

# Effects of Nitrogen Deposition on Insect Herbivory: Implications for Community and Ecosystem Processes

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## ABSTRACT

The deposition of anthropogenically fixed nitrogen (N) from the atmosphere onto land and plant surfaces has strong influences on terrestrial ecosystem processes. Although recent research has expanded our understanding of how N deposition affects ecosystems directly, less attention has been directed toward the investigation of how N deposition may affect ecosystems indirectly by modifying interactions among organisms. Empirical evidence suggests that there are several mechanisms by which N deposition may affect interactions between plants and insect herbivores. The most likely mechanisms are deposition-induced shifts in the quality and availability of host plant tissues. We discuss the effects of N deposition on host plant chemistry, production, and phenology, and we review the evidence for the effects of N deposition on insect herbivores at the individual, population, and community levels. In general, N deposition has positive effects on individual insect performance, probably due to deposition-induced improvements in host

plant chemistry. These improvements include increased N and decreased carbon-based defensive compound concentrations. The evidence to date suggests that N deposition may also have a positive effect on insect populations. These effects may have considerable ecological, as well as economic consequences if the rates of herbivory on economically important timber species continue to increase. Deposition-induced changes in plant–herbivore relationships may affect community and ecosystem processes. However, we predict that the larger-scale consequences of interactions between N deposition and herbivory will vary based on site-specific factors. In addition, interactions between N deposition and other global-scale changes may lead to nonadditive effects on patterns of herbivory.

**Key words:** acid deposition; herbivory; global change; nitrogen deposition; plant–insect interactions; pollution.

## INTRODUCTION

The deposition of anthropogenically fixed nitrogen (N) from the atmosphere onto plant and soil sur-

faces is one of the most important factors currently causing global-scale changes to terrestrial ecosystems. According to recent estimates, anthropogenic activities are doubling the amount of fixed N entering the terrestrial N cycle annually (Galloway and others 1994; Vitousek and others 1997). This N enrichment causes changes in soil N availability, and the acidic nature of many nitrogenous com-

Received 29 July 2002; accepted 24 January 2003; published online 2 March 2004.

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pounds affects soil and soil solution chemistry. Because N is important in controlling biological processes, from organismal to ecosystem levels of organization, deposition-induced changes in N availability may have substantial consequences for natural systems (Vitousek and Howarth 1991; Chapin 1980). Increased N deposition may act either directly on biological processes (for example, nutrient cycling) or indirectly (for example, causing shifts in herbivory that result from altered host plant biology).

Although the direct effects of N deposition have received considerable attention over the past 2 decades, scientists have paid less attention to its indirect effects. However, there is a growing body of evidence suggesting that N deposition may substantially affect the interactions between plants and insect herbivores. Large-scale changes in herbivory caused by N deposition could affect ecosystem productivity and carbon (C) storage, as well as the dynamics of the cycling of N and other elements. In addition, changes in herbivory could have large economic consequences; they impact the growth and mortality patterns of commercially important species, such as northern conifers.

In this article, we first briefly review the chemical and spatial nature of N deposition and its direct effects on terrestrial ecosystems. We then examine the indirect effects of N deposition, focusing on its impact on interactions between herbivores and plants and the ways in which these individual-scale effects may translate to changes in population, community, and ecosystem processes. Finally, we assess the potential for interactions between N deposition and other global-scale changes, such as changes in climate and atmospheric carbon dioxide (CO<sub>2</sub>) levels, on herbivory and ecosystems.

### Chemical and Spatial Nature of N Deposition

Inorganic N in the atmosphere enters terrestrial systems as either dry deposition (direct deposition of gases and particulate matter), wet deposition (via precipitation), or cloud water deposition (Lovett 1994; Ollinger and others 1993). Deposited N arrives in reduced form as NH<sub>x</sub> (primarily volatilized from agricultural activities) or in an oxidized state as NO<sub>y</sub> (primarily as the result of fossil fuel combustion). The relative concentrations of the reduced and oxygenated forms of N depend on regional human activities. Deposited N becomes incorporated into the biota through roots or microbial uptake of N deposited into the soil surface and via foliar uptake of gaseous and particulate N compounds (Rennenberg and others 1998; Aber and

others 1998; Lovett 1994; Hosker and Lindberg 1982).

Spatial patterns of deposition vary greatly on both local and regional scales. At the local scale, deposition rates can differ across scales of tens to hundreds of meters, such as when a plume of fixed N moves from a point source of emission across the landscape (Armolaitis 1998; Pitcairn and others 1998; Whytemare and others 1997). At the regional scale, the highest rates of deposition generally occur downwind of major urban or agricultural areas and decrease with distance from the source area. In addition, rates of N deposition tend to increase with altitude because of the increased importance of cloud water deposition (Lovett 1994; Weathers and Likens 1997). In the United States, deposition rates range from near zero to up to 40 kg N ha<sup>-1</sup> y<sup>-1</sup> in high-elevation locations in the Northeast, and deposition rates in the Netherlands may exceed 100 kg N ha<sup>-1</sup> y<sup>-1</sup> (Ollinger and others 1993; Draaijers and others 1989).

### Direct Ecosystem Effects of N Deposition

Nitrogen deposition directly affects ecosystem processes in two general ways. Deposition-induced increases in soil inorganic N availability lead to fertilization effects, while the often acidic nature of N deposition leads to acidification effects (Fenn and others 1998; Aber and others 1998; Vitousek and others 1997). Rates of N mineralization and nitrification tend to increase with atmospheric inputs, although mineralization rates may decline after soils become N saturated (Aber and others 1998). One of the consequences of increased rates of N cycling is an increase in the flux rates of trace gases from soils. Increased rates of N<sub>2</sub>O and NO emission as a result of N deposition may have substantial consequences for atmospheric chemistry (Hall and Matson 1999). The deposition of acidic precipitation, such as nitric acid, alters soil chemistry and leads to changes in element cycling. Deposition-induced soil leaching causes the depletion of essential cations, including magnesium (Mg), calcium (Ca), and potassium (K) (Likens and others 1996). Depending on the rates of acid input and the acid-buffering capacity of the soil, acid deposition can exceed the buffering capacity of the soil and reduce pH (Schulze 1989; Fenn and others 1998). Decreases in soil pH lead to the mobilization of aluminum (Al) into the soil solution; this Al is detrimental to plant growth due to both direct toxicity and interference with Ca uptake (Schulze 1989; Shortle and Smith 1988).

Deposition-induced changes in plant physiology may also lead to changes in net primary productiv-

ity (NPP). The strong correlation between plant N status and photosynthetic rates (Field and Mooney 1986) means that N deposition can have a strong positive influence on leaf-level photosynthetic rates. Simulated and "natural" deposition studies at both the leaf and stand levels have shown increases in photosynthesis, which may in turn lead to increased C storage in the terrestrial biosphere (Townsend and others 1996; Holland and others 1997; Schindler and Bayley 1993; but see Nadelhoffer and others 1999). In contrast to the effects of low to moderate levels of deposition, chronic high levels of deposition eventually lead to decreases in NPP (Aber and others 1998). Decreases in productivity are likely the result of base cation deficiencies and the toxic effects of mobile Al (Schulze 1989).

### EFFECTS OF N DEPOSITION ON HERBIVORY

Nitrogen deposition can potentially affect plant-herbivore interactions via several pathways (Figure 1). First, the deposited N may be toxic to insects. Although direct toxicity effects have been documented for other types of air pollution (Alstad and others 1982), there is little evidence to show that such direct effects result from N deposition (a possible exception is the toxicity of high concentrations of gaseous N oxides) (Feir and Hale 1983). Second, deposition-induced changes in food quality, quantity, and phenology may alter herbivore population dynamics. For insect herbivores, the N concentration of the host plants strongly controls processes such as growth, survivorship, population levels, and outbreak frequency. Changes to these processes result from both the direct effects of N on host plant quality and its influences on plant defensive chemistry. Finally, N deposition may affect plant-herbivore interactions by altering relationships between herbivores and their natural enemies, leading to changes in herbivore survival and population dynamics.

Because the first mechanism is a rare response to N deposition, this review is focused on the second and third mechanisms. To distinguish the impacts of N deposition from higher-level rates of fertilization (such as occurs in agricultural fertilization practices), we have limited this review to studies that use N deposition rates of no greater than  $100 \text{ kg N ha}^{-1} \text{ y}^{-1}$ .

#### Individual Plant and Insect Responses to N Deposition

There are two central questions that are especially pertinent to the potential effects of deposition on

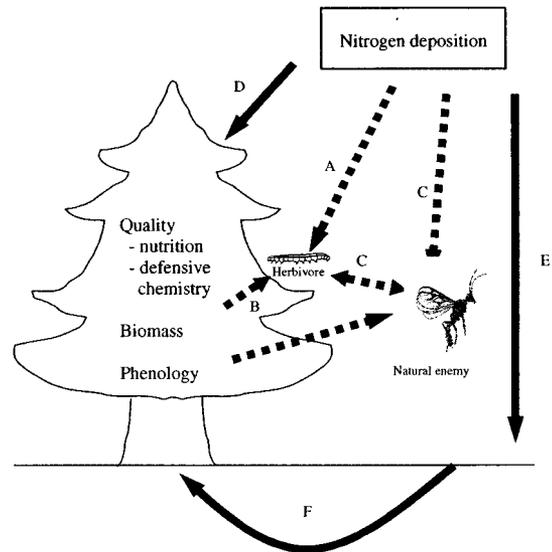


Figure 1. Possible mechanisms by which N deposition could affect interactions between plants and insect herbivores. Nitrogen deposition could potentially directly affect insects (A), although there is scant evidence to support this mechanism. More likely are deposition-mediated changes in host-plant suitability (B) or deposition-mediated changes in herbivore susceptibility to predators, parasites, or pathogens (C). Changes in host-plant quality may be the result of either foliar uptake of fixed nitrogen compounds (D) or deposition to soil surface (E) and subsequent changes in the availability of fixed nitrogen, base cations, or aluminum for root uptake (F). The processes shown with solid arrows have been reasonably well researched, whereas processes represented by dashed arrows are less well understood.

herbivore performance via changes in host plant quality. First, does N deposition alter the composition of plant tissue in such a way as to affect insect herbivores? Second, if herbivores do respond to changes in tissue quality, what is the direction of that response? We focus primarily on leaf tissue responses and consequent impacts on folivores because these responses have been studied more thoroughly than the responses of other plant tissue types and other insect feeding guilds. Nonfolivorous insects may also be affected by deposition induced changes in their host plant tissue. For example, Latty and others (forthcoming) draw a link between N deposition and attack by scale insects. We caution, however, that different plant tissues (for example, foliar tissue versus phloem sap) may have dissimilar responses to N deposition, which may lead to different responses among insect feeding guilds.

*Plant N Allocation and Insect Response.* Aber and others (1998) have suggested that N deposition

Table 1. Response of Foliar Nitrogen to Nitrogen Deposition

Species	N Addition	Length of N Addition	Foliar N (%)—Low Deposition	Foliar N (%)—High Deposition	% Change	Reference
<i>Pinus resinosa</i>	N addition to natural stand (50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	6 y	1.03	1.34	+30 (?)	Magill and others 1997
<i>Acer rubrum</i>	N addition to natural stand (50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	6 y	1.61	1.73	+7 (?)	Magill and others 1997
<i>Quercus velutina</i>	N addition to natural stand (50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	6 y	2.15	2.29	+6 (?)	Magill and others 1997
<i>Betula lenta</i>	N addition to natural stand (50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	6 y	2.26	2.49	+10 (?)	Magill and others 1997
<i>Calluna vulgaris</i>	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> addition to natural stand (0, 10, 50, 90 kg N ha <sup>-1</sup> y <sup>-1</sup> )	27 mo	1.22	1.25, 1.41, 1.56	+2.4, +16, +28	Prins and others 1991
<i>Betula lenta</i>	Gradient from poultry farm (12 and 50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	—	2.38	3.21	+35 (?)	Pitcairn and others 1998
<i>Fagus sylvatica</i>	Gradient from poultry farm (12 and 50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	—	2.47	2.76	+12 (?)	Pitcairn and others 1998
<i>Pinus sylvestris</i>	Gradient from poultry farm (12 and 50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	—	1.69	2.24	+33 (?)	Pitcairn and others 1998
<i>Picea sitchensis</i>	Gradient from poultry farm (12 and 50 kg N ha <sup>-1</sup> y <sup>-1</sup> )	—	1.31	1.79	+37 (?)	Pitcairn and others 1998
<i>Picea rubens</i>	N addition to natural stand (0, 25, 56 kg kg N ha <sup>-1</sup> y <sup>-1</sup> )	1–3 y	0.93	1.03, 1.06	+10.5, +13.8 NS	Magill and others 1996
<i>Fagus grandifolia</i>	N addition to natural stand (0, 25, 56 kg kg N ha <sup>-1</sup> y <sup>-1</sup> )	1–3 y	2.09	2.26, 2.30	+8.2, +10.0 <sup>b</sup>	Magill and others 1996
<i>Betula alleghaniensis</i>	N addition to natural stand (0, 25, 56 kg kg N ha <sup>-1</sup> y <sup>-1</sup> )	1–3 y	2.06	2.21, 2.23	+7.2, +8.3 <sup>b</sup>	Magill and others 1996
<i>Betula papyrifera</i>	Simulated deposition (one-time application, 2:1 NaNO <sub>3</sub> :NH <sub>3</sub> SO <sub>4</sub> ), 0 and 100 kg N ha <sup>-1</sup> y <sup>-1</sup>	—	2.3	2.6	+13	Erelli and others 1998
<i>Betula papyrifera</i>	Low- and high-elevation leaves (high-elevation receive greater deposition loads)	—	2.50	2.85	+13	Erelli and others 1998
<i>Abies balsamea</i>	Low- and high-elevation leaves	—	1.83	1.57	-14	Erelli and others 1998
<i>Picea rubens</i>	Low- and high-elevation leaves	—	1.11	1.24	+12	Erelli and others 1998
<i>Nardus stricta</i>	Open-top chambers and simulated acid rain	1 growing season	1.4	1.69	+21 NS	Leith and others 1999
<i>Erica cinerea</i>	Open-top chambers and simulated acid rain	1 growing season	0.84	1.57	+87	Leith and others 1999
<i>Eriophorum vaginatum</i>	Open-top chambers and simulated acid rain	1 growing season	1.43	1.85	+29	Leith and others 1999
<i>Vaccinium vitis-idaea</i>	Open-top chambers and simulated acid rain	1 growing season	0.73	1.74	+138	Leith and others 1999
<i>Crataegus</i> spp.	Ambient roadside and filtered air	4 wk	1.95	2.27	+16	Braun and Flückiger 1985

