

Species Diversity Across Nutrient Gradients: An Analysis of Resource Competition in Model Ecosystems

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ABSTRACT

The capture and efficient use of limiting resources influence the competitive success of individual plant species as well as species diversity across resource gradients. In simulations, efficient nutrient acquisition or nutrient retention by species were key predictors of success when nutrients were limiting. Increased nutrient supply favored species with characteristics that improved light interception or light use. Ecological theory suggests that low diversity on fertile sites may be a consequence of competitive exclusion by one or a few species with superior light-interception characteristics. On infertile sites, competitive exclusion may be a function of superior nutrient-acquisition characteristics in species. At intermediate fertility, a shift from single-resource specialization to a balanced effort in the acquisition of multiple resources should allow for greater species diversity. Thus, a unimodal relationship between diversity and nutrient

supply, vegetation biomass, or productivity is predicted. However, simulations demonstrated alternate relationships depending on the ecosystem characteristic to which diversity was compared. Diversity was greatest at intermediate total biomass but increased monotonically with net primary production and nitrogen (N) supply. The highest diversity occurred midrange on a scale of community-level leaf area to fine-root length ratios, which in the context of the model indicates that the vegetation as a whole was simultaneously limited by both N and light and that effort toward the acquisition of both resources is distributed in such a way that both resources are equally exploited. Diversity was lowered by the presence of species with a superior ability to sequester resources.

Key words: diversity; competition; nutrient use; light use; biogeochemical model.

INTRODUCTION

In this article, we explore how the functional characteristics of plant species can affect competitive success across a nutrient supply gradient. We demonstrate that the highest species diversity occurs where there is a high degree of complementarity in resource specialization among coexisting species. We apply a biogeochemical model that accommodates multiple competing species and couples ele-

ments cycling between plants and soil, and is therefore influenced by feedbacks consequent to changes in community composition. Our goal is to examine some earlier proposed relationships between plant species diversity and a few key ecosystem characteristics.

Competition as used here refers exclusively to the capture of resources, defined as “the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space” (Grime 1973a). *Competitive success* means survival and *competitive exclusion* means local extinction.

Competition has been invoked as a mechanism

Received 6 September 2002; accepted 20 March 2003; published online 2 April 2004.

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driving successional replacements of species and relationships between species diversity, biomass, and productivity (Connell and Orias 1964; Grime 1973b, 1979; Connell and Slatyer 1977; Tilman 1982, 1990; Rosenzweig and Abramski 1993; Huston 1994; Abrams 1995). Nutrient requirements and mechanisms of nutrient acquisition drive competition when nutrient supply rate is low, leading to communities composed of species that are effective in nutrient acquisition or tolerant of low nutrient supply (Reader and others 1994; Guo and Berry 1998). Biomass and productivity increase with nutrient supply rate, causing competition to shift from belowground resources to aboveground resources and placing greater importance on mechanisms that improve light interception and light-use efficiency (Olf and others 1993; Grace 1993; Wilson and Tilman 1995). Consequently, it is possible for one or a few species to cause local extinctions at either end of a nutrient supply gradient (Margalef 1963; Huston and DeAngelis 1994; Abrams 1995).

Early observations suggest that the number of species increases monotonically with either productivity or biomass [for example, see Darwin (1872) and Preston (1962)]. The concept is supported by hypotheses equating energy flow rate through ecosystems with the number of species serving as energy conduits (MacArthur 1955; Elton 1958). Because the number of species for which resources are above some minimum requirement increases with resource supply, and because productivity, an indicator of energy flow, is also positively correlated with resource supply, diversity should increase with productivity (Schoener 1976; Abrams 1988).

Alternatively, Grime (1973b, 1979) and Al-Mufti and colleagues (1977) proposed a unimodal model describing the relationship between species diversity and biomass (including necromass). The unimodal model involves multiple resources and is particularly useful when considering trade-offs between mechanisms for aboveground and belowground resource acquisition across gradients of resource supply. With the assumption that biomass is positively correlated with resource supply, the unimodal model suggests that a superior competitor for belowground resources (for example, nutrients or water) can limit diversity when belowground resources are limiting, and that a superior competitor for aboveground resources (for instance, light) can limit diversity when belowground resources are not limiting. *Tolerance*, the ability to survive growth-limiting conditions (that is, stress), may also influence diversity (Grime 1979). Others have elaborated on mechanisms of the unimodal model, but a universal relationship remains in dispute (Rosenz-

weig 1992; Tilman and Pacala 1993; Huston and DeAngelis 1994; Gough and others 1994; Abrams 1995; Tilman 1997; Grace 1999; Waide and others 1999).

Despite this large volume of literature devoted to relationships between species diversity or richness and habitat productivity or fertility, theory and observation are mixed (Mittelbach and others 2001). We suspect that explicit attention to the light–nutrient and aboveground–belowground trade-offs may provide insight into the different findings from these studies.

In this article, we use the multiple-element limitation (MEL) model (Rastetter and Shaver 1992; Rastetter and others 1997) to explore functional characteristics of species that can affect competition for nutrients and light across a nitrogen (N) deposition gradient, and the consequences of competition on species diversity. For this purpose, the model has been modified to partition vegetation among multiple species competing for the same resources (Herbert and others 1999). Because MEL couples plant and soil nutrient pools, changes in litter quality consequent to shifts in species dominance produce feedbacks on decomposition, N mineralization, and element leaching from the soil. In turn, those feedbacks can drive further shifts in nutrient supply and species composition (Herbert and others 1999).

Resource heterogeneity on spatial or temporal scales can also affect species diversity (Tilman and Pacala 1993; Huston and DeAngelis 1994; Abrams 1995; Zobel and Liira 1997; Mittelbach and others 2001). However, in the present analyses, we examine discrete points across the N deposition gradient, each representing a spatially and temporally homogeneous environment. This approach restricts interpretation to the interactions of species on the sole basis of their functional characteristics.

THE MULTIPLE-ELEMENT LIMITATION MODEL

The MEL model was originally derived to examine constraints on plant growth associated with two limiting elements (Rastetter and Shaver 1992). A later modification includes element recycling within the ecosystem through detrital pools (Rastetter and others 1997). Inputs to detrital pools are made via litter deposition and microbial uptake of inorganic N, whereas losses occur through leaching and mineralization (Figure 1). Microorganisms consume organic carbon (C) and N at rates proportional to detrital C and N abundance, and the rate of organic matter mineralization depends on total mi-

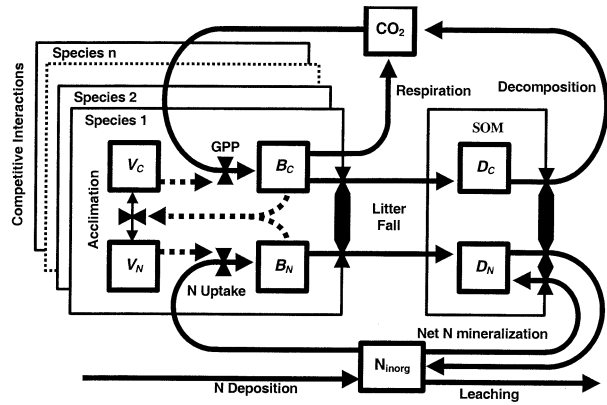


Figure 1. The multiple-element limitation (MEL) model applied to carbon (C) and nitrogen (N) cycles in a terrestrial ecosystem. As presented, the C and N in biomass (B_C and B_N) and the effort expended toward the uptake of C and N (V_C and V_N) are represented for multiple species. The elements are cycled among vegetation, soil organic matter (SOM), and inorganic pools (N_{inorg}) and are linked through the vegetation and microbial processes. Solid arrows indicate material fluxes, and dotted arrows indicate the transfer of information used to calculate those fluxes. CO_2 , carbon dioxide; and GPP, gross primary production.

crobal consumption and a microbial efficiency. Adjustments in the rate of inorganic N uptake by microorganisms (that is, N immobilization) compensate for shortfalls in the organic N supply (Rastetter and others 1997).

