Research review

Plants actively control nitrogen cycling: uncorking the microbial bottleneck

Author for correspondence:
Samantha K. Chapman
Tel: +1 928 699 2231
Fax: +1 928 523 7500
Email: Samantha.Chapman@nau.edu

Samantha K. Chapman[1,3], J. Adam Langley[1,3], Stephen C. Hart[2,3] and George W. Koch[1,3]

[1]Department of Biological Sciences, [2]School of Forestry, and [3]Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011, USA

Summary

Ecologists have tried to link plant species composition and ecosystem properties since the inception of the ecosystem concept in ecology. Many have observed that biological communities could feed back to, and not simply result from, soil properties. But which group of organisms, plants or microorganisms, drive those feedback systems? Recent research asserts that soil microorganisms preclude plant species feedback to soil nitrogen (N) transformations due to strong microbial control of soil N cycling. It has been well documented that litter properties influence soil N cycling. In this review, we stress that under many circumstances plant species exert a major influence over soil N cycling rates via unique N attainment strategies, thus influencing soil N availability and their own fitness. We offer two testable mechanisms by which plants impart active control on the N cycle and thereby allow for plant–litter–soil–plant feedback. Finally, we describe the characteristics of plants and ecosystems that are most likely to exhibit feedback.

Introduction

Over 120 years ago, the Russian soil scientist Dokuchaev hypothesized that climatic and geological factors were largely responsible for the development of the dominant characteristics of soils (Jenny, 1941). His work and that of contemporaries and predecessors such as Darwin (1883) prompted ecologists to recognize that soil fertility influences plant species distribution, but the degree to which established plant species feed back to control soil fertility remains a controversial issue in ecology. Empirical studies over the last 30 years have documented important influences of plant species on nutrient cycling, particularly for nitrogen (N), which is often growth-limiting (Hobbie, 1992; Binkley & Giardina, 1998; Menyailo *et al.*, 2002; Lovett *et al.*, 2004). In addition to the acknowledged concept that plants can alter nutrient cycling via nutrient use efficiency (*sensu* Vitousek, 1982), several researchers have suggested other mechanisms by which plant species mediate soil nutrient availability. Evidence to date indicates that plant species, through differences in litter quality and

specifically polymeric composition and polymer to nitrogen (N) ratios, can influence nutrient cycling (Scott & Binkley, 1997; Schweitzer *et al.*, 2004). This line of research has prompted many researchers to question whether plant species can, through litter feedback, influence their own fitness (Berendse, 1994)?

Researchers have invoked contradictory hypotheses to explain the magnitude and mechanisms of control of N cycling processes by plant species. In order to reconcile these disparate perspectives, empirical studies and literature reviews have lucidly outlined: (1) some potential mechanisms by which plant species may affect N cycling (Hobbie, 1992; Binkley, 1996; Binkley & Giardina, 1998), and (2) the alternative, nonplant, biological controls on N cycling (Holmes & Zak, 1999; Knops *et al.*, 2002). In a recent review, Knops *et al.* (2002) assert that because most litter N must pass through, and can be sequestered in, the 'microbial loop', N availability and cycling in ecosystems must be ultimately under microbial control. While this mechanism may predominate in some ecosystems, much evidence argues against a dominant microbial 'bottleneck' in forests. Knops *et al.* (2002) acknowledge that plant species can influence N inputs and losses (i.e. N fixation), but refute their role as the primary regulators of internal ecosystem N cycling because of the time lag between production of plant litter and the N release from that litter, negating the potential for nutritional feedback from plant litter to plant growth and fitness.

The novelty of this paper is twofold. First, we attempt to refute and refine the conclusions of the Knops review with recent empirical evidence showing that plants can and do supersede this microbial 'bottleneck'. Second, the idea that plants can create feedback to soil N cycling via litter chemistry has been thoroughly explored (Gosz, 1981; Hobbie, 1992; Binkley & Giardina, 1998). We merge this line of evidence for plant influence on N cycling with the idea that the importance of plant species extends beyond merely passive influences on soil quality via litter to active N access strategies. We advance the previous reviews on this topic by emphasizing how plant species employ unique active strategies to access N (organic) via mycorrhizal symbionts and by merging evidence for plant species' influence on litter quality feedback to N cycling with plant species' active control of N cycling.

