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EDITORIAL

Towards a predictive understanding of belowground process responses to climate change: have we moved any closer?

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Summary

1. Belowground processes, including root production and exudation, microbial activity and community dynamics, and biogeochemical cycling interact to help regulate climate change. Feedbacks associated with these processes, such as warming-enhanced decomposition rates, give rise to major uncertainties in predictions of future climate.

2. Uncertainties associated with these processes are more likely to be reduced if two key challenges can be met: increasing interdisciplinarity among researchers, and measuring belowground ecosystem structure and function at relevant spatial and temporal scales. For instance, recognizing the relationship between belowground primary production and soil respiration enhances modelling of global-scale C cycle temperature responses. At the opposite end of the spectrum, applying genomic techniques at the scale of microns improves mechanistic understanding of root–microbe interactions.

3. Progress has been made in understanding interactions of belowground processes with climate change, although challenges remain. We highlight some of these advances and provide directions for key research needs in this Special Feature of Functional Ecology, which results from a symposium that was convened at the Soil Science Society of America National Meeting in November, 2006.

Key-words: soil organic matter, soil respiration, microbial community, global change, global warming, carbon cycle, root, mycorrhiza, biogeochemical cycle

Belowground process responses to climate change

Soils contain about 70% of terrestrial organic C, and belowground processes regulate fluxes to the atmosphere that are approximately 10 times the current anthropogenic CO_2 loading rate (Chapin, Matson & Mooney 2002). Soil processes are also responsible for a substantial portion of the uncertainty in predicting ecosystem carbon cycle interactions with climate, particularly global warming (Davidson, Janssens & Luo 2006). These issues were addressed during the Symposium ‘Towards a predictive understanding of belowground process responses to climate change,’ held during the Soil Science Society of America Annual Meeting in 2006.

Key challenges identified by organizers and speakers attending the Symposium revolved around two main issues: a need for improved interdisciplinarity, and the difficulty of studying belowground processes at relevant spatial and temporal scales. Traditional research boundaries must be crossed in order to understand the complex linkages and interactions among primary producers, microbial communities and the physical environment (Fig. 1). For instance, while it has long been known that aboveground processes, particularly gross primary production (GPP) and plant community dynamics, strongly control belowground C and nutrient cycling, the specific roles of roots have been less clear. Roots provide energy to microbes in the form of labile, or fast-cycling, C compounds such as sugars and amino acids, as well as slow-cycling, structural C compounds such as cellulose and lignin. These subsidies, which are sensitive both to root growth rates and tissue quality, can structure decomposer and symbiotic communities and the processes they carry out; understanding these linkages requires improved communication between root biologists and soil ecologists. Plant–microbe interactions

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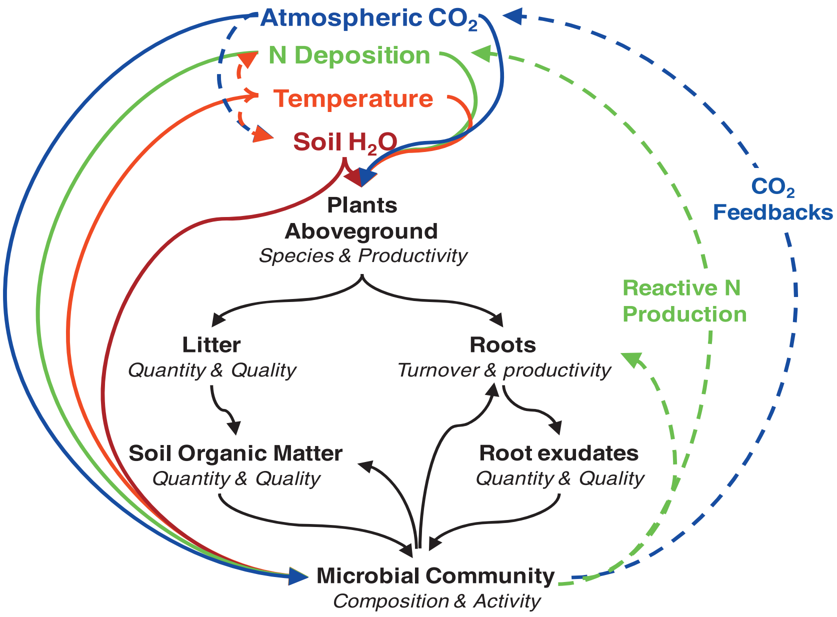

