REVIEW

Mechanisms of plant species impacts on ecosystem nitrogen cycling

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Abstract

Plant species are hypothesized to impact ecosystem nitrogen cycling in two distinctly different ways. First, differences in nitrogen use efficiency can lead to positive feedbacks on the rate of nitrogen cycling. Alternatively, plant species can also control the inputs and losses of nitrogen from ecosystems.

Our current understanding of litter decomposition shows that most nitrogen present within litter is not released during decomposition but incorporated into soil organic matter. This nitrogen retention is caused by an increase in the relative nitrogen content in decomposing litter and a much lower carbon-to-nitrogen ratio of soil organic matter. The long time lag between plant litter formation and the actual release of nitrogen from the litter results in a bottleneck, which prevents feedbacks of plant quality differences on nitrogen cycling. Instead, rates of gross nitrogen mineralization, which are often an order of magnitude higher than net mineralization, indicate that nitrogen cycling within ecosystems is dominated by a microbial nitrogen loop. Nitrogen is released from the soil organic matter and incorporated into microbial biomass. Upon their death, the nitrogen is again incorporated into the soil organic matter. However, this microbial nitrogen loop is driven by plant-supplied carbon and provides a strong negative feedback through nitrogen cycling on plant productivity. Evidence supporting this hypothesis is strong for temperate grassland ecosystems. For other terrestrial ecosystems, such as forests, tropical and boreal regions, the data are much more limited. Thus, current evidence does not support the view that differences in the efficiency of plant nitrogen use lead to positive feedbacks. In contrast, soil microbes are the dominant factor structuring ecosystem nitrogen cycling. Soil microbes derive nitrogen from the decomposition of soil organic matter, but this microbial activity is driven by recent plant carbon inputs. Changes in plant carbon inputs, resulting from plant species shifts, lead to a negative feedback through microbial nitrogen immobilization.

In contrast, there is abundant evidence that plant species impact nitrogen inputs and losses, such as: atmospheric deposition, fire-induced losses, nitrogen leaching, and nitrogen fixation, which is driven by carbon supply from plants to nitrogen fixers. Additionally, plants can influence the activity and composition of soil microbial communities, which has the potential to lead to differences in nitrification, denitrification and trace nitrogen gas losses. Plant species also impact herbivore behaviour and thereby have the potential to lead to animal-facilitated movement of nitrogen between ecosystems.

Thus, current evidence supports the view that plant species can have large impacts on ecosystem nitrogen cycling. However, species impacts are not caused by differences in plant quantity and quality, but by plant species impacts on nitrogen inputs and losses.

Keywords

Feedbacks, nitrogen cycling, nitrogen inputs, nitrogen losses, nitrogen use efficiency, species impacts.

Ecology Letters (2002) **5**: 454–466

INTRODUCTION

Plant species are an integral part of ecosystems nitrogen cycling because plants take up nitrogen and produce biomass, which subsequently decomposes and releases nitrogen. However, plants species differ in their rates of nitrogen uptake, litter quality, and the efficiency with which they produce biomass per unit of nitrogen. All have major consequences for decomposition and ultimately nitrogen cycling. These plant species differences have long been recognized (Waksman & Tenney 1927), and many studies document how species differ and how those species differences correlate with nitrogen pools and fluxes (Aerts & Chapin 2000). However, there are also many studies documenting that plant species are largely redundant or have only minor impacts on ecosystem functions (Reich et al. 1997). Here we construct a conceptual framework to reconcile these differences, which allows us to examine: (1) why species differ; (2) which mechanisms are important in determining their ecosystem impacts; and (3) if species can cause positive or negative feedbacks on nitrogen cycling within ecosystems.

First, we want to emphasize that determining how species influence ecosystems requires studying entire ecosystems as well as examining how species impact nitrogen cycling within ecosystems. Many studies examine individual species within ecosystems, such as trees within grass savannas, but this approach confounds two issues. Species can influence nitrogen cycling of entire ecosystems, but species can also change the spatial distribution of nitrogen within ecosystems. For instance, trees have been documented to have large positive impacts on soil nitrogen pools in a grassland savanna (Vetaas 1992). Based on this result alone, one might conclude that the nitrogen accumulation was the result of a positive feedback on nitrogen cycling. However, by also examining the grassland areas, an alternative mechanism becomes apparent. Nitrogen is being spatially redistributed by the trees rather than a positive feedback occurring on nitrogen cycling throughout the entire ecosystem.

Second, we have chosen to focus on nitrogen cycling, because carbon cycling is intimately linked to nitrogen cycling. Nitrogen often limits productivity, decomposition and the long-term accumulation of carbon in the soil (Knops & Tilman 2000).

Theories of when plant species identity does impact ecosystem nitrogen cycling: plant feedbacks vs. inputs/outputs of nitrogen

Ecosystems are hypothesized to be sensitive to species composition as a result of a positive feedback in which higher soil nitrogen availability results in higher tissue quality, faster decomposition and higher nitrogen availability

and vice versa (Fig. 1) (Vitousek 1982; Pastor et al. 1984). Alternatively, plant species can also change ecosystem nitrogen cycling by controlling nitrogen input rates, such as symbiotic nitrogen fixation (Vitousek et al. 1987; Binkley et al. 1992) or nitrogen losses (Fig. 1) (Wedin & Tilman 1990). These two views differ in the mechanism by which species influence ecosystems.

The plant nitrogen use theory predicts an internal positive feedback in which initial differences within ecosystems magnify over time and result in different stable endpoints. However, a recent modelling study (Tateno & Chapin 1997) suggested that within closed systems (e.g. no nitrogen inputs or outputs), productivity converges under contrasting species. This convergence can be caused by a negative feedback of a high biomass, resulting in a high litter carbon : nitrogen ratio and low nitrogen mineralization. Alternatively, productivities may converge as a result of a positive feedback in which low biomass results in a low carbon : nitrogen ratio of litter and higher nitrogen mineralization.