In this paper, we highlight the most recent evidence that illustrates how plants, owing to species-specific differences in litter chemistry, can directly impact ecosystem N cycling. We then explore the evidence suggesting that plant control of soil nutrient inputs, via litterfall, can feed back to affect plant fitness. We also detail some additional mechanisms by which some plant species can minimize the dominance of the microbial loop and precipitate plant-to-soil N availability feedback because of differences in plant litter and other characteristics related to N cycling. We do not review previous studies that document plant litter–soil feedback to plant growth, because fairly recent syntheses on this topic already exist in the literature (Hobbie, 1992; Binkley, 1996). Rather, we delineate the ecological situations in which plant species feedback is likely to supersede the microbial bottleneck. Our objective is to advance theory on how plant species may regulate N cycling processes and to propose empirically testable, mechanistic hypotheses of potential plant species-N cycling links.

Recent evidence supporting the plant species–N cycling link

In addition to the studies reviewed by Binkley (1996), several recent empirical (Chen & Stark, 2000; Van der Krift & Berendse, 2001; Lovett *et al.*, 2004) and modeling studies (Miki & Kondoh, 2002) support the idea that plant species can have important effects on N cycling that feed back to plant function and species composition. Here, we highlight some of the recent studies not previously reviewed.

Many common garden experiments have outlined how plant species can affect N status of soils (France *et al.*, 1989; Binkley & Valentine, 1991; Menyailo *et al.*, 2002). Some recent studies using other approaches have also provided insight into the mechanisms by which plants can affect N cycling processes. For example, McKane *et al.* (2002) employed an ^{15}N tracer study in the arctic tundra and found that certain plants have differential access to soil N through specialized timing of N uptake, rooting depth or N form accessed. Their advantage over other co-occurring plants could have large impacts on ecosystem N cycling. Using monospecific tree plots in the Catskill Mountains, USA, Lovett *et al.* (2004) found that species identity strongly influenced the soil C to N ratio and potential rates of net N mineralization and nitrification. In these same plots, Templer *et al.* (2003) found that four out of the five tree species examined preferentially take up soil ammonium rather than nitrate, thus affecting the form of N primarily available for other plants and microbes. Scott (1998) performed two common garden experiments in which he compared the effects of six grass species and five tree species on organic matter and C and N mineralization, as mediated by soil aggregation. He showed that though grass species and tree species affected net N mineralization, grass species had no effect on soil organic matter concentration. However, although both of these recent studies document species effects on soil N processes, they do not directly suggest feedback to plant success or fitness.

Other studies documenting the plant species–N cycling link go further in demonstrating that potential feedback to plant success and survival can occur. A common garden experiment performed by Van der Krift and Berendse (2001) showed that the species identities of grasses are an important determinant of ecosystem N cycling. Specifically, species from high fertility habitats increased gross N mineralization and nitrification more than species from low fertility habitats. Increased N mineralization was not solely due to increased

production but was also a consequence of increased litter turnover rate, likely because of increased litter quality. The results from this study suggest that plants growing in high fertility sites reinforce the fertility regimes they inhabit, thus potentially promoting their existence in these sites. Chen & Stark (2000) examined shifts in plant community structure due to shrub invasion of grasslands. They conducted laboratory incubations with soils from 15-yr-old experimental plots that differed in the distribution of sagebrush (*Artemisia tridentata*) and crested wheatgrass (*Agropyron desertorum*). They found that soil samples collected beneath grasses had significantly greater total N and nitrate concentrations than those collected beneath sagebrush plants. They concluded that plant species significantly but subtly influenced N cycling (and C cycling) rates. Chen & Stark's (2000) study also suggests that plant species normally inhabiting more fertile sites (wheat grass) can generate these conditions in nonnative sites, thus creating a more suitable habitat for their future growth and reproduction. Miki & Kondoh (2002) developed a model to investigate the role of species-specific litter decomposability in determining plant community structure by plant–soil nutrient feedback. Their model predicts that positive feedback between plants and soil may generate multiple community equilibria with different species composition. The state of the community or 'output' is determined by the initial abundance of species and their associated traits. Modeling studies such as this are useful in investigating feedback because we would expect such feedback to occur over long periods of time, making it difficult to test in empirical settings. Perhaps the strongest evidence for the influence of plant species on N cycling feedback comes from the Binkley & Giardina (1998) paper where they summarized that the average difference in net N mineralization across plant species plots in a common garden was 50%. This extreme difference in soil N supply due to plant species in common garden settings necessitates that microbial control of N cycling cannot operate independent of plant species. Finally, intraspecific variation in leaf chemistry may also be important in propagating plant-soil feedback. For example, Schweitzer *et al.* (2004) found that genetically variant levels of condensed tannins in litter explained 55–65% of the variation in soil net N mineralization rates under both field and laboratory conditions. These recent studies, conducted in a variety of contrasting ecosystem types, provide compelling evidence suggesting that plant species, through their effects on soil fertility and N cycling, may feed back to affect their own future fitness.

