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Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics

Mark D. Hunter

Institute of Ecology, University of Georgia, Athens, GA 30602-2202, U.S.A

Introduction

I've been thinking a lot lately about death and decomposition. I don't know if it's the onset of a mid-life crisis or waiting for the academic 'deadwood' in my own institution to be recycled into the peak productivity of new faculty but, either way, it's been on my mind. I was primed therefore for the appearance of a couple of recent publications that explore links between insect herbivore activity and the recycling of nutrients in ecosystems. The first of these is a new insect ecology text book (Schowalter, 2000), which promotes the view that insects are regulators of cybernetic systems (i.e. ecosystems). The second is an article by Belovsky & Slade (2000) in the Proceedings of the National Academy of Sciences, which documents the effects of grasshopper populations on nutrient availability and primary production in grasslands. It is well established, of course, that insects are major decomposers of non-living tissue such as leaf litter, faeces, wood and cadavers (Speight *et al.*, 1999). Their role as regulators of ecosystem processes by the consumption of living tissue is more controversial. The publications by Schowalter (2000) and Belovsky & Slade (2000) suggest that consumption of living foliage by insect herbivores can have significant impacts upon the cycling of nutrients in systems, their subsequent availability to plants, and the growth and productivity of plant communities.

These arguments might sound familiar. The initial idea that herbivores can regulate nutrient cycling and primary production date back to the 1960s and 1970s (Pitelka, 1964; Schultz, 1964, 1969; Chew, 1974; Mattson & Addy, 1975; Kitchell *et al.*, 1979) and led to the general view that moderate herbivory can increase rates of nutrient cycling (Schowalter, 1981; Seastedt & Crossley, 1984; DeAngelis, 1992). However, the view that insect herbivores act to increase nutrient availability and subsequent productivity became inappropriately linked with the 'herbivores as mutualists' hypothesis (Dyer & Bokhari, 1976; Owen & Wiegert, 1976, 1981), in which herbivores were seen to increase the fitness of the plants upon which they feed. The concept of herbivores as mutualists has caused considerable controversy in the literature (Paige & Whitham, 1987; Bergelson & Crawley, 1992; Paige, 1992; Belsky *et al.*, 1993; Turner *et al.*, 1993; Moon *et al.*, 1994; Dyer *et al.*, 1995) and may have diluted the interest of some terrestrial insect ecologists in herbivore–ecosystem interactions.

Correspondence: Mark D. Hunter. Tel.: +1 706 542 1801; fax: +1 706 542 6040; e-mail: mhunter@sparc.ecology.uga.edu; website: www.ecology.uga.edu/hunter.html

In reality, the idea that insect herbivores may regulate nutrient availability and primary production has no fundamental link with theories of mutualism or plant fitness. Plant productivity is measured in different units (carbon per m² per year) and at a different level of organization (the community) than is fitness (proportional representation in the next generation measured at the level of individual plants). Theories of herbivore-mediated changes in nutrient cycling need not be found guilty by association with controversial views of herbivores as mutualists. Given the recent interest in the role of species in ecosystems (Jones & Lawton, 1995) and publications by Schowalter (2000) and Belovsky & Slade (2000), it is worth re-examining potential effects of insect herbivores on ecosystem function. The discussion that follows is limited to the effects of foliar-feeding herbivores on soil nutrient dynamics and subsequent productivity. Effects of wood-boring insects on nutrient dynamics are well-documented (e.g. Dale *et al.*, 1990) and, although root-feeding insects can influence nutrients in soils (Maron & Connors, 1996; Maron & Jefferies, 1999; Hunter, 2001), the effects of below-ground fauna on nutrient dynamics are a whole other can of worms, so to speak. In addition, although the focus of this article will be insect folivores, I beg your indulgence if a few four-legged and eight-legged herbivores make brief appearances to illustrate an occasional ecological principle.

