

Competition for nitrogen between plants and soil microorganisms

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Many experiments have examined controls over plant available nitrogen (N), yet the mechanism of N limitation to temperate agricultural and wildland plants is poorly understood¹⁻⁵. Direct mechanisms of N limitation include N immobilization by clay fixation and reduced N diffusion due to low soil moisture. Indirect mechanisms of N limitation include low litter N content, low soil temperature, and carbon (C) or phosphorus limitation of soil microorganisms¹⁻⁷. Indirect mechanisms cause N limitation to plants by affecting microbial manipulation of the N cycle.

Ecologists have generally considered competition among plants for 'available' N to be an important determinant of plant growth and reproductive success because of the similar requirements of plants for this limited soil resource. However, soil microorganisms also use inorganic N, and inter-kingdom competition for N between plants/mycorrhizae and soil microorganisms may be an important mechanism controlling N limitation to plants. Mycorrhizae, which engage in mutualistic symbioses with most plants, probably play a role in plant-microbe competition¹. Despite the potential importance of this interaction, the degree and nature of competition for soil N between plants and soil microorganisms remain unclear.

Recent research on plant-microbe competition in wildland ecosystems^{8,9} and plant uptake of organic N (Ref. 1) has renewed interest in plant-microbe competition for soil N. In addition, ongoing increases in atmospheric CO₂ concentrations may increase litter C:N ratios, augmenting microbial demand for inorganic N (Ref. 10), and potentially intensifying plant-microbe competition. This review explores theoretical and experimental evidence for competition between plants and soil microorganisms for soil N. We use the resource competition conceptual model¹¹ as the basis for our discussion of plant-microbe competition. In this model of N competition, competition only exists if each competitor is N-limited and utilizes the same N resource.

The theoretical basis of competition for inorganic N

Plants and their mycorrhizal symbionts may compete with heterotrophic microorganisms for ammonium (NH₄⁺) or nitrate (NO₃⁻) or with autotrophic nitrifiers for NH₄⁺. Many ecologists have hypothesized that plants and heterotrophic microorganisms do not compete for soil resources because heterotrophic microorganisms are C-limited^{6,12}, while temperate plants are known to be N-limited². However, this generalization depends strongly on detrital C:N ratios.

Heterotrophic bacteria and fungi have C:N ratios ranging from 4:1 to 12:1; however, they respire about 50% of their C

Experiments suggest that plants and soil microorganisms are both limited by inorganic nitrogen, even on relatively fertile sites. Consequently, plants and soil microorganisms may compete for nitrogen. While past research has focused on competition for inorganic nitrogen, recent studies have found that plants/mycorrhizae in a wide range of ecosystems can use organic nitrogen. A new view of competitive interactions between plants and soil microorganisms is necessary in ecosystems where plant uptake of organic nitrogen is observed.

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uptake, and some organic matter fractions are not assimilated (e.g. lignin)⁶. Consequently, there is a theoretical critical detritus C:N ratio of approximately 30:1, above which heterotrophic microorganisms are N-limited and below which they are C-limited⁶. When heterotrophic microorganisms are C-limited, net N mineralization increases soil inorganic N, which may increase plant N uptake and decrease the C:N ratio of plant litter. Low plant litter C:N ratios decrease the C:N ratio of soil organic matter, facilitating net N mineralization and further increasing plant N uptake. When heterotrophic microorganisms are N-limited, they may use exogenous sources of N such as soil NH₄⁺ or NO₃⁻ while decomposing detritus^{8,13}. The majority of plant detrital inputs to soil organic

matter have C:N ratios greater than 30:1 (Ref. 6). The disparity between the critical C:N ratio of 30:1 and the C:N ratios of plant detritus provides strong theoretical support for the occurrence of competition between plants and heterotrophic microorganisms.

Competition may also exist between plants/mycorrhizae and soil autotrophic nitrifiers that use NH₄⁺, rather than C, as an energy source⁶. Early researchers hypothesized that autotrophic nitrifiers were minor sinks for NH₄⁺ and that plant-nitrifier competition was minimal¹⁴. Recent work shows that autotrophic nitrifiers may use substantial amounts of NH₄⁺ and that competition probably exists^{9,13}. However, plant-nitrifier interactions are more complex than this. Autotrophic nitrifiers gain energy by converting NH₄⁺ to NO₃⁻, which diffuses through soil much more readily than NH₄⁺ (Ref. 6). Therefore, while autotrophic nitrifiers may compete with plants for NH₄⁺, nitrifiers also produce a highly mobile N source which may be more accessible to plants¹⁵.