A key feature of the model is that vegetation acclimates to changes in the availability of two resources, C and N in this case, by continuously adjusting effort expended toward their acquisition [V_C and V_N (Appendix 1)]. Effort in this sense represents the sum of all internal resources allocated toward the acquisition of external resources, but is assumed strongly correlated with leaf area (S_C) and fine-root length (S_N). Acclimation is the redistribution of acquisition effort, meant to represent all compensatory responses of vegetation to nutritional imbalance with the end result of resource optimization (Bloom and others 1985; Rastetter and others 2001). In the model, continuous adjustments in the distribution of effort drive plant C–N ratios toward an optimum (Eqs. 6, 7, and 17 in Appendix 1) that is assumed to be set by genetic constraints and changes only with allometry (Eqs. 8 and 9). Resource acquisition effort is constrained by the requirement that V_C and V_N sum to 1; thus, V_C and V_N represent the fraction of effort expended toward the uptake of C and N, respectively (Rastetter and Shaver 1997). Total effort increases as the

amount of active biomass (B_A) increases, which is then partitioned into leaf and root biomass based on V_C and V_N , respectively (Eqs. 8, 10, and 11).

A recent modification pertinent to the present examination incorporates interactions among multiple species competing for N and light (Herbert and others 1999). Here we briefly describe those changes.

An allometric equation (Eq. 8) accounts for stand-level changes in resource-acquiring tissues of species with changes in total stand biomass (for example, change in allometry with canopy closure). The equation accounts for a broad range of allometric patterns, including effects of interspecific and intraspecific competition; for example, the allometry of solitary trees (vertically even leaf distribution and high leaf to stem ratio) compared to that of trees in forests or plantations (vertically restricted leaf distribution and low leaf to stem ratio).

Photosynthetic and N uptake equations (Eqs. 12 and 13) account for interspecific and intraspecific resource competition and are based on a probabilistic representation of resource acquisition analogous to that used in the derivation of the Beer–Lambert law (Monsi and Saeki 1953). Thus, photosynthesis and N uptake are proportional to the fraction of light intercepted by the canopy and the fraction of soil volume exploited by fine roots, respectively. As leaves fill the canopy or fine roots extend into unexploited regions of the soil, there is a diminishing return on the increase in uptake per unit leaf or root added. The light-interception extinction coefficient (k_l) is the same as the Beer–Lambert extinction coefficient. An analogous coefficient for soil exploitation (k_s) defines the effectiveness of fine roots exploring a heterogeneous soil N environment from fertile patches to increasingly infertile and marginal areas.

Intercepted light or exploited soil volume is partitioned among n species based on a canopy-dominance or soil-dominance parameter for each species (f_{Ci} and f_{Ni} , respectively). If the leaf area of species i is entirely above the leaf area of all other species, then the fraction of incident light absorbed by species i is

$$(1 - e^{-K_l S_{Ci}}) e^{K_l (S_{Cj} - S_{Ci})} = \frac{(1 - e^{-K_l S_{Ci}})}{e^{-K_l S_{Ci}}} \prod_{j=1}^n e^{-K_l S_{Cj}}$$

The formulation in Eq. 12a (Appendix 1) allows partitioning of light between these two extremes, with the relative dominance of species i being evaluated against each of the other species individually. Thus, if $f_{Ci} \gg f_{Cj}$, then species i will outtop species j ; and, if $f_{Cj} \gg f_{Ci}$, then species j will outtop species

Table 1. Plant N Acquisition, Light Interception, N-use and Light-use Parameter Limits.

Parameter	Description	Units	Minimum	Maximum
k_{Ni}	Half saturation constant for N uptake	g N m ⁻²	0.1	1
g_{Ni}	Maximum N uptake rate per unit ground area	g N m ⁻² y ⁻¹	26	42
g_{Ci}	Light-use efficiency	g C GJ ⁻¹	152	226
m_{Ai}	Active-tissue turnover rate	y ⁻¹	0.3	1
q_{Ai}	Litter C:N ratio of active-tissue	g C g ⁻¹ N	30	55
$c_{ii}(f_{Ci})$	Allometry; active tissue vs. woody tissues and canopy dominance ($f_{Ci} = 0.58/C_{ii}$)	no units	0.1 (5.8)	1 (0.58)
q_{Ni}/k_{Ni}	N uptake efficiency	year ⁻¹	29	304
q_{Ai}/m_{Ai} q_{mini}	N retention (q_{mini} = active tissue C:N and is not varied)	years	1.4	7.8

i. The equations for root competition are derived in an analogous way.

MODEL PARAMETERIZATION

In this exercise, it was essential that the model ecosystem have the potential to accumulate enough biomass to become limited by nutrients and/or light. To meet this requirement, a model ecosystem was constructed approximating the C and N pools and fluxes measured in an eastern North American deciduous forest [Appendix 2 (Rastetter and others 2001)]. This high-biomass ecosystem was selected because N is known to be a limiting resource and because light can become a limiting resource as the canopy closes.

Our analysis was based on 40 simulated communities in which five species competed for N and light at ten N deposition rates (400 simulations total). In each community, six functional characteristics were selected for each of the five species from a uniform-random distribution on either side of the parameter values for a standard species (Table 1). The parameters for this standard species were set by assuming a monospecific stand at steady state and calibrating the model to the aggregate characteristics of the mature stand (Appendix 2). The parameters differentiating the six functional characteristics were selected from realistic ranges and are described in detail next.

Parameters Affecting Nitrogen Acquisition and Light Interception

Nitrogen acquisition is affected by the half-saturation constant for N uptake (k_{Ni}) and the maximum N uptake rate per unit root length (g_{Ni}). The rate of N uptake increases with g_{Ni} and small k_{Ni} enables effective N acquisition at low N concentration. The efficiency of N uptake at low N supply is defined by

the quotient g_{Ni}/k_{Ni} , with a larger quotient defining greater efficiency.

Leaf mass and fine-root mass are collectively the active tissues (B_{Ai}). Allometry of active tissue relative to total plant mass (B_{Ci}) affects both N acquisition and light interception; the allometric parameter (c_{ii}) defines the $B_{Ai}-B_{Ci}$ ratio at low biomass ($0 < c_{ii} < 1$). If c_{ii} is small, then B_{Ai} slowly approaches B_{Amaxi} in a manner similar to the growth of trees, which must produce structural tissues to support the vertical display of leaf area before acquiring maximum leaf area. If C_{ii} is large, then B_{Ai} approaches B_{Amaxi} when B_{Ci} is still relatively small, similar to the growth of herbaceous plants. In the same manner, c_{ji} defines the effect of other species in the community on a species' allometry. In our simulations, $c_{ji} = c_{ij}$, which means that the allometry of species *i* is affected equally by interspecific and intraspecific shading and fine-root interactions.

Parameters for canopy dominance (f_{Ci}) and allometry (c_{ii}) define species architecture. These two parameters were correlated based on the assumption that both small c_{ii} and large f_{Ci} best define the allometry of tall species and that a tall species can display part or all of its leaf area above a shorter species. To account for this correlation, c_{ii} was selected as a uniform-random variable between 0.1 and 1, and f_{Ci} was set to $0.58/c_{ii}$. This nonuniform distribution for f_{Ci} was imposed to be consistent with the proportionally small number of species that can be described as canopy emergent. The range in Table 1 includes architectural forms from understory species with minimal structural tissue to canopy emergent species.