Mechanisms

There are seven broad mechanisms by which the activity of insect herbivores can cause changes in nutrient cycles and nutrient availability in soils. I will mention each of them briefly here and then focus on some of their effects in more detail below. First, insect herbivores can deposit significant quantities of faecal material (frass) onto litter and soil. Nitrogen returned to soils in insect frass can exceed that in leaf litter (Fogal & Slansky, 1985; Grace, 1986) and can double overall rates of nitrogen return from plants to soil (Hollinger, 1986). Second, nutrients returned to soils in insect cadavers are more easily decomposed than those in leaf litter (Schowalter *et al.*, 1986) and can stimulate the decomposition of litter during defoliator outbreaks (Swank *et al.*, 1981; Schowalter & Crossley, 1983; Seastedt & Crossley, 1984). Third, insect defoliation changes the nutrient content of precipitation as it passes through plant canopies. Folivory influences the nutrient chemistry of this 'throughfall' primarily through increased rates of nutrient leaching from damaged leaves (Tukey & Morgan, 1963) and through the dissolution of frass from foliage. Fourth, herbivory

can change the quantity and quality of leaf litter that falls from plant canopies to the soil. Herbivore-mediated changes in litter inputs can occur through premature leaf abscission (Faeth *et al.*, 1981), petiole clipping and foliar fragmentation (Risley, 1986), wound-induced increases in foliar phenolics (Findlay *et al.*, 1996), root mortality (Ruess *et al.*, 1998) and community-wide changes in the relative abundance of plant species or genotypes that vary in their litter quality (Pastor *et al.*, 1993; Kielland *et al.*, 1997; Uriarte, 2000). Fifth, herbivore-mediated changes in plant community composition not only influence litter quality, but may also affect the utilization of soil nutrients by the new community (Kielland *et al.*, 1997). Sixth, herbivory may influence root exudates or interactions between roots and their symbionts (Bardgett *et al.*, 1998; Hunter, 2001), both of which are known to influence nutrient dynamics. Finally, herbivores can influence the structure of plant canopies and the cover that they provide, with concomitant changes in light availability, soil temperature and moisture. Changes in soil microclimate that result from herbivore activity can alter the cycling of nutrients (Mulder, 1999). Similarly, herbivore-induced changes in light availability may influence litter quality through effects on leaf chemistry (Hunter & Forkner, 1999; Strand *et al.*, 1999) or plant productivity and diversity (Van der Wal *et al.*, 2000).

These seven mechanisms are likely to vary in the speed with which they influence nutrient dynamics and primary production. Nutrient cycles are likely to respond rapidly to inputs of frass, cadavers and modified throughfall because they do not require the decomposition of complex organic matter. These effects are analogous to the 'fast cycle' of McNaughton *et al.* (1988). In contrast, herbivore-mediated changes in litter quality, canopy cover and community composition will probably influence nutrient dynamics more slowly and are analogous to the 'slow cycle' of McNaughton *et al.* (1988). It is possible that fast and slow responses to herbivore activity may differ in both magnitude and direction. For example, herbivore activity may increase rates of nitrogen cycling and primary production in the short term while causing both to decline in the long term (Uriarte, 2000). A more detailed understanding of fast and slow responses of ecosystems to herbivory may help to resolve some of the debates that have arisen in the literature on herbivore–ecosystem interactions (Belovsky & Slade 2000).

Shit happens and then you die – the influence of frass and cadavers

Having worked in the field during outbreaks of the winter moth in England and the gypsy moth in the United States, I can vouch for the importance of a comb as an essential piece of field equipment. Inputs of insect frass and cadavers from plant canopies are large during defoliator outbreaks and represent a steady rain of labile carbon and nutrients during the growing season, even under endemic insect densities. More importantly, in temperate systems, frass inputs occur at a different time of year from natural litter fall and include resources that would, in the absence of herbivory, be resorbed by perennial plants before leaf drop. About 70% of foliar nitrogen is resorbed by plants prior to senescence under low levels of herbivory. Under heavy defoliation, however, resorption can account for less than 25% of foliar nitrogen, with 29% occurring in premature leaf fall, 23% in

insect frass, and 8% in insect biomass (G. M. Lovett, personal communication, 2000). Under isolated California oak trees, for example, up to 70% of both the nitrogen and phosphorus that returns to the soil is in the form of frass and cadavers during outbreaks of the California oak moth (Hollinger, 1986). Although a considerable proportion of forest canopies can be turned over annually by insect herbivores (Lowman, 1992), inputs are obviously much smaller in the absence of outbreaks. Under endemic insect densities (less than 10% foliage removed), herbivores are thought to consume around 2–3% of annual leaf production in *Eucalyptus* forest and return less than 4% of nitrogen, phosphorus and potassium to the forest floor as frass or cadavers (Ohmart *et al.*, 1983).