Some ecologists have assumed that heterotrophic microorganisms are superior competitors for soil inorganic N (Refs 4,5,16); indeed, the basis of most plant N availability indices rests on this assumption. Based on this view, plants assimilate N that is 'left over' after heterotrophic microorganisms are no longer N-limited. Rather than competing with plants for N, heterotrophic microorganisms mediate plant N uptake by controlling available N. This theory is bolstered by strong correlations between plant N uptake and net N mineralization rates^{4,7} (Fig. 1), and by short-term ¹⁵N experiments, which show that inorganic N uptake by heterotrophic microorganisms is unaffected by plants^{9,13}.

Experimental evidence for competition for inorganic N

Experimental evidence for plant-microbe competition for inorganic N comes from long- and short-term ¹⁵N experiments. In short-term ¹⁵N experiments, the soil inorganic N

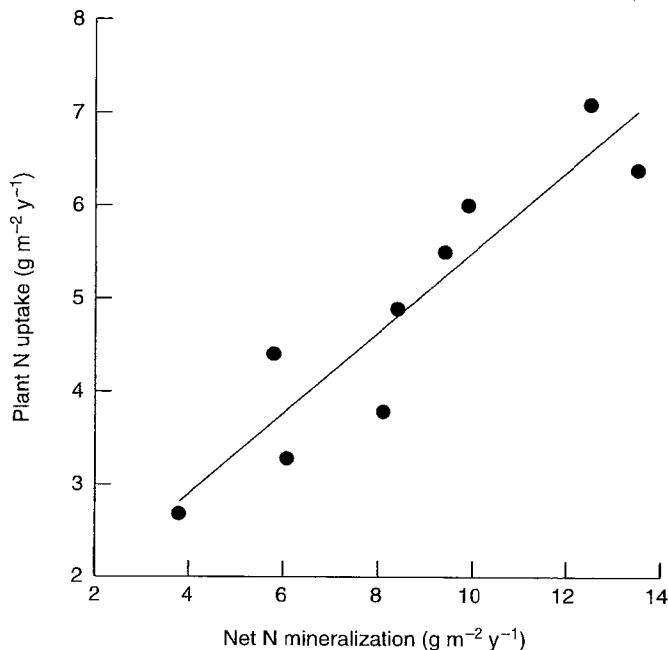


Fig. 1. Above-ground plant N uptake in relation to net N mineralization in soil (0–20 cm; from data in Ref. 4). $y = 1.5 + 0.43x$; $r^2 = 0.85$.

pool is enriched with $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$, and the ^{15}N label is measured in plant, microbial, and inorganic N pools after a few days. Long-term experiments use the same tracer techniques; however, the fate of the ^{15}N is determined after weeks or months. While specific plant–microbe competition events take place over minutes or days, the monthly or annual fate of N depends on the cumulative outcome of several individual short-term competition events^{5,15}.

Because plants have long life spans relative to soil microorganisms, plants may be able to take advantage of the high N fluxes resulting from microbial turnover. A single atom of

N may cycle through the soil microbial biomass many times during a year¹², or through above-¹⁷ or below-ground⁴ plant biomass many times during a decade. Thus, even if plants/mycorrhizae are relatively unsuccessful competitors for N during individual competition events, they can accumulate N for growth by competing several times for the same N atom and then storing N in plant tissues. Long-term ^{15}N experiments do not reveal the outcome of a specific competition event; they yield a point estimate of the long-term fate of N as calculated by the net amount of added ^{15}N residing in a pool after a specific amount of time.

Long-term ^{15}N uptake by soil heterotrophic microorganisms indicates that they assimilate N exogenous to the organic compounds from which they draw energy, and consequently have the potential to become N limited. Similar long-term N uptake rates between plants and heterotrophic microorganisms, or greater uptake by heterotrophic microorganisms, indicate the potential for competition due to mutual resource limitation. Greater long-term N uptake by plants suggests that: (1) the longevity of plants affords them greater N sink potentials; or (2) soil microorganisms use primarily organic N, leaving most of the inorganic N to plants. If (1) is true then long-term experiments reveal little information about short-term competition events. If (2) is true then greater N uptake by plants suggests a lack of competition because plants and soil microorganisms use different N sources.

The fate of added ^{15}N varied substantially among ecosystems in some recent, long-term experiments; however, all ecosystems showed significant microbial uptake of inorganic N (Table 1). Recovery of ^{15}N in managed pastures was consistently greater in plants than in soil microorganisms^{3,18}. However, ^{15}N recovery in a managed forest and an unmanaged annual grassland was similar in plants and soil microorganisms or greater in the microbial biomass, respectively^{19,20}. Based on these experiments, plant–microbe competition for inorganic N appears to occur in at least some ecosystems.