Table 1. (Continued)

Species	N Addition	Length of N Addition	Foliar N (%)—Low Deposition	Foliar N (%)—High Deposition	% Change	Reference
<i>Picea abies</i>	Simulated wet deposition in closed chambers (0, 30, 90 kg N ha <sup>-1</sup> y <sup>-1</sup> s NH <sub>3</sub> NO <sub>4</sub> )	27 mo	0.47 (at 420 ppm CO <sub>2</sub> )	0.49, 0.70	+4.3, +49 <sup>b</sup>	Hättenschwiler and Schafellner 1999
<i>Picea engelmannii</i>	Sites with high (3–5 kg N ha <sup>-1</sup> y <sup>-1</sup> ) versus low (1–2 kg N ha <sup>-1</sup> y <sup>-1</sup> ) N deposition	—	0.96	1.09	+13.5 NS	Baron and others 2000
<i>Pinus sylvestris</i>	Stands w/high- and low-deposition loads (~0.27 versus 7.5 kg N ha <sup>-1</sup> y <sup>-1</sup> throughfall)	—	1.44	1.75	+21.5	Huhn and Schulz 1996
<i>Calluna vulgaris</i>	Simulated deposition added to natural stands (7.7 and 15.4 kg N ha <sup>-1</sup> y <sup>-1</sup> )	—	1.12 (shoots) <sup>a</sup>	1.31, 1.34 (shoots) <sup>a</sup>	+17, +20	Power and others 1998

<sup>a</sup>Excluded from calculation of mean change in foliar N, because nonfoliar tissue was included in the chemical analysis.

<sup>b</sup>Value for change in response to higher N addition used for calculating mean change in foliar N.

Studies include "natural" and simulated deposition experiments

Studies were selected for inclusion based on the criteria that foliar N concentrations were available for both deposition and control sites, and that addition rates were  $\leq 100$  kg for simulated deposition experiments. Statistically significant changes are noted in bold; nonsignificant changes are denoted as NS; changes for which results of statistical analyses were not reported are denoted (?).

leads to a monotonic increase in foliar N concentration as stands move toward N saturation. We compiled data on foliar N response to natural or simulated N deposition (Table 1). Although there are differences in experimental design among studies (for example, differences in N loads, length of N applications, chemical composition of deposition, and species-specific differences) that make it difficult to draw generalizations, some interesting patterns emerge from these data. First, N deposition has a very strong positive effect on leaf N concentration. In 24 of 25 cases, deposition led to an increase in foliar N. Second, there was a difference in response between coniferous and deciduous woody species. The mean increase in foliar N for conifers was 21.76% ( $\pm 6.09$  SE), whereas deciduous trees had a mean increase of only 13.03% ( $\pm 2.62$  SE).

In addition to affecting total foliar N, deposition can lead to changes in the form of N present in leaf tissue. We compiled data on foliar free amino acid concentration in response to N deposition. We found that the concentration of reported foliar free amino acids—in particular, arginine and glutamine—tends to increase in plants subjected to high deposition inputs (Table 2). It is unclear from these data how generalized these responses are, because four of the eight studies were conducted on *Pinus sylvestris*, all but two studies used conifers, and most studies reported data from only a limited number of amino acids. These data do indicate, however, that N deposition can cause drastic changes in relative allocation patterns among different amino acids. Similarly, N additions can cause increases in total foliar protein and altered protein profiles in leaf tissue (Rao and others 1993; Pietila and others 1991). The concentration of soluble N may increase in plants with deficiencies of nutrients such as K and Mg (White 1984). Foliar nitrate concentrations increase in foliage once the N requirements for growth or nitrate assimilation capacity are exceeded (Fenn and others 1996, 1998; Stams and Schipholt 1990; Hogbom and Hogberg 1991). Finally, increased N availability can increase allocation to N-based secondary chemicals such as alkaloids (Gerson and Kelsey 1999; Waterman and Mole 1989). We hypothesize that a general pattern showing a positive correlation between N availability and N-based secondary chemicals would become evident under N deposition, although to our knowledge no studies to date have investigated this relationship.

The N concentration in host-plant tissue consistently serves as the single best predictor of host plant quality for insect herbivores. This pattern has

been reviewed extensively elsewhere, and a strong positive relationship has been documented between foliar N concentration and insect survivorship, development, growth, and reproductive rates (Mattson and Scriber 1987; Mattson 1980; White 1993; Scriber and Slansky 1981). In contrast, insect response to N may vary in terms of individual consumption rates. Some species increase consumption rates in the presence of N-rich food, whereas others tend to decrease individual feeding rates to keep N intake constant (for example, see Slansky and Feeny 1977; Raubenheimer 1992; Meyer 2000; Woods 1999; Muthukrishnan and Selvan 1993). However, there appears to be an optimal N concentration in host foliage for most insects, and decreased performance is likely when tissue N exceeds this level (Mattson 1980; White 1984). The optimal foliar N concentration seems to differ greatly among different insect herbivores. For example, in an experiment where common ragweed (*Ambrosia artemisiifolia*) was grown under varying N levels, cabbage looper (*Trichoplusia ni*) larvae had greatest survival under the highest foliar N (6.76% N), whereas the survival rates of larvae of a leaf beetle, *Ophraella communa*, declined as foliar N rose above the lowest foliar N concentration (2.20% N). In this case, differential insect response to foliar N concentration may be related to N-based secondary metabolites or foliar nitrate accumulation (Throop 2002).

Given the important influence of N deposition on leaf N concentration and the strong effect of leaf N concentration on insect herbivores, it seems likely that N deposition could play an important role in influencing patterns of herbivory. But a critical question remains: Are current or predicted future levels of deposition great enough to influence herbivory? In a review of fertilization studies, Ayers (1993) found that experimental fertilization increased foliar N concentrations by an average of 38%. In contrast, we found that the average foliar N response to simulated or “natural” deposition (with N deposition rates of 3–100 kg N ha<sup>-1</sup> y<sup>-1</sup>) is around 13% (Table 1). In general, this enhancement of foliar N should have a positive effect on insect performance, provided that foliar N does not exceed the optimal levels for insect herbivores (Mattson 1980; Scriber and Slansky 1981). The apparent difference in foliar N response between deciduous and coniferous plants suggests that N deposition may have fundamentally different effects on herbivores of coniferous trees than herbivores of deciduous trees. Specifically, N deposition might be expected to have a more positive impact on herbivore performance on coniferous trees than on deciduous trees.

**Table 2.** Response of Foliar Free Amino Acid Concentration to Nitrogen Fertilization

Plant	Amino Acid	% Increase (or Decrease)	No. Amino Acids Reported			Deposition Rate	Reference
			+	-	NS		
<i>Fagus sylvatica</i>	Asparagine	+240	4	0	5	-40 kg N ha <sup>-1</sup> y <sup>-1</sup> (fertilization)	Påhlsson 1992 (low-N treatment)
	Aspartate	+100					
	Glutamine	+76					
	Glutamate	+70					
<i>Pseudotsuga menziesii</i>	Glutamine	+3450 <sup>a</sup>	5 <sup>a</sup>	0	0	Ambient versus fertigated (balanced nutrient) sites, both receiving ~40 kg N ha <sup>-1</sup> y <sup>-1</sup> ambient deposition	Perezsoba and Devisser 1994
	Arginine	+1316					
	Histidine	+303					
	Proline	+120					
<i>Pinus sylvestris</i>	Arginine	+250 <sup>a</sup>	4 <sup>a</sup>	1	0	Ambient versus fertilized & irrigated (balanced nutrient) sites, both receiving ~40 kg N ha <sup>-1</sup> y <sup>-1</sup> ambient deposition	Perezsoba and Devisser 1994
	Histidine	+188					
	Glutamine	+127					
	Proline	+52					
<i>Picea abies</i>	Glutamate	-19				Stands with low and high ambient deposition loads (~3 versus ~20–30 kg N/ha/y)	Edfast and others 1990; data from "medium quality" sites
	Arginine	+6266	1	0	5		
<i>Pinus sylvestris</i>	Arginine	+2400	2	0	4	Stands with low and high deposition loads (~3 versus ~20–30 kg N/ha/y)	Edfast and others 1990; data from "medium-quality" sites
	Glutamine	+162					
<i>Pinus sylvestris</i>	Arginine	+12600, +27780 <sup>b</sup>	19 <sup>b</sup>	1	5	NH <sub>4</sub> <sup>+</sup> deposition gradient from a large fox farm; needles collected at 50, 150, and 700 m from farm	Pietila and others 1991
	Cysteine	+600, +500					
	Ornithine	+386, +400					
	Leucine	+225, +355					
<i>Pinus sylvestris</i>	Histidine	+102, +288				Stands w/low and high deposition loads (~0.27 versus 7.5 kg N/ha/y throughfall)	Huhn and Schulz 1996
	Arginine	+753	7	1	1		
	Aspartate	+141					
	Serine	+89					
	Glycine	+83					
	Glutamine	+64					
	Glutamate	+54					
	Asparagine	+38					
<i>Deschampsia flexuosa</i>	Proline	-76				0.5 versus 50 kg N/ha/y (1-y application)	Nordin and others 1998)
	Asparagine	+90	1	0	2		

<sup>a</sup>No statistical analyses presented.

<sup>b</sup>No statistical analyses presented; values given here are the five amino acid with the greatest percent change of the 25 free amino compounds presented.

Studies include "natural" and simulated deposition experiments. For simulated deposition experiments, only addition rates ≤ 100 kg N ha<sup>-1</sup> y<sup>-1</sup> are included. Amino acids with statistically significant differences in concentration are included in the table, and the number of free amino acids that increase, decrease, or do not change in response to deposition are reported. Note that half of the studies use the same species, *Pinus sylvestris*.

Although a vast number of studies have investigated the impacts of quantitative changes in tissue N on insect herbivores, relatively little research has explicitly examined how changes in the form of N in leaves affect insect herbivores. Shifts in allocation to different N-rich compounds may have a substan-

tial impact on insect herbivores. Because free amino acids are a readily available form of N for insects, deposition-induced increases in foliar amino acid concentrations will most likely cause a disproportionate increase in the amount of N available to herbivores (White 1984). The feeding patterns of

**Table 3.** Response of Carbon-based Secondary Chemicals to Nitrogen Deposition

Species	N Addition	Secondary Metabolite	% Change	Reference
<i>Picea abies</i>	Simulated deposition in closed chambers at 420 ppm CO <sub>2</sub> (0, 30, 90 kg N ha <sup>-1</sup> y <sup>-1</sup> )	Tannins (condensed)	<b>-3.6, -8.0<sup>a</sup></b>	Hättenschwiler and Schafellner 1999
<i>Picea abies</i>	Simulated deposition in closed chambers at 420 ppm CO <sub>2</sub> (0, 30, 90 kg N ha <sup>-1</sup> y <sup>-1</sup> )	Phenolics	<b>-9.1, -9.1<sup>a</sup></b>	Hättenschwiler and Schafellner 1999
<i>Calluna vulgaris</i>	Open-top chambers, 35 (year 1) & 70 (year 2) kg N ha <sup>-1</sup> y <sup>-1</sup>	Phenolics	-9.47 NS	Kerslake and others 1998
<i>Betula papyrifera</i>	High versus low elevation	Tannins (condensed)	<b>-41.4</b>	Erelli and others 1998
<i>Betula pubescens</i>	Simulated wet deposition ~6 kg aN ha <sup>-1</sup> y <sup>-1</sup> s HNO <sub>3</sub> , also H <sub>2</sub> SO <sub>4</sub>	Phenolics	+5.2 NS <sup>b</sup>	Suomela and others 1998
<i>Fagus sylvatica</i>	Fertilization with ~40 kg N ha <sup>-1</sup> y <sup>-1</sup> as NH <sub>4</sub> NO <sub>3</sub> , 5 y	Phenolics	<b>-28</b>	Påhlsson 1992; low N treatment
<i>Picea engelmannii</i>	Sites with high (3–5 kg N ha <sup>-1</sup> y <sup>-1</sup> ) versus lower (1–2 kg N ha <sup>-1</sup> y <sup>-1</sup> ) N deposition	Lignin	-2.1 NS	Baron and others 2000

<sup>a</sup>Significance level for overall N treatment effect; data not presented for comparison between N treatments

<sup>b</sup>Grand mean of presented means from several subplots and sampling dates

Studies include "natural" deposition and simulated deposition experiments. For simulated deposition experiments, only addition rates of ≤ 100 kg N ha<sup>-1</sup> y<sup>-1</sup> are included. Statistically significant changes are in bold face and nonsignificant changes are denoted as NS.

some herbivores suggest that they may be limited by amino acid availability and feed to maximize amino acid intake (Parsons and de la Cruz 1980). However, herbivore performance may be reduced in some situations if the altered amino acid profiles are suboptimal; such a response to changes in amino acid profiles has been found in several aphid species (Sandstrom and Pettersson 1994; Ponder and others 2000). In the event that N inputs lead to an accumulation of nitrate in plant tissues, some herbivores may be susceptible to nitrate toxicity (Mattson 1980). However, the data on deposition-induced foliar nitrate concentrations and insect responses to nitrate are not adequate to establish whether deposition would ever lead to nitrate levels high enough to cause a decrease in insect performance. Finally, the potential for N deposition to increase N-based secondary chemicals suggests that the performance of herbivores feeding on plants with these compounds will decrease.

