Towards a rhizo-centric view of plant-microbial feedbacks under elevated atmospheric CO₂

The stimulatory effects of elevated CO₂ on plant productivity have been reported for many ecosystems (Ainsworth & Long, 2005), but whether such effects will persist in the face of increasing nutrient limitation is unclear. In nitrogen (N)-limited ecosystems, elevated CO₂ has been hypothesized to decrease nutrient availability as the N becomes sequestered in plant and soil pools with slow turnover rates. Alternatively, an elevated CO₂ may increase nutrient availability by stimulating N release from soil organic matter (SOM), resulting in positive feedbacks to primary production. Previous reports on the effects of elevated CO₂ on N cycling have been variable, with reports of increases, decreases or no change in soil N dynamics under elevated CO₂ (Zak et al., 2000). One major source of uncertainty is the degree to which potential changes in root-derived C affect the microbial regulation of soil N availability. In this issue of New Phytologist (pp. 778–786), de Graaf et al. describe a novel approach to examining the effects of elevated CO₂ on root-derived inputs of N to soil. Their results support an emerging ‘rhizo-centric’ view, whereby root–microbial interactions may be the central processes in controlling the magnitude and duration of plant productivity responses under elevated CO₂.

‘... roots and rhizosphere microbes play a more important role than has been previously considered in mediating soil N availability under elevated CO₂.’

By labeling plants with ¹⁵N via foliar uptake, de Graaf et al. quantified the magnitude and fate of N from rhizodeposition in wild and cultivated genotypes of wheat and maize exposed to ambient and elevated levels of CO₂. Their study reported that rhizodeposition was a strong sink for foliar-applied N in all plants (5–10% of the total uptake from leaves), and that elevated CO₂ increased this flux in those plants that also increased in total biomass (e.g. wheat but not maize). Moreover, this study reports that CO₂-induced increases in rhizodeposition decreased soil N availability, as greater amounts of root-derived N were immobilized in the rhizosphere of the labeled plants and lesser amounts were taken up by unlabeled, ‘receiver’ plants growing in the same pots.

Increased C fluxes from roots to soil under elevated CO₂ have been reported previously but the consequences of such changes for soil N cycling are unclear (Cheng, 1999). de Graaf et al. suggest that greater N immobilization by rhizosphere microbes and decreased N uptake by receiver plants are evidence of enhanced N limitation. However, an alternative interpretation of this is that plants grown under elevated CO₂ retain a greater proportion of rhizodeposited N within their rhizosphere. This could be accomplished through CO₂-induced increases in rhizosphere microbial biomass as a result of increased root exudation. Such immobilization would not necessarily represent a major loss of N from an individual plant because much of the N would be available for subsequent uptake due to the rapid turnover of the rhizosphere microbial biomass (Paton, 2003). Furthermore, the loss of root-derived N would likely be minor relative to potential N gains from increased root growth and/or root-induced stimulation of decomposition (Cheng & Kuzyakov, 2005). Both hypotheses are consistent with the data, and suggest that roots and rhizosphere microbes play a more important role than had previously been thought in mediating soil N availability under elevated CO₂.

Rhizosphere feedbacks under elevated CO₂

Previous conceptual models of plant–microbial interactions under elevated CO₂ have focused on bulk soil processes (Fig. 1a). Although such models are appropriate for understanding ecosystem responses in the long term, they do not consider how spatially and temporally dynamic processes occurring in the rhizosphere can influence ecosystem response to elevated CO₂. This may explain, in part, why several studies have been unable to account for CO₂-induced increases in N in ecosystem budgets (Johnson, 2006). At the Duke Forest free-air carbon dioxide enrichment (FACE) site (North Carolina, USA), the N content of the canopy trees has increased in response to elevated CO₂ despite there being no evidence of increased net N mineralization rates in the soil (Finzi et al., 2006). Because net N mineralization is measured in the absence...
of roots, it is plausible that the unaccounted-for canopy N is derived from enhanced N availability due to rhizosphere processes. A more rhizo-centric view would account for how changes in the intensity of root–microbial interactions under elevated CO$_2$ affect soil N availability and feedbacks to plant productivity (Fig. 1b).

