

Root morphology and architecture respond to N addition in *Pinus tabuliformis*, west China

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Abstract Belowground dynamics of terrestrial ecosystems are responding to global increases in anthropogenic N deposition with important consequences for productivity and ecosystem health. We compared root characteristics across five root orders in *Pinus tabuliformis* plantations treated for 3 years to a gradient of N addition (0–15 g m⁻² year⁻¹). In reference plots, the roots of *P. tabuliformis* were finer and with higher specific root length than reported for other pine species, suggesting severe N limitation. Addition of N resulted in slightly reduced fine root biomass and significant changes in root morphology, responses that were associated primarily with first and second order roots. In particular, root number, cumulative root length, individual root length, and specific root length all declined with increasing N addition for first and second order roots, with most of the responses elicited

at <9 g m⁻² year⁻¹ N addition. These responses (1) support the concept of ephemeral root modules consisting of first and second orders and (2) are consistent with a change in functional demand from uptake to transport with increasing soil resource availability. Traditionally, fine roots have been identified by a somewhat arbitrary diameter cut-off (e.g., 1 or 2 mm); as an index of fine root function, diameter would fail to reveal most of the functional response.

Keywords Belowground allocation · Forest ecosystem · Nitrogen saturation · Nutrient uptake · Fine root plasticity

Introduction

Global environmental changes are rapidly and profoundly altering soil resource availability, with potential consequences for vegetation composition, structure, and dynamics. In many regions, nitrogen (N) deposition has increased markedly as a result of anthropogenic generation of reactive N, leading to increases in the availability of this often growth-limiting nutrient (Vitousek et al. 1997; Galloway et al. 2008). Aber et al. (1998) proposed a general theory of ecosystem responses to excessive N deposition, and empirical studies (Driscoll et al. 2003; Fenn et al. 2003; Bobbink et al. 1998, 2010) illustrate a variety of vegetation responses. Understanding the interactions of N deposition and other global change drivers is of particular importance because of the potential feedbacks that could affect global ecosystem responses (Hungate et al. 2003). Although increased N availability can be expected to stimulate primary productivity in many N-limited ecosystems, the mechanisms contributing to this response are complex. One important component of forest growth

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responses to increased nutrient availability is reduced C allocation to root systems (Haynes and Gower 1995), allowing proportionally higher aboveground growth (Keyes and Grier 1981); however, the mechanisms contributing to this response are poorly understood, and increased root production has sometimes been observed in response to forest N addition (King et al. 2002).

In accordance with general theory (Bloom et al. 1985), plant fine root systems are assumed to be well adapted to maximize soil resource capture (water, mineral nutrients) while minimizing the energetic cost of construction, maintenance, and resource uptake. Many traits of root systems exhibit variation that influences the efficiency of the root system in resource acquisition, including total fine root biomass, diameter distribution, average longevity, branching patterns, and specific root length (length/mass ratio). These traits vary as a result of genetic control (e.g., interspecific differences) and of phenotypic plasticity, depending on the soil environment, and the responses of root traits to changing soil resource availability represent a series of trade-offs that result in complex patterns of variation both among species and environments (Yanai et al. 1995; Eissenstat 1997). At the level of the root system of individual trees, this complexity also encompasses the branching patterns of fine roots.

Traditionally, fine roots of perennial plants have been identified by a somewhat arbitrary diameter cut-off (e.g., 1 or 2 mm), but recent studies emphasize that the dynamics and functions of fine roots vary markedly within this diameter range (Hendricks et al. 2006; Guo et al. 2008b). Fine root order—the position of individual roots within the hierarchical branching system—has been proposed as a classification system (Fitter 1982) that can greatly reduce the within-class variation in fine root traits of perennial plants (Borken et al. 2007) and thereby improve the characterization of root system function. For example, several studies have documented interspecific variation in root system characteristics among trees based on root order (Pregitzer et al. 2002; Guo et al. 2008b), demonstrating the value of the concept for quantifying root system function. Notably, nitrate availability influences lateral branching (Nibau et al. 2008; Wang et al. 2009) and thereby the efficiency of resource acquisition of the root system. However, few studies have evaluated how the plastic response of other fine root traits to changes in soil resource availability varies among root orders (Pregitzer et al. 2002; Wang et al. 2006). An improved conceptualization of these responses is essential for understanding the effects of global change drivers on terrestrial ecosystem dynamics.