**Plant C Allocation and Insect Response.** Nitrogen deposition may also alter plant–herbivore interactions by affecting patterns of allocation to C-based compounds. In general, the concentration of both total nonstructural carbohydrates (TNC) and total structural carbohydrates (TSC) are negatively correlated with leaf protein concentration (Poorter and Villar 1997). However, only a few researchers have specifically investigated the effects of N deposition on carbohydrate concentrations. The experimental response of carbohydrate allocation patterns to N

deposition has been mixed. In *Deschampsia flexuosa*, leaf sucrose concentration was negatively correlated with leaf N concentration both along a deposition gradient and in experimentally fertilized plots (Hogbom and Hogberg 1991). However, simulated N deposition in environmental chambers did not significantly affect the TNC concentrations in beech, spruce, or three understory species (Landolt and Pfenninger 1997; Hättenschwiler and Korner 1996).

Several plant-allocation models predict that increased N availability leads to decreased allocation to C-based secondary chemicals such as phenolics (including lignin and tannins) and terpenes (Coley and others 1985; Herms and Mattson 1992; Jones and Hartley 1998). Plants allocate proportionately more C to C-based defenses when resources such as N are scarce and plant growth is limited by N. In contrast, when N abounds, C is allocated to growth (Lorio 1986; Bryant and others 1983). In six of seven simulated deposition studies, the concentration of C-based secondary chemicals decreased in response to increasing N availability (the seventh study showed a nonsignificant increase), suggesting that decreased allocation to these compounds is a common response to N deposition (Table 3). Carbon-based secondary chemicals tend to have strong detrimental influences on insect performance (Rosenthal and Janzen 1979), suggesting that deposition-induced changes in C-based secondary chemical allocation may have large influences on

insect performance. In addition, C-based structural defenses (for example, trichomes) can be an important form of defense, particularly for sucking insects (Agrawal 2000). In contrast, there is little evidence to show that deposition-induced influences on plant carbohydrate concentrations strongly affect insect herbivores—perhaps because carbohydrates are rarely limiting to insects, although starch may increase digestibility (Goverde and others 1999).

*Plant Mineral Nutrition and Insect Response.* In addition to its impact on foliar N concentration, N deposition can affect substantially the foliar concentrations of other elements and alters the ratios among them. The acidic nature of much N deposition can lead to acidification of the soil and soil solution and consequent leaching of cations from the soil. Increases in N deposition are coupled with declines in both soil and foliar concentrations of base cations (Katzensteiner and others 1992; Duquesnay and others 2000). Consequently, a monotonic decline in foliar cation: N ratios such as Ca:N and Mg:N is expected as stands become N saturated (Aber and others 1998). In contrast, acid deposition leads to increased mobility of Al in the soil; consequently, it may increase foliar Al concentrations (Wilson and Skeffington 1994).

Insects require a number of mineral elements for physiological processes. Deposition-induced changes in foliar mineral composition may therefore affect herbivore performance. Phosphorus (P), K, and Mg are among the most abundant mineral elements in insect tissues, although little is known about the specific concentrations required for these and other elements (Mattson and Scriber 1987). Because these base cations typically decline in response to N deposition, it is possible that insect herbivores experience mineral deficiencies under high-deposition conditions. Soil acidification from acid deposition has been shown to cause Ca losses great enough to affect snail abundances (Wäreborn 1992; Graveland and others 1994). In contrast, experimental studies of the response of insect herbivores to Ca availability suggest that high levels of Ca may in fact be detrimental because it interferes with insect ability to take up other essential elements from foliage (Clancy and King 1993). Thus, N deposition-induced declines in Ca content may enhance food quality for folivores if pre-deposition Ca levels were higher than optimal. Similarly, the performance of insect herbivores has been linked to complex interactions between Mg and P availability. Generally higher insect performance has been observed with lower concentrations of both these elements (Clancy and King 1993). Diets in that study, however, were based on moderate to high levels of

Mg and P in host plant tissue (0.83–1.95 mg g<sup>-1</sup> Mg and 2.74–4.95 mg g<sup>-1</sup> P) (Clancy and King 1993), so it is unclear whether very low nutrient levels from deposition could in fact be suboptimal for folivores. Ratios between elements may be even more important than absolute values, because they may affect the bioavailability of other nutrients (Clancy and King 1993). Further research into the response of insects to the foliar element ratios found under deposition scenarios would help to clarify this issue.

Deposition-induced increases in foliar Al levels may also affect herbivore performance. Harmful effects of Al on whitebacked planthoppers (*Sogatella furcifera*) have been demonstrated in rice plants with foliar Al levels of 228–268 mg kg<sup>-1</sup> (Salim and Saxena 1992). Reported foliar Al levels in natural forest stands are considerably lower (20–160 mg kg<sup>-1</sup> Al) (Raynal and others 1990), so it is not clear whether the acidification caused by N deposition could create foliar Al levels great enough to affect insect performance.

Clearly, further research on acidification, plant mineral content, and insect performance is needed for a fuller understanding of the implications of N deposition in affecting plant–herbivore relationships. This area of research is particularly critical because of the different influences of agricultural-level N fertilization and atmospheric N deposition on base cation availability.

*Whole-Plant Effects.* In addition to having qualitative effects on plant tissues and a subsequent impact on insect herbivores, N deposition may also affect the quantity of food available to herbivores, either by changing the total amount of plant tissue available or by altering plant phenology and thus changing the timing of the availability of specific tissues. Moderate rates of N deposition (around 5–20 kg N ha<sup>-1</sup> y<sup>-1</sup> of “natural” deposition in northern Europe) have been linked to increases in total plant biomass (Kauppi and others 1992), thereby potentially increasing the quantity of food for insect herbivores. Increases in plant biomass may be more pronounced in deciduous species than in coniferous species because conifers appear to be more likely to allocate additional N to enhancing foliar N concentration (Table 1). Under conditions where very high or sustained loads of N deposition lead to N saturation (for example, 150 kg N ha<sup>-1</sup> y<sup>-1</sup> in an experimental fertilization experiment in a pine stand at Harvard Forest; Aber and others 1998), biomass production often decreases or even ceases (Aber and others 1998; Kauppi and others 1992), leading to a decrease in food availability to insect herbivores. In terrestrial systems, however,

primary consumer populations appear to be limited less by total food availability than by the quality of food and predation pressure from higher trophic levels (Hairston and others 1960; White 1993).

Insect herbivores may respond to deposition-induced changes in the availability of certain plant tissues. Nitrogen fertilization has been shown to increase rates of new leaf flushing in indeterminate plants and to affect leaf development rates (Dickson and Isebrands 1991; Wait and others 1998). Many folivores typically prefer new leaf tissues because of their relatively high N content and low toughness, and changes in flushing phenology can substantially affect interactions between plants and insect herbivores (White 1993; Coley 1980; Fox and others 1997). Similarly, N fertilization can increase herbivory by accelerating the rate of leaf development (Wait and others 1998). It is also possible that N deposition affects the quality of food for herbivores at the whole-plant level by stressing plants and initiating a suite of physiological responses to stress (Koricheva and Larsson 1998; White 1984; Waring and Cobb 1992). Indeed, many forest pest outbreaks are associated with host-plant stress (Waring and Cobb 1992; White 1984). Unfortunately, the exact physiological changes that characterize the stress response have not been well defined. Suggested plant responses to stress have included increased concentrations of free amino acids and decreased allocation to defensive compounds (Haglund 1980; Koricheva and Larsson 1998); in the case of N deposition, these changes may be explained by shifts in nutrient availability rather than a stress-specific response. Recent work suggests that acid deposition may leach membrane-associated foliar Ca. Subsequent disruptions in the membrane structure and function may predispose plants to damage from environmental factors, including herbivory, pathogens, and freezing (DeHayes and others 1999). More research is needed to determine exactly what these physiological stresses are, whether they differ from plant response to deposition-induced changes in nutrient availability, and how they affect insect herbivores.

*Individual-Level Summary.* Changes in tissue chemistry mediated by atmospheric N deposition can affect insect performance both positively and negatively. The available literature suggests that moderate levels of N deposition generally affect insect performance positively by causing increases in total foliar N and amino acids and decreases in C-based defensive chemicals. In addition, moderate deposition may benefit individual insects by increasing plant biomass and the availability of newly flushed leaves. In contrast, very high levels of dep-

osition may negatively affect individual herbivore performance by causing detrimentally high rates of foliar nitrate and a decrease in plant production. Of eight studies that investigated the impacts of simulated or natural N deposition (at rates of up to 100 kg N ha<sup>-1</sup> y<sup>-1</sup>) on individual folivore performance, all showed a positive response to N deposition in at least one measure of insect performance (Table 4). In addition, eight studies with phloem-sucking aphids also showed positive individual-level responses (Table 4). Unfortunately, due to the lack of similarity in the response variables investigated in these studies, it is difficult to make specific predictions about the nature of the particular responses of individual insects to N deposition. However, all of the response variables measured (for example, survival, relative growth rate, adult mass, development time) are strong factors that impact on insect performance and potential fecundity (Awmack and Leather 2002). These data thus provide a solid indication that atmospheric N deposition has strong and measurable positive effects on herbivore performance.

#### Deposition and Susceptibility of Herbivores to Predators and Pathogens

One of the most interesting, but least studied, avenues by which N deposition could affect herbivory is through impacts on predators and pathogens of herbivores. In several ecosystems that have been studied in detail, predators on herbivores play a major role in regulating insect herbivory (Krause and Raffa 1996; Rosenheim and others 1993; Cappuccino and others 1998). For example, in northern coniferous forests, parasitoid wasps can be significant controllers of lepidopteran populations and thus influence folivory (Cappuccino and others 1998). Only a few studies to date have explored the consequences of N deposition on the susceptibility of insect herbivores to predators and pathogens. Changes in rates of predation as a result of N deposition, however, may in turn influence herbivore populations.

Higher trophic levels may, in some cases, be more prone to toxicity from air pollutants than herbivores due to trophic amplification of toxins. For example, Price and others (1974) found that lead (Pb) concentrations were higher in predatory insects than herbaceous ones in a roadside area with high (Pb) emissions (10.3, 15.5, and 35.0 ppm (Pb) for sucking insects, folivores, and predators, respectively). Trophic amplification seems much less likely from N deposition because direct toxicity does not occur in response to most of the forms of N that are likely to be present in herbivores. In contrast, in

**Table 4.** Individual Insect Responses to Simulated Nitrogen (N) Deposition

Insect	Plant	Study Type	N Addition	Low % N	High % N	Performance Change	Reference
<i>Operophtera brumata</i>	<i>Calluna vulgaris</i>	Open-top chambers	35 (year 1) & 70 (year 2) kg N ha <sup>-1</sup> y <sup>-1</sup>	32.8	20.1	Survival +58%	Kerslake and others 1998
Lepidoptera				C:N	C:N	Growth rate +37%	
<i>Lochmaea suturalis</i>	<i>Calluna vulgaris</i>	Field plots with simulated acid rain (NH <sub>3</sub> SO <sub>4</sub> )	7.7 and 15.4 kg N ha <sup>-1</sup> y <sup>-1</sup>	1.12%	1.31%, 1.34%	Pupal weight +23% 5-d RGR+12%, +14% 10-d RGR +7.3%, +12.7% 15-d RGR -3%, +6% 20-d RGR +6%, +3% Pupal mass +9%, +21% Adult mass +2%, +12% 70-d mass 0%, +19%	Power and others 1998
<i>Lymantria monarcha</i>	<i>Picea abies</i>	Mesocosms (at 420 ppm CO <sub>2</sub> )	0, 30, 90 kg N ha <sup>-1</sup> y <sup>-1</sup>	0.47%	0.49%, 0.70%	Larval mass +22%, 36% <sup>a</sup> Consumption +23%, 12% <sup>a</sup> RGR +45.2%, +52.4% <sup>a</sup> RGR +8.4%, -4.3% <sup>a</sup>	Hättenschwiler and Schafellner 1999
<i>Lymantria dispar</i>	<i>Betula papyrifera</i>	High versus low elevation (other factors may covary)	Natural deposition loads	~2.5% <sup>b</sup>	~2.9% <sup>b</sup>	1 <sup>st</sup> instar RGR -4.4%, +18.6% <sup>c</sup> 3 <sup>rd</sup> instar RGR -11.0%, +2.4% <sup>c</sup> 3 <sup>rd</sup> instar consumption -2.6%, -6.7% <sup>c</sup>	Erelli and others 1998
Lepidoptera							
<i>Orgyia leucostigma</i>	<i>Betula papyrifera</i>	High versus low elevation (other factors may covary)	Natural deposition loads	~2.5%	~2.8%	1 <sup>st</sup> instar RGR +5.3%, +6.7% <sup>c</sup> 4 <sup>th</sup> instar RGR -6.4%, +20.1% <sup>c</sup> 4 <sup>th</sup> instar consumption -14.0%, -16.1% <sup>c</sup>	Erelli and others 1998
Lepidoptera							
<i>Neodiprion sertifer</i>	<i>Pinus sylvestris</i>	Field plots with simulated acid rain	~0.14 & 8.4 g N ha <sup>-1</sup> y <sup>-1</sup> , as HNO <sub>3</sub> ; H <sub>2</sub> SO <sub>4</sub> also added			RGR +6% Larval duration +0.5% (illigible), -1.6% (illigible) Cocoon mass +3.7% (illigible), -0.5% (illigible) Larval biomass +26% <sup>b</sup>	Saikkonen and others 1995
Hymenoptera							
<i>Phratora polaris</i>	<i>Betula pubescens</i> ssp. <i>tortuosa</i>	Field plots with simulated acid rain	-0.14 & 8.4 g N/ha/y, as HNO <sub>3</sub> ; H <sub>2</sub> SO <sub>4</sub> also added				Palokangas and others 1995
Coleoptera							
<i>Euceraflhis punctipennis</i>	<i>Betula pubescens</i>	Chamber fumigation	9, 57, 105, 157 nl/L NO <sub>2</sub>			MRGR +15%, +30%, +9%	McNeill and Whittaker 1990