Parameters Affecting Nitrogen Use and Light Use

At steady state, N-use efficiency equals one divided by the N concentration of the total litter (Vitousek

1982). Two parameters were varied to affect N-use efficiency: q_{Ai} , the C–N ratio of litter from active biomass, and m_{Ai} , the turnover rate of active biomass. The value of q_{Ai} affects N-use efficiency directly because it determines the N concentration of litter from active tissues. The value of m_{Ai} has an indirect effect on N-use efficiency because it affects the ratio of woody-tissue (high C–N) versus active-tissue (low C–N) litter. As m_{Ai} increases in magnitude, N-use efficiency declines toward q_{Ai} .

The plant C-uptake parameter (g_{Ci}) defines a maximum potential light-use efficiency. The actual light-use efficiency approaches this maximum as carbon dioxide (CO_2) concentration (E_C) increases. Because we keep E_C constant and k_C , the CO_2 half-saturation constant, the same for all species, the among-species differences in light-use efficiency are proportional to the differences among their g_{Ci} values.

SIMULATIONS

Simulations were designed to examine how plant diversity might change as a result of interactions among species functional characteristics and N supply rate. Two hundred variants of the standard (unmodified) species were defined by random assignment of the seven previously discussed parameters (affecting N acquisition, N use, light interception, and light use) within the ranges described in Table 1. The method of random assignment allows for all possible combinations of functional characteristics that impart competitive ability for N or light (or the lack thereof) to be represented in species. Random assignment of the 200 species, without replacement, was used to define 40 communities consisting of five species each.

Inorganic N supply rate was controlled by a constant N deposition rate, and simulations with each model ecosystem were run to steady state at each of ten rates: 0.005, 0.0075, 0.01, 0.02, 0.05, 0.075, 0.1, 0.2, 0.5, and 1.0 g N m⁻² y⁻¹. This range encompasses measured rates from a broad sampling of ecosystems, including Chilean temperate mixed forest with less than 0.01 g m⁻² y⁻¹ (Hedin and others 1995), arctic Alaskan tundra with approximately 0.06 g m⁻² y⁻¹ (Giblin and others 1991), tropical Amazon rainforest with approximately 0.25 g m⁻² y⁻¹ (Lesack and Melack 1991), and temperate North American eastern deciduous forest with 1.0 g m⁻² y⁻¹ or more (Lovett and others 2000).

In all simulations, atmospheric CO_2 and incident radiation were assumed constant at 350 ppmv and

2.5 GJ m⁻² y⁻¹, respectively. Temperature and other environmental conditions were also assumed constant. These assumptions of constant environmental conditions preclude environmental feedback effects—for example, the effect of light extinction by plant canopies on soil temperature and moisture, which feedback on microbial populations, diversity, and activity, and therefore nutrient supply rates via mineralization.

Initial vegetation mass of a community was set to 100 g C m⁻² per species (less than 3% of vegetation mass in the calibrated system) with C–N ratio = 80. Simulations were run until a new steady state was attained at each of the ten N deposition rates. Steady state was inferred from stable mass of surviving species and an ecosystem N loss rate equal to deposition.

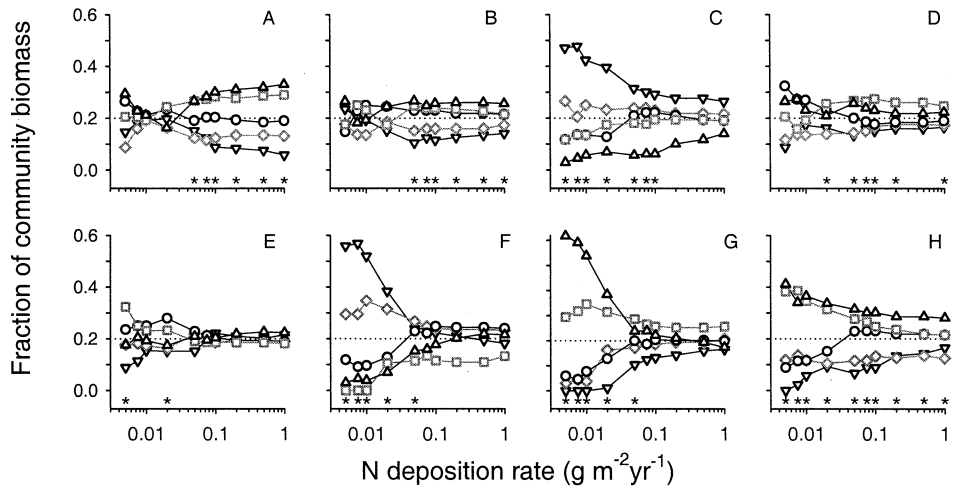
RESULTS AND ANALYSES

Competitive Success Depends on Nutrient Availability

Results were analyzed to assess which functional characteristics imparted a competitive advantage at each point on the fertility gradient. Species that went extinct at a particular N deposition rate were removed from the analysis at that N rate to avoid confounding the results with coincident co-occurrences of one characteristic with other detrimental characteristics. All 200 species (40 communities × 5 species each) were ranked for each functional characteristic, from low to high, based on parameter values defining the characteristic. This ranking was used to partition species into five classes with equal numbers. The fraction of community biomass for species in each class was averaged and plotted against N deposition (Figure 2). One-way analysis of variance (ANOVA) was used to determine whether there were differences among classes at each N deposition rate.

The analysis provides evidence that characteristics enhancing N uptake, N retention, and N use were advantageous when N deposition rates were low. Mass and leaf area increased with N deposition, shifting competitive success onto characteristics that improved light interception. Thus, the importance of different functional characteristics changed with N deposition rate.

Leaf display high in the canopy (large f_{Ci}) proved advantageous when high N deposition reduced belowground competition, increased leaf area, and thereby limited light interception by understory species [$P < 0.05$ (Figure 2A)]. The advantage was



Parameter class	A		B	C	D	E	F	G	H
	c_{ij}	f_{ci}	g_{Ci}	m_{Ai}	q_{Ai}	g_{Ni}	k_{Ni}	g_{Ni}/k_{Ni}	$q_{Ai}/m_{Ai}q_{mini}$
1 ∇	0.86 - 1.0	0.58 - 0.67	152 - 169	0.30 - 0.44	30.0 - 34.9	26.0 - 29.6	0.10 - 0.27	28.6 - 41.7	1.45 - 2.24
2 \diamond	0.67 - 0.86	0.68 - 0.88	170 - 184	0.45 - 0.57	35.0 - 39.0	29.7 - 32.8	0.28 - 0.47	41.8 - 50.7	2.25 - 2.76
3 \circ	0.52 - 0.66	0.89 - 1.15	185 - 198	0.58 - 0.69	39.1 - 44.1	32.9 - 35.7	0.48 - 0.64	50.8 - 73.7	2.77 - 3.39
4 \square	0.34 - 0.51	1.16 - 1.72	199 - 211	0.70 - 0.83	44.2 - 50.3	35.8 - 38.7	0.65 - 0.87	73.8 - 130	3.40 - 4.51
5 \triangle	0.10 - 0.33	1.73 - 5.80	212 - 226	0.84 - 1.00	50.4 - 55.0	38.8 - 42.0	0.88 - 1.00	131 - 304	4.52 - 7.85

eliminated at N deposition less than $0.04 \text{ g m}^{-2} \text{ y}^{-1}$, but tended to reappear below $0.01 \text{ g N m}^{-2} \text{ y}^{-1}$ (although $P > 0.05$ at this low end of the gradient). An advantage at the lowest N supply rate was because of low N requirements per unit mass in wood versus herbaceous tissue (that is, high nutrient-use efficiency in woody plants). The active-tissue allometry (c_{ij}) associated with a potentially tall species requires relatively large amounts of structural tissue when total plant mass is small (for example, dwarf shrubs); therefore, plants generally have a high C–N ratio.