As mentioned above, long-term experiments measure the fate of N after several rounds of short-term competition events. Short-term ^{15}N experiments are the best way to assess plant–microbe competition events, because short turnover times of soil microorganisms, leaves and fine roots confound longer experiments. In complementary laboratory and field experiments, Schimel *et al.*¹⁵ and Jackson *et al.*⁸ added $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ separately to soils in a California annual grassland and measured the partitioning of these N sources after 24 hours. In the field, recovery of added $^{15}\text{NH}_4^+$ was greater in the microbial biomass (46–61%) than in plants (9–11%)⁸. Plants recovered from 17–26% of added $^{15}\text{NO}_3^-$ compared with 37–50% recovered by soil microorganisms. Laboratory microcosm results were similar to the field experiment, but the microcosm studies also showed microbial consumption of $^{15}\text{NH}_4^+$ was similar with and without plants¹⁵.

Zak *et al.*⁹ conducted similar experiments in a deciduous forest in Michigan. Excluding tree roots, they found 1% of added $^{15}\text{NH}_4^+$ and 3% of added $^{15}\text{NO}_3^-$ in spring ephemerals compared with 22% of added $^{15}\text{NH}_4^+$ and 32% of added $^{15}\text{NO}_3^-$ in the microbial biomass after 48 hours. The exclusion of all plants caused the extractable $^{15}\text{NO}_3^-$ pool to increase fivefold when $^{15}\text{NH}_4^+$ was injected, but did not change microbial assimilation of NH_4^+ or NO_3^- . Again, soil microorganisms recovered more ^{15}N than plants, and microbial assimilation of NH_4^+ was unaffected by the presence of plants.

Norton and Firestone¹³ found that added $^{15}\text{NH}_4^+$ to potted ponderosa pine (*Pinus ponderosa*) seedlings was distributed fairly evenly among the processes of plant uptake (30%), microbial immobilization (40%), and nitrification (30%) after

Table 1. Recent studies of the long-term fate of $^{15}\text{N}^a$

Site treatment	Substrate added	Duration (months)	% ^{15}N recovered in	
			Plants	Microbial biomass
Dairy pasture ^b (New Zealand)	^{15}N -Urea	4–6	31–63	6–7
Grass–legume association ^c (Italy)	^{15}N -Urea	1.9	24	6
		5.8	25	11
		18	28	11
		27	29	12
Annual grassland ^d (California, USA)	$^{15}\text{NH}_4^+$	8.4	6	13
		12.5	5	11
Loblolly pine clearcut ^e (N. Carolina, USA)	$^{15}\text{NH}_4^+$	5	11,13	12,15

^aFrom data in Ref. 20.

^bRange indicates variable time of application and duration of experiment. Plant recovery includes shoots only. The main species was *Lolium perenne*¹⁸.

^cPlant recovery includes shoots only. Species present were *Dactylis glomerata*, *Lolium* spp., *Medicago sativa* and *Lotus corniculatus*³.

^dPlant recovery includes shoots only. Main species were *Bromus mollis*, *Hordeum hystris*, *Avena barbata*, *B. madritensis* and *Lolium multiflorum*²⁰.

^eValues are from two different site preparation treatments. The main species was 22 year-old *Pinus taeda*¹⁹.

48 hours. Removing plants increased nitrification, but microbial assimilation of NH_4^+ remained constant. In a $^{15}\text{NO}_3^-$ amended system, plants recovered 70% of added ^{15}N and soil microorganisms recovered 30% (Ref. 13). When plants were removed from this system, nitrification increased while microbial NO_3^- assimilation did not change. In another experiment, microbial immobilization of $^{15}\text{NH}_4^+$ increased with increasing NH_4^+ addition, suggesting that the heterotrophic microorganisms were N-limited¹³. Nitrogen limitation in microbial heterotrophs was also indicated by the smaller amount of $^{15}\text{NH}_4^+$ assimilation that occurred compared with the amount predicted by a C-availability model.