Table 4. (Continued)

Insect	Plant	Study Type	N Addition	Low % N	High % N	Performance Change	Reference
Homoptera <i>Aphis fabae</i> Homoptera	<i>Vicia faba</i>	Chamber fumigation	0.21 ppm NO <sub>2</sub> for 7 d			MRGR +7.7%	Dohmen 1988
<i>Aphis pomi</i> Homoptera	<i>Crataegus</i> spp.	Chamber fumigation	Ambient roadside and filtered air (ambient air has elevated CO, NO, NO <sub>2</sub> , O <sub>3</sub> , SO <sub>2</sub> , dust, lead, zinc)	1.95%	2.27%	Population growth +132% <sup>b</sup>	Braun and Flückiger 1985
<i>Aphis fabae</i> Homoptera	<i>Vicia faba</i>	Chamber fumigation	Filtered and NO <sub>2</sub> air (100 and 150 nl/L NO <sub>2</sub> )			RGR +10.5%, +21.9%	Masters and McNeill 1996
<i>Aphis fabae</i> Homoptera	<i>Vicia faba</i>	Chamber fumigation	Filtered and ambient air (enriched NO, NO <sub>2</sub> , SO <sub>2</sub> )			MRGR -19.9%	Houlden and others 1991
<i>Acyrtosiphon pisum</i> Homoptera	<i>Vicia faba</i>	Chamber fumigation	Filtered and ambient air (enriched NO, NO <sub>2</sub> , SO <sub>2</sub> )			MRGR +14.6%	Houlden and others 1991
<i>Triphaba geminata</i> Coleoptera	<i>Encelia farinosa</i>	Short fogging episodes	Acid (pH 2.5; 2.5:1 HNO <sub>3</sub> :H <sub>2</sub> SO <sub>4</sub> ) and control (pH 6.3-6.4) fogs			Adult consumption rate +60% Larval consumption rate +333%	Paine and others 1993
<i>Sitobion avenae</i> Homoptera	<i>Triticum aestivum</i>	Chamber fumigation	Charcoal-filtered air or filtered air + 100 nl/L NO <sub>2</sub>			MRGR +20%	Houlden and others 1990
<i>Aphis fabae</i> Homoptera	<i>Vicia faba</i>	Chamber fumigation	Charcoal-filtered air or filtered air + 100 nl/L NO <sub>2</sub>			MRGR +10%	Houlden and others 1990

RGR, relative growth rate; MRGR, mean relative growth rate

<sup>a</sup>Significance level for overall N treatment effect; data not presented for comparison between N treatments

<sup>b</sup>Data pooled from several sampling dates

<sup>c</sup>Data from trees from two locations; significance for overall N effect; data not presented for comparison between sites

Statistically significant changes are in boldface; nonsignificant changes are denoted as NS.

Caution should be exercised in interpreting the results of chamber fumigation studies because rates of gaseous N application cannot be easily compared to wet deposition rates.

**Table 5.** Herbivore Population Responses to Nitrogen Deposition

Insect	Plant(s)	Study Type	Deposition Load	Direction of Response	Reference
<i>Phyllaphis fagi</i> Homoptera	<i>Fagus sylvatica</i>	Fertilization of potted plants	0, 25, 50, 100 <sup>a</sup> kg N ha <sup>-1</sup> y <sup>-1</sup>	+	Flückiger and Braun 1998
<i>Orgyia antiqua</i> and other lepidopteran larvae	<i>Vaccinium myrtillus</i>	Measurement of damage rates but not actual populations	0, 5, 12.5, 25, 50 kg N ha <sup>-1</sup> y <sup>-1</sup>	+	Nordin and others 1998
Various grassland herbivores	Various grassland plants	N-fertilized plots	0–100 <sup>a</sup> kg N ha <sup>-1</sup> y <sup>-1</sup>	+	Haddad and others 2000
<i>Ips typographus</i> Coleoptera	<i>Picea abies</i>	Correlative (point-source)	Gradient of deposition from an N fertilizer plant (sulfur deposition rates also affected)	+	herbivore-induced tree mortality downwind of plant Armolaitis 1998
<i>Pissodes piniphilus</i> , <i>Monochamus galloprovincialis</i> , <i>Myelophitus piniperda</i> , <i>Acanthocinus aedilis</i> , <i>Ips sexdentatus</i> , <i>Orthotomicus laricis</i> , <i>Ips acuminatus</i> Coleoptera	Conifers	Correlative (point source)	Gradient of deposition from an N fertilizer plant	+	attack of dead or dying trees (reportedly damaged as a result of N emissions) Sierpinski 1971

<sup>a</sup>Study also includes N applications > 100 kg N ha<sup>-1</sup>y<sup>-1</sup>. Studies include "natural" deposition along gradients from point source pollutants and simulated deposition. For simulated deposition experiments, only addition rates of  $\geq 100$  kg N/ha/y are included.

cases where specialist herbivores sequester N-based secondary compounds that are detrimental to parasitoids or predators (for example, quinolizidine alkaloids produced by *Lupinus* spp.; Wink 1992), a negative relationship may be seen between N deposition and predation rates.

Experimental results exploring insect susceptibility to predators and pathogens under N deposition have been mixed. Several studies on the European sawfly (*Neodiprion sertifer*) and its nuclear polyhedrosis virus found that young larvae fed on leaves treated with acid rain (composed of both nitric and sulfuric acids) were less susceptible to initial mortality than larvae fed control leaves (Neuvonen and others 1990; Saikkonen and Neuvonen 1993). In contrast, leaf beetles reared on acid-treated foliage (again, nitric and sulfuric acids) were generally more susceptible to predation by ants, carabids, and birds than larvae reared on control foliage (Palo-kangas and others 1995). Studies of the impact of N deposition on predators and parasitoids should focus on ecosystems where insectivorous taxa are known to play key roles in regulating herbivore populations and where N deposition is known to be a serious and growing problem—for example, the coniferous forests of northeastern North America (Ollinger and others 1993; Cappuccino and others 1998).

## POPULATION-LEVEL IMPLICATIONS

### Patterns of N Deposition Effects

Deposition-induced changes in plant tissue quality may not only drive changes in individual insect performance but may also influence herbivore population dynamics. An exact one-to-one correlation between individual performance and population size is unlikely due to the influence of other factors, such as weather and predators, in affecting herbivore population dynamics. However, in many cases, host-plant N concentration is believed to have a strong effect on population dynamics (White 1993; Mattson 1980), and a positive correlation between N fertilization and the abundance of some herbivores species has been found in several studies investigating population-level responses to traditional N fertilization experiments (Kytö and others 1996; Haddad and others 2000). However, higher trophic levels are often also affected by N fertilization, and these factors can counteract the positive effects of N enrichment at the level of herbivore populations (Kytö and others 1996; Forkner and Hunter 2000; Strauss 1987). For example, in an *Artemisia ludoviciana* monoculture, beetle damage

was lower in fertilized than unfertilized plots. This shift was apparently the result of a positive aphid and membracid population response to N fertilization, which in turn led to an increase in the number of ants. These ants tended the honeydew-producing aphids and deterred beetle feeding (Strauss 1987).

Experimental evidence linking N deposition and herbivore population dynamics is limited. We were able to find only five population-level studies that suited the criterion of deposition applications with N loads no higher than  $100 \text{ kg N ha}^{-1} \text{ y}^{-1}$  (Table 5). To increase the number of studies, we included several studies with nonfolivorous insects (bark beetles and non folivorous grassland herbivores). Several of these studies are correlative observations of insect population dynamics in the proximity of a pollution source; in these cases, other pollutants may covary with N. Despite differences in experimental design, insect type, and deposition loads, it is striking that all of the studies showed a positive increase in herbivore population levels in response to N deposition.

### *Factors Underlying Changes in Population Dynamics.*

There are a number of factors that may affect the susceptibility of particular herbivore species to deposition-induced changes in population dynamics. Potential factors that could affect susceptibility are life history traits, feeding guild, and the relative importance of top-down versus bottom-up factors in controlling population dynamics and outbreak susceptibility. Although both predators and food quality affect the population dynamics of most herbivorous insects, the relative importance of these factors varies from species to species. Insects that are strongly controlled by top-down factors are not likely to experience strong population increases in response to deposition-induced enhancement of host quality, unless N deposition acts detrimentally on their natural enemies.

In contrast to species with “steady-state” population dynamics, herbivorous species prone to outbreak dynamics may have distinct population-level responses to N deposition. Rosenzweig (1971) suggested that nutrient additions may destabilize plant-herbivore interactions over time (the so-called paradox of enrichment). In the paradox demonstrated by theoretical models, greater resource availability to plants can cause a dramatic increase in the exploitation of plants by herbivores, which may in turn put populations of the host plant at risk of extinction (Rosenzweig 1971). It has been suggested that destabilizing effect of N deposition on plant-herbivore interactions is the cause of a recent increase in frequency of outbreaks of the monophagous heather beetle (*Lochmaea suturalis*)

on *Calluna vulgaris* in the Netherlands. *Lochmaea suturalis* is prone to periodic outbreaks. From 1915 to 1980, they occurred about every 20 years; but since 1980, the outbreak frequency has increased to less than eight years, possibly as a result of increased host N availability (Bobbink and others 1998). In this system, N deposition rates are extremely high, with reported average N deposition loads in the Netherlands at  $40 \text{ kg N ha}^{-1} \text{ y}^{-1}$  (Van der Eerden and others 1998), and *C. vulgaris* tissue N concentration responds positively to N additions (Hicks and others 2000; Pitcairn and others 1995; Power and others 1998). Several investigators have demonstrated a relationship between N fertilization and *L. suturalis* performance in terms of growth rates, larval development rates, and adult mass (Brunsting and Heil 1985; Van der Eerden and others 1991; Power and others 1998); it has been suggested that these changes in beetle performance are responsible for increased outbreak frequency (Bobbink and others 1998). Nitrogen-rich industrial air pollution has also been cited as a possible cause for outbreaks of bark beetles in Poland (Sierpinski 1971).

An increase in the frequency or severity of outbreak would have severe ecological consequences for systems in which herbivory is characterized by periodic outbreaks. In addition, because many of the economically-important timber species in North America are affected by outbreak of insects such as the spruce budworm (*Choristoneura fumiferana*), western spruce budworm (*Choristoneura occidentalis*), gypsy moth (*Lymantria dispar*), mountain pine beetle (*Dendroctonus ponderosae*), and southern pine beetle (*Dendroctonus frontalis*) (Peltonen and others 2002), N deposition may have considerable economic consequences for the North American timber industry. Given the apparent stronger foliar N response to N deposition in conifers, we suggest that these impacts will be greater on coniferous species than deciduous ones.

## COMMUNITY AND ECOSYSTEM-LEVEL IMPLICATIONS

### Deposition Effects on Herbivore Communities

There are several mechanisms through which N deposition may influence the composition of herbivore communities. First, deposition-induced changes in host plant quality may directly affect the composition of insect communities. Insect feeding guilds or individual herbivore species may respond differently to deposition-induced changes in the

quality of the host plant (Awmack and Leather 2002), leading to changes in the relative abundance of herbivore species. Second, deposition-induced shifts in plant community composition may affect herbivore community composition. Plant community composition can change in response to N deposition (Heil and Diemont 1983; Rainey and others 1999; Pitcairn and others 1998), and changes in the abundance or diversity of host plants are likely to have strong impacts on herbivore communities. For example, in herbaceous communities, N deposition may favor plants that rely on N-based defenses, such as members of the Solanaceae. Because there are only a few specialized herbivore taxa that feed on solanaceous plants (Clark 1999), N deposition could profoundly change the insect herbivore community in these systems.

Deposition effects on plant N concentration and productivity may cascade up such that they affect the composition of insect herbivore communities, particularly if taxa or feeding guilds differ in their relative response to deposition. In a recent study in the San Bernadino Mountains of southern California, herbivore community composition was assessed on three different host plant species in response to experimental N additions and naturally occurring variation in deposition rates. Deposition altered the patterns of insect diversity within host plants; the herbivore fauna associated with ferns increased in diversity in response to deposition but it decreased on pines (M. Eatough personal communication). In an N fertilization study (in which low to very high levels of N were added) in an *Artemisia ludoviciana* monoculture, the abundance of sucking insects increased with deposition whereas beetle abundance decreased (Strauss 1987). In this study, a positive response in the population of sucking insects to host plant quality appeared to lead to an increase in aphid-tending ants. The increase in ant density was cited as the probable cause for the decreased in beetle abundance.