Light-use efficiency (g_{Ci}) improved success when N deposition was $0.05 \text{ g m}^{-2} \text{ y}^{-1}$ or more (Figure 2B). Lower N deposition rates were insufficient for canopy closure in most cases. Increased vegetation mass and leaf area at high N supply resulted in a diminished understory light environment that improved the success of understory species having high light-use efficiency.

Low production rates of fine litter (small m_{Ai}) increase N retention time and decrease annual N requirements, thereby increasing the success of species competing for N (Figure 2C). A high litter C–N ratio (q_{Ai}) also increases N retention time and decreases annual N requirements, but in this analysis there was no clear influence of litter C–N ratio on success (Figure 2D). This lack of a significant influ-

ence of q_{Ai} is the result of its interaction with m_{Ai} in determining N-loss rates in active litter. This N-loss rate is proportional to m_{Ai}/q_{Ai} [Eq. 15 in (Appendix 1)]. Because m_{Ai} varied by a factor of more than 3 and q_{Ai} by less than a factor of 2 in our simulations, the effect of m_{Ai} swamped out the influence of q_{Ai} on the competitive interactions.

Maximum N uptake rate per unit fine-root length (g_{Ni}) had no clear effect on success (Figure 2E). This lack of effect is the result of other parameter influences on total fine-root length (that is, N-absorbing surface area) and an overwhelming influence of the half-saturation constant for N uptake (k_{Ni}), which has a strong influence on a plant's ability to capture soil inorganic N at very low concentrations (Figure 2F). Nitrogen uptake efficiency [g_{Ni}/k_{Ni} (Figure 2G)] and the retention time of N in active tissue [$q_{Ai}/(m_{Ai} q_{mini})$ (Figure 2H)] both had a large influence over species success, especially at low N supply [see also Aerts and Chapin (2000)].

A Trade-off Between Traits for Acquisition and Use of Nutrient and Light

There was a trade-off in the value of functional characteristics affecting resource use and acquisition relative to resource availability. To assess this tradeoff, we regressed the fraction of vegetation

Figure 2. Competitive success indicated by the biomass fraction of individual species in steady-state ecosystems. Each panel depicts the mean biomass fraction relative to one growth characteristic. At each nitrogen (N) deposition rate, the surviving species (of 200 from 40 communities) were pooled and subdivided into five discrete classes ranked from low to high parameter value as 1 to 5, each with equal numbers of species. Deviation of steady-state biomass fraction from 0.2 (dotted reference line) indicates an effect. A significant effect is indicated by the asterisk above the x-axis [one-way analysis of variance (ANOVA), $P < 0.05$]. Parameter units are in Table 1.

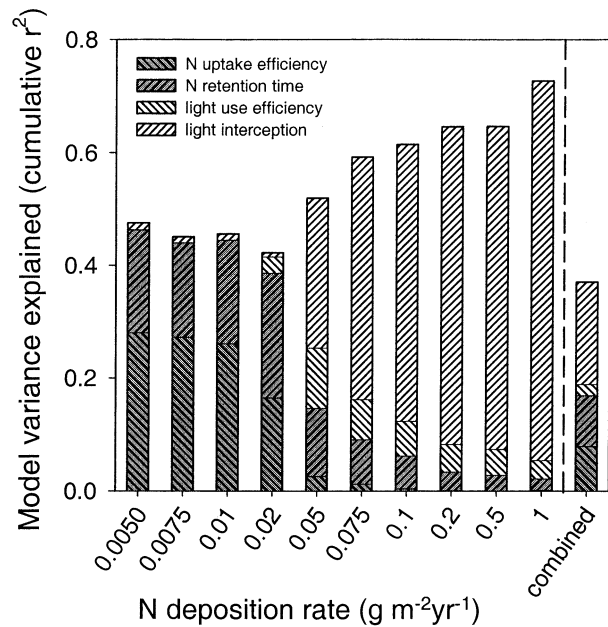


Figure 3. Trade-offs in the importance of functional characteristics affecting acquisition and use of nutrients and light with increasing nitrogen (N) deposition. Bars represent cumulative r^2 in stepwise regressions in which the sequence of independent variables added (functional characteristics) were determined by best model approach as described in text.

biomass in a species against growth characteristics represented by a range of values derived from four combinations of parameters: (a) N uptake efficiency (g_{Ni}/k_{Ni}), (b) active-tissue N retention time [$q_{Ai}/(m_{Ai}q_{mini})$], (c) light-use efficiency (g_{Ci}), and (d) light-interception capacity (represented by the co-varying parameters c_{ii} and f_{Ci}). Stepwise regression with forward selection and backward elimination procedures validated by adjusted r^2 and the Mallows C_p statistic was used to determine the best model (Sokal and Rohlf 1980). Regressions were calculated for the combined pool of 200 species at each N deposition rate.

At low N deposition rates, N uptake efficiency and active-tissue N retention time explained 40%–50% of the variance in species biomass fraction, whereas light-interception capacity and light-use efficiency explained less than 5% of the variance (Figure 3). The pattern was reversed with high N deposition, where 60%–70% of the variance was explained by light-interception capacity and light-use efficiency. These results logically follow extensive analyses elsewhere, both theoretical and empirical (Chapin 1980; Bloom and others 1985; Aerts and Chapin 2000).

Alternate Diversity Patterns for Nitrogen Supply, Net Primary Production, and Biomass Gradients

The Shannon–Wiener index, H' , as applied in community ecology, has been used as a measure of species diversity that incorporates evenness of biomass distribution among species [see Magurran (1988)]. By definition,

$$H' = \sum_{i=1}^n (p_i)(\log_2 p_i)$$

where H' is diversity, n is the number of species, p_i is the fraction of total biomass belonging to species i , and $\log_2 p_i$ is the base 2 log of that fraction. As an ecological measure, we use H' to describe the distribution of biomass among species and how that distribution changes as N deposition increases. In our simulations, H' varies from 0 for monocultures to 2.32 for a community of five equally represented species.

Patterns of diversity across the N deposition gradient differed depending upon the ecosystem characteristic used in quantifying fertility (Table 2). Generally, species richness (the number of species present) and H' increased monotonically if N supply or net primary production (NPP) was used as the indicator of site fertility, but unimodal distributions were not rare. If biomass was used as the indicator, then unimodal distributions became apparent in half of the communities.

The results from the 40 communities were pooled to establish relationships between productivity and diversity relative to N supply in the broadest range of the simulations. A general pattern emerged in which biomass, NPP, species richness, and H' increased with N supply (Figure 4). Species richness and H' increased with NPP, but there was a unimodal relationship with biomass (Figure 5). The unimodal pattern arises because of the rarity of species with the ability to survive at very low N supply, the positive relationship between biomass and N supply, and the likelihood that superior light competitors will exclude species at high N supply.

High Diversity Occurs When Resource Acquisition Effort Is Balanced

A unimodal diversity pattern relative to the aggregated vegetation leaf area to fine-root length ratio provides additional insight into mechanisms controlling species diversity across resource gradients (Figure 6A and B). Low leaf area to root length ratios occur when N is highly limiting, suggesting

Table 2. Patterns of Species Richness and Shannon-Weiner H'

Ecosystem characteristic	Strong unimodal		Weak unimodal		Monotonic		Other	
	richness	H'	richness	H'	richness	H'	richness	H'
Biomass	7	9	17	11	12	15	4	5
NPP	3	5	5	7	23	25	9	3
N deposition	0	3	4	3	35	33	1	1
Gross N mineralization	0	3	4	3	35	33	1	1
Net N mineralization	4	4	2	3	28	27	6	6

Results represented in the 40 simulated communities relative to nutrient supply, community biomass, and NPP. Across gradients of ecosystem characteristics the strong unimodal pattern was defined by a greater than 50% decline from peak richness or H' . The weak unimodal pattern was defined by a 30% to 50% decline from peak richness or H' . A richness or H' pattern that declined <30% from peak was defined as monotonic. Patterns with multiple peaks or no change in richness or H' were classified as "other." Values represent the number of simulated communities falling into each category.

that the vegetation is investing a greater amount of effort (allocation of internal resources) into the acquisition of N. The reverse is true with an essentially unlimited N supply, and effort is allocated toward light interception. Intermediate leaf area to root length ratios indicate that both N and light limit the community and there is an approximately equal allocation of effort toward the acquisition of both resources. The unimodal diversity pattern is more defined when indices are plotted against the ratio of light intercepted to N uptake by the vegetation (Figure 6C and D). Thus, in these simulations, diversity is greatest where uptake effort is distributed among species in such a way that aboveground and belowground resources are more or less equally exploited and the community is limited by both N and light.

