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Minireview

Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems

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Summary

Experimental evidence from a diverse set of forested ecosystems indicates that CO_2 enrichment may lead to deeper rooting distributions. While the causes of greater root production at deeper soil depths under elevated CO_2 concentration ([CO_2]) require further investigation, altered rooting distributions are expected to affect important ecosystem processes. The depth at which fine roots are produced may influence root chemistry, physiological function, and mycorrhizal infection, leading to altered nitrogen (N) uptake rates and slower turnover. Also, soil processes such as microbial decomposition are slowed at depth in the soil, potentially affecting the rate at which root detritus becomes incorporated into soil organic matter. Deeper rooting distributions under elevated [CO_2] provide exciting opportunities to use novel sensors and chemical analyses throughout the soil profile to track the effects of root proliferation on carbon (C) and N cycling. Models do not currently incorporate information on root turnover and C and N cycling at depth in the soil, and modification is necessary to accurately represent processes associated with altered rooting depth distributions. Progress in understanding and modeling the interface between deeper rooting distributions under elevated [CO_2] and soil C and N cycling will be critical in projecting the sustainability of forest responses to rising atmospheric [CO_2].

Introduction

Belowground processes are increasingly recognized as an important foundation for ecosystem responses to rising atmospheric CO_2 concentration ([CO_2]). Fine roots (i.e. roots < 2 mm in diameter) are important in water and nutrient uptake, and are the main interface between trees and the soil ecosystem. Because of their intimate association with the soil profile, fine-root inputs are often more important than leaf litter in driving soil organic matter accumulation (Russell *et al.*, 2004). Rising atmospheric [CO_2] is expected to increase carbon (C) and nitrogen (N) allocation to fine roots, especially in N-limited forests (Norby & Jackson, 2000). Increased fine-root allocation could drive changes in soil C storage and N cycling because fine roots turn over quickly in forests (Gill & Jackson, 2000), and contribute a large amount of C and N to the soil system (Iversen *et al.*, 2008).

Experimental evidence from a diverse set of forested ecosystems indicates that fine roots of trees exposed to elevated [CO_2] are distributed more deeply in the soil profile relative to trees grown under ambient [CO_2] (Table 1). A multitude

Table 1 Fine-root (i.e. roots < 2 mm diameter) depth distributions in CO_2-enriched woody ecosystems

Experimental manipulation and site location	Species examined	Target [CO_2] (ppm)	Year initiated	Root measurement methodology	Soil depth (cm)	Fine-root depth distribution under elevated [CO_2]	Proportion root biomass deeper than *c.* 15 cm		
							Treatment year	Ambient [CO_2]	Elevated [CO_2]
Free-air CO_2 enrichment									
Duke Forest, Orange County, NC, USA	*Pinus taeda* L.	Ambient + 200	1997	Minirhizotrons and soil cores	30	**Not reported**			
						Matamala & Schlesinger (2000)	–	–	–
						Deeper			
						Pritchard *et al.* (2008a)	7	0.25	0.39
						Pritchard *et al.* (2008b)[1]	8	0.51	0.92
Rhinelander, WI, USA	*Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Acer saccharum* Marsh.	560	1997	Minirhizotrons and soil cores	10-25	**Not reported**			
						King *et al.* (2001)	–	–	–
						King *et al.* (2005)	–	–	–
						Pregitzer *et al.* (2008)	–	–	–
Oak Ridge National Laboratory, TN, USA	*Liquidambar styraciflua* L.	565	1998	Minirhizotrons and soil cores	60	**Deeper**			
						Iversen *et al.* (2008)	1	0.43	0.66
Viterbo, Italy	*Populus alba* L., *Populus nigra* L., *Populus* × *euramericana* Dode (Guinier)	550	1999	Soil cores	40	**Deeper**			
						Lukac *et al.* (2003)	3	0.24	0.38
						Liberloo *et al.* (2006)[2]	6	0.24	0.27
						No response			
						Liberloo *et al.* (2009)	–	–	–
Stillberg, Davos, Switzerland	*Larix deciduas* Mill., *Pinus uncinata* Mill. ex Mirb.	550	2001	In-growth cores	10	**Not reported**			
						Handa *et al.* (2008)	–	–	–
Basel, Switzerland	*Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., *Carpinus betulus* L., *Tilia platyphyllos* Scop., *Acer campestre* L., *Prunus avium* L.	540	2001	Soil cores	10	**Not reported**			
						Keel *et al.* (2006)	–	–	–
Open-top chamber									
US Forest Service Institute of Forest Genetics, Placerville, CA, USA	*Pinus ponderosa* Dougl. Ex Laws.	525, 700	1991	Minirhizotrons	46	**No response**			
						Tingey *et al.* (2005)	–	NR	NR