A comprehensive examination of forest litter chemistry effects on N cycling across ecosystems also provides evidence suggesting that plant species may create self-sustaining feedback mediated by litter quality. Scott & Binkley (1997) synthesized the effects of forest floor litter chemistry and mineral soil chemistry on net N mineralization. They found a strong correlation ($r^2 = 0.74$) between lignin : N ratio (a litter quality parameter) of both the forest floor (litter) and the mineral soil (soil organic matter) and the net N mineralization rate of forest soils. The fact that lignin : N ratios of both litter and soil organic matter (SOM) were correlated with net N mineralization rates suggests that soil microorganisms do not completely remove the legacies of litter chemistry as they convert fresh plant litter to soil humus. The persistence of species-dependent lignin : N ratios in SOM points to a prolonged effect of plants on net N mineralization and thus availability.

Knops *et al.* (2002) used grasslands as their model system to describe plant species effects on N cycling. Scott & Binkley (1997) found that, unlike forests, grasslands did not exhibit an apparent correlation between litter chemistry and net N mineralization. This suggests that trees, and especially the temperate species examined by Scott and Binkley, may be more likely than grasses to propagate plant-soil feedback. In order for this relationship between forest litter quality and net N mineralization to be so strong, N must be mineralized and released from decomposing litter – and not just from an small active SOM pool, as Knops *et al.* (2002) suggest – in a systematic and predictable way, thus feeding back to the trees that produced the litter. Further, the size and dynamics of the active soil organic matter pool may be controlled by the nature of the plant litter inputs, adding more weight to the influence that plant species can have on N mineralization (Quideau *et al.*, 2001). We have focused on foliar litter, but forests also produce highly recalcitrant litter such as coarse woody debris, creating even more variability in forest litter quality.

Grasslands may differ from forests in that the chemical quality of grass litter is generally more readily decomposable and less variable among species than forest litter. Thus, only when viewed in the larger context of the global, cross-ecosystem level can we see that grasses do exert an effect on N cycling. The labile carbon compounds released from grass litter tend to cause immobilization of N in litter and thus, in effect, regulate the rate at which this N is mineralized from soil organic matter. This effect of grasses on N cycling differs drastically from the effect of most forest species but still represents an important control on nutrient cycling. When comparing grasslands with forests, in terms of N cycling control, the identity of a plant as a grass, but not necessarily as a specific grass species, matters. High rates of grass litter decomposition and the homogeneity of grass litter quality are likely to minimize the appearance of litter impacts on nutrient availability and promote greater apparent microbial control of N availability within grasslands. We feel that the strong correlation between litter quality and net N mineralization found across forests suggests that the microbial loop proposed by Knops *et al.* (2002) is not the primary regulator of N availability in forest ecosystems. The conclusions of Knops *et al.* (2002) were based primarily on their observations of grasslands, within which plant species control of nutrient cycling is not likely to be apparent because the above-mentioned lack of chemical variation in grass species' litter.
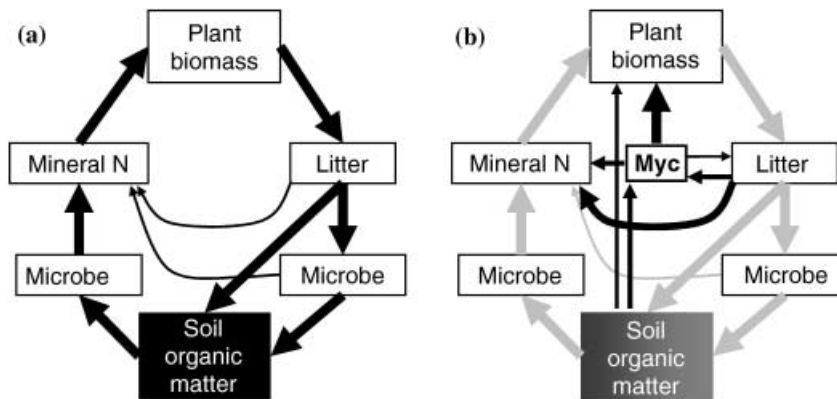
Fig. 1 Two representations of the nitrogen (N) cycle. In each case, arrows represent N fluxes, thickness is approximately proportional to the magnitude of the flux. (a) The N cycle, as described by Knops *et al.* (2002); (b) our representation includes several superimposed fluxes (in bold) that create a tighter, plant-oriented loop that allows for plant litter-mediated feedback. Myc, mycorrhizas.

