Research review

Root dynamics and global change: seeking an ecosystem perspective

RICHARD J. NORBY[1]* AND ROBERT B. JACKSON[2]

[1]*Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831–6422, USA*

[2]*Department of Botany and Nicholas School of the Environment, Duke University, Durham, NC 27708, USA*

SUMMARY

Changes in the production and turnover of roots in forests and grasslands in response to rising atmospheric CO_2 concentrations, elevated temperatures, altered precipitation, or nitrogen deposition could be a key link between plant responses and longer-term changes in soil organic matter and ecosystem carbon balance. Here we summarize the experimental observations, ideas, and new hypotheses developed in this area in the rest of this volume. Three central questions are posed. Do elevated atmospheric CO_2, nitrogen deposition, and climatic change alter the dynamics of root production and mortality? What are the consequences of root responses to plant physiological processes? What are the implications of root dynamics to soil microbial communities and the fate of carbon in soil? Ecosystem-level observations of root production and mortality in response to global change parameters are just starting to emerge. The challenge to root biologists is to overcome the profound methodological and analytical problems and assemble a more comprehensive data set with sufficient ancillary data that differences between ecosystems can be explained. The assemblage of information reported herein on global patterns of root turnover, basic root biology that controls responses to environmental variables, and new observations of root and associated microbial responses to atmospheric and climatic change helps to sharpen our questions and stimulate new research approaches. New hypotheses have been developed to explain why responses of root turnover might differ in contrasting systems, how carbon allocation to roots is controlled, and how species differences in root chemistry might explain the ultimate fate of carbon in soil. These hypotheses and the enthusiasm for pursuing them are based on the firm belief that a deeper understanding of root dynamics is critical to describing the integrated response of ecosystems to global change.

Key words: fine roots, root dynamics, turnover, climatic change, global change, elevated CO_2, nitrogen deposition, mycorrhizas.

INTRODUCTION

Tansley (1935) in describing the concept of the ecosystem commented on '…the necessity for investigation of all the components of the ecosystem and of the ways they interact to bring about approximation to dynamic equilibrium. That is the prime task of the ecology of the future.' With respect to the current mandate to scientists to unravel the complexity of terrestrial ecosystem responses to global change, the future is now. Whether the current research (or policy) question concerns the capacity for forests and grasslands to sequester carbon as the atmosphere becomes progressively enriched with CO_2, or the resistance of communities

to changing water and temperature regimes, or the fate of anthropogenic nitrogen compounds deposited onto ecosystems, the key components of ecosystem response may reside out of sight – the belowground system of roots, soil and associated microorganisms.

Changes in the production and turnover of roots in forests and grasslands in response to rising atmospheric CO_2 concentrations, elevated temperatures, altered precipitation, or N deposition could be a key link between plant responses and longer-term changes in soil organic matter and ecosystem C balance. While Tansley's call for integrated studies of all ecosystem components has long been embraced, ecosystem-level observations of root production and mortality in response to global change variables are just starting to emerge. The papers in this volume highlight the current state of knowledge

*Author for correspondence (tel +1 865 576 5261; fax +1 865 576 9939; e-mail rjn@ornl.gov).

about root responses to atmospheric and climatic change and their interaction with ecosystem properties.

This collection revolves around three central questions:

- Do elevated atmospheric CO_2, N deposition, and climatic change alter the dynamics of root production and mortality?
- What are the consequences of root responses to plant physiological processes?
- What are the implications of root dynamics to soil microbial communities and the fate of C in soil?

These questions are considerably easier to ask than they are to answer. Ecosystem-scale experiments on global change phenomena are few and recent (or ongoing). Results are often ambiguous, contradictory and confounded by methodological problems. Although the body of knowledge may be immature for a definitive synthesis, we have an opportunity to highlight the critical uncertainties, generate new hypotheses, and improve our techniques in current and future research programs.

BACKGROUND

Before delving into the results of manipulative experiments, it is useful to understand the scope of the issues of root dynamics and the physiological and ecological controls that may be sensitive to global change factors. The system of small, ephemeral roots is an important part of terrestrial metabolism. Jackson *et al.* (1997) estimated that as much as 33% of global annual net primary productivity is used for the production of fine roots, which have a relatively short life before they die and begin decomposing. A central concept in our discussion is that root turnover is a key component of the C and nutrient cycling in ecosystems and will probably be sensitive to many global change factors (Gill & Jackson, 2000; Eissenstat *et al.*, 2000). As discussed further here, root turnover is variously defined, but generally it is a measure of the production and mortality of roots relative to the size of the standing crop of roots. A plant that maintains roots longer (lower turnover) allocates less C to the production of new roots, but expends more energy (i.e. root respiration) in maintaining roots that may be less efficient at nutrient uptake compared to a root newly deployed in a nutrient-rich microsite. When roots die and decompose, some of their C is released to the atmosphere and some may remain as soil organic matter (SOM). Hence, root turnover is a major component of ecosystem C fluxes and the potential of an ecosystem to sequester atmospheric C.

Clues to how global change factors might alter root turnover, and therefore nutrient and C cycling, come from an analysis of the variation in root turnover across environmental gradients. Gill & Jackson (2000) assembled root turnover data for major biomes across the globe and analyzed the data set for broad-scale patterns along climatic gradients. Turnover rates of fine roots increased exponentially with mean annual temperature in forests and grasslands, but surprisingly, there was no relationship with precipitation once temperature effects were accounted for. Does this result suggest that root turnover will increase in response to climatic warming? Not necessarily. Gill & Jackson (2000) found that the global relationship did not predict the relationship to interannual variability in climate at a particular site.