Superior Resource Competitors Reduce Diversity

Diversity (H') was greatest in communities composed of species similar in their ability to exploit available resources. Plotted as a response surface relative to community indices for species similarity in soil volume exploited by roots and light intercepted by leaves, H' declined with increasing dissimilarity (Figure 7). In simulations where species coexisted, similarity in either exploitation of soil resources or interception of light was calculated as a community average Euclidean distance, d_{ij} , as follows:

$$d_{ij} = \frac{\left[\sum_{i=1}^{n-1} \sum_{j=i+1}^n (r_i - r_j)^2 \right]^{1/2}}{\frac{n(n-1)}{2}}$$

where r_i and r_j are the fractions of total resource

acquired by species i and j , and n is the number of species in the community. Equations 12 and 13 (Appendix 1) were used to calculate the fraction of light intercepted and fraction of soil volume exploited. A similarity index value (d_{ij}) near 0 indicates that species in the community were similar in their ability to acquire the resource in question, whereas values approaching 1 indicate increasing dissimilarity caused by one or more species acquiring a large share of the resource. Therefore, H' decreased when communities contained a species with superior ability to sequester light or soil resources (high d_{ij}) because of deleterious effects on resource acquisition by other species.

DISCUSSION

Our model is in general agreement with current fertility diversity theories. Our contributions are (a) an assessment of the relative importance of several functional characteristics on competitive ability relative to N supply rate, (b) mechanistic evidence that patterns of diversity may differ depending on the fertility index applied (N deposition, NPP, or biomass), and (c) a demonstration that the highest diversity is realized when potentially limiting external resources are equally exploited by the community as a whole.

Functional characteristics that improved N uptake efficiency or lengthened N retention time diminished in importance as N deposition increased, whereas characteristics that improved light-interception or light-use efficiency increased in importance. Thus, the model illustrates a trade-off in the importance of functional characteristics to competitive success across a resource gradient and demonstrates transitions from species that are effective in N acquisition or efficient in N use to species that are

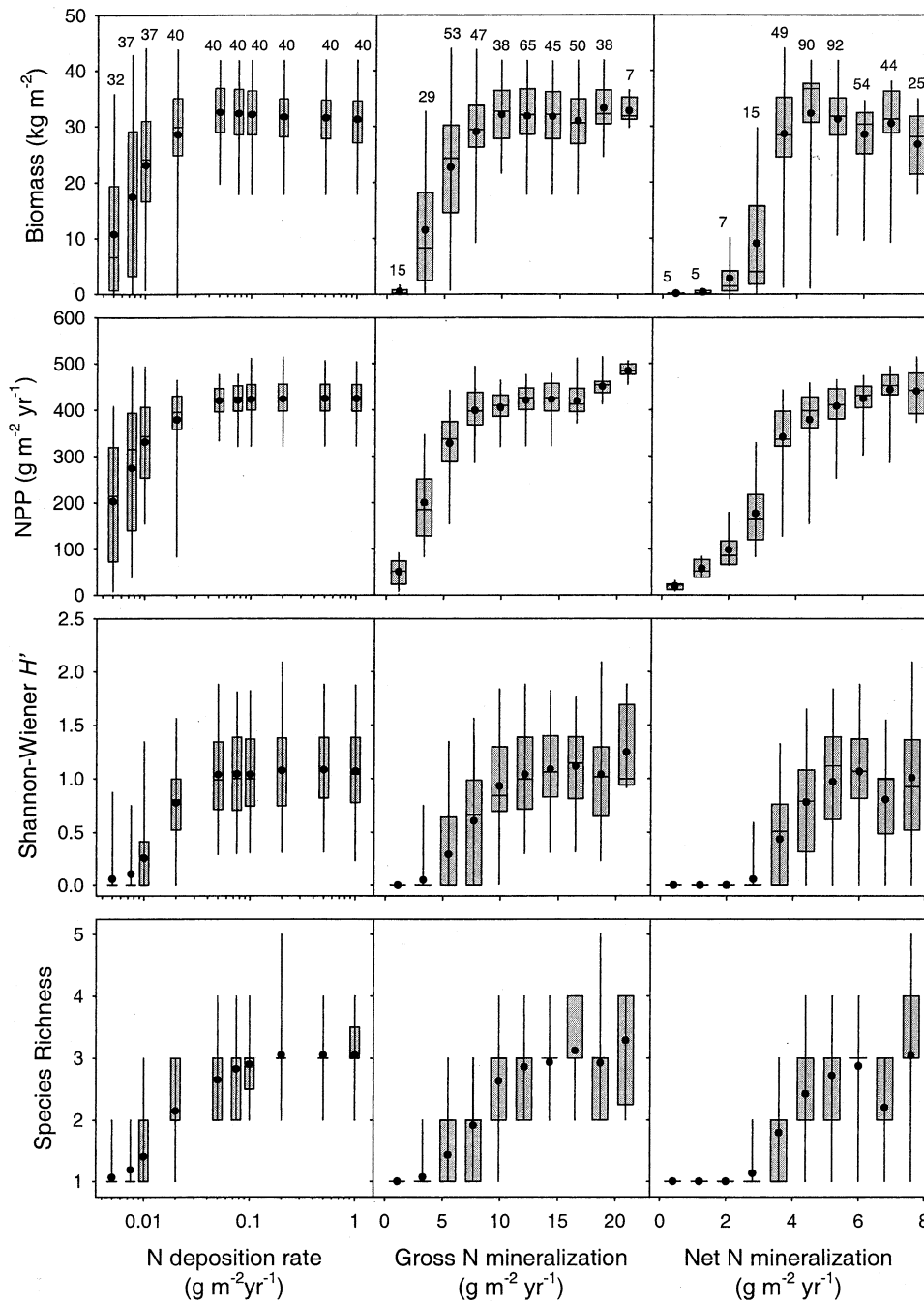


Figure 4. Biomass, net primary production (NPP), Shannon–Wiener index (H'), and species richness relative to three nitrogen (N) availability indices. H' is 0 for a monoculture and is 2.32 for a community of five equally represented species. Box plots are defined as follows: vertical lines indicate the range of observations, horizontal lines indicate the median observation, boxes encompass the 25th and 75th percentile observation, and filled bullets are means. Values at the top box plots (top figures) indicate the number of simulations represented by the independent variable.

effective in light interception or efficient in light use (Tilman 1982, 1990; Aerts 1990; Wilson and Tilman 1991; Aerts and Chapin 2000).

Competition coupled with a trade-off in resource use has been invoked as a mechanism explaining unimodal species diversity relationships when resources are spatially or temporally homogeneous (Tilman 1982, 1990; Huston and DeAngelis 1994; Abrams 1995). Our results support this trade-off mechanism. Diversity increased with N availability

because of the increase in the number of species having their minimum N requirements satisfied and because of relief from N competition [see also Schoener (1976), Tilman (1982), Abrams (1988), and Tilman and Pacala (1993)]. Light competition increased with N availability because of increased biomass, NPP, and leaf area. Consequently, greater success by the effective light competitors could exclude other species and thereby cause the unimodal pattern.