In some cases, the deposition of insect frass and cadavers appears to influence nutrient cycling and subsequent availability (Fogal & Slansky, 1985; Lightfoot & Whitford, 1990). For example, defoliation by the fall cankerworm in the southern Appalachians in the U.S. results in marked changes in nutrient cycling and export of nitrate in forest streams (Swank *et al.*, 1981). Defoliation is followed by an increase in primary productivity, increases in litterfall, increases in nutrient inputs to the soil in frass and throughfall, increases in soil nitrogen pools and increases in soil microflora. Likewise, infestations of black locust by the locust stem borer in the same forests coincide with nitrate export in forest streams (Crossley *et al.*, 1988). Similar increases in nitrate export have been observed following gypsy moth defoliation (Eshleman *et al.*, 1988; Webb *et al.*, 1995). Recently, a moderate outbreak (40% leaf area removed) of the oak-feeding sawfly *Periclista* sp. (Hymenoptera: Tenthredinidae) in the Appalachians led to a tripling of average frass inputs and a five-fold increase in soil nitrate availability. Summer increases in soil nitrate were followed by two-fold increases in stream nitrate export in autumn and winter (Reynolds *et al.*, 2000).

In addition to direct nutrient inputs in frass, insect faeces may also provide a source of nutrients for decomposers that can then accelerate the decomposition of natural litter fall. For example, Schowalter & Sabin (1991) reported increases in litter arthropod diversity and abundance following defoliation of saplings. However, in their study, effects of defoliator inputs were not distinguished from defoliator-induced changes in litter microclimate. Experimental additions of frass to forest floors in the southern Appalachians have resulted in blooms of Collembola, fungal-feeding nematodes, bacterial-feeding nematodes and predatory mites (B. C. Reynolds and M. D. Hunter, unpublished data). Presumably, these soil invertebrates are responding to fungal and bacterial blooms (Coleman & Crossley, 1996) resulting from the nutrient additions in frass.

In contrast to studies that have associated the deposition of insect frass with increases in nitrate in soils and streams (Swank *et al.*, 1981; Crossley *et al.*, 1988; Eshleman *et al.*, 1988; Webb *et al.*, 1995; Reynolds & Hunter, 2001), other studies have failed to observe significant effects of frass deposition on nutrient availability. For example, gypsy moth defoliation of hybrid poplar in Michigan produced large quantities of frass, but little change in soil nitrate (K. R. Kosola, personal communication, 2000). The frass remained largely undecomposed on the dry soil surface, suggesting that the lack of increased nitrate availability was not due to rapid uptake by the plants. Similarly, Lovett &

Ruesink (1995) reported microbial immobilization of essentially all extractable nitrogen in gypsy moth frass. This immobilization would prevent uptake of mineral nutrients by vegetation or the leaching of nutrients from soil. Their initial experiments were conducted in laboratory microcosms without natural densities of soil fauna which may be responsible for remobilizing nutrients from the microbial community (see above). However, recent field experiments by Lovett and colleagues have again failed to show increases in nutrient leaching following frass deposition (G. M. Lovett, personal communication, 2000), with most nitrogen retained in recalcitrant organic matter. Given that there is no significant volatilization of nitrogen in the form of ammonia from gypsy moth guts (Lovett *et al.*, 1998), nitrogen appears to be highly conserved at Lovett's sites. These differences in results may be due to variation in the quality of frass, variation in abiotic conditions, variation in forest age, or variation in the fauna and flora of forest soils where the research was conducted.

The effects of honeydew production on ecosystem processes have generally received less attention than those of frass production, even though honeydew was a component of Owen & Wiegert's (1981) hypothesis that plants might benefit from herbivory. Questions of fitness aside, the labile carbon in insect honeydew can act as a fuel for decomposers (Choudhury, 1985) and might be expected to influence soil nutrient dynamics. Clearly, there is still much to learn about the effects of insect faecal material on soil nutrient availability and ecosystem productivity.

Throughfall

There is strong evidence that defoliation influences nutrient concentrations in precipitation as it passes through the canopies of plants (Tukey & Morgan, 1963; Seastedt & Crossley, 1984; Hollinger, 1986; Haines *et al.*, 1991; Schowalter *et al.*, 1991). Such herbivore-mediated changes in throughfall chemistry can be quite large (Kimmins, 1972; Seastedt & Crossley, 1984). For example, in a study of herbivores on black locust and red maple in the southern Appalachians, a nominal 8% increase in leaf consumption resulted in a 70% increase in leaching of potassium from foliage (Seastedt *et al.*, 1983). There were also minor defoliation-induced increases in leaching of phosphorus. These effects were generated through experimental manipulation of endemic herbivore densities and suggest that even background levels of leaf damage can influence throughfall chemistry.