Table 1 (Continued)

Experimental manipulation and site location	Species examined	Target $[CO_2]$ (ppm)	Year initiated	Root measurement methodology	Soil depth (cm)	Fine-root depth distribution under elevated $[CO_2]$	Proportion root biomass deeper than *c.* 15 cm		
							Treatment year	Ambient $[CO_2]$	Elevated $[CO_2]$
Merritt Island, Kennedy Space Center, FL, USA	*Quercus* spp.	700	1992 (Pilot study)	Minirhizotrons	61	**Deeper** Day *et al.* (2006)	2	0.43	0.46
Headley, Hampshire, UK	*Quercus petraea* L., *Fraxinus excelsior* L., *Pinus sylvestris* L.	700	1994	In-growth cores	30	**Not reported** Crookshanks *et al.* (1998)	–	–	–
Oak Ridge National Laboratory, Oak Ridge, TN, USA	*Acer rubrum* L., *Acer saccharum* Marsh.	Ambient + 300	1994	Minirhizotrons and soil cores	60	**Not reported** Wan *et al.* (2004)	–	–	–
University of Michigan Biological Station, Pellston, MI, USA	*Populus tremuloides* Michx.	700	1994	Minirhizotrons and soil cores	45	**Not reported** Pregitzer *et al.* (2000)	–	–	–
Birmensdorf, Switzerland	*Fagus sylvatica* L., *Picea abies* Karst.	570	1995	Soil cores	42	**Not reported** Spinnler *et al.* (2002)	–	–	–
Christchurch, New Zealand	*Pinus radiata* D. Don	650	1995	Minirhizotrons and soil cores	90	**Deeper** Thomas *et al.* (1999)	2	0.44	0.50
Swiss Federal Research Institute for Forest, Snow and Landscape Research, Switzerland	*Fagus silvatica* L., *Picea abies* (L.) Karst.	Ambient + 200	1995	Soil cores	40	**No response** Wiemken *et al.* (2001)	4	0.44	0.40
Merritt Island, Kennedy Space Center, FL, USA	*Quercus* spp.	700	1996	Minirhizotrons and soil cores	101	**Deeper** Day *et al.* (2006)	2	0.51	0.58
						Not reported Brown *et al.* (2009)	–	–	–
University of Antwerp, Wilrijk, Belgium	*Pinus sylvestris* L.	Ambient + 400	1996	Soil cores	50	**Not reported** Jach *et al.* (2000)	–	–	–

Table 1 (Continued)

Experimental manipulation and site location	Species examined	Target [CO_2] (ppm)	Year initiated	Root measurement methodology	Soil depth (cm)	Fine-root depth distribution under elevated [CO_2]	Proportion root biomass deeper than *c.* 15 cm		
							Treatment year	Ambient [CO_2]	Elevated [CO_2]
USDA-ARS National Soil Dynamics Laboratory, Auburn, AL, USA	*Pinus palustris* Mill., *Aristida stricta* Michx., *Quercus margaretta* Ashe, *Crotalaria rotundifolia* Walt., *Aesclepias tuberosa* L.	720	1998	Minirhizotrons	32.5	**Deeper** Pritchard *et al.* (2001)	1	0.43	0.56
Closed chamber									
US EPA, Corvallis, OR, USA	*Pseudotsuga menziesii* (Mirb.) Franco	Ambient + 200	1994	Minirhizotrons	78	**Deeper** Johnson *et al.* (2006)[3]	4	0.20	0.50
US EPA, Corvallis, OR, USA	*Pinus ponderosa* Dougl. Ex Laws.	Ambient + 270	1998	Minirhizotrons and soil excavation	93	**No response** Phillips *et al.* (2009)	3	0.89	0.88