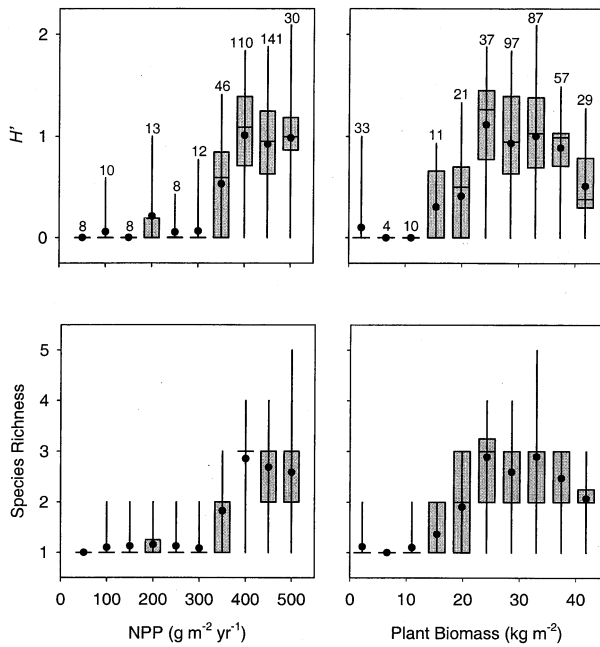


Figure 5. Shannon–Wiener index (H') and species richness relative to net primary production (NPP) and biomass. Box plots are defined in Figure 4. Values at the top box plots (top figures) indicate the number of simulations represented by the independent variable.

Empirical analyses have often used biomass or productivity as indices for underlying patterns of resource availability in plant communities. However, our simulations illustrate that diversity patterns associated with nutrient availability, biomass, or NPP are not necessarily equivalent [see also Grace (1999)]. We found two distinctly different species diversity patterns within the same sets of simulations, depending on the ecosystem characteristic used as the index of fertility. Species diversity usually increased monotonically with increased N supply rate, and an envelope with a monotonically increasing upper limit encompassed all simulations [see also Marrs and others (1996)]. Monotonic diversity–N supply relationships support the earliest observations and hypotheses concerning productivity or energy flow and numbers of species receiving their minimum resource requirements (Darwin 1872; MacArthur 1955; Elton 1958; Preston 1962; Currie 1991). Although unimodal diversity–NPP relationships were not rare in our simulations, we found that unimodal diversity–biomass relationships were in fact common, and that there was a strongly unimodal envelope encompassing diversity–biomass relationships in all simulations. Unimodal patterns support later hypotheses and observations associated with community biomass,

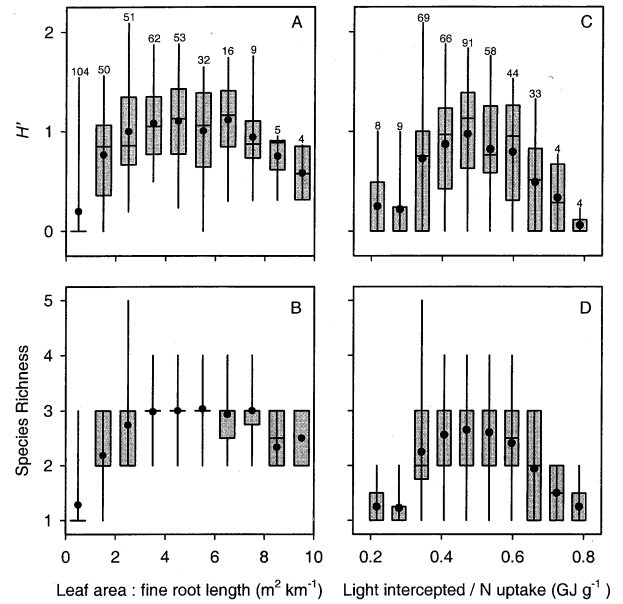


Figure 6. Shannon–Wiener index (H') and species richness relative to (A and B) the ratio of community leaf area to fine-root length, and (C and D) the quotient of light intercepted and nitrogen (N) uptake by the community as a whole. The quotient represents the balance of effort allocated to the acquisition of aboveground and belowground resources in the community. Box plots are defined in Figure 4. Values at the top box plots (top figures) indicate the number of simulations represented by the independent variable.

complementary resource use by multiple species, and the presence of tolerant or competitively superior species (Grime 1973, 1979; Al-Mufti and others 1977).

The identification of multiple diversity patterns within any given data set has important implications for the interpretation of results from past and ongoing empirical studies. Conflicting results from earlier studies may be a consequence of fitting observed patterns to inappropriate mechanisms, or the use of surrogate data such as biomass or productivity as interchangeable indices of resource availability. Alternatively, experimental design may not incorporate enough data relevant to the measurement of resource acquisition and the balance of resource use in plant communities. Clearly, a more unified understanding of mechanisms relevant to the controls over species diversity in ecosystems must be a priority in the design and interpretation of future and ongoing empirical studies.

Low diversity in a high-biomass system was not directly associated with N availability. Rather, the pattern was defined by the allocation of effort toward resource acquisition by species within the

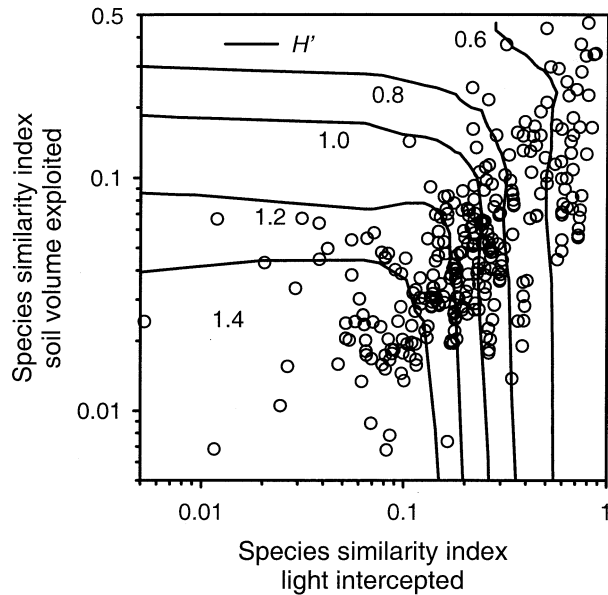


Figure 7. Shannon–Wiener index (H') (contour lines) relative to community-level indices for species similarity in soil volume exploited by roots and light intercepted by leaves. A small index value indicates high similarity among species for acquisition of a resource. Values next to contour lines indicate average H' . Symbols indicate communities having species coexistence.

community as a whole (illustrated by leaf area to fine-root length ratio), suggesting that the greatest diversity can occur when all resources are fully exploited. Therefore, diversity is not necessarily a function of nutrient availability, productivity, or biomass. Instead, low diversity in high-biomass systems is a function of the rarity of species that can fully exploit aboveground and/or belowground resources to the exclusion of other species, both in our random assemblages and in the evolutionary selection of traits in nature. Diversity at high biomass will be lower if these competitively dominant species are present and limiting resources are sequestered. Thus, a process analogous to that used to explain low diversity at the low end of the fertility gradient causes low diversity at the high end of the fertility gradient—specifically, the chance occurrence of species with the ability to exploit extreme environmental ranges. Unique to the low-fertility case is the chance occurrence of species that can survive abiotic extremes and are likely the greatest contributors to low diversity when resources are scarce.

