

The Effect of Recycling on Plant Competitive Hierarchies

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ABSTRACT: Evidence from field studies suggests that some plant species enhance their persistence by reinforcing patterns of N availability through differences in litter quality. Using mathematical models of nutrient flow, we explore whether and how recycling affects plant growth, competition, and coexistence and whether it leads to positive feedbacks. Two mechanisms are considered: the ability of plants to access two forms of soil N, complex (e.g., organic) and simple (e.g., nitrate), and the effect of density-dependent limitation of growth. Except in the trivial case of limitation by N in one form without density dependence, differences in litter quality can prevent the establishment of competitors. Feedback can, conversely, facilitate the invasion of competitors. At equilibrium, the rate of decomposition does not affect the outcome of competition. Species affect their long-term persistence if they alter the fraction of nitrogen that is returned to the soil and becomes available for plant uptake. Increasing the fraction of N that is recycled favors specialists in complex nitrogen and species that suppress the growth of others at high nitrogen availability. Increasing the rate of microbial decomposition of complex nitrogen favors specialists in simple nitrogen.

Keywords: nitrogen, recycling, model, R^* , resource competition, mineralization.

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Observation of patterns in plant traits across gradients of nitrogen availability has led to the hypothesis that plants are able to affect the availability of N in their immediate environment through the quality of their litter (Pastor et al. 1984; Grime et al. 1997; Aerts 1999). Trade-offs between plant traits such as growth rates, litter quality, and longevity of biomass are thought to lead to positive feedback where plants produce litter that further enhances their competitive dominance (Tilman 1988; Chapin 1991; Hobbie 1992; van Breemen 1995). This has even led to the hypothesis that plant litter is an important component of plant fitness (Berendse 1994). Thorough analysis of the conditions required for such positive feedback to exist has never been presented. Here we present a model of N cycling and plant competition and investigate the conditions that can lead to such feedback effects.

In terrestrial ecosystems, the majority of the N in the soil is in a complex organic form or is bound to organic matter and becomes available as inorganic N as the litter decays and the N-containing compounds within it are mineralized by microorganisms. Rates of litter decay and mineralization are determined by both abiotic effects, such as climate, and species traits, such as the C : N ratio and lignin content of litter (Meentemeyer 1978; Vitousek et al. 1994; Aerts and de Caluwe 1997). Plants take up nitrogen, affecting N availability directly. They also affect availability indirectly by changing rates of mineralization and leaching, and this results in the potential for feedback between plant competitive ability and the availability of N in the soil. Species from infertile habitats tend to retain nutrients, grow slowly, have long-lived, unpalatable organs, and produce litter high in lignin and secondary compounds that lead to slow decomposition rates and low rates of mineralization, further lowering fertility. Species from fertile habitats tend to have high growth rates and palatable, short-lived organs and produce high-quality litter low in lignin and secondary compounds that decomposes rapidly, leading to high rates of mineralization and increasing fertility (Grime 1977; Pastor et al. 1984; Reich et al. 1992; Berendse 1994; Cornelissen et al. 1999; Aerts and Chapin 2000). In a study of 43 common British plants, Grime et al. (1997) found evidence for a trade-off between the capacity for rapid growth, when nutrients were not limiting,

and the ability to sustain growth, when nutrients were limiting.

Correlation between species traits and N availability does not prove that plants are actually controlling the availability of N, however (Hobbie 1992). Mathematical models have been used to establish when recycling litter changes N availability. DeAngelis (1992) showed that increased levels of recycling increased the amount of nutrient at equilibrium in an autotroph-herbivore system. Pastor et al. (2002) showed how alternative climax communities depended on both rates of input and loss from the system and plant life-history traits in a model of plant-moss competition and N cycling in peatland ecosystems. The way in which feedback affects competitive hierarchies is unresolved (Knops et al. 2002). Miki and Kondoh (2002) showed that in closed systems, turnover rates affect nutrient availability, whereas de Mazancourt and Loreau (2000) showed that in open systems, nutrient availability can be changed only through changing inputs or losses of nutrient from the ecosystem.

In a simple, single-resource model, Tilman (1982) concluded that recycling could not affect the identity of the competitive dominant. Tilman (1990) stated that if multiple limiting resources or factors are considered, recycling N through litter can affect the competitive outcome (see also Wedin and Tilman 1990). However, he did not explore the conditions that lead to different effects of recycling on the competitive outcome and the kind of trade-offs that lead to positive feedbacks.

We present two mechanisms that lead to a possible shift in competitive ability with changes in N availability. For each mechanism, we explore the specific trade-offs required for feedback-driven founder control and facilitation to be possible and then present a parameterized example. Finally, we present the complete model, which includes both mechanisms.

Our first mechanism is that plants have access to different forms of N. Although simple models of competition for N have considered soil N to be a single homogeneous resource (de Wit 1960; Tilman 1982; DeAngelis 1992), N is available in different forms that are accessible to the plant (Lipson and Nasholm 2001; McKane et al. 2002). All plants access N as ammonium and nitrate. More recently, the ability of plants to access N in the form of amino acids has been found in mycorrhizal (Falkengren-Grerup et al. 2000; Hodge et al. 2001; Bardgett et al. 2003; Miller and Bowman 2003) and nonmycorrhizal plants (Chapin et al. 1993; Raab et al. 1999) in a variety of habitats. Some plants are even able to utilize complex organic substrates, such as short peptides, directly as a nitrogen source (Kerley 1993; Persson et al. 2003). Our model represents the plant-available soil N as two pools of N in different forms, linked through the metabolic activity of

microbes. We do not model N in recalcitrant soil organic matter explicitly. An interpretation of the two pools is that form 1 represents the plant-available organic N and form 2 is the plant-available inorganic N. The pools could also represent two forms of inorganic N, with form 1 being ammonium and form 2 being nitrate. In some ecosystems (such as heathlands; Bajwa and Read 1985; Kerley and Read 1998), the two pools could represent insoluble (hydrolyzable) organic N and soluble (organic and inorganic) N.

Our second mechanism is the limitation of plant growth rate by other resources, such as space, other nutrients, water, or light, at high levels of N availability. Nitrogen is unlikely to be the only limiting resource across all reasonable levels of availability (Ingestad and Agren 1995). In productive environments, plant growth rate has been shown to be limited by the availability of other resources or other factors (Tilman 1988) in a density-dependent manner (Goldberg et al. 1999). In order to yield general predictions about other limiting resources, we did not specify the mechanism or the other limiting resource explicitly in the model. This flexibility allows for parameterization of the model using data from reciprocal transplant experiments, which measure the intensity of density-dependent inter- and intraspecific competition for unspecified resources by measuring growth of target plants in the presence and absence of neighbors (Emery et al. 2001; Pastor et al. 2002; Suding et al. 2005).