In addition to the studies reported in the table, there were also several open-top chamber experiments that began in or before 1992 that did not examine rooting depth distribution (e.g. Murray *et al.*, 1996; Norby *et al.*, 1995; Rey & Jarvis, 1997; Tingey *et al.*, 1997; Tissue *et al.*, 1997). In some cases, multiple manuscripts from the same experiment were included when they encompassed different treatment years. Wiemken *et al.* (2001), Spinnler *et al.* (2002), Lukac *et al.* (2003), Day *et al.* (2006), Liberloo *et al.* (2006), Johnson *et al.* (2006), and Phillips *et al.* (2009) reported the depth distribution of root standing crop, not production. Raw data to determine the proportion of root biomass distributed deeper than *c.* 15 cm in the soil (actually deeper than 10–25 cm depending on the depth increment measured in the individual study) were obtained from each manuscript from tables, or from figures using digital calipers. In the case of Lukac *et al.* (2003), the proportional responses of *Populus alba* and *Populus nigra*, the species in which the depth distribution was significantly different under elevated [CO_2], were averaged. In the case of Liberloo *et al.* (2006), the proportion of coarse roots deeper in the soil was averaged over all three *Populus* species. In the case of Wiemken *et al.* (2001), proportional responses were averaged over calcareous and siliceous soil types. In all cases, I chose the treatment year in which the largest differences in proportional depth distribution between ambient and elevated [CO_2] were reported. While potentially useful as a rough comparison among studies, proportional root distribution in the soil profile below 15 cm should be interpreted with caution, given that this will differ depending on the absolute depth of measurements (i.e. 30 cm compared with 100 cm), does not necessarily correspond to the year in which absolute root production at depth in the soil was greatest (i.e. Iversen *et al.*, 2008; Pritchard *et al.*, 2008a), and neglects rooting responses localized to specific soil depths (i.e. Day *et al.*, 2006; Iversen *et al.*, 2008; Johnson *et al.*, 2006).

[1]Deeper distribution of mycorrhizal production.

[2]Deeper distribution of coarse roots under elevated [CO_2].

[3]Deeper root distribution with no overall effect of elevated [CO_2] on root production.

NR, depth distribution not reported.

of important soil properties change with soil depth; for example, oxygen content, soil moisture, bulk density, temperature and soil texture (Schenk, 2005). Thus, as soil depth increases, microbial activity, nutrient availability, and root decomposition rates often decline (Gill & Burke, 2002). While rooting depth distribution under elevated [CO_2] was described as a major unknown 15 yr ago (Rogers *et al.*, 1994), the consequences of increased fine-root proliferation and turnover at depth are still poorly understood; this is in part because belowground research is often truncated at relatively shallow soil depths (*c.* 20 cm). The objective of this review is to examine the potential mechanisms for, and consequences of, deeper rooting distributions under elevated [CO_2] as they relate to ecosystem C and N cycling. The main focus is on forest ecosystems exposed to elevated [CO_2] in relatively intact soil systems (i.e. free-air CO_2 enrichment experiments and open-top chambers).

Evidence for deeper rooting distributions under elevated [CO_2]

Deeper rooting distributions under elevated [CO_2] have been observed in a variety of experiments and ecosystems, ranging from free-air CO_2 enrichment (FACE) experiments in mature forest plantations to tree seedlings and saplings planted in open-top chambers (Table 1). Fine roots developed under elevated [CO_2] are not necessarily found deeper in the soil than fine roots developed under ambient [CO_2]. Rather, the relative increase in root production under elevated [CO_2] is often greatest below *c.* 15 cm depth, resulting in a larger proportion of root biomass at deeper soil depths under elevated [CO_2] (Table 1). For example, in a FACE experiment in a sweetgum (*Liquidambar styraciflua* L.) plantation, Iversen *et al.* (2008) found that, over 9 yr, there was a 220% stimulation in cumulative C inputs from fine roots under elevated [CO_2] at 45–60 cm soil depth, compared with a 30% stimulation of root C inputs at 0–15 cm depth. At least half of root-derived C and N inputs in this sweetgum plantation were deeper than 30 cm under elevated [CO_2]. Pritchard *et al.* (2008a) found a similar response in a CO_2-enriched loblolly pine (*Pinus taeda* L.) plantation, where elevated [CO_2] resulted in a larger stimulation of root production at 15–30 cm depth compared with 0–15 cm depth. Deeper rooting distributions under elevated [CO_2] have also been observed in seedlings in pot studies (1.6-m-deep pots; Derner *et al.*, 2005). Of those experiments that examined rooting depth responses to elevated [CO_2], 73% found deeper rooting distributions (Table 1).

While rooting depth is functionally determined by species and ecosystem type (Jackson *et al.*, 1996), observations of rooting responses at depth in the soil are limited by the effort applied and the technology used. For example, the minirhizotrons used by Pritchard *et al.* (2008a) reached to only *c.* 30 cm, and the authors indicated that deeper tubes were recently installed to determine whether rooting responses deeper than 30 cm exist. Iversen *et al.* (2008) and Pritchard *et al.* (2008a) both used minirhizotron technology to determine root dynamics in mature forest plantations, but investigations of root dynamics in other experiments have used methodology ranging from soil coring to in-growth cores (Table 1).

