Literature Review: Canopy Herbivory and Soil Ecology, the Top-Down Impact of Forest Processes

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ABSTRACT. Insects that feed on the foliage of trees can influence the quality of forest soils by dropping frass (feces) and leaf fragments to the floor. They can also modify the chemistry of rainwater that passes through the forest canopy. The effects of herbivore activity on forest soil processes are poorly understood. Potentially, insects may change soil fertility and the rates of decomposition of leaves that have fallen to the ground. This literature review examines our present understanding of these top-down impacts of forest canopy herbivory on soil processes.

Key words: Forest canopy, herbivory, microarthropod, leaf phenology, defoliation, decomposition, leaf litter, forest soil

Introduction
Ecological Linkages in the Canopy

To know the forest, we must study it in all aspects, as birds soaring above its roof, as earth-bound bipeds creeping slowly over its roots.
(Alexander F. Skutch 1992)

The word, canopy, is principally a botanical term and, for our purposes, refers to all above-ground vegetation in a plant community (Nadkarni 1995, Parker 1995, Moffett 2000). According to scientists in the field, each plant community has a canopy (Seastedt & Crossley 1984). Each tree has a canopy (see Lowman 1995b, Reynolds & Crossley 1997). A temperate forest and a tropical forest each have a canopy. Technically speaking, even an orchard, a lawn, a golf course, and a kelp forest have canopies. This systems-wide term includes plants and all their aboveground associations. Contrast this with the word "crown" which, in the parlance of professional forestry, refers exclusively to the upper part of a tree but not to its attending flora and fauna (Winters 1977). The term, canopy, denotes community architecture as well as species composition, nutrient cycling, energy transfer, plant-animal interactions, and conservation issues from the ground to the community-atmosphere interface. For the purposes of this article, however, the term refers specifically to forest systems.

Forest canopies largely have been ignored in ecological studies because of the logistic challenges of access and the difficulty of carrying out experiments many meters above the ground (Lowman et al. 1993, 1996, Lowman 1995a, Reynolds & Crossley 1995, Rinker et al. 1995). From a perspective of sampling design, the components of the canopy include (1) the tree crown itself, (2) sessile organisms (e.g., trees, vines, epiphytes and epiphylls), (3) mobile organisms (e.g., birds, mammals, and insects), and (4) canopy processes (e.g., herbivory and nutrient cycling) (Lowman & Moffett 1993, Lowman & Wittman 1996). Canopy processes are perhaps the most difficult to study experimentally because they require measurements of both sessile and mobile components over time. The study of canopy processes, however, is crucial because of the ecological linkages between the treetops and the forest floor (see Seastedt & Crossley 1984, Lowman & Morrow 1998).

Herbivores as Mediators of Forest Processes

By consuming plant material, herbivores influence decomposition and nutrient cycling in communities (Pitelka 1964, Schultz 1964, 1969, Kitchell et al. 1979, Swank et al. 1981, Pastor & Cohen 1997). Experimental studies have confirmed the role of vertebrate herbivores as mediators of decomposition processes in terrestrial systems (McInnes et al. 1992, Molvar et al. 1993, Pastor et al. 1993, Ritchie et al. 1998). Both empirical

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(Ruess & Seagle 1994, Lovett & Ruesink 1995) and theoretical studies (Loreau 1995, De Mazancourt et al. 1998, De Mazancourt & Loreau 2000) suggest that herbivory, by both vertebrates and invertebrates, can have significant effects on decomposition and nutrient availability in soils.

Canopy herbivory and soil processes in forest systems, however, have not yet been linked in one study. Canopy processes (e.g., defoliation) are coupled to forest floor processes (e.g., decomposition) through inputs of leaf and twig litter, canopy throughfall, and inputs from frass, the excretory products of insect digestion (Schowalter & Sabin 1991, Schowalter et al. 1991, Lovett & Ruesink 1995). Defoliation by insects in forests may impact primary productivity and nutrient cycling (Mattson & Addy 1975, Kitchell et al. 1979). Wilson (1987) argued forcibly that insects in forests are vital components of the ecosystem with effects more pronounced than those of vertebrates. Although the impact of insects on forest systems is controversial (Terborgh 1988), it remains largely untested by experimental manipulation. A considerable proportion of forest canopies can be turned over annually by insect herbivores (Lowman 1992), yet the consequences of herbivory for decomposers such as soil fauna are largely unexplored. Schowalter and Sabin (1991) reported increases in litter arthropod diversity and abundance following defoliation of saplings, but effects of defoliator inputs were not distinguished from defoliator-induced changes in microclimate.