Investigations of global change effects on root dynamics should be based on a good understanding of the internal and external controls of root production and longevity. Without such a framework, observations from a manipulative experiment are strictly phenomenological and difficult to apply to the broader and more complicated issue of global change. Eissenstat *et al.* (2000) reviewed comprehensive studies indicating fine-root longevity to be related to a number of root characteristics such as diameter, tissue density, mycorrhizal infection, N concentration, and basal respiration rates, analogous to relationships that have been described for leaves (Reich *et al.*, 1997). These characteristics can be used to predict root longevity through an analysis of the costs of constructing and retaining roots, and this can provide a framework for sorting out the net effect on root systems of the myriad influences that atmospheric and climatic change could have on plants and the soil environment (Eissenstat *et al.*, 2000).

The internal controls on root deployment and longevity require an understanding of C allocation processes in plants. Farrar & Jones (2000) developed a hypothesis of C allocation in plants that suggests control is shared by roots and shoots, with two mechanisms underlying the distribution of control – regulation of phloem transport and control of gene expression by resource compounds (e.g. sugars and N compounds). In discussing the implications of this model to predictions of climatic change impacts, Farrar & Jones (2000) are careful to distinguish a shorter-term response, which might simply be bigger plants with larger roots systems and little change in C partitioning, from longer-term responses that occur after the plants begin to deplete soil resources. This scale-related consideration is especially important when attempting to extend the responses of individual plants to that of ecosystems (Norby *et al.*, 1999), and must, therefore, be kept at the forefront in all of our discussions.

METHODOLOGY AND APPROACHES

Any discussion about root biology is inevitably intertwined with methodological issues. It is, of course, much more difficult to make *in situ* obser-

vations (qualitative or quantitative) of roots than of aboveground portions of plants, and the relevance of responses of roots extracted from their soil environment is always suspect. As a result the data base on root responses to global change factors is much smaller than that for aboveground processes, and without standard methods for researchers to rely on, much of the data that does exist is confounded by methodological differences. Novel techniques are being developed, but progress in understanding and quantifying root dynamics and function – especially with an ecosystem perspective – will lag until the new techniques are widely used and accepted.

One particularly frustrating problem is the substantial confusion created by inconsistent use of important terms, such as fine root and turnover. In considering trees and forests, it is important to differentiate the responses of relatively small, ephemeral roots from those of larger, woody perennial roots, and failure to do so creates critical errors in scaling responses from seedlings to mature trees (Norby, 1994). But there remains considerable variation within the category of 'small, ephemeral roots', and the word 'fine' is variously used for all or parts of that category. The term fine root is meaningless with grasses – all of the roots are fine, although not all are ephemeral.

Perhaps more important than establishing a precise definition of a fine root is the recognition that processes and responses vary not just with root diameter but with other root characteristics as well. Eissenstat *et al.* (2000) emphasize the importance of root order, that is, the position of a root within the branched hierarchy of the root system. Fine roots with no daughter roots generally have higher N concentration, respiration rate, specific root length, and a shorter life span than similar roots with branches. While the very small diameter roots are generally thought to turn over most rapidly, and many observations support this view, very fine roots (especially of an earlier order in the branching sequence) may live a remarkably long time. An innovative technique by Gaudinski *et al.* (2000; also pers. comm.) utilized ^{14}C created during the early 1960s from thermonuclear testing to date the C in fine roots collected from a forest. Though very fine (<1 mm in diameter), some of these roots were surprisingly long-lived, ranging from 2 to 16 yr. Clearly there is need for caution in associating fine roots with fast turnover. Heterogeneity of roots increases the complexity of our investigations further.

The definition of root turnover has also created confusion in the literature and in discussion, which can hinder effective communication. In a systems science approach, turnover is typically defined as flux divided by pool size, or the proportion of the root biomass that is produced or dies annually. Unfortunately, both the flux and the pool for root studies are somewhat ambiguous. Turnover was defined by Gill & Jackson (2000) in their global survey as annual belowground production divided by maximum belowground standing crop, following the definition employed by Dahlman & Kucera (1965). Using this approach, an annual plant that maintains its roots through the growing season would have a turnover equal to one, where maximum biomass is equal to belowground production. Other researchers have based turnover on the mean or minimum annual standing crop rather than the maximum. Nadelhoffer (2000) defines turnover as annual root death divided by mean fine root biomass. Note that if annual net root productivity (annual increment) is zero, as might be expected in a fully developed perennial system or in an annual system in which all roots die at the end of the season, then mortality is equal to production. Other researchers have used the term 'turnover' as annual root production or mortality in grams per square meter (e.g. DeLucia *et al.*, 1999). Tingey *et al.* (2000) refer to annual root mortality as absolute turnover in contrast to relative turnover, which they call turnover index. The distinction is especially important when the standing crop of roots is changing from year to year, as during stand development or under the influence of a changing environment. If the primary research interest is in rates of C and N fluxes from roots to soil, then the absolute turnover rate (which could be called annual root mortality) may be most useful, but for studies of root demography or to link with ecosystem models, then relative turnover (or simply 'turnover' as already defined) is the appropriate metric (Tingey *et al.*, 2000).

