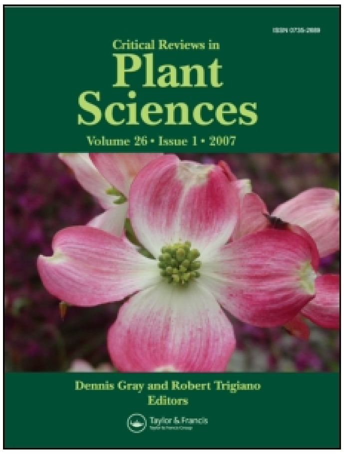

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Brian W. Brassard [a]; Han Y. H. Chen [a]; Yves Bergeron [b]
[a] Faculty of Forestry and the Forest Environment, Lakehead University, Ontario, Canada [b] Chaire industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec, Canada

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Influence of Environmental Variability on Root Dynamics in Northern Forests

Brian W. Brassard,[1] Han Y. H. Chen,[1] and Yves Bergeron[2]
[1]*Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Rd., Thunder Bay, Ontario, Canada, P7B 5E1*
[2]*Chaire industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, Québec, Canada, J9X 5E4*

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Address correspondence to Brian W. Brassard, Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Rd., Thunder Bay, Ontario, Canada, P7B 5E1. E-mail: bbrassar@lakeheadu.ca

Plant root systems are highly dynamic over various temporal and spatial scales, and are responsive to changes in environmental conditions. The objective of this review is to describe the dynamics of root structure and function in boreal and northern temperate forests and examine how edaphic and climatic characteristics and intra- and interspecific root competition impact root dynamics. Fine roots exhibit distinct seasonal trends of production and mortality. Over the extent of stand development, coarse root biomass increases until maturity, while the response of fine roots remains unclear. Roots are predominantly restricted to the upper soil layers, and spatial variability of roots in the horizontal direction decreases with decreasing root size. Root/shoot ratio decreases gradually through stand development. On nutrient-rich sites, roots are more concentrated around respective stems and root systems are more branched than on nutrient-poor sites. Plants generally root deeper under low soil moisture conditions, while roots tend to grow horizontally into rich rather than poor patches of soil. Plants adapt their biomass allocation strategies to edaphic and climatic variation according to the functional equilibrium hypothesis. Although root production is projected to increase, providing nutrients are not limiting, following elevated carbon dioxide concentrations and temperatures, how root turnover and above- and below-ground carbon allocation may change remains uncertain. Stands composed of species with different rooting characteristics may attain greater root production compared to single-species stands or mixtures of similar species from reduced exploitative competition. Alternatively, plants can produce greater root biomass with a competing plant than growing alone as a result of self root discrimination. Future research is needed to address how elevated carbon dioxide concentrations and temperatures will feedback upon soil resource availability to influence plant responses from the organism- to the ecosystem-level.

Keywords increased atmospheric carbon dioxide concentration, soil nutrient availability, root production and turnover, root structure, resource competition, plant allometry

I. INTRODUCTION

The evolution of a dynamic and complex root system is arguably the single most important adaptation that has allowed higher plants to thrive in terrestrial environments (Harper *et al.*, 1991). Roots are commonly differentiated into the following two arbitrary classes in the literature, based on their size and function: fine and coarse roots. Fine roots are small, absorbing roots that are predominantly responsible for the uptake of water and mineral nutrients from the soil, carbon (C) transport below ground, and mycorrhizal and microbial interactions (Fredericksen and Zedaker, 1995; Millikin and Bledsoe, 1999; Burton *et al.*, 2000; Eissenstat *et al.*, 2000; Trumbore and Gaudinski, 2003; Norby *et al.*, 2004). In contrast, coarse roots are large, structural roots that provide support and anchorage for the above-ground component, and are of paramount importance in nutrient storage and transport (Eis, 1974; Foster, 1985; Lavigne and Krasowski, 2007; Ouimet *et al.*, 2008).

Although fine roots and their associated mycorrhizae may only represent a small fraction of total biomass in boreal and northern temperate forests (Harris *et al.*, 1977; Vogt *et al.*, 1996; Hertel and Leuschner, 2002), their production and maintenance can account for between one-third and three-quarters of annual total net primary production (Grier *et al.*, 1981; Keyes and Grier, 1981; Fogel and Hunt, 1983; Comeau and Kimmins, 1989; Hendrick and Pregitzer, 1992; Fredericksen and Zedaker, 1995; Helmisaari *et al.*, 2002; Ostonen *et al.*, 2005). In comparison to fine roots, a relatively small proportion of annual total net primary production is allocated to develop and sustain coarse roots (Grier *et al.*, 1981; Comeau and Kimmins, 1989; Helmisaari *et al.*, 2002). However, classification of roots into fine and coarse root categories does not account for the continuum between roots that are very small and exclusively for absorption and those that are large and exclusively anchor and support (Pregitzer *et al.*, 2002; Pregitzer *et al.*, 2007). Nor do these broad categories reflect that roots of similar sizes, depending on species and environment, can exhibit highly contrasting morphology and physiology (Eissenstat, 1992; Pregitzer *et al.*, 1997; Comas and Eissenstat, 2004).