In contrast, the input/output theory assumes that the crucial facet determining the endpoint of change is the way in which species impact nitrogen input and losses (de Mazancourt et al. 1998). Many studies show that plant species affect nitrogen inputs and losses. Below we will review how plant species influence atmospheric deposition, fire, symbiotic and asymbiotic nitrogen fixation and nitrogen losses (Fig. 2). We will also consider indirect interactions, such as herbivore impacts on plant biomass and plant species abundances as well as the translocation of nitrogen via animal movement.
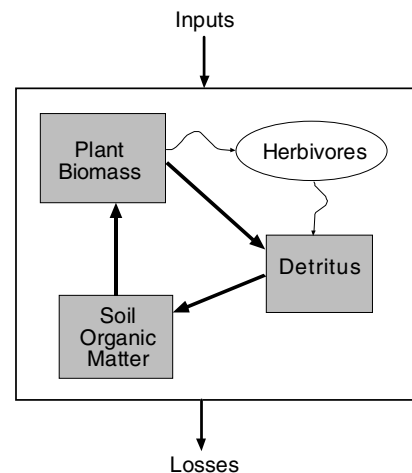

Figure 1 Major nitrogen flows within an ecosystem among plants, herbivores, detritus and soil organic matter. This paper addresses the relative importance of within-ecosystem nitrogen flows vs. inputs and losses in determining plant species impacts on ecosystem nitrogen cycling.
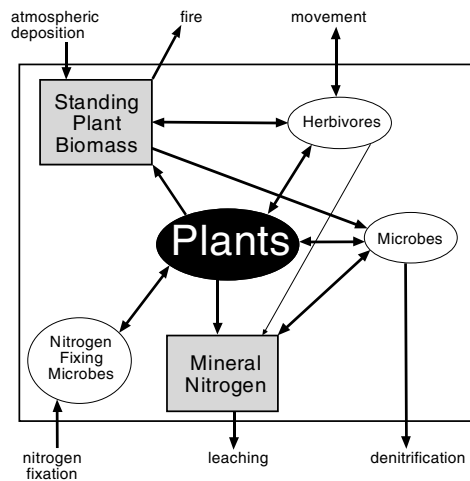
Figure 2 The major pathways of nitrogen inputs (atmospheric deposition, animal movement and nitrogen fixation) and losses (fire, animal movement, leaching and denitrification) and the direct and indirect pathways by which ecosystem components impact the nitrogen inputs and losses.

These theories are not mutually exclusive, but understanding the relative importance of these two mechanisms is crucial to generate predictive hypotheses about how shifts in plant species may impact ecosystem nitrogen cycling. For instance, *Acacia* invasions into grasslands have been shown to strongly influence the available nitrogen pool as well as nitrogen cycling within the system (Stock & Baker 1995). Acacias differ from grasses in both their growth form, which impacts their nitrogen use, and their ability to fix nitrogen. Changes in ecosystem nitrogen cycling are likely to be a result of both increased nitrogen inputs and changes in efficiency of nitrogen use, although it is difficult to untangle the relative importance of these two mechanisms. Similarly, in Hawaii, grasses are invading sites dominated by native shrubs. These grass invasions change the fire regime and subsequently, nitrogen losses. However, the dominant growth form is also leading to changes in efficiency of nitrogen use (D'Antonio & Vitousek 1992). These species-based studies do not allow us to separate the relative importance of changes in plant species nitrogen use from their impact on nitrogen inputs and outputs. Because the two mechanisms are confounded, we are unable to make generalizations about how species shifts may alter nitrogen cycling in other ecosystems.

INPUT–OUTPUT THEORY

Plant species differ in several important traits that can affect either nitrogen inputs or losses (Fig. 2). Some species have symbiotic relationships, which result in the fixation of atmospheric nitrogen. There are reports that some plant

species can influence asymbiotic nitrogen fixation within the root rhizosphere and the soil. In addition, the canopy of plants can also alter atmospheric deposition rates. Plant species also affect nitrogen losses by their differential abilities to lower soil mineral nitrogen levels, thereby changing the amount of nitrogen available for leaching. The seasonality of plant activity is also important, because it might not match the seasonality of nitrogen supply from microbial decomposers. Plants' seasonality and growth form may influence the susceptibility of fire-induced nitrogen losses and impact animal-facilitated movement of nitrogen. In total, there are many direct and indirect ways that plant species impact the inputs and losses of nitrogen from ecosystems. Below, we review the main pathways and how plant species affect these fluxes.

Symbiotic nitrogen fixation

Much is known about symbiotic nitrogen fixation, and there is abundant evidence that such fixation, often in association with a single plant species, can facilitate the input of significant amounts of nitrogen (Vitousek *et al.* 1987; Maron & Jeffries 1999). Legume abundance is also a significant factor which influences the rate of carbon and nitrogen accumulation in abandoned agricultural fields (Knops & Tilman 2000). In addition, nitrogen-fixing leguminous trees are key invaders of savannas and grasslands on several continents (Archer 1994).

Asymbiotic nitrogen fixation

The impact of plant species on asymbiotic nitrogen fixation has not been extensively investigated as a contributing factor to nitrogen inputs. Asymbiotic nitrogen fixation has been estimated in most ecosystems to contribute on the order of 0–5 kg of nitrogen per ha per year (Cleveland *et al.* 1999). There is also evidence that the availability of carbon (Granhall 1981) and the ratio of soil phosphorus to nitrogen might be important factors in controlling asymbiotic fixation rates (Smith 1992). Several studies have shown that some plant species, especially trees, can increase nitrogen accumulation in soil at substantially higher rates than can be accounted for by symbiotic nitrogen fixation or atmospheric deposition (Richards 1962; Switzer *et al.* 1966). Our work at Cedar Creek has also documented nitrogen inputs into trenched plots occupied by *Pinus strobus* of the order of 50 kg ha^{-1} year^{-1}. These large nitrogen inputs cannot be accounted for by other factors (Knops *et al.* 2000). These rates are similar to those reported by Bormann *et al.* (1993) for completely enclosed sandboxes, which eliminated soil mining by roots outside the plots as a possible factor. Soil mining is unlikely also in our plots, given that the area these trees would have to mine to account for this amount of

nitrogen is five times the area that each plot occupies. However, neither our study nor Bormann et al. (1993) showed acetylene reduction rates to match these input rates (Barkman & Schwitzer 1998). Richards (1973) showed conclusive laboratory evidence that Pinus radiata increased asymbiotic nitrogen fixation in the rhizosphere, and there is some corroboration for this from field studies (Richards 1962).

