Research review

Root stress and nitrogen deposition: consequences and research priorities

Author for correspondence:
Erica A. H. Smithwick
Tel: +1 814 865 6693
Email: smithwick@psu.edu

Erica A. H. Smithwick[1], David M. Eissenstat[2], Gary M. Lovett[3], Richard D. Bowden[4], Lindsey E. Rustad[5] and Charles T. Driscoll[6]

[1]Department of Geography and Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, PA, 16802, USA; [2]Department of Ecosystem Science and Management and Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, PA, 16802, USA; [3]Cary Institute of Ecosystem Studies, Millbrook, NY, 12545, USA; [4]Department of Environmental Science, Allegheny College, Meadville, PA, 16335, USA; [5]USDA Forest Service, Northern Research Station, Durham, NH, 03824, USA; [6]Department of Civil and Environmental Engineering, Syracuse University, Syracuse, NY, 13244, USA

Summary

Stress within tree roots may influence whole-tree responses to nutrient deficiencies or toxic ion accumulation, but the mechanisms that govern root responses to the belowground chemical environment are poorly quantified. Currently, root production is modeled using rates of forest production and stoichiometry, but this approach alone may be insufficient to forecast variability in forest responses when physical and chemical stressors alter root lifespan, rooting depth or mycorrhizal colonization directly. Here, we review key research priorities for improving predictions of tree responses to changes in the belowground biogeochemical environment resulting from nitrogen deposition, including: limits of the optimum allocation paradigm, root physiological stress and lifespan, contingency effects that determine threshold responses across broad gradients, coupled water-biogeochemical interactions on roots, mycorrhizal dynamics that mediate root resilience and model frameworks to better simulate root feedbacks to aboveground function. We conclude that models incorporating physiological feedbacks, dynamic responses to coupled stressors, mycorrhizal interactions, and which challenge widely-accepted notions of optimum allocation, can elucidate potential thresholds of tree responses to biogeochemical stressors. Emphasis on comparative studies across species and environmental gradients, and which incorporates insights at the cellular and ecosystem level, is critical for forecasting whole-tree responses to altered biogeochemical landscapes.

Introduction

To inform biogeochemical models that are capable of forecasting ecosystem responses to nitrogen (N) deposition, improved understanding of belowground responses to biogeochemical stressors is needed. Yet, few studies have focused on how cumulative root responses to elevated N (including shifts in root lifespan, production, depth distribution and physiology) affect whole-ecosystem function. Models that incorporate these dynamics mechanistically could help elucidate the conditions that promote ecosystem resilience to atmospheric N deposition and help explain heterogeneous patterns in tree productivity (Thomas *et al.*, 2010)

that are not easily attributed to N loads, species, or environmental gradients (Pardo *et al.*, 2011).

Currently, root biomass and turnover are modeled through passive responses to aboveground allocation and shifts in stoichiometry (especially leaf carbon (C) : N) that appear to regulate ecosystem function adequately under most conditions. However, when systems are stressed, shifts in allocation and stoichiometry alone are insufficient to simulate increases in root mortality (decreases in lifespan), which may have direct consequences on nutrient or water uptake and aboveground productivity. Rather, root tissues in contact with ions at toxic levels in soil solution may experience mortality directly through cellular physiological

responses, independent of changes in allocation or stoichiometry. Changes in rooting depth or function in response to increased mortality might increase tree susceptibility to subsequent disturbances such as drought, with broad ecosystem consequences. How much of a change in allocation, stoichiometry and tissue physiology is required to alter ecosystem productivity is unknown and likely depends on initial conditions (e.g. concentrations of nutrients or toxins in soil, roots, and shoots), stressors (e.g. N loads), and associated changes in soil solution chemistry (e.g. acidity, base cation concentrations).

Motivation for understanding root responses to elevated N derives from recent research that shows that, despite intensive and long-term studies, forest responses to elevated N remain frustratingly complex, with some forests showing positive responses to added N (Thomas *et al.*, 2010) and others showing decreased productivity and sometimes increased mortality (Wallace *et al.*, 2007). Overall, these effects are spatially heterogeneous and difficult to disentangle from factors such as form of added N, climate, land use, lithology, or tree species composition.