Evidence exists, however, indicating that defoliation can influence forest soil processes. Insect herbivory can actually enhance nitrogen export from forest ecosystems (Swank et al. 1981, Reynolds et al. 2000). Low-to-moderate defoliation levels by forest insects can have significant effects on nutrient cycling (Schowalter et al. 1991). Some evidence suggests that nitrogen is immobilized in frass by fungal decomposers (Lovett & Ruesink 1995), although a field test of nitrogen dynamics following defoliation is sorely needed (Lerdau 1996). Likewise, the evidence is strong that defoliation influences the chemistry of throughfall (Seastedt & Crossley 1984, Schowalter et al. 1991) and subsequent nutrient export (Swank et al. 1981). Interactions among canopy herbivores, soil fauna, and the processes of decomposition, however, remain to be quantified (Schowalter et al. 1986, Risley & Crossley 1993, Reynolds & Hunter 2001).

PLANT PHENOLOGY AND HERBIVORY

Trees exhibit significant variation in both budburst date and the timing of leaf abscission (Hunter 1992). Variation in the phenology of leaf flush and leaf loss occurs at several spatial scales with differences among forest types, among tree species, among different populations of the same tree species, among individual trees within the same population, and even among canopy layers within individual plants (Lowman 1992, 1995a, Heatwole et al. 1997). The origins of such phenological variation (genetic, ontogenetic, and/or environmental) and the ecological consequences for the trees and the communities within which they live remain matters for debate (Phillipson & Thompson 1983, Hunter 1992). Phenological variation in leaf flush and leaf fall, however, clearly provides the kind of spatial and temporal heterogeneity in resource availability that determines the form of interactions among organisms in natural communities (Dajoz 2000). For example, several authors have suggested that differences among trees in their budburst dates are related to insect herbivore performance and population density. In general, oaks that burst bud early in spring have higher insect herbivore densities and suffer greater levels of defoliation than those that burst bud late (Hunter 1990, 1992). Spatial variation in budburst phenology determines herbivore load and, consequently, influences canopy-wide defoliation levels and the distribution of frassfall and greenfall to the forest floor. In at least one system, variation in the timing of leaf expansion of forest trees is thought to have a cascading effect through the trophic system from plants through insect herbivores to avian predators (Hunter & Price 1992).

Leaf abscission is another critical event in the dynamics of a forest. Spatial and temporal variation in the timing of leaf fall influences herbivore densities and may determine patterns of foraging by herbivores within and among trees. Leaf fall also represents one major pulse of resource input into the decomposer community on the forest floor. Thus, spatial and temporal variations in leaf abscission are reflected in variation in the activities of decomposers.

LEAF PHENOLOGY AS A REGULATOR OF INSECT HERBIVORY

Generalities about differences between temperate and tropical forests must first acknowledge the broad variation in a single latitude (Lowman 1995a). Nonetheless, most broadleaved trees in temperate forests produce new foliage in spring and drop old foliage in fall. Foliage is largely absent for the rest of the year, as are insect folivores; and the availability of young expanding leaves shows a marked peak in the spring.

In European temperate forests, dominated by oaks, the temporal distributions of herbivores closely track leaf expansion. The work by Feeny (1970) on the English oak, *Quercus robur*, demonstrated a spring-skewed species richness of oak herbivores. A second smaller peak in late summer/fall includes species that respond to a second flush of oak foliage resulting from spring defoliation. Yet more than 95% of the total defoliation on *Q. robur* occurs between budburst in April and the beginning of June, presumably because of seasonal declines in foliage quality (Feeny 1970, McNeill & Southwood 1978). As leaves age, they generally become lower in total nitrogen and water (Mattson 1980) and are often higher in fiber, lignin, and polyphenols than are younger leaves (Cates 1980). Inevitably, examples occur of insect herbivores that prefer mature foliage (Cates 1980), but defoliation events are most usually associated with young leaves (Dajoz 2000). In rain forests, young leaves are more extensively grazed by insect herbivores than are old leaves (Lowman 1984, 1992). In most deciduous forests in the eastern United States, folivory also is skewed toward leaf emergence (Reichle et al. 1973).

