Are microorganisms more effective than plants at competing for nitrogen?

Angela Hodge, David Robinson and Alastair Fitter

Plant scientists have long debated whether plants or microorganisms are the superior competitor for nitrogen in terrestrial ecosystems. Microorganisms have traditionally been viewed as the victors but recent evidence that plants can take up organic nitrogen compounds intact and can successfully acquire N from organic patches in soil raises the question anew. We argue that the key determinants of ‘success’ in nitrogen competition are spatial differences in nitrogen availability and in root and microbial distributions, together with temporal differences in microbial and root turnover. Consequently, it is not possible to discuss plant–microorganism competition without taking into account this spatiotemporal context.

Nitrogen (N) is the primary limiting nutrient in most terrestrial ecosystems. Competition between plants and microorganisms for this nutrient is believed to be intense. Traditionally, it was assumed that plants can access only the inorganic forms of N made available via the mineralization of soil organic matter. It was also assumed that microorganisms are the superior competitors for this N (Ref. 4) because of their major role in the mineralization process, large surface area/volume ratios and rapid growth rates compared with plant roots. Some mineral N will also be released by eukaryotic organisms and by the action of exoenzymatic activities within the rhizosphere (the volume of soil surrounding and influenced by the plant root) is densely populated with microorganisms and so there will be competition for this mineral N also.

However, some plants can also take up organic N compounds directly via their roots or when in association with some types of mycorrhizal fungi, thereby bypassing the dependency on microbial mineralization. This can only be a partial bypass because microorganisms can also use organic N sources and thereby will compete with plants for these, too. Consequently, the widespread importance of this mechanism to the N supply of plants remains debatable.

Inorganic nitrogen

Production and pools

Inorganic N is made available by the mineralization of organic N to ammonium (NH$_4^+$) and subsequent nitrification (mainly autotrophic) to nitrate (NO$_3^-$) (Fig. 1). Additionally, NO$_3^-$ can be produced from organic N by certain heterotrophic bacteria and fungi, mainly in acid soils, thereby avoiding the ammonification step (Fig. 1). Microbial mineralization and nitrification are generally thought to be the rate-limiting steps in the N cycle and it has thus been assumed that microorganisms are able to acquire inorganic N before plants.

It is difficult to assess direct competition between plants and microorganisms for soil N because (1) there are multiple loops and pathways through which N cycles at variable rates and in varying amounts between different pools (Fig. 1), and (2) some plants and some fungi in any ecosystem will be in a mycorrhizal symbiosis, providing an additional pathway for N movement.

The use of $^{15}$N-pool-dilution techniques has helped to resolve many uncertainties about N-pool fluxes. For example, $^{15}$N-labelling of the NH$_4^+$ and NO$_3^-$ pools of a grassland soil revealed that, even though the NH$_4^+$ pool was always moderately large, it was extremely dynamic and had a turnover time of ~1 day. The NO$_3^-$ ‘pool’ was even more dynamic, being consumed as rapidly as it was produced. Similarly, the mean residence time of small amounts of NO$_3^-$ in an undisturbed coniferous forest was only ~15 h (Ref. 11), indicating intense microbial activity. On a longer timescale, pulses of NH$_4^+$ in an acid woodland soil were short-lived persisting for a few weeks (Ref. 11).

Influence of the C:N ratios of soil organic matter

Most soil microorganisms are usually limited by the supply of easily decomposed carbon (C) in soil. However, most soil N transformations are carried out by microbial heterotrophs that depend on the supply of available organic C. The chemoaautotrophic nitrifiers *Nitrosomonas* and *Nitrobacter* are notable exceptions, using inorganic C as their C source and obtaining their energy from the oxidation of inorganic N compounds. Therefore the N and C cycles cannot be considered in isolation. This point is highlighted particularly by the influence of C:N ratios on the balance between N mineralization and immobilization.

