Effects of nitrogen deposition and insect herbivory on patterns of ecosystem-level carbon and nitrogen dynamics: results from the CENTURY model

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Abstract

Atmospheric nitrogen deposition may indirectly affect ecosystems through deposition-induced changes in the rates of insect herbivory. Plant nitrogen (N) status can affect the consumption rates and population dynamics of herbivorous insects, but the extent to which N deposition-induced changes in herbivory might lead to changes in ecosystem-level carbon (C) and N dynamics is unknown. We created three insect herbivory functions based on empirical responses of insect consumption and population dynamics to changes in foliar N and implemented them into the CENTURY model. We modeled the responses of C and N storage patterns and flux rates to N deposition and insect herbivory in an herbaceous system. Results from the model indicate that N deposition caused a strong increase in plant production, decreased plant C:N ratios, increased soil organic C (SOC), and enhanced rates of N mineralization. In contrast, herbivory decreased both vegetative and SOC storage and depressed N mineralization rates. The results suggest that herbivory plays a particularly important role in affecting ecosystem processes by regulating the threshold value of N deposition at which ecosystem C storage saturates; C storage saturated at lower rates of N deposition with increasing intensity of herbivory. Differences in the results among the modeled insect herbivory functions suggests that distinct physiological and population response of insect herbivores can have a large impact on ecosystem processes. Including the effects of herbivory in ecosystem studies, particularly in systems where rates of herbivory are high and linked to plant C:N, will be important in generating accurate predictions of the effects of atmospheric N deposition on ecosystem C and N dynamics.

Keywords: carbon cycle, CENTURY model, herbivory, nitrogen deposition, SOC

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Introduction

Atmospheric deposition of anthropogenically fixed nitrogen (N) is a major component of global change, making understanding the ecosystem-level impacts of this deposited N a high research priority. Recent estimates suggest that human activities have at least doubled the rate of annual input of inorganic N into the terrestrial N cycle, and increases in N inputs are expected to continue to grow during the next few decades as a result of human population growth, increasing fossil fuel consumption, and increasing reliance on industrially produced fertilizers (Galloway et al., 1994; Galloway et al., 1995; Vitousek et al., 1997).

Nitrogen deposition has been linked to a number of changes in terrestrial biogeochemical cycles. Rates of N mineralization and nitrification tend to increase with atmospheric inputs, although mineralization rates may decline after soils become N saturated (Aber et al., 1998). Increased rates of N_2O and NO emission as a result of N deposition may have substantial consequences

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for atmospheric chemistry (Hall & Matson, 1999). Patterns of carbon (C) storage and cycling are also being influenced by N deposition. Increased availability of fixed N to plants may lead to increased photosynthetic rates due to strong correlations between foliar N concentration and photosynthetic rates (Field & Mooney, 1986; Reich et al., 1998; Peterson et al., 1999). Simulated deposition studies at both the leaf and stand levels have revealed increases in photosynthesis or enhanced aboveground production (Aber et al., 1993; Leith et al., 1999). Models suggest that these patterns may lead to increased terrestrial C storage in vegetation due to enhanced primary production (Schindler & Bayley, 1993; Townsend et al., 1996; Holland et al., 1997; but see Nadelhoffer et al., 1999).

Nitrogen deposition may also have more indirect impacts on ecosystem process through modifying interactions between plants and insect herbivores. Because foliage is low in N-based proteins and amino acids, the N concentration of host plant tissue is typically the single best predictor of host plant quality for insect herbivores (Mattson, 1980). Deposition-induced shifts in plant C:N may therefore strongly affect plant–herbivore interactions. A strong positive relationship between foliar N concentration and insect survivorship, development, growth, and reproductive rates has been demonstrated for many insect species (Mattson, 1980; Scriber & Slansky, 1981; Mattson & Scriber, 1987; White, 1993). In contrast, insect consumption response to N varies, as some species exhibit increased consumption rates in the presence of N-rich food while other species decrease individual feeding rates to keep N intake constant (Slansky & Feeny, 1977; Raubenheimer, 1992; Muthukrishnan & Selvan, 1993; Woods, 1999; Meyer, 2000). These differences suggest species-specific physiological differences in insect metabolic response to foliar N or other compounds that might be affected by plant N availability (e.g. secondary metabolites). Positive effects of N deposition at the individual level can scale up to enhanced population sizes, although this response is not universal (Strauss, 1987; Waring & Cobb, 1992; Kytö et al., 1996; Meyer & Root, 1996; Siemann, 1998).

Deposition-induced changes in the rates of insect herbivory may have ecosystem-level consequences because insect herbivory can affect ecosystem processes. Numerous studies have linked grazing by large and small mammals to changes in primary production and altered rates of N and C cycling (McNaughton, 1976; McNaughton, 1979; Holland & Detling, 1990; Holland et al., 1992; Kielland et al., 1997; Pastor & Cohen, 1997). Less well understood, however, is the extent to which insect herbivory, both at low levels and in outbreak situations, affects ecosystem processes.

Defoliation from high levels of insect herbivory can decrease net primary productivity (Mattson & Addy, 1975; Grier & Vogt, 1990; Belovsky & Slade, 2000; Tikkanen & Roininen, 2001). Herbivory can also lead to changes in decomposition and mineralization rates by affecting the quantity and quality of leaf litter and frass (insect waste) inputs (Swank et al., 1981; Seastedt et al., 1983; Seastedt & Crossley, 1984; Grier & Vogt, 1990; Schowalter & Sabin, 1991; Lovett & Ruesink, 1995; Stadler et al., 1998; Belovsky & Slade, 2000). In addition, ecosystem functioning can be substantially impacted by herbivore-induced plant mortality and changes in plant community composition (Jenkins et al., 1999).