Description of the Model

Nitrogen Cycling

We present a general model of N cycling and plant competition (fig. 1). The model describes the flow of N through an ecosystem. The ecosystem is divided into several compartments, each holding a certain amount of living or dead matter that contains N. The amounts of N in the plant and soil pools are the state variables of the model. The amount of N can be translated into the amount of matter by assuming a one-to-one correspondence between the amount of N and the amount of matter in each pool. This correspondence is not necessarily linear; that is, the stoichiometry is not necessarily constant. Plants can access N in two forms, form 1 (complex) and form 2 (simple), at different rates.

The model is described in terms of first-order ordinary differential equations representing the rates of flow of N between the plant and soil compartments (eqq. [1]–[4]). Table 1 presents a description of the variables and parameters, with their units. The behavior of the pools is given as rate of change of N in plant species *i* biomass,

$$\frac{dP_i}{dt} = \frac{n_{1i}N_1 + n_{2i}N_2}{1 + k_{ii}P_i + k_{ji}P_j} P_i - d_i P_i, \quad (1)$$

rate of change of N in plant species i litter,

$$\frac{dL_i}{dt} = d_i \mu_i P_i - q_i L_i, \quad (2)$$

rate of change of soil N in form 1,

$$\begin{aligned} \frac{dN_1}{dt} = & i_1 + q_i L_i + q_j L_j - \frac{n_{1i}N_1}{1 + k_{ii}P_i + k_{ji}P_j} P_i \\ & - \frac{n_{1j}N_1}{1 + k_{jj}P_j + k_{ij}P_i} P_j - \frac{c_i P_i + c_j P_j}{P_i + P_j} N_1 - l_1 N_1, \end{aligned} \quad (3)$$

and rate of change of soil N in form 2,

$$\begin{aligned} \frac{dN_2}{dt} = & i_2 + \frac{c_i P_i + c_j P_j}{P_i + P_j} N_1 - \frac{n_{2i}N_2}{1 + k_{ii}P_i + k_{ji}P_j} P_i \\ & - \frac{n_{2j}N_2}{1 + k_{jj}P_j + k_{ij}P_i} P_j - l_2 N_2. \end{aligned} \quad (4)$$

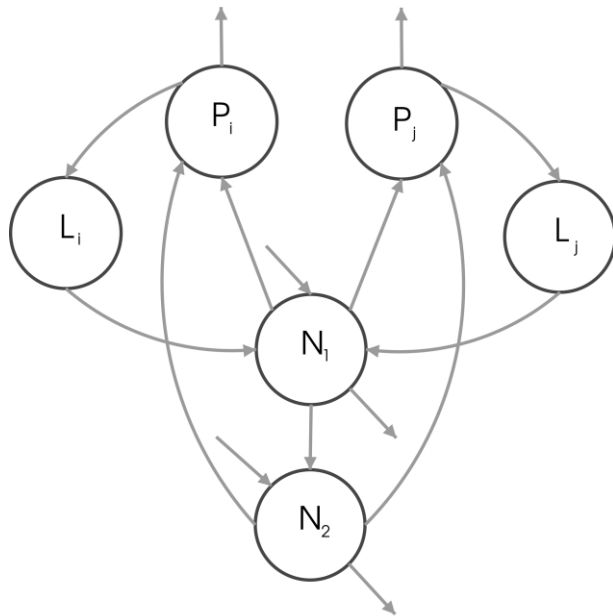


Figure 1: Model of N cycling and plant competition. The model comprises two soil compartments representing pools of N in plant-available complex (N_1) and simple (N_2) forms. Nitrogen held in the recalcitrant soil organic matter is not modeled explicitly. Each species (i and j) comprises a pool of N held in living biomass (P_i , P_j) and a pool of N in dead litter (L_i , L_j). Arrows represent N entering and leaving the ecosystem and moving between the pools.

In this model, uptake increases linearly with each pool of soil N at rates n_{1i} for N in form 1 and n_{2i} for N in form 2 (Ingestad and Agren 1995; Reich et al. 1997). In appendix B in the online edition of the *American Naturalist*, we show that our result would hold if nonlinear uptake rates (e.g., Michaelis-Menten uptake kinetics) were used. Growth is limited through inter- and intraspecific competition for resources other than N when plant abundance is high. The intensity of this limitation is dependent on the amount of plant biomass. If there is a one-to-one correspondence between the amount of plant biomass and the amount of plant N, then the effect of this limitation on growth rate can be expressed in terms of its effect on the rate of uptake of N; thus, the factor $1/(1 + k_{ii}P_i + k_{ji}P_j)$ occurs in the term for plant growth:

$$\frac{n_{1i}N_1 + n_{2i}N_2}{1 + k_{ii}P_i + k_{ji}P_j} P_i. \quad (5)$$

Individual plants lose N throughout their lifetime through mortality of both above- and belowground plant parts, root exudation, herbivory, and many other processes (Berendse et al. 1987). In this model, plants lose N at a rate proportional to the amount of N in the plant ($d_i P_i$). This process of uptake and loss is summarized in equation (1), which describes the rate of change of the N in the biomass of species i .

Once biomass from species i is no longer living, it enters a pool of litter (L_i). This pool represents dead biomass from both above- and belowground plant parts. A certain fraction of this dead biomass ($1 - \mu_i$) is either lost from the ecosystem or bound up in highly recalcitrant secondary compounds and will not become available to the plant over the timescales considered here (Campbell et al. 1967). This recalcitrant fraction of litter can be estimated from the “limit value” of litter, the asymptote of the regression of percent litter N loss against time (Berg and Meentemeyer 2002). Although this fraction is retained within the ecosystem in the pool of recalcitrant soil organic matter, it does not become available to the plant, has the same effect as a loss, and will be discussed as such. The remainder (μ_i) is recycled within the ecosystem and enters the pool of plant-available complex N as the litter breaks down at a constant rate q_i (Aerts et al. 2003). The rate of change of N in the litter of species i is described in equation (2) (fig. 2).