Conceptual models of N saturation have traditionally focused on understanding ecosystem-level responses over time (Aber *et al.*, 1998), but emerging frameworks (i.e. Lovett & Goodale, 2011) suggest that changes in N cycling resulting from experimental N additions may be best determined by differential abilities of ecosystem sinks (soil, vegetation, microbial pools) to absorb short-term N additions relative to N inputs. We consider here the unexamined role of roots and root feedbacks to aboveground function, which have not previously been integrated explicitly into these frameworks.

We suggest that tissue-level root physiology and architecture can be understood alongside traditional paradigms of aboveground and belowground dynamics in response to elevated N, by evaluating five alternate pathways (Fig. 1). First, we suggest that fine root proliferation and extension is governed by the availability of C for root growth, which is determined by absolute or relative allocation of photosynthate partitioned belowground (pathways 1 and 2). The idea that the fraction of C allocated to the root system increases as nutrient supply limits whole-plant growth is modeled traditionally under the assumption of functional equilibrium or optimal growth allocation (Brouwer, 1983; Ingestad & Ågren, 1991). Alternatively, we suggest that root lifespan is controlled by physiological responses of roots to elevated N (pathway 3), in which reactive N or oxygen species accumulate in cell tissues leading to oxidative or respiratory stress (Delledonne *et al.*, 2001; Hancock *et al.*, 2008). Similarly, direct exposure to aluminum (Al) (pathway 4) via declines in base cation (Bc) to Al ratios (USEPA, 2009) can inhibit cell division and elongation (Kochian *et al.*, 2005) and have adverse effects on tree growth or nutrition (Cronan & Grigal, 1995). In addition, shifts in rooting depth (pathway 5) may occur in response to increased physiological stress within root tissues in adverse conditions (van Bodegom *et al.* 2008) or increased activity and sink strength of roots in favorable soil locations (Farrar & Jones, 2000), with implications for understanding interactions between N deposition and drought. Finally, complex interactions between roots and the symbiotic fungal community are likely important for determining whole-ecosystem responses to elevated N. Changes in fungal biomass or shifts in fungal communities may alter tolerance of roots to herbivory or ions at toxic levels, and
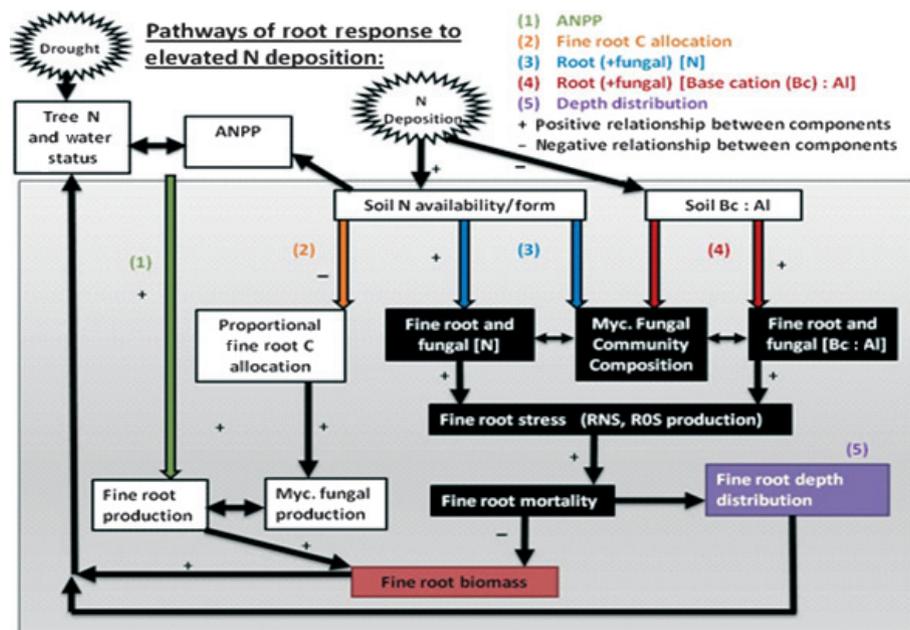
Fig. 1 Five mechanisms by which nitrogen (N) addition may modify fine root mortality and production. (1) Total allocation: increased nutrient supply increases aboveground net primary productivity (ANPP) and total belowground allocation. (2) Relative allocation: elevated N availability changes fine root production by shifting relative carbon (C) allocation from belowground to aboveground tissues. (3) N stress: root stress may increase via increases in fine root N concentrations leading to increased reactive N and oxygen species. (4) Aluminum (Al) stress: elevated rates of nitrification and NO_3^- leaching decrease soil base cation (Bc) : Al ratios, leading to increased Al toxicity and elevated levels of reactive N and oxygen species. (5) Rooting depth: decreased C allocation or increased root stress decreases rooting depth and increases vulnerability to additional stressors such as drought. +, A positive correlation between A and B; −, an inverse correlation between A and B.