Deeper root distribution under elevated [CO_2] appears to be a relatively dynamic response. Root proliferation at depth did not occur in all experiments exposed to elevated [CO_2] (Table 1), and when it did occur, it was both dynamic (i.e. occurring in some treatment years and not others; e.g. Day *et al.*, 2006; Iversen *et al.*, 2008; Liberloo *et al.*, 2009) and species-specific (e.g. occurring in two poplar clones, but not a third, in Lukac *et al.*, 2003). Deeper rooting distributions have also been observed under elevated [CO_2] without an overall increase in root production (i.e. a redistribution of roots belowground; cf. Johnson *et al.*, 2006). Increased proliferation at depth in the soil has not been limited to fine roots; increased production of mycorrhizas (Pritchard *et al.*, 2008b) and coarse roots (Liberloo *et al.*, 2006) also occurred deeper in the soil under CO_2 enrichment.

A historical focus on roots in shallower soils (i.e. the 'plow layer') contributes to the fact that rooting depth responses remain unexamined or unreported in many CO_2-enrichment studies (Table 1). For example, it was assumed at the start of the sweetgum FACE experiment that the roots had fully occupied the soil volume in the closed-canopy stand (Norby *et al.*, 2004); the subsequent capture of the rooting depth response was largely fortuitous and a consequence in large part of the depth at which the minirhizotron tubes were installed.

Potential causes of deeper rooting distributions under elevated [CO_2]

While much work has been done to examine root proliferation in the soil in response to resource patches (reviewed in Hodge, 2004), the causes of increased root proliferation throughout the soil under elevated [CO_2] remain relatively unexplored (Pritchard *et al.*, 1999). A conceptual diagram (Fig. 1) may serve as a framework for future hypothesis testing to determine the potential mechanisms for, and feedbacks from, greater root production at depth in a CO_2-enriched atmosphere. Deeper rooting distributions under elevated [CO_2] are probably related to three factors: increased resource demand as forest production increases in response to CO_2 enrichment; increased C available for allocation to root growth; and limited resource availability in shallower soil as a result of increased microbial or plant competition. These three factors will probably interact to control root 'decisions' (i.e. Hodge, 2009) that determine root distribution throughout the soil profile.

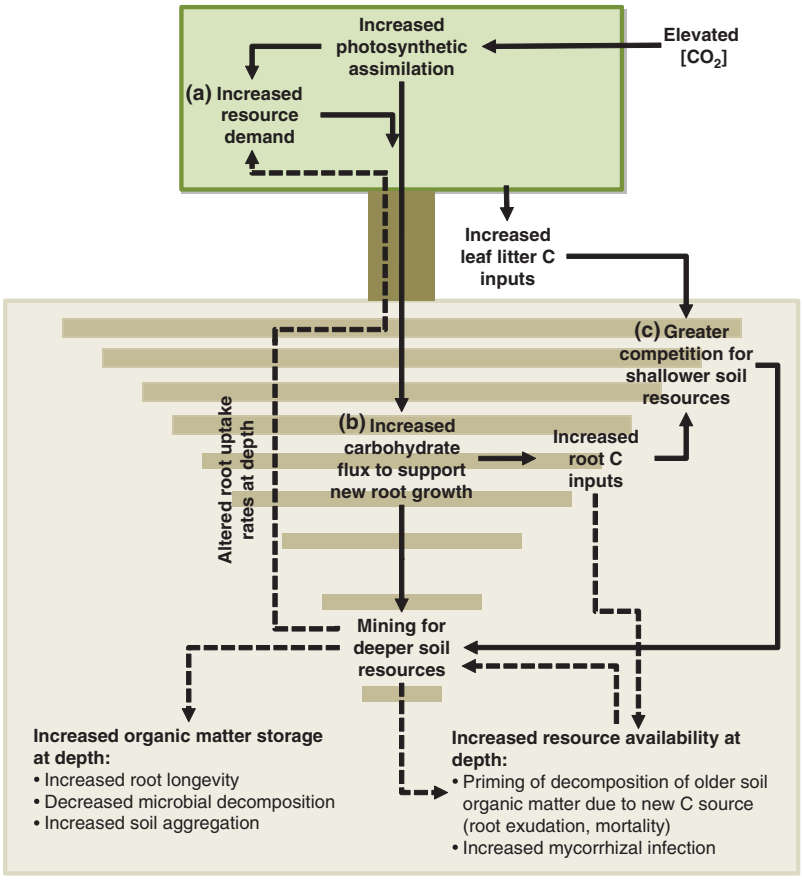

Fig. 1 A conceptual model of the processes leading to deeper rooting distributions under elevated CO_2 concentration ($[CO_2]$) (solid lines), and potential feedbacks from the production of deeper roots (dashed lines). Deeper rooting distributions in CO_2-enriched forests are probably a result of three interacting factors: (a) increased resource demand by trees, (b) greater carbon (C) available for allocation belowground, and (c) increased competition for scarce resources in shallower soil from microbes or other roots. I have specifically chosen to use the phrase 'resources' in the conceptual model rather than 'nutrients' to indicate that essential plant resources other than nutrients (e.g. water) may also control rooting distributions under elevated $[CO_2]$.