The increased importance of rhizosphere processes under elevated CO$_2$ results from both increased rhizodeposition and changes in rhizosphere N availability. Elevated CO$_2$ can increase rhizosphere C flux through increases in fine root biomass (Norby et al., 1987; Uselman et al., 2000) and/or increases in mass-specific exudation (Phillips et al., 2006). Moreover, elevated CO$_2$ may also induce changes in the chemical composition of exudates (Hodge & Millard, 1998; Phillips et al., 2006). Will such CO$_2$-induced changes in the quantity and chemical quality of exudates influence the microbial processing of soil N? Most root exudates are low molecular weight organic compounds (sugars, amino acids, organic acids) that have traditionally been viewed in light of their effects on P and Fe availability (Marschner, 1995). However, exudates are also the preferred substrates for the rhizosphere microflora (Cheng, 1999), and the rapid assimilation of exudates creates a ‘rhizosphere effect’ around roots where the tight coupling between substrate availability and soil microbial activity is likely to influence soil N availability (Paterson, 2003).

**Rhizosphere effects on soil N availability**

There are several ways in which roots may increase soil N availability under elevated CO$_2$ (Table 1). First, rhizodeposition may stimulate decomposition through priming effects (Cheng & Kuzyakov, 2005). This has the potential to dramatically increase soil N availability because of the large size of the N pool in SOM. Second, increased C allocation to roots and mycorrhizal fungi under elevated CO$_2$ could increase N availability through increased foraging in soil. Moreover, mycorrhizal fungi (and some plants) may increase N availability through the uptake of organic N (Jones et al., 2005). A third rhizosphere process which may provide a

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**Table 1** Potential rhizosphere effects on soil N availability under elevated CO$_2$

<table>
<thead>
<tr>
<th>Rhizosphere process</th>
<th>Mechanism</th>
<th>Effects on N*</th>
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<tbody>
<tr>
<td>Exudate-induced decomposition</td>
<td>Increased SOM decomposition due to priming of rhizosphere microbes</td>
<td>++</td>
</tr>
<tr>
<td>Mycorrhizal growth</td>
<td>Increased soil exploration, exo-enzyme activity, organic N acquisition</td>
<td>++</td>
</tr>
<tr>
<td>Fine root growth</td>
<td>Increased soil exploration; expansion of rhizosphere extent</td>
<td>+</td>
</tr>
<tr>
<td>Associative N fixation</td>
<td>Increased fixation due to high C availability and low O$_2$ potentials</td>
<td>+</td>
</tr>
<tr>
<td>Grazing of rhizosphere microbes</td>
<td>Increased release of NH$_4$ via the microbial loop</td>
<td>+</td>
</tr>
<tr>
<td>Release of novel compounds</td>
<td>Increased/decreased N due to exudate effects on specific microbial taxa; decreased root competition from allelochemical release</td>
<td>+ or –</td>
</tr>
<tr>
<td>Root allocation of metabolites</td>
<td>Increased N immobilization due to higher C : N of root exudates</td>
<td>–</td>
</tr>
<tr>
<td>Rhizosphere denitrification</td>
<td>Increased N loss due to high C availability and low O$_2$ potentials</td>
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</table>

*Indicates the magnitude and direction of change (increase +; decrease –) in soil N availability resulting from each process.
new source of N under elevated CO$_2$ is associative N fixation. Although there have been few reports of increased fixation under elevated CO$_2$, increased rates may occur in the rhizosphere where enhanced substrate availability and low O$_2$ potentials may provide more favorable conditions than in the bulk soil (Dakora & Drake, 2000).

In addition to accessing new sources of N, rhizosphere processes may accelerate or slow-down N turnover under elevated CO$_2$ (Table 1). The grazing of rhizosphere microflora by soil fauna may accelerate N turnover if increased rhizodeposition stimulates rhizosphere microbes and NH$_4$ release through the microbial loop (Bønkowski, 2004). Second, the production of novel compounds under elevated CO$_2$ could increase or decrease N availability if certain microbial taxa with specific enzymatic capabilities are affected. Finally, CO$_2$-induced increases in the C:N of rhizodeposits may decrease N availability if the roots allocate more C-rich or less N-rich metabolites to root secretions (Paterson, 2003).

Unresolved questions and future research needs

Our present understanding of how rhizosphere processes will affect feedbacks to plant productivity under elevated CO$_2$ is constrained by the lack of appropriate methods. Most studies of CO$_2$ effects on root-derived C have been conducted with small plants growing in an artificial medium (Grayston et al., 1996), and most studies of CO$_2$ effects on N mineralization have been conducted in soil cores from which the roots have been excluded (Zak et al., 2000). Thus, a fundamental challenge in adopting a more rhizo-centric view is that there are few good methods for quantifying rhizosphere processes in intact root–soil systems. This is especially true in the case of root exudation, which has rarely been measured in situ. Such a knowledge gap has limited our understanding of some very basic questions. For example, what are the effects of a root’s age, diameter, order or mycorrhizal status on the quantity and chemical quality of exudates? How do abiotic factors such as soil temperature, moisture and fertility affect exudation? Although recent reviews have highlighted our progress in understanding controls on exudation (Jones et al., 2004), more efforts are needed to develop field-based approaches, with the larger goal of integrating the results from field observations with those from highly controlled experimental systems (e.g. growth chambers, FACE sites).