Mechanisms by which plants subvert the microbial loop

Nitrogen limits primary production in most terrestrial systems (Chapin *et al.*, 2002). Adaptation of plants under conditions of high N competition or low organic N availability has selected plants with diverse mechanisms of obtaining N (Zak *et al.*, 1990; Kaye & Hart, 1997; Aerts & Chapin, 2000). Here, we describe how plants can obtain N directly from plant litter and illustrate some of the mechanisms by which plants compete with and therefore subvert the microbial control of the N cycle proposed by Knops *et al.* (2002).

Is soil organic matter the primary source of N for plants?

The notion of the N cycle advanced by Knops *et al.* (2002) necessitates that the vast majority of the N contained in plant litter is incorporated into the SOM pool (Fig. 1a). They state that the long period of time between the deposition of plant litter to the soil and the liberation of N from that source in a form utilizable by plants prevents any direct positive feedback of plant species on N cycling from occurring. In their model, N from plant litter must pass through the SOM pool before it is available to plants. Soil organic matter certainly contains the largest amount of N in ecosystems (Schlesinger, 1997), and most of this N is thought to be unavailable to plants over the short-term. However, much evidence refutes the generalization that most of the N released by microbes during decomposition of plant litter is incorporated into the SOM pool.

   Plants need an annual supply of N in order to synthesize enzymes (including photosynthetic enzymes), DNA and other compounds required for growth and respiration. The majority of this N has cycled through ecosystem components. The amount of N recycled through terrestrial vegetation is about an order of magnitude greater than the input of N to these ecosystems from the atmosphere (Paul & Clark, 1996; Chapin *et al.*, 2002). Over 80% of terrestrial plant uptake of N is obtained through ecosystem recycling (Whittaker *et al.*,

1979; Schlesinger, 1997). This recycled N is obtained by roots (often in association with mycorrhizas) or is retained in plants by resorption from senescing tissues. In many ecosystems, the majority of the N captured by roots is in the inorganic form (ammonium and nitrate) and originates by one of the following mechanisms: (1) leaching or mineralization of N from decomposing plant litter and microbial biomass; (2) mineralization of N from SOM (humus); (3) inorganic N released following fixation of N from the atmosphere by bacteria in symbioses with a plant; and (4) N deposition from the atmosphere. In order for meaningful direct plant–litter feedback to exist, pathway 1 (leaching or mineralization of N) must contribute a significant amount of N to plant nutrition (Fig. 1b).

   Several field studies using ^{15}N-labeled plant litter applied to the soil have shown that a substantial proportion of the N taken up by plants comes either directly from N released from decomposing plant litter, or from recent litter-released N that passes briefly through the microbial biomass without being incorporated into the SOM pool. These studies have been conducted in a variety of ecosystems (i.e. annual grassland, deciduous forest, agricultural fields) and generally show that from 2 to 25% of the added ^{15}N is taken up by the plant after a year of application to the soil (Hart, 1990; Zeller *et al.*, 2000). The actual N flux from plant litter to growing plants is likely much greater than these values suggest because: (1) generally only above-ground plant parts considered in calculating plant uptake; (2) usually only leaf litter is evaluated; and (3) most of the N residing in the litter has not been released by the end of the study (typically 1–3 yr). However, there are at least two other mechanisms by which plants compete with and therefore subvert the microbial control of the N cycle proposed by Knops *et al.* (2002) even if only a small amount of litter-N passes directly from the decomposing litter to the live vegetation.