Complex N in the soil can suffer three fates. It can be taken up by a plant, as described above, and incorporated into living biomass, provided the species in question is able to do so. It can be leached out of the soil and lost from the ecosystem (Qualls 2000; Perakis and Hedin 2002) at a constant rate (l_1). Finally, it can be converted into

Table 1: Variables and parameters used in this model

Parameter/ variable	Definition	Units
c_i	Rate of conversion (depolymerization, mineralization, or nitrification) of soil N from complex form 1 to simple form 2 under species i	year^{-1}
d_i	Rate of detritus (above- and belowground plant parts) produced by species i	year^{-1}
i_1	N form 1 input into soil	$\text{kg N ha}^{-1} \text{ year}^{-1}$
i_2	N form 2 input into soil	$\text{kg N ha}^{-1} \text{ year}^{-1}$
k_{ii}	Limiting effect of biomass on the uptake rate of species i on species i (intraspecific competition)	$\text{kg}^{-1} \text{ N ha}$
k_{ji}	Limiting effect of biomass on the uptake rate of species j on species i (interspecific competition)	$\text{kg}^{-1} \text{ N ha}$
l_1	Leaching rate from soil N pool 1	year^{-1}
l_2	Leaching rate from soil N pool 2	year^{-1}
μ_i	Fraction of N recycled within the ecosystem in the timescales considered here by species i	Dimensionless
n_{1i}	Rate of uptake of complex N by species i	$\text{kg}^{-1} \text{ N ha year}^{-1}$
n_{2i}	Rate of uptake of simple N by species i	$\text{kg}^{-1} \text{ N ha year}^{-1}$
q_i	Rate of decay of plant litter from species i	year^{-1}
L_i	Total litter N from species i	kg N ha^{-1}
N_1	Soil N form 1 (complex), e.g., ammonium or organic N	kg N ha^{-1}
N_2	Soil N form 2 (simple), e.g., nitrate or inorganic N	kg N ha^{-1}
P_i	Plant N in species i	kg N ha^{-1}

simple nitrogen at a net rate determined by species litter quality (c_i) and enter the pool of simple N (N_2 ; Schimel and Bennett 2004). In this article, the continuum from fresh litter to soil organic N to mineral N in the soil is represented by three pools of N, each with first-order kinetics. As such, it is a simplification of the highly complex and poorly understood process of decomposition and mineralization (Benbi and Richter 2002). In particular, this model may not describe the non-steady state behavior of ecosystems well, because it does not describe the initial immobilization phase of decomposition and does not include a pool of N in microbial biomass explicitly. Even in this simplified form, it is a challenge to parameterize the model. The model provides a useful tool to test intuition about the effect of recycling on the outcome of competition in the long term. The rate of change of complex soil N is described in equation (3).

As with the complex N, simple N in the soil can be taken up by a plant and incorporated into living biomass, as described above, or it can be leached from the soil and lost from the ecosystem at a constant rate (l_2). Nitrogen enters the ecosystem through deposition of N-containing compounds from the atmosphere (and in the case of complex N, from recalcitrant soil organic matter), which enter the soil pools (N_1 and N_2) at constant rates (i_1 and i_2).

Litter quality effects are represented by three parameters: the rate of decay of litter and release of any nonrecalcitrant N contained therein (q_i ; fig. 2), the proportion of litter that is not recycled ($1 - \mu_i$), and the rate of conversion of complex N to simple N (c_i). Clearly, such parameters can

covary (Fog 1988; Berg 2000), but no assumptions about their relationship are made here.

Calculating the Invasion Condition

The effects of traits on the relative competitive ability of a species are determined by examining the invasion condition (Metz et al. 1992). This inequality describes the situation when a rare population of plants is able to invade (i.e., have a positive growth rate in) a resident population of plants that are at a stable equilibrium. In this situation, the rare population is so small that it has no effect on the environment. If a strategy is able to invade another when rare, then it will persist, even at a low density. If both strategies are able to invade each other, then they are able to permanently coexist.

The invasion condition of a rare strategy (r) in a resident (R) at equilibrium is

$$\frac{dP_r}{dt} > 0, \quad (6)$$

that is,

$$\frac{n_{1r}N_{1r}^* + n_{2r}N_{2r}^*}{1 + k_{r,r}P_r^*} - d_r > 0, \quad (7)$$

where N_{1r}^* , N_{2r}^* , and P_r^* are the equilibrium soil N in forms 1 and 2 and plant N of the resident, respectively.

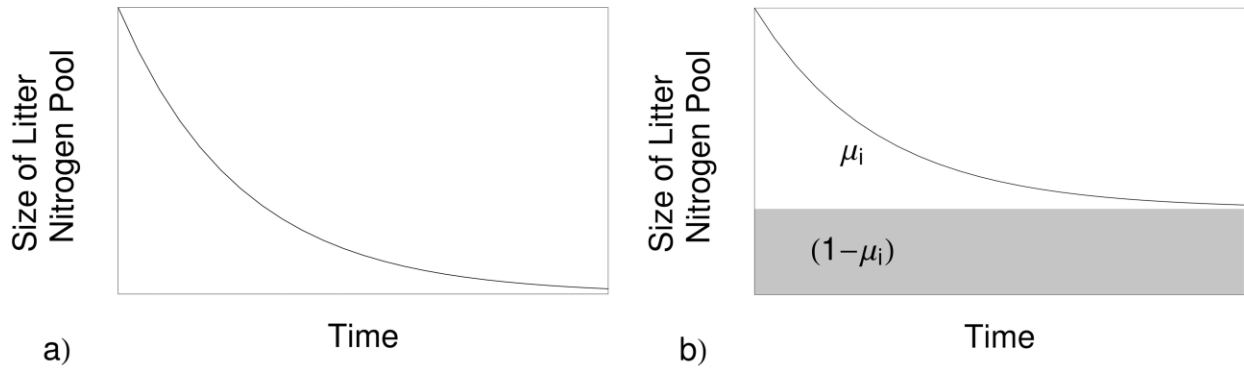


Figure 2: Illustration of the difference between q_i (the rate of decay of litter) and μ_i (the fraction of N recycled within the ecosystem via the plant in the timescales considered here). *a.* Litter pool is chemically homogeneous and decays at a constant rate (q_i) over reasonable ecological timescales (e.g., hundreds of years). *b.* Litter is heterogeneous, with a certain fraction (μ_i) of the litter decomposing at rate q_i , and the remainder ($1 - \mu_i$; gray) decomposing at a much slower rate and effectively never being decomposed over the time shown here.

Results

The behavior of the model is first examined when N in only one form limits growth. The effect of incorporating other resources or factors is then considered. First, the effect of competition for multiple forms of N is presented, followed by the effect of limiting plant growth through competition for resources other than N. Finally, the behavior of the full model is presented, where both mechanisms are included.

