores will find and exploit acceptable resources (9, 28, 33, 81, 84, 135). Patterns of herbivory within and among trees and stands reflect variation in resource availability and acceptability. Defoliation by the spruce budworm decreases as the proportion of balsam fir decreases or as the proportion of hardwoods in the overstory increases (9, 89).

Availability of nonfood resources (as affected by stand development, fire, etc) also influences herbivore populations. Many folivores spend portions of their life cycles in nonfoliage modules (e.g. in bark crevices or litter), thereby gaining protection against predators, temperature extremes, or other mortality agents (22, 81). Vertical stratification in forested ecosystems ensures a range of foliage phenology, tree age, size, and degree of canopy closure (84, 107, 135), providing refugia from which to exploit favorable conditions.

Changes in tree age, size, density, species composition, and vertical stratification, across stands and through time, influence patterns of forest herbivory at the ecosystem and landscape levels of resolution (28, 33, 54, 107, 114, 134, 135, 146). Pitman et al (117) reported that defoliation by the European pine sawfly (*Neodiprion sertifer* Geoffr.) was concentrated in unthinned 25–30-year-old Scots pine stands compared to adjacent young (7-year-old) and thinned, old (105-year-old) stands. Trees along the border with the young and old stands grew faster and slower, respectively, and sustained less defoliation than the remainder of the 25–30-year-old stands. Border effects may reflect predator-parasite abundance in ecotones (150) or disruption of pheromone communication at stand edges (44). In addition, trees growing close to edges experience differing exposure and edaphic factors, altering insect survival as well as tree physiology and phenology (9, 22, 107, 146, 135).

TREE RESPONSES TO HERBIVORY

Obvious effects of herbivory on foliage and wood production have received considerable attention (80, 89). Less conspicuous effects on resource allocation patterns and growth form remain poorly understood.

Effects on Individual Trees

The impact of folivory at the genet level is largely a function of the value of affected foliage (38, 124, 128). Foliage loss results from consumption by grazing folivores (19, 80), premature shedding of damaged leaves (1, 45, 75, 110, 120, 121), and tissue necrosis following introduction of salivary toxins

and foliage pathogens (72, 99, 125, 144). Small folivore populations can cause disproportionately large foliage losses by feeding on vegetative buds or unexpanded foliage (59, 106, 127, 168). Repeated piercing by sucking herbivores during feeding site selection may result in foliage deformation and distortion of growth (99, 125, 135). Foliage consumption in the spring amounting to 2–3% of foliage standing crop can reduce photosynthetic capability 9–10% by autumn (109); consumption of 13% of leaf production can reduce foliage biomass 74% (168). Similarly, the impact of a leaf miner upon total plant production may be greatly increased if mining activity induces premature leaf fall (25, 45, 120, 121; see the section on Physical Defenses, above).

Significant but less conspicuous loss of nutrients or metabolites and disruption of plant growth can result from feeding activities of forest herbivores. Phloem-feeding Homoptera can remove up to four times their dry biomass per day and up to several times the nutrient standing crops that are present in foliage over the growing season (125, 137, 154, 165). Salivary enzymes of Homoptera [e.g. *Adelges piceae* (Ratzeburg)] and Hemiptera (e.g. *Lygus* spp.) may stimulate plant growth, inducing deformation or gall formation (99). Feeding on vegetative buds interferes with bud development, influencing tree growth and geometry (69, 100, 156). Folivory increases leaching of nutrients, especially P and K, from damaged leaves (76, 141). A difference of 8% in leaf consumption resulted in a 70% increase in canopy leaching of K during a four-month period on a southern Appalachian watershed (142). Leaves pierced by sucking herbivores show elevated transpiration rates (165), but defoliation by chewing herbivores reduces transpiration rate (107).

The importance of folivory for tree productivity and survival depends on the value of affected foliage, the tree life history strategy, and the tree condition (9, 38, 134, 135, 156–158). The value of damaged foliage is the most important factor determining the severity of impact. Foliage value, a measure of contribution to tree fitness, is evaluated by several criteria, including foliage age, life expectancy, and position in the forest canopy (25, 38, 101, 108, 118, 124). The value of old or mature leaves differs markedly from that of expanding or young leaves (29). Young leaves of some tree species, especially those with rapid foliage turnover, have high photosynthetic efficiencies and, therefore, higher value than older leaves (25, 38, 101, 124). Douglas fir, on the other hand, stores energy in older needles (156). This energy is mobilized to produce new needles, but old needles constitute 30–90% of foliage biomass (depending on tree age and growth rate). For these reasons, preferential consumption of new needles by the Douglas-fir tussock moth can reduce resource requirements without seriously reducing photosynthetic capacity in open-growing trees (156). Sunlit leaves have higher photosynthetic rates than shaded leaves, regardless of age (101, 107, 156). Insects feeding on shaded leaves affect the host less severely than insects feeding on sunlit leaves (107, 157, 158).

Tree species characterized by rapid foliage turnover can tolerate considerable sustained folivory (18, 38, 59); deciduous hardwoods and conifers adapted for periodic foliage loss and replacement often refoliate following complete defoliation by insects (33, 74, 78, 157, 168). Evergreen conifers, on the other hand, often lose substantial canopy volume or die as a result of intense herbivory (33, 78, 80, 89, 100).