decrease potential nutrient acquisition, with feedbacks to above-ground function.

Using this conceptual model as a guide, we review belowground responses to altered soil chemistry, aligning traditional ecosystem paradigms with emerging understanding of root physiology and belowground dynamics. We focus on exploration of six research priorities that emerge from our understanding of roots and N deposition: (1) recognition of the limits of the optimum allocation paradigm for understanding diminished root function and declines in root lifespan under elevated N; (2) incorporation of direct root physiological stress into understanding root response to elevated N; (3) the role of contingency effects (e.g. soil conditions) that mediate threshold responses of roots across broad environmental gradients; (4) increased understanding of how chronic elevated N may influence root responses to stressors such as drought; (5) the role of mycorrhizal dynamics on root resilience; and (6) the development of new model frameworks that embed root responses to chemical and physical stressors alongside traditional allocation approaches.

Understanding both direct and indirect responses of roots to elevated N may provide a generalizable framework for understanding mechanistic, belowground responses to altered soil biogeo-chemistry. Nitrogen deposition has received significant policy and management attention (Pardo *et al.*, 2011) and has been the focus of a variety of long-term experimental and observational studies; yet, specific rhizosphere-level mechanisms remain unclear and cannot yet explain the observed variability in ecosystem-level responses to elevated N in experimental studies. Root responses to N deposition thus serve as an opportunity to explore aboveground–belowground interactions more generally, bridge disciplinary boundaries and improve understanding of the conditions that determine ecosystem resilience under biogeochemical stressors.

Research priorities

Optimum allocation

Effects of N availability on the allocation of C to the root system is often modeled under the assumption of functional equilibrium or optimal growth allocation (e.g. Ingestad & Ågren, 1991), where the fraction of C allocated to the root system is proportional to nutrient and water limitation for whole-plant growth. Specifically, fine root proliferation and extension is governed by the availability of C for root growth, determined by aboveground net primary productivity (ANPP) and the portion of photosynthate allocated to the root system. Increased leaf area resulting from elevated N availability, combined with increases in photosynthesis caused by increases in leaf N and rubisco, could increase absolute belowground alloca-tion. Elevated N availability may also lead to reductions in relative fine root production by shifting C allocation from belowground to aboveground tissues (Hendricks *et al.*, 1993).

Poorter & Nagel (2000) suggested that more support exists for functional equilibrium in the case of nutrient supply than light, CO_2 or water. For N, evidence suggests that much of the control over allocation is at the leaf-level, where C is retained preferentially for shoot growth when N is not limiting (Ingestad & Ågren, 1991). Although the mechanisms have been challenged previously (e.g.

Farrar & Jones, 2000), the dominant paradigm of optimal equilibrium remains widely accepted (see recent reviews by Poorter & Nagel, 2000; Brassard *et al.*, 2009) and has been used to develop mathematical models that predict whole-plant growth (van Noordwijk *et al.*, 1998).

However, most studies supporting optimal allocation have been conducted using young plants in pots where allocation shifts have been confounded with ontogenetic shifts associated with plant size (Reich, 2002); studies clearly supporting optimal allocation under field conditions are rare. Studies that have explored the responses of tree fine roots to enhanced soil N availability indicate the entire range of possible responses – increases, decreases or no change in belowground biomass (Brassard *et al.*, 2009). Thus, a generalized application of optimal allocation theory to forested environments experiencing enhanced N deposition may not be sufficient to explain heterogeneous forest responses.