Because roots of all sizes are inherently difficult to sample (Böhm, 1979), below-ground plant structure and function is generally less studied, and therefore less understood, than above-ground. The purpose of this review is to improve understanding of the below-ground ecology of North American boreal and northern temperate forests (hereafter referred to as simply northern forests) by examining how abiotic and biotic factors affect root system dynamics. Specifically, this review will: (*i*) develop a generalized conceptual framework of how root system production and mortality, structure, and C allocation to above and below-ground plant parts differ over short- and long-term temporal scales, (*ii*) examine how root production and turnover, below-ground C pools, and root to shoot biomass allocation patterns and morphology respond to variability in soil nutrient availability, specifically nitrogen (N) and moisture, and elevated atmospheric temperatures and carbon dioxide (CO_2) concentrations, and (*iii*) investigate how plant inter- and intraspecific competition influences root production, system morphology, and C allocation to plant structures above and below ground.

II. PRODUCTION, STRUCTURE, AND CARBON ALLOCATION DYNAMICS

A. Root Production, Mortality, and Biomass over Short- and Long-Term Temporal Scales

Root production, mortality, and biomass are highly dynamic over various temporal and spatial scales in northern forests. Since the implications of climate change on below-ground C pools will undoubtedly depend on how rising global temperatures and CO_2 atmospheric concentrations influence root production and mortality, soil decomposition by microbes, herbivory, soil moisture, and soil fertility, improving our knowledge of general short- and long-term trends of root dynamics is fundamental to enhancing our understanding of C allocation and storage in terrestrial ecosystems. Therefore in this section, we will describe the following: (*i*) the seasonal patterns of root production and mortality and (*ii*) the dynamic changes in root biomass over the extent of stand development, which are generally ubiquitous of most northern forests.

1. *Seasonal Fluctuations of Root Production and Mortality*

The timing of fine root production and mortality is highly synchronized with foliage growth and senescence in northern forests. Fine roots have annual flushes of growth that intimately coincide with foliage production (Vogt *et al.*, 1987; Comeau and Kimmins, 1989; Hendrick and Pregitzer, 1993a; Burke and Raynal, 1994; Fahey and Hughes, 1994; Majdi *et al.*, 2005). Fine root production generally increases in early spring and peaks in late spring to mid-summer before decreasing in the fall (Tryon and Chapin III, 1983; Gholz *et al.*, 1986; Joslin and Henderson, 1987; Hendrick and Pregitzer, 1992; Hendrick and Pregitzer, 1993a; Burke and Raynal, 1994; Fahey and Hughes, 1994; Hendrick and Pregitzer, 1996; Steele *et al.*, 1997; King *et al.*, 1999b; Burton *et al.*, 2000; Konôpka *et al.*, 2005) (Fig. 1A). In the spring, trees and understory plants must produce extensive fine root networks to meet their high demands for soil mineral nutrients and water during foliage production and photosynthesis. Flushes of fine root growth often precede foliage growth (Hendrick and Pregitzer, 1996; Côté *et al.*, 1998; King *et al.*, 2002; Konôpka *et al.*, 2005), which ensures that a framework for nutrient uptake is in place prior to leaf-out.