Nutrients in throughfall may actually decline following attack by herbivores. For example, feeding by aphids on Norway spruce reduces the concentrations of nitrate and ammonium in throughfall (Stadler & Michalzik, 1999). In this case, high concentrations of dissolved organic carbon (sugars) are thought to fuel microbial immobilization of inorganic nitrogen and so reduce the amount of nitrate and ammonium reaching the forest floor.

While it has been assumed that defoliation-induced changes in throughfall chemistry are related to subsequent nutrient dynamics in soils and streams (Swank *et al.*, 1981; Crossley *et al.*, 1988), this is not simple to test experimentally. In one manipulative study, the addition of artificial throughfall to forest soils was accompanied by increases in Collembola and

nematode populations (B. C. Reynolds and M. D. Hunter, unpublished data). However, not all studies support a strong role for leached nutrients from damaged leaves in subsequent nutrient dynamics (Hollinger, 1986; Schowalter, 1999). Experimental defoliation of Douglas fir saplings by the silver-spotted tiger moth had a statistically significant but ecologically minor influence on throughfall chemistry (Schowalter, 1999). Likewise, an outbreak of the California oak moth did not result in increased leaching losses of nutrients from the foliage of *Quercus* spp. (Hollinger, 1986). It would appear, therefore, that although defoliation can sometimes affect fluxes of nitrogen, phosphorus, potassium and calcium to the forest floor in leachate (Seastedt & Crossley, 1984; Schowalter *et al.*, 1991), the magnitude of the changes to throughfall and their subsequent impact on ecosystem processes, are contingent on the systems under study (Schowalter, 1999).

The quality of litter, species turnover and microclimate

In contrast to the potentially rapid effects of frass, cadavers and throughfall on soil nutrient dynamics, herbivore-mediated changes in litter quality are likely to influence ecosystem processes much more slowly because they require the decomposition of complex organic material (McNaughton *et al.*, 1988; Belovsky & Slade, 2000). Changes in litter quality can result from premature leaf abscission, wound-induced decreases (or increases) in litter quality, the mortality of roots, and the replacement of species or genotypes in communities.

Premature leaf abscission is a pervasive response by plants to herbivory (Faeth *et al.*, 1981; Chabot & Hicks, 1982; Pritchard & James, 1984). Defoliation-induced litterfall can return 10 times as much nitrogen to the forest floor as would normally return in natural litterfall (Klock & Wickman, 1978) because resorption of nutrients from damaged leaves may not be complete before they fall. Many leaf-chewing insects are also messy eaters, dropping clipped leaves or fragments of leaves (greenfall) to the forest floor (Risley, 1986). There have been few systematic studies of the importance of greenfall for soil nutrient dynamics but the carpet of green leaf material that can occur under canopies defoliated by gypsy moth suggest that such inputs can be important periodically. When insect herbivores are at endemic densities, greenfall is thought to represent about 5% of leaf production and about 6% of the nitrogen normally returned during autumnal litterfall (Risley & Crossley, 1993). These figures are greater than the combined estimates of nutrient return in insect frass and cadavers from endemic densities of insects (Risley & Crossley, 1988). Greenfall is a high-quality substrate (relative to other surface litter) available for rapid use by decomposer organisms, and may increase rates of nutrient cycling (Risley & Crossley, 1988). Unlike potassium, nitrogen is not readily leached from damaged leaves on trees and so its concentration in greenfall may represent a more significant transfer from the canopy to the forest floor than does its concentration in throughfall (see above). In a recent experiment, we excluded natural greenfall from the floor of a southern Appalachian forest (Reynolds & Hunter, 2001). We observed a decline in soil respiration, suggesting that decomposer activity had been reduced. An extreme form of 'greenfall' is generated by

Pikas (*Ochotona princeps*: Lagomorpha) in alpine habitats where they deposit caches of vegetation that serve as food during winter. Soils beneath these caches are higher in nitrogen, and plants growing on caches have higher tissue nitrogen and greater productivity than those in surrounding areas (Aho *et al.*, 1998).