To understand fine root productivity in response to N gradients, alternative perspectives may be necessary to supplement or replace the optimal allocation paradigm. For example, under the paradigm of lifetime efficiency (Eissenstat & Yanai, 1997), production and longevity interact to optimize nutrient foraging: as roots become exposed to unfavorable soil microsites, they may be shed and produced elsewhere within the rooting zone. Soil chemistry may influence root lifespan directly through changes in root efficiency (i.e. the benefit the root provides compared with its C costs of construction and maintenance). Under N limitation, increasing N availability may increase lifespan if the benefit (N uptake of a root) is increased relative to the C cost. Physiologically, this may occur through greater carbohydrate allocation to inducible defenses, maintenance of membrane potentials and production of enzymes that can scavenge reactive oxygen and N species, and reduced expenditure of photosynthate for those roots providing little benefit. If plants become N saturated, the marginal gain of taking up additional N could be of lower value than the marginal cost of carbohydrates expended on root maintenance, leading to shorter root lifespan. This leads to the prediction that as systems become N-saturated, added N could reduce root lifespan and fine root biomass.

A greater appreciation of lifetime efficiency (trade-offs between costs and benefits) does not preclude the generalization of the optimum allocation paradigm. Multiple factors are likely to be operating simultaneously. However, methods for measuring turnover and lifespan are often confounded methodologically, limiting the ability to separate changes in biomass resulting from aboveground allocation vs those induced by shifts in efficiency. New frameworks should extend equilibrium ideas of mass and nutrient partitioning to those that incorporate factors influencing production as well as those that influence root lifespan directly. Efforts focused solely on relative and absolute biomass allocation in response to leaf N concentrations may be too simplistic and are likely biased toward an aboveground-driven view of root responses.

Root physiology and root lifespan

Direct physiological activity within roots may be altered under environmental stress leading to decreases in root lifespan. Studies

have documented strong positive correlations of root N concentration with root respiration (e.g. Burton *et al.*, 2002). Respiration is associated with critical root functions of uptake, assimilation and transport, and may also increase the generation of reactive oxygen species (e.g. oxygen ions, free radicals and peroxides, both inorganic and organic). In addition, roots that have excess N may be unable to completely reduce nitrate to amino acids, leading to accumulation of reactive N species (e.g. nitric oxide (NO); Delledonne *et al.*, 2001). Because reactive N and oxygen species have unstable redox states, they react readily with root membranes, nucleic acids and proteins, and can impair root cellular function (Zaninotto *et al.*, 2006). Production and scavenging of these reactive species may be perturbed by a number of adverse abiotic stress factors, including drought, high temperatures, nutrient deficiencies and imbalances, and elevated concentrations of Al or other toxic ions (Clijsters *et al.*, 1999). Conversely, roots may avoid accumulation of reactive N species by direct uptake of amino acids or ammonium (NH_4^+), or relationships between respiration and root N may be obscured by the accumulation of storage proteins, especially in woody roots (Burton *et al.*, 2012).

In addition to interactions with reactive N and oxygen species, plant roots are adversely affected by direct exposure to elevated concentrations of Al that may occur following N deposition. Aluminum can bind to nucleotides and nucleic acids, inhibiting cell division and elongation, and interfering with energy and soil solution transfer across root cell walls, causing irreversible damage to plant cells (Vanguelova *et al.*, 2005). Sverdrup & Warfvinge (1993) developed a logistic relationship relating root biomass to soil solution base cation to Al ratios that describes root dynamics in response to acidification (see Fig. 2). In this model, threshold responses occur when soil solution molar ratio concentrations are < 1. The risk of 'adverse impacts on tree growth or nutrition' has been estimated as 50% when soil solution Ca : Al is 1.0, increasing to 90–100% when the ratio is 0.2 (Cronan & Grigal, 1995; p. 209). However, complicating our ability to generalize is the fact that the
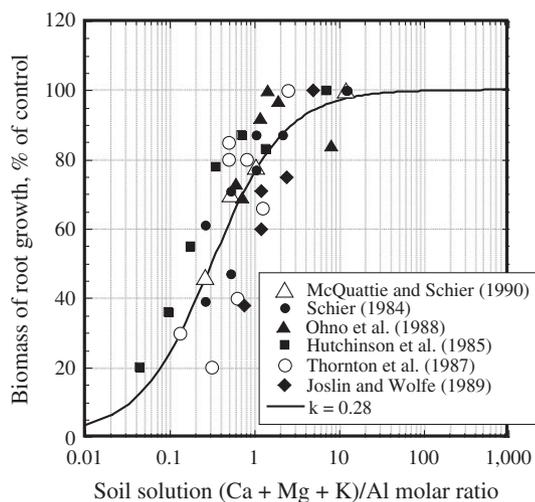
effects of Al on root mortality may vary considerably among plant species, and even within species roots may be able to acclimatize *in situ* to minimize toxicity (Richter *et al.*, 2007).