Further studies will allow better characterization of the relative impacts of N deposition on insect taxa and feeding guilds. Changes in guild structure such as those described by Strauss (1987) could alter ecosystem processes by changing patterns of litterfall, the input of frass, and the relative proportion of litter that enters as labile C and N (Lerdau 1996). For example, honeydew produced by aphids is extremely labile and has been shown to affect ecosystem-level C and N dynamics (Stadler and others 1998; Grier and Vogt 1990), so deposition-induced increases in the relative inputs of honey-

dew due to increased density of sucking insects has the potential to affect element cycling.

Herbivore community composition may also be affected by deposition-induced changes in plant community composition. Several studies have found a negative correlation between N deposition and plant diversity (Pitcairn and others 1998; Aerts and Berendse 1988; Inouye and Tilman 1995; Bobbink and others 1998). Deposition-induced changes in plant community composition have implications for herbivores due to the shift in host food available to herbivores. Observations on arthropod community diversity after long-term N fertilization ( $0\text{--}270\text{ kg N ha}^{-1}\text{ y}^{-1}$ ) in a grassland system showed that fertilization-induced declines in plant species richness were mirrored by a decrease in herbivore species richness (Haddad and others 2000), although the positive effects of N fertilization on predators may act negatively on herbivore richness (Siemann 1998). In addition, shifts in plant community composition can affect insect communities by facilitating the establishment of novel herbivores in the community. In the Netherlands, needle damage caused by the adults of the red-black pine bug *Haematoloma dorsatum* (Homoptera: Cercopidae), was first observed in Dutch pine stands in the mid-1980s (Moraal 1996). Native to the Mediterranean, the red-black pine bug appeared to spread northward in the 1920s. Moraal hypothesized that deposition-induced increases in the density of the grass *Deschampsia flexuosa*, apparently the only host plant of pine bug nymphs, facilitated the establishment of pine bug populations.

The few studies (discussed above) that explicitly examined the effects of N deposition on insect communities have found profound impacts, and several studies that investigated the impacts of insects on ecosystems have also documented large effects. The question then is how to connect the community to the ecosystem scale. The issues that arise when we try to make this connection are fundamental to ecological research across a variety of subdisciplines: the extent to which species identities are crucial in ecosystem processes and the sensitivity of different processes to the identities of the species present in the ecosystem (Lerdau and Slobodkin 2002). One of the general ways in which N deposition will affect plant communities and their insect herbivores will be through favoring plants that respond positively to N deposition. In general, such plants tend to allocate more of their resources to growth and fewer to defense. Because of higher leaf quality, these plants may be more palatable to herbivores, and the litter they produce may decompose quickly because of its higher nutrient content. The

details of relationships such as this one, and their implications, require careful empirical study using both observational and experimental frameworks.

### Ecosystem-level Implications

Greater knowledge of the influence of N deposition on altered patterns of herbivory will afford a more complete understanding of how N deposition affects ecosystem functioning. Nitrogen deposition has the potential to influence the role of insect herbivores in regulating ecosystem processes through several mechanisms. First, if N deposition strongly affects herbivore population sizes and/or the rates of herbivory, there might be a shift in the relative importance of herbivores to ecosystem processes. Second, the inputs of nutrients into a system due to combination of insect herbivory and N deposition may lead to different influences than the inputs from one process alone. Finally, ecosystem processes such as N cycling can be altered substantially by herbivore-induced plant mortality or shifts in plant species composition (Jenkins and others 1999; Ritchie and others 1998); interactions between N deposition and herbivory might increase the frequency of these herbivore-induced shifts in community composition. We predict that the combined effects of N deposition and herbivory will substantially affect ecosystem-level processes, but that the magnitude of these effects will be system-specific. We will focus on herbivore impacts on C and N dynamics to illustrate how herbivory might interact with N deposition to affect ecosystems.

Carbon dynamics can be strongly affected by herbivory through its effects on photosynthetic rates, soil respiration, and litter decomposition rates. Herbivory can lead to decreases in primary productivity during both conditions of herbivore outbreaks and conditions of background rates of herbivory (Morrow and Lamarche 1978; Grier and Vogt 1990; Mattson and Addy 1975). We predict that these negative impacts of herbivory on productivity will increase under deposition due to increased performance and larger populations of insect herbivores. Decreases in production will be particularly pronounced in cases where N deposition leads to increases in the frequency or severity of outbreaks. However, simultaneous positive impacts of N deposition on primary production may, at least to some degree, counteract enhanced herbivory. For example, fertilization experiments with high loads of N ( $350\text{ kg ha}^{-1}\text{ N}$ ) led to increases in the performance of western spruce budworm (*Choristoneura occidentalis*) during an outbreak, but negative impacts on primary production from enhanced herbivory ap-

pear to have been offset by positive impacts of fertilization (Mason and others 1998, 1992).

In addition to its impact on productivity, herbivory can affect N and C dynamics by altering the quantity and quality of litter inputs. These changes may in turn affect rates of litter turnover, N mineralization, decomposition, and soil respiration. Herbivory typically leads to a reallocation of N, where foliar N that would be resorbed prior to leaf abscission is instead transferred to soil N pools via greenfall, frass deposition, and dead insect biomass (Lovett and others 2002). Several studies have found that litterfall mass or litter N concentrations is enhanced in forests experiencing outbreak or background rates of herbivory (Grace 1986; Risley and Crossley 1993; Hollinger 1986; Tiedemann and Furniss 1985). Throughfall inputs of N may also be enhanced by moderate rates of defoliation (Seastedt and others 1983; Schowalter and others 1991; Reynolds and others 2000). Similarly, the amount and quality of C transferred into soil pools is altered by herbivory, with an increase in the relative amount of labile C from frass with increased rates of herbivory (Lovett and others 2002). Field and laboratory experiments with gypsy moths (*Lymantria dispar*) suggest that N in litterfall frass is rapidly immobilized by microbes (Lovett and others 2002; Christenson and others 2002). Mineralization rates may be enhanced, however, when herbivore feeding leads to considerable greenfall inputs in addition to frass inputs (Brown 1994). Along similar lines, N deposition has been found to enhance N mineralization, litter decomposition, and soil respiration rates due to increases in the quality or quantity of litter inputs (Aber and others 1998; Baron and others 2000; Morecroft and others 1994; Magill and others 2000). This suggests that when N deposition occurs in concert with herbivory, rates of C and N mineralization will be further enhanced by this doubly-enhanced litter quality. Increases in N and C mineralization may have differential consequences for ecosystem N and C storage. Enhanced N mineralization may lead to increased plant N uptake, whereas increased C mineralization may lead to decreases in the soil C pool due to enhanced soil respiration (Cardon and others 2001, 2002).

As discussed earlier N deposition can alter the concentrations of both free amino acids and nitrate in leaves. In the absence of herbivory, these compounds are likely to be resorbed prior to senescence and thus will not affect soil N cycling. However, herbivory has the potential to short-circuit resorption by increasing the direct deposition of green leaves to the soil. That is, herbivory disrupts internal N cycling and increases the delivery of labile N.

We suggest that the combination of increased concentrations of free amino acids and nitrate that are caused by N deposition in conjunction with increased greenfall caused by herbivory could have profound impacts on N availability in soils, and the crucial step in this complex relationship is the reduction in resorption effected by herbivory. Of course, nonfolivory-based types of herbivory—for example, phloem or xylem feeding—will not have this effect.

The combined effects of N deposition and herbivory may have particularly profound impacts on ecosystem nutrient losses. Short-term increases in streamwater nitrate levels in response to watershed-level defoliation events have been reported in a number of studies (Webb and others 1995; Swank and others 1981; Reynolds and others 2000; Lewis 1998; Eshleman and others 1998), although these patterns may be reversed several years after defoliation (Drohan and DeWalle 2002). The biogeochemical mechanisms leading to this elevated nitrate flux are not well established, but enhanced nitrification rates, leaching from insect frass and leaf fragments, herbivory-induced tree mortality, enhanced water runoff, faster decomposition of second-flush leaves, and decreased plant production may be involved (Eshleman and others 1998; Lewis 1998; Swank and others 1981; Lovett and others 2002; Hutchens and Benfield 2000). We hypothesize that under scenarios of high or chronic deposition loads in which stands are moving toward N saturation, herbivory will cause further increases in levels of streamwater nitrate, which are already high due to deposition. Enhanced nitrate loss in streamwater is especially likely under outbreak conditions; deposition-induced changes in outbreak frequency or severity may thus affect ecosystem-level patterns of N retention. These impacts could have profound ecological, human health, and economic consequences due to the role of nitrate in decreasing water quality.

The impact of N deposition on patterns of herbivory will vary among ecosystems according to site-specific differences in resource availability. Nitrogen-limited ecosystems, including many temperate and high-latitude ones, are likely to show strong and complex effects because N deposition in these systems will probably change plant tissue composition, total plant production, and plant community composition (Jefferies and Maron 1997; Fenn and others 1998; Aber and others 1998; Rainey and others 1999). In contrast, P-limited systems, including many lowland tropical forests and some grasslands, will likely show very little growth response to N deposition because of P limitations (Lee and Ca-

porn 1998; Matson and others 1999). In these systems, additional N will probably be incorporated into plant tissue, thus altering the quality of food available to herbivores. One might expect then that herbivore populations will increase in response to this improvement in host quality. Our knowledge of grasslands is more tenuous. Although mammalian herbivory is also important in these systems, insects are often responsible for more herbivory in grasslands than are mammals (Scholes and Hall 1996; Belovsky and Slade 2000). Insect herbivory in grassland systems is often regulated by foliar moisture and N, which almost always covary (Mattson and Scriber 1987; Scriber and Slansky 1981). Nitrogen deposition has the potential to decouple these two factors and thus rewrite the rules regulating herbivore behavior. Specific experimental studies of chronic low-level N additions are needed to develop predictions of herbivore responses.

## GLOBAL CHANGE AND N DEPOSITION

In addition to the effects of N deposition alone discussed above, there are important interactions between herbivory, N deposition, and other large-scale environmental changes—for example, rising atmospheric CO<sub>2</sub> levels, elevated levels of ozone and other pollutants, biological invasions, temperature shifts, and changes in the patterns and timing of precipitation. There are relatively few studies of the interactions between N deposition and these other changes compared to the attention that single-factor effects (for example, changes in CO<sub>2</sub> concentration) has received. However, given the prevalence of simultaneous anthropogenic perturbations and the possibility that single-factor experiments do not capture important interactions, it is important to study these interactions so that we can generate accurate predictions of how ecosystems will respond to multiple perturbations (Percy and others 2002).

### Interactions Between N Deposition and Elevated CO<sub>2</sub>

Although N deposition varies at local to regional scales and CO<sub>2</sub> concentrations are relatively invariant globally, the ubiquity of N deposition as an issue across the globe demands that deposition and CO<sub>2</sub> increases be considered together. Given our current understanding of the impacts of CO<sub>2</sub> and N deposition on plant tissue chemistry and herbivory, one would predict that increasing levels of these factors would tend to negate each other. That is, as CO<sub>2</sub> rises, tissue C:N ratio should increase; and as N

deposition grows, C:N should fall. Environmental chamber studies that have investigated the relative importance of elevated CO<sub>2</sub> and soil N availability have found primarily additive (and not interactive) effects of CO<sub>2</sub> and N on both foliar nutrition indices and insect performance (Hättenschwiler and Schafellner 1999; Kinney and others 1997). For example, Kinney and others (1997) found that gypsy moth (*Lymantria dispar*) consumption rates were significantly positively affected by both atmospheric CO<sub>2</sub> concentration and the N fertilization level under which host plants were grown. Interactions between CO<sub>2</sub> concentration and N fertilization level on consumption rates were not significant. However, several longer-term empirical studies argue against this straightforward perspective. In studies where elevated CO<sub>2</sub> exposure has been maintained for several growing seasons, photosynthetic rates tend to decline and C:N ratios are reduced (Luo and Reynolds 1999). Although this down-regulation takes longer to occur in plants receiving fertilization, it is not yet known whether low levels of chronic N addition can prevent this acclimation to elevated CO<sub>2</sub>. Because the effects of elevated CO<sub>2</sub> on leaf N are much larger in fresh tissue than in senesced leaves (Norby and others 2001), the impacts of elevated CO<sub>2</sub> on herbivory are likely to be larger than the direct impacts on nutrient cycling. Furthermore, studies of the impact of elevated CO<sub>2</sub> on field-grown plants suggest that one of the most important effects of elevated CO<sub>2</sub> is a reduction in stomatal conductance (Jackson and others 1994). In contrast, foliar N concentration is positively correlated to stomatal conductance (Reich and others 1999). Conductance may have significant impacts on tissue palatability to herbivores by altering C and N allocation patterns or tissue moisture content. It is unknown how these two potentially contradictory impacts on conductance interact to affect herbivores.

Another possible effect of simultaneous increases in atmospheric CO<sub>2</sub> and N deposition is that plants could both grow larger and maintain higher levels of chemical defense against herbivores no matter what their dominant mode of antiherbivore defense. Plant taxa dependent on alkaloids or other N-based defenses may be able to increase both growth and allocation to defense in a doubly perturbed world. Taxa that use primarily C-based defenses such as phenolics might be able to increase both growth and allocation to defense.