The objective of the present study was to quantify the response of key morphological traits of the fine root system of *Pinus tabulaeformis* to increased soil N availability. We hypothesized that increased N availability would reduce the overall abundance of fine roots, following previous

observations for various temperate zone conifer species (Vogt et al. 1996). We also expected that the proportion of absorptive, low-order roots would be reduced as constraints on soil N acquisition were relaxed. We hypothesized that the morphology (length, diameter, specific root length) of low-order roots would be more responsive than that of higher-order roots in conformity with the concept of ephemeral root modules of perennial plants (Pregitzer et al. 2002; Xia et al. 2010). In particular, an increase in the diameter and a reduction in the average length and specific root length of fine roots were expected, reflecting a relative increase in transport functions over uptake functions.

Materials and methods

Research site

This research was carried out in the Songyugou watershed in the Loess Plateau region, Shaanxi Province, China (35°39'N, 110°06'E). The watershed has a mainland monsoon-type climate with an average annual precipitation of about 585 mm and a mean annual temperature of 9.7 °C. The soil is gray forest soil with clay, silt, and sand contents of 36.8, 24.3, and 38.9 %, respectively. The organic matter content is $13.6 \pm 1.3 \text{ g kg}^{-1}$ (mean \pm SD); soil total N content is $1.54 \pm 0.24 \text{ g kg}^{-1}$; soil total P content is $1.42 \pm 0.38 \text{ g kg}^{-1}$; and soil pH is 8.6. The natural vegetation was mixed deciduous broadleaf–needle leaf forest with the dominant canopy species being *Quercus liaotungensis*, *P. tabulaeformis*, and *Betula platyphylla*. However, both the original and secondary forests at this site were destroyed prior to the 1960s. In the 1960s, the Chinese government organized local farms to plant a *P. tabulaeformis* forest with 1,667 stems/ha, the same as the original stand density. Since 1986, some of these forests have been monitored for ecological and hydrological research by the Institute of Soil and Water Conservation, Chinese Academy of Sciences. The mean canopy tree height was $12.6 \pm 1.4 \text{ m}$ (mean \pm SE) in 2010.

Experimental design

In 2008, six plots were established within *P. tabulaeformis* planted forests to quantify the root dynamics after N fertilization. The six plots were on a northeast-facing slope between 980 and 1,130 m elevation with slope angle ranging from 20° to 28°. The plot areas ranged from 0.8 to 1.4 ha. In each plot, six 10 \times 10 m subplots were established for fertilization treatments. The fertilization treatment levels are 0 (as control), 3, 6, 9, 12, and 15 g N m⁻² year⁻¹ of urea. The six treatments were assigned at random to each of the six replicate sub-plots.

Beginning in 2008, N fertilizer was added into the subplots before rain in early April every year.

Fine root excavation and dissection

Root sampling was conducted in May 2011. Five locations were chosen in each subplot under a randomly chosen individual tree, and a shovel was used to remove a soil block of $20 \times 20 \times 20$ cm. Thus, a total of 30 soil blocks were excavated for each treatment. Each block was gently loosened by hand in the field and intact segments of fine roots were removed from the soil blocks. Great care was taken to extract segments that were intact with minimal breakage. The samples were tapped to remove loose organic matter and mineral soil. They were immediately placed in a plastic box with ice as a cooler and then transported within several hours to the laboratory and frozen for dissection at a later date.

In the laboratory, fine roots contained in each soil block were sorted following a process from Pregitzer et al. (2002). Before dissection, root segments were cleaned of residual soil particles with forceps in deionized water (1 °C). Individual roots were dissected by order, with the distal roots numbered as first-order roots. Only live roots were measured; dead roots were removed and discarded. Because only a few soil blocks contained up to six root orders, only the first five orders were included in the analysis. For roots on broken segments, the order designation was based on the similarity in diameter and length between these roots and the roots whose branching order had been conclusively determined. In our study, these residual root segments represented only a small portion (<3 %) of total biomass of all five orders combined.