The quantification of root production and mortality is difficult and controversial. Researchers use several methods to determine root production and mortality, each with strengths and limitations. Historically, sequential harvesting of roots was the most widely used method to determine root production. Although several sources of error hamper this method, numerous algorithms have been developed to increase the value of harvest data and new methods and technologies continue to be introduced that may alleviate some problems with harvest methods (Singh *et al.*, 1984; Burke & Raynal, 1994). By contrast, Nadelhoffer (2000) believes that methods based on sequential root harvests are flawed and give the wrong conclusion about the effect of N availability on root turnover. He estimates root turnover by constraining it with an N budget, a promising method but one that is sensitive to estimates of N mineralization rates (Lauenroth, 2000). Minirhizotrons are in increasing use in global change studies, providing a method for frequent, nondestructive quantification of root length production and mortality (Hendrick & Pregitzer, 1992). They are not without problems, however. For an ecosystem C budget it is necessary to convert data on

root length production per minirhizotron to grams of C per square meter; a method for doing this is described by Tingey *et al.* (2000). Another problem can be the definition of root death, especially in minirhizotron images where tactile cues and staining techniques are not possible. Typically root disappearance is used instead, but this may include initial stages of decomposition (Tingey *et al.*, 2000). The definition of root death is ambiguous under any circumstances since death occurs gradually and part of a root can die and cease function while the remaining root still maintains important functions such as transport (Comas *et al.*, 2000).

ROOT DYNAMICS IN A CHANGING ENVIRONMENT

Will root production, mortality, or turnover change in response to increasing atmospheric CO_2 concentration, N deposition, or climatic warming and changing patterns of precipitation? We are aware that the number of field studies that can address this question with the appropriate ecological focus is extremely limited. In asking the question, we are essentially highlighting the tremendous uncertainty in the interpretation of the meager data set, but in so doing, we may be outlining the highest priority research questions and key measurements for new experiments as they get started. The largest emphasis here is on the effects of elevated atmospheric CO_2, because that is the global change factor on which there have been the most manipulative experiments. Furthermore, we presume there is a direct feedback between root turnover responses to increased CO_2 and the cycling of C through ecosystems and back to the atmosphere. Root dynamics in elevated CO_2 has therefore been identified by the Global Change and Terrestrial Ecosystems (GCTE) Project as an especially important issue for assessments of global change response (Canadell *et al.*, 1999).

Responses to elevated CO₂

Root dynamics have been investigated in field CO_2 experiments in forests, grasslands, and agricultural systems. Fundamental differences in these ecosystems and their root systems lead to distinct research questions, as well as distinct methodological issues. In forests (or in tree seedling studies meant to address forest issues), it is particularly important to differentiate the responses of large woody roots, which may be important in C storage, from those of fine roots, which are important in nutrient and water uptake and C flux (Norby, 1994). Forests are very difficult to include in manipulative experiments, and the available data on root responses to elevated CO_2 in forests is very limited. Grassland systems, on the other hand, can be studied as intact ecosystems in manipulative experiments (e.g. Fitter *et al.*, 1997), and the arbitrary separation of responses by fine

roots and coarse roots is unnecessary. In an annual crop system, the important research questions are more likely to revolve around root deployment and resource capture rather than equilibrium responses and C flux (Fitter *et al.*, 1991). Root turnover is likely to be impacted by CO_2 differently in annual versus perennial plants (Pritchard & Rogers, 2000).

In discussing the responses of crop roots to elevated CO_2, Pritchard & Rogers (2000) emphasize the importance of cell expansion and cell division and suggest that a key to understanding how root growth will change in a high-CO_2 environment is to understand how carbohydrates, especially sucrose, functions both as a substrate for growth and as a regulatory molecule. From this perspective, they review the literature and conclude that roots in a high CO_2 environment will be larger and more highly branched, but less efficient in nutrient and water uptake (also see Berntson & Bazzaz, 1996; Rogers *et al.*, 1999). Root turnover is not an important issue with annual crop plants: Fitter *et al.* (1996) found no changes in root turnover in CO_2-enriched wheat because there is little or no mortality of wheat roots until they all die synchronously at the end of the life cycle.

Arnone *et al.* (2000) surveyed the literature on root responses to CO_2 in native grassland ecosystems. Results have been inconsistent, with less than half of the studies showing increased root growth in elevated CO_2. In their own study in a calcareous grassland in Switzerland, Arnone *et al.* (2000) used minirhizotrons to test their hypothesis that increased root production and mortality would explain the observed increase in net ecosystem CO_2 uptake in this system. After 2 yr of CO_2 enrichment, there were no differences in root production or mortality. There was a shift, however, in the distribution of roots, with more being found in the upper soil layer in the CO_2-enriched plots, which may have been a result of increased soil moisture in elevated CO_2.

The scale of forests has made them more difficult to study in manipulative experiments, and in their synthesis of the responses of coniferous trees, Tingey *et al.* (2000) had to rely mainly on data from experiments with seedlings and saplings. Fine-root growth increased in elevated CO_2 across a range of species and experimental conditions, but there was no clear indication that CO_2 enrichment altered the proportion of C allocated to roots. For example, the ratio of fine root to needle mass did not change in a consistent pattern in these studies. If root mass or fine-root density increases in elevated CO_2 simply because of a coordinated whole-plant growth response rather than a specific response of roots, we really have not learned anything new: bigger plants have bigger root systems. However, we cannot expect these observations of young, isolated plants to persist over time as trees develop into a forest. Eventually, we might expect fine-root density in a forest to reach

a maximum value, analogous to the aboveground canopy reaching a maximum leaf area index (LAI) (although can a concept similar to 'canopy closure' apply below ground?) It then becomes especially important to focus on the dynamics of the root system – the longevity of roots and the turnover of root systems. The few observations of CO_2 effects on root turnover in field experiments with conifers have shown an increased rate of root loss, but the response of relative turnover has been inconsistent (Tingey *et al.*, 2000). In the free-air CO_2 enrichment (FACE) experiment in a 15-yr-old *Pinus taeda* stand in North Carolina, USA, Allen *et al.* (2000) reported that fine-root production increased 37% in elevated CO_2, and mortality plus decomposition (or absolute turnover) increased 26% (not statistically significant), but in this system turnover rate relative to production did not change.