In the long run, it may turn out that these interacting effects are less important at ecosystem scales than initial modeling studies suggested (for example, Townsend and others 1996) because only a

small fraction of N is incorporated into biomass whereas relatively large quantities are stored in the soil or lost from the system via leaching (Nadelhoffer and others 1999; but see Jenkinson and others 1999). In addition, in lowland tropical ecosystems that are often limited by P (forests) or systems limited by water (grasslands), N deposition may have little influence on growth. This may lead not to an increase in the quantity of the plant tissue as food for herbivores but to a shift in food quality due to an increase in N concentration. Given that both atmospheric CO<sub>2</sub> and N deposition are increasing simultaneously across much of the Earth's surface, the only way to address these unknowns is through empirical studies in which the mode of N addition mimics deposition patterns rather than agricultural fertilization practices.

### N Deposition and Climate Change

Patterns of herbivory may also be affected indirectly by the accumulation of CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O, and other greenhouse gases in the atmosphere and consequent changes in the Earth's climate. Recent models of the Earth's climate suggest that increases in greenhouse gases may be raising maximum temperatures and accelerating the onset of warm temperatures in spring (IPCC 2001). Regional precipitation patterns are predicted to change in response to elevated greenhouse gas concentrations (IPCC 2001). Previous reviews of the effects of changes in temperature on herbivory have suggested that higher temperatures are likely to speed up development rates and reproductive rates and to increase the number of generations per year; this may lead to increases in potential population sizes, particularly in multivoltine species (Ayres and Lombardero 2000; Landsberg and Smith 1992; Morimoto and others 1998; Yamamura and Kiritani 1998).

Little attention, however, has been devoted to studying how N deposition and temperature changes might interact to affect insects. Changes in temperature and increases in deposition could disrupt the tight relationships between insect and leaf phenology. Numerous studies have documented the close association between spring temperature or budbreak and larval hatch times (for example, see Futuyma and Wasserman 1980; Parry and others 1998; Visser and Holleman 2001). If these relationships are disrupted as a result of temperature-mediated impacts on insects and N-mediated effects on plants, early-season herbivory levels might be altered due to a shift in the abundance of leaf tissue available for larvae. In addition, if increased N enables leaves to develop faster, they may pass more

quickly through their expansion stage, the stage at which they are most vulnerable to herbivores.

Altered precipitation patterns may interact particularly strongly with N deposition to affect plant-herbivore interactions. Plant physiological theory suggests a tradeoff between N-use efficiency and water-use efficiency so that increases in N availability, as caused by deposition, could lead to a relaxing of the constraints imposed by water stress and thus higher growth and/or changes in tissue quality (Field and Mooney 1986). Although predicted changes in precipitation patterns are still not definitive, a general trend toward more extreme precipitation events, such as droughts and heavy rains, is expected (IPCC 2001). There is a strong correlation between leaf water status and rates of herbivory, partially due to the strong correlation between foliar concentrations of water and N (Scriber and Slansky 1981; Mattson and Scriber 1987). In addition, drought stress tends to cause numerous physiological changes in plants, increasing their susceptibility to insect herbivory (Mattson and Haack 1987). Interactions between N deposition and drought stress may exacerbate physiological changes from each single factor, in turn leading to greater plant susceptibility to herbivores.

### DIRECTIONS FOR FUTURE STUDIES

The paucity of studies investigating the effects of N deposition on herbivory underscores the need for well-planned experimental work. Much of the data currently available depend on either short-term experimental studies or correlative studies in which N deposition is not clearly separated from other pollutants. Additional research is needed to improve our understanding of the influences of N deposition on insect herbivory and how deposition-induced changes in herbivory affect populations, communities, and ecosystem processes. We suggest a two-pronged approach that includes both correlative and manipulative studies designed to investigate the relationships between N deposition and herbivory. Within this framework, experimental work should address the effects on herbivory at the scales of individual insects, populations, communities, and ecosystems, as well as potential interactions between N deposition and other processes undergoing global change.

Many questions remain regarding how individual insects will respond to N deposition. In particular, studies using multiyear low-level treatments (for example, 5–30 kg N ha<sup>-1</sup> y<sup>-1</sup>) would increase our knowledge of how chronic low-level deposition affects insect herbivory and the different ways in

which insects respond to atmospheric N deposition versus agricultural-level N fertilization.

At the population, community, and ecosystem scales, it is exceedingly difficult to accurately mimic the spatial and temporal scales of deposition. Short-term studies (for example, 1 year, Nordin and others 1998; Flückiger and Braun 1998) offer a glimpse of the potential implications of N deposition for patterns of herbivory, but they fail to capture other factors, such as natural enemy population dynamics, that may come into play over longer time scales. Some investigators have created spatially small deposition plots (from a single plant to several square meters) and then measured changes in herbivore population dynamics within these plots (see, for example, Nordin and others 1998; Haddad and others 2000; Flückiger and Braun 1998). Although such experiments laudably attempt to measure the effects of stimulated N deposition under field conditions, they inadvertently create environmental "hot spots" of plant material with N-rich tissue. Mobile herbivores can preferentially colonize these hot spots, confounding the effects of N on insect performance with its effects on insect preference. Manipulative studies in environmental chambers may help to assess bottom-up effects of simulated N deposition on herbivore population dynamics while restricting the possibility of preferential migration, although such studies are limited in their ability to address questions at community or ecosystem scales.

Correlative studies could serve as powerful tools for investigating the relationship between N deposition and herbivory. Unfortunately, much of the existing evidence from correlative studies comes from small sample sizes or experimental designs that lack adequate replication. Furthermore, correlations often emerge from a pollution source without well-distinguished components (nitrogenous compounds co-occur with other pollutants such as ozone and sulfur dioxide for example, Kainulainen and others 1993; Heliövaara and Väisänen 1990; Viskari and others 2000). In addition, correlative studies run the risk of confounding changes in the rates of herbivory or consequences of herbivory with changes in plant susceptibility to herbivory due to stresses imposed by high N deposition. Several investigators have reported changes in defoliation intensity or potentially herbivore-induced tree mortality in areas of high N deposition (Hain and Arthur 1985; Armolaitis 1998; Sierpinski 1971), but these changes may result from either deposition-induced changes in insect population dynamics or higher probability of plant mortality from herbivory in high-deposition areas due to other stresses asso-

ciated with deposition. Correlative studies set over gradients of N deposition may be especially valuable, particularly those where the gradient has few co-occurring pollutants (such as N fertilizer plants) and other abiotic factors remain constant (Whyte-mare and others 1997), although large-scale gradients (see, for example, Burton and others 1991) are likely to include changes in other abiotic factors as well. To make studies over gradients more definitive, it is crucial to monitor factors such as deposition rates and plant tissue chemistry as well as herbivore population dynamics, community changes, and rates of ecosystem processes.

While knowledge of the effects per se of N deposition on herbivory is important, it is even also crucial to understand how N deposition will affect herbivory in the context of other global-scale changes. Experimental manipulation of multiple aspects of global change and careful observation of the patterns of insect herbivory, as in the recent Free Air CO<sub>2</sub> Enrichment (FACE) work with combinations of elevated CO<sub>2</sub> and ozone (Percy and others 2002), provide one possible avenue for such research.

## CONCLUSIONS

Atmospheric N deposition can have strong direct effects on community and ecosystem processes, and these direct effects have received considerable research attention. In addition, N deposition may affect communities and ecosystems indirectly through impacts on interactions among organisms. Specifically, N deposition affects the concentration and chemical form of N and mineral elements and the relative availability of amino acids and secondary metabolites; all of these compounds can strongly influence insect herbivores. Our survey of the potential effects of N deposition on herbivory at the scales of individual and populations levels suggests that it will generally have a strong positive impact on individual insect performance and lead to an increase in herbivore populations. These effects are likely to be more pronounced on conifers than deciduous plants due to the more positive foliar N responses of conifers. At the ecosystem level, herbivory in combination with N deposition will exacerbate enhanced N mineralization and nitrate leaching caused by N deposition. Changes in the rates and consequences of herbivory as a result of N deposition may be substantial. Predictions of the impacts of N deposition on ecological processes and the economic consequences are likely of N deposition underestimated unless deposition effects medi-

ated by changes in herbivory are also taken into consideration.

## ACKNOWLEDGEMENTS

The manuscript benefited from the insightful comments of G. Bharathan, D. Futuyma, J. Gurevitch, E. Holland, L. Hyatt, M. Litvak, T. Schowalter, and two anonymous reviewers.

## REFERENCES

- Aber J, McDowell W, Nadelhoffer K, Magill A, Bernston G, Kamakea M, McNulty S, Currie W, Rustad L, Fernandez I. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. *BioScience* 48:921–34.
- Aerts R, Berendse F. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Veg- etatio* 76:63–9.
- Agrawal AA. 2000. Benefits and costs of induced plant defense for *Lepidium virginicum* (Brassicaceae). *Ecology* 81:1804–13.
- Alstad DN, Edmunds GF Jr., Weinstein LH. 1982. Effects of air pollutants on insect populations. *Annu Rev Entomol* 27:369–84.
- Armolaitis K. 1998. Nitrogen pollution on the local scale in Lithuania: vitality of forest ecosystems. *Environ Pollut* 102:55–60.
- Awmack CS, Leather SR. 2002. Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* 47:817–44.
- Ayers MP. 1993. Global change, plant defense, and herbivory. In: Kareiva PM, Kingsolver JG, Huey RB, Eds. *Biotic interactions and global change*. Sunderland (MA): Sinauer. p 75–94.
- Ayers MP, Lombardero MJ. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci Total Environ* 262:263–86.
- Baron JS, Rueth HM, Wolfe AM, Nydick KR, Allstott EJ, Minear JT, Moraska B. 2000. Ecosystem responses to nitrogen deposition in the Colorado Front Range. *Ecosystems* 3:352–68.
- Belovsky GE, Slade JB. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proc Natl Acad Sci U S A* 97:14412–7.
- Bobbink R, Hornung M, Roelofs JGM. 1998. The effects of airborne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J Ecol* 86:717–38.
- Braun S, Flückiger W. 1985. Increased population of the aphid *Aphis pomi* at a motorway. Part 3. The effect of exhaust gases. *Environ Pollut (A)* 39:183–92.
- Brown DG. 1994. Beetle folivory increases resource availability and alters plant invasion in monocultures of goldenrod. *Ecology* 75:1673–83.
- Brunsting AMH, Heil GW. 1985. The role of nutrients in the interactions between a herbivorous beetle and some competing plant species in heathlands. *Oikos* 44:23–36.
- Bryant J, Chapin FS III, Klein D. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357–68.
- Burton AJ, Pregitzer KS, Reed DD. 1991. Leaf-area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. *For Sci* 37:1041–59.
- Cappuccino N, Lavert D, Bergeron Y, Regniere J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114:236–42.
- Cardon ZG, Czaja AD, Funk JL, Vitt PL. 2002. Periodic carbon flushing to roots of *Quercus rubra* saplings affects soil respiration and rhizosphere microbial biomass. *Oecologia* 133:215–23.
- Cardon ZG, Hungate BA, Cambardella CA, Chapin FS III, Field CB, Holland EA, Mooney HA. 2001. Contrasting effects of elevated CO<sub>2</sub> on old and new soil carbon pools. *Soil Biol Biochem* 33:365–73.
- Chapin FS III. 1980. The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–60.
- Christenson LM, Lovett GM, Mitchell MJ, Groffman PM. 2002. The fate of nitrogen in gypsy moth frass deposited to an oak forest floor. *Oecologia* 131:444–52.
- Clancy KM, King RM. 1993. Defining the western spruce budworm's nutritional niche with response surface methodology. *Ecology* 74:442–54.
- Clark T. 1999. Evolution and adaptive significance of larval midgut alkalization in the insect superorder Mecoptera. *J Chem Ecol* 25:1945–60.
- Coley PD. 1980. Effects of leaf age and plant life-history patterns on herbivory. *Nature* 284:545–6.
- Coley PD, Bryant JP, Chapin I FS. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–9.
- DeHayes D, Schaberg P, Hawley G, Strimbeck G. 1999. Acid rain impacts of calcium nutrition and forest health. *BioScience* 49:789–800.
- Dickson RE, Isebrands JG. 1991. Leaves as regulators of stress response. In: Mooney HA, Winner WE, Pell EJ, Eds. *Responses of plants to multiple stresses*. San Diego: Academic Press. p 1–34.
- Dohmen GP. 1988. Indirect effects of air pollutants: changes in plant/parasite interactions. *Environ Pollut* 53:197–207.
- Draaijers GPJ, Ivens WPMF, Bos MM, Bleuten W. 1989. The contribution of ammonia emissions from agriculture to the deposition of acidifying and eutrophying compounds onto forests. *Environ Pollut* 60:55–66.
- Drohan P, DeWalle D. 2002. Defoliation and atmospheric deposition influences on spring baseflow chemistry in 56 Pennsylvania mixed land-use watersheds. *Water Air Soil Pollut* 133: 31–48.
- Duquesnay A, Dupouey JL, Clement A, Ulrich E, Le Tacon F. 2000. Spatial and temporal variability of foliar mineral concentration in beech (*Fagus sylvatica*) stands in northeastern France. *Tree Physiol* 20:13–22.
- Edfast AB, Nasholm T, Ericsson A. 1990. Free amino acid concentrations in needles of Norway spruce and Scots pine trees on different sites in areas with two levels of nitrogen deposition. *Can J For Res* 20:1132–6.
- Erelli MC, Ayres MP, Eaton GK. 1998. Altitudinal patterns in host suitability for forest insects. *Oecologia* 117:133–42.
- Eshleman K, Morgan R, Webb J, Deviney F, Galloway J. 1998. Temporal patterns of nitrogen leakage from mid-Appalachian forested watersheds: role of insect defoliation. *Water Resour Res* 34:2005–16.
- Feir D, Hale R. 1983. Growth and reproduction of an insect model in controlled mixtures of air pollutants. *Int J Environ Studies* 20:223–8.
- Fenn ME, Poth MA, Aber JD, Baron JS, Bormann BT, Johnson DW, Lemly AD, McNulty SG, Ryan DE, Stottlemeyer R. 1998. Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. *Ecol Appl* 8:706–33.