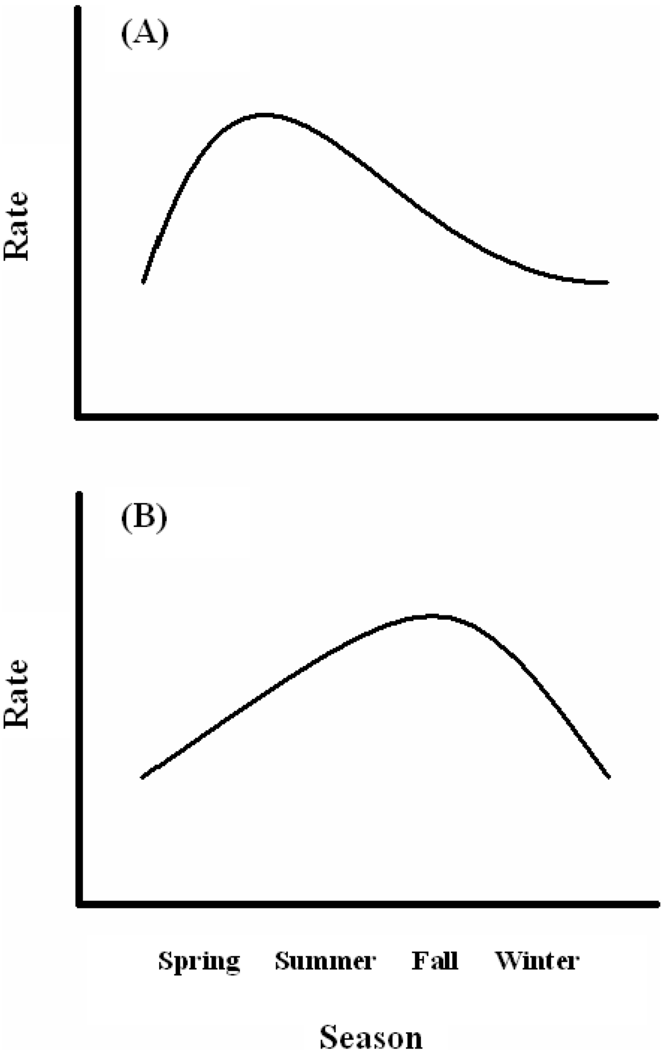

FIG. 1. Seasonal fluctuations of fine root (A) production and (B) mortality.

As the demand for nutrients is reduced in late summer and fall in preparation for leaf senescence and overwintering, there is a reduction in fine root production and maintenance and a subsequent increase in fine root mortality. Although fine root mortality is more evenly distributed throughout the year (Hendrick and Pregitzer, 1996; Burton *et al.*, 2000), there appears to be a loose temporal synchrony between fine root mortality and foliage senescence, particularly for broadleaf species (Hendrick and Pregitzer, 1992; Hendrick and Pregitzer, 1993a; Burke and Raynal, 1994). Mortality is generally highest in late summer and fall and low in the spring (Hendrick and Pregitzer, 1993a; Burke and Raynal, 1994; Hendrick and Pregitzer, 1996; Steele *et al.*, 1997; Norby *et al.*, 2004) (Fig. 1B). Fine root production and mortality is minimal over the winter months, attributed to cold and frozen soils that hinder water uptake and microbial activity (Burke and Raynal, 1994; Steele *et al.*, 1997; Konôpka *et al.*, 2005). Although annual foliage mortality is not as substantial for coniferous species, fine root mortality patterns in conifer-dominated stands typically resemble that of broadleaf stands (Steele *et al.*, 1997; Coleman *et al.*, 2000; Konôpka *et al.*, 2005), suggesting similarity in response for most northern forests that must tolerate extremes in seasonal temperatures and precipitation. Initiation of fine root production in the spring and mortality in the fall is largely related to photoperiod and temperature cues from the environment (Burke and Raynal, 1994; Pregitzer *et al.*, 2000a). Temporal variation in the timing of these cues may ultimately be responsible for the moderately different patterns of root growth and death observed among regions in northern forest ecosystems.

Annual fine root biomass dynamics may lag behind trends of production and mortality, as time is needed for pulses of each to be reflected in below-ground biomass pools (Comeau and Kimmins, 1989; Hendrick and Pregitzer, 1992; Coleman *et al.*, 2000). Fine root biomass generally peaks in mid to late summer and is minimal in late fall to early winter, while the biomass of coarse roots on an annual scale does not exhibit significant seasonal fluctuations (Fogel, 1983; Gower *et al.*, 1992; Ericsson *et al.*, 1996).

2. *Changes in Root Biomass Through Stand Development*

The long-term dynamics of fine root biomass remains one of the least understood aspects of forest ecology. A synthesis of studies that reported changes in fine root biomass over time using various chronosequence approaches, suggests that fine root biomass increases from stand initiation to a maxima at a later stage of stand development, which can vary from canopy closure to maturity (Vogt *et al.*, 1981; Vogt *et al.*, 1983b;