In the few CO_2-enrichment studies with deciduous trees under field conditions, the roots have been more responsive to CO_2 enrichment than those of conifers. In six studies, fine-root density (the mass of roots per unit ground area) increased from 60 to 140% in elevated CO_2 (Norby *et al.*, 1999). Contrasting with the conclusion of Tingey *et al.* (2000), fine-root density increased more than leaf area in every case, suggesting that the stimulation of fine-root production was a specific response to elevated CO_2. In addition to these static measures of root response, fine-root production and mortality have increased in CO_2-enriched deciduous trees in the few studies that used minirhizotrons to measure root dynamics. Fine-root length production, mortality and net production all increased with CO_2 enrichment in an *Acer saccharum–Acer rubrum* assemblage in open-top chambers in Oak Ridge, TN, USA (E. G. O'Neill, pers. comm.). Elevated CO_2 increased the diameter and length of individual roots of *Populus tremuloide*s trees in open-top chambers (Pregitzer *et al.*, 2000b). Fine-root length production and mortality and fine-root biomass all were increased by CO_2 enrichment, but only in trees grown in high-N soil; there were no CO_2 effects in low-N soil.

Fine-root turnover was studied in the deciduous forest FACE experiment in a *Liquidambar styraciflua* stand in Tennessee using minirhizotrons (E. G. O'Neill, pers. comm.). In 2 yr of exposure to elevated CO_2, there has been no effect on annual net production (i.e. standing crop does not change), but both production and mortality are higher in CO_2-enriched stands, indicating increased turnover and increased input of C to the soil. These observations contrast with the *Pinus taeda* FACE (Allen *et al.*, 2000), perhaps because the deciduous forest has higher tree density and LAI and has roots that fully occupy the soil, whereas the root system is still expanding in the pine stand. Another possible explanation for the apparent difference in root turnover response, consistent with the tentative conclusion of Pregitzer *et al.* (2000b), is that lower N availability in the pine stand (R. Oren, pers. comm.) limits the response of fine roots to elevated CO_2 compared to that in the more fertile hardwood stand. A third possibility, and an unfortunate one, is that the apparent differences in response results from the different techniques for assessing root turnover (sequential harvest versus minirhizotron).

Clearly, there have not been enough experiments attempted of sufficient duration or spatial scale to permit conclusions about the effect of elevated atmospheric CO_2 on root dynamics. Root production and mortality have been increased by CO_2 enrichment in some studies and not in others (but have not been seen to decrease). Differences in response might be related to system-level properties or interactions with other environmental drivers, and new hypotheses are needed to guide new and ongoing experiments.

Response to climatic change

Atmospheric CO_2 can influence root dynamics through its direct interaction with C uptake and allocation in plants, but the increasing concentration of CO_2 in the atmosphere can also be expected to alter root dynamics indirectly through its role as a greenhouse gas affecting temperature and precipitation patterns. As air temperature warms globally, soil temperature can be expected to rise concomitantly (Schlesinger & Andrews, 2000). Root growth and mortality often increase with increasing temperature as long as soil moisture and nutrient availability are adequate (Pregitzer *et al.*, 2000a), conditions which must however be rare in natural ecosystems. Generalizations can be difficult because different populations of plants have evolved to cope with a wide range of air and soil temperature regimes. Fitter *et al.* (1998), for example, concluded that root growth in their grassland site was controlled by radiation flux, not by temperature. In addition, soil temperature has other effects, notably a change in N mineralization rate, and interacts with other environmental factors to influence root functioning. Pregitzer *et al.* (2000a) also discuss the importance of seasonality in root dynamics, especially in perennial plants, and speculate that global warming will result in earlier root growth in the spring. Their analysis suggests that the flux of C from leaves to roots and into soil should increase with warming. Analyses of ecosystem response to warming often focus on the presumed increase in heterotrophic respiration and the loss of C from the system (Schlesinger & Andrews, 2000), and it is important that the likelihood of a (partially) counterbalancing increase in C input by roots also be considered.

Interannual variation in precipitation clearly can affect plant productivity, but the specific responses

of roots are not clear. At a global scale, precipitation did not explain patterns of fine-root turnover across different ecosystems once the effects of temperature were accounted for, although turnover was related to precipitation at the local scale (Gill & Jackson, 2000). Joslin *et al.* (2000) conclude that responses of roots to irrigations treatments have been mixed and at any rate are difficult to extend to long-term change in precipitation at the ecosystem scale. They report on the 'Throughfall Displacement Experiment' in which the long-term effects of both decreasing and increasing water inputs to the forest floor of a mature deciduous forest in Tennessee are being investigated. After 5 yr of minirhizotron observations of fine roots in this experiment, clear evidence of significant changes at the stand level to drought has yet to emerge. Differences across treatments in net fine-root production were small and non-significant, although a trend of increasing net production (due to less mortality) in the dry plot was noted. Perhaps the most important finding of this study has been the resilience of the forest in maintaining an active root system with relatively constant fine-root mass despite the interannual and imposed variation in soil moisture (Joslin *et al.*, 2000).