- Fenn ME, Poth MA, Johnson DW. 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. *For Ecol Manage* 82:211–30.
- Field C, Mooney HA. 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ, Eds. *On the economy of plant form and function*. Cambridge: (UK) Cambridge University Press. p 25–54.
- Flückiger W, Braun S. 1998. Nitrogen deposition in Swiss forests and its possible relevance for leaf nutrient status, parasite attacks and soil acidification. *Environ Pollut* 102(S1):69–76.
- Forkner RE, Hunter MD. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81:1588–600.
- Fox CW, Waddell KJ, Groeters FR, Mousseau TA. 1997. Variation in budbreak phenology affects the distribution of a leaf-mining beetle (*Brachys tessellatus*) on turkey oak (*Quercus laevis*). *Ecoscience* 4:480–9.
- Futuyma DJ, Wasserman SS. 1980. Resource concentration and herbivory in oak forests. *Science* 210:920–2.
- Galloway JN, Levy HI, Kasibhatla PS. 1994. Year 2020: Consequences of population growth and development on deposition of oxidized nitrogen. *Ambio* 23:120–3.
- Gerson EA, Kelsey RG. 1999. Piperidine alkaloids in nitrogen fertilized *Pinus ponderosa*. *J Chem Ecol* 25:2027–39.
- Goverde M, Bazin A, Shykoff JA, Erhardt A. 1999. Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO<sub>2</sub> and plant genotype. *Funct Ecol* 13:801–10.
- Grace J. 1986. The influence of gypsy moth on the composition and nutrients content of litter fall in a Pennsylvania oak forest. *For Sci* 32:855–70.
- Graveland J, van der Wal R, van Balen JH, van Noordwijk AJ. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature* 368:446–8.
- Grier CC, Vogt DJ. 1990. Effects of aphid honeydew on soil nitrogen availability and net primary production in an *Alnus rubra* plantation in western Washington. *Oikos* 57:114–8.
- Haddad NM, Haarstad J, Tilman D. 2000. The effects of long-term nitrogen loading on grassland insect communities. *Oecologia* 124:73–84.
- Haglund BM. 1980. Proline and valine—cues which stimulate grasshopper herbivory during drought stress? *Nature* 288:697–8.
- Hain FP, Arthur FH. 1985. The role of atmospheric deposition in the latitudinal variation of Fraser fir mortality caused by the Balsam Woolly Adelgid, *Adelges piceae* (Ratz.) (Hemipt., Adelgidae): a hypothesis. *Zeitschr Angew Entomol* 99:145–52.
- Hairton NG, Smith FE, Slobodkin LB. 1960. Community structure, population control, and competition. *Am Nat* 94:421–5.
- Hall SJ, Matson PA. 1999. Nitrogen oxide emissions after nitrogen additions in tropical forests. *Nature* 400:152–5.
- Hättenschwiler S, Korner C. 1996. Effects of elevated CO<sub>2</sub> and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems. *Oecologia* 106:172–80.
- Hättenschwiler S, Korner C. 1998. Biomass allocation and canopy development in spruce model ecosystems under elevated CO<sub>2</sub> and increased N deposition. *Oecologia* 113:104–14.
- Hättenschwiler S, Schafellner C. 1999. Opposing effects of elevated CO<sub>2</sub> and N deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia* 118:210–7.
- Heil GW, Diemont WH. 1983. Raised nutrient levels change heathland into grassland. *Vegetatio* 53:113–20.
- Heliövaara K, Väisänen R. 1990. Changes in population dynamics of pine insects induced by air pollution. In: Watt AD, Leather SR, Hunter MD, Kidd NAC, Eds. *Population dynamics of forest insects*. Andover (UK): Intercept. p 209–18.
- Hermes DA, Mattson WJ. 1992. The dilemma of plants: to grow or to defend. *Q Rev Biol* 67:283–335.
- Hicks WK, Leith ID, Woodin SJ, Fowler D. 2000. Can the foliar nitrogen concentration of upland vegetation be used for predicting atmospheric nitrogen deposition? Evidence from field surveys. *Environ Pollut* 107:367–76.
- Hogbom L, Hogberg P. 1991. Nitrate nutrition of *Deschampsia flexuosa* (L) Trin in relation to nitrogen deposition in Sweden. *Oecologia* 87:488–94.
- Holland EA, Braswell BH, Lamarque JF, Townsend A, Sulzman J, Muller JF, Dentener F, Brasseur G, Levy H, Penner JE and others. 1997. Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *J Geophys Res (Atmos)* 102: 15849–66.
- Hollinger D. 1986. Herbivory and the cycling of nitrogen and phosphorous in isolated California oak trees. *Oecologia* 70: 291–7.
- Hosker RP, Lindberg SE. 1982. Review: atmospheric deposition and plant assimilation of gases and particles. *Atmos Environ* 16:889–910.
- Houlden G, McNeill S, Aminu-Kano M, Bell JNB. 1990. Air pollution and agricultural aphid pests. I. Fumigation experiments with SO<sub>2</sub> and NO<sub>2</sub>. *Environ Pollu* 67:305–14.
- Houlden G, McNeill S, Bell JNB. 1991. Air pollution and agricultural aphid pests. II. Chamber filtration experiments. *Environ Pollut* 72:45–55.
- Huhn G, Schulz H. 1996. Contents of free amino acids in Scots pine needles from field sites with different levels of nitrogen deposition. *New Phytol* 134:95–101.
- Hutchens J Jr., Benfield E. 2000. Effects of forest defoliation by the gypsy moth on detritus processing in southern Appalachian streams. *Am Midl Nat* 143:397–404.
- Inouye RS, Tilman D. 1995. Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology* 76:1872–87.
- IPCC. 2001. *Climate change 2001: the scientific basis*. Cambridge (UK): Cambridge University Press, pp 944.
- Jackson RB, Sala OE, Field CB, Mooney HA. 1994. CO<sub>2</sub> alters water-use carbon gain, and yield for the dominant species in a natural grassland. *Oecologia* 98:257–62.
- Jefferies RL, Maron JL. 1997. The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. *Trends Ecol Evol* 12:74–8.
- Jenkins JC, Aber JD, Canham CD. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Can J For Res* 29:630–45.
- Jenkinson DS, Goulding K, Powlson DS. 1999. Nitrogen deposition and carbon sequestration. *Nature* 400:629–30.
- Jones CG, Hartley SE. 1998. Global change and plant phenolic concentrations: species level predictions using the protein competition model. In: De Kok LJ, Stulen I, Eds. *Responses of plant metabolism to air pollution and global change*. Leiden (The Netherlands): Backhuys. p 23–50.
- Kainulainen P, Satka H, Mustaniemi A, Holopainen JK, Oksanen

- J. 1993. Conifer aphids in an air-polluted environment. 2. Host plant-quality. *Environ Pollut* 80:193–200.
- Katzensteiner K, Glatzel G, Kazda M. 1992. Nitrogen induced nutritional imbalances—a contributing factor to Norway spruce decline in the Bohemian Forest (Austria). For *Ecol Manage* 51:29–42.
- Kauppi PE, Mielikainen K, Kuusela K. 1992. Biomass and carbon budget of European forests, 1971 to 1990. *Science* 256:70–4.
- Kerslake JE, Woodin SJ, Hartley SE. 1998. Effects of carbon dioxide and nitrogen enrichment on a plant–insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytol* 140:43–53.
- Kinney KK, Lindroth RL, Jung SM, Nordheim EV. 1997. Effects of CO<sub>2</sub> and NO<sub>3</sub><sup>-</sup> availability on deciduous trees: phytochemistry and insect performance. *Ecology* 78:215–30.
- Koricheva J, Larsson S. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Annu Rev Entomol* 43:195–216.
- Krause SC, Raffa KF. 1996. Defoliation tolerance affects the spatial and temporal distributions of larch sawfly and natural enemy populations. *Ecol Entomol* 21:259–69.
- Kytö M, Niemelä P, Larsson S. 1996. Insects on trees: population and individual response to fertilization. *Oikos* 75:148–59.
- Landolt W, Pfenninger I. 1997. The effect of elevated CO<sub>2</sub> and soil type on non-structural carbohydrates in beech leaves and Norway spruce needles growing in model ecosystems. *Acta Oecol* 18:351–9.
- Landsberg J, Smith MS. 1992. A functional scheme for predicting the outbreak potential of herbivorous insects under global atmospheric change. *Aust J Bot* 40:565–77.
- Latty EF, Canham CD, Marks PL (2003) Beech bark disease in northern hardwood forests: the importance of nitrogen cycling and forest history for disease severity. *Can J For Res.* 33: 257–268
- Lee JA, Caporn SJM. 1998. Ecological effects of atmospheric reactive nitrogen deposition on semi-natural terrestrial ecosystems. *New Phytol* 139:127–34.
- Leith ID, Hicks WK, Fowler D, Woodin SJ. 1999. Differential responses of UK upland plants to nitrogen deposition. *New Phytol* 141:277–89.
- Lerdau M. 1996. Insects and ecosystem function. *Trends Ecol Evol* 11:151.
- Lerdau M, Slobodkin L. 2002. Trace gas emissions and species-dependent ecosystem services. *Trends Ecol Evol* 17:309–12.
- Lewis G. 1998. Response of stream chemistry to forest insect defoliation on the Allegheny High Plateau, Pennsylvania [dissertation]. Ithaca (NY): Cornell University
- Likens GE, Driscoll CT, Buso DC. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* 272:244–6.
- Lorio PL. 1986. Growth–differentiation balance—a basis for understanding southern pine beetle–tree interactions. For *Ecol Manage* 14:259–73.
- Lovett G, Christenson L, Groffman P, Jones C, Hart J, Mitchell M. 2002. Insect defoliation and nitrogen cycling in forests. *BioScience* 52:335–41.
- Lovett GM. 1994. Atmospheric deposition of nutrients and pollutants in North America: an ecological perspective. *Ecol Appl* 4:629–50.
- Luo YQ, Reynolds JF. 1999. Validity of extrapolating field CO<sub>2</sub> experiments to predict carbon sequestration in natural ecosystems. *Ecology* 80:1568–83.
- Magill AH, Aber JD, Berntson GM, McDowell WH, Nadelhoffer KJ, Melillo JM, Steudler P. 2000. Long-term nitrogen additions and nitrogen saturation in two temperate forests. *Ecosystems* 3:238–53.
- Magill AH, Aber JD, Hendricks JJ, Bowden RD, Melillo JM, Steudler PA. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. *Ecol Appl* 7:402–15.
- Magill AH, Downs MR, Nadelhoffer KJ, Hallett RA, Aber JD. 1996. Forest ecosystem response to four years of chronic nitrate and sulfate additions at Bear Brooks Watershed, Maine, USA. For *Ecol Manage* 84:29–37.
- Mason RR, Wickman BE, Beckwith RC, Paul HG. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part I. Insect response. For *Sci* 38:235–51.
- Mason RR, Wickman BE, Paul HG, Torgersen TR. 1998. A pilot experiment of forest fertilization during an outbreak of the western spruce budworm in northeastern Oregon. USDA Forest Service Pacific Northwest Research Station Research Paper. P 1–+
- Masters GJ, McNeill S. 1996. Evidence that plant varieties respond differently to NO<sub>2</sub> pollution as indicated by resistance to insect herbivores. *Environ Pollut* 91:351–4.
- Matson PA, McDowell WH, Townsend AR, Vitousek PM. 1999. The globalization of N deposition: ecosystem consequences in tropical environments. *Biogeochemistry* 46:67–83.
- Mattson WJ. 1980. Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11:119–61.
- Mattson WJ, Addy ND. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190:515–22.
- Mattson WJ, Haack RA. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37:110–18.
- Mattson WJ, Scriber JM. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. In: Slansky F Jr., Rodriguez JG, Eds. Nutritional ecology of insects, mites, spiders, and related invertebrates. New York: Wiley. p 105–46.
- McNeill S, Whittaker JB. 1990. Air pollution and tree-dwelling aphids. In: Watt AD, Leather SR, Hunter MD, Kidd NAC, Eds. Population dynamics of forest insects. Andover (UK): Intercept. p 195–208.
- Meyer GA. 2000. Interactive effects of soil fertility and herbivory on *Brassica nigra*. *Oikos* 88:433–41.
- Moraal LG. 1996. Bionomics of *Haematoloma dorsatum* (Hom, Cerpocidae) in relation to needle damage in pine forests. *Anz Schädli Pflanz Umwelt* 69:114–8.
- Morecroft MD, Sellers EK, Lee JA. 1994. An experimental investigation into the effects of atmospheric deposition on two semi-natural grasslands. *J Ecol* 82:475–83.
- Morimoto N, Imura O, Kiura T. 1998. Potential effects of global warming on the occurrence of Japanese pest insects. *Appl Entomol Zool* 33:147–55.
- Morrow PA, Lamarche VC. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. *Science* 201:1244–6.
- Muthukrishnan J, Selvan S. 1993. Fertilization affects leaf consumption and utilization by *Porthesia scintillans* Walker (Lepidoptera, Lymantriidae). *Ann Entomol Soc Am* 86:173–8.
- Nadelhoffer KJ, Emmett BA, Gunderson P, Kjønnass OJ, Koop-