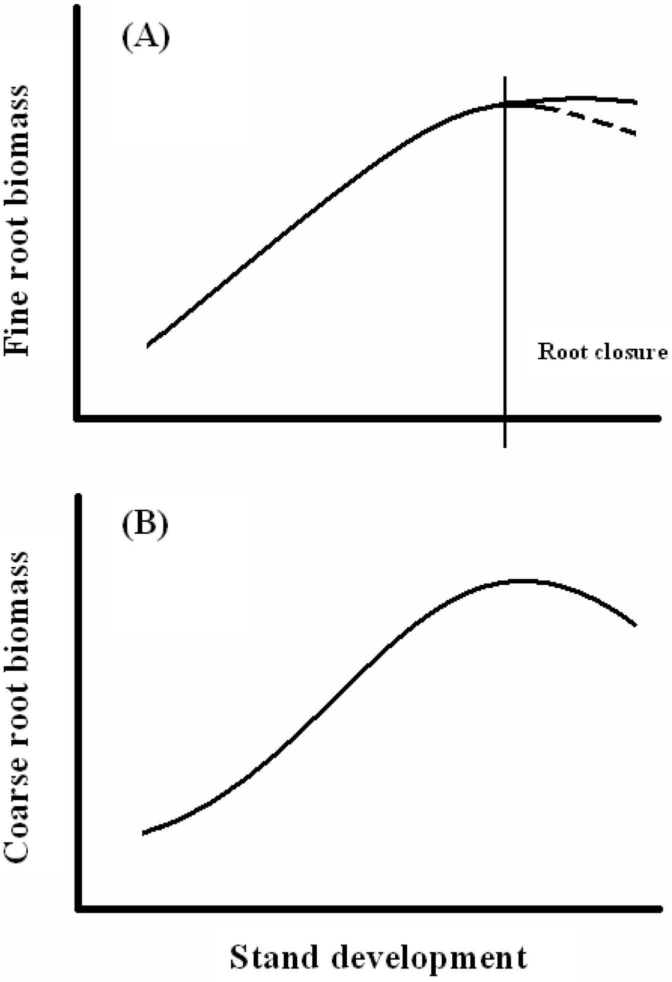

FIG. 2. Trends of (A) fine and (B) coarse root biomass through stand development.

Ruark and Bockheim, 1987; Vogt *et al.*, 1987; Helmisaari *et al.*, 2002; Bond-Lamberty *et al.*, 2004; Claus and George, 2005; Yanai *et al.*, 2006), suggesting possible differences among study stands in respective rates of development (Fig. 2A). Beyond the period of maximum fine root biomass, i.e., root closure, contrasting responses were reported, where fine root biomass leveled off and remained relatively static or decreased. Variability in site characteristics and species assemblages over time may largely be responsible for the different stand development trends of fine root biomass reported in the literature (Vogt *et al.*, 1987; Finér *et al.*, 1997; Coleman *et al.*, 2000; John *et al.*, 2001; Bond-Lamberty *et al.*, 2004; Yanai *et al.*, 2006). However, Johnson and Miyanishi (2008) recently questioned the validity of using chronosequences to infer dynamic patterns from static estimates in 'space-for-time substitution', suggesting that some differences among studies may be attributed to inherit methodological deficiencies.

As fine roots are continuously being produced and dying throughout the development of a stand (Persson, 1983; Hendrick and Pregitzer, 1993b; Coleman *et al.*, 2000; Trumbore and Gaudinski, 2003), their death and decomposition contribute a small but continuous input of C and other nutrients to the soil (Gholz *et al.*, 1986; Tate *et al.*, 1993; Gill and Jackson, 2000; King *et al.*, 2007). Remarkably, fine root mortality may produce detritus that exceeds annual contributions from litterfall (Nadelhoffer and Raich, 1992; Fahey and Hughes, 1994), emphasizing that fine root mortality and decomposition can constitute an important pathway for nutrient cycling between the biosphere and the atmosphere (Fahey *et al.*, 1988; Allen *et al.*, 2000; Norby and Jackson, 2000; Wan *et al.*, 2004) by generating C inputs to the soil even greater than foliage (Fogel and Hunt, 1983; Vogt *et al.*, 1983a; Joslin and Henderson, 1987; Hendrick and Pregitzer, 1993a). At the landscape-level, managing forest age structure and overstory species compositions may be an important strategy for managing C storage capacity by influencing below-ground C dynamics.

Similar to above-ground stemwood, coarse root biomass increases with stand development from initiation to maturity (Vanninen *et al.*, 1996; Millikin and Bledsoe, 1999; John *et al.*, 2001; Helmisaari *et al.*, 2002; Yanai *et al.*, 2006; Peichl and Arain, 2007) (Fig. 2B). Expansion in size and complexity is driven by both increased growth of the current coarse root stock and the transition of certain fine roots into the perennial root system as a consequence of secondary thickening. As trees, the dominant vegetation in forest ecosystems, grow larger in size, they must continuously allocate photosynthetic resources to the development of a larger and more complex coarse root system to provide adequate support for the expanding above-ground stemwood component, resulting in greater coarse root biomass at the stand-level with stand development (Santantonio *et al.*, 1977; Millikin and Bledsoe, 1999; John *et al.*, 2001; Helmisaari *et al.*, 2002; Lavigne and Krasowski, 2007; Ouimet *et al.*, 2008).

Beyond maturity, stand-level coarse root biomass tends to remain relatively static or decline marginally (Foster, 1985; Vanninen *et al.*, 1996; Bond-Lamberty *et al.*, 2004), depending upon the balance between losses (longevity-related mortality of pioneering trees) and inputs (establishment and growth of later successional trees) to the coarse root pool. When substantial numbers of coarse roots die due to longevity-related tree mortality, they contribute pulses of C and N to the soil (Grier *et al.*, 1981; King *et al.*, 2007) that can promote microbial activity and tree establishment (Lõhmus and Ivask, 1995; Gill and Jackson, 2000; Norby *et al.*, 2004).