Several studies have found evidence that soils dominated by grasses (Abbadie et al. 1992; Brejda et al. 1994) and forbs (McKone & Biesboer 1986) also have unaccounted nitrogen inputs that may be explained by asymbiotic nitrogen fixation. In total, however, little is known about asymbiotic nitrogen fixation and even less regarding the degree of plant control over this phenomenon (Hendrickson 1990).

Atmospheric nitrogen deposition

Plant canopy surfaces can intercept the small particles contained in both wet, such as fog, dew and mist, and dry deposition (Lovett 1991). Thus, species that differ in canopy architecture can change atmospheric deposition markedly in some (Knops et al. 1996), but not all ecosystems (Kellman & Carty 1986). Differences between tree species in deposition rates have also been observed (Draaijers et al. 1992). In addition, forest edges have greater deposition rates than the interior of forests (Weathers et al. 2000).

Nitrogen losses

Much of the nitrogen lost from ecosystems results from the leaching of NO_3 (Magill et al. 1997). However, most studies have been conducted in temperate Northern Hemisphere ecosystems, which are subject to widespread anthropogenic nitrogen pollution. Recent evidence shows that nitrogen losses from unpolluted, undisturbed forest are much lower and mainly in the form of dissolved organic compounds (Perakis & Hedin 2002). The soil NO_3 pool is low because of rapid uptake by plants and microbes. However, individual plant species can influence the level of depletion (Wedin & Pastor 1993). The total amount of nitrogen that cycles through this pool in a year is large (Wedin & Tilman 1990; Wedin & Pastor 1993). The timing of uptake and the degree of depletion of NO_3 by plants may therefore control rates of nitrogen loss from ecosystems (Wedin & Tilman 1990).

At Cedar Creek, we found (Wedin & Tilman 1993); Knops & Tilman, unpubl. data.) that experimentally maintained monocultures of Schizachyrium scoparium (a C_4 grass) and Agropyron repens (a C_3 grass) had significantly different levels of available nitrate in the surface soil (mean of six measurements, Schizachyrium 0.144 NO_3-nitrogen per g dry soil, Agropyron 0.213, t-test, $F = 9.7$, $n = 12$, $P < 0.05$). Total plant nitrogen (roots, shoots and litter) was significantly divergent after 6 years, e.g. Schizachyrium 7.4 g

nitrogen m^{-2}, and Agropyron 3.0 (t-test, $n = 12$, $F = 10.7$, $P < 0.01$). The soil contained about 6.0 g nitrogen m^{-2}, and atmospheric deposition was on the order of 1–1.5 g nitrogen m^{-2} y^{-1}. Knops & Tilman (2000) argued that Schizachyrium plots essentially retained all atmospheric deposited nitrogen, whereas Agropyron plots retained only half. The other half was most likely lost through leaching (Wedin & Tilman 1996). Thus, it is clear that plant species can strongly impact ecosystem nitrogen leaching.

Soil microbes are often limited by carbon (Jackson & Caldwell 1992). Root exudates and root turnover are important sources of carbon for soil microbes (Grayston et al. 2001). The quality and quantity of this carbon supplied by plants can determine the rate of net nitrogen mineralization (Schmidt et al. 1997), which, in turn, can influence the total amount of NO_3 produced as well as leached from ecosystems. Plant species also interact with soil microbial communities, which can have strong impacts on nitrification and therefore nitrate leaching (Lata et al. 1999). As a result, plants can influence and control nitrogen loss from ecosystems in a number of ways. However, there are few comprehensive field studies that document the impact of individual plant species on these rates in a field setting.

Fire

Plant species can change fire regimes (D'Antonio & Vitousek 1992). This may impact nitrogen losses both directly by fire-induced losses (Wan et al. 2001) and by a temporary decrease in vegetation biomass. The loss of vegetation lowers water and nitrogen uptake, leading to an increase in soil water and nitrate pools. The nitrate can then be lost through increased leaching (Mack et al. 2001). In a meta-analysis, Wan et al. (2001) reported that most fire studies found no real detectable changes within the soil nitrogen pool, although fire did show a significant impact on the standing biomass nitrogen above ground. Because soil nitrogen is the dominant nitrogen pool in ecosystems, the impact of fire seems limited (Wan et al. 2001). It is important to note that most of these studies are short-term. A few studies do show a strong impact of long-term fire regime on total ecosystem nitrogen (Blair 1997; Knops et al. 2000) and modelling studies support this (Ojima et al. 1994).

Animal movements

Migratory grazers have the potential to process and redistribute a large amount of nitrogen within a landscape (Frank & Evans 1997). Additionally, within spatially complex habitats such as savannas, animals may spend a disproportionate amount of their time in or under trees, because trees can be a food resource, and can also supply nesting sites and shade. This can also lead to a redistribution

of nitrogen within a landscape. Long-distance movement of animals, such as salmon (Helfield & Naiman 2001), birds (Erskine *et al*. 1998), ants (Sagers *et al*. 2000) and termites (Lopez 2001) can also transport a significant amount of nitrogen into ecosystems. This nitrogen input can also be transferred from aquatic to riparian ecosystems (Helfield & Naiman 2001). Thus, if moving animals preferentially select habitats dominated by specific species, these plant species might indirectly increase nitrogen input into ecosystems.