Root imaging and statistics

All the segments of the fine roots were dried on absorbent filter paper and then spread over a rectangular, transparent, plastic sheet so that no two segments touched. A scanner was used to scan the roots on the plastic sheet at a resolution of 300 dpi. Images of the roots were recorded in tiff format. The fine root length, area, and diameter were measured using CIAS 2.0 image analysis software (CID, USA). Before the roots were scanned, the scanner and software were calibrated with CIAS image standards for length and area. Root diameter classes were set at 0.1-mm intervals. Root diameter and length were measured. After being scanned, the roots were oven-dried at 70 °C for 48 h before being weighed. The root length and root biomass were obtained by dividing the cumulative root length and root biomass by the area (20×20 cm) of the soil block. The specific root length was obtained by dividing the root length by the root biomass.

Data analysis

Differences between any two treatments in root characteristics (i.e., individual root number, root length, root biomass, root diameter, specific root length) were tested in SPSS 13.0 statistical software package using a one-way blocked ANOVA (SPSS, USA) with each plot representing a block. The root data were tested for normal distributions and, when required, logarithmic transformations were used. Homogeneity-of-variances were tested by the Levene test. Post hoc separation of means was performed using Duncan's test.

Results

The morphological characteristics of the fine roots of *P. tabuliformis* growing in the control plots varied markedly among root orders. The cumulative root length and individual root number both decreased sharply with increasing root order (Table 1). The cumulative root length of the first three root orders comprised over 90 % of the total length of fine roots. In contrast, the proportion of total fine root biomass tended to increase with ascending root order (Table 1), with nearly half of the fine root biomass in the fourth- and fifth-order roots. The average individual root length significantly increased with root order from 2.5 mm in the first order to 89.9 mm in the fifth order. The mean root diameter ranged from 0.19 mm in the first order to 1.26 mm in the fifth order (Table 1), while the specific root length decreased significantly from 96.3 m g^{-1} for the first order to 2.3 m g^{-1} on the fifth order.

Many of these root morphological traits responded significantly to N fertilization, and the responses varied across root orders and levels of N addition (Fig. 1). In general, the lower order roots were most responsive. In particular, individual root number and cumulative root length both decreased with increasing N addition with significant responses in first- and second-order roots. Biomass of the first- and second-order roots declined significantly with increasing N addition, but higher-order roots did not respond. Total fine root biomass was significantly reduced only in the two highest N addition treatments (Fig. 1). For the two lowest-order roots, individual root length decreased and mean root diameter increased with N addition, but the magnitude of these responses was relatively small. In contrast, specific root length declined by 20 % in the two lowest root orders with most of the response being elicited at the lowest N addition levels. Root tissue density did not differ significantly either with root order or with N treatment. In summary, key root morphological characteristics

Table 1 The morphological characteristics of five root orders in 0–20 cm soil depth of *Pinus tabuliformis* growing in control plots on the Loess Plateau, western China

Root order	Cumulative root length		Root number		Root biomass		Individual root length (mm)	Root diameter (mm)	Specific root length (m/g)
	Density (m/m ²)	Percent (%)	Density (×10 ³ ind./m ²)	Percent (%)	Density (g/m ²)	Percent (%)			
1st	828.3 a	52.4	335.3 a	88.0	8.6 d	11.2	2.5 e	0.19 e	96.3 a
2nd	361.9 b	22.9	33.5 b	8.8	9.1 d	11.8	10.8 d	0.30 d	39.9 b
3rd	239.1 c	15.1	9.6 c	2.5	12.0 c	15.6	32.0 c	0.43 c	19.9 c
4th	83.1 d	5.3	1.8 d	0.5	17.4 b	22.7	47.3 b	0.88 b	4.7 d
5th	68.4 e	4.3	0.8 e	0.2	29.8 a	38.8	89.9 a	1.26 a	2.3 e

The same letters indicate that values are not significantly different ($p = 0.05$)

that affect the efficiency of soil resource acquisition (individual root number, cumulative root length, individual root length, mean root diameter and specific root length of low-order roots) responded to increased soil N availability.