The combination of strong controls over the rates of herbivory by N availability and links between herbivory and ecosystem processes suggest that N deposition and herbivory may interact to affect patterns of productivity and C and N cycling. Experimentally assessing the extent to which deposition-induced changes in insect herbivory affects ecosystem processes is exceedingly difficult due to the large spatial and temporal scales required for these experiments. Simulation models of ecosystem processes can be used to explore how ecosystems might respond to these perturbations and to generate a suite of predictions to be tested in future experiments. We used CENTURY, a well-validated ecosystem model that tracks the pools and fluxes of C and N, to explore how N deposition and herbivory might interact to affect ecosystem processes. We parameterized the model with data from an experiment that assessed the influences of herbivory and simulated N deposition on the production of an annual plant. Because physiological differences between insect species can lead to distinct effects of N on consumption rates and population dynamics, we created several herbivory functions in which the impact of N deposition affected rates of herbivory differentially.

Model description

The CENTURY model simulates plant production and soil organic matter (SOM) dynamics. CENTURY has been extensively validated and has been used to model many different vegetation types worldwide (Schimel et al., 1994). It is described in detail elsewhere (Parton et al., 1987, 1988). Briefly, the model simulates the pools and fluxes of C and N in soil and plant compartments in monthly time-steps (Fig. 1). Monthly potential plant above- and belowground production is calculated based on annual precipitation without regard to nutrient availability. Actual monthly production values are lower than the potential values if insufficient inorganic N is available to maintain the vegetation between specified minimum and maximum C:N ratios.
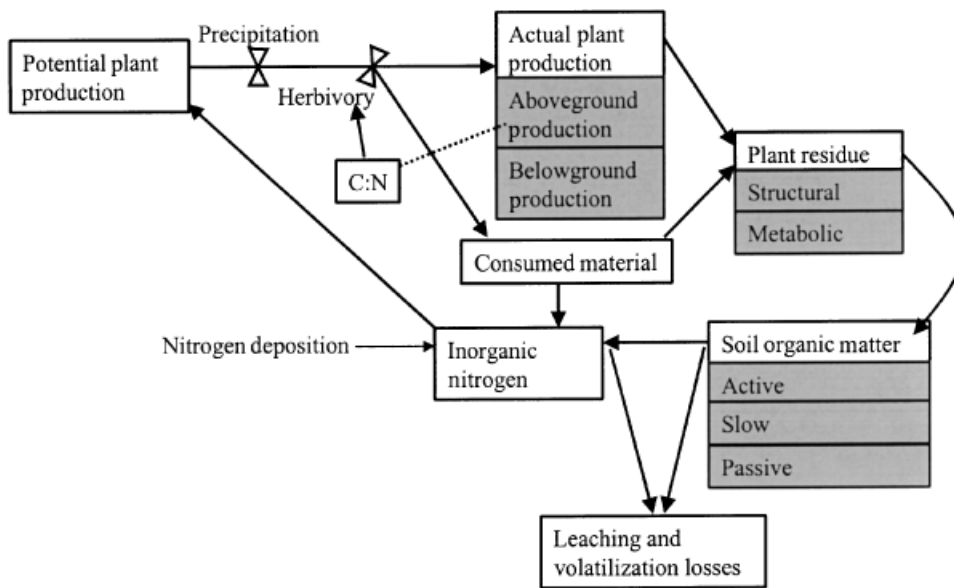
Fig. 1 Major pools and flows of nutrients in the CENTURY model. Shaded boxes represent components of the unshaded boxes above them. The dynamic effect of C:N on herbivory rates is a modification of the model presented in this paper.

Upon death, plant material is transferred into the litter pools. Dead litter is divided into above- and below-ground structural (1–5-year turnover) and metabolic (0.1–1-year turnover) pools (Parton *et al.*, 1987, 1988). Turnover times vary based on the chemical and structural composition of the litter. Material moves from the litter pools to the SOM pools. The SOM material is partitioned into three pools based on turnover time. Turnover time ranges from 1 to 5 years in the active SOM pool, 20 to 40 years in the slow pool, and 200 to 1500 years in the passive SOM pool (Parton *et al.*, 1987, 1988). The decomposition rate of SOM and litter pools are extrinsically controlled by soil temperature and water content. Input variables for the model include average minimum and maximum monthly temperature and precipitation; lignin, C, N, P, and S content of plant material and SOM; soil texture; and atmospheric N inputs (Parton *et al.*, 1987, 1988).

The CENTURY model explicitly integrates herbivory with plant production and nutrient flows. The pre-existing grazing functions in CENTURY take into account user-specified values for the proportions of live and dead shoots removed per month by grazing (Holland *et al.*, 1992). Grazing is specified to cause no effect, a linear decrease, or a quadratic effect (initial increase followed by a decrease) on aboveground production and the root:shoot ratio. Nitrogen dynamics are affected by herbivory in the model both by altering plant production and through N inputs to the soil as feces and urine (Holland *et al.*, 1992).

Previous simulations with the CENTURY grazing functions have been used to explore the implications of large grazing mammals and prairie dogs on grassland systems (Parton *et al.*, 1987; Holland *et al.*, 1992; Seastedt *et al.*, 1994). These original grazing functions simulate removal of a constant proportion of plant tissue from the system each month, regardless of the nutrient content of the plant tissue. Given that empirical studies indicate that insect herbivores are typically strongly limited by the N concentration of their diet (Slansky & Feeny, 1977; Mattson, 1980; Mattson & Scriber, 1987), these original CENTURY grazing functions were not appropriate for modeling the combined effects of N deposition and insect herbivory on ecosystem processes.

The objectives of this study were to implement new insect herbivory functions into CENTURY that reflect a dynamic response of consumption rate to plant C:N and to explore how these functions interact with N deposition to affect C and N pools and transformations. We hypothesized that both N deposition and herbivory would lead to changes in C and N storage patterns and flux rates. In particular, we expected that herbivory would counteract the strong positive impacts of N deposition on C and N storage and transformations when herbivore consumption rates and population sizes increased with increasing N deposition.