Mycorrhizal fungi: soil microbes bound to plant species

Mycorrhizal fungi elude simple classification because they are morphologically and energetically coupled with autotrophs,
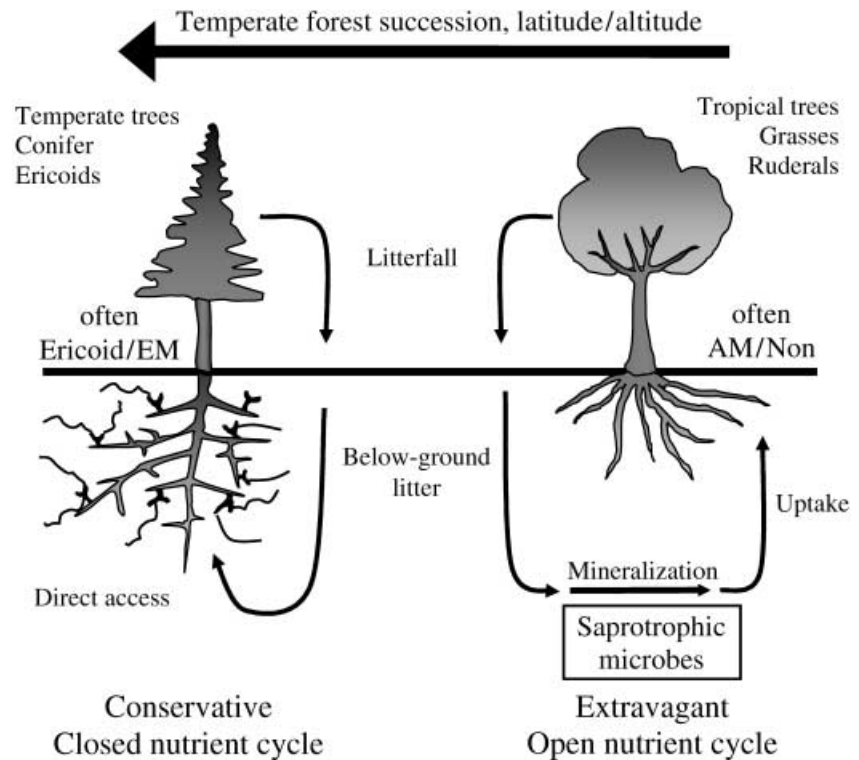
Fig. 2 Two extremes of plant–litter feedback potential. Conservative plants cycle nitrogen (N) tightly while extravagant plants allow, and rely on, free-living microbes to process much of the N in their litter. AM, arbuscular mycorrhizas; EM, ectomycorrhizas.

yet many possess nutrient mineralizing capabilities historically attributed only to free-living microbial heterotrophs. All gymnosperms and 80% of angiosperms form mycorrhizas (Wilcox, 1991). Mycorrhizal taxa differ widely in functioning, and plant functional groups coincide with that species' mycorrhizal strategy. For example, Cornelissen *et al.* (2001) found that fast-growing plant species produce nutrient-rich litter and tend to form arbuscular mycorrhizas, while slow-growing plants with poor litter quality more often associate with ectomycorrhizal or ericoid mycorrhizal fungi. Mycorrhizal type, which differs widely in function and in host plant associates, could mediate the influence of plant species on N cycling (Fig. 2).

Mycorrhizas can alter N cycling and contribute to plant–litter feedback by efficiently accessing mineral N, and by actively releasing N from organic matter (Zeller *et al.*, 2000) (Fig. 1b). Colonization by mycorrhizal fungi can increase the nutrient absorbing surface area of a plant by a factor of 60 (Simard, 2002) by producing hyphal surface areas of up to $200 \ m^2 \ m^{-2}$ of field soil (calculated from length data in Miller *et al.*, 1995). Further, mycorrhizal hyphae can extend into the soil to exploit narrow soil pores for resources otherwise unavailable to plants. Moreover, mycorrhizal hyphae can rapidly respond to new resource availability (Perez-Moreno & Read, 2000). Although the EM fungi may not be primary decomposers (Colpaert & van Tichelen, 1996) they can directly compete with saprotrophic species for nutrients (Leake *et al.*, 2002). Laboratory culture studies have shown that ericoid

mycorrhizal fungi can degrade an array of complex polymers. Laboratory studies have also demonstrated that some ectomycorrhizal fungi are proficient at breaking down simple polymers such cellulose, as well as having the capacity to degrade more complex biomolecules such as chitin and lignin (Read, 1991). Further, arbuscular mycorrhizal fungi may facilitate the uptake of simple organic molecules (Hodge *et al.*, 2001). Within each type, mycorrhizal fungi likely vary functionally among species and afford host plants varied access to soil N resources (Fig. 2).