The tropics are not aseasonal. Most plants in the tropics produce new leaves periodically rather than continuously, and some synchrony occurs among different plant species, suggesting adaptive responses to biotic or abiotic variables (Van Schaik et al. 1993). Nonetheless, leaf emergence in tropical wet forests does not exhibit the same pronounced seasonal peak as in temperate forests. Much more interspecific variability in leaf flush and leaf fall exists in tropical wet forests than in temperate forests. For example, in a French Guianan forest, each deciduous tree species appears to exhibit its own endogenous periodicity for shedding leaves (Loubry 1994). A 12-year study of flowering for 173 tree species at La Selva Biological Station in Costa Rica concluded that tree phenology was highly diverse, irregular, and complex (Newstrom et al. 1994). The authors also concluded that many tropical tree species show greater variation in phenology than do temperate species. Data on fruit fall from the Luquillo Experimental Forest in Puerto Rico suggest that, despite strong seasonal pulses in fruit production, a stand in some part of the forest is always in peak fruit production (Lugo & Frangi 1993). Tree species in Australian rain forests show a diversity of leaf flush phenologies from seasonal to continuous (Lowman 1992). Tropical dry forests show more seasonal patterns of leaf flush than do tropical wet forests, and the production of new foliage appears to peak toward the end of the dry season, perhaps avoiding the peak emergence of insect folivores that begins with the rains (Aide 1992). Even in tropical dry forest, however, more interspecific variability in phenology is apparent than in temperate forests.

The phenological responses of insect herbivores to leaf emergence are arguably even more pronounced in tropical wet forests than they are in temperate forests (Dajoz 2000). Most herbivory on tropical forest leaves occurs very early during expansion and may be even more skewed toward young leaves than defoliation in temperate forests (Reichle et al. 1973). The accumulation of herbivory throughout the forest should still occur more evenly through the year in wet tropical forests than in temperate forests. Despite clear pulses of leaf expansion in tropical wet forests, new leaves are still produced over extended periods. Data presented by Coley and Aide (1991) suggest, for example, that during eight months in Oak Ridge, Tennessee, no new leaves were produced on trees compared with only two months at La Selva, Costa Rica, and four months in Semego, Sarawak. Although both tropical wet forests and temperate forests exhibit seasonal peaks in leaf expansion, those peaks are broader in the tropics.

SOIL PROCESSES IN TEMPERATE AND TROPICAL SYSTEMS

Leaf litter decomposition is a continuous process in wet tropical forests (Cuevas & Medina 1988) as opposed to a pulsed process in temperate forests. The annual litter input at the Coweeta Long-Term Ecological Research (LTER) site in North Carolina, for example, occurs mostly from November to January (Swank & Crossley 1986). In other months, a small amount of greenfall occurs with minor inputs into nitrogen pools in the forest floor (Risley & Crossley 1993). Tropical forest leaf litter varies widely in decomposition rates and resource quality because of such leaf features as phytochemistry and toughness. Some dominant trees may respond to droughts by dropping leaves, thus producing a peak of litter inputs (Cuevas & Medina 1986). The general pattern for wet tropical forests is one of continual litter inputs, continual nutrient inputs via throughfall, and continual herbivory in the canopy (Cuevas & Medina 1986, 1988).

Forest soil fauna may be richer and denser than previously estimated. Because of selective sampling, extracting, sorting, and identifying, we may have considerably underestimated the numbers of species in forest soils (Andre et al. 1994). Most species are collembolan and mite (Andre et al. 1994, Coleman & Crossley 1996). Yet it may be the functional rather than the tax-

onomic diversity of microarthropods that impacts ecosystems (Crossley et al. 1992, Heneghan et al. 1999). These "plankton of the soil" (Johnston 2000) consume fungi and bacteria and comminute detritus, thereby affecting primary production, decomposition, nutrient cycling, microbial structure and activity, and food-web stability (Moore et al. 1988, Heneghan et al. 1999). Their effects on decomposition of organic matter and the maintenance of soil fertility can be significant enough that a trophic cascade results from their influences (see Strong et al. 1996, Heneghan et al. 1999, Wardle 1999).