Herbivores can slow down nitrogen cycling by preferentially eating high quality plant such as nitrogen fixing legumes (Ritchie *et al*. 1998) or fast-growing highly productive plant species (Pastor *et al*. 1993). Alternatively, herbivory can also speed up nitrogen cycling (McNaughton 1979). Grazing within grasslands can influence primary productivity in three ways. First, herbivory can stimulate plant growth (McNaughton 1979). For instance, biomass allocation can change from below-ground to above-ground tissues, thereby increasing above-ground primary productivity (Oesterheld & McNaughton 1991). Second, herbivores can act as "decomposition vessels" by providing microbial decomposers with a much more favourable environment for decomposition than the soil environment (Van Soest 1982). This can markedly speed up the rate of organic matter decomposition, and an herbivore's waste products can provide a readily available pool of nitrogen for plants (Frank & Groffman 1998). Third, above-ground herbivory can result in a rapid release of easily decomposable carbon from roots (Holland *et al*. 1996), which can increase soil microbial populations, decomposition rates and nitrogen mineralization (Eason & Newman 1990; Hamilton & Frank 2001). However, none of these mechanisms change the overall nitrogen fluxes or lead to long-term changes in nitrogen cycling if they do not alter nitrogen inputs and/or losses (de Mazancourt & Loreau 2000). Note that herbivores browsing preferentially on legumes do decrease nitrogen pools, by lowering plant-associated nitrogen fixation (Ritchie *et al*. 1998).

PLANT NITROGEN USE THEORY

Plant nitrogen use efficiency is the biomass produced per unit of nitrogen uptake (Garnier & Aronson 1998; Aerts & Chapin 2000). Plant nitrogen use varies among plant species, because plant species differ in the components that determine plant nitrogen use efficiency such as: allocation patterns, photosynthetic nitrogen use efficiency, tissue longevity and litter quality. In addition, there are also unavoidable trade-offs between various components such as leaf longevity and maximum photosynthetic rates (Reich *et al*. 1992).

Nitrogen use efficiency can be considered as having two components: nitrogen productivity and mean nitrogen residence time (Berendse & Aerts 1987), which is mainly

determined by tissue longevity. Species differ markedly in their photosynthetic nitrogen use efficiency, because of photosynthetic pathways (e.g. C_3 and C_4), allocation patterns and leaf structure. Longevity of tissues also differs strongly between species. These differences between species are considered important in structuring ecosystem nitrogen cycling and are hypothesized to result in positive and negative feedbacks on nitrogen availability and productivity (Vitousek 1982; Pastor *et al*. 1984; Wedin & Tilman 1990).

Nitrogen pools and nitrogen use

Soil organic matter is the largest nitrogen pool within terrestrial ecosystems, accounting for more than 90% of total ecosystem nitrogen (Fig. 3d). Soil organic matter is the largest nitrogen pool partly because it has a carbon-to-nitrogen ratio of 10–20 (Batjes 1996; Knops & Tilman 2000), whereas live plant biomass has a carbon-to-nitrogen ratio of 50–100 and abscised, dead plant material has a carbon-to-nitrogen ratio of 100–200 (Aerts 1996; Killingbeck 1996). Many litter decomposition studies show an exponential mass loss over time, corresponding with an exponential increase in percent nitrogen of the litter during decomposition (Melillo *et al*. 1982; Hobbie 1996).

If we assume that dead plant material shows an exponential carbon loss, with 20% eventually being incorporated into soil organic matter (Fig. 3a) and that the percentage nitrogen increases during decomposition from an initial percentage of 0.75 to 3.75 (Fig. 3b), we find that all initial litter nitrogen is retained and incorporated into soil organic matter (Fig. 3c). Different initial litter nitrogen content impacts the mineralization and immobilization of nitrogen into the decomposing litter. But, as Fig. 3 (b,c) shows, even at an initial litter nitrogen concentration of 1.5% the decomposing litter still retains 50% of its nitrogen, whereas at any litter concentration below 0.75%, nitrogen is strongly immobilized. Thus, most of the nitrogen is always incorporated into the soil organic matter, and soil organic matter decomposition primarily determines nitrogen mineralization and thereby plant-available nitrogen and primary productivity (Fig. 3e, Knops unpubl. data). Any changes in the quality of other ecosystem nitrogen pools must percolate through the soil organic matter pool.

Changes in plant quality are slow to influence nitrogen release because of the time lag created by their passage through soil organic matter (Fig. 3d). As a result of this bottleneck, species litter quality has a much smaller impact on nitrogen availability, compared to nitrogen released from soil organic matter. Consequently, differences in plant species quality have only a limited impact on nitrogen cycling within ecosystems. Experimental litter decomposition studies support the strong retention of nitrogen

Figure 3 Within-ecosystem nitrogen cycling. (A) Litter decomposition generally follows an exponential decay over time and (B) percentage nitrogen increases exponentially over time to 3.75% (C : N = 12), which is the nitrogen content of well decomposed soil organic matter (Knops, unpubl. data). (B, C, solid circles) This results in no net nitrogen release from litter, if the initial nitrogen content of the litter is 0.75%. Changes in initial litter quality result in changes in nitrogen retention, but most of the nitrogen is retained and results (D) in the large observed nitrogen content of the soil organic matter pool. Forest data in (D) is the average of 19 stands from Cole & Rapp (1981); Cedar Creek data is from Wedin & Tilman (1996); Konza Prairie data is from Knapp *et al.* (1998). (E) Conceptually, plants incorporate mineral nitrogen into biomass, subsequently litter, and most of the nitrogen is incorporated into soil organic matter. Soil organic matter decomposes slowly and acts as a bottleneck.
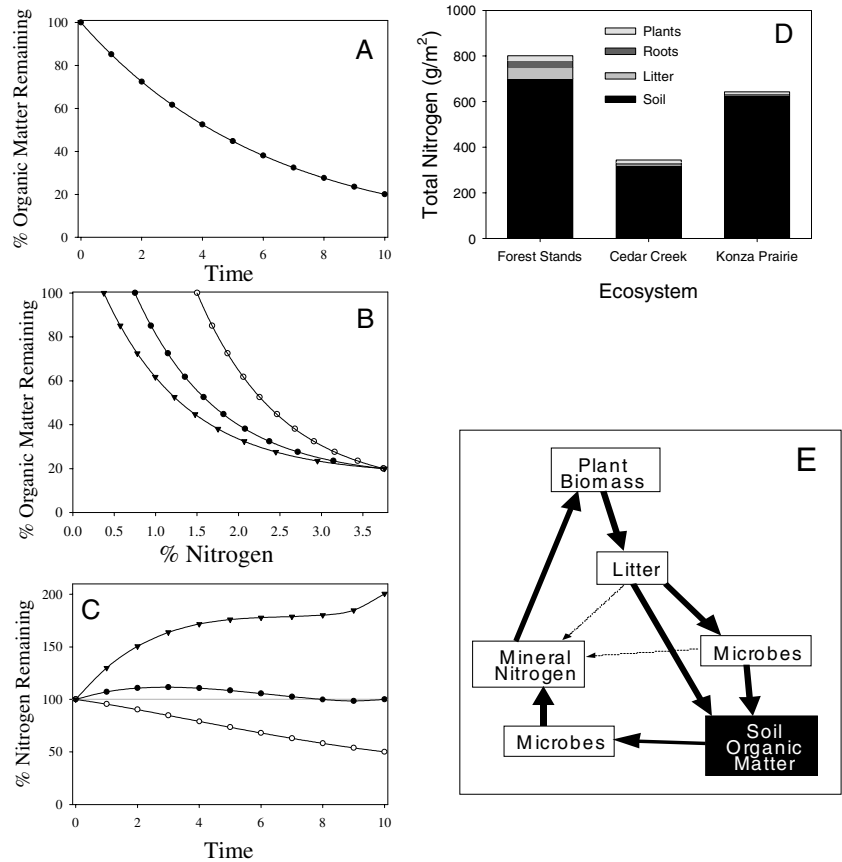
within decomposing litter, although there are few reliable long-term studies, because of inherent method problems, such as fragmentation and new root ingrowth. For instance, Wedin *et al.* (1995) and Wedin (unpubl. data) have shown that most of the nitrogen initially present in the litter (above- and below-ground) of five grass species was retained after 3 years of decomposition, even though these species differed fourfold in their nitrogen contents (0.37% to 1.66% nitrogen, Fig. 4).