Traditional approaches to root system classification rely on root diameter largely because of the greater ease of measurement in samples obtained using root cores. We examined the transformation from diameter class data (e.g., collected by auger or soil coring) to root order data for *P. tabuliformis* (see Resources 1–5 of the electronic supplementary material, ESM). Only two steps are needed for the transformation: (1) collecting branch order samples and calculating the diameter divisions of 75 % confidence intervals of root numbers for first to fifth order, respectively (Resource 4 of the ESM), and (2) calculating the “critical values” of root characteristics for each root order, defined as the value which best separates the adjacent root orders (e.g., order 1 vs. 2). For example, the results indicated that the first diameter class (0, 0.25] mm for the control plots included 78.3 % of root length (Fig. 2), 80.8 % of the root number, and 76.5 % of root biomass of the first order (Resources 1–3 of the ESM). Thus, the first diameter class represented largely the characteristics of the first order. Similarly, the diameter classes from the second to fifth classes represented mainly the characteristics of the second- to fifth-order roots (Resources 2 and 3 of the ESM). Moreover, despite the large responses of root morphology to the N fertilization treatments, there were very small differences of critical values for the same diameter class pair among different N treatments (Resource 5 of the ESM). No less than 67.3 % of the root information (root number, root length, and root biomass) of the root orders was included in the corresponding diameter classes for the control (Fig. 2; Resources 2 and 3 of the ESM); similarly, no less than 67.5, 64.3, 60.1, 61.6, and 64.9 % of the root information of root orders were included for 3, 6, 9, 12, and 15 g N m⁻² year⁻¹, respectively (data not presented).