Current experiments in North Carolina and Puerto Rico (e.g., see Reynolds and Hunter 2001) are evaluating the significance of microarthropod populations for rates of litter decomposition. The continual nature of leaf litterfall in wet tropical forests may be a factor contributing to somewhat lower microarthropod populations in those forest floors. Apparently, the numbers of these soil invertebrates are related to standing crops of organic matter on forest floors, and wet tropical forests have minimal standing crops. One study from Nigeria suggests that collembolan populations are influenced in only minor ways by climatic variability and that life-history phenomena dominate their seasonal fluctuations (Badego & Van Straalen 1993). In contrast, temperate forests support microarthropod densities that appear to peak in synchrony with leaf flush and leaf fall or during wet months (Schowalter & Sabin 1991).

Any pulse of leaf litter inputs contributed by herbivory may have a significant impact on forest floor processes. Nutrient inputs, for example, may be strongly affected by defoliation. B.L. Haines and D.A. Crossley (unpubl. data) recorded large inputs of ammonium and phosphate to forest floors via throughfall that were enriched during an insect outbreak. Lovett and Ruesink (1995) described experiments in which gypsy moth frass was added to laboratory incubations, causing microbial immobilization of N with little mineralization after 120 days. Though he did not specify herbivory as a causal agent, McDowell (1998) documented the alteration of precipitation chemistry by contact with the forest canopy where herbivores are active ecological components. Considering the nutrient limitations and low soil fertility of some tropical wet forests, the effect of herbivory on nutrient inputs into forest floor processes may be significant. This effect may be heightened by overall herbivory levels in tropical forests that appear to be higher than those in temperate forests.

Conclusion: Few Studies Connect Canopy to Ground

Few studies have directly compared ecological processes between tropical and temperate systems (but see Coley & Aide 1991, Lowman & Wright 1994). One major difficulty of across-site comparisons has been the lack of standardized protocols for field measurements. At a recent National Science Foundation (1995) workshop on database management, contributors stressed the value of standardized protocols for accurate comparisons among sites. Another recognized difficulty is the strong influence that climate and vegetation exert on soil properties (Hobbie 1992). Tropical rain forests are typically low-nutrient ecosystems, while temperate forests are generally high-nutrient areas. Rates of nutrient allocation and demand, along with local climate and soil microbes, make across-site comparisons difficult. Plant and animal assemblages in tropical forests also exhibit various extreme patterns when compared to those in temperate forests (MacArthur 1969), compounding any comparative ecological studies for these biomes.

Another challenge to across-site comparisons has been the lack of a conceptual model that links insect herbivory in forest canopies to soil processes. Defoliation takes two major routes in influencing decomposition on the forest floor. First, solid materials drop to the floor during or following herbivory. Specifically, insect frass, greenfall (leaf fragments dropped by defoliators), and prematurely abscised leaves represent major inputs to the soil community resulting from herbivory (Schowalter & Sabin 1991, Schowalter et al. 1991, Lovett & Ruesink 1995). Second, rainfall collects some products of herbivory and introduces those products to the soil in liquid form. This canopy throughfall represents the combined effects of dissolved insect frass and modified leachates from damaged foliage. Both pathways result in the input of carbon, nitrogen, and phosphorus to the decomposer community. Because plant decomposition and soil respiration are major interdependent processes of consequence to detritus ecology (Singh & Grupta 1977), measurement of soil respiration is used as an index of soil metabolism. Thus, tools are available for the development of conceptual models that link forest canopy and soil processes.

Canopy ecologists are shifting their emphasis from a descriptive autecology of individuals to a more complex ecological approach (Lowman & Wittman 1996, Reynolds & Hunter 2001). The complexity of forest systems demands such an interdisciplinary avenue of study. Canopy researchers have predicted for some time that the

emphasis of their work inevitably would adjust to address relationships between plants and animals (Schowalter et al. 1986) and between canopy and forest floor (Lowman & Wittman 1996). Ecological studies that link vegetation strata, address intrinsic differences in biota and seasonality, and compare temperate and tropical associations are not only timely studies; they are indispensable for a realistic understanding of our living planet.