Given the near-ubiquitous occurrence of wound-induced changes in the palatability of leaves (Agrawal *et al.*, 1999), it is surprising that the decomposition of leaves damaged by herbivores, and the consequences for nutrient dynamics, have received so little attention. In the one study that I could find, Findlay *et al.* (1996) reported that damage by mites to the leaves of cottonwood results in a 50% decline in the rate of litter decomposition. Reductions in decomposition rate were associated with damage-induced increases in phenolic compounds and were predicted to increase the accumulation of soil organic matter and reduce the rates of nutrient return. Of course, effects of polyphenols on decomposition and nutrient dynamics are well-established (reviewed in Haettenschwiler & Vitousek, 2000), as is the phenomenon of polyphenol induction (Schultz & Baldwin, 1982; Rossiter *et al.*, 1988). There is clearly a gaping hole in our understanding of how phenolic induction in living tissue can influence soil nutrient dynamics during decomposition (Choudhury, 1988).

Some types of herbivory on plants can cause subsequent increases in foliage quality. Browsing by mammals, because it removes meristems as well as leaves, can result in the production of regrowth tissue with fewer leaves of higher average nutritional content (Kielland *et al.*, 1997). When these high-quality leaves abscise, rates of nutrient cycling can increase (Mulder, 1999). As entomologists, we may wish to explore whether insect herbivores that damage meristematic tissue have a different effect on soil nutrient dynamics than those that remove portions of leaves.

Not all litter 'falls' above ground. Senescing roots provide a source of carbon and nutrients below ground that can influence nutrient availability, and root senescence following above-ground herbivory may influence soil processes (Seastedt *et al.*, 1988). In arctic systems, herbivory appears to result in a significant reduction in fine root production and an increase in root mortality (Ruess *et al.*, 1998). In combination, herbivores cause an increase in fine root turnover. However, fine roots from defoliated areas appear to decompose more slowly than those from undefoliated areas, making direct effects of herbivore-mediated root mortality on soil nutrient availability uncertain. Moreover, we are just beginning to understand the potential impact of fine-root exudates on soil ecosystem processes (Bardgett *et al.*, 1998). In artificial defoliation experiments (i.e. with no inputs of frass, greenfall or throughfall) defoliation levels of 50% have not been shown to influence soil nutrient availability (Mikola *et al.*, 2000), suggesting that independent effects of root mortality may be minimal. Similarly, gypsy moth defoliation of hybrid poplar in Michigan had no effect on root mortality and only minor effects on the production of new roots (K. R. Kosola, personal communication, 2000). It remains possible, however, that nitrogen export following severe defoliation of forested watersheds that is generally attributed to inputs of frass and throughfall (Swank *et al.*, 1981; Crossley *et al.*, 1988; Reynolds *et al.*, 2001) may depend, in part, upon root mortality. Given our ignorance of the contributions of root

senescence to nutrient dynamics, it would appear to be a priority for future research efforts.

Perhaps the greatest potential for insects to influence the dynamics of ecosystems comes when they alter the relative abundance of plant species within communities. Species differ markedly in the quality of litter that they produce and in the speed with which it decomposes (Wedin & Tilman, 1990; Hobbie, 1992; Haettenschwiler & Vitousek, 2000). If herbivores are choosy, they may gradually reduce or eliminate the contribution of particular species to the overall litter pool. In addition, herbivores that influence the progress of succession (Ritchie *et al.*, 1998; Van Wijnen *et al.*, 1999) will mediate changes in nutrient inputs and nutrient use. An example of the former is provided by Belovsky & Slade (2000). During a 5-year experiment, they excluded grasshoppers from prairie habitat and monitored the subsequent effects on nitrogen dynamics, plant productivity and species abundance. In the presence of grasshoppers, rates of nitrogen cycling increased and productivity rose by 18%. Grasshoppers increased the quality of available litter (nitrogen content, rate of decomposition) and their effects on productivity depended more on their influence on litter quality (slow-cycle effects) than on the deposition of faecal material or cadavers (fast-cycle effects). Specifically, effects were mediated by a relative reduction in the abundance of plants that produced low-quality litter caused, in part, by preferential consumption.