The integration of the amount of herbivory, leaf value, and host condition determines tree growth and survival. Low-intensity consumption on low-value leaves of trees growing under optimal conditions will result in little reduction in (if not slight benefit to) tree fitness. As consumption intensity increases, involving higher-value leaves, or as tree condition deteriorates, severely affected crown portions may die, altering competitive status (see the section on Effects on Community Development, below) and predisposing the tree to various mortality factors; intense folivory often kills stressed trees (14, 33, 78, 80, 89, 100, 104, 134, 135, 156–158).

Tree Condition and Response to Herbivory

For a given tree species, tree condition largely determines individual response to herbivory. Refoliation or induced defense requires reallocation of resources from other metabolic pathways. Injury, stress, or resource limitation may reduce the ability of trees to respond to herbivory in ways that contribute to survival (134, 135, 157, 158, 168).

Fertilization often increases tree resistance to defoliators (6, 16, 59). On the other hand, higher foliar nutrients in fertilized trees may make them especially attractive to consumers as a high-quality food source (21, 93, 145, 158, 167). Increased N translocation associated with fertilization or refoliation contributes to population growth of phloem feeders and consequent damage to translocation systems and transmission of pathogens (135, 137, 154, 165). Black locust trees fertilized with N, P, and K initially incurred higher losses to chewing insects, but subsequently gained some protection from herbivory (59). This shift in canopy herbivory after fertilization may help explain conflicting reports in the literature concerning the impact of host nutrition on herbivory (see 59).

IMPACT OF HERBIVORY ON FORESTED ECOSYSTEMS

Effects of herbivory at stand and ecosystem levels reflect the integration of effects on individual trees. Studies during the past decade have begun to address folivore effects on forest community structure and long- and short-term nutrient cycling processes.

Nominal and Short-Term Effects

Nominal folivory typically accounts for less than 10% of annual foliage standing crops (56, 82, 94, 106, 109, 137, 142). Trees tolerate low levels of folivory

with little or no growth loss, perhaps because only low-value foliage is ordinarily consumed at low herbivore population densities (38, 101, 107, 124, 156). Nominal levels of herbivory also may affect short-term nutrient cycling (109, 136, 137).

Stands are predisposed to folivore population outbreaks through changes in the abundance and distribution of suitable resources (see the section on Forest Structure, above). Folivore populations growing on suitable hosts often disperse to nearby trees (54, 81, 135). Even trees resistant to nominal herbivory may be sufficiently stressed by the feeding of large numbers of folivores to contribute to further growth of herbivore populations (117, 135). Foliage loss can reach 100% of foliage standing crops at stand, ecosystem, and landscape levels of resolution (28, 33, 51, 74, 78, 80, 89, 100, 114, 117, 146, 148, 168).

Effects on Community Development

Concentration of herbivory on susceptible trees or tree species accelerates changes in forest structure and community development (20, 134, 135, 141). Defoliation and tree mortality open the canopy and change the pattern of light penetration to the understory. Altered growth rates resulting from herbivory can reduce or enhance the ability to compete with neighboring trees for light and nutrients.

Concentration of herbivory on particular tree species favors competing species and results in a successional transition in stand composition (20, 31, 134, 135). Concentration of folivory on stressed trees accelerates the demise of such trees and releases competing vegetation, homeostatically mitigating the stressful conditions (134, 135). Stands composed largely of suitable host trees often suffer extensive decimation of canopy and subcanopy (100). In such cases, ecological succession is reset to the herb, shrub, or sapling stage (77, 89, 134). Fuel accumulation resulting from extensive tree mortality predisposes stands to fire and reinitiation of succession (135). However, compensatory growth by surviving trees often reduces the long-term impact of herbivory (97, 112, 166, 168).

Effects on Nutrient Cycling

Herbivory affects short- and long-term nutrient cycling processes in forest ecosystems. Defoliated trees may have reduced demand for some nutrients because of reduction in metabolically active foliage tissue (156). Trees recovering from defoliation, however, may show increased photosynthetic efficiency and starch replacement (156). Oaks, maples, and birches showed increased CO_2 assimilation in residual and regrowth foliage following manual defoliation (66, 122). Changes in transpiration rates brought about by herbivore activity affect rates of nutrient uptake (77, 107, 165). Nutrient uptake by grazed trees, especially nutrient-demanding species, increases as tree mortality in the stand

reduces competition for light, water, and nutrients following herbivore population outbreaks (18, 134, 135, 166, 168). However, general reduction in transpiration rates during periods of defoliation often increases streamflow and nutrient export (77, 148).

The addition of foliage, insect tissues, and feces results in considerable nutrient transfer to the litter layer (134, 136, 141, 148). Premature litterfall resulting from artificial defoliation returned ten times as much nitrogen to the litter as would normal litterfall (77). Even at nominal levels of folivory (< 7% foliage biomass reduction) folivores can return as much as 30% of foliage standing crop of K and 300% of foliage standing crop of Na to the litter (137). Substantial amounts of mobile elements such as K are returned indirectly by folivory as a result of increased leaching from damaged foliage during precipitation events (76, 113, 142).