Nitrogen deposition

Terrestrial ecosystems around the world, but especially in North America and Europe, are receiving unprecedented amounts of N compounds, ammonia and nitrogen oxides. The primary route by which these compounds enter ecosystem cycles after being deposited from the air is through the soil pools of nitrate and ammonium. Therefore, understanding how N deposition might influence root dynamics comes largely from analyzing the response of roots to natural or applied gradients of N availability. Different approaches to measuring fine roots have yielded different conclusions about the relationship between N availability and fine-root turnover in forests, but Nadelhoffer (2000) argues that the best evidence indicates that with increasing N availability, fine-root biomass typically decreases and turnover increases. He develops the hypothesis that if N deposition increases N mineralization, nitrification, or N availability to plants, then fine-root biomass will decrease but fine-root production and turnover will increase. In forests at late stages of N saturation (Aber *et al.*, 1985), the decreased root biomass will contribute to a loss of nitrate from the system, and after prolonged and highly elevated N deposition, nutrient imbalances could disrupt fine-root functions.

A complete understanding of the interaction between N deposition and root dynamics depends on many interacting factors, particularly the native fertility of the soil. Gifford *et al.* (1996) concluded that the assumption about how the exogenous N is initially taken up (directly by foliage or through a soil pathway) is a critical one that should be further investigated. Other global change factors, including CO_2, temperature and precipitation, which co-occur with increasing N deposition globally, are likely to modify root responses to increasing N availability. Various modeling approaches to exploring the interactive effects of CO_2 and N deposition (discussed in Norby, 1998) illustrate that the responses to N deposition and CO_2 enrichment are not likely to be simple or additive. This is not surprising given the close linkages and feedbacks between the C and N cycles in a plant, and roots are at a key intersection between those cycles. Different assumptions about allocation are particularly important to the net effect of N deposition and CO_2 enrichment (Norby, 1998), which emphasizes the importance of developing a better understanding of the control of C allocation to roots (Farrar & Jones, 2000).

ROOT PHYSIOLOGY AND GLOBAL CHANGE

While our focus here is on root dynamics at the ecosystem scale, there is an important interplay between root production, deployment, and turnover and the physiological activity of roots, and this interplay must be part of our analyses of the impacts of global change. For example, increased nutrient uptake might be observed in an isolated plant in elevated CO_2 as a result of a larger plant having a large root system. Scaling this observation to an ecosystem, however, requires additional information on whether there are ecosystem-level constraints to the total size of the root system, coupled with physiological information on the response of root-specific nutrient uptake efficiency. Some of the presumed controls (or correlates) of root turnover, including respiration rate or nutrient and carbohydrate content, relate directly to the physiological activity of the root. The challenge of incorporating plant physiology into global change predictions is the trade-off between a more mechanistic basis to the predictions and picking which physiological attributes scale to meaningful ecosystem-level changes.

A sustained growth response of plants to elevated CO_2 in unmanaged ecosystems is expected to require increased N availability because short-term increases in nutrient-use efficiency cannot be sustained indefinitely (Norby *et al.*, 1986; Bazzaz, 1990; Lloyd & Farquhar, 1996). The capacity for a plant to take up nutrients depends on both the size of the root system and its efficiency to deploy roots at the time and place nutrients are present (Fitter *et al.*, 1991), as well as on the efficiency by which a particular root segment can take up a nutrient from the soil solution. BassiriRad (2000) has analyzed the latter issue through careful studies of the kinetics of NH_4^+ and NO_3^- uptake and the influence of CO_2 enrichment, soil temperature and N deposition. The response of

uptake kinetics as reported in the literature is highly variable, but BassiriRad (2000) suggests that much of this variability may be attributable to experimental protocol (though there is insufficient evidence yet to know), such as whether both high and low affinity transport systems were involved or only the more ecologically relevant high affinity system. Nevertheless, there do appear to be species-specific differences in response to elevated CO_2, and this raises the possibility of shifts in community composition resulting from $CO_2 \times$ nutrient interactions (Berntson *et al.*, 1998; BassiriRad, 2000). Increased soil temperature generally increases N uptake capacity, but the response seems to be greater in species from warm climates with fluctuating soil temperatures than from those in cold climates (BassiriRad, 2000).

Nutrient uptake is an energy-demanding process that accounts for a significant fraction of root respiration. Atkin *et al.* (2000) considered how root respiration rates might respond to climatic warming. Root respiration is an important part of the C budget of ecosystems, although the C flux from root respiration is often lumped with respiration by soil heterotrophs. Root respiration is very sensitive to changes in temperature, yet it is very difficult to predict its response to climatic warming because it can acclimate rapidly to changes in growth temperature, and the degree of acclimation varies among species (Atkin *et al.*, 2000). Pregitzer *et al.* (2000a), however, cite several examples where there was no evidence of acclimation of root respiration to changing temperature. They suggest that the natural seasonal and diurnal fluctuations in soil temperatures that occur in temperate and boreal ecosystems might prevent significant acclimation in the field, in contrast to laboratory conditions with controlled, constant temperature. Further complicating the extension to an ecosystem scale, respiration responses are likely to be confounded by any factor (e.g. elevated CO_2 or air temperature) that affects shoot activity and C supply to roots (Atkin *et al.*, 2000).