Methods

Insect herbivory functions

We created three new functions with dynamic relationships between plant C:N and insect herbivory and

Table 1 Studies used for generating consumption response functions

Order	Species	Experiment type	Response sign	References
Lepidoptera	*Lymantria monacha*	Fertilized plants	+	Hättenschwiler & Schafellner (1999); A
Lepidoptera	*Porthesia scintillans*	Fertilized plants	+	Muthukrishnan & Selvan (1993); B
Lepidoptera	*Lymantria dispar*	Fertilized plants (2 species)	+	Kinney *et al.* (1997); C, D
Coleoptera	*Ophraella communa*	Fertilized plants	+	Throop (2002); E
Lepidoptera	*Trichoplusia ni*	Fertilized plants	+	Throop (2002); F
Lepidoptera	*Spodoptera eridania*	Fertilized plants	+	Manuwoto & Scriber (1985); G
Orthoptera	*Melanoplus differentialis*	Fertilized plants	+	Johnson & Lincoln (1991); H
Lepidoptera	*Galleria mellonella*	Artificial diets	−	Jindra & Sehnal (1989); I
Lepidoptera	*Spodoptera eridania*	Artificial diets	−	Karowe & Martin (1989); J
Lepidoptera	*Lymantria dispar*	Artificial diets	−	Lindroth *et al.* (1997); K
Orthoptera	*Locusta migratoria*	Artificial diets	−	Raubenheimer (1992); L
Lepidoptera	*Spodoptera exigua*	Fertilized plants (3 species)	−	Al-Zubaidi & Capinera (1984); M–O
Lepidoptera	*Smerinthus ocellatus*	Fertilized plants (2 moisture treatments)	−	Thomas & Hodkinson, (1991); P, Q

Response sign indicates whether individual insects increased or decreased their consumption rates in response to increased nitrogen concentration of their food. Data for insects that increased their consumption rates were used for the positive consumption response function and data for insects that decreased their consumption rates were used to generate the negative consumption response function. Letters in the reference column refer to the letters used to denote different experiments in Fig. 2.

implemented them into CENTURY. These functions were based on data compiled from measurements assessing the impact of diet N concentration on individual insect consumption rates (Table 1). We randomly selected 13 studies from the literature in which herbivores were fed either on leaf tissue from plants grown under different fertilizer regimes or on artificial diets with varying N content. For each study we normalized the consumption and N concentration values such that the values for both consumption and N concentration were equal to one at the lowest N concentration (Fig. 2a). Normalizing the data provided a means for comparing data from a diverse array of studies on common axes, thus allowing us to explore whether any general patterns of consumption response to changes in dietary N concentration occurred. Visual inspection of the data sets indicated that normalization did not mask patterns evident in the raw data. Although the literature search was carried out with no *a priori* assumptions on the direction of herbivore response, we found two distinct consumption response patterns. In half of the cases, herbivores responded to increased food N content by increasing their consumption rates (hereafter the 'positive consumption response' function), while in the other half they decreased their consumption rates. The decrease in consumption rate led to a nearly stable N intake rate as the N concentration increased (hereafter the 'negative

consumption response' function). These two functions reflect two physiologically distinct consumption responses to N availability.

We generated equations to describe the two generalized consumption response functions. The data were best described by exponential curves (Fig. 2a). These two new functions were implemented into CENTURY in order to generate values for monthly consumption rates. Monthly consumption of live shoots was modeled to be 10% when aboveground live C:N was greater than or equal to 50 and then varied as C:N declined as specified by the herbivory functions (Fig. 2b). We chose a relatively high baseline rate of herbivory to reflect the extensive herbivory observed on *Ambrosia artemissifolia* plants used for model parameterization (H. L. T., personal observation; see 'Model Parameterization' section for details on study system).

A 'population response' function was created to simulate a positive impact of N deposition on both consumption and herbivore population density. Because all the herbivory functions calculate monthly removal as a percentage of standing live biomass, there is an inherent assumption that herbivore populations increase in proportion to increased biomass. The population response function, however, simulates a disproportionate increase in population with respect to biomass. In this function, population size responds linearly to plant C:N, with a doubling of the normalized
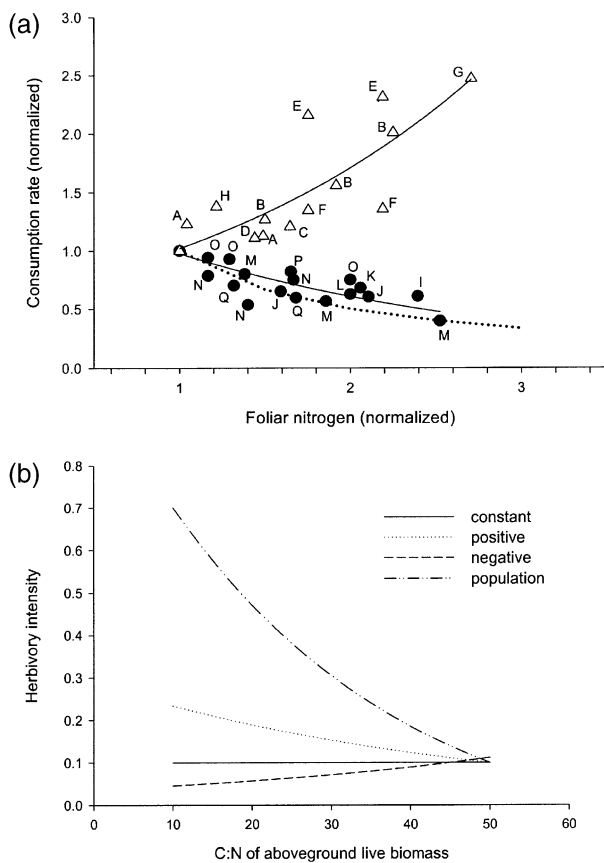
Fig. 2 (a) Empirical data on individual insect consumption response to changes in foliar nitrogen concentration. Data are from studies listed in Table 1. For each study, the values for the consumption rates and foliar nitrogen concentration were both normalized to one at the values obtained for the lowest nitrogen concentration. Each study has at least two points on the curve (one with nitrogen at 1, and one greater than 1). Letters correspond to different studies. Triangles represent the positive consumption response function ($y = 0.6167e^{0.5005x}$) and circles represent the negative consumption response ($y = 1.5263e^{-0.4592x}$). The equations describing these curves were implemented as the consumption functions in the model. The dashed line represents the theoretical value for an entirely stable nitrogen intake response in which daily nitrogen intake was constant despite changes in foliar nitrogen concentration. (b) Change in consumption for each of the four herbivory functions in response to changes in the C:N of aboveground live biomass. Herbivory intensity (H) is the proportion of aboveground live biomass that is removed by herbivores each month. The constant consumption rate function is the unmodified CENTURY grazing function in which the herbivory intensity is static regardless of C:N. For the positive consumption response function, $H = 0.2889e^{-0.0213 \times C:N}$. For the negative consumption response function, $H = 0.0365e^{0.0224 \times C:N}$. For the population response function, $H = (0.2889e^{-0.0213 \times C:N})(-0.05 \times C:N + 3.5)$. This equation describes a positive consumption response multiplied by a linear effect of C:N on herbivore population size. Herbivore population size doubles if C:N declines from 50 to 30.