The rate of mineralization of organic N depends first on the C:N ratio of the substrate being decomposed and second on the decomposer community’s need for N relative to its need for C. Fungi generally assimilate substrate more efficiently than bacteria, which have a smaller C:N ratio and consequently a larger N demand per unit C (Ref. 10; Fig. 2). If the C:N ratio of the substrate being decomposed exceeds that of the decomposers (after taking account of respired CO$_2$) then those microorganisms will not release inorganic N during decomposition and might supplement their N requirements from the soil’s inorganic N pool, reducing the availability of that pool to plants by the act of immobilization.

Conversely, if the C:N ratio of the substrate being decomposed is less than that of the decomposers (after taking account of respired CO$_2$) then those microorganisms will liberate excess N, often as NH$_4^+$, adding to the soil’s inorganic N by the process of mineralization. Thus, at C:N ratios less than about 12:5, neither fungi nor bacteria will require additional N, and net N release (mineralization) will occur. At C:N ratios greater than about 30:1, both fungi and bacteria will require additional N and net immobilization will occur (Fig. 2).

Under natural conditions, the situation is more complex. The heterogeneous nature of soil organic matter and the presence of a range of decomposers in soil ensure that N mineralization and immobilization occur simultaneously; net mineralization will occur typically at soil-organic-matter C:N ratios below ~25:1 (Ref. 13). Nit N immobilization after the addition of organic residues to soil can reduce plant growth, an effect that can be reversed by adding available N (Ref. 14). The rate of plant N capture generally increases as the C:N ratio of the substrate decreases (Table 1).

Plant–microorganism competition and spatiotemporal variations

There is abundant evidence that plants use N that is left over from microbial metabolism, at least in non-agricultural soils. For example, 24 h after the injection of NH$_4^+$ and NO$_3^-$ into a grassland soil, most of the $^{15}$N label was recovered in the microbial biomass (Table 1). Because the labelled N was added as an external source rather than produced via microbial processes, true competition between microorganisms and plants for the available N source would have been expected, rather than roots simply accessing N that had been discarded by the microorganisms. This study shows that, on a short timescale, soil microorganisms do...
compete better than plants for the added N, particularly for NH$_4^+$; its uptake by microorganisms was five times faster than that by plants. The NO$_3^-$ uptake rate by microorganisms was double that of plants.

By marked contrast, after 12 d, plants in an alpine ecosystem acquired 93–96% of an (15$^N$H$_4$$_2$SO$_4$ solution applied, compared with 4–7% recovered in the microbial biomass$^{15}$. However, in this study$^{15}$, the N supplied was sprayed directly onto the plots and it is possible that roots absorbed the labelled surface solution before it could penetrate into the soil; however, direct adsorption by the foliage was ruled out$^{15}$. Although microorganisms are better short-term competitors for N, it has been suggested that plants will win out in the longer term$^3$. Microbial cells turn over more rapidly than plant roots do, therefore releasing N back into the soil, whereas plants are able to retain captured N to a greater extent.

There is much evidence to support this view. For example, 49 d after the addition of discrete patches of organic material of low C:N ratio (i.e. <4) to Lolium perenne swards, about half of the added N (45–54%) was found in the plants$^{16}$, compared with <10% in the microbial biomass (Table 1). Furthermore, the organic material added was labelled with both 15$^N$ and 13$^C$, and, although 15$^N$ enrichments were detected in the plant tissues, plant 13$^C$ was never enriched. This implies that microbial decomposition of these patches occurred first and that the plants took up N in inorganic form rather than as intact organic compounds. However, plants captured only 11% of the N from a patch with a higher C:N ratio (i.e. 21:1), a comparable amount to the microbial biomass (Table 1), and most of this patch remained undecomposed. These quantities of N in the microbial biomass are similar to the 6–15% reported from long-term field studies (1.9–27.0 months) after the addition of either urea or NH$_4^+$ (reviewed in Ref. 17).