B. Vertical and Horizontal Distribution of Roots within the Soil Profile

A tree root system is a spatially complex arrangement of roots that vary extensively in size, shape, structure, function, and health. The root systems of higher plants branch hierarchically (Pregitzer *et al.*, 1997; Pregitzer *et al.*, 2002; Robinson *et al.*, 2003), i.e., large roots branch into smaller roots, which branch into even smaller roots, and so forth, until terminating as very fine absorbing roots with or without mycorrhizal associations and root hairs. Soil physically constrains the movement of roots within the soil profile (Brady and Weil, 2002; Richter *et al.*, 2007), and its chemical composition, i.e., distribution and availability of soil nutrients, can significantly influence vertical and horizontal rooting characteristics. The physical, biological, and chemical properties of soil, in conjunction with species-specific genetic plant predispositions, are the predominant contributors to the variability in root system depth, size, and branching characteristics observed among plant communities in northern forests. Similar to other reviews (e.g., Hutchings and John, 2003), we have chosen below to describe structural rooting patterns in the vertical and horizontal directions separately.

1. *Vertical Rooting Patterns*

In northern forests, roots are generally restricted to the upper soil layers, with most roots occurring within the first 30 to 50 cm of the soil profile (Persson, 1980; Persson, 1983; Strong and La Roi, 1983a; Tryon and Chapin III, 1983; Comeau and Kimmins, 1989; Finér *et al.*, 1997; Millikin and Bledsoe, 1999; Wang *et al.*, 2002; Püttsepp *et al.*, 2006). In order to maximize their potential for nutrient uptake, fine roots are highly concentrated in the organic and upper mineral soil horizons (Kimmins and Hawkes, 1978; Vogt *et al.*, 1983b; Finér *et al.*, 1997; Steele *et al.*, 1997), as concentrations of available nutrients and soil temperatures decline abruptly with increasing soil depth (Steele *et al.*, 1997; Bennett *et al.*, 2002). However, maximum potential rooting depth (Robinson *et al.*, 2003) and vertical penetration of soil nutrients (Brady and Weil, 2002) generally decreases along an increasing northward latitudinal gradient (in the Northern Hemisphere), resulting in tree species from northern hardwood forests, for example, generally rooting deeper than those from the more northern boreal. To minimize the likelihood of uprooting from strong winds, coarse roots develop to greater depths than fine roots. As the stem grows with stand development, the coarse root system must expand vertically and horizontally to provide increasing support and stability (Eis, 1974; Strong and La Roi, 1983a; Strong and La Roi, 1983b; Ouimet *et al.*, 2008).

While the fine root component can represent only a small fraction of total root weight (Bi *et al.*, 1992; Steele *et al.*, 1997; Millikin and Bledsoe, 1999; Jach *et al.*, 2000; Wang *et al.*, 2002), it can comprise the majority of total root length (Bi *et al.*, 1992; Burke and Raynal, 1994; Pregitzer *et al.*, 1998). Because shallow soil layers contain most of the fine roots in northern forests, researchers have traditionally overlooked the role of deeper fine roots. Evidence suggests that deeper fine roots may be less involved in soil mineral nutrient acquisition and C cycling than shallower fine roots, but of greater importance for water capture (Persson, 1983; Tryon and Chapin III, 1983; Hendrick and Pregitzer, 1996; Burton *et al.*, 2000; Bennett *et al.*, 2002). More research is needed to characterize the different functional roles among roots within the different horizons of the soil profile.

2. *Horizontal Rooting Patterns*

Spatial variability of roots in the horizontal direction generally decreases with decreasing root size (Ruark and Bockheim, 1987; Mou *et al.*, 1995; Wang *et al.*, 2002), i.e., large roots are aggregated around the stem, whereas small roots are interspersed more evenly throughout the stand. While the literature is in general agreement on patterns of coarse root distribution within a stand (Strong and La Roi, 1983a; Millikin and Bledsoe, 1999; Ouimet *et al.*, 2008), there is discrepancy concerning how fine roots are distributed. Some researchers have found that fine roots proliferate horizontally relatively evenly within the soil profile (Puri *et al.*, 1994; Mou *et al.*, 1995; Millikin and Bledsoe, 1999), implying that fine roots extensively forage and compete with individuals of the same and other species intensely, whereas others indicate that fine root systems are more concentrated around their respective stems (Persson, 1980; Leuschner *et al.*, 2001; Yanai *et al.*, 2006), thereby reducing among-individual-competition. Alternatively, a stand's stage of development may be important in determining patterns of fine root distribution. In stands where root closure has been reached, a relatively horizontally homogeneous distribution of fine roots may be required in order for the plant community to maximize their collective access to soil resources. In younger stands, however, where root closure has not yet occurred, fine roots may show some aggregation around respective stems, a consequence of plants not yet having fully exploited the soil.