population size if C:N drops from 50 to 30 (Fig. 2b). This population response approximates the herbivore population response found in a fertilization experiment in a grassland community (Siemann, 1998). Overall consumption in the population response function is the product of this linear population response and the positive consumption response function. Finally, we used one of the original CENTURY herbivory functions (the 'constant consumption rate' function) to simulate a constant monthly consumption rate of 10% of live aboveground biomass regardless of the C:N content (Fig. 2b).

All functions were stipulated to have a linear effect on aboveground production and no effect on the root:shoot ratio (grazing effect 1 in Parton et al., 1992). Monthly aboveground production was calculated following Parton et al. (1992) as

$$\text{AGP}_{out} = (1.0 - 2.21H)\text{AGP}_{in},$$

where AGP_{in} is the monthly aboveground production prior to herbivory ($gC m^{-2}$), AGP_{out} is the total monthly production after the herbivory routine ($gC m^{-2}$), and H is the percentage of aboveground live biomass removed by herbivory each month (H is the parameter flgrem of Parton et al., 1992). A fraction of N and C removed in herbivory is returned to the soil as frass. The N in frass is modeled as a combination of urea and organic N compounds. Plant production is constrained by water availability and minimum and maximum C:N ratios. These bounds on C:N prevent either N deposition or herbivory from driving C:N to unrealistically high or low values. An executable version of the CENTURY model that includes the insect herbivory functions is available from the CENTURY website (http://www.nrel.colostate.edu/projects/century/herbivory1.htm).

Model parameterization

The plant production submodel parameterization was based on experimental work with the herbaceous annual Ambrosia artemisiifolia (Asteraceae, common ragweed). The production response of A. artemisiifolia to beetle herbivory and N deposition was studied in a common garden experiment in an old field at Brookhaven National Laboratory in Upton, NY, USA (Throop, 2002). Twenty plants grew in each of eight 0.5×2 m plots. Nitrogen deposition was simulated with weekly applications of a liquid N solution during the growing season at rates of 0 or $5 gN m^{-2} yr^{-1}$. Beetle herbivory was manipulated by caging specialist leaf beetles (Ophraella communa, Coleoptera: Chrysomelidae) on plants using mesh bags. Control plants were enclosed in bags but maintained free of herbivores.

Aboveground biomass response was assessed with an end-of-season destructive harvest. Aboveground C:N ratios were calculated by determining relative biomass allocation to aboveground components (shoots, leaves, and stems) and measuring both the C and N content for each component. Plant input variables affecting plant production rates and C:N were adjusted from the CENTURY plant input file describing weed vegetation in agricultural areas (the 'E' crop parameterization) in order to achieve a modeled response to N deposition and herbivory similar to the experimental response of *A. artemisiifolia*. Plant production input values used for the simulation runs are listed in Throop (2002).

Site files from a temperate grassland (Konza Prairie, KS, USA) were used to specify site-specific soil and climate input variables for the model. Of the available site files, this site file most closely approximated the conditions of the experimental plot. Examination of the modeled and measured plant production response suggests that the dynamics of the system were captured well. Nitrogen deposition was simulated by dividing the desired annual N inputs into 12 equal portions and added monthly with the CENTURY fertilization routine.

Model runs

All simulations began with an initial 2500-year run with no N deposition or herbivory. These spin-up runs allowed equilibrium conditions in soil organic C (SOC) values to develop. Nitrogen deposition was initiated in year 2501 and ran for 30 years prior to insect herbivory. This reflects the global ramp-up of N deposition that has occurred since the 1950s as a result of increased fossil fuel combustion, industrial fixation of N for fertilizer, and agricultural intensification (Holland *et al.*, 1999). An initial set of runs was used to explore plant and soil responses to N deposition alone. We ran these simulations in $1\,g\,N\,m^{-2}\,yr^{-1}$ increments spanning wide range of deposition values currently occurring worldwide, $0–10\,g\,N\,m^{-2}\,yr^{-1}$ (deposition rates topping $10\,g\,N\,m^{-2}\,yr^{-1}$ have been reported in the Netherlands; Draaijers *et al.*, 1989). A second set of model runs simulated the combination of N deposition and herbivory. We initiated herbivory in year 2531 and ran it for 30 years. Deposition rates in these studies were 0, 1, 2, 3, 4, and $5\,g\,N\,m^{-2}\,yr^{-1}$. These rates of deposition were chosen to represent the range of current N deposition rates in the United States, where deposition ranges from near zero to up to $4\,g\,N\,m^{-2}\,yr^{-1}$ in high elevation locations in the Northeast (Ollinger *et al.*, 1993). We ran the model for all possible combinations of the four herbivory functions (none, constant consumption rate, positive consumption response, negative

consumption response, and population response) and the six deposition rates.