After an initially rapid N capture and the assimilation of inorganic N by soil microorganisms, as short-term studies indicate (Table 1), the microbial biomass appears to reach a steady state. One possible explanation is that the microbial biomass again becomes limited by C rather than by N. As the microbial biomass turns over, there is insufficient C to maintain its fast initial growth rates and therefore N is released into the soil, there becoming available to plants. The relative turnover times of roots and microorganisms are therefore likely to be a key determinant of competitive success; it is the rapid turnover of microbial biomass that gives the roots an opportunity to capture released N through microbial cell lysis. However, there can be large differences between microbial populations in turnover time: mycelial structures (fungi and actinomycetes) can recycle N internally and their N turnover therefore can be much slower than for bacteria. Similarly, perennial plants also recycle N internally by remobilizing N from senescent tissues, thus reducing N losses to the external environment relative to those from annuals.

Freeze–thaw and drying–rewetting events disrupt microbial cells$^{18,19}$, thus reducing microbial populations. Such events might provide the plant with a competitive opportunity because roots both compete with a decreased microbial population and have additional N available via microbial-cell lysis. Most of this N will be organic, especially in prokaryotes, whose production of proline and glutamate generally increases with osmotic stress$^{10}$. Plants such as the arctic sedge (Kobresia myosuroides), which is common in systems prone to freeze–thaw and dry–rewet events, can take up amino acids directly$^{19}$.

The pronounced heterogeneity of soils profoundly affects all plant–microorganism interactions. The organic matter from which NH$_4^+$ and NO$_3^-$ are produced is patchily distributed throughout the soil in both space and time, and its decomposition creates nutrient-rich patches.
Many plant species proliferate their roots within such patches (Fig. 3). However, this proliferation can take a long time to establish (e.g. ~35 d for a range of grass species), during which the microbial biomass might have turned over many times and decomposition thus be complete. Nevertheless, plants can acquire a large fraction of N from an organic patch relatively quickly, simply because the slower turnover of roots and the potential for internal recycling makes the plant N pool an effectively self-absorbing sink.

The important point here is that not only does plants capture N from the turn-over of older soil organic matter but they can also capture substantial amounts from the turnover of more-recent additions, in spite of the microorganisms apparently getting the N first. Why then do plants proliferate roots in N-rich patches at all?

Inorganic N (particularly $\text{NO}_3^-$, which is more mobile in soil than $\text{NH}_4^+$) will diffuse readily through the soil to the root surface and the speed at which new roots can be produced will never match that of the turnover rates of microbial cells. Indeed, in plant monoculture, the extent of root proliferation is unrelated to plant N capture from decomposing complex physical and chemical organic patches (e.g. L. perenne shoot material) in the soil.

However, more recent evidence has shown that, when plants are grown in competition with other plant species, there is a direct relationship between root proliferation and N capture. Thus, although roots might not be produced quickly enough to compete directly with microorganisms for inorganic N in the

short term, the relative length density of the root systems and hence root production are crucial when they compete with the roots of other plants. This is particularly true in complex organic patches, in which microbial decomposition continually produces inorganic $\text{N}$ throughout the patch; consequently, the spatial placement of roots becomes much more important. The greater the root-length density maintained by a plant within the patch, the more likely roots are to be present when and where mineralized $\text{N}$ is released. Thus, localized root proliferation has two ecologically relevant functions: it enhances N capture for the plant that has produced the most roots; and it reduces N capture by competitors.

Organic nitrogen

In some ecosystems (e.g. tundra, boreal and temperate forests, and heathlands), the rate of N mineralization is insufficient to meet the known rate of N uptake by the vegetation. This might reflect a simple underestimate of N mineralization or the existence of N-acquisition mechanisms that allow direct uptake by plants of unmineralized (i.e. organic) N (Refs 5,6). Much emphasis has been placed on the ability of plants to take up organic N compounds directly, so reducing plants' dependency on mineralization. However, many studies of this phenomenon have been at unrealistic temperatures, with unlikely nutrient enrichments and in the absence of microorganisms. The amino acid glycine, commonly used as a putative organic N source for plants, is a relatively poor substrate for microbial growth. This, in itself, does not argue against the uptake of organic N by roots (indeed, it might be that a capacity to take up this amino acid has evolved in roots for this very reason) but it does question whether true microorganism-plant competition is occurring.