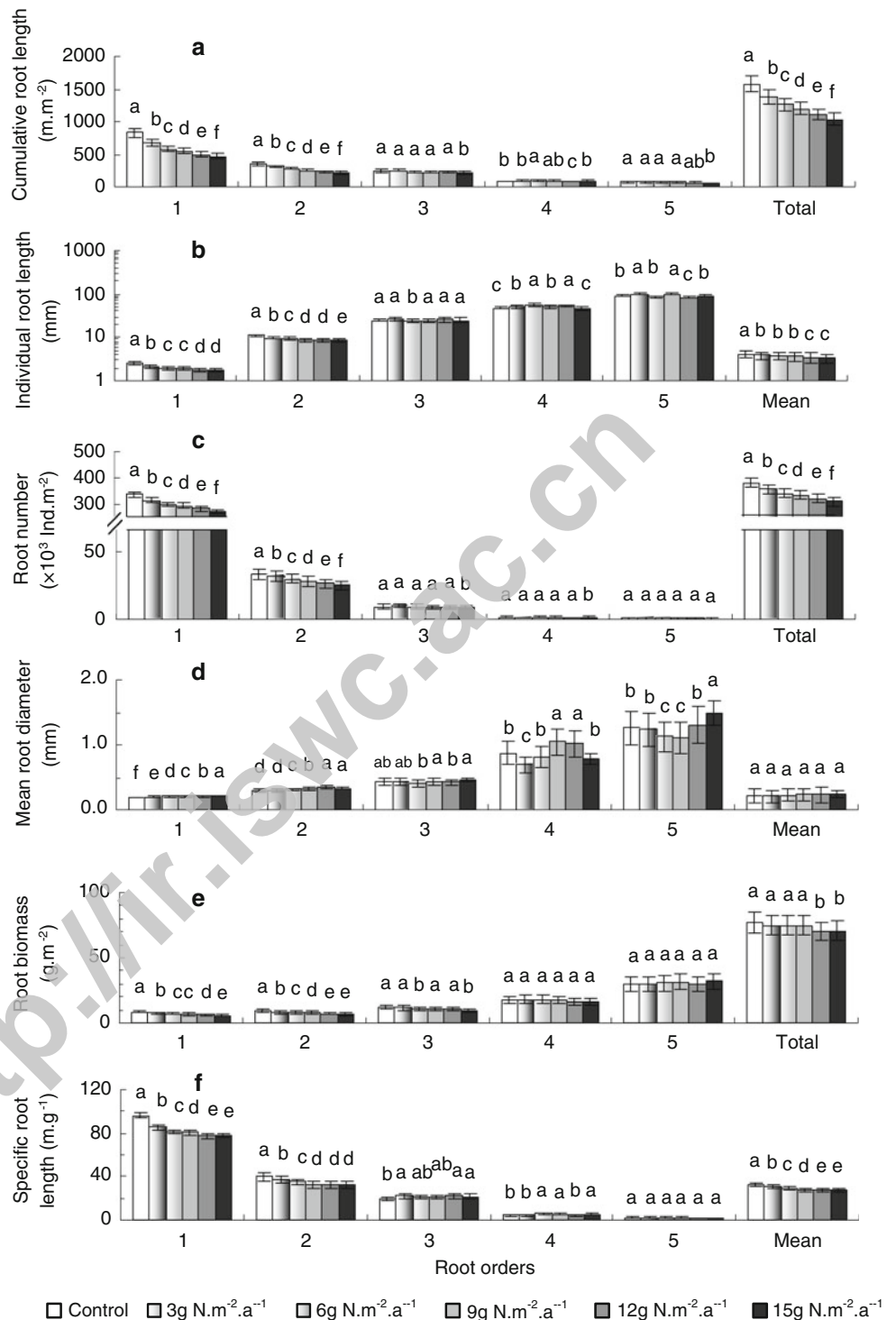
Discussion

Response of fine root morphology and architecture to N addition

The effects of continuing anthropogenic loading of reactive N on global ecosystem dynamics and health remain highly uncertain because of the complex mechanisms underlying ecosystem responses and interactions with other local and global drivers of environmental change. One key uncertainty in forest ecosystem response to N loading is belowground carbon allocation and fine root production and turnover. For example, higher N availability may reduce fine root production and turnover (Burton et al. 2000); however, because of the difficulties of measurement and the heterogeneity of responses, arguments to the contrary have been proposed (Nadelhoffer 2000), and the evidence is mixed (King et al. 2002). One feature of fine roots that contributes to this uncertainty is the complex morphology and architecture of fine roots, typically defined by an arbitrary diameter cut-off (e.g., <1 mm). If the morphology and architecture of forest tree root systems responds to N addition, then careful accounting of these changes would be needed to clarify the effects of anthropogenic N deposition on belowground dynamics. We examined the response of fine root architecture and morphology of monoculture stands of *P. tabuliformis* forest to an experimental gradient of increasing N addition to contribute to a better understanding of this key component of terrestrial ecosystem change.

The sites we fertilized on the Loess Plateau of China are primarily N limited like many temperate zone forests (LeBauer and Treseder 2008). For example, foliar N concentrations in our control plots averaged less than 1.0 %, suggestive of severe N limitation (Binkley 1986). Additionally, regional studies of *P. tabuliformis* plantations on the Loess Plateau (Han and Wang 1998; Sun and Wang 2006) concluded that N was the most limiting nutrient for tree growth, and a greenhouse study using the soils from our plantations indicated that

Fig. 1 Effect of N fertilization on **a** cumulative root length, **b** individual root length, **c** root numbers, **d** mean root diameter, **e** root biomass, and **f** specific root length for each root order (mean \pm SE, $n = 6$ plots; The extreme right-hand mean is the arithmetic mean of the indices in the six plots, and the indices in each plot were the arithmetic means of the indices of six sub-plots, and the mean in six sub-plots is the weighted mean of 1–5 order roots, where the weight is the occurrences of 1–5 order root numbers) of *Pinus tabulaeformis* growing on the Loess Plateau, west China. Different letters indicate significant differences for a given index among the different N additions ($p < 0.05$)



growth of pine seedlings increased in response to N addition levels identical to those used in our field experiment (Liu 2011). The N addition gradient in the present study spanned a range from moderately high (3 g m⁻² year⁻¹) to excessive (15 g m⁻² year⁻¹) in comparison to N loading in polluted regions (Son and Hwan 2003), comparable to loading in other forest N saturation studies (Aber et al. 1993).