Results

Simulated plant response to N deposition

Nitrogen deposition strongly affected patterns of plant productivity and C storage in the simulation runs. All soil and vegetative variables were stable at the end of the 2500-year spin-up runs. After 30 years of simulated N deposition, above- and belowground production were essentially stable, with little inter-annual variability, but SOC was still increasing. Plant production exhibited a strong increase with N deposition until the response saturated at $7\,g\,N\,m^{-2}\,yr^{-1}$ of N deposition. Plant C:N ratios decreased in response to N deposition, but this response saturated around $7\,g\,N\,m^{-2}\,yr^{-1}$ of N deposition. Nitrogen deposition also caused a substantial increase in SOC, and the response saturated at $8\,g\,m^{-2}\,yr^{-1}$ of deposition.

Herbivory functions

The intensity of simulated herbivory responded differentially to N deposition for the four herbivory functions (Fig. 3). For the negative consumption response, average monthly biomass removed by herbivory declined from 9.9% at no deposition to 8.8% at $5\,g\,N\,m^{-2}\,yr^{-1}$, although total N removed by herbivory remained nearly constant. Herbivory increased with deposition for the positive consumption response
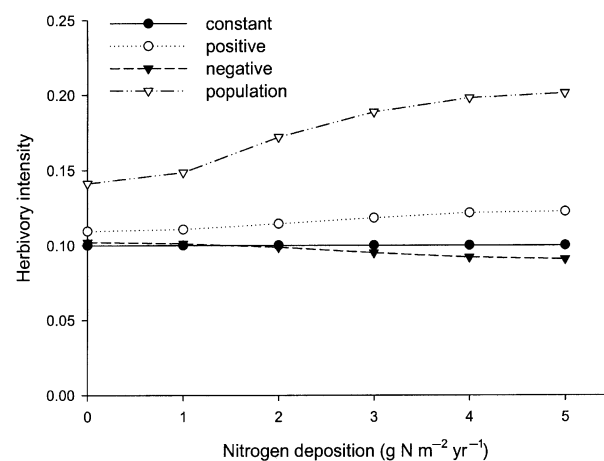

Fig. 3 Influences of nitrogen deposition on modeled monthly herbivory intensity. Herbivory intensity is the proportion of aboveground live biomass that is removed each month by herbivores. Each symbol represents a different herbivory function (see text). Values are simulation results from July after 30 years of nitrogen deposition and 30 years of herbivory and nitrogen deposition after a 2500-year climate stabilization run.
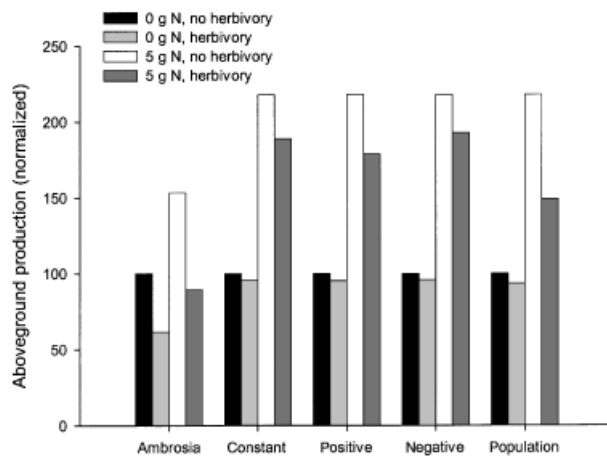
Fig. 4 Measured vs. modeled response to nitrogen deposition and herbivory in terms of aboveground biomass production. *Ambrosia* data are results from the field experiment with caged beetles, and all other data are simulation results. To facilitate comparisons, biomass production values are normalized to 100 at no nitrogen deposition and no herbivory for each herbivory type.

function (11.3% with no deposition to 12.7% at $5\,g\,N\,m^{-2}\,yr^{-1}$) and for the N-deposition positive population response (15.4% with no deposition to 21.7% at $5\,g\,N\,m^{-2}\,yr^{-1}$). The relative influence of changes in N deposition in affecting monthly herbivory rate differed among herbivory functions.

Effect on production response: comparison with data

Aboveground production increased in response to N deposition more strongly in the simulations than in the field experiments (Fig. 4). Because overall aboveground production was higher in the simulation results than the field experiments, we normalized the data to enable comparisons of relative changes in production (see Fig. 4). In the absence of added N deposition, none of the modeled herbivory functions suppressed aboveground production as much as occurred in the field experiment. Considerable variation existed in the modeled effect of herbivory at $5\,N\,g\,m^{-2}\,yr^{-1}$, with the population response function leading to the strongest suppression of aboveground production.