LITERATURE CITED

Aide, T.M. 1992. Dry season leaf production: an escape from herbivory. Biotropica 24: 532–537.

André, H.M., M.-I. Noti and Philippe Lebrun. The soil fauna: the other last biotic frontier. Biodiversity & Conserv 3: 45–56.

Badejo, M.A. and N.M. Van Straalen. 1993. Seasonal abundance of springtails in two contrasting environments. Biotropica 25: 222–228.

Cates, R.G. 1980. Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. Oecologia 46: 22–31.

Coleman, D.C. and D.A. Crossley. 1996. Fundamentals of Soil Ecology. Academic Press, San Diego.

Coley, P.D. and T.M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pp. 25–49 in P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson, eds. Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. John Wiley and Sons, New York.

Crossley, D.A., B.R. Mueller and J.C. Perdue. Biodiversity of microarthropods in agricultural soils: relations to processes. Agric., Ecosyst. & Environm. 40: 37–46.

Cuevas, E. and E. Medina. 1986. Nutrient dynamics within Amazonian forests: Part I, nutrient flux in fine litter fall and efficiency of nutrient utilization. Oecologia 68: 466–472.

———. 1988. Nutrient dynamics within Amazonian forests: Part II, fine root growth, nutrient availability, and litter decomposition. Oecologia 76: 222–235.

Dajoz, Roger. 2000. Insects and Forests: The Role and Diversity of Insects in the Forest Environment. Lavoisier, Paris.

De Mazancourt, C., M. Loreau and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? Ecology 79: 2242–2252.

De Mazancourt, C.L. and Michel Loreau. 2000. Effect of herbivory and plant species replacement on primary production. Amer. Nat. 155(6): 735–754.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51(4): 565–581.

Heatwole, H., M.D. Lowman, C. Donovan and M. McCoy. 1997. Phenology of leaf-flushing and macroarthropod abundances in canopies of *Eucalyptus* saplings. Selbyana 18(2): 200–214.

Heneghan, L., D.C. Coleman, X. Zou, D.A. Crossley and B.L. Haines. 1999. Soil microarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. Ecology 80(6): 1873–1882.

Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. Trends Ecol. & Evol. 7: 336–339.

Hunter, M.D. 1990. Differential susceptibility to variable plant phenology and its roles in competition between two insect herbivores on oak. Ecol. Entomol. 15: 401–408.

———. 1992. A variable insect-plant interaction: the relationship between tree budburst phenology and population levels of insect herbivores among trees. Ecol. Entomol. 17: 91–95.

Hunter, M.D. and P.W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724–732.

Kitchell, J.F., R.V. O'Neill, D. Webb, G.A. Gallep, S.M. Bartell, J.F. Koonce and B.S. Ausmus. 1979. Consumer regulation of nutrient cycling. Bioscience 29: 28–34.

Johnston, J.M. 2000. The contribution of microarthropods to aboveground food webs: a review and model of belowground transfer in a coniferous forest. Amer. Midland Nat. 143: 226–238.

Lerdau, M. 1996. Insects and ecosystem function. Trends Ecol. & Evol. 11: 151.

Loreau, M. 1995. Consumers as maximizers of matter and energy flow in ecosystems. Amer. Nat. 145: 22–42.

Loubry, D. 1994. Phenology of deciduous trees in a French Guianan forest (5 degrees latitude north): case of a determinism with endogenous and exogenous components. Canad. J. Bot. 72: 1843–1857.

Lovett, G.M. and A.E. Ruesink. 1995. Carbon and nitrogen mineralization from decomposing gypsy moth frass. Oecologia 104: 133–138.

Lowman, M.D. 1984. An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? Biotropica 16(4): 264–268.

———. 1992. Leaf growth dynamics and herbivory in five species of Australian rain forest canopy trees. J. Ecol. 80: 433–447.