However, there may be ecosystems where other sources of nitrogen are the dominant source of plant nitrogen. For instance, Abbadie *et al.* (1992) found indirect evidence that the most plant nitrogen originated from root decay in an African grassland. Also, legumes have the potential to be completely independent of soil organic matter for nitrogen and depend entirely on nitrogen fixation (Ehleringer *et al.* 1992).

Feedbacks and nitrogen use

Most evidence supporting nitrogen-use feedbacks is based on species replacement along natural fertility gradients (Vitousek 1982; Pastor *et al.* 1984). However, many initial conditions and environmental factors vary along the same

gradients, which might confound their interpretation. Current analysis shows that plant species do not show a different response to productivity, that productivity is linearly correlated with soil nitrogen supply (Reich *et al.* 1997; Knops & Koenig, unpubl. data) and that the species replacement along soil fertility gradients does not correspond with differences in nutrient use efficiency (Knops *et al.* 1997). This lack of a species-specific response supports the notion that nitrogen use efficiency does not play an important role in determining long-term productivity differences among ecosystems. Many correlational studies (Waring & Schlesinger 1985) also have found much higher net mineralization rates of deciduous trees, with a high nitrogen use efficiency, compared to evergreen trees, with a low nitrogen use efficiency. However, recent studies (Stark & Hart 1997; Verchot *et al.* 2001; Verchot *et al.* unpubl. data) showed that net nitrification rates strongly underestimated gross nitrification rates, because of strong microbial immobilization. These and other recent studies suggest that plant species differences in net nitrogen mineralization and nitrification are not caused by gross differences, but instead by differences in microbial immobilization. It is becoming increasingly clear that it is essential to consider microbial dynamics because microbial
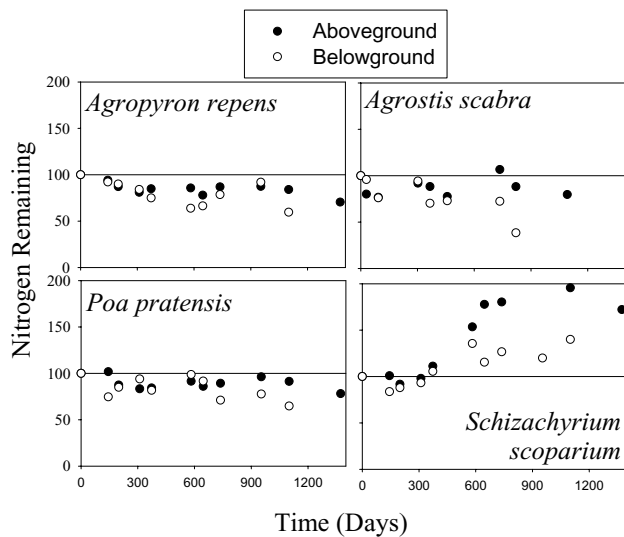
Figure 4 Above- and below-ground nitrogen remaining as a percentage of initial nitrogen content vs. decomposition time of *Agrostis scabra* (above-ground 1.05% nitrogen, 17.4% lignin, below-ground 1.66% nitrogen, 9.5% lignin), *Agropyron repens* (above-ground 1.21% nitrogen, 12.5% lignin, below-ground 0.89% nitrogen, 15.9% lignin), *Poa pratensis* (above-ground 0.92% nitrogen, 10.7% lignin, below-ground 0.75% nitrogen, 17.0% lignin), and *Schizachyrium scoparium* (above-ground 0.37% nitrogen, 15.4% lignin, below-ground 0.49% nitrogen, 22.5% lignin). All data are from Wedin *et al.* (1995) and Wedin, unpublished.

activity exerts a strong influence over patterns of nitrogen mineralization.