Our results differ markedly from similar multi-species modeling exercises—specifically those that assume that soil solution element concentration

can be reduced by an equilibrational monoculture to a level that ultimately excludes all competition for that element, R^* (Tilman 1987, 1990). In our analyses, CO_2 is a nondepletable resource and therefore R^* does not apply (Rastetter and Shaver 1992). Also, it has been demonstrated that R^* does not apply to light (Tilman 1990; Tilman and Wedin 1991; Wedin and Tilman 1993). This leaves N as the single resource to which R^* might pertain, and the R^* model predicts one species per limiting resource at steady state (one niche, one species). However, multiple species can persist per limiting resource in the R^* model if the resource uptake function is replaced with a nonlinear, concave downward function of biomass (Rastetter and Ågren 2002). An uptake function of this form would be expected, for example, if there were a diminishing return on biomass allocation to resource acquisition. The uptake function in our model is of this form and therefore accommodates coexistence of multiple species competing for a single limiting resource.

We have identified several important functional characteristics of plants that affect patterns of diversity across nutrient gradients—specifically, characteristics affecting nutrient acquisition, nutrient use, light interception, and light use. We have demonstrated that if competing species within a community optimize their individual C–N ratios within the constraints of ecosystem C and N mass balances, then diversity is greatest at intermediate levels of total biomass while increasing monotonically with NPP and N supply. These mechanisms and their impacts on diversity patterns should be tested further in future empirical studies. We have also illustrated that a community may exhibit multiple diversity patterns if the community is examined in multiple ways. We therefore recommend that researchers use a uniform approach when comparing and contrasting diversity patterns across multiple ecosystems. Such an approach will best satisfy the test of an hypothesis if it includes identification and verification of underlying resource supply and/or gradients, and differentiation between characteristics of energy flow through vegetation (NPP or N flux in this analysis) and energy storage in biomass.

ACKNOWLEDGEMENTS

National Science Foundation grant DEB95-09613 provided funding support for this research. We thank Bonnie Kwaitkowski for assistance in development of the MEL model and Jim Grace for substantive comments on the manuscript.

Appendix 1. Model Equations, Variables, and Parameters.

$$\frac{dE_N}{dt} = R_{Ne} + R_{Nm} - L_{Ne} - U_{Nm} - U_{Nvi} \quad (1)$$

$$\frac{dB_{Ci}}{dt} = U_{Cvi} - R_{Cvi} - L_{Cvi} \quad (2)$$

$$\frac{dB_{Ni}}{dt} = U_{Nvi} - L_{Nvi} \quad (3)$$

$$\frac{dD_C}{dt} = L_{Cvi} - R_{Cm} - L_{CD} \quad (4)$$

$$\frac{dD_N}{dt} = L_{Nvi} + U_{Nm} - R_{Nm} - L_{ND} \quad (5)$$

$$\frac{dV_{Ci}}{dt} = -a_i A_i V_{Ci}; \text{ if } A_i \geq 0 = -a_i A_i V_{Ni}; \text{ if } A_i < 0 \quad (6)$$

$$\frac{dV_{Ni}}{dt} = -\frac{dV_{Ci}}{dt} \quad (7)$$

$$B_{Ai} = \frac{B_{Amaxi} c_{ii} B_{Ci}}{B_{Amaxi} + \sum_{j=1}^n c_{ji} B_{Cj}} \quad (8)$$

$$q_i = \frac{B_{Ci} q_{mini} q_{maxi}}{B_{Ai} q_{maxi} + (B_{Ci} - B_{Ai}) q_{mini}} \quad (9)$$

$$S_{Ci} = b_{Ci} V_{Ci} B_{Ai} \quad (10a)$$

$$S_{CT} = \sum_{j=1}^n S_{Cj} \quad (10b)$$

$$S_{Ni} = b_{Ni} V_{Ni} B_{Ai} \quad (11a)$$

$$S_{NT} = \sum_{j=1}^n S_{Nj} \quad (11b)$$

$$w_{Ci} = \frac{2(1 - e^{-k_i S_{Ci}})}{(1 + e^{-k_i S_{Ci}})} \prod_{j=1}^n \left(\frac{f_{Cj} e^{-k_j S_{Cj}} + f_{Ci}}{f_{Ci} + f_{Cj}} \right) \quad (12a)$$

$$U_{Cvi} = \frac{g_{Ci} E_C w_{Ci} I(1 - e^{-k_i S_{Cv}})}{(k_{Ci} + E_C) \sum_{j=1}^n w_{Cj}} \quad (12b)$$

$$w_{Ni} = \frac{2(1 - e^{-k_i S_{Ni}})}{(1 + e^{-k_i S_{Ni}})} \prod_{j=1}^n \left(\frac{f_{Nj} e^{-k_j S_{Nj}} + f_{Ni}}{f_{Ni} + f_{Nj}} \right) \quad (13a)$$

$$U_{Nvi} = \frac{g_{Ni} E_N w_{Ni} (1 - e^{-k_i S_{Nv}})}{(k_{Ni} + E_N) \sum_{j=1}^n w_{Nj}} \quad (13b)$$

$$L_{Cvi} = m_{Ai} B_{Ai} + m_{wi} (B_{Ci} - B_{Ai}) \quad (14)$$

$$L_{Nvi} = \frac{q_i B_{Ni}}{B_{Ci}} \left[\frac{m_{Ai}}{q_{Ai}} B_{Ai} + \frac{m_{wi}}{q_{wi}} (B_{Ci} - B_{Ai}) \right] \quad (15)$$

$$R_{Cvi} = r_{Ai} B_{Ai} + r_{wi} (B_{Ci} - B_{Ai}) \quad (16)$$

$$A_i = \ln \left(\frac{B_{Ci}}{q_i B_{Ni}} \right) + h_i \left(\frac{1}{B_{Ci}} \frac{dB_{Ci}}{dt} - \frac{1}{B_{Ni}} \frac{dB_{Ni}}{dt} \right) \quad (17)$$

$$L_{Ne} = \beta_{Ne} E_N^\gamma \quad (18)$$

$$L_{CD} = \beta_{CD} D_C \quad (19)$$

$$L_{ND} = \frac{\beta_{CD}}{\eta} D_C \quad (20)$$

$$\theta = \frac{\epsilon_N \phi}{\epsilon_C} \quad (21)$$

$$U_{Nm} = \frac{\psi \alpha_N D_C^2 E_N}{\theta D_N (\kappa_{Nm} + E_N)} \quad (22)$$

$$M_N = \psi D_N + U_{Nm} \quad (23)$$

$$\Lambda_C = \frac{\epsilon_C \theta M_N}{\psi D_C + \theta M_N} \quad (24)$$

$$\Lambda_N = \frac{\epsilon_N \psi D_C}{\psi D_C + \theta M_N} \quad (25)$$

$$R_{Cm} = \psi D_C (1 - \Lambda_C) \quad (26)$$

$$R_{Nm} = M_N (1 - \Lambda_N) \quad (27)$$

Table 3.