Physiological responses within root cells have received relatively little attention at the ecosystem level and thus are sorely lacking in most ecosystem process models. This contrasts with the extensive incorporation of cellular physiology within photosynthesis (Farquhar & Sharkey, 1982) in ecosystem models. In certain biogeochemical environments, decreases in root lifespan caused by cellular physiological stress might not occur in parallel with changes in net root productivity; rather, shifts in aboveground and belowground C allocation may be independent of changes in root mortality. Thus, future research on root dynamics requires knowledge of physiological factors that affect fine root productivity and lifespan, accounting for both direct and indirect causes of shifts in root biomass. Moreover, in addition to biogeochemical stress, root lifespan is controlled by many other factors, including C availability, herbivory, pathogens and other abiotic factors such as water stress (Eissenstat & Yanai, 1997), which must be considered alongside direct biogeochemical factors.
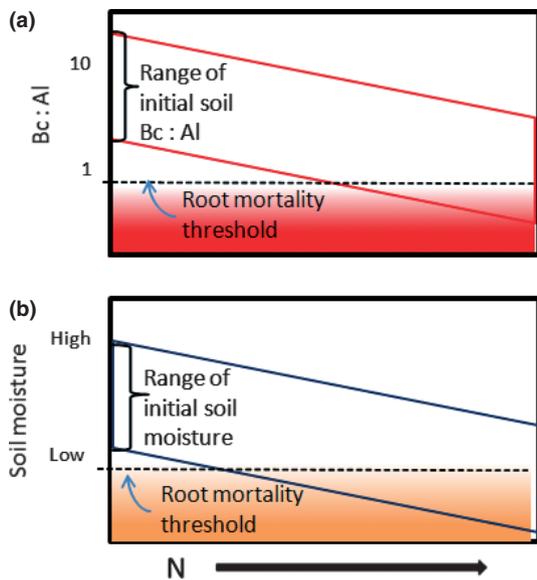
Contingent effects

Local conditions can strongly influence ecosystem dynamics and thus are likely to govern or mediate root responses to specific chemical soil solution stressors. Stand age, background nutrient availability, seasonality and differences among individuals, species and communities can all influence specific root responses at a given location (Brassard *et al.*, 2009). For example, Richter *et al.* (2007) found that root tip development was correlated with initial base saturation conditions, declining as root Ca : Al ratio and base saturation decreased. Thus, across gradients in N deposition, the sum of environmental conditions may mediate root lifespan responses and may thus conceal complex interactions between initial conditions, stressors and ecosystem responses (Fig. 3).

With increases in N deposition, root tissue damage caused by declining Bc : Al ratios may not be observed if soil is characterized initially by high Bc : Al. However, if geological conditions create a soil that is characterized initially by low Bc : Al, root damage may occur at lower levels of N deposition (Fig. 3a). Similarly, if increasing N deposition increases leaf area, then increased transpiration can reduce soil moisture availability, resulting in root stress if moisture is limiting (Fig. 3b). Thus, within a forest landscape receiving equal rates of N deposition, environmental gradients of soil, substrate and climate, may determine the vulnerability of roots to tissue damage. These thresholds may be crossed under specific environmental conditions that are geographically and temporally contingent and must be explicitly included in model parameterization.

Coupled water–nutrient interactions

Roots respond morphologically and physiologically to differential nutrient or moisture availability within their rooting zones. Understanding the coupled interactions between nutrient acquisition and access to deep water has received significant attention in

Fig. 2 The relationship between soil solution base cation (Bc) : aluminum (Al) ratio and biomass or root growth in red spruce (from Sverdrup & Warfvinge, 1993; reproduced, with permission). Ca, calcium; K, potassium (K); Mg, magnesium.