This idea is further supported by the experimental work of Wedin & Tilman (Wedin & Tilman 1990; Tilman & Wedin 1991; Wedin & Pastor 1993; Wedin & Tilman 1993; Wedin *et al.* 1995), who examined five grass species that differed in nitrogen use efficiency by a factor of 3.5 (Fig. 5). Species were planted along a soil fertility gradient. In the first year, soil mineral nitrate availability differed among species in the high soil fertility plots. The differences in soil nitrate availability probably related to the rate of establishment and differences in longevity among the species. However, by the second year, all soil mineral nitrate levels had converged to very low levels except for *Agrostis scabra* at high soil fertility (Fig. 5e,f). Above-ground productivity was higher at higher soil fertility, but there was no long-term pattern of species with higher nitrogen use efficiency achieving consistent increases in biomass on low fertility soil and low nitrogen use efficiency species increasing at high fertility soil (Fig. 5a,b). In the fifth year of the experiment, *Agrostis scabra*, the species with the lowest nitrogen use efficiency, had more above-ground standing biomass on the low fertility soil than on the high fertility soil (Fig. 5a,b). *Agrostis scabra* was the only species that showed a sustained increase in net nitrogen mineralization with time

on the high soil fertility plots. All other species showed a decrease in net nitrogen mineralization over time in the high fertility plots and a convergence at lower fertility levels.

From these results, it is clear that nitrogen use efficiency did not lead to a change in productivity on low soil fertility. At high soil fertility, four out the five species converged in their net nitrogen mineralization rates. *Agrostis scabra* was the only species whose mineralization rate did not match the pattern of the other four species. A probable explanation for this result is that *Agrostis* had a much lower below-ground productivity than the other four grasses (Fig. 5g). This difference in below-ground allocation leads to fewer carbon inputs and probably less microbial immobilization of nitrogen. Note that the same trend of increased nitrogen mineralization for *Agrostis* also occurs at low soil fertility. However, we are unable to determine if this pattern under *Agrostis* was actually caused by lower carbon inputs, which lead to decreases in microbial biomass, activity and immobilization rates, because no gross nitrogen mineralization rates are available from this experiment.

It is clear from this experiment that species which differ three and a half times in nitrogen use efficiency do not show any positive feedbacks on nitrogen cycling. In contrast, four out of the five species showed a negative feedback on net nitrogen mineralization based on their nitrogen use efficiency. This lack of consistent feedback supports our hypothesis that soil organic matter is the bottleneck through which nitrogen has to pass. The long turnover time of the soil organic matter leads to a negative feedback, where increased productivity leads to bigger pools of litter and soil organic matter and thus prevents any positive feedbacks from occurring. However, species-specific soil nitrate concentrations do lead to differences in leaching loss. Wedin & Tilman (1996) showed that soil mineral nitrate levels strongly correlated with nitrogen retention or loss from old fields.

Additionally, Wedin & Tilman (1993) found that these five plant species did not change total soil carbon and total soil nitrogen over 5 years, which is consistent with their other results. Wedin & Pastor (1993) did find a short-term difference in net laboratory nitrogen mineralization, but no long-term difference. Those results support the view that the balance between microbial immobilization and mineralization rates drives the net mineralization patterns, and that these patterns result from differences in below-ground carbon inputs from plants.

Species impacts on nitrogen mineralization

We can summarize our current understanding of species impacts on net nitrogen mineralization with two alternate concepts. In the first model, plants produce detritus of different qualities (Fig. 6). Part of the detritus is incorporated into a large inactive soil organic matter pool that
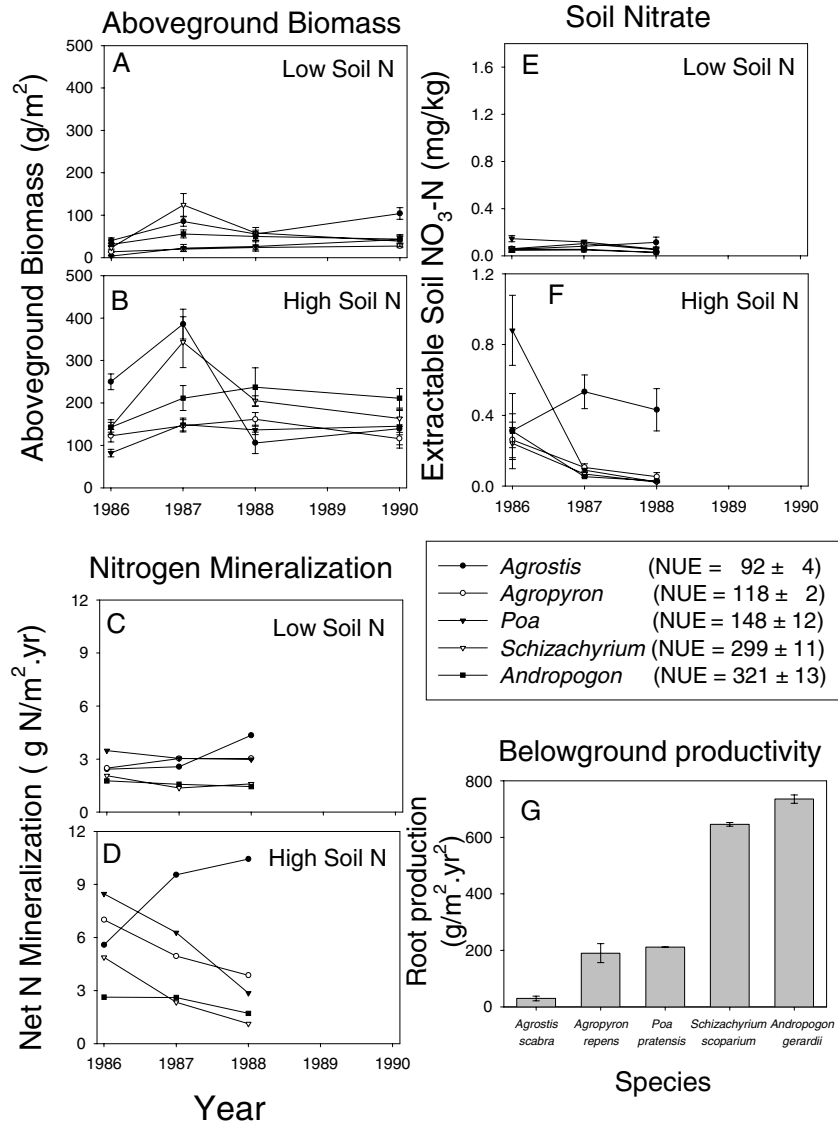
Figure 5 (A, B) Above-ground biomass, (C, D) nitrogen mineralization, (E, F) soil mineral nitrate levels and (G) below-ground net primary productivity of monocultures of *Agrostis scabra*, *Agropyron repens*, *Poa pratensis*, *Schizachyrium scoparium* and *Andropogon gerardii* established on low soil fertility (182 mg nitrogen/kg soil, SE 9, *n* = 10 per species) and high fertility (833 mg nitrogen/kg soil, SE = 30, *n* = 10 per species). Above-ground biomass is from one harvest per plot per year (see Tilman & Wedin 1991 for details. Nitrogen mineralization rates are the projected levels for the soil fertility levels of the plots (see Wedin & Tilman 1990) for details. Soil nitrate is the average of six measurements per year with a 1-M KCl extractions (Wedin 1990). Annual below-ground productivity is a 2-year average from high soil fertility plots only and is the difference between the maximum and minimum of 12 sequential corings per year (Wedin 1990).