Response of low order roots to N addition

The response of fine roots of pine to N addition in the present study indicates that morphological and architectural changes in roots are an important component of forest ecosystem responses to anthropogenic N loading. In particular, fewer, shorter roots of lower specific root length

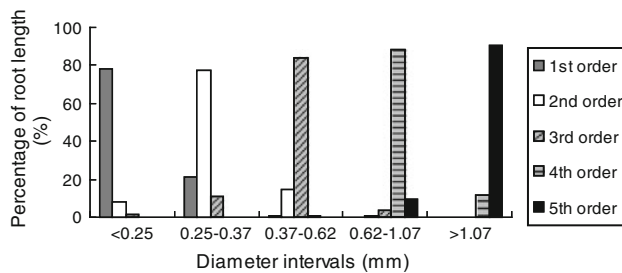


Fig. 2 Percentage of root length for first- to fifth-order roots of *Pinus tabulaeformis* included in the five root diameter intervals in control plots on the Loess Plateau, western China

were produced with increasing N addition, and much of this response was elicited at the lowest level of N loading; progressively smaller incremental responses were generally observed at higher N loading at least up to $9 \text{ g m}^{-2} \text{ year}^{-1}$. These responses suggest a possible reduction in C allocation to root growth under high N availability, as is typical for conifer forests on N-limited sites (Haynes and Gower 1995; Wang et al. 2006). That is, by reducing relative investment in low-order roots of high specific root length, C allocation would be reduced because a suite of related traits affecting the cost of roots would be expected to change. In particular, low-order roots of higher specific root length have markedly shorter lifespans (Guo et al. 2008c) and higher respiration rates associated with higher tissue N concentration (Burton et al. 2002). In the present study, root tissue N concentration decreased steadily from order 1 and 2 (0.85 %) to order 5 (0.36 %) in the reference plots (G. Wang, unpublished data). These results conform with the principles of whole-plant cost-benefit in multiple resource acquisition (Bloom et al. 1985; Yanai et al. 1995) and would appear to support the observations of Burton et al. (2012) of declining fine root turnover but constant fine root biomass under elevated N. Our results are the first to demonstrate that a change in fine root system morphology and architecture contributes to belowground responses of forests to increased N availability, and to suggest the interpretation that under high N availability the transport function of fine root systems is enhanced over the soil volume exploitation and uptake functions (Burton et al. 2000). In conformity with the concept of ephemeral root modules of perennial plants (Pregitzer et al. 2002; Xia et al. 2010), we hypothesized that the distal first- and second-order roots of pines would be most responsive to changes in soil resource availability. Our results support this hypothesis as increased soil N availability resulted in reduction in fine root biomass and changes in fine root morphology mostly for the first- and second-order roots. The limited response of higher order roots could be attributed in part to their greater average lifespan (Valenzuela-Estrada et al. 2008) and a consequent delay in their response.

However, a minirhizotron study (Guo et al. 2008a) indicated mean lifespan of third-order roots of about 2 years; hence, if the roots in the present study are comparable, most of the third-order roots would have been replaced during the time frame of the present study (3 years). Thus, rather than a delayed response due to slow turnover, the minimal response of the third-order roots to the N treatments may actually reflect limited plasticity in morphology of these roots or lack of benefits from potential morphological changes.