- mans CJ, Schleppei P, Tietema A, Wright RF. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* 398:145–8.
- Neuvonen S, Saikkonen K, Haukioja E. 1990. Simulated acid rain reduces the susceptibility of the European pine sawfly (*Neodiprion sertifer*) to its nuclear polyhedrosis virus. *Oecologia* 83:209–12.
- Norby RJ, Cotrufo MF, Ineson P, O'Neill EG, Canadell JG. 2001. Elevated CO<sub>2</sub>, litter chemistry, and decomposition: a synthesis. *Oecologia* 127:153–65.
- Nordin A, Nasholm T, Ericson L. 1998. Effects of simulated N deposition on understorey vegetation of a boreal coniferous forest. *Funct Ecol* 12:691–9.
- Ollinger SV, Aber JD, Lovett GM, Millham SE, Lathrop RG, Ellis JM. 1993. A spatial model of atmospheric deposition for the northeastern U.S. *Ecol Appl* 3:459–72.
- Påhlsson AMB. 1992. Influence of nitrogen fertilization on minerals, carbohydrates, amino acids and phenolic compounds in beech (*Fagus sylvatica* L.) leaves. *Tree Physiol* 10:93–100.
- Paine TD, Redak RA, Trumble JT. 1993. Impact of acidic deposition on *Encelia farinosa* Gray (Compositae: Asteraceae) and feeding preferences of *Trirhabda geminata* Horn (Coleoptera: Chrysomelidae). *J Chem Ecol* 19:97–105.
- Palokangas P, Neuvonena S, Haapala S. 1995. The effects of simulated acid rain on growth and susceptibility to predation of *Phratora polaris* (Col., Chrysomelidae). *Environ Pollut* 89:67–71.
- Parry D, Spence JR, Volney WJA. 1998. Budbreak phenology and natural enemies mediate survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocampidae). *Environ Entomol* 27:1368–74.
- Parsons KA, de la Cruz AA. 1980. Energy flow and grazing behavior of conocephaline grasshoppers in a *Juncus roemerianus* marsh. *Ecology* 61:1045–50.
- Peltonen M, Liebhold AM, Björnstad ON, Williams DW (2002) Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology*. 83: 3120–3129
- Percy K, Awmack C, Lindroth R, Kubiske M, Kopper B, Isebrands J, Pregitzer K, Hendrey G, Dickson R, Zak D and others. 2002. Altered performance of forest pests under atmospheres enriched by CO<sub>2</sub> and O<sub>3</sub>. *Nature* 420:403–7.
- Perezsoza M, Devisser PHB. 1994. Nitrogen metabolism of Douglas fir and Scots pine as affected by optimal nutrition and water supply under conditions of relatively high atmospheric nitrogen deposition. *Trees Struct Funct* 9:19–25.
- Pietila M, Lahdesmaki P, Pietilainen P, Ferm A, Hytonen J, Patila A. 1991. High nitrogen deposition causes changes in amino acid concentrations and protein spectra in needles of the Scots pine (*Pinus sylvestris*). *Environ Pollut* 72:103–15.
- Pitcairn CER, Fowler D, Grace J. 1995. Deposition of fixed atmospheric nitrogen and foliar nitrogen content of bryophytes and *Calluna vulgaris* (L.) Hull. *Environ Pollut* 88:193–205.
- Pitcairn CER, Leith ID, Sheppard LJ, Sutton MA, Fowler D, Munro RC, Tang S, Wilson D. 1998. The relationship between nitrogen deposition, species composition and foliar nitrogen concentrations in woodland flora in the vicinity of livestock farms. *Environ Pollut* 102(S1):41–8.
- Ponder KL, Pritchard J, Harrington R, Bale JS. 2000. Difficulties in location and acceptance of phloem sap combined with reduced concentration of phloem amino acids explain lowered performance of the aphid *Rhopalosiphum padi* on nitrogen deficient barley (*Hordeum vulgare*) seedlings. *Entomol Exp Appl* 97:203–10.
- Poorter H, Villar R. 1997. The fate of acquired carbon in plants: chemical composition and construction costs. In: Bazzaz FA, Grace J, Eds. *Plant resource allocation*. San Diego: Academic Press. p 39–72.
- Power SA, Ashmore MR, Cousins DA, Sheppard LJ. 1998. Effects of nitrogen addition on the stress sensitivity of *Calluna vulgaris*. *New Phytol* 138:663–73.
- Price PW, Rathcke BJ, Gentry DA. 1974. Lead in terrestrial arthropods: evidence for biological concentration. *Environ Entomol* 3:370–2.
- Prins AH, Berdowski JJM, Latuhihin MJ. 1991. Effect of NH<sub>4</sub>-fertilization on the maintenance of a *Calluna vulgaris* vegetation. *Acta Bot Neerl* 40:269–79.
- Rainey SM, Nadelhoffer KJ, Silver WL, Downs MR. 1999. Effects of chronic nitrogen additions on understory species in a red pine plantation. *Ecol Appl* 9:949–57.
- Rao MV, Khujneri S, Dubey PS, Kumawat DM. 1993. Response of eight tropical plants to enhanced ammonia deposition under field conditions prevalent with SO<sub>2</sub> and NH<sub>3</sub>. *Water Air Soil Pollut* 71:331–45.
- Raubenheimer D. 1992. Tannic-acid, protein, and digestible carbohydrate—dietary imbalance and nutritional compensation in locusts. *Ecology* 73:1012–27.
- Raynal DJ, Joslin JD, Thornton FC, Schaedle M, Henderson GS. 1990. Sensitivity of tree seedlings to aluminum. III. Red spruce and loblolly pine. *J Environ Qual* 19:180–7.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80:1955–69.
- Rennenberg H, Kreuzer K, Papen H, Weber P. 1998. Consequences of high loads of nitrogen for spruce (*Picea abies*) and beech (*Fagus sylvatica*) forests. *New Phytol* 139:71–86.
- Reynolds B, Hunter M, Crossley DA Jr. 2000. Effects of canopy herbivory on nutrient cycling in a northern hardwood forest in western North Carolina. *Selbyana* 21:74–8.
- Risley LS, Crossley DA. 1993. Contribution of herbivore-caused greenfall to litterfall nitrogen flux in several southern Appalachian forested watersheds. *Am Midl Nat* 129:67–74.
- Ritchie ME, Tilman D, Knops JMH. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–77.
- Rosenheim JA, Wilhoit LR, Armer CA. 1993. Influence of intra-guild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96:439–49.
- Rosenthal GA, Janzen DH. 1979. *Herbivores: their interactions with secondary plant metabolites*. New York: Academic Press.
- Rosenzweig ML. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–7.
- Saikkonen KT, Neuvonen S. 1993. Effects of larval age and prolonged simulated acid rain on the susceptibility of European pine sawfly to virus infection. *Oecologia* 95:134–9.
- Saikkonen K, Neuvonen S, Kainulainen P. 1995. Oviposition and larval performance of European pine sawfly in relation to irrigation, simulated acid rain and resin acid concentration in Scots pine. *Oikos* 74:273–82.
- Salim M, Saxena RC. 1992. Iron, silica, and aluminum stresses and varietal resistance in rice—effects on whitebacked planthopper. *Crop Sci* 32:212–9.
- Sandstrom J, Pettersson J. 1994. Amino acid composition of

- phloem sap and the relation to intraspecific variation in pea aphid (*Acyrtosiphon pisum*) performance. *J Insect Physiol* 40: 947–55.
- Schindler DW, Bayley SE. 1993. The biosphere as an increasing sink for atmospheric carbon—estimates from increased nitrogen deposition. *Global Biogeochem Cycles* 7:717–33.
- Scholes R, Hall D. 1996. The carbon budget of tropical savannas, woodlands and grasslands. In: Breymer A, Hall D, Melillo J, Agren G, Eds. *Global change: effects on coniferous forests and grassland*; vol 56. Chichester (UK): Wiley. p 69–100.
- Schowalter TD, Sabin TE, Stafford SG, Sexton JM. 1991. Phytophage effects on primary production, nutrient turnover, and litter decomposition of young Douglas-fir in western Oregon. *For Ecol Manage* 42:229–43.
- Schulze E-D. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* 244:776–83.
- Scriber JM, Slansky F Jr. 1981. The nutritional ecology of immature insects. *Annu Revi Entomol* 26:183–211.
- Seastedt TR, Crossley DA, Hargrove WW. 1983. The effects of low level consumption by canopy arthropods on the growth and nutrient dynamics of black locust and red maple trees in the southern Appalachians. *Ecology* 64:1040–8.
- Shortle WC, Smith KT. 1988. Aluminum-induced calcium deficiency syndrome in declining red spruce. *Science* 198:1017–8.
- Siemann E. 1998. Experimental test of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–70.
- Sierpinski Z. 1971. Secondary noxious insects of pine in stands growing on areas with industrial air pollution containing nitrogen compounds. *Sylvan* 115:11–8.
- Slansky F, Feeny P. 1977. Stabilization of rate of nitrogen accumulation by larvae of cabbage butterfly on wild and cultivated food plants. *Ecol Monogr* 47:209–28.
- Stadler B, Michalzik B, Muller T. 1998. Linking aphid ecology with nutrient fluxes in a coniferous forest. *Ecology* 79:1514–25.
- Stams AJM, Schipholt IJL. 1990. Nitrate accumulation in leaves of vegetation of a forested ecosystem receiving high amounts of atmospheric ammonium sulfate. *Plant Soil* 125:143–5.
- Strauss SY. 1987. Direct and indirect effects of host-plant fertilization on an insect community. *Ecology* 68:1670–8.
- Suomela J, Neuvonen S, Ossipova S, Ossipov V, Pihlaja K. 1998. A long-term study of the effects of simulated acid rain on birch leaf phenolics. *Chemosphere* 36:639–44.
- Swank WT, Waide JB, Crossley DA J, Todd RL. 1981. Insect defoliation enhances nitrate export from forest ecosystem. *Oecologia* 51:297–9.
- Throop HL. 2002. Linking nitrogen deposition and herbivory: implications for insects, plants, and ecosystems [dissertation]. Stony Brook (NY): State University of New York. 226 p
- Tiedemann A, Furniss M. 1985. Soil and litter nutrient responses to looper defoliation of curleaf mountain mahogany. *For Sci* 31:382–8.
- Townsend AR, Braswell BH, Holland EA, Penner JE. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. *Ecol Appl* 6:806–14.
- Van der Eerden L, De Vries W, Van Dobben H. 1998. Effects of ammonia deposition on forests in the Netherlands. *Atmos Environ* 32:525–32.
- Van der Eerden LJ, Dueck TA, Berdowski JJM, Greven H, Van Dobben HF. 1991. Influence of NH<sub>3</sub> and (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> on heathland vegetation. *Acta Bot Neerl* 40:281–97.
- Viskari EL, Kossi S, Holopainen JK. 2000. Norway spruce and spruce shoot aphid as indicators of traffic pollution. *Environ Pollut* 107:305–14.
- Visser ME, Holleman LJM. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc R Soc London [B]* 268:289–94.
- Vitousek PM, Aber JA, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* 7:737–50.
- Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13:87–115.
- Wait DA, Jones CG, Coleman JS. 1998. Effects of nitrogen fertilization on leaf chemistry and beetle feeding are mediated by leaf development. *Oikos* 82:502–14.
- Wäreborn I. 1992. Changes in the land mollusc fauna and soil chemistry in an inland district in southern Sweden. *Ecography* 15:62–9.
- Waring GL, Cobb NS. 1992. The impact of plant stress, on herbivore population dynamics. In: Bernays EA, Eds. *Insect-plant interactions*; vol 4 Boca Raton (FL): CRC Press. p 167–226.
- Waterman PG, Mole S. 1989. Extrinsic factors influencing production of secondary metabolites in plants. In: Bernays EA, Eds. *Insect-plant interactions*; vol I Boca Raton (FL): CRC Press. p 107–34.
- Weathers KC, Likens GE. 1997. Clouds in southern Chile: an important source of nitrogen to nitrogen-limited ecosystems? *Environ Sci Technol* 32:210–3.
- Webb J, Cosby B, Deviney F, Eshleman K, Galloway J. 1995. Change in the acid-base status of an Appalachian mountain catchment following forest defoliation by the gypsy moth. *Water Air Soil Pollut* 85:535–40.
- White TCR. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63:90–105.
- White TCR. 1993. *The inadequate environment: nitrogen and the abundance of animals*. New York: Springer-Verlag, pp 425.
- Whytemare AB, Edmonds RL, Aber JD, Lajtha K. 1997. Influence of excess nitrogen deposition on a white spruce (*Picea glauca*) stand in southern Alaska. *Biogeochemistry* 38:173–87.
- Wilson EJ, Skeffington RA. 1994. The effects of excess nitrogen deposition on young Norway spruce trees. 2. The vegetation. *Environ Pollut* 86:153–60.
- Wink M. 1992. The role of quinolizidine alkaloids in plant-insect interactions. In: Bernays EA, Eds. *Plant-insect interactions*; vol 4 Boca Raton (FL): CRC Press. p 131–66.
- Woods HA. 1999. Patterns and mechanisms of growth of fifth-instar *Manduca sexta* caterpillars following exposure to low- or high-protein food during early instars. *Physiol Biochem Zool* 72:445–54.
- Yamamura K, Kiritani K. 1998. A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. *Appl Entomol Zool* 33:289–98.