I was surprised by the results of Belovsky & Slade (2000). Leaves that are palatable to generalist herbivores are usually those that decompose most rapidly (Jefferies *et al.*, 1994; Cornelissen *et al.*, 1999). Through preferential consumption of palatable species, herbivores might often be expected to increase the biomass of plants that produce recalcitrant litter and so slow rates of nutrient cycling. This prediction is opposite to the effects found by Belovsky and Slade. One possible explanation is that selection by herbivores has led to a relative increase in tolerant rather than resistant plants. Plants that tolerate defoliation by rapid regrowth may produce litter that is easily decomposed (R. Van der Wal, personal communication). Clearly, correlated variation in the palatability and decomposition rates of plant material is critical to an understanding of the roles of herbivores in nutrient cycling and productivity (Pastor & Cohen, 1997). The question that remains is how often the activities of herbivores push the balance towards the production of high-quality vs. low-quality litter.

In at least a few other systems, herbivory appears to increase the relative abundance of plants that produce high quality litter. For example, moose browsing in the Alaskan arctic is associated with an increase in the rate of nutrient cycling. The mechanisms for this effect are multiple and include changes in litter accumulation, canopy cover, soil characteristics, species turnover and the quality of litter inputs (Kielland *et al.*, 1997; Kielland & Bryant, 1998; Mulder, 1999). Over the long-term, moose browsing favours a transition from willow to nitrogen-fixing alder with yet further impacts upon soil ecosystems. The positive effects of herbivores on nutrient availability in the arctic may not be herbivore-specific. For example, moderate grazing by geese in Alaska also appears to stimulate primary production, at least in part due to fertilization by goose faeces (Ruess *et al.*, 1997).

However, in their long-term studies of moose browsing on Isle Royale, Michigan, Pastor *et al.* (1993) found trends opposite to those in Alaska. Long-term exclusion of moose resulted in increased nutrient availability in soils, higher microbial activity and higher rates of nitrogen mineralization. Moose on Isle Royale mediate a change in the plant community towards conifers over hardwoods and depress both the quality and quantity of litter returned to the soil. This work has recently been extended to investigate the impacts of herbivores across landscapes (Pastor *et al.*, 1998) and supports the notion that herbivore activity generates patches of low nutrient availability (and low temporal variance) at the landscape level. Similar results have been reported following the long-term exclusion of herbivores in Uganda (Hatton & Smart, 1984) and the exclusion of insects and mammals from oak savanna in the United States (Ritchie *et al.*, 1998). In this last case, herbivore exclusion caused an increase in both the cover and biomass of a nitrogen-fixing legume. Above- and below-ground tissues and plant litter were therefore higher in nitrogen, so mediating an increase in soil nitrate availability. Herbivores decreased rates of nitrogen-cycling by selectively removing plants with high tissue nitrogen. Overall, herbivore-free plots were twice as productive as those with herbivores (Knops *et al.*, 2000).

In direct contrast, however, Georgiadis & McNaughton (1990) have associated high levels of herbivore activity with increasing nutritional quality across landscapes in East African savanna, suggesting once again that herbivory increases rates of nutrient availability. Contrasting results in disparate systems may depend upon the relative importance of plant species replacement and herbivore fertilization effects on nutrient dynamics. Van Wijnen *et al.* (1999) suggested that, when grazing normally halts the process of succession, the absence of grazing can lead to an increase in fuel for microbial decomposers and concomitant increases in mineralization rates. In their study, long-term effects on species composition and the biomass of plant material available to decompose were consistently more important than effects of fertilization by faeces. Responses may also be conditional upon the general availability of water and nutrients (Georgiadis *et al.*, 1989).

It was necessary to consider the effects of mammals on nutrient dynamics in order to set the stage for the only long-term study of which I am aware, in which insect densities were manipulated in order to study effects on ecosystem processes. Recently, Uriarte (2000) reported that long-term exclusion of insect herbivores from goldenrod fields resulted in an increase in nutrient availability and an increase in plant tissue quality. The long-term reduction in soil nutrients mediated by herbivore activity was in contrast to short-term increases resulting from frass deposition and increased light penetration. Given that there was little species turnover during the 17-year experiment, Uriarte (2000) speculates that within-species selection of high quality plants by goldenrod herbivores may lead to an accumulation of low-quality plants producing low quality litter as succession proceeds.