Increased C allocation to fine roots under elevated $[CO_2]$ is mainly observed in nutrient-limited forest ecosystems (Table 1). Further, CO_2 enrichment has increased plant demand for nutrient acquisition in a number of forests (Finzi *et al.*, 2007). Roots often proliferate throughout the soil in response to patches of nutrient availability (Prior *et al.*, 2003; Hodge, 2004), and it stands to reason that mining for nutrients is one of the main reasons for greater root proliferation in deeper soil under elevated $[CO_2]$ (Fig. 1a). Others have shown that nutrients are available for plant uptake at depth in the soil (Jobbágy & Jackson, 2001; McKinley *et al.*, 2009), and that the proliferation of new roots can stimulate the mineralization of older organic matter (i.e. priming; Dijkstra & Cheng, 2007). However, there is still much uncertainty regarding the cues for root proliferation throughout the soil, as well as the benefits from such proliferation (Hodge, 2004), and little work has been done to examine root proliferation at depth in the soil in response to nutrients. Roots also proliferate in water zones (Hodge, 2004), and greater root production at depth may also occur in response to increased tree water use under elevated $[CO_2]$ (Uddling *et al.*, 2008). However, water limitations may be rarer under elevated $[CO_2]$ if decreased stomatal conductance at the leaf level (Medlyn *et al.*, 2001) results in less transpiration at the canopy level.

Terrestrial ecosystems are often limited by multiple factors, including light and nutrient availability (Fahey *et al.*, 1998). In nutrient-limited forest ecosystems, greater C fixation in response to rising atmospheric $[CO_2]$ may help to alleviate previous constraints on root development and resource acquisition (Pritchard *et al.*, 1999; Stitt & Krapp, 1999). Cost–benefit models have been used to explain root construction and maintenance (Eissenstat *et al.*, 2000), and C gains under elevated $[CO_2]$ may shift the cost–benefit balance in favor of root production (Fig. 1b), especially in deeper soil where the benefit of smaller resource gains may have previously been outweighed by C costs. The benefit of root proliferation at depth may be further enhanced by strong competition from microbes, and intra- and interspecific interactions with other plant roots, for limited resources in shallower soil (Fig. 1c), especially as increased litter inputs under elevated $[CO_2]$ are expected to increase microbial immobilization of available nutrients (Zak *et al.*, 2000).

Plant root systems are controlled by complex interactions between genetic constraints and environmental conditions (Nibau *et al.*, 2008). Thus, differences in the rooting depth distributions observed under elevated $[CO_2]$ across a range of experiments (Table 1) are probably determined by the interplay between genetically determined species character-

istics such as plant physiology, biochemistry, and root architecture (Bradley & Pregitzer, 2007; Nibau *et al.*, 2008), and ecosystem properties such as climate and soil texture (Jobbágy & Jackson, 2000), resource heterogeneity (Prior *et al.*, 2003), and water table depth (Imada *et al.*, 2008). For example, this review focuses on forested ecosystems, but, in contrast to forests, crop and grassland ecosystems tend to have shallower rooting distributions under elevated [CO_2] (as reviewed in Arnone *et al.*, 2000; Pritchard & Rogers, 2000). Elevated [CO_2] has been shown to stimulate the development of lateral roots (Crookshanks *et al.*, 1998; Pritchard *et al.*, 1999). Therefore, root proliferation in shallower soils may be the result of shallower rooting distributions in crop and grassland ecosystems compared with those in forested ecosystems (Jackson *et al.*, 1996), or shallower rooting distributions in annual compared with perennial plants (Holmes & Rice, 1996). Greater access to nutrients or water at shallower soil depths in crop or grassland ecosystems (Prior *et al.*, 2003; Nippert & Knapp, 2007) may also help to explain the contrasting response.

Potential consequences of deeper rooting distributions under elevated [CO_2]

While pinpointing the mechanisms of deeper rooting distributions under elevated [CO_2] requires more experimentation, the potential consequences of increased root production at depth can be inferred from current knowledge regarding changing ecosystem processes with soil depth.