Fig. 1. Global change feedbacks mediated by belowground processes. Interacting effects of global change forcing factors on belowground processes act directly on plant communities to alter primary productivity, litter quantity and quality, and root production rates. Atmospheric CO_2 concentrations have indirect effects on soil moisture, while temperature can alter N and moisture availability. The quantity and quality of soil organic matter and labile root exudates interact with microbial communities to alter rates of biogeochemical cycles. The interface between roots and microbes is seen as an emerging frontier of belowground global change research. Microbial activity regulates belowground feedbacks to climate change by altering rates of decomposition and reactive N (e.g. N_2O) production. Solid lines, direct effects; dashed lines, indirect effects or feedbacks.

coupled with physical soil conditions determine the nutrient status of ecosystems, which is being altered by increasing reactive N production globally. Production rates of CO_2 in soils, and thus the magnitude of the CO_2 feedback to climate, are determined by microbial decomposition as well as root maintenance respiration and growth rates, which interact with plant phenology, and all of these are regulated by temperature and moisture (Fig. 1).

Belowground processes are notoriously obscure, in part because of inadequate methods to make observations across a wide range of spatial and temporal scales. Predictive understanding of C cycling processes that improve the accuracy of global climate change forecasts requires diurnal resolution of microscopic processes occurring beneath our feet. Recent advances in sensor technology have improved measurements of CO_2 concentrations such that relevant plant physiological processes can be detected in belowground CO_2 production rates. The application of genomics to soil microbial communities has the potential to vastly enhance understanding of the biology underlying biogeochemical cycling. Stable isotope techniques continue to provide insight into nutrient and C cycling interactions and responses to climate change that would be undetected by studying gross pools or fluxes.

The Belowground Response to Climate Change Symposium brought together experts on roots, rhizosphere processes, microbial ecologists, ecosystem ecologists and biogeochemists for a productive discussion of fundamental mechanisms governing processes that will determine the direction of belowground feedbacks to climate change. These presentations showed that major conceptual and technical breakthroughs are occurring or are imminent.

The Special Feature represents a subset of topics presented at the Symposium, beginning with a review of belowground net primary production (BNPP) and its response to temperature in forested ecosystems across the globe (Litton & Giardina 2008). This paper presents strong evidence that belowground C cycling is regulated by aboveground production, and demonstrates that annual rates of GPP, BNPP and soil respiration (or total belowground C flux, TBCF) all increase with increasing mean annual temperature. Importantly, this synthesis suggests that allocation of TBCF to BNPP increases with increasing temperature, which would potentially provide a negative feedback to atmospheric CO_2 concentrations if the spatial pattern is applicable to gradual warming. The Special Feature continues with a discussion of conditions under which mycorrhizae may act as decomposers by producing extracellular lytic enzymes that mineralize organic substrates and lead to net soil C losses (Talbot, Allison & Treseder 2008). Decomposition by mycorrhizae is hypothesized to occur in three possible scenarios, all of which would be mediated by global changes to alter inputs and losses from soil C stocks.

Field and laboratory studies employing stable isotope techniques are a mainstay in assessing biogeochemical responses to environmental changes, and have been put to good use in two papers included in this Special Feature to distinguish effects of nutrient availability on soil C and N cycling. Bradford, Fierer & Reynolds (2008), in a series of substrate addition – incubation experiments, demonstrated that decomposition of older organic matter can be enhanced ('primed') by moderate inputs of labile C, but the priming effect diminishes with higher inputs, presumably because microbes favouring labile compounds outcompete those that rely on the older, more stable compounds. Interestingly, additions of N and P had opposing effects on decomposition rates; N suppressed decomposition of organic matter, whereas P amendment stimulated decomposition. In a long-term field experiment, Dijkstra *et al.* (2008) found that plant N uptake was enhanced under doubled atmospheric CO_2 concentrations, probably because N mineralization was enhanced as an indirect effect of increased soil moisture. A novel ^{15}N pool-dilution approach demonstrated higher dilution rates with elevated CO_2, and further showed that certain plant species benefited from the available N more than others. Although these new findings are important, gaps remain in understanding biogeochemical responses to global change. In particular, the role of priming, its response to warming and elevated CO_2 and interaction with N mineralization and uptake, should be a target for future investigations.