———. 1995a. Herbivory in Australian forests-a comparison of dry sclerophyll and rain forest canopies. Proc. Linn. Soc. 115: 77–87.

———. 1995b. Herbivory as a canopy process in rain forest trees. Pp. 431–455 in M.D. Lowman and N.M. Nadkarni, eds. Forest Canopies. Academic Press, San Diego.

Lowman, M.D., R.L. Kitching and Genevieve Carruthers. 1996. Arthropod sampling in Australian subtropical rain forests—how accurate are some of the more common techniques? Selbyana 17: 36–42.

Lowman, M.D. and Mark Moffett. 1993. The ecology of tropical rain forest canopies. Trends Ecol. Evol. 8(3): 104–107.

Lowman, M.D., M.W. Moffett and H.B. Rinker. 1993. A new technique for taxonomic and ecological sampling in rain forest canopies. Selbyana 14: 75–79.

Lowman, M.D. and Patrice Morrow. 1998. Insects and their environment: plants. Pp. 290–316 *in* W.S. Romoser and J.G. Stoffolano, eds. The Science of Entomology. WCB McGraw-Hill, Boston.

Lowman, M.D. and P.K. Wittman. 1996. Forest canopies: methods, hypotheses, and future directions. Ann. Rev. Ecol. & Syst. 27: 55–81.

Lowman, M.D. and S.J. Wright. 1994. A comparison of herbivory in the rain forest canopies of Panama and Australia. Selbyana 15: 35.

Lugo, A.E. and J.L. Frangi. 1993. Fruit fall in the Luquillo Experimental Forest, Puerto Rico. Biotropica 25: 73–84.

MacArthur, R.H. 1969. Patterns of communities in the tropics. Biol. J. Linn. Soc. 1(April): 19–30.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. & Syst. 11: 119–161.

Mattson, W.J. and N.D. Addy. 1975. Phytophagous insects as regulators of forest primary production. Science 190: 515–522.

McDowell, W.H. 1998. Internal nutrient fluxes in a Puerto Rican rain forest. J. Trop. Ecol. 14: 521–536.

McInnes, P.F., R.J. Naiman, J. Pastor and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73: 2059–2075.

McNeill, S. and T.R.E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships. Pp. 77–98 *in* J.B. Harbourne, ed. Biochemical Aspects of Plant and Animal Coevolution: Proceedings of the Phytochemical Society Symposium, Reading, April 1977. Academic Press, New York.

Moffett, M.W. 2000. What's 'Up'? A critical look at the basic terms of canopy biology. Biotropica 32(4a): 569–596.

Molvar, E.M., R.T. Boyer and V. Vanballengerghe. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94: 472–479.

Nadkarni, Nalini. 1995. Good-bye, Tarzan. Sciences 35(1): 28–33.

National Science Foundation. 1995. Proceedings of the NSF Canopy Database Workshop. Evergreen State College, Olympia, Washington.

Newstrom, L.E., G.W. Frankie and H.G. Baker. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. Biotropica 26: 141–159.

Parker, G.G. 1995. Structure and microclimate of forest canopies. Pp. 73–106 *in* M.D. Lowman and N.M. Nadkarni, eds. Forest Canopies. Academic Press, San Diego.

Pastor, J., B. Dewey, R.J. Naiman, P.F. McInnes and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74: 467–480.

Pastor, J. and Y. Cohen. 1997. Herbivores, the functional diversity of plant species, and the cycling of nutrients in boreal ecosystems. Theor. Pop. Biol. 51: 165–179.

Phillipson, J. and D.J. Thompson. 1983. Phenology

and intensity of phytophage attack on *Fagus sylvatica* in Wytham Woods, Oxford. Ecol. Entomol. 8: 315–330.

Pitelka, F.A. 1964. The nutrient-recovery hypothesis for arctic microtine cycles. I. Introduction. Pp. 55–56 *in* D.J. Crisp, ed. Grazing in Terrestrial and Marine Environments. Blackwell, Oxford.

Reichle, D.E., R.A. Goldstein, R.I. Van Hook and G.J. Dodson. 1973. Analysis of insect consumption in a forest canopy. Ecology 54: 1076–1084.