Turnover of mycorrhizal litter itself can represent a large input of available N in many forests and may contribute to the specificity of plant–litter feedback (Fig. 1b). Fungi have high N concentrations compared with plant tissue, but this N is often bound within chitin, which resists decomposition (Swift *et al.*, 1979; Langley & Hungate, 2003). Ericoid fungi are proficient at digesting chitin; hence, the N contained within this pool may be more available to ericaceous plants (Kerley & Read, 1997). In nutrient-poor soils where ericaceous plants dominate, ericoid litter N may be relatively unavailable to organisms outside of the plant–mycorrhiza system (Read, 1991; Northup *et al.*, 1997; Lindahl *et al.*, 2002; Langley & Hungate, 2003).

Organic N uptake by plants

Organic N has only recently been explored as a potentially important pool of available N (Atkin, 1996; Chapin, 1995).

A variety of nonmycorrhizal plant species, ranging from arctic to tropical regions, have been shown to employ organic-N uptake to meet their N requirements (Chapin *et al.*, 1993; Kielland, 1994; Raab *et al.*, 1999). Mycorrhizal fungi can also access forms of organic N (ectomycorrhizas and ericoid mycorrhizas, Read, 1991, possibly arbuscular mycorrhizas, Hodge *et al.*, 2001) to a greater extent than nonmycorrhizal roots.

The microbial bottleneck proposed by Knops *et al.* (2002) is potentially obviated by the ability of plants and their associated mycorrhizal fungi to exploit organic N (Fig. 1b). Organic N uptake allows plants to access directly the N contained within their own litter. Nitrogen cycling feedback to plant success could be pronounced where exploitation of litter is spatially and temporally confined to the individual. Such positive feedback has been proposed in ecosystems where plants produce litter with high levels of phenolic compounds, which are effective at tightly binding N in protein (Jones & Hartley, 1999). Northup *et al.* (1997) suggested that these plants host ectomycorrhizas that can effectively take up the N that is bound to phenolics in plant litter. However, there is controversy regarding whether this is a regular occurrence in ecosystems. Chen *et al.* (2001) documented ectomycorrhizal genes encoding for the breakdown of lignin and other phenolic products. However, Wu *et al.* (2003) experimentally demonstrated that although mycorrhizas can access simpler forms of organic N, they were not able to access phenolic-bound N in a red pine system. Regardless, the exploitation of organic N by certain plant species likely has important implications for the fate of litter N and the ecosystem pools through which it passes.

Plant species effects: which species are likely to utilize the above-mentioned mechanisms?

We have outlined some mechanisms explaining how plants can actively subvert microbial control of N resources. The precise strategy of subversion may vary by species. Here, we describe the plant traits that we expect to be associated with stronger and weaker feedback to N cycling and contrast the plant functional groups likely to follow these distinctions. We separate plants into 'conservative' and 'extravagant' types with respect to N cycling.

Aerts & Chapin (2000) previously proposed elegant plant groupings that separated plants according to their strategies of nutrition. Our conservative and extravagant distinctions intimately overlap with their plant groupings in consideration of both the nitrogen form predominantly used and tissue quality. Our plant groups differ in one essential way from those outlined by Aerts & Chapin (2000). Conservative and extravagant plants are not defined by the 'nutritional ecology' or nutrient availability environment that they inhabit. Rather, conservative and extravagant plants (and their mycorrhizal symbionts) actively employ strategies within the plant–

mycorrhiza continuum that, to an extent, determine the nutrient environment they inhabit. Further, these plant types are not simply explained by assigning them to a mycorrhizal group as has been done by Cornelissen *et al.* (2001) but do, like most plant functional type groupings, correlate with broad patterns of mycorrhizal types.

Nitrogen-conservative plants

Nitrogen-conservative plants have characteristics that promote N transfers within the soil-plant continuum. We define species with the following characteristics as N-conservative plants: (1) support of high levels of mycorrhizal colonization; (2) dependence on mycorrhizal fungi for nutrient uptake; (3) ability to access organic N; and (4) production of low-quality, recalcitrant litter (Fig. 2, left side). Plant species exemplifying this category include conifers, broadleaf evergreen trees, ericaceous plants (tundra) and mangrove species. Most but not all N-conservative plants are ectomycorrhizal. For example, dipterocarps are ectomycorrhizal but have much higher litter quality than most plants in our conservative grouping and likely do not exhibit the same influence on nutrient cycling. Similarly, arbuscular plant species in poor soils may produce poor litter but have mechanisms of accessing the nutrients that would make them more conservative.