Arguably, the most important recent advances contributing to improved understanding of belowground processes involve techniques allowing resolution of fine-scale mechanisms in space and time. An exciting development is the application of genetically engineered microbiosensors to soils, as reviewed in Gage *et al.* (2008). These tools provide insights into processes such as N uptake at the scale of individual root tips, allowing observation of plant–microbe interactions on scales at which they actually occur, instead of being masked by a whole-core average. Microbes can be engineered to detect rapid changes in labile C compounds within the rhizosphere, such as could be explained by shoot–root translocation and allocation dynamics. Linkages between soil water availability and root growth can be made using a microbiosensor induced by low water potential. While reporter gene systems such as described by Gage *et al.* (2008) elucidate enzymatic functions at the interface between plants and microbes within the physical soil environment, quantifying biogeochemical fluxes resulting from these reactions remains a challenge. Phillips *et al.* (2008) have developed an approach to extracting root exudates from trees grown in the field, and quantifying the resulting C flow based on root biomass. Although root exudation is believed to represent only 1–10% of annual NPP, it provides substrates that fuel larger decomposition fluxes, mediate nutrient cycling and stimulate microbial activity, therefore playing a potentially critical role in determining feedbacks of belowground processes to global change.

A critical unresolved issue requiring investigation at fine temporal scales is the temperature dependence of soil respiration, and deploying automated sampling systems provides data on diurnal variations in flux rates from an increasing number of ecosystems. In the final paper in this Special Feature, Savage, Davidson & Richardson (2008) present a pragmatic approach to analysing large datasets generated by high-frequency sampling systems that facilitates quality control, uncertainty analysis and data-model fusion. While some details of this approach are specific to dynamic, closed-chamber systems, the conceptual steps are also useful when considering how to analyse data collected from ecosystem gas exchange chambers (e.g. Arnone & Obrist 2003) and solid state sensors for estimating fluxes from soil CO_2 profile gradients (e.g. Tang *et al.* 2003). Importantly, Savage *et al.* (2008) provide guidelines to determining effective sampling strategies to meet specific research objectives. For example, side-by-side comparisons showed that biweekly manual sampling provided a reasonable estimate of seasonal or annual average respiration rates, but hourly or half-hourly measurements were critical for assimilating into ecosystem models of C-cycling dynamics (e.g. Hanson *et al.* 2004).

Progressing toward prediction

Belowground processes are coming into finer focus as new sensor technology is applied, with the potential of improving the reliability of predictions of responses to altered atmospheric CO_2 concentrations, warming temperatures and nutrient deposition. Several advances are bringing us closer to a functional understanding of belowground ecosystem structure. These include (i) the ability to quantify root exudation of labile substrates and their potential role in organic matter formation and decomposition (e.g. Bradford *et al.* 2008; Phillips *et al.* 2008), (ii) linking biogeochemical processes to soil microbial community dynamics using microarray-based genomic techniques (e.g. He *et al.* 2007), even at the scale of fine roots (Gage *et al.* 2008), and (iii) developing scaled-down electronic sensors with advanced data-handling capabilities. Together, these provide opportunities to better understand diurnal soil CO_2 concentration dynamics with depth in the soil and efflux at the surface (e.g. Tang *et al.* 2003; Savage *et al.* 2008). These advances, and others, will be required to answer pressing questions regarding the nature and stability of soil organic matter as it is exposed to climate change, allocation of C from recent photosynthate to belowground processes and pools, and indirect effects of soil moisture and nutrient availability on C cycling.

Most recent advances have allowed better resolution of fine-scale processes, and have highlighted that we need to understand these processes to develop adequate predictions of larger scale phenomena. However, extrapolating to decadal time scales and regional to global spatial scales requires implementing these key processes into models, as well as additional research on long-term responses of ecosystems to interacting global change forcing factors – we can't validate long-term projections with short-term, single-factor experiments (e.g. Zhou, Weng & Luo 2008). Nevertheless, the present state of knowledge suggests that soils, especially at high latitudes, are unlikely to act as a negative feedback to help limit climate change, unless advances in techniques for enhancing sequestration maintain pace with CO_2 emissions and warming. Present understanding also suggests that the risks of strong positive feedbacks, in the form of substantial natural methane and CO_2 emissions resulting from permafrost melting and increased temperature sensitivity of resistant organic matter, are large (Fischlin *et al.* 2007). Climate and carbon policy should recognize and respond to the likelihood that soil processes may act as an amplifier of climate change in the near future.

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