There is also evidence that many plants might in practice be unable to take up organic N compounds in competition with microorganisms, as shown by the lack of detectable $^{13}$C enrichments in the plant tissues when $^{13}$N-$^{13}$C-labelled substrates have been applied. However, it is possible that small amounts of $^{13}$C might have been absorbed and then lost via catabolism over the experimental period in these studies. Furthermore, if only small amounts of $^{13}$C were present then they might have been below detectable limits. Alternatively, amino acid influx into roots has been proposed as a mechanism by which roots could control the availability of nutrient supplies and hence regulate the size and activity of their associated rhizosphere microbial population. The true ecological significance of the phenomenon of organic N uptake currently remains obscure.

Role of mycorrhiza

Most plants are colonized by mycorrhizal fungi under natural conditions. Although the
Table 1. Plant and microbial partitioning of added $^{15}$N substrates

<table>
<thead>
<tr>
<th>Material added</th>
<th>Substrate C:N ratio</th>
<th>Plant species</th>
<th>Duration</th>
<th>% N captured</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lolium perenne</em> shoots</td>
<td>31.0:1.0</td>
<td><em>Festuca arundinacea</em></td>
<td>39 d</td>
<td>3.6 ND</td>
<td>20</td>
</tr>
<tr>
<td><em>Lolium perenne</em> shoots</td>
<td>31.0:1.0</td>
<td><em>Poa pratense</em></td>
<td>39 d</td>
<td>3.5 ND</td>
<td></td>
</tr>
<tr>
<td><em>Lolium perenne</em> shoots</td>
<td>31.0:1.0</td>
<td><em>Poa pratense</em></td>
<td>39 d</td>
<td>3.2 ND</td>
<td></td>
</tr>
<tr>
<td><em>Lolium perenne</em> shoots</td>
<td>31.0:1.0</td>
<td><em>Dactylis glomerata</em></td>
<td>39 d</td>
<td>4.8 ND</td>
<td></td>
</tr>
<tr>
<td><em>Lolium perenne</em> shoots</td>
<td>31.0:1.0</td>
<td><em>Lolium perenne</em></td>
<td>39 d</td>
<td>5.0 ND</td>
<td></td>
</tr>
<tr>
<td><em>Lolium perenne</em> shoots</td>
<td>21.0:1.0</td>
<td><em>Lolium perenne</em> sward</td>
<td>49 d</td>
<td>11.0 12*</td>
<td>16</td>
</tr>
<tr>
<td>Algal amino acids</td>
<td>3.1:1.0</td>
<td><em>Lolium perenne</em> sward</td>
<td>49 d</td>
<td>54.0</td>
<td>9*</td>
</tr>
<tr>
<td>Algal cells</td>
<td>3.2:1.0</td>
<td><em>Lolium perenne</em> sward</td>
<td>49 d</td>
<td>45.0</td>
<td>9*</td>
</tr>
<tr>
<td>L-lysine</td>
<td>2.4:1.0</td>
<td><em>Lolium perenne</em> sward</td>
<td>49 d</td>
<td>46.0</td>
<td>9*</td>
</tr>
<tr>
<td>Urea</td>
<td>0.4:1.0</td>
<td><em>Lolium perenne</em> sward</td>
<td>49 d</td>
<td>53.0</td>
<td>7*</td>
</tr>
<tr>
<td>$^{15}$NH$_4^+$</td>
<td>NA</td>
<td>CA, USA grassland (field study)</td>
<td>1 d</td>
<td>9.0–11.0</td>
<td>46–61</td>
</tr>
<tr>
<td>$^{15}$NO$_3^-$</td>
<td>NA</td>
<td>CA, USA grassland (field study)</td>
<td>1 d</td>
<td>20.0–26.0</td>
<td>38–50</td>
</tr>
<tr>
<td>($^{15}$NH$_4$)$_2$SO$_4$</td>
<td>NA</td>
<td>Alpine moist meadow, CO, USA (field study)</td>
<td>12 d</td>
<td>93.0–96.0</td>
<td>4–7</td>
</tr>
</tbody>
</table>

* N in microbial biomass not measured directly but indirectly using protozoan biomass values

Abbreviations: ND, not determined; NA = not applicable.