Carbon storage response

Nitrogen deposition increased C storage in plant biomass, but this response was strongly mediated by herbivory. Herbivory always led to reduced total plant production, but the extent to which production was reduced varied with N deposition intensity and the herbivory function used (Fig. 5a). Herbivory functions
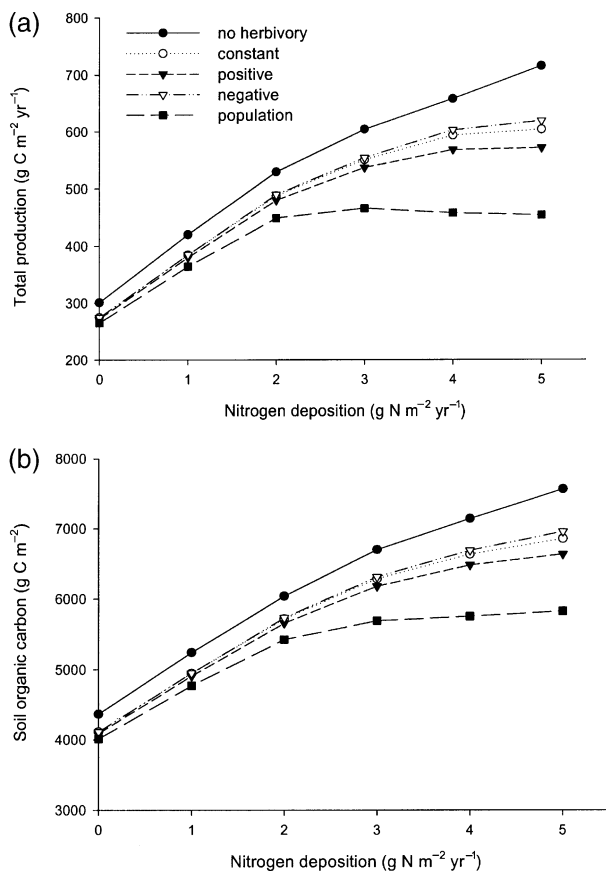

Fig. 5 Influences of nitrogen deposition and the four herbivory functions on carbon dynamics. Values are from the final year of a simulation run that included a 2500-year climate stabilization, 30 years of nitrogen deposition, and 30 years of herbivory and nitrogen deposition. (a) Total annual biomass production (sum of above and belowground production) in terms of g carbon accumulation $m^{-2}\,yr^{-1}$. (b) Total pools of soil organic carbon.

that led to higher monthly consumption suppressed the positive influence of N deposition on plant C storage, and led to a saturation of production with increased N deposition. Herbivory thus lowered the N deposition threshold at which vegetative C storage saturated. The influences of N deposition and herbivory on C storage in vegetation led to parallel effects on SOC (Fig. 5b). Although SOC was still increasing at $5\,N\,g\,m^{-2}\,yr^{-1}$ in the absence of herbivory, the response was nearly saturated at this deposition rate with the population response function.

Nitrogen dynamics

Nitrogen dynamics were affected both by N deposition and herbivory. Net N mineralization rates were generally enhanced by N deposition and depressed
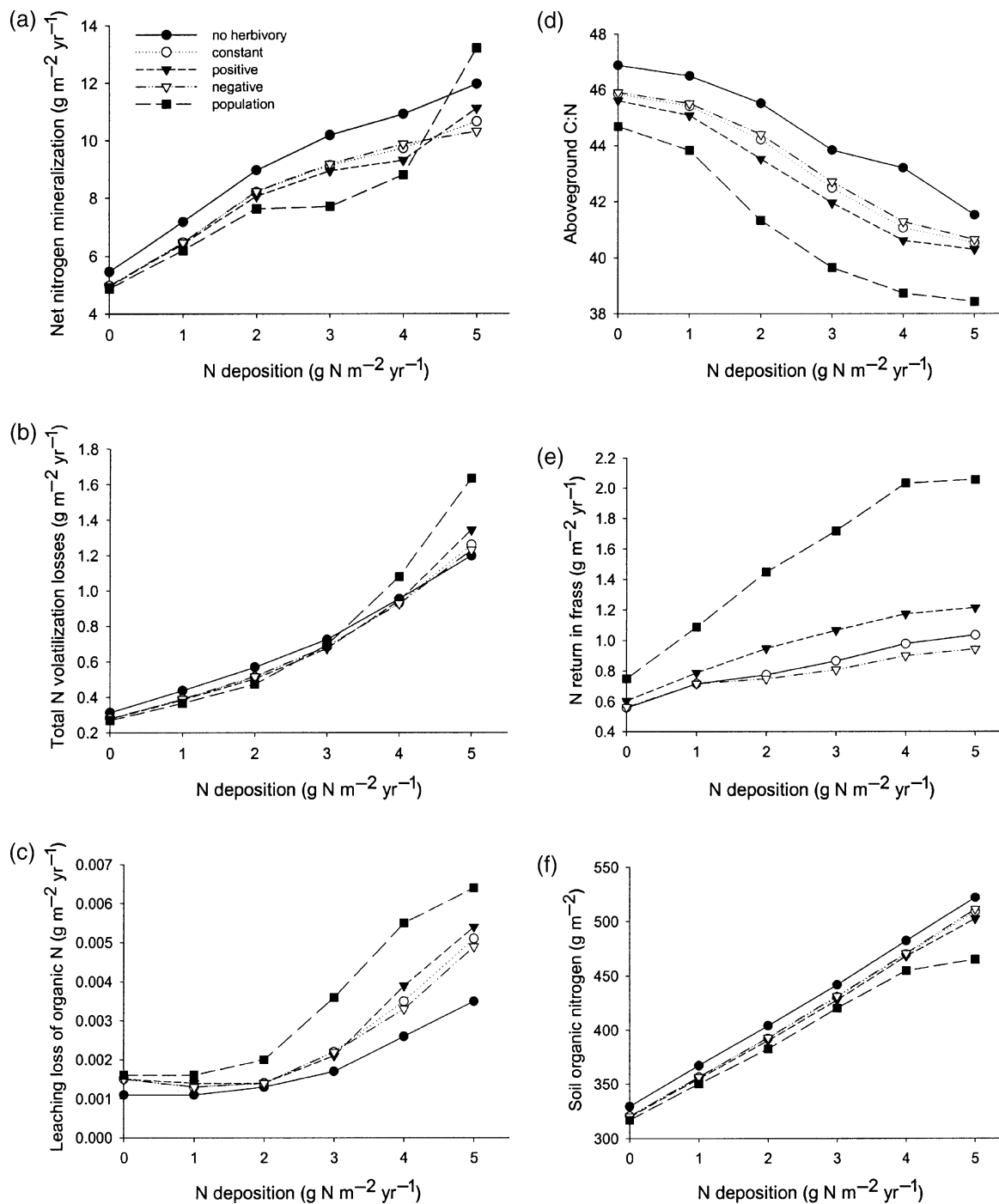
Fig. 6 Influences of nitrogen deposition and the four herbivory functions on nitrogen pools and fluxes. Values are cumulative annual rates from the final year of a simulation run that included a 2500-year climate stabilization, 30 years of nitrogen deposition, and 30 years of herbivory and nitrogen deposition. (a) Net nitrogen mineralization. (b) Total nitrogen losses by volatilization (as a result of nitrification and denitrification). (c) Nitrogen losses through leaching of organic nitrogen compounds. (d) Mid-season (July) C : N ratios of aboveground live biomass. (e) Annual cumulative nitrogen return to the soil as insect frass. (f) Pool sizes of total soil organic nitrogen.