C. Carbon Allocation between Roots and Shoots—Influence of Species Ontogeny

The accumulation of biomass to the shoot and root systems during plant development is highly synchronous (Raich and Nadelhoffer, 1989; Burke *et al.*, 1992; Hendrick and Pregitzer, 1993a; Gedroc *et al.*, 1996; Niklas, 2005; Wang *et al.*, 2006). A close coordination between the two is necessary, as one system cannot grossly outgrow the other without risk to the overall fitness of the plant. An inadequate-sized root system will not be able to provide sufficient soil mineral nutrients, water, and anchorage to support the above-ground portion, whereas an inadequate-sized shoot system will not be able to produce enough carbohydrate to sustain the below-ground portion. It is still far from certain what factors are primarily responsible for regulating the acquisition of C and the partitioning of photosynthate to the root and shoot systems (Gower *et al.*, 1996). In their review, Farrar and Jones (2000) provided strong evidence that control over C acquisition and allocation rests partially with the roots and partially with the shoots. Plants, like other organisms, have genetically determined species-specific patterns of growth and development (ontogeny). However, environmental factors can be strong drivers of growth and development trajectories, as most organisms exhibit a certain degree of phenotypic plasticity in response to environmental heterogeneity.

If patterns of C allocation to above and below-ground plant parts are largely under genetic control, then plants of the same species growing under different edaphic and climatic

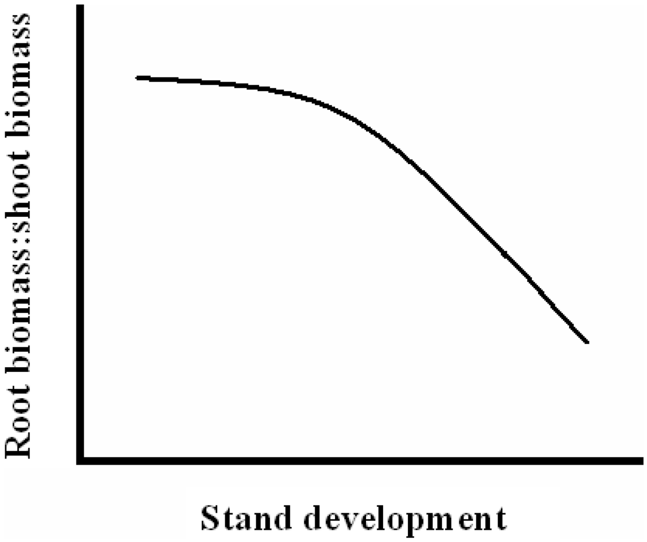

FIG. 3. Ratio of root biomass to shoot biomass through stand development.

conditions in different geographical regions should exhibit similar root/shoot ratios during their development. In support of this conjecture, below- to above-ground biomass relationships have been shown to be generally consistent over a wide range of site types and geographical locations (Harris *et al.*, 1977; Hendrick and Pregitzer, 1993a; Vanninen *et al.*, 1996; Cairns *et al.*, 1997; King *et al.*, 1999b; Enquist and Niklas, 2002; Peng and Dang, 2003; Coyle and Coleman, 2005). If, as studies in the literature suggest, ontogenetic development exerts strong control over the allometry of root/shoot relationships, then two possible temporal relationships between roots and shoots could exist: (*i*) root/shoot allometric relationships are isometric and remain largely unchanged over the extent of stand development, i.e., constant allometry (Enquist and Niklas, 2002), or (*ii*) root/shoot allometric relationships vary depending on plant or stand age, i.e., ontogenetic drift (Gedroc *et al.*, 1996). Ontogenetic drift has been reported for many species of trees and shrubs, i.e., over the course of plant development, the relative allocation of photosynthate is shifted from below to above ground (Vanninen and Mäkela, 1999; Litton *et al.*, 2003; Coleman *et al.*, 2004; Coyle and Coleman, 2005; Mokany *et al.*, 2006; King *et al.*, 2007; Peichl and Arain, 2007) (Fig. 3). Consequently, for short-lived plant species, root/shoot allometry may remain relatively constant over the extent of development (Jackson *et al.*, 1996; Niklas, 2005), while for longer-lived plant species, annual increases to stem increment eventually exceed annual below-ground biomass production, resulting in a gradual decrease in root/shoot ratio.

III. ABIOTIC INFLUENCES

In all terrestrial ecosystems, from deserts to tropical rainforests, plants exhibit different rooting strategies depending on soil nutrient concentrations and distributions. On the young, post-glacial soils that characterize northern forests, plant growth and development is often limited by the availability of soil N (Curtis *et al.*, 1994; Oren *et al.*, 2001; Hungate *et al.*, 2003; Lambers *et al.*, 2008). In contrast, however, soil moisture availability generally decreases along a north to south latitudinal gradient and a longitudinal gradient from coastal to inland, as the extent to which water availability constrains plant growth and development is highly dependent on latitude and longitude and related precipitation patterns.