Fig. 3 Interactions of increasing soil nitrogen (N) with base cation to aluminum ratios (Bc : Al) and soil moisture concentrations. Potential for root tissue damage depends on initial conditions, which are a function of plant species, geographic location (e.g. substrate) and external drivers (e.g. climate). In (a), increasing N deposition decreases because of increased Al concentrations. Different plant species may have a damage threshold lower or higher than Bc : Al of 1. In (b), increasing N deposition decreases soil moisture because of increasing leaf area. Root stress increases with increasing N and decreasing Bc : Al, but root mortality thresholds are crossed at lower levels of N deposition if initial conditions are more sensitive.

arid regions where these factors are often co-limiting, and where sharp responses in vegetation function have been observed. However, little is known about how rooting depth responds to chronically adverse biogeochemical environments in which nutrients are in oversupply, or how these responses may influence ecosystem function following episodic stressors (e.g. drought). Under elevated N deposition, increased acidity may decrease root biomass in organic layers but increase root distribution in deeper, mineral soil horizons where soil pH is buffered more strongly (Adamek *et al.*, 2011). Relaxation of this stress may show the opposite response (Zang *et al.*, 2011). By contrast, other studies indicate that N addition can preferentially shift root length density to more surface soil layers (Coleman, 2007), whereas some have shown that N additions have no effect on root distribution (Leyshon, 1991).

Together, biogeochemical and water stress may influence root distribution and lifespan changes with soil depth, but the strength or direction of these interactions have not been explored (McMurtrie *et al.*, 2012). Arguably, if fine roots in northern temperate forests are already stressed from elevated N soil, then they may be more vulnerable to drought because of decreases in lifespan and root standing crop that could reduce water uptake. If these changes in lifespan and standing crop were coupled to shifts to shallower root distribution, limited access to deep water may exacerbate water stress during drought. Arguably, fewer roots in upper horizons could also increase water stress if water availability was limited to organic horizons during dry periods. The specific physiological tolerance necessary to sustain root lifespan in

response to coupled stressors may be a key indicator of tree mortality thresholds and is likely to vary across species, ages and geographic locations. Importantly, roots are involved in foraging for multiple nutrients in addition to water, so root depth distribution in heterogeneous belowground environments likely involves trade-offs in efficiency, which manifest at very fine spatial and temporal scales and are driven by multiple factors, including CO_2 concentrations (Iversen, 2010; McMurtrie *et al.*, 2012). Interestingly, Makita *et al.* (2011) concluded that as chemical stress is alleviated, root biomass recovers to prestress conditions, suggesting a plastic response of root dynamics to stressors. Together, these trade-offs may promote whole-tree and ecosystem resilience, but it is not known to what extent this resilience varies across different plant species or types of stress. It may be that certain combinations of stress push roots across thresholds beyond which no recovery is possible. If responses are species specific, shifts in species composition could be expected under projected changes in climate and atmospheric N deposition. Clearly, models and experimental studies should explore depth- or horizon-specific responses to coupled chemical and water stress and the degree to which these are sensitive to species or plant functional type. Importantly, flexibility in model frameworks to account for root redistribution and recovery under chemical or moisture stress will be necessary to forecast dynamics of aboveground–belowground feedbacks.

Mycorrhizas

Mycorrhizal roots are central to quantifying and predicting the balance of N retention and loss from ecosystems (Nadelhoffer, 2000; Jussy *et al.*, 2004). Integrated with an understanding of rhizosphere dynamics that include both fungal and microbial function (e.g. Högberg *et al.*, 2011), mycorrhizal roots may be critical for forecasting forest response to elevated N deposition. Previous reviews of mycorrhizal response to elevated N (Treseder, 2004) suggest that an assessment of fungal symbiotic relationships aids understandings of the heterogeneity of belowground dynamics and subsequent effects on ecosystem function. Several studies have shown a decline in arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) in response to elevated soil N (van Diepen *et al.*, 2010), including changes in EMF community composition (Lilleskov *et al.*, 2001). Interestingly, Högberg *et al.* (2011) showed a recovery of ectomycorrhizal communities following reduced N loading in northern Sweden.