Root form and function

The depth at which fine roots are produced may influence intrinsic root properties (Fig. 1). For example, roots produced in deeper soils tend to have a lower risk of mortality (Wells *et al.*, 2002; Guo *et al.*, 2008). Roots in deeper soil also often have increased diameter (Wells *et al.*, 2002), lower average root N concentration (Pregitzer *et al.*, 1998), and decreased root respiration rates (Pregitzer *et al.*, 1998). Changes in root form and function at depth in the soil may interact with reduced root [N] and maintenance respiration expected to occur under elevated [CO_2] (i.e. Eissenstat *et al.*, 2000). Altered root chemistry and physiology may in turn result in altered N uptake rates (Göransson *et al.*, 2008), slowed rates of C and N input to the soil as a result of increased root longevity (Joslin *et al.*, 2006), and reduced decomposability (Cotrufo & Ineson, 1995).

Deeper rooting distributions under elevated [CO_2] may also affect root infection by symbionts (Fig. 1). Mycorrhizal fungi, which receive a significant portion of the C taken up by the host plant in exchange for nutrient uptake, are important players in ecosystem C and nutrient cycling. Further, mycorrhizal abundance has been shown to increase up to 50% in response to elevated [CO_2] (Treseder, 2004). Mycorrhizal colonization is closely related to root distribution in the soil across multiple biomes, and, while infection rates tend to decline with soil depth in natural ecosystems (Treseder & Cross, 2006), there is evidence that both ectomycorrhizas and arbuscular mycorrhizas increase root infection rates deeper in the soil profile in response to elevated [CO_2] (Rillig & Field, 2003; Pritchard *et al.*, 2008b).

Root inputs and soil organic matter cycling

The vertical distribution of organic matter and nutrients in the soil is strongly related to rooting patterns (Jobbágy & Jackson, 2000, 2001). Thus, the increased proliferation of roots at relatively unexplored depths under elevated [CO_2] (Fig. 2) may affect previously stable organic matter pools deeper in the soil. The energy gained in deeper soils from fresh inputs of labile C and N compounds from root exudation (de Graaff *et al.*, 2007), or of detritus from root turnover (Iversen *et al.*, 2008), may be more important than temperature and moisture in stimulating the decomposition of ancient C deeper in the soil profile (Fontaine *et al.*,

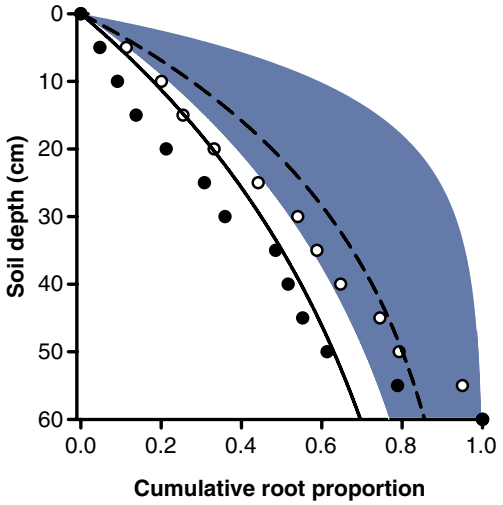

Fig. 2 Forest responses to elevated CO_2 concentration ([CO_2]) may result in rooting distributions that differ from current ecosystems. Open symbols are data from the ambient [CO_2] treatment, and closed symbols are from the elevated [CO_2] treatment, in the Oak Ridge National Laboratory (ORNL) free-air CO_2 enrichment experiment (FACE) in a sweetgum plantation (Iversen *et al.*, 2008). Data are proportional root production throughout the soil profile (to 60 cm deep) in 2001, which was the year of the largest increase in root biomass production at depth under elevated [CO_2] at ORNL FACE. The lines are equal to $1 - \beta^d$, where d is soil depth and β is the fitted parameter (larger values imply deeper rooting depth; adapted from Jackson *et al.*, 1996). At ORNL FACE, $\beta = 0.972$ (dashed line, $R^2 = 0.93$) under ambient [CO_2], and $\beta = 0.981$ (solid line, $R^2 = 0.85$) under elevated [CO_2]. The shaded area represents the global range in rooting depth distributions, ranging from $\beta = 0.914$ in the tundra to $\beta = 0.976$ in the temperate coniferous forest (Jackson *et al.*, 1996).