While much is known concerning the impacts of potential future climatic change on grassland and agricultural systems (Norby, 1994; Canadell *et al.*, 1996; Fitter *et al.*, 1996; Hungate *et al.*, 1997; Cheng and Johnson, 1998; Fitter *et al.*, 1999; Reich *et al.*, 2006), how forests may respond is not as well understood. In this section, we first describe how variation in soil N and moisture availability and atmospheric concentrations of CO_2 and temperatures affect root production, turnover, and below-ground C pools in northern forests. Next, we examine how root system morphology and carbon allocation to above- and below-ground plant parts may differ depending on the status of the aforementioned environment characteristics.

A. Influence of Edaphic and Climatic Characteristics on Root Production, Turnover, and Below-ground C Pools

1. *Soil Nutrient Availability*

Although it is apparent that soil N availability exerts a strong influence on root dynamics in northern forests, it has yet to be resolved how variation in soil N availability affects trends of root production, turnover, and biomass, since reports in the literature are extremely contradictory. Both increases and decreases in annual estimates of fine root production and turnover, and static approximations of fine root biomass, have been commonly reported in association with increasing soil N availability in various northern forest stand types (Table 1). As evidenced by these inconsistencies, it appears that no generalized relationships can be used to characterize how all northern forests respond to differing soil N concentrations, making it problematic to predict long-term changes in plant community structure and function under differing soil N regimes. As we will describe below, plant responses to elevated atmospheric CO_2 concentrations and temperatures in both the short- and long-term, may be highly dependent on soil N availability (Zak *et al.*, 2000; Reich *et al.*, 2006; Huang *et al.*, 2007; Pregitzer *et al.*, 2007), highlighting the difficulty associated with predicting broad-scale vegetation dynamics under conditions of rising atmospheric temperatures, CO_2 concentrations, and N deposition across various forest biomes.

2. *Increased Atmospheric Temperatures and CO_2 Concentrations*

Providing photosynthesis is not limited by the availability of soil nutrients, annual total net primary production (Curtis *et al.*, 1994; DeLucia *et al.*, 1999; Jach *et al.*, 2000; Tingey *et al.*, 2000; Finzi *et al.*, 2002; Norby and Iversen, 2006) and annual

TABLE 1
Responses of fine root production, turnover, and biomass to enhanced soil nitrogen availability reported in the literature

Study	Fine root production	Fine root turnover	Fine root biomass
Aber *et al.* (1985)	Increase	Increase	Decrease
Albaugh *et al.* (1998)	Decrease	–	–
Burke *et al.* (1992)	Increase	–	–
Burton *et al.* (2000)	Increase	Decrease	–
Côté *et al.* (1998)	Decrease	–	Decrease
Curt *et al.* (2001)	–	–	Increase
Ericsson (1995)	Increase	–	–
Fahey and Hughes (1994)	–	Decrease	–
Gower *et al.* (1992)	Decrease	–	–
Grier *et al.* (1981)	Decrease	–	–
Haynes and Gower (1995)	Decrease	–	Decrease
Hendricks *et al.* (1993)	Increase	Increase	–
Kern *et al.* (2004)	Increase	–	Increase
King *et al.* (1999a)	–	–	Decrease
King *et al.* (1999b)	Increase	Increase	–
King *et al.* (2002)	Increase	–	–
Majdi (2001)	Increase	–	Increase
Nadelhoffer and Raich (1992)	Increase	–	Decrease
Nadelhoffer *et al.* (1985)	Increase	Increase	Decrease
Persson (1980)	–	–	Increase
Pregitzer *et al.* (1993)	Increase	Decrease	–
Pregitzer *et al.* (1995)	Increase	Increase	–
Pregitzer *et al.* (2000b)	Increase	–	Increase
Ruess *et al.* (1996)	–	Decrease	–
Safford (1974)	–	–	Increase
Schmid and Kazda (2002)	–	–	Decrease
Vogt *et al.* (1996)	Decrease	–	Decrease