Because the solutions to the equations presented above are complex, they are described in this section and reproduced in full in appendix A in the online edition of the *American Naturalist*.

The Basic Model: Competition for Nitrogen in One Form Only, with No Other Competitive Factors

When competition for one form of N only is considered, with no other resources limiting ($n_{1_i} = k_{ii} = k_{ji} = 0$), the model reverts to a single-resource R^* model (Tilman 1980, 1990; Berendse 1985; Huisman 1994) where only one species can persist in the long term. Coexistence is impossible because in this model, N availability cannot change the competitive hierarchy: every species has an R^* value, and the species with the lowest R^* always dominates, whatever the conditions. The identity of the superior long-term competitor is determined by the ability of the species to deplete the limiting resource (N) to a lower level than any other competing species. The identity of the superior competitor is independent of any trait representing litter decomposition rate, amount of N recycled, or conversion rate (app. A). This result confirms predictions made by Tilman (1990) that when N is the only limiting resource,

feedback between plant and soil through differences in litter quality has no effect on the identity of the dominant species.

The Effect of Competition for Multiple Resources

Competition for Nitrogen in Two Forms, with No Other Competitive Factors. If competition for multiple forms of N is considered, with no other resources limiting ($k_{ii} = k_{ji} = 0$), the rate of decomposition (q_i) has no effect on N availability or on plant competitive ability. The amount of recycling (μ_i) and the rate of conversion (c_i) can change competitive hierarchies if there is a trade-off between the ability of a species to deplete the level of N in form 1 and the ability of the species to deplete the level of N in form 2. A species (j) is a complex specialist if it is more able to deplete N in form 1 than its competitor when only complex N is present:

$$\frac{d_i}{n_{1_j}} < \frac{d_i}{n_{1_i}}. \quad (8)$$

A species (j) is a simple specialist if it is better able to deplete N in form 2 than its competitor when only simple N is present:

$$\frac{d_i}{n_{2_j}} < \frac{d_i}{n_{2_i}}. \quad (9)$$

Given a species specializing in N in form 1 (eq. [8]) and a species specializing in N in form 2 (eq. [9]), increasing the amount of N recycled in the ecosystem (μ_i) increases the size of the complex pool relative to the simple

pool by increasing the total amount of N available, thus increasing the amount of plant biomass, which in turn results in a reduction in the size of the simple pool through an increased amount of uptake (eq. [A8] in the online edition of the *American Naturalist*). This favors the complex specialist (fig. 3a). Recycling less favors the simple specialist. If the simple specialist recycles less and the complex specialist recycles more (fig. 3b), multiple stable states exist where either species can create conditions favorable to themselves and dominate in the long term. If the simple specialist recycles more and the complex specialist recycles less, then each species can create conditions favorable to the other and coexistence between the two species can be maintained (fig. 3c). Conversion rates affect the outcome of competition through changing the relative size of the pools of complex and simple N. Increasing the conversion rates favors the simple specialist because it increases the size of the pool of simple N. If species have conversion rates that favor their own persistence, this can lead to founder control. Conversely, if species have conversion rates that favor their competitors, this can lead to “facilitation” (app. A). Coexistence requires that the complex specialist is not able to reduce the amount of simple N to

a lower level than the simple specialist and vice versa (app. A):

$$\begin{aligned} N_{1_i}^* &< N_{1_j}^*, \\ N_{2_j}^* &< N_{2_i}^*. \end{aligned} \tag{10}$$

Figure 4 shows how differences in relative preference for forms of N between species can change predictions about the relative competitive ability of species. The parameters for this example are derived from experiments on dry heathland in the Netherlands. The two species are *Calluna vulgaris*, an evergreen shrub with ericoid mycorrhiza, and *Molinia caerulea*, a graminoid with arbuscular mycorrhiza. When only the rates of uptake and loss of inorganic N are considered, *Molinia* is predicted to dominate in the long term, since it uses N more efficiently. However, *Calluna*’s ericoid mycorrhiza allow it to access amino acids and proteins directly (Bajwa and Read 1985), giving it a higher relative preference for organic N. This is predicted to greatly enhance its ability to compete with and even exclude *Molinia* by recycling more N in its litter (fig. 4b). At high levels of N availability, *Calluna*’s increased susceptibility to attack by the heather beetle *Lochmaea*