Shifts in fungal biomass and mycorrhizal communities in response to increased N are likely to have consequences for subsequent nutrient acquisition by roots and mediation of toxic soil conditions. However, the mycorrhizal fungal community may exacerbate or mediate root responses, follow similar trajectories as roots in response to increased N, or may be decoupled from root responses. Methodologically it is difficult to know whether mycorrhizal fungal response is a direct or indirect mechanism causing tree mortality. If mycorrhizas are preferentially sensitive to increased N, the loss of this symbiotic relationship could reduce nutrient uptake by tree roots. Alternatively, mycorrhizal fungi may

decouple root uptake from these toxic conditions of bulk solution (van Scholl *et al.*, 2008), shielding roots from toxic soil conditions. If mycorrhizal fungi act as a buffer to help alleviate moisture stress (Fusconi & Berta, 2012), then reduced mycorrhizal colonization of roots under elevated N may actually increase vulnerability to coupled water–nutrient stress. An exciting area of further investigation is the degree to which mycorrhizal fungal communities in stressful soil environments govern root dynamics or respond secondarily to alterations in root biomass or function.

Biogeochemical models

Numerous models synthesize understanding of ecosystem nutrient cycling and productivity to help forecast ecosystem responses to changing biogeochemical conditions. In most contemporary biogeochemical or ecosystem models, uptake of nutrients (e.g. N or phosphorus (P)) is allocated among plant, litter and soil pools by comparing actual vs optimal stoichiometry of mineral nutrients with C (e.g. C : N or C : P ratios). Feedbacks within the vegetation–soil system are generally limited to litter quality and decomposition, nutrient mineralization rates and nutrient availability. Root mass or C is often embedded within belowground 'black boxes' that serve as passive conduits of elemental storage and flow, responsive to system inputs and outputs but with little internal sensitivity. However, optimum allocation approaches that govern aboveground and belowground allocation, and that are commonplace in most biogeochemical models, are unlikely to forecast the heterogeneity and complexity of ecosystem responses to biogeochemical stressors described earlier because they lack mechanisms for interpreting fine root responses. Modeled C storage and productivity appear sensitive to rooting depth and fine root C : N (Tatarinov & Cienciala, 2006) but integration of root dynamics and internal chemistry into biogeochemical models has been limited, and root dynamics are known to alter model output considerably. For example, in the dynamic vegetation model, MC1, rooting depth had a greater influence on ecosystem productivity and vegetation distribution than did shifts in the size of biogeochemical pools under climate change (Daly *et al.*, 2000). Given the number of studies that have focused on understanding coupled nutrient-C-climate dynamics, this result highlights the need for renewed emphasis on root module development.

Currently there is a paucity of models that explore responses of roots to the stressful soil conditions resulting from atmospheric N deposition. Black box approaches have provided valid first-order approximations for simulating ecosystem growth and development, but models to date have not been able to predict increased tree mortality in response to N deposition. Incorporation of more integrated feedbacks among roots, the soil environment and aboveground function may improve these modeling efforts. For example, McMurtrie and colleagues recently formalized a modeling strategy to link N uptake with root distributions that is suitable for incorporation into ecosystem process models and would allow for comparisons of root-depth distributions across ecosystems and alongside root traits (McMurtrie *et al.*, 2012).

Conclusions

We conclude with several specific research recommendations, integrating the topics already described:

• **Experimental studies examining root stress caused by nutrient deficiencies or toxic stress are needed to scale laboratory and glasshouse studies to the ecosystem level.** An opportunity exists for controlled studies (e.g. glasshouse, common garden) to examine the conditions that lead to changes in root lifespan across chemical gradients, and to then examine the places on the landscape where these conditions exist. While extrapolation from seedlings in microcosms to trees in actual landscapes is nontrivial, isolation of key physiological mechanisms in an experimental setting can develop hypotheses to be tested at broader scales. Specifically, studies are needed that compare direct effects of root tissue chemistry and lifespan alongside shifts in productivity and allocation. In these efforts, novel approaches (e.g. tracers, molecular tools) may be necessary to unravel aboveground–belowground linkages.