These four experiments^{8,9,13,15} share some consistent results with respect to plant-microbe competition for inorganic N. Recovery of ^{15}N was similar between soil microorganisms and plants or greater in soil microorganisms, plant removal caused an increase in nitrification^{9,13}, and uptake of N by heterotrophic microorganisms was unaffected by plant N uptake^{8,9,13,15}. These results suggest that plants and soil microorganisms are mutually limited by, and consequently compete for, inorganic N. However, the results also provide evidence that heterotrophic microorganisms are much stronger competitors for inorganic N than plants, and that plants take up most of their N after heterotrophic microorganisms have assimilated enough inorganic N to eliminate their N limitation. Increases in nitrification following plant removal^{9,13} suggest that plants and autotrophic nitrifiers compete for NH_4^+ , and that plants may be the superior competitor.

Current perspectives on plant-microbe competition for organic N

Competition for organic N between plants and soil heterotrophic microorganisms is not often considered in N cycling studies because it is usually assumed that neither plant roots nor their mycorrhizal symbionts are capable of significant direct uptake or mineralization of organic N (Refs 4-6,13). Under this paradigm, which is indirectly supported by close relationships between net N mineralization rates and plant N uptake in some ecosystems (Fig. 1), N mineralization is solely the domain of heterotrophic microorganisms, and plants must rely on microbial mineralization and/or nitrification to liberate NH_4^+ or NO_3^- (Fig. 2). While this paradigm dominates the soil ecology field, there is abundant contrary theoretical and experimental evidence. Most terrestrial ecosystems are simultaneously N-limited and have high soil organic N:inorganic N ratios, suggesting that selection pressures for plant/mycorrhiza uptake of organic

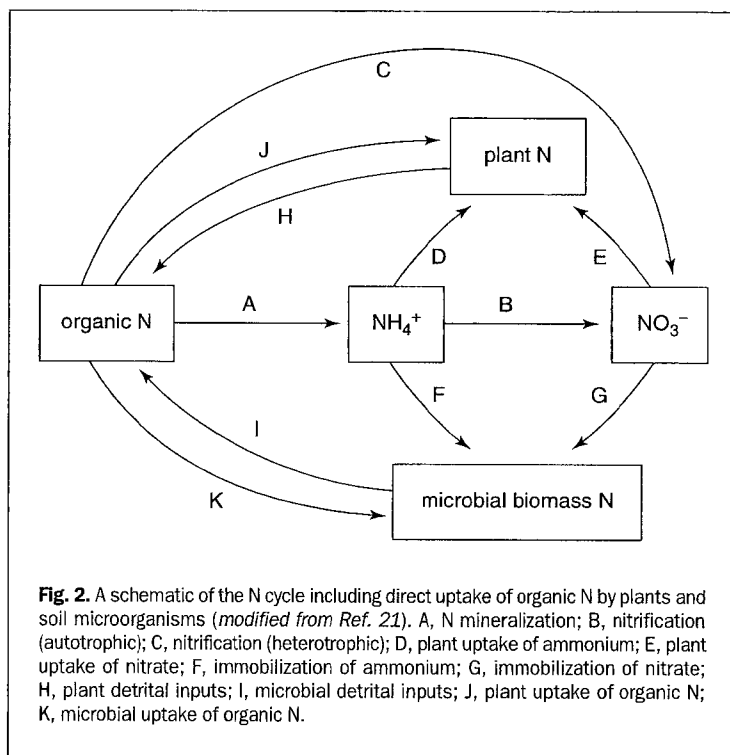


Fig. 2. A schematic of the N cycle including direct uptake of organic N by plants and soil microorganisms (modified from Ref. 21). A, N mineralization; B, nitrification (autotrophic); C, nitrification (heterotrophic); D, plant uptake of ammonium; E, plant uptake of nitrate; F, immobilization of ammonium; G, immobilization of nitrate; H, plant detrital inputs; I, microbial detrital inputs; J, plant uptake of organic N; K, microbial uptake of organic N.

Table 2. A summary of recent studies showing substantial plant uptake of organic N