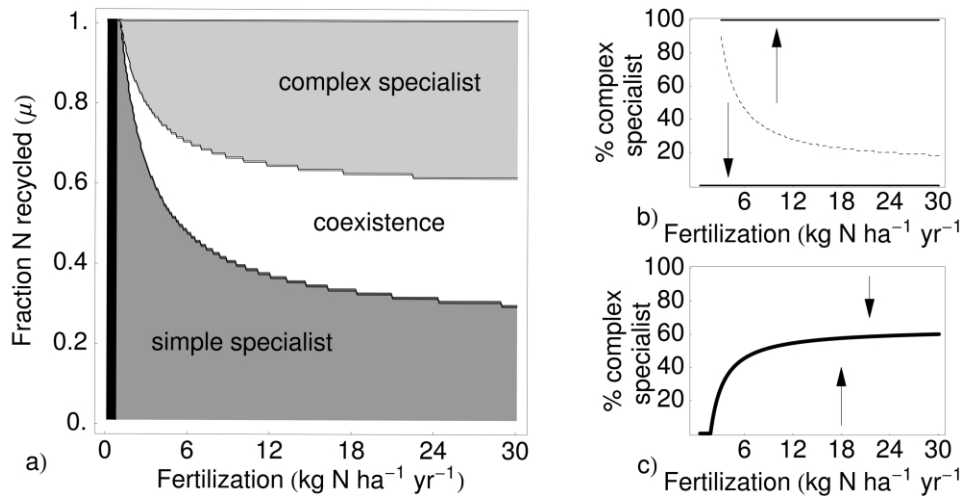


Figure 3: Results of a model including uptake of multiple forms of N, no other limiting resources, and a trade-off between the ability to deplete the two forms of N. *a*, Effect of fertilization and fraction of N recycled on the competitive outcome. The persistence of the complex specialist and the simple specialist depends on fertilization (*X*-axis) and recycling traits (*Y*-axis). Both species recycle the same proportion of N in the long term ($\mu_i = \mu_j = \mu$). *b*, Percent abundance of the complex specialist at equilibrium as a function of fertilization and initial abundance. The complex specialist recycles a large amount of N ($\mu_i = 0.9$), and the simple specialist recycles a small amount ($\mu_j = 0.1$). At certain levels of fertilization, multiple stable states exist where both species are capable of preventing invasion and persistence of the other. The final state arrived at depends on the initial abundances of the two species. *c*, Percent abundance of the complex specialist at equilibrium as a function of fertilization and initial abundance. The complex specialist recycles a small amount of N ($\mu_i = 0.1$), and the simple specialist recycles a large amount ($\mu_j = 0.9$). In this case, coexistence is maintained because each species creates conditions that allow the other to invade. Parameters (where *i* is the complex specialist and *j* is the simple specialist): $n_{1_i} = 0.1$, $n_{1_j} = 0.06$, $n_{2_i} = 0.58$, $n_{2_j} = 1.53$, $d_i = 0.9$, $d_j = 1.32$, $l_1 = 0.129$, $l_2 = 0.407$, $c_i = 0.246$, $c_j = 0.288$, $i_1 = 0$, $q_i = 0.159$, $q_j = 0.317$, $k_{ii} = 0.0$, $k_{jj} = 0.0$, $k_{ij} = 0.0$, $k_{ji} = 0.0$.

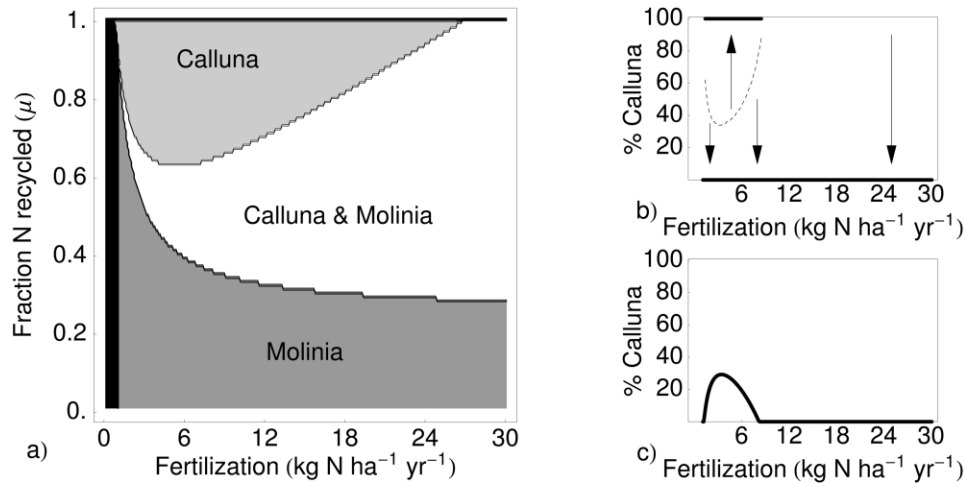


Figure 4: Competition between an evergreen shrub with ericoid mycorrhiza, *Calluna vulgaris*, and a graminoid, *Molinia caerulea*, for inorganic and organic N in a dry heath in the Netherlands (no other resources are limiting; app. C in the online edition of the *American Naturalist*). *a*, Effect of fertilization and fraction of N recycled on the competitive outcome. Both species recycle the same proportion of N in the long term ($\mu_M = \mu_C = \mu$). *Molinia* is slightly more efficient at using inorganic N than *Calluna* and therefore has an advantage in very unproductive environments (eq. [9]). If *Calluna* is slightly more efficient at using organic N than *Molinia*, it is predicted to have an advantage when intermediate amounts of N are recycled within the ecosystem (eq. [8]). At high levels of fertilization or recycling, *Calluna* is excluded because of the large losses of N incurred by heather beetle outbreaks (Heil and Dietmont 1983). *b*, Percent abundance of *Calluna* at equilibrium as a function of fertilization and initial abundance. *Calluna* recycles a larger amount of N ($\mu_C = 0.9$) than *Molinia* ($\mu_M = 0.1$). In this situation, founder control is possible over some intermediate levels of fertilization, but at higher levels of fertilization *Calluna* is excluded. *c*, Same as *b*, but here *Calluna* recycles a smaller amount of N ($\mu_C = 0.1$) than *Molinia* ($\mu_M = 0.9$). Coexistence is possible at intermediate levels of fertilization, but at high levels of fertilization *Calluna* is excluded. Parameters are given in appendix C.

suturalis Thoms. increases its mortality rate and reduces its competitive ability (Heil and Bobbink 1993a).

Calluna is predicted to favor its persistence by increasing μ_i (the amount of N that is recycled in reasonable ecological timescales), because it increases the size of the pool of complex N. This result is counterintuitive—litter from *Calluna* decomposes slowly (Van Vuuren et al. 1993). However, “founder control” is also possible if species have different mineralization rates (c_i). *Calluna* can favor its persistence through lowering mineralization rates, because this increases the size of the pool of complex N relative to the pool of simple N.

Nitrogen Accessible in One Form Only, with Competition for Other Resources or Factors. If inter- and intraspecific competition for resources other than N are considered and N is accessible in one form only ($n_{i_i} = 0$), then the amount of N that is recycled (μ_i) can change competitive hierarchies if there is a trade-off between the ability of a species to deplete the level of N in the soil and the ability of the species to suppress the growth of its competitor when growth is not limited by N. The rate of decomposition (q_j) has no effect on N availability or on plant competitive ability. The ability of a species to deplete the amount of N in the soil is determined by the ratio of its detritus

production rate to its uptake rate, as well as the ratio of input to leaching of N from the soil pool and the intensity of intraspecific competition for resources other than N (app. A, eq. [A18]). The species (j) that is able to deplete N the most at low N availability is called the R^* species:

$$\frac{n_{2_i}}{d_i} < \frac{n_{2_j}}{d_j}. \quad (11)$$

The ability of a species to suppress the growth of its competitor when growth is not limited by N is dependent on the intensity of inter- and intraspecific competition for resources other than N being relatively low. A species (j) that is able to suppress the growth of its competitor relative to its own growth when community biomass is high is called a k -type species:

$$1 < \frac{k_{ji}}{k_{jj}}. \quad (12)$$

Increasing N availability through inputs or the amount of N recycled in the ecosystem (μ_i) favors the k -type species (app. A), whereas decreasing it favors the R^* species. Figure 5a shows how the invasibilities of an R^* species and a k -

type species change with increasing N availability. If the R^* species recycles less and the k -type species recycles more (fig. 5b), multiple stable states can exist where either species can dominate in the long term. If the R^* species recycles more and the k -type species recycles less, then coexistence between the two species can be maintained (fig. 5c). Rates of conversion alter the competitive outcome by increasing or decreasing the N availability through changing the rate of loss from the system via the pool of complex N.