Changes in the rate, composition, and timing of litterfall all result from herbivory and can affect rates of biotic processing and conservation of nutrients in the litter layer (106, 136). Nutrient return to litter as feces may be less than as an equivalent mass of foliage (77, 141, 160). However, feces are more easily processed by soil organisms. Sequestering of antibacterial tannins in the gut of the green oak leaf roller (*Tortrix viridana* L.) reduced the tannin content of the feces and stimulated litter decomposition (168). Swank et al (1981) observed increased standing crops of nitrifying bacteria and increased NO_3-N export associated with defoliation of mixed-hardwood forests by the fall cankerworm, [*Alsophila pometaria* (Harris)]. Homopteran honeydew may stimulate nitrogen fixation under host trees (111), but this effect has proven difficult to demonstrate experimentally (27, 115). Interception of honeydew by ants stimulates feeding and growth rate of homopteran populations (137) and concentrates nutrients in underground colonies. Abandoned ant nests show accelerated reforestation (73).

Nutrients returned as insect tissues also are more biologically active than those in fallen foliage. Nutrients removed from foliage during digestion are concentrated in herbivores (77), especially in caterpillar tissues (136). These nutrient pools may stimulate litter decomposition during defoliator outbreaks (136, 141, 148, 168).

Residual and regrowth foliage of defoliated trees has higher phenolic content than foliage of undamaged trees (129, 139; see the section on Chemical Defenses, above). Induced defenses may reduce litter decomposition rates as well as future herbivory (168). The importance of herbivore-controlled canopy/litter transfer for nutrient cycling rates in forested ecosystems depends on several factors, including plant species composition, the particular herbivores involved, changes in microclimate resulting from canopy opening, and the amount, composition, and seasonal pattern of material transferred relative to normal litterfall (106, 136, 168).

Effects on Forest Uses

Herbivore impacts on tree growth and timber production have been the focus of previous reviews (38, 51, 78, 80). Increased emphasis on multiple-use, sustained-yield management of forest resources has led to increased attention to herbivore impacts on nontimber uses of forests (33).

Reduction in radial growth and increased mortality to terminals or genets are immediate and conspicuous folivore impacts (see the section on Effects on Individual Trees, above). Longer-term effects, however, may be more covert. Wickman (166) found that defoliated white fir grew significantly faster than undefoliated white fir for 36 years following a Douglas-fir tussock moth outbreak, despite similar radial growth rates prior to defoliation. The traditional short-term view of herbivore impact on timber production overestimates impact because it fails to recognize long-term recovery through compensatory growth.

Foliage loss reduces both interception of rainfall (113) and transpiration rate, and consequently affects watershed hydrology (33, 77, 148, 160). Increased runoff and increased litter turnover rate could lead to increased erosion, but increased water yield is a positive effect of folivory. If folivory promotes forest succession from deciduous to evergreen species, streamflow may be reduced by herbivore activity (160).

Addition of feces and organic debris, mobilization of soil nutrients, and increased water temperature brought about by folivores can affect water quality (33, 77, 148, 160). Folivory appears not to affect water quality significantly in the northeastern United States (17, 160), perhaps because of high baseline concentrations of nutrients in these streams (148). Nitrate-impoverished streams in the southeastern United States, however, show significant increases in NO_3-N concentrations during periods of defoliation (148). Increased stream temperatures resulting from canopy-opening influence biological and chemical characteristics of streamwater (33, 77, 160).

Increased herbivory provides increased food resources for insectivorous fish, birds, and mammals (33, 77). Reduced canopy cover may affect shelter and nesting sites, but provides increased forage for vertebrate grazers. Increased stream temperature and sedimentation may affect fish habitat during periods of defoliation (33, 77). The long-term contribution of herbivory to stand productivity and heterogeneity (77, 135), however, benefits fish and wildlife by improving food and habitat resources.

CONCLUSIONS

The study of plant/insect relationships is in its infancy, yet it is already clear that valid generalizations will be rare. Problems of scale, previous history, specificity of response, separation of cause and effect, and confounding variables plague those who would characterize plant/herbivore interactions. In forested

ecosystems, practical problems of canopy access and random sampling in the heterogeneous volume represented by the canopy confound experimental design. Short- and long-term responses to herbivory can be very different, even opposite (59, 166).

A need for carefully designed, critical, long-term manipulative experiments is obvious (70). Searching for single-factor explanations will often be futile. Even if one factor is largely causal, this may be extremely difficult to establish unambiguously. Classical scientific method, where all variables but one are held constant, is clearly impossible in most instances. New emphasis on multivariate, factorial, and discriminant techniques may prove more profitable.

Despite these problems, undeniable progress has been made toward understanding herbivory in forested systems. The less-restrictive perception of herbivore/plant interaction as a mutualistic non-zero-sum game (*sensu* Axelrod, 7) represents one example of such progress, as does the viewpoint that considers plants as heterogeneous resources in time and space. We anticipate that future research will continue to provide stimulating results.

ACKNOWLEDGMENTS

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