2007). For example, rhizosphere priming through exudation by living roots has been shown to stimulate the decomposition of organic matter (Dijkstra & Cheng, 2007), and also stimulate N mineralization (de Graaff *et al.*, 2009). As up to 50% of soil C is stored below 20 cm in forests (Jobbágy & Jackson, 2000), even small changes in C inputs at depth in the soil can have drastic consequences for long-term soil C storage (Fig. 1). However, root exudation is notoriously difficult to measure, especially *in situ* in the soil, and measurements are often restricted to shallower soil layers (Phillips *et al.*, 2008). Further, more integration is needed to link root C and N inputs with the cycling of organic matter at depth in the soil, where declining oxygen and temperature may be expected to halve microbial activity (Gill & Burke, 2002).

In contrast to the stimulatory effect of fine-root inputs on the decomposition of organic matter at depth in the soil, root-derived inputs have been shown to be disproportionately important for the formation of stable microaggregates in the soil system (Gale *et al.*, 2000). As the process of microaggregate formation depends not only on the organic nucleus of root detritus, but also on soil texture, bulk density, and microbial activity (Six *et al.*, 2002), the rate of formation could be expected to differ throughout the soil profile, though this has not been examined in detail.

Tools and measurements

Novel analyses may be required to determine the consequences of increased root proliferation at deeper soil depths under elevated [CO_2] for ecosystem C and N cycling. For example, while minirhizotron measurements are currently the best way to track the dynamics of ephemeral root populations (Johnson *et al.*, 2001), improved methods of extrapolating measurements of root length and diameter obtained from digitized images to root mass and N content (Iversen *et al.*, 2008) and root respiration (Makita *et al.*, 2009) will be key in tracking root-derived C and N cycling at depth in the soil. Other recent tools are also available to track C fluxes throughout the soil that may be attributable to fine roots. For example, the effect of deeper rooting distributions on gradients of soil [CO_2] can be determined with CO_2 sensors that are coupled with minirhizotron tubes (e.g. Vargas & Allen, 2008). Also, the flux of ^{13}C-CO_2 from the soil surface in experiments where root material is labeled with a depleted ^{13}C signal can be measured on diurnal scales with tunable diode lasers (e.g. Bahn *et al.*, 2009). Novel analyses of compound-specific isotopes (Filley *et al.*, 2001) and tissue-specific biopolymers (Filley *et al.*, 2008) may also aid in the identification of root-derived compounds. Along with C fluxes, new strategies are needed to link measurements of soil N availability with root dynamics throughout the soil profile (as reviewed in Frank & Groffman, 2009), as current metrics to examine soil nutrient cycling often exclude the effects of roots.

Incorporating rooting depth in projected forest responses to rising CO_2

An important goal of climate change research is the integration of experimental data with ecosystem models (Classen & Langley, 2005). The plant–soil interface is one of the largest areas of uncertainty in current global models, both because of the difficulty in representing complex belowground processes, and also because of the scarcity of data that will allow the development and parameterization of improved model frameworks (Ostle *et al.*, 2009). While the effects of rooting depth distribution on the distribution of C and nutrients in the soil indicate that the interface between fine roots and soil nutrient cycling should be considered throughout the soil profile (Jackson *et al.*, 2000), the most commonly used belowground ecosystem models simulate the mineralization of organic matter at relatively shallow soil depths (i.e. *c.* 20 cm; Parton *et al.*, 1988).

There are at least a dozen ecosystem or land surface models that are used to project C and nutrient cycling in forest ecosystems (Hanson *et al.*, 2004). The output from these models is an important intermediate step between data obtained from field experiments and the information needed for global models used by the Intergovernmental Panel on Climate Change Report to project future climatic conditions (Denman *et al.*, 2007). However, these models differ in the way in which they represent root distributions and nutrient cycling in the soil profile (Fig. 3). Some models do not have a framework to explicitly consider interactions between fine-root production and soil nutrient cycling (cf. Jackson *et al.*, 2000), and therefore greater root proliferation throughout the soil would not affect nutrient uptake rates by the forest system. While other models contain soil layers that represent different depth increments, and prescribe fractional root allocation among soil layers, these layers (represented by dashed lines in Fig. 3) are typically included to represent water dynamics rather than nutrient dynamics (e.g. Thornton *et al.*, 2007). Decomposition dynamics, and therefore soil C and N mineralization, are modeled as one 'box' (heavy outline in Fig. 3), and are typically parameterized with data measured at relatively shallow soil depths (Parton *et al.*, 1988).