In this case, founder control or coexistence can also occur without litter feedback effects. If neither species is a k -type, then both species suppress their own growth more than they suppress the growth of the other species, resulting in coexistence. If both species are k -types, then there is founder control at high levels of fertilization and/or recycling (“The Full Model: Competition for Nitrogen in Two Forms and for Resources Other than Nitrogen”).

Figure 6 gives an example of how competition for resources other than N becomes more important as the amount of N in the soil increases. The parameters for this example are derived from experiments on an alpine moist meadow on Niwot Ridge, Colorado. The two species are *Acomastylis rossii*, a slow-growing, rhizomatous forb, and

Deschampsia caespitosa, a relatively fast growing bunchgrass. Empirical results have led to the hypothesis that *Acomastylis* is able to dominate by reducing the rates of cycling of N and that increasing N inputs from pollution would lead to increased amounts of *Deschampsia* (Bowman 2000).

However, because of *Deschampsia*'s ability to use inorganic N efficiently (Bowman et al. 1995) and the lack of any significant difference in the two species' preference for inorganic and organic N (Miller and Bowman 2002, 2003), *Deschampsia* is predicted to be a superior competitor when the amount of N in the soil is low. Because intraspecific competition is more intense than interspecific competition (Suding et al. 2005), increased fertilization or recycling is predicted to lead to coexistence between the two species. Rates of mineralization (c_i) do not seem to make any difference to the outcome of competition.

The Full Model: Competition for Nitrogen in Two Forms and for Resources Other than Nitrogen. When competition for multiple forms of N and other limiting resources is considered (i.e., when n_{1j} , k_{ij} , and k_{ji} are greater than 0), recycling can affect the outcome of competition through raising or lowering the size of the N pools in the soil. The

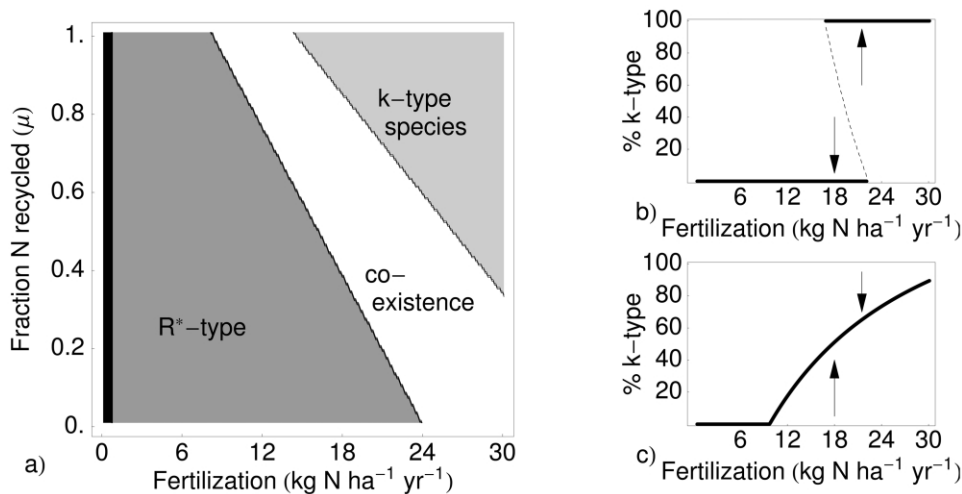


Figure 5: Results from a model including N accessible in one form only, inter- and intraspecific competition for resources other than N, and a trade-off between the ability of species to compete for different resources. *a*, Effect of fertilization and fraction of N recycled on the competitive outcome. Both species recycle the same proportion of N in the long term ($\mu_i = \mu_j = \mu$). The persistence of a k -type species and an R^* species depends on fertilization (X -axis) and recycling (Y -axis). *b*, Percent abundance of the k -type species at equilibrium as a function of fertilization and initial abundance. The k -type species recycles a large amount of N ($\mu_i = 0.9$), and the R^* species recycles a small amount ($\mu_j = 0.1$). At certain levels of fertilization, multiple stable states exist where both species are capable of preventing the long-term persistence of the other; this is founder control. *c*, Percent abundance of the k -type species at equilibrium as a function of fertilization and initial abundance. The k -type species recycles a small amount of N ($\mu_i = 0.1$), and the R^* species recycles a large amount ($\mu_j = 0.9$). In this case, coexistence is maintained because each species creates conditions that allow the other to invade. Parameters (where i is the k -type species and j is the R^* species): $n_{1i} = n_{1j} = 0$, $n_{2i} = 0.58$, $n_{2j} = 1.53$, $d_i = 0.9$, $d_j = 1.32$, $l_1 = 0.129$, $l_2 = 0.407$, $c_i = 0.246$, $c_j = 0.288$, $i_1 = 0$, $q_i = 0.159$, $q_j = 0.317$, $k_{ii} = 0.05$, $k_{ji} = 0.1$, $k_{ij} = 0.11$, $k_{ji} = 0.03$.