Distinctions previously made about nutrient-rich plants and nutrient-poor plants were often based on the levels of available soil mineral N (which was probably liberated from the SOM) (Hobbie, 1992; Binkley & Giardina, 1998). Conservatively N-cycling plants do not necessarily suffer from chronic nutrient shortage. Rather, these plants possess one or more of the above-mentioned strategies for obtaining and retaining N within the plant–mycorrhiza system that allows them to persist in nutrient poor soils. Regardless of soil N availability, these plants may actually preserve relatively more N within their biomass and that of their symbionts than plants found in nutrient richer soils.

Nitrogen-extravagant plants

Nitrogen-extravagant plants are leaky with respect to cycling of litter N in the plant-soil continuum. We define N-extravagant plants as having one or more of the following traits: (1) relatively low levels of mycorrhizal colonization, minimizing their dependence on mycorrhizas for nutrient uptake; (2) inability to access organic N; and (3) production of high-quality, nutrient-rich litter (Fig. 2, right side). Plant species that are representative of this category include grasses, some broadleaf deciduous trees, most forbs, and most tropical plants. We predict that these species, such as grasses which were the focus of the Knops *et al.* (2002) hypothesis, will often access N after it has been mineralized from the SOM pool. Because of the rapid and direct transfer of N from plant litter to heterotrophic microbes with these types of plants, N

cycling in these ecosystems may indeed be under control of the microbial loop, as proposed by Knops *et al.* (2002).

The majority of studies investigating and documenting the plant species-N cycling link have been performed in grasslands and other herbaceous plant-dominated ecosystems. However, even in these ecosystems some studies have provided evidence that plant species can be an important driver of N cycling (Chen & Stark, 2000; Van der Krift & Berendse, 2001). Perhaps, as Knops *et al.* (2002) suggest, soil microorganisms control N cycling processes in these ecosystems primarily through plant inputs of relatively available carbon (C) compounds; these compounds, in turn, affect the rate at which microorganisms immobilize and release N. The greater quantity of high-quality C compounds produced in grasslands than in forests is consistent with this hypothesis. Further support for this view is provided by Chen & Stark's (2000) suggestion that the differences in N cycling rates observed in soil under the two types of plants were likely due to greater fraction of labile C (and labile N) present beneath the wheatgrass plants. Clearly, more research is needed to better understand how plant litter chemistry alters C and N interactions during microbial decomposition of plant litter.

It is unlikely that plant species–N cycling feedback mechanisms operate only on a one-dimensional continuum of conservative to extravagant plants, wherein litters are simply stable or labile. Instead, plants may mediate feedback by more idiosyncratic mechanisms involving several nutrients bound in an array of compounds. Plant access to those nutrients depends on the nutrient uptake capacity of a given plant species. This continuum allows for species to exhibit some of the N attainment mechanisms mentioned above without completely obviating the microbial loop. For example, during one point in the year when N is less available, plants may rely more heavily upon organic N uptake but during times of greater N availability they access mineral N, and thus are more dependent on the activities of soil microorganisms (Schimel & Bennett, 2004).

Conclusions

There have been reviews discussing the feedback of species-specific litter quality (Hobbie, 1992) and reviews documenting the active control of N cycling by plant species due to symbionts (Read & Perez-Moreno, 2003). However, these two concepts have not yet been discussed in the same paper. The merging of these two inherently different ways in which plants can influence N cycling advances our understanding of this topic and connects two diverse lines of evidence for this influence. We have presented some testable hypotheses that will further the theory on the link between plant species and N cycling. Empirical studies could test our proposed mechanisms regarding: (1) the importance of plant litter as an immediate source of plant available N; (2) mycorrhizal facilitation of N uptake and influence on litter quality; and (3) plant and mycorrhizal uptake of organic N.

It is likely that the microbial bottleneck hypothesis of Knops *et al.* (2002) is supported in some situations, but there is ample evidence that plant characteristics and interactions do in fact exert strong control on N cycling processes in many settings. The next challenge in this field of study is determining where and how plants influence N cycling. We believe plant control of N cycling is most likely to be found in strongly N-limited systems. When fast N cycling occurs, N is rapidly converted to SOM and microbial N, and species effects weaken. We predict that plant species that fall into the conservative category will more strongly regulate N cycling than plant species exhibiting extravagant N-management.

Acknowledgements

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