As discussed by Farrar & Jones (2000), carbohydrate supply to roots is a key process linking environmental effects on shoot physiology to the changes in the growth and function of roots. Total nonstructural carbohydrate (TNC) can comprise from 4 to 23% of fine-root dry mass (Pregitzer *et al.*, 2000a). In a simulation of root processes, Pregitzer *et al.* (2000a) show that regardless of the TNC concentration *Acer saccharum* fine roots can live only a short time without a continual supply of TNC. Respiratory acclimation to temperature is a critical factor in determining the lifespan of a root in relation to leaf activity and the supply of TNC. They conclude that during the growing season rates of fine-root respiration and root longevity are likely to be closely linked to the rate of photosynthesis and whole-plant source–sink relationships. Clearly, responses of roots to global change cannot be studied in isolation from the rest of the plant and the myriad influences of multiple, fluctuating, environmental factors.

INTERACTIONS BETWEEN ROOTS AND SOIL

In addition to their fundamental role in the growth and physiology of plants, roots also are important conduits by which C enters the soil. Root turnover is a critical mediator of C cycling in ecosystems, and it follows that the response of roots to global change factors will be an important determinant of net ecosystem production and the potential for ecosystems to sequester fossil-derived C in long-term pools.

In nature, the roots of almost all plants are joined symbiotically with fungi to form the mycorrhizal partnership. The fungal partner resides at the interface between plant and soil and is a link in the chain of transfers by which C moves from plant to soil (Staddon *et al.*, 1999). Hence, the effect of elevated CO_2 or other global change factors (which are less studied) on the establishment, growth and turnover of mycorrhizal fungi is an important factor in assessment of C cycling in ecosystems. The literature describing effects of CO_2 enrichment on mycorrhizal colonization is inconclusive, largely because of the failure to separate the overall effect of CO_2 on plant growth from any specific effect on mycorrhizas (a problem in many other aspects of CO_2 research). A more mechanistic understanding of how elevated CO_2 could affect mycorrhizas must come from an improved understanding of C fluxes in mycorrhizal plants under varying CO_2 concentration (Fitter *et al.*, 2000). They argue that research on mycorrhizas has been too 'plant centered' and to better understand mycorrhizal responses to global change there should be a new emphasis on the biology of the fungal partner – a 'mycocentric' approach. In particular, the diversity among fungal species in their responses to CO_2 and the services they provide to the plant (e.g. P uptake) warrant more study.

Mycorrhizal tissue comprises a substantial fraction of soil organic matter in many systems (Treseder & Allen, 2000), and aspects of the biology and chemistry of mycorrhizal hyphae can influence the cycling of C to soil. Although microarthropods graze on live hyphae, they do not have a big impact on C cycling, which is determined by the turnover rate of hyphae. Hyphal turnover is almost certainly greater than that of roots (Fitter *et al.*, 2000), but an important fraction of the hyphal mass is recalcitrant compounds like chitin and glomalin that can account for a significant pool of soil organic matter (Treseder & Allen, 2000). Field studies (e.g. Rillig *et al.*, 1999) have suggested effects of elevated CO_2 on mycorr-

hizal community composition and the productivity and decomposition of hyphae could lead to an increase in the amount of C sequestered in intact hyphae and their residual components. Hyphal responses to increases in N availability (as might result from N deposition) have been inconsistent, and the most general response may be shifts in community composition based on differential sensitivity to N. Because mycorrhizal groups differ in their growth rate and recalcitrant chitin content, these shifts could have implications for C immobilization in SOM, but a great deal more work on mycorrhizal physiology is needed before any predictions can be made (Treseder & Allen, 2000).

What then is the net result of the CO_2 effects on fine-root productivity, turnover, and the flux of C through mycorrhizas on the fate of C in soil and sequestration in long-lived SOM pools? Zak *et al.* (2000) attempted to address this question by summarizing data from 47 reports on soil C and N cycling under elevated CO_2, focusing on those pools and processes that are important control points for the belowground flow of C and the closely linked N fluxes. Soil and microbial respiration were almost always more rapid under elevated CO_2 because more C entered the soil and the additional substrate was metabolized by soil microorganisms. This leaves as an open question the net effect of increased influx and increased efflux, and Zak *et al.* (2000) found that microbial biomass, gross N mineralization, microbial immobilization and net N mineralization had such a high degree of variability that there was no basis for any prediction about how microbial activity and rates of soil C and N cycling will change with CO_2 enrichment. To remedy this fundamental gap in our understanding of ecosystem response to global change, Zak *et al.* (2000) argue that we need to understand better how differences between plant taxa in fine-root production, mortality and biochemistry may influence microbial metabolism and lead to different patterns of soil C and N cycling.

SYNTHESIS: EXTENDING OBSERVATIONS TO
PREDICTIONS OF ECOSYSTEM RESPONSE

Most of the papers in this volume conclude that not enough is known to draw any firm conclusions about how global change factors will impact root dynamics or how changes in root dynamics might affect plant physiology or C cycling in soil. The problems are manifold:

- Daunting methodological problems in measuring unseen roots without disturbing the system of study.
- An inability to sense belowground variables remotely at regional and global scales.
- Experimental challenges in simulating future atmospheric and climatic conditions at a useful spatial scale.

- Complications of uncontrolled, interacting environmental variables.
- Difficulties in generalizing in the face of broad variability in responses among plants, fungal partners and soil microbes, as well as the variability introduced by methodology.

All of these issues, and many others, have been invoked in this set of papers. But at the same time new hypotheses have been introduced to suggest why responses of root turnover might differ in contrasting systems, how C allocation to roots is controlled, and how species differences in root chemistry might explain the ultimate fate of C in soil.