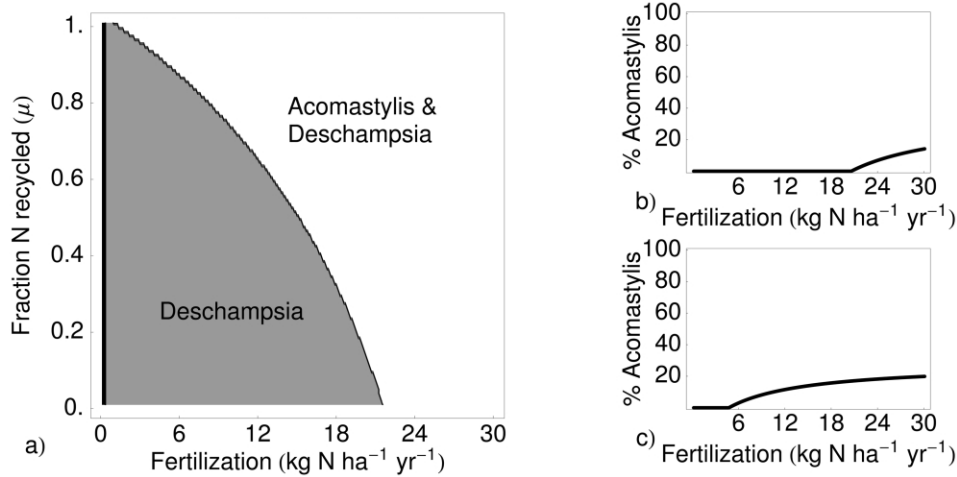


Figure 6: Competition between *Acomastylis rossii* and *Deschampsia caespitosa* for inorganic N and other limiting resources on an alpine moist meadow system on Niwot Ridge, Colorado (N is available only in the inorganic form; app. C in the online edition of the *American Naturalist*). *Acomastylis* is a slow-growing, rhizomatous forb. *Deschampsia* is a relatively fast-growing bunchgrass. *a*, Effect of fertilization and fraction of N recycled on the competitive outcome. Both species recycle the same proportion of N in the long term ($\mu_A = \mu_D = \mu$). Contrary to expectations, *Deschampsia* appears to be the superior competitor at low levels of N availability because it has a much higher uptake rate of inorganic N, compared to its loss rate, than *Acomastylis*. As the amount of N increases in the system, increased coexistence is predicted because *Acomastylis* is less affected by competition for resources other than N overall. *b*, *c*, Percent abundance of *Acomastylis* at equilibrium as a function of fertilization and initial abundance. *Deschampsia* is predicted to dominate at low levels of fertilization. As fertilization increases, competition for resources other than N become more important, and the two species are able to coexist. *b*, *Acomastylis* recycles more ($\mu_A = 0.9$) than *Deschampsia* ($\mu_D = 0.1$). *c*, *Acomastylis* recycles less ($\mu_A = 0.1$) than *Deschampsia* ($\mu_D = 0.9$). Parameters are given in appendix C.

net effect of recycling on the outcome of competition is the product of the mechanisms discussed in “Competition for Nitrogen in Two Forms, with No Other Competitive Factors” and “Nitrogen Accessible in One Form Only, with Competition for Other Resources or Factors.” Depending on species traits, the effect of recycling on competitive hierarchies can be mainly driven by differences in relative preference for multiple forms of N, resulting in a system that behaves as in “Competition for Nitrogen in Two Forms, with No Other Competitive Factors,” or it can be mainly driven by differences in inter- and intraspecific competition for resources other than N, resulting in a system that behaves as in “Nitrogen Accessible in One Form Only, with Competition for Other Resources or Factors.”

If the simple specialist (eq. [9]) is also the complex specialist (eq. [8]), then the behavior of the system is qualitatively like that in “Nitrogen Accessible in One Form Only, with Competition for Other Resources or Factors,” except that because of the greater availability of N in both complex and simple forms, regions of coexistence, dominance, or founder control caused by inter- or intraspecific competition for resources other than N occur at lower levels of fertilization and/or recycling (cf. fig. 7a–7e [without complex N uptake] to fig. 7g–7k [with complex N

uptake when the simple specialist is also the complex specialist]). If the simple specialist is not the complex specialist, then the simple specialist dominates at low levels of fertilization and recycling, and complex specialist is always able to dominate at some high level of recycling and low level of fertilization. High levels of fertilization and recycling lead to five different outcomes that result from combining the two mechanisms outlined in “Competition for Nitrogen in Two Forms, No Other Competitive Factors” and “Nitrogen Accessible in One Form Only, with Competition for Other Resources or Factors” (cf. fig. 7a–7e [without complex N uptake] to fig. 7m–7q [with complex N uptake when the simple specialist is not the complex specialist]).

Discussion

Competitive ability must change with N availability for feedback to be able to affect the outcome of competition. The basic model considers competition for N in one form only, with no other resources limiting. In this case no such trade-off is possible, so a single species will dominate across all levels of resource availability. With mechanisms that consider a single resource in multiple forms (“Competition for Nitrogen in Two Forms, with No Other Com-