by herbivory (Fig. 6a). Similarly, losses of N from the system through volatilization from nitrification and denitrification were enhanced by N deposition and

depressed by herbivory (Fig. 6b). Leaching of organic N was enhanced by both N deposition and herbivory (Fig. 6c). Nitrogen deposition led to decreased aboveground

C:N under all herbivory functions (Fig. 6d). Nitrogen return from insect frass was enhanced with N deposition as a function of deposition-induced changes in the rate of herbivory (Fig. 6e). There was a nearly linear response of SON to N deposition, with herbivory causing only a small decrease in pool size (Fig. 6f). However, this relationship broke down at high N deposition with the population herbivory response when the pool size appeared to saturate.

Discussion

Implications for C dynamics

Although N deposition more strongly affected ecosystem processes than did herbivory, the simulation results suggest that herbivory may alter the magnitude of the effect of N deposition on ecosystem processes. This is particularly pronounced under high N deposition with the herbivory functions in which there is a negative correlation between C:N and herbivory rates. Under these conditions, herbivory lowers the threshold value for N deposition at which C storage saturates. These changes in the threshold N value for C saturation appear to occur due to a decoupling of the relationship between rates of N and C returns caused by herbivory (Holland et al., 1992). Different physiological responses of herbivores to N deposition, represented by the four herbivory functions, differ in the extent to which they affect the saturation threshold.

The interactions between N deposition and herbivory have a particularly strong effect on C storage in vegetation. Nitrogen deposition-induced increases in vegetative C storage were dampened in the presence of herbivory. Mechanistically, decreased C storage from herbivory was caused both by biomass removal due to consumption and the modeled impact of herbivory in suppressing of future biomass production. Parallel changes in SOC pools were driven primarily by herbivory- and nitrogen-induced changes in plant production. SOC accumulation may have been overestimated in our simulation runs, however, because herbivory had no modeled effect on root:shoot ratio. Herbivore-induced changes in root:shoot allocation can be an important regulator of SOC (Holland & Detling, 1990).

The apparent role of herbivory in lowering both the N deposition threshold for saturation of C storage and the amount of system-wide C storage suggests that herbivores could play an important role in mitigating the impacts of N deposition in herbaceous systems. As the modeled system is composed entirely of annual plants, changes in vegetative C sequestration in this system are of little long-term consequence since C in herbaceous tissue has a relatively short residence time prior to decomposition (Townsend et al., 1996). Changes in the saturation threshold could be important to the global C cycle, however, if they occurred in forest ecosystems where there is greater long-term C storage potential. Strong links between C:N and rates of consumption exist in woody plants (Mattson & Scriber, 1987), and herbivory has been shown to decrease C sequestration in woody tissues (Morrow & Fox, 1989; Muzika & Liebhold, 1999; Tikkanen & Roininen, 2001). Research exploring N deposition and herbivory in forests will be crucial in determining whether herbivory affects the N saturation threshold in forested ecosystems.

The positive influence of N deposition on C storage in vegetation may be somewhat overestimated in CENTURY for several reasons. First, base cation availability is not incorporated into CENTURY, although deposition-induced base cation losses can reduce productivity (Shortle & Smith, 1988; Schulze, 1989; Katzensteiner et al., 1992). Root:shoot allocation is not dynamic in response to N availability in CENTURY, although decreased root:shoot ratios are a common response to increased N availability (Brouwer, 1983). Thus, simulated belowground production is higher and aboveground production is lower than they would be if root:shoot was affected by N availability. Since tissue removed by herbivory is calculated as a proportion of aboveground biomass, the effect of herbivory under high levels of N deposition is underestimated with this static biomass allocation algorithm. Finally, C storage may have been overestimated because CENTURY typically exhibits N saturation at higher N loads than is found empirically (E. A. H., personal observation).

Implications for N dynamics

Nitrogen deposition and herbivory had conflicting influences on modeled N storage because of their contrasting impact on biomass production. Nitrogen deposition enhanced N storage in vegetation and soil by increasing above- and belowground biomass. In contrast, herbivory generally slightly depressed SON due to decreased aboveground production. Nitrogen deposition caused a disproportionately large increase in total N storage in vegetation relative to total biomass because N deposition caused modeled plant C:N to decrease.