Plant species	Native habitat	Mycorrhizal species	N source	Source
<i>Vaccinium macrocarpon</i>	Heathland (UK)	ericoid endomycorrhiza	Glycine Alanine Aspartic acid Glutamic acid Glutamine	22
<i>Vaccinium corymbosum</i>	Heathland (UK)	<i>Hymenoscyphus ericae</i>	L-alanine Peptides of alanine ^a	34
<i>Betula pendula</i>	Birch woodland (France)	<i>Hebeloma crustuliniforme</i>	protein L-alanine Peptides of alanine	32 33
		<i>Amanita muscaria</i>	L-alanine Peptides of alanine	
		<i>Paxillus involutus</i>	L-alanine Peptides of alanine	
<i>Picea mariana</i>	Black spruce forest (Canada)	<i>H. crustuliniforme</i>	protein	32
<i>Picea sitchensis</i>	Sitka spruce plantation (UK)	<i>H. crustuliniforme</i>	protein	23
<i>Pinus contorta</i>	Pine forest (Canada)	<i>H. crustuliniforme</i> Unknown pink hyphae	protein	23 35
<i>Eriophorum vaginatum</i>	Tussock tundra (Alaska)	none	Glycine Glutamate Aspartate	23,25,30
<i>Betula nana</i>	Dry heath (Alaska) Tussock tundra (Alaska) Shrub tundra (Alaska)	no data	Glycine Glutamic acid Aspartic acid	23
<i>Carex aquatilis</i>	Wet meadow (Alaska)	none	Glycine	23,30
<i>Eriophorum angustifolium</i>			Glutamic acid Aspartic acid	23 23
<i>Carex bigelovii</i>	Tussock tundra (Alaska)	no data	Glycine	23
<i>Ledum palustre</i>			Glutamic acid Aspartic acid	
<i>Salix pulchra</i>	Tussock tundra (Alaska) Shrub tundra (Alaska)	no data	Glycine Glutamic acid Aspartic acid	23

^aDi-, tri-, tetra-, penta- and hexa-alanine.

N may be strong^{6,22}. Furthermore, plant N often exceeds potentially available inorganic N in alpine, arctic, boreal and temperate sites^{5,23,24}. Organic N, which is abundant as insoluble detritus or dissolved organic N (DON) in these ecosystems, may be an alternative N source for plants^{23,26-28}.

If plants/mycorrhizae in a range of ecosystems use organic N, then competition with heterotrophic microorganisms probably exists. Heterotrophic microorganisms are known to use N associated with the organic C from which they draw energy^{6,29}, although it is unclear whether a majority of the N assimilated is mineralized externally or taken up directly^{29,30}. However, if symbiotic fungi are capable of direct uptake of organic N, it is likely that heterotrophic fungi are as well.

Went and Stark³¹ first suggested that direct uptake of organic N by tropical mycorrhizae may be important to plant nutrition. They observed fungal hyphae in aboveground plant litter, detrital roots and decaying stumps in Brazil. While these authors did not measure fungal uptake of organic N, such experiments have subsequently been carried out in other ecosystems (Table 2).

Recent studies of the organic N assimilative capabilities of plants show a wide range of organic N assimilation rates, but organic N uptake was always a substantial fraction of total plant N uptake (Table 2). Some species used organic forms of N preferentially over NH_4^+ (Ref. 25). Others had organic N uptake rates equal to or higher than NH_4^+ (Refs 22, 30,32). Even some non-mycorrhizal plants assimilated organic N (Refs 25,30,32). Ammonium often had higher maximum plant uptake rates (V_{max}) than organic N, but plant affinity (K_m) for organic compounds was often higher than for NH_4^+ when Michaelis-Menten kinetics of plant N uptake were calculated^{23,25}. As expected, uptake rates decreased with increasing size of the organic compound²³.

The geographic and taxonomic ranges of plant species that use organic sources of N are substantial (Table 2). Including the study of Went and Stark³¹, the ecosystems in which such plants occur include: tropical forests, boreal forests, temperate forests, heathlands and arctic tundra. Furthermore, many species that use organic N, such as lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*), are commercially important.

Plant uptake of organic N is rarely considered in temperate systems where N mineralization rates are high. However, as we discussed earlier, microbial competition may limit plant uptake of inorganic N even on relatively fertile sites. Plants on fertile sites could face the same selection pressures for organic N uptake as those on infertile sites. Consequently, it is plausible that plant-microbe competition for organic and inorganic N occurs simultaneously in ecosystems ranging from the tropics to the tundra.

Conclusion

To demonstrate plant-microbe competition for N in soil unequivocally, mutual N limitation and use of the same N resource must be shown¹¹. Nitrogen limitation of an organism can be demonstrated convincingly by increased N assimilation and growth, after N fertilization in the absence of competitors. Use of the same N resource (i.e. NH_4^+ , NO_3^- , or organic N) is best established using short-term ¹⁵N experiments with all competitors present; ¹⁵N recovery in the biomass of each competitor indicates use of the same N resource. Although in this review we have summarized a substantial amount of indirect and direct evidence in support of the hypothesis that some degree of competition exists between plants and soil microorganisms, no single study has clearly satisfied both conditions for the existence

of N competition between these distantly related taxa. The existence and extent of plant-microbe competition for inorganic and organic N resources need to be elucidated in ecosystems of contrasting structure and productivity before the nature of N limitation in terrestrial ecosystems can be fully understood.

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