decomposes at a constant decay rate. However, a part of the detritus is incorporated into a small active soil organic matter pool, and litter quality differences control the decomposition rate of this pool. Thus, small changes in the total soil organic matter caused by species differences can lead to a large change in net nitrogen mineralization, because of substantial changes in the size and decomposition rate of a small active soil organic matter pool (Parton *et al.* 1987; Wedin & Pastor 1993). In the alternate model,

we can view net nitrogen mineralization as being largely determined by nitrogen immobilization (Fig. 7). Plants fix carbon and supply carbon either directly, through root exudates, or indirectly in detritus, to soil microbial decomposers (Schmidt *et al.* 1997).

Soil organic matter is formed from retained recalcitrant components of the detritus, but also from dead microbes. Microbes decompose both soil organic matter, recent litter inputs and root exudates. Their net mineralization rate
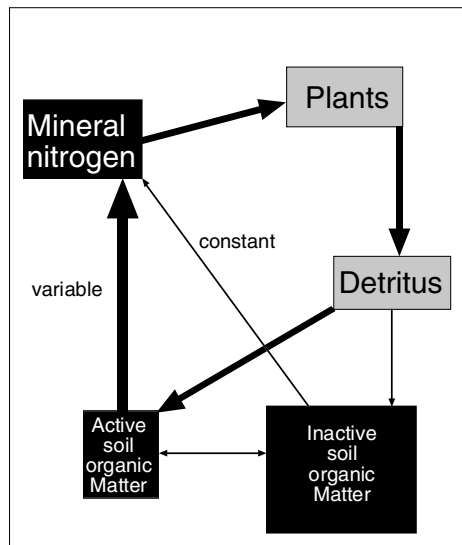
Figure 6 Soil organic matter pools and nitrogen cycling. Plant species may change a small active soil organic matter pool that differs in decomposition rates depending on plant litter quality. Net nitrogen mineralization is the sum of a constant mineralization from a large recalcitrant soil pool. Plant species determine the nitrogen mineralization rate from a small active soil organic matter pool (Parton *et al.* 1987; Wedin & Pastor 1993; Wedin *et al.* 1995).

depends on the relative amount of carbon inputs from plants (high in carbon, low in nitrogen), plant detritus (intermediate in nitrogen) and soil organic matter (high in nitrogen). Recent studies have shown in forests and grasslands that gross nitrogen mineralization is often an order of magnitude higher than net nitrogen mineralization and does not differ among plant species (Stark & Hart 1997; Verchot *et al.* 2001; Verchot *et al.* unpubl. data).

The rates of gross mineralization indicate that a microbial nitrogen loop strongly dominates nitrogen cycling. This loop consists of decomposition of soil organic matter for nitrogen, the incorporation of nitrogen into microbial biomass, and the return of nitrogen to the soil organic matter upon microbial death. The idea of a microbial-dominated nitrogen loop fits into our current understanding of nitrogen cycling, which is viewed as a complex network of both mutualistic and competitive interactions between the primary producers and decomposers (Harte & Kinzig 1993). Plant-available nitrogen is determined by what is left over from microbial uptake. The microbial nitrogen loop is driven by below-ground plant carbon inputs, because it provides microbes with a more easily degradable source of carbon than soil organic matter (Hart *et al.* 1994). However, plant species strongly differ in below-ground carbon inputs. For instance, Wedin *et al.* (1995) showed 25-fold differences in below-ground net primary productivity, whereas above-ground productivity only varied twofold (Fig. 5). The
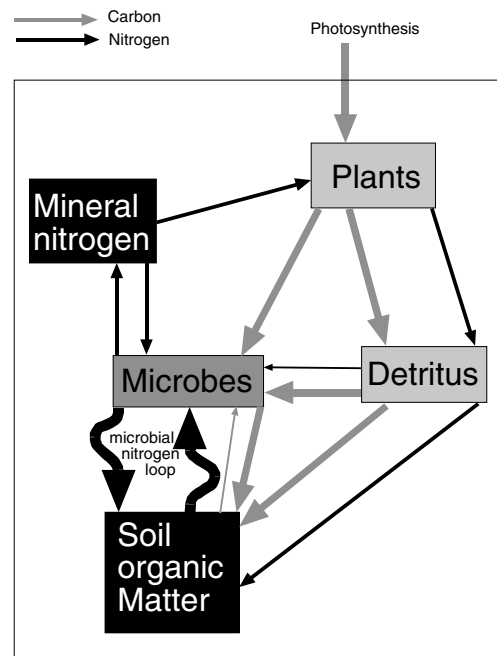

Figure 7 Controls of nitrogen flow within ecosystems. Arrow thickness indicates the relative importance of the flux. Soil microbes decompose soil organic matter, which provides them with nitrogen, whereas they derive most of their carbon directly or indirectly from plants. Most of the microbial nitrogen is incorporated into soil organic matter after microbial death. This microbial loop, which dominates nitrogen cycling within ecosystems, is driven by new plant carbon inputs. Net mineralization and immobilization rates depend on the ratio of new carbon inputs vs. the decomposition of soil organic matter. Thus, net nitrogen mineralization dynamics are regulated by the microbes, but driven by plant carbon supply to the microbes.

species with the lowest below-ground productivity (*Agrostis scabra*) also showed much higher soil nitrate levels and much higher net nitrogen mineralization, consistent with the view that plant carbon drives the microbial nitrogen loop and determines net nitrogen mineralization rates (van der Krift *et al.* 2001).