Even if all the problems were resolved, our assembled data would still be insufficient for addressing the larger issues in which we are all ultimately interested. That is, how will atmospheric and climatic change alter the net productivity of ecosystems over decadal time scales? Such far reaching questions can be addressed only with the use of simulation models. Ideally, those models are informed by the results of experiments and the best compilation of our understanding of processes and responses.

Woodward & Osborne (2000) summarize how roots are currently considered in models used to address global change issues (see also Jackson *et al.*, 2000). The range of approaches used for simulating root behavior in models has been fairly narrow, and modeling has not been as fruitful at providing new ideas to explore experimentally for belowground processes as for aboveground processes. The level of detail currently used in models varies dramatically depending on the model and whether the goal might be to simulate water uptake for transpiration or the role of roots in soil C storage. Woodward & Osborne (2000) rightly point out that many global models perform well for today's conditions with little or no representation of roots. One reason for this agreement is that the major root activities of resource capture are often correlated (e.g. uptake of N and transpired water). However, we do not know if these correlations will stay the same in the future. Furthermore, extensive land use and land cover change are creating novel combinations of climate and plant life forms for which such relationships may not hold. The moderate success of all approaches (including those that ignore roots completely), the lack of appropriate global root data sets, and trade-offs between mechanistic detail and over-parameterization all call into question how extensively root data can and will be incorporated into global models in the future (Woodward & Osborne, 2000).

Here we have a major challenge. Root biologists accept on faith that a deeper understanding of roots is critical to describing the integrated response of ecosystems to global change, yet many global models

appear to work fairly well for today's conditions with only rudimentary information on roots. Furthermore, the broad patterns in root turnover observed globally cannot necessarily be explained by detailed local observations (Gill & Jackson, 2000). We cannot yet answer the questions put forth in the beginning of this paper. There are insufficient data to support any generalizations about effects of elevated CO_2 on root turnover or the consequence of root turnover on the C flux to long-lived soil C pools. The responses to increased temperature are obscured by the occurrence of acclimation, but this issue at least appears to be tractable. The challenge, then, is to overcome the serious methodological and analytical problems and assemble a more comprehensive data set with sufficient ancillary data that differences between ecosystems can be explained. Efforts to link root attributes mechanistically or correlatively with remotely sensed variables are needed. An additional challenge is further to develop conceptual and predictive models of C allocation in plants so that environmental influences on leaves can be translated into the responses that follow in roots. New ideas that might account for the large uncertainty in the ultimate fate of the C in roots need to be tested. And clear challenges remain: to integrate above- and belowground plant functioning and to demonstrate that roots matter – that global predictions of terrestrial response to atmospheric and climatic change will be improved with a better characterization of root dynamics.

REFERENCES

Aber JD, Melillo JM, Nadelhoffer KJ, McClaugherty C, Pastor J. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability. A comparison of two methods. *Oecologia* **66**: 317–321.

Allen AS, Andrews JA, Finzi AC, Matamala R, Richter DD, Schelsinger WH. 2000. Effects of free-air CO_2 enrichment (FACE) on belowground processes in a *Pinus taeda* forest. *Ecological Applications* **10**: 437–448.

Arnone JA III, Zaller JG, Spehn E, Niklaus PA, Wells CE, Körner Ch. 2000. Dynamics of root systems in native grasslands: effects of elevated atmospheric CO_2. *New Phytologist* **147**: 73–85.

Atkin OK, Edwards EJ, Loveys BR. 2000. Response of root respiration to changes in temperature and its relevance to global warming. *New Phytologist* **147**: 141–154.

BassiriRad H. 2000. Kinetics of nutrient uptake by roots: responses to global change. *New Phytologist* **147**: 155–169.

Bazzaz FA. 1990. The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology and Systematics* **21**: 167–196.

Berntson GM, Bazazz FA. 1996. The allometry of root production and loss in seedlings of *Acer rubrum* (Aceraceae) and *Betula papyrifera* (Betulaceae): implications for root dynamics in elevated CO_2. *American Journal of Botany* **83**: 608–616.

Berntson GM, Rajakaruna N, Bazzaz FA. 1998. Growth and nitrogen uptake in an experimental community of annuals exposed to elevated atmospheric CO_2. *Global Change Biology* **4**: 607–626.

Burke MK, Raynal DJ. 1994. Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. *Plant and Soil* **162**: 135–146.

Canadell J, Ingram J, Noble I, eds. 1999. *Global Change and Terrestrial Ecosystems Implementation Plan. IGBP Report 47. Focus 1: Ecosystem Physiology and Global Change.* http://www.gcte-focus1.org/publications/Focus1Implementation.pdf

Comas LH, Eissenstat DM, Lakso AN. 2000. Assessing root death and root system dynamics in a study of grape canopy pruning. *New Phytologist* **147**: 171–178.

Dahlman RC, Kucera CL. 1965. Root productivity and turnover in native prairie. *Ecology* **46**: 84–89.

DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, Matamala R, Mohan JE, Hendrey GR, Schlesinger WH. 1999. Net primary production of a forest ecosystem with experimental CO_2 enrichment. *Science* **284**: 1177–1179.

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL. 2000. Building roots in a changing environment: implications for root longevity. *New Phytologist* **147**: 33–42.

Farrar JF, Jones DL. 2000. The control of carbon acquisition by roots. *New Phytologist* **147**: 43–53.