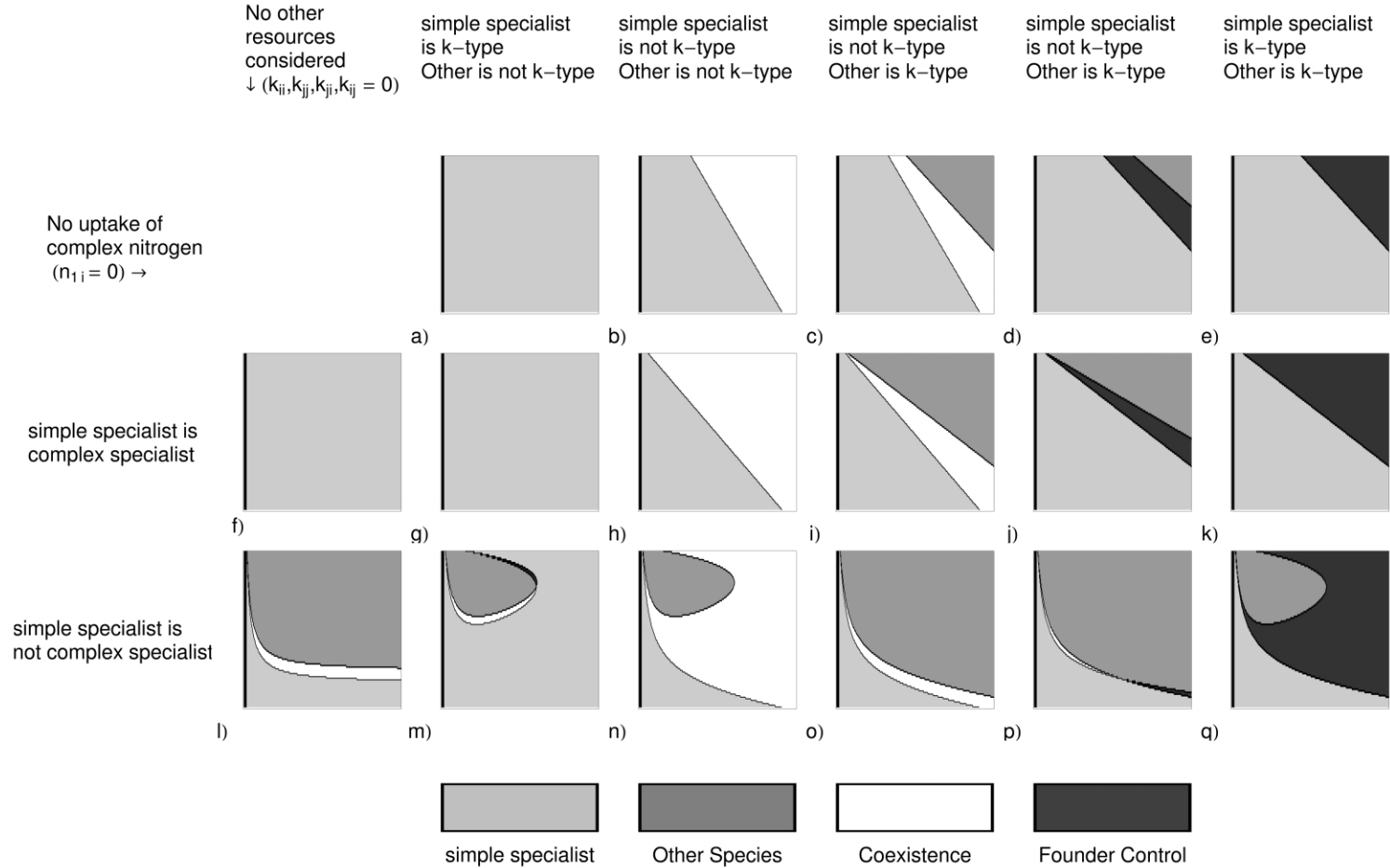


Figure 7: Effect of fertilization and fraction of N recycled on the competitive outcome between two species in a model including both uptake of multiple forms of N and inter- and intraspecific competition for resources other than N. The X-axis of each graph represents the rate of input of simple N (i_2) from 0 to 30 kg ha⁻¹ year⁻¹, and the Y-axis of each graph represents the amount of recycling (μ) from 0 to 1. *a-e*, Both species recycle the same proportion of N in the long term ($\mu_i = \mu_j = \mu$). The plots show the behavior of the model when N is accessible in one form only, with competition for other resources or factors ($n_{1i} = 0$). The ability of the R^* species to suppress the growth of its competitor when N is not limiting is lower in *c* than in *d*. *f, l*, Two plots show the behavior of the model when competition for N in two forms is considered, with no other competitive factors ($k_{ii} = k_{jj} = k_{ji} = k_{ij} = 0$). *g-k, m-q*, Behavior of the full model (with competition for N in two forms and for resources other than N). In each case, light gray represents the simple specialist (eq. [9]) dominating exclusively, medium gray represents the other species, white represents coexistence between the two species, and dark gray represents founder control, where both species can exclude the other, with the identity of the dominant species being determined by initial conditions.

petitive Factors”) or multiple resources (“Nitrogen Accessible in One Form Only, with Competition for Other Resources or Factors”), trade-offs between the abilities of plant species to compete for different resources are possible (as discussed in Tilman 1990), and feedback can alter the competitive outcome in three different ways.

The first outcome is that one species can dominate because it fosters conditions that prevent its competitor invading. If both species recycle N so that it is harder for the other to invade, multiple stable states are possible (Suding et al. 2004). This situation leads to founder control, whereby species are able to persist through positive feedback where their presence reinforces their ability to persist. In this case, the identity of the long-term dominant is dependent on the initial abundances of the two species. Pastor et al. (1984) found that species growing on poor soils that were good competitors for N produced litter with high C : N ratios that resulted in low mineralization rates. If these lead to greater losses of N, this would be a mechanism through which they might favor their own persistence. Wedin and Tilman (1990) planted monocultures of five perennial grass species and found that the two species that had the highest competitive ability for N (the lowest R^*) also had litter that resulted in low rates of mineralization. In both cases, the link between mineralization and losses is unknown.

A second outcome is that one species can establish initially and alter the environment so that the other is able to invade and then drive the initial species to extinction. This successional process is an extreme form of facilitation, because one species creates a negative feedback where its presence allows other species to invade and cause the initial species to go extinct. Wedin and Tilman (1990) suggested that N-fixing plants in low-fertility, primary successions are good examples of species that facilitate the invasion of other species.

A third outcome is that each species alters the environment so that the other is able to invade and the two species coexist. This situation may also be seen as facilitation, but in this case both species create a negative feedback whereby their presence reinforces the persistence of the other. The ecosystem presented in figure 6 could be an example of this kind of outcome, provided that the species that is best at depleting soil N (contrary to expectations, *Deschampsia*) recycles more N than the other species (*Acomastylis*). *Acomastylis* enhances microbial immobilization (Bowman et al. 2004) and is unlikely to lead to greater losses, because microbial immobilization probably reduces snow melt leaching of inorganic nitrogen (Brooks and Williams 1999).

In all cases, the rate of decomposition of litter (q_i) and transient processes, such as immobilization, have no effect on the outcome of competition. Slowing down or speeding

up the rate of change of N availability can potentially affect competitive ability in disturbed (nonequilibrium or spatially heterogeneous) ecosystems by allowing species to persist for longer (Berendse 1994). This is a transient effect and does not allow for long-term founder control.

Other aspects of litter quality can change the outcome of competition. When N is accessed in two forms, litter quality changes the outcome of competition by changing the relative sizes of the pools of complex and simple N. Increasing the amount of N that is recycled in the long term (μ_i) increases the pool of complex N and decreases the size of the pool of simple N, favoring the complex specialist. Increasing the rate of conversion (c_i) increases the pool of simple N and decreases the size of the pool of complex N, favoring the simple specialist. Given that as many species can potentially coexist on one limiting resource (nitrogen) as there are distinct forms of N in the soil, this could provide a possible explanation as to how many plant species can coexist when N is the limiting resource (Tilman 1982; McKane et al. 2002). When growth is limited by N in a single form and resources other than N, increasing the amount of N that is recycled in the long term (μ_i) favors k -type species because it increases the availability of N by reducing losses of complex N. Rates of conversion matter only if they change losses of complex N.

Plant species show significant differences in uptake rates of organic and inorganic N. Although the rate of uptake of organic N is usually lower than that of inorganic N (Kielland 1994; Falkengren-Grerup et al. 2000; Miller and Bowman 2003), the results presented in “Competition for Nitrogen in Two Forms, with No Other Competitive Factors” show that uptake rates of complex N do not need to be the same order of magnitude as uptake rates of simple N for differences in uptake rate of complex N to affect the competitive outcome. The complex specialist does not necessarily have the highest uptake rate of complex N. It is the best at depleting complex N to the lowest level when simple N is not present. This depends on the rate of uptake of complex N and the rate of production of detritus (eq. [8]).

These results put a new perspective on the effect of recycling on plant competitive ability. Recycling can determine the outcome of competition, provided that growth is limited by multiple resources and that the competitive hierarchy changes across a gradient of N availability. In the long term, turnover rates cannot affect the outcome of competition. Positive or negative feedback results from three different mechanisms: differences in plant litter quality, through differences in conversion rate between different forms of plant-accessible N; differences in plant litter quality, through differences in the fraction of N recycled in reasonable ecological timescales; and three differences

in inter- and intraspecific competition for resources other than N. Experiments are needed to show which mechanism actually drives the outcome of competition in the field.

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