These two alternative views are not mutually exclusive. It is likely that there are different soil organic matter pools, and that there is a continuum from litter to soil organic matter (Melillo *et al.* 1982), which turn over at different rates. However, it is clear that the microbial decomposers control ecosystem nitrogen cycling and plants depend on the nitrogen left over from microbial uptake. Paradoxically, this microbial immobilization is largely driven by plant carbon inputs. Larger plant productivity leads to increased microbial nitrogen immobilization and smaller net nitrogen mineralization, whereas a decrease in plant productivity leads to an increase in net nitrogen mineralization. This provides a powerful negative feedback mechanism that contradicts any plant

species quality or quantity differences. Do note that there is strong evidence to support this for grassland ecosystems, but that the evidence supporting this productivity–nitrogen mineralization in forest ecosystems is much more limited. Mature forest stands show a linear relationship between productivity and nitrogen mineralization (Reich *et al.* 1997) and differences among stands and species are reflected in the soil organic matter pools (Finzi *et al.* 1998). However, no experimental studies comparable to grassland studies that examine short-term species differences in productivity in relation to nitrogen mineralization are available, as far as we know. Magill *et al.* (1997) examined nitrogen pools and fluxes in a 6-year nitrogen forest fertilization experiment that increased nitrogen inputs six- and 17-fold. However, they found that the net nitrogen mineralization rates only increased 8–80%, depending on the forest type and nitrogen addition levels. Many other forest fertilization studies show a similar pattern (Polglase *et al.* 1992; Prescott *et al.* 1992), but very high levels of nitrogen fertilization can result in an equivalent increase in nitrogen mineralization (Matson *et al.* 1992). Thus, there is strong evidence from low and intermediate nitrogen fertilization studies that increased nitrogen availability does lead to increased productivity and nitrogen storage in plants and soil organic matter, and that fertilization does not lead to a proportional increase in nitrogen mineralization. Nitrogen tracer studies also show that the soil organic matter is the dominant, while plants are the secondary long-term sink for nitrogen (Johnson *et al.* 2000; Zogg *et al.* 2000). Consequently, current evidence supports the hypothesis that increased productivity also leads to a negative feedback through nitrogen availability within temperate forest ecosystems.

In summary, there are two reasons that plant species do not directly cause short-term feedbacks within ecosystem nitrogen cycling. First, most nitrogen is retained in the decomposing litter and incorporated into soil organic matter, which prevents any immediate feedbacks. Second, the microbial nitrogen loop is driven by plant carbon and provides a negative feedback on any plant species quantity or quality differences. There is also increasing evidence that plants, especially in arctic and boreal regions, can take up, and are able to compete with microbes, for organic forms of nitrogen (Nasholm *et al.* 1998) and that different plant species differ in their uptake patterns of ammonium, nitrate and amino acids (McKane *et al.* 2002). In addition, mycorrhizal fungi have the potential to transfer nutrient from decomposers, as has been shown for phosphorus (Lindahl *et al.* 1999) and nitrogen from dead nematodes (Perez-Moreno & Read 2001), to plants, thereby circumventing the mineral pool (Fig. 7). Thus, it is increasingly clear that nitrogen cycling is controlled by microbes and by microbial interactions among decomposers, below-ground food webs and symbiotic mycorrhizae (Lindahl *et al.* 2002).

Pastor *et al.* (1993) used species shifts among non-nitrogen fixing tree species caused by herbivore presence to examine nitrogen mineralization and long-term soil fertility changes. However, this study found no significant differences in total soil nitrogen or nitrogen mineralization. Uriarte 2000 examined long-term non-nitrogen fixing species differences among plots caused by the presence of experimentally manipulated insect herbivores. She found no difference in nitrogen mineralization, but did find a significant, 45% change in total soil nitrogen. However, this corresponds to a total change of 2700 kg of nitrogen per ha (or an annual change of 159 kg nitrogen per ha), which seems highly unlikely because legumes are rare within this study. No other mechanisms of sustained nitrogen inputs or losses can be linked with the plant species changes within this system (Carson & Root 2000).

Thus, there is no compelling evidence from experiments that directly or indirectly manipulate non-nitrogen fixing plant species to support any strong long-term impact of plant species nitrogen use on ecosystem fertility.

SYNTHESIS

In conclusion, there is abundant evidence that plant species can have major impacts on nitrogen inputs and losses (Fig. 2). Many of these impacts are indirect and caused by plant species interactions with herbivores, soil microbial decomposers and symbioses with nitrogen fixing bacteria. However, many studies only address specific aspects of plant species impacts on ecosystems. Thus, there is an urgent need for more integrated ecosystem studies that study all components and their interactions. We think that such integrated studies are essential to gain a better understanding of both the mechanisms by which plants species influence nitrogen cycling and the relative importance of these mechanisms.

It is also becoming clear that plant species impacts on nitrogen cycling are primarily caused by their impacts on nitrogen inputs and losses. Internal nitrogen use efficiency differences among species are much less important. Species differences in nitrogen use efficiency do not result in strong feedbacks in nitrogen cycling for two reasons. First, most of the nitrogen present in plant detritus is retained during decomposition and incorporated into soil organic matter. This leads to a bottleneck within ecosystem nitrogen cycling, where a long time delay in the release of nitrogen precludes any feedback. Second, most of the nitrogen mineralized from soil organic matter is immobilized in microbial biomass, which is subsequently incorporated back into the soil organic matter. This microbial nitrogen loop is driven by more recent plant carbon inputs and provides an immediate negative feedback. Thus, the role of microbial decomposers in nitrogen cycling is much

more important than that of the plants, but microbes are dependent on the plants for carbon, e.g. energy. Microbes control the nitrogen cycling, but plants regulate carbon inputs that control microbial activity. Plant quality controls nitrogen cycling not because of a direct impact on nitrogen mineralization, but because plant carbon controls microbial immobilization.

ACKNOWLEDGEMENTS

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