Fitter AH, Graves JD, Self GK, Brown TK, Bogie DS, Taylor K. 1998. Root production, turnover and respiration under two grassland types along an altitudinal gradient: influence of temperature and solar radiation. *Oecologia* **114**: 20–30.

Fitter AH, Graves JD, Wolfenden J, Self GK, Brown TK, Bogie D, Mansfield TA. 1997. Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. *New Phytologist* **137**: 247–255.

Fitter AH, Heinemeyer A, Staddon PL. 2000. The impact of elevated CO_2 and global climate change on arbuscular mycorrhizas: a mycocentric approach. *New Phytologist* **147**: 179–187.

Fitter AH, Self GK, Wolfenden J, van Vuuren MMI, Brown TK, Williamson L, Graves JD, Robinson D. 1996. Root production and mortality under elevated atmospheric carbon dioxide. *Plant and Soil* **187**: 299–306.

Fitter AH, Stickland TR, Harvey ML, Wilson GW. 1991. Architectural analysis of plant–root systems. 1. Architectural correlates of exploitation efficiency. *New Phytologist* **118**: 375–382.

Gaudinski JB, Trumbore SE, Davidson EA, Zheng S. 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry*. (In press.)

Gifford RM, Lutze JL, Barrett D. 1996. Global atmospheric change effects on terrestrial carbon sequestration: exploration with a global C- and N-cycle model (CQUESTN). *Plant and Soil* **187**: 369–387.

Gill RA, Jackson RB. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**: 13–31.

Hendrick RL, Pregitzer KS. 1992. The demography of fine roots in a northern hardwood forest. *Ecology* **73**: 1094–1104.

Jackson RB, Mooney HA, Schulze ED. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences, USA* **94**: 7362–7366.

Jackson RB, Schenk HJ, Jobbágy EG, Canadell J, Colello GD, Dickinson RE, Field CB, Friedlingstein P, Heimann M, Hibbard K, Kicklighter DW, Kleidon A, Neilson RP, Parton WJ, Sala OE, Sykes MT. 2000. Belowground consequences of vegetation change and their treatment in models. *Ecological Applications* **10**: 470–483.

Joslin JD, Wolfe MH, Hanson PJ. 2000. Effects of altered water regimes on forest root systems. *New Phytologist* **147**: 117–129.

Lauenroth WK. 2000. Methods of estimating belowground net primary production. In: Sala OE, Jackson RB, Mooney HA, Howarth R, eds. *Methods in ecosystem science*. New York, USA: Springer, 58–71.

Lloyd J, Farquhar GD. 1996. The CO_2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO_2 concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. *Functional Ecology* **10**: 4–32.

Nadelhoffer KJ. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytologist* **147**: 131–139.

Norby RJ. 1994. Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. *Plant and Soil* **165**: 9–20.

Norby RJ. 1998. Nitrogen deposition: a component of global change analyses. *New Phytologist* **139**: 189–200.

Norby RJ, Pastor J, Melillo JM. 1986. Carbon–nitrogen interactions in CO_2-enriched white oak: physiological and long-term perspectives. *Tree Physiology* **2**: 233–241.

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R. 1999. Tree responses to rising CO_2: implications for the future forest. *Plant, Cell & Environment* **22**: 683–714.

Pregitzer KS, King JS, Burton AJ, Brown SS. 2000a. Responses of tree fine roots to temperature. *New Phytologist* **147**: 105–115.

Pregitzer KS, Zak DR, Maziasz J, DeForest J, Curtis PS, Lussenhop J. 2000b. Fine root growth, mortality, and morphology in a factorial elevated atmospheric $CO_2 \times$ soil N availability experiment. *Ecological Applications* **10**: 18–33.

Pritchard SG, Rogers HH. 2000. Spatial and temporal deployment of crop roots in CO_2-enriched environments. *New Phytologist* **147**: 55–71.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* **94**: 13730–13734.

Rillig MC, Wright SF, Allen MF, Field CB. 1999. Rise in carbon dioxide changes soil structure. *Nature* **400**: 628.

Rogers HH, Runion GB, Prior SA, Torbert HA. 1999. Responses of plants to elevated atmospheric CO_2: root growth, mineral nutrition, and soil carbon. In: Luo Y, Mooney HA, eds. *Carbon dioxide and environmental stress*. San Diego, CA, USA: Academic Press, 215–244.

Schlesinger WH, Andrews JA. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* **48**: 7–20.

Singh JS, Lauenroth WK, Hunt HW, Swift DM. 1984. Bias and random errors in estimators of net root production: a simulation approach. *Ecology* **65**: 1760–1764.

Staddon PL, Robinson D, Graves JD, Fitter AH. 1999. The $\delta^{13}C$ signature of the external phase of a *Glomus* mycorrhizal fungus: determination and implications. *Soil Biology and Biochemistry* **31**: 1067–1070.

Tansley AG. 1935. The use and abuse of vegetational concepts and terms. *Ecology* **16**: 284.

Tingey DT, Phillips DL, Johnson MG. 2000. Elevated CO_2 and conifer roots: effects on growth, life span and turnover. *New Phytologist* **147**: 87–103.

Treseder KK, Allen MF. 2000. Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. *New Phytologist* **147**: 189–200.

Woodward FI, Osborne CP. 2000. The representation of root processes in models addressing the responses of vegetation to global change. *New Phytologist* **147**: 223–232.

Zak DR, Pregitzer KS, King JS, Holmes WE. 2000. Elevated atmospheric CO_2, fine roots and the response of soil microorganisms: a review and hypothesis. *New Phytologist* **147**: 201–222.