Reynolds, B.C. and D.A. Crossley. 1995. Use of a canopy walkway for collecting arthropods and assessing leaf area removed. Selbyana 16(1): 21–23.

———. 1997. Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. Ecol. Entomol. 25: 348–356.

Reynolds, B.C. and M.D. Hunter. 2001. Responses of soil respiration, soil nutrients, and litter decomposition to inputs from canopy herbivores. Soil Biol. & Biochem. 33(12,13): 1641–1652.

Reynolds, B.C., M.D. Hunter and D.A. Crossley. 2000. Effects of canopy herbivory on nutrient cycling in a northern hardwood forest in western North Carolina. Selbyana 21(1,2): 74–78.

Rinker, H.B., M.D. Lowman and M.W. Moffett. 1995. Africa from the treetops. Amer. Biol. Teacher 57(7): 393–401.

Risley, R.S. and D.A. Crossley. 1993. Contribution of herbivore-caused greenfall to litterfall nitrogen flux in several southern Appalachian forested watersheds. Amer. Midland Nat. 129: 67–74.

Ritchie, M.E., D. Tilman and J.M.H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79: 165–177.

Ruess, R.W. and S.W. Seagle. 1994. Landscape patterns in soil microbial processes in the Serengeti National Park, Tanzania. Ecology 75: 892–904.

Schowalter, T.D. and T.E. Sabin. 1991. Litter microarthropod responses to canopy herbivory, season and decomposition in litterbags in a regenerating conifer ecosystem in western Oregon. Biol. & Fertil. Soils 11: 93–96.

Schowalter, T.D., T.E. Sabin, S.G. Stafford and J.M. Sexton. 1991. Phytophage effects on primary production, nutrient turnover, and litter decomposition of young Douglas fir in western Oregon. For. Ecol. & Managem. 42: 229–243.

Schowalter, T.D., W.W. Hargrove and D.A. Crossley. 1986. Herbivory in forested ecosystems. Ann. Rev. Entomol. 31: 177–196.

Schultz, A.M. 1964. The nutrient-recovery hypothesis for arctic microtine cycles. II. Ecosystem variables in relation to arctic microtine cycles. Pp. 57–68 *in* D.J. Crisp, ed. Grazing in Terrestrial and Marine Environments. Blackwell, Oxford.

———. 1969. A study of an ecosystem: the arctic tundra. Pp. 77–93 *in* G.V. Dyne, ed. The Ecosystem Concept in Natural Resource Management. Academic Press, New York.

Seastedt, T.R. and D.A. Crossley. 1984. The influence of arthropods on ecosystems. BioScience 34: 157–161.

Singh, J.S. and S.R. Gupta. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. 43: 449–528.

Skutch, A.F. 1992. A Naturalist in Costa Rica. University Press of Florida, Gainesville, Florida.

Strong, D.R., J.L. Maron and P.G. Connors. 1996. Top down from underground? The underappreciated influence of subterranean food webs on aboveground ecology. Pp. 170–175 *in* G.A. Polis and K.O. Winemiller, eds. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.

Swank, W.T. and D.A. Crossley. 1986. Coweeta Hydrologic Laboratory: background and synthesis. Pp. 23–32 *in* M.I. Dyer and D.A. Crossley, eds. Coupling of Ecological Studies with Remote Sensing. U.S. Department of State Publication 9504, Washington, D.C.

Swank, W.T., J.B. Waide, D.A. Crossley Jr. and R.L. Todd. 1981. Insect defoliation enhances nitrate ex-

port from forest ecosystems. Oecologia 51: 297–299.

Terborgh, John. 1988. The big things that run the world—a sequel to E.O. Wilson. Conserv. Biol. 2: 402–403.

Van Schaik, C. P., J.W. Terborgh and S.J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Rev. Ecol. & Syst. 24: 353–377.

Wardle, D.A. 1999. How soil food webs make plants grow. Trends Ecol. & Evol. 14(11): 418–420.

Wilson, E.O. 1987. The little things that run the world: the importance and conservation of invertebrates. Conserv. Biol. 1: 344–346.

Winters, R.K. 1977. Terminology of Forest Science Technology Practice and Products. Society of American Foresters, Bethesda, Maryland.