A disconnect between observed root dynamics and modeled nutrient availability has confounded projections of forest responses to elevated [CO_2]. While models predict that soil N availability will limit forest responses to elevated [CO_2] (Thornton *et al.*, 2007), many of the forested FACE experiments found a sustained increase in N uptake from the soil in response to CO_2 enrichment (Finzi *et al.*, 2007). There has been much speculation on the source of this 'extra' N (Johnson, 2006), and a greater cumulative amount

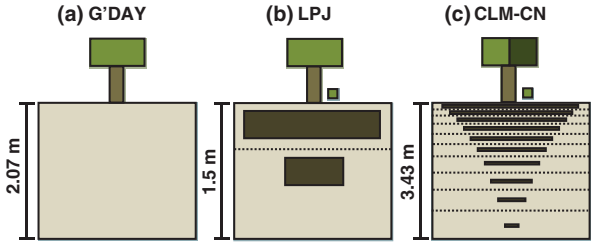

Fig. 3 A small subsample of ecosystem and land surface models, where forest vegetation pools are represented by schematic diagrams. The diagrams are separated into canopy, stem, roots, and soil system. Aboveground, a canopy with multiple boxes indicates sun/shade dynamics, while smaller boxes below the canopy indicate multiple species. Belowground, dotted lines indicate soil layers. Thus far, the soil layers are used solely to model water distribution and transpiration dynamics; soil C and N dynamics are modeled as one 'depth' (dark outline) in all three models. Total soil depth is indicated on the left of each diagram. Three models are shown, representing a range in model treatment of rooting distributions: (a) G'DAY (Pepper *et al.*, 2007) does not explicitly consider the interaction between fine roots and soil, (b) LPJ (Sitch *et al.*, 2003) allocates proportional root distribution in two soil layers, where the fraction in each layer depends on the plant functional type, and (c) CLM-CN (Thornton *et al.*, 2007) prescribes a linear decline in root distribution with soil depth, where the soil system is divided into 10 layers which are exponentially larger as soil depth increases. Model diagrams are based on the framework used in Hanson *et al.* (2004).

of N available at depth in the soil may be the answer (i.e. a 'bigger box' of N when deeper soil depths are considered). However, shallower soil depths have been the main focus of N cycling research in forested FACE experiments to date (i.e. Zak *et al.*, 2003).

A modeling framework that integrates root dynamics and soil N availability at depth may help to pinpoint the cause of increased root proliferation at depth in response to rising [CO_2] (i.e. shifting nutrient or water limitations) and explain the dynamic nature of the rooting depth response observed in a number of ecosystems. A framework for examining the interaction among rooting responses and soil C and N cycling at different soil depths currently exists in at least some ecosystem or land surface models (i.e. dashed lines in Fig. 3). However, more data are needed to accurately parameterize root and nutrient dynamics at depth in the soil. Data-model synthesis will be further improved by communication among researchers as to the relevant depth increments for observation of root and nutrient dynamics (Table 1).

Conclusions

Increased root proliferation at depth may be a key response of forested ecosystems to rising atmospheric [CO_2]. However, it is uncertain to what extent this is a common phenomenon (Table 1). While I have focused on the responses of woody ecosystems to rising atmospheric [CO_2], rooting depth distributions in other ecosystems, such as grasslands and crops, also exert important controls over C and N storage in the soil. Contrasting rooting depth distributions of forested compared with cropped and grassland ecosystems under elevated [CO_2] merit further study, and could help to elucidate the proximal controls over altered rooting distributions in a CO_2-enriched atmosphere.

Deeper rooting distributions under elevated [CO_2], and the interaction of those roots with a soil environment depleted in oxygen and microbial activity, could lead to changes in root form and function, as well as changes in the rate at which root detritus is incorporated into soil organic matter. Altered rooting distributions also provide exciting opportunities for research on C and N cycling in the soil. Advances in the measurement of processes occurring at the root–soil interface that take advantage of novel methodologies such as sensors embedded throughout the soil profile, isotopic partitioning of C fluxes, compound specific chemistry, and measurements of nutrient cycling at depth will provide data needed to inform ecosystem models.

It is important to accurately represent and parameterize processes occurring throughout the soil profile in models. The interactions among elevated [CO_2] and global change factors such as rising temperatures and altered precipitation regimes will almost certainly affect the responses described here, albeit in uncertain ways. Furthermore, the reconfiguration of current model frameworks to accept data on rooting distributions and nutrient cycling at depth in the soil will facilitate the testing of new hypotheses such as those conceptualized in Fig. 1. Continued progress in understanding the interface between root growth and turnover and soil C and N cycling, especially at depth in the soil, will provide critical information needed for understanding current ecosystem function, as well as predicting future ecosystem responses to environmental change.

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