The model provides several mechanisms by which herbivory and N deposition affected N transformation rates. Nitrogen mineralization is controlled in CENTURY by the C:N and pool sizes of SOM metabolic pools. Both these factors were enhanced by modeled N deposition. Similar positive relationships between N deposition and mineralization rates have been found in

empirical studies (Fenn *et al.*, 1996; Magill *et al.*, 1997; Lee & Caporn, 1998). In contrast, herbivory affected N mineralization through several different mechanisms. Herbivory negatively affected N mineralization rates because consumption decreased organic N pools. These decreases were somewhat negated, however, by herbivory-induced decreases in plant C : N and through inputs of readily mineralizeable components of frass.

Physiological and population responses of herbivores

The presence of the two distinct consumption responses suggests that there may be a few main physiological mechanisms by which insects respond to changes in foliar composition. Increased consumption may be a response to higher food quality due to increased N or decreased C-based secondary metabolites and consequent impacts on growth rates and insect size (Mattson, 1980; Scriber & Slansky, 1981; Mattson & Scriber, 1987). In contrast, decreased consumption could be the result physiological limitations to upregulating metabolism of N on N-based secondary metabolites. It is interesting to note that all of the studies using artificial diets fell out in the negative consumption response group, suggesting that the positive consumption response is influenced by changes in foliar composition besides proteins and amino acids (the main N-containing compounds in the artificial diets).

The differing effects of the positive consumption response and population response functions illustrate the potential ecosystem consequences of numerical responses of insect herbivores. Because insect population sizes can change by several orders of magnitude (Ostfeld *et al.*, 1996), we suggest that population responses may be more plastic, and thus ultimately more influential on ecosystem processes, than consumption responses. Experimental work assessing the impact of N deposition on insect populations poses considerable technical challenges (Throop & Lerdau, in press), but is needed in order to fully assess the ecosystem-level impacts of N deposition.

The four herbivory functions all modeled folivorous larvae and differed only in the extent to which plant C : N affected herbivory rates; many additional factors may influence affect herbivory-ecosystem process relationships. For example, herbivores differ in the extent to which tissue removal affects plant biomass and frass production. Herbivores from other feeding guilds, such as phloem sap suckers or cell contents feeders, are likely to cause very different effects than the modeled folivores (Karban & Strauss, 1993; Meyer, 1993; Throop & Lerdau, in press). In addition, scaling from individual consumption responses to ecosystem-level consequences is complicated by changes in other factors that are affected by N availability, such as insect

development rates, plant architecture, tritrophic interactions, and individual insect survival.

Directions for future modeling studies

While this modeling effort represents a first step toward incorporating herbivory into ecosystems models, further refinement will more fully capture the complicated relationships between herbivory, N deposition, and ecosystem processes. Results from this modeling effort underscore the need for models that integrate across traditional boundaries of ecological organization. Processes at the physiological, population, and community levels need to be taken into account for ecosystem modeling incorporating herbivory.

Our model simplifies the physiological response of both plants and insects to N deposition. For example, links between soil N availability and secondary metabolite production are not modeled in CENTURY. Changes in secondary metabolism can be important in affecting ecosystem processes such as decomposition rates (Aerts, 1997; Hobbie, 2000). In addition, insect consumption may be affected by mixtures of nutrients and secondary metabolites (Raubenheimer, 1992; Simpson & Raubenheimer, 2001). Incorporating changes in plant allocation and herbivore metabolism to N deposition into ecosystem models will require that models include more physiological complexity. A drawback is that models will become more species-specific, reflecting physiological characteristics of specific plants and insects.

We modeled herbivory as a relatively constant, low-level phenomenon. While this is a realistic situation for many systems, including many herbaceous systems such as the modeled system, in other systems, such as forests, ecological and economically important herbivory often occurs as episodic outbreaks of intense herbivory (Haack & Byler, 1993). Application of ecosystem models that include herbivory in systems characterized by herbivore outbreaks will require inclusion of factors that trigger outbreaks.

Future iterations of ecosystem models should also explore the relationships between herbivory, N deposition, and plant community composition. Plant communities are known to change both in response to herbivory (Brown, 1990; Ritchie *et al.*, 1998; Carson & Root, 1999; Jenkins *et al.*, 1999) and in response to N deposition (Heil & Diemont, 1983; Pitcairn *et al.*, 1998; Rainey *et al.*, 1999). Since changes in plant community composition can affect ecosystem processes (Hobbie, 1992; Finzi *et al.*, 1998a; Finzi *et al.*, 1998b; Jenkins *et al.*, 1999; Hibbard *et al.*, 2001), future empirical and modeling efforts should assess the patterns and consequences of these interactions. In addition, preferential herbivory on N-rich plant parts, genotypes, or

species may affect plant C : N (Pastor *et al.*, 1993; Ritchie *et al.*, 1998; Sirotnak & Huntly, 2000; Uriarte, 2000).

Conclusions

The results from these modeling simulations demonstrate that herbivory could have a substantial impact on ecosystem processes, but that these impacts may change with levels of N deposition. In particular, herbivory lowered the threshold level of N deposition at which ecosystem C storage saturated and decreased C storage capacity. Current discrepancies exist between modeled and measured influences of N deposition on ecosystem C sequestration (Holland *et al.*, 1997; Jenkinson *et al.*, 1999; Nadelhoffer *et al.*, 1999). Inclusion of herbivory in ecosystem models may help close this gap. The presence of several distinct consumption responses to N deposition suggests that species- or guild-specific responses to N deposition will need to be included in ecosystem models. Other aspects of global change, such as altered temperature, elevated atmospheric CO_2, and air quality may also affect patterns of herbivory (Williams & Leibhold, 1995; Bezemer & Jones, 1998; Ayres & Lombardero, 2000; Niemela *et al.*, 2001). Future modeling and empirical studies should examine the extent to which changes in herbivory patterns as a result of these factors, singly and in combination, might affect ecosystems. In addition, in order to assess the relevance of these modeled results to 'real world' situations, additional empirical studies on N deposition and herbivory at the individual, population, community, and ecosystem levels are required.

Acknowledgments

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