The arbuscular mycorrhizal association is the most common type, and the role of these fungi in accessing organic N for plants is the most controversial. Direct uptake of glycine by ecto-, ericoid and arbuscular mycorrhizal plants has been shown in the field, although most (>60%) of the amino acid remained in the soil. There is also some evidence from laboratory experiments that roots colonized by arbuscular mycorrhizal fungi showed enhanced uptake of intact serine compared with uncolonized controls. However, other microorganisms were excluded in this study, preventing any direct competition for the substrate between plants and microorganisms or between microorganisms; in addition, serine, like glycine, is a poor substrate for microbial growth compared with many other amino acids.

When a more-complex substrate (*L. perenne* shoots) was added to soil containing either an indigenous arbuscular mycorrhiza inoculum or an indigenous and an additional inoculum (*Glomus mosseae*), there was no direct uptake of intact organic N (Ref. 26). Nitrogen capture from the mineralized organic material was, however, related to the proportion of vesicles (fungal storage organs) in the roots. Arbuscular mycorrhizal fungi might enhance plant N capture from inorganic sources27, presumably by being more effective than roots as competitors with soil microorganisms for mineralized N. Evidence that arbuscular mycorrhizal fungi contribute to the direct uptake of intact N from organic sources that are also potential substrates for other microorganisms remains equivocal. Perhaps this is not surprising; both fungal and plant partners in the arbuscular mycorrhizal association have generally coevolved in soils deficient in available phosphorus but not N, unlike the partners in the ectomycorrhizal and the ericoid associations. Therefore, for most plant species that form arbuscular mycorrhizal associations, it is unlikely that fungal N capture is an important factor in root–microorganism competition.

**Fig. 3.** Root growth into an N-rich organic patch composed of lyophilized algal cells viewed using a minirhizotron tube and a borescope camera. Each image is ~7 mm in diameter. (a) 21 days after the patch has been added, a single root is seen growing into the nitrogen-rich zone. (b) The same image four days later shows increased root production and root-hair development in the nitrogen-rich zone.
of this N. When N is in the form of discrete patches of low C:N ratio, these longer periods might be only a few days, apparently because of the longer lifespan of root systems compared with most soil microorganisms. For most plant species, both the direct uptake of simple organic compounds and arbuscular mycorrhizal assistance appear to be unimportant in N capture. The principal weapon that plants possess is their ability to sequester N for much longer periods than most microorganisms. Root-proliferation responses are more important to understanding plant–plant than plant–microorganism competitive interactions.

We still know little about the precise factors regulating the expansion, activity and diversity of the microbial biomass in the rhizosphere, which are responsible for the localized transformations of complex N substrates into plant-available forms. In addition, we do not yet have sufficient information about the contributions of specific components of the microbial biomass to particular N transformations. Recent advances have revealed important new information about gene expression in certain N-transforming microorganisms, in signalling between plants and rhizosphere microorganisms, and between external NO₃ and roots. These suggest that tools are now available to approach the ecologically important question of plant–microorganism competition for N at molecular scales.

Acknowledgements

We thank three anonymous reviewers for their perceptive comments. A.H. is funded by a fellowship awarded by the Biotechnology and Biological Sciences Research Council (BBSRC), UK.

References


Angela Hodge* and Alastair Fitter are at the Dept of Biology, PO Box 373, University of York, York, UK Y010 5YW; David Robinson is at the Dept of Plant and Soil Science, University of Aberdeen, Aberdeen, UK AB24 3UJ.

*Author for correspondence (tel +44 1904 432878; fax +44 1904 432860; e-mail ah29@york.ac.uk).

Letters to Trends in Plant Science

Correspondence in Trends in Plant Science may address topics raised in very recent issues of the magazine, or other matters of general current interest to plant scientists. Letters should be no more than 700–800 words long with a maximum of 12 references and one small figure. Letters should be sent, together with an electronic copy on disc to the Editor (or e-mail your text to plants@current-trends.com). The decision to publish rests with the Editor, and the author(s) of any article highlighted in Correspondence will normally be invited to reply.