Increased N availability resulted in decreased root branching, as the proportion of first-order roots declined in all the N addition treatments (Fig. 1). Although this response appears counter to the observed effect of high soil NO_3^- in signaling greater root branching in model herbaceous plant root systems (Hodge et al. 1998), the latter stimulus is elicited primarily on individual roots growing in NO_3^- -enriched patches. The interactions among whole-plant, endogenous, and environmental control of root branching are complex (Pregitzer 2008). Although tree root systems also exhibit a branching response to nutrient-enriched patches (Hodge et al. 1998; Nibau et al. 2008), chronic, broad-scale nutrient enrichment may result in decreased branching to reduce the carbon cost of whole-plant soil resource acquisition under high N supply (Eissenstat 1997; Burton et al. 2000).

Widespread changes of root morphology and soil environment by N addition

The morphological changes we observed may also reflect unmeasured responses of ectomycorrhiza (ECM) formation. Previous observations of conifer ECM response to increasing soil N do not indicate any large reductions in ECM formation (i.e., nearly 100 % colonization of root tips; Wallenda and Kottke 1998); however, changes in species composition of ECM fungi and consequent differences in ECM morphology have been observed (Lilleskov et al. 2002). Moreover, reductions in extra-matrical hyphae of arbuscular mycorrhizae were observed under high N loading in maple forests (van Diepen et al. 2010), and a parallel response in ECM of pine has been observed under more controlled conditions (Aber et al. 1993). The fact that most of the morphological responses were elicited at relatively low rates of N addition indicates the high sensitivity of these N-limited pine forests to levels of N addition similar to those observed in many polluted parts of China (Son and Hwan 2003). Hence, we anticipate that continued excessive deposition of reactive N will cause widespread changes in pine root systems in coming years.

The overall root system architecture and morphology of *P. tabulaeformis* exhibited patterns that are consistent with previous studies of other forest trees (Pregitzer et al. 2002; Wang et al. 2006; Yu et al. 2007), but in comparison with

other species of pine (Pregitzer et al. 2002; Guo et al. 2004), the roots in the reference plots of the present study were smaller in mean root diameter and higher in specific root length. The finer roots may facilitate the acquisition of water in arid soil and nutrients in infertile soil (Yanai et al. 1995).

Increased N availability may cause ecosystems previously limited by N to become limited by P and/or K (Mohren et al. 1986; Fujita et al. 2010), and N fertilization also often causes reduced soil pH (Driscoll et al. 2003). The soils in the present site are very well buffered (pH 8.6) and no significant reduction in soil pH was observed after 3 years of N addition. However, a switch to P or K limitation could induce root system responses. For example, P limitation is known to affect a variety of root features including formation of cluster roots and root hairs (Bates and Lynch 1996), elongation of lateral and adventitious roots (Dolan 1997), and changes in basal root growth angle (Liao et al. 2001). Factorial trials with N, P, and K addition are needed to clarify the role of changing limiting factors in eliciting root responses.

Obscured responses with a conventional classification system

Fine roots have conventionally been defined on the basis of an arbitrary diameter cut-off, typically <1 mm. Because this diameter class encompassed all the first- to third-order roots and most of the fourth-order roots (Fig. 2), many of the distinctive responses we observed would have been obscured with a conventional classification system. For example, whereas individual root number, cumulative root length, and specific root length of the third- and fourth-order roots did not respond to the N treatments, all these traits declined significantly for the 0- to 1-mm roots. Clearly, the lumping of small roots with differing morphology and function into the standard category of fine roots (<1 or 2 mm) has confused the interpretation of belowground ecosystem function.

Ecological implications

Additional measurements of root system response to anthropogenic N loading are needed to provide a conclusive interpretation of the implication for terrestrial ecosystem dynamics. For example, although reduced specific root length would result in reduced nutrient uptake efficiency, uptake per unit root length also varies markedly among species and across sites (Reich et al. 1998), with concomitant effects on efficiency. Moreover, coincident shifts in the cost of root construction and maintenance and in root lifespan will contribute to the efficiency of soil resource acquisition in a changing environment (Yanai

et al. 1995). The complexity of these responses is emphatically demonstrated by the recent observation that the relationship of fine root tissue N to root respiration rate is altered by chronic N deposition (Burton et al. 2012). Future work on belowground responses to N addition is urgently needed to facilitate regional and global modeling of terrestrial ecosystem dynamics.

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