Similarly, relatively few studies have examined the effects of exudate chemistry on soil N transformation rates under rhizosphere-relevant conditions. For example, how much C is needed (and in what chemical form) to stimulate net N mineralization? Does the response depend on the physical, chemical, or biotic properties of the soil? A future research priority should be to develop methods which can better simulate the rhizosphere environment in order to provide a more mechanistic understanding of the fate of root exudates in soil under realistic conditions.

An emerging view in elevated CO$_2$ research is that root–microbial interactions are likely to play an increasingly important role in controlling ecosystem-scale responses to global change. This would argue for a more rhizo-centric view of the interactions between plants and soil microbes, and a better understanding of how roots influence soil N availability. Because today’s rhizosphere is yesterday’s (and tomorrow’s) bulk soil it is critical to integrate rhizosphere mechanisms into models of bulk soil processes in order to better understand the long-term response of ecosystems to global change.

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References


Fungal endophytes and other clandestine citizens that reside within plants are increasingly appreciated for the role they play in community ecology. In a well-designed study examining the interaction between the fungal endophyte Neotyphodium lolii and perennial ryegrass, Lolium perenne, Rasmussen et al. (this issue; pp. 787–797) address the question of whether the fungal alkaloid content of the host plant is a function of enhanced alkaloid biosynthetic rates within the endophyte, or of increased endophyte populations in the plant. The authors’ investigations provide much-needed insight into how genetic and abiotic interactions affect the fungal endophyte–grass host relationship, and how these in turn could influence multidirectional biotic interactions within an agronomic grassland community.

‘This would suggest that the host plant’s C and N metabolite pool status conditions its ability to effectively limit fungal colonization.’

A clearer view through the looking-glass at interacting genomes

Plants respond to a myriad of endogenous and environmental cues by modulating their utilization of available carbon and nitrogen resources, which serve to accommodate the resource demands of growth, development and reproduction, as well as interactions with other organisms. The metabolic networks that promote allocation of C and N resources to different plant parts, and partitioning of those resources into different biosynthetic pathways, not only are under exquisite genetic control, but also are incredibly responsive to cues such as C and N resource status. For example, genome-wide analyses of gene expression have demonstrated that extensive reconfiguration of the transcriptome occurs in response to differential N availability, which effects dramatic changes in primary and secondary metabolism as well as growth and developmental processes (e.g. Scheible et al., 2004). But how do changes to a plant’s resource status affect the association of the plant with interacting organisms such as endophytic fungi?

Rasmussen et al. investigated how the resource status of L. perenne affects communications between the host plant and its fungal endophyte, N. lolii. To this end, the authors manipulated the resource status of L. perenne through increasing N availability as well as by use of cultivars exhibiting contrasting levels of soluble carbohydrate.

Two manifestations of resource-mediated interactions between the host plant and its fungal endophyte may be altered colonization of the host plant by N. lolii, and/or a change in the fungal endophyte’s partitioning of resources to alkaloid biosynthesis. Without a reliable means of quantifying fungal biomass, these two scenarios remain confounded. Rasmussen et al. shed light on these questions by using quantitative PCR as a means to estimate N. lolii fungal biomass within the host, L. perenne. The sensitivity and specificity of quantitative PCR is having a transformative effect on the study of interacting genomes. The ability to quantify the extent of colonization of a plant host by microbial associates provides a powerful lens through which to view these interacting species (Schena et al., 2004; Mumford et al., 2006). The addition of spatial or temporal dimensions to these analyses allows a means of exploring the dynamics of plant–microbe interactions. The utility of quantitative PCR is nicely illustrated by the authors’ investigations of the N. lolii–L. perenne symbiont.

Rasmussen et al.’s quantitative PCR analyses revealed that fungal endophyte biomass was negatively correlated with increasing plant-soluble resource pools, measured either as soluble carbohydrates or N sources (amino acids and proteins). In the case of the soluble carbohydrate pools these differences are a function of host plant differences at the genetic level, whereas in the case of the soluble N pools these differences result from N fertilization. Thus fungal endophyte population levels can be influenced by both the host’s genotype and the environment. The authors present a plausible argument that the difference in fungal DNA levels in these high soluble-N or high soluble-C plants is not a consequence of a ‘dilution effect’, that is, caused by