Uriarte (2000) presents an interesting twist to the 'species replacement' effects described above. 'Genotype replacements' during long-term exposure to herbivores may also be important to the nutrient dynamics of ecosystems and there exists some evidence that this may be so. Holland *et al.* (1992) simulated the

responses of grazing-tolerant and grazing-intolerant plant populations to defoliation. They found positive effects of herbivores on nitrogen cycling and productivity only in the grazing-tolerant populations. This suggests that herbivore pressure, acting through the process of natural selection, may ultimately determine the effects of herbivores on nutrient dynamics and primary productivity.

One final effect of herbivores on nutrient cycling can be mediated by changes in the architecture of plant canopies and subsequent effects on soil microclimate. The processes of decomposition and nutrient cycling are often driven by soil temperature and humidity (Meentemeyer, 1978; Swift *et al.*, 1979; Meentemeyer & Berg, 1986), which may change following damage by herbivores to above-ground vegetation. For example, increased sunlight on the soil surface is thought to contribute to elevated rates of nutrient cycling following browsing by moose in the arctic (Kielland *et al.*, 1997).

Conclusions and future directions

In the experiments reported by Belovsky & Slade (2000), net primary production was greatest at intermediate grasshopper densities. This provides empirical support for the modelling work of de Mazancourt & Loreau (2000), who suggest that a bell-shaped relationship between defoliation and plant productivity can occur either through an increase in the rate of nutrient cycling in current plant communities or through herbivore-mediated replacement of plant species. Non-linear relationships between herbivory and nutrient dynamics, bell-shaped or otherwise, should be no surprise. Given spatial and temporal variation in both insect densities and in host-plant preferences, we might expect that the effects of insects on nutrient dynamics will also vary in space and time. The literature provides clear examples of both positive effects (Swank *et al.*, 1981; Seastedt & Crossley, 1984; DeAngelis, 1992; Belovsky & Slade, 2000; Reynolds *et al.*, 2001) and negative effects (Hatton & Smart, 1984; Pastor *et al.*, 1993; Pastor *et al.*, 1998; Ritchie *et al.*, 1998; Knops *et al.*, 2000) of herbivory on rates of nutrient cycling. The interesting question is why.

Several lines of investigation may provide answers. As Uriarte (2000) points out, we need to distinguish between short- and long-term effects of herbivores on nutrient dynamics and productivity; interactions that are initially positive can change to negative over time. Second, we need long-term experiments that manipulate the degree of herbivory rather than simple presence or absence. There is no reason to believe that endemic densities of insect herbivores will have the same effects on ecosystem processes as do epidemic densities. Third, we must surely try to associate degrees of herbivore specialization with their impacts on nutrient dynamics. Given that preferential consumption appears to be a mediator of changes in nutrient cycling via species turnover (Pastor *et al.*, 1993; Knops *et al.*, 2000), we might predict that specialist herbivores will have impacts through 'slow-cycle' effects, whereas the impacts of generalists may be more restricted to 'short-cycle' effects. Fourth, as entomologists, we might wish to consider whether insects have effects on ecosystems that are fundamentally different from other taxa of herbivores. The induction of phenolic defences by leaf-chewing insects differs from the

effects of browsing on leaf quality and may influence the subsequent decomposition of litter (Findlay *et al.*, 1996). Fifth, the proposition that herbivore-mediated turnover of plant genotypes can result in the selection of morphs with recalcitrant litter (Uriarte, 2000) is an exciting suggestion that requires attention. It is possible that many of the effects of herbivores on ecosystem processes will be 'invisible' to us until we characterize the genetic architecture of plant populations in the presence and absence of herbivores, and quantify the phenotypic traits (lignin, polyphenols, nutrient content) that mediate the decomposition process.

Finally, herbivores do not simply influence nutrient dynamics in ecosystems, but also respond to ecosystem change. Positive feedbacks may exist whereby herbivore-induced increases in nutrient cycling and productivity act to stimulate further insect population growth. Increased nutrient availability has been shown in some cases to decrease foliar defences (Hunter & Schultz, 1995), increase both the quality and quantity of foliage (Forkner & Hunter, 2000) and 'cascade up' the trophic system to influence herbivore and predator densities (Forkner & Hunter, 2000). Put simply, defoliation at one moment in time may favour defoliation in the future through effects on nutrient availability and productivity. In any case, the potential interactions between insect herbivores and the ecosystems in which they live and die are many and diverse. They provide an area of interface where the disciplines of population ecology and ecosystem science can fruitfully interact.

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