• **Observational studies should explore contingent effects – in space and time – that influence threshold responses of root lifespan and tree mortality to biogeochemical stress.** These studies should explore variation across species, plant functional types and disturbances across broad abiotic gradients and focus on the interaction among chemical elements on both root lifespan and root production. As such, interactions and coupled responses should be anticipated, the magnitude and direction of which may differ depending on the place along the gradient. Arguably, this is a challenge for root studies that are often laborious and previously restricted to a few, intensive study locations. However, if responses can be generalized along existing gradients, for example, soil, climate or lithology, then root constraints on aboveground productivity could be extended across broader biogeochemical landscapes.

• **Experiments and observational studies should focus on a deeper understanding of conditions in which mycorrhizal fungal colonization, both in amount and fungal composition, influence root resilience and vulnerability to stressful soil solutions.** Of particular interest is whether mycorrhizal colonization buffers, exacerbates, or is independent of root cellular chemistry when roots are exposed to adverse chemical environments. To facilitate this effort, comparisons of mycorrhizal colonization and composition in response to chemical modifications should be made routinely alongside 'root' studies.

• **Belowground dynamics in ecosystem models should examine the consequences of including: physiological feedbacks, dynamic responses to soil solution and root biogeochemistry (nutrients and water), relaxation of the optimum allocation paradigm and inclusion of mycorrhizal dynamics when appropriate.** In the shorter term, focusing objectives on a limited set of root parameters and processes that can be measured and modeled readily with available information and technology may improve our understanding of shifts in belowground function in response to biogeochemical stress. For example, given that quantifiable, mechanistic understanding of mycorrhizal–root interactions is largely untenable at the current time, models could

start by heuristically exploring the consequences of mediating influences of fungal symbionts by employing an additional 'limiting factor' (or its opposite) on root function for a given mycorrhizal functional group and a given level of environmental (e.g. N + drought) stress, as is commonly done for moisture and temperature constraints to aboveground growth. Models could also be improved to incorporate direct changes in aboveground productivity in response to declines in root lifespan, separately from feedbacks related to soil nutrient availability. These changes could be used to complement traditional allocation-driven frameworks. Furthermore, models should be used to explore more generalizable belowground response to stressors other than N.

In summary, despite decades of inquiry through monitoring, process studies, and experimental N additions, ecosystem consequences of excess soil N remain a research priority and a research opportunity. Focus on N may be illustrative of more general responses of roots to altered chemical environments. For example, mixed responses of temperate trees to N deposition, ranging from increases to sharp declines, may reflect more general trade-offs between belowground and aboveground function along complex biogeochemical gradients determined by species, soil, lithology, climate and magnitude of stressor. Mechanisms underpinning tree decline under elevated N are not well understood, but may result from shifts in belowground root structure and function caused by physiological responses that influence both productivity and longevity. Roots that are sensitive to chemical and moisture stress in soils with elevated N and lower nutrient Bc : Al ratios may exhibit reduced productivity, decreased root longevity, or shifts in root distribution that may increase tree vulnerability to drought. These effects may occur simultaneously with other responses that are more consistent with traditional conceptual models (e.g. optimal allocation theory and N-saturation theory) in which changes in aboveground productivity from elevated N as well as feedbacks between altered root biomass and aboveground productivity influence overall tree response.

Nitrogen deposition is a critical stress facing forest ecosystems worldwide and remains a policy concern. An increased emphasis on how tissue-level, root physiology governs tree responses to N deposition and drought may help explain the large variations in ecosystem responses. Moreover, understanding of N deposition may lead to more generalizable insights into root responses to a variety of ecosystem perturbations, such as fire, insects or disease, that influence soil chemistry. Given the rich experimental and analytical approaches to date, models can now be improved to include these mechanistic responses to N specifically, as well as other nutrients and conditions more heuristically. Finally, these goals will be best achieved through focused collaborations among microbial ecologists, plant physiological ecologists, ecosystem ecologists and landscape modelers. Ultimately, this dialogue is likely to provide a forum for increased interdisciplinary understanding of complex landscape dynamics of a biogeochemically evolving world.

Acknowledgements

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