A_i	acclimation potential
a_i	acclimation rate (y^{-1})
B_{Ai}	active-tissue C in plants ($g\ C\ m^{-2}$)
B_{Amaxi}	maximum B_{Ai} ($g\ C\ m^{-2}$)
B_{Ci}	C in plant biomass ($g\ C\ m^{-2}$)
b_{Ci}	leaf area per unit C ($m^2\ g^{-1}\ C$)
B_{Ni}	N in plant biomass ($g\ N\ m^{-2}$)
b_{Ni}	root length per unit C ($m\ g^{-1}\ C$)
c_{ji}	allometric effect of species j on i
D_C	C in soil detritus ($g\ C\ m^{-2}$)
D_N	N in soil detritus ($g\ N\ m^{-2}$)
E_C	CO ₂ concentration ($ml\ m^{-3}$)
E_N	inorganic N ($g\ N\ m^{-2}$)
f_{Ci}	canopy dominance parameter
f_{Ni}	soil dominance parameter
g_{Ci}	plant C-uptake rate ($g\ C\ m^{-2}\ y^{-1}$)
g_{Ni}	plant N uptake rate ($g\ N\ m^{-2}\ y^{-1}$)
h_i	acclimation damping (y)
I	irradiance ($GJ\ m^{-2}\ y^{-1}$)
k_{Ci}	1/2-saturation for CO ₂ ($ml\ m^{-3}$)
k_I	light extinction ($m^2\ m^{-2}$)
k_{Ni}	plant 1/2-saturation for N ($g\ N\ m^{-2}$)
k_S	soil-resource extinction ($m^2\ m^{-1}$)
L_{CD}	organic-C leaching ($g\ C\ m^{-2}\ y^{-1}$)
L_{Cvi}	litter C production ($g\ C\ m^{-2}\ y^{-1}$)
L_{ND}	organic-N leaching ($g\ N\ m^{-2}\ y^{-1}$)
L_{Ne}	inorganic-N leaching ($g\ N\ m^{-2}\ y^{-1}$)
L_{Nvi}	N in litter production ($g\ N\ m^{-2}\ y^{-1}$)
m_{Ai}	active-tissue-litter loss rate (y^{-1})
m_{Wi}	woody-tissue-litter loss rate (y^{-1})
q_i	plant optimal C:N ($g\ C\ g^{-1}\ N$)
q_{Ai}	active-tissues-litter C:N ($g\ C\ g^{-1}\ N$)
q_{maxi}	maximum plant C:N ($g\ C\ g^{-1}\ N$)

(Continued)

Table 3. (Continued)

q_{mini}	minimum plant C:N ($g\ C\ g^{-1}\ N$)
q_{Wi}	woody-tissue-litter C:N ($g\ C\ g^{-1}\ N$)
r_{Ai}	active-tissue respiration rate (y^{-1})
R_{Cm}	microbial respiration ($g\ C\ m^{-2}\ y^{-1}$)
R_{Cvi}	plant respiration ($g\ C\ m^{-2}\ y^{-1}$)
R_{Ne}	external N supply ($g\ N\ m^{-2}\ y^{-1}$)
R_{Nm}	N mineralization ($g\ N\ m^{-2}\ y^{-1}$)
r_{Wi}	woody-tissue respiration rate (y^{-1})
S_{Ci}	species i leaf area ($m^2\ m^{-2}$)
S_{Ni}	species i root length ($m\ m^{-2}$)
S_{CT}	total leaf area ($m^2\ m^{-2}$)
S_{NT}	total root length ($m\ m^{-2}$)
t	time (y)
U_{Cvi}	gross photosynthesis ($g\ C\ m^{-2}\ y^{-1}$)
U_{Nm}	microbial N uptake ($g\ N\ m^{-2}\ y^{-1}$)
U_{Nvi}	plant N uptake ($g\ N\ m^{-2}\ y^{-1}$)
V_{Ci}	plant C-uptake effort
V_{Ni}	plant N uptake effort
w_{Ci}	canopy scaling factor
w_{Ni}	root scaling factor
α_N	microbial N uptake ($g\ N\ g^{-1}\ C$)
β_{CD}	organic-C loss (y^{-1})
β_{Ne}	inorganic-N loss ($g^{1-\gamma}\ N\ m^{-2+2\gamma}\ y^{-1}$)
γ	inorganic-N loss exponent
ϵ_C	maximum microbial C efficiency
ϵ_N	maximum microbial N efficiency
η	leached organic matter C:N ($g\ C\ g^{-1}\ N$)
θ	C:N microbial consumption ($g\ C\ g^{-1}\ N$)
κ_{Nm}	microbial 1/2-saturation for N ($g\ N\ m^{-2}$)
Λ_C	microbial C efficiency
Λ_N	microbial N efficiency
M_N	microbial N consumption ($g\ N\ m^{-2}\ y^{-1}$)
ϕ	C:N microbial byproducts ($g\ C\ g^{-1}\ N$)
ψ	decomposition rate (y^{-1})

Appendix 2

Table 4. Variables, Fluxes and Parameters used in Defining the Simulation of an Eastern Deciduous Forest.

Term	Definition	Units	Value
Variables			
B_C	plant C	$g\ C\ m^{-2}$	22000
B_N	plant N	$g\ N\ m^{-2}$	110
B_A	active tissue C	$g\ C\ m^{-2}$	340
S_C	leaf area	$m^2\ m^{-2}$	10
S_N	fine root length	$m\ m^{-2}$	5000
b_C	leaf area per g C	$m^2\ g^{-1}\ C$	0.0455
b_N	fine root length per g C	$m\ g^{-1}\ C$	43.0
D_C	C in soil detritus	$g\ C\ m^{-2}$	13000
D_N	N in soil detritus	$g\ N\ m^{-2}$	520
E_C	atmospheric CO ₂	ppmv	350
E_N	soil inorganic N	$g\ N\ m^{-2}$	1.0

(Continued)

Table 4. (Continued)

Term	Definition	Units	Value
Fluxes			
U_{Cv}	gross photosynthesis	$\text{g C m}^{-2} \text{y}^{-1}$	940
U_{Nv}	plant N uptake	$\text{g N m}^{-2} \text{y}^{-1}$	7.5
R_{Cv}	plant respiration	$\text{g C m}^{-2} \text{y}^{-1}$	497
L_{Cv}	litter C loss	$\text{g C m}^{-2} \text{y}^{-1}$	446
L_{Nv}	litter N loss	$\text{g N m}^{-2} \text{y}^{-1}$	7.5
U_{Nm}	microbial N uptake	$\text{g N m}^{-2} \text{y}^{-1}$	7.1
R_{Nm}	N mineralization	$\text{g N m}^{-2} \text{y}^{-1}$	14.6
R_{Cm}	microbial respiration	$\text{g C m}^{-2} \text{y}^{-1}$	446
R_{Ne}	N deposition	$\text{g N m}^{-2} \text{y}^{-1}$	1.0
L_{Ne}	inorganic N leaching	$\text{g N m}^{-2} \text{y}^{-1}$	1.0
Plant Parameters			
m_A	active tissue litter rate	y^{-1}	0.85
m_w	woody tissue litter rate	y^{-1}	0.0074
r_A	active tissue respiration	y^{-1}	2.0
r_w	woody tissue respiration	y^{-1}	0.0148
q	optimal plant C:N	$\text{g C g}^{-1} \text{N}$	196
q_A	active tissue litter C:N	$\text{g C g}^{-1} \text{N}$	42.5
q_w	woody tissue litter C:N	$\text{g C g}^{-1} \text{N}$	225
k_C	1/2 saturation for CO_2	ml m^{-2}	350
k_N	1/2 saturation for N	g N m^{-2}	0.5
B_{Amax}	maximum B_A	g C m^{-2}	350
q_{max}	maximum plant C:N	$\text{g C g}^{-1} \text{N}$	22
q_{min}	minimum plant C:N	$\text{g C g}^{-1} \text{N}$	225
V_C	plant C uptake effort		0.5
V_N	plant N uptake effort		0.5
k_l	light extinction	m m^{-2}	0.5
k_s	soil resource extinction	m m^{-1}	0.00008
Microbial Parameters			
α_N	N uptake	$\text{g N g}^{-1} \text{C}$	0.008
β_{Ne}	N loss	$\text{g}^{1-\gamma} \text{N m}^{-2+\gamma}$	0.0025
ϵ_C	maximum C efficiency		0.60
ϵ_N	maximum N efficiency		0.65
θ	C:N consumption	$\text{g C g}^{-1} \text{N}$	7.765
κ_{Nm}	N 1/2 saturation constant	g N m^{-2}	1
Λ_C	C efficiency		0.1696
Λ_N	N efficiency		0.4642
M_N	N consumption	$\text{g N m}^{-2} \text{y}^{-1}$	27.24
ϕ	C:N	$\text{g C g}^{-1} \text{N}$	8
ψ	decomposition rate	y^{-1}	0.042

Values have been derived from sources detailed in Rastetter and others 2001.

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