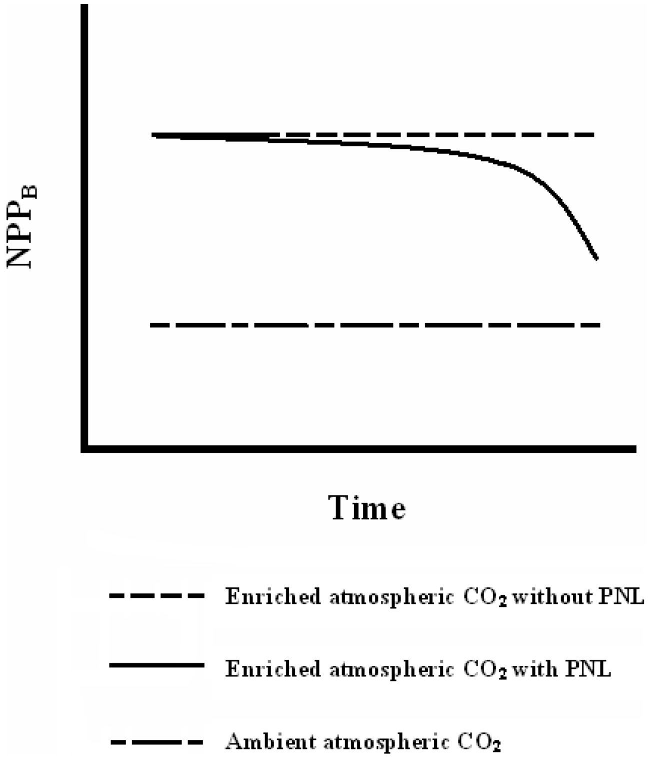

FIG. 4. Rates of annual below-ground net primary production (NPP_B) over time under scenarios of ambient atmospheric (CO_2), enriched atmospheric CO_2 without progressive nitrogen limitation (PNL), and enriched atmospheric CO_2 with PNL.

below-ground net primary production (Pregitzer *et al.*, 1995; King *et al.*, 1999b; Allen *et al.*, 2000; Matamala and Schlesinger, 2000; Pregitzer *et al.*, 2000a; Pregitzer *et al.*, 2000b; Tingey *et al.*, 2000; King *et al.*, 2001; Pregitzer, 2002; Pendall *et al.*, 2004; Wan *et al.*, 2004; Heath *et al.*, 2005; King *et al.*, 2005; Norby and Iversen, 2006) is projected to increase in response to CO_2 enrichment from accelerated rates of photosynthesis (Norby *et al.*, 1992; Tingey *et al.*, 2000; Huang *et al.*, 2007) and enhanced N availability (Zak *et al.*, 1993; Norby, 1994; Fitter *et al.*, 1999). Beyond temperature extremes that result in significant plant mortality (Taiz and Zeiger, 2002), increased atmospheric temperatures have also been reported to increase annual total and below-ground net primary production irrespective of CO_2 enrichment when soil nutrients are not limiting. When soil nutrient availabilities are limiting, however, elevated atmospheric CO_2 concentrations and temperatures may not significantly increase root production, as reduced soil N availability, for example, can significantly restrict potential increases in plant growth (Pregitzer *et al.*, 2000b; Zak *et al.*, 2000; Pritchard *et al.*, 2001; King *et al.*, 2005). Ultimately, long-term increases in annual below-ground and above-ground net primary production in association with climatic change in forested ecosystems may be constrained by progressive nitrogen limitation, facilitated by N sequestration into long-term biomass pools, decreased N mineralization, and reduced plant N use efficiency or uptake potential (Birk and Vitousek, 1986; Oren *et al.*, 2001; Finzi *et al.*, 2002; Luo *et al.*, 2004; Norby and Iversen, 2006; Yuan and Chen, 2009) (Fig. 4).

The flux of carbon and nutrients of root origin into the soil per unit area per unit time is often referred to as root turnover (Pregitzer *et al.*, 2007). Rates of root turnover are driven predominantly by root lifespan and rates of microbial decomposition, which collectively control the retention time of root-derived C in the soil, i.e., time from root production to complete mineralization. Therefore, any factor which increases below-ground production or root death and decomposition will increase absolute root turnover (Lauenroth and Gill, 2003).

Reports in the literature on the effects of CO_2 enrichment and increased global temperatures on root turnover are conflicting.

Some research indicates that root turnover may increase under CO_2 enrichment and higher global temperatures (Pregitzer *et al.*, 1995; Pregitzer *et al.*, 2000b; King *et al.*, 2001; Pendall *et al.*, 2004), attributed to higher root respiration rates that decrease root lifespan (Boyer *et al.*, 1971; Eissenstat, 1992; King *et al.*, 2001) and more rapid microbial decomposition (Joslin and Henderson, 1987; King *et al.*, 1999b; Pendall *et al.*, 2004). Other research, however, reports that root turnover may decline, attributed to plants retaining fine roots for longer or reallocating assimilates to develop a greater proportion of perennial structural roots at the expense of ephemeral absorbing roots (Canadell *et al.*, 1996; Fitter *et al.*, 1996; King *et al.*, 1996; Tingey *et al.*, 2000). Furthermore, some studies have shown that root turnover may not change substantially (Allen *et al.*, 2000; Matamala *et al.*, 2003; Norby *et al.*, 2004).

If we assume that elevated atmospheric temperatures and concentrations of CO_2 will cause a significant increase in root production from that of ambient levels, and that root and microbial responses will not be constrained by nitrogen limitation in the long run, we can predict how below-ground C pools, both root biomass and soil C, may respond to variation in root turnover under future climatic change:

(i) *Scenario I: Increased root turnover*: Under this scenario, as increased root production may be largely offset by greater root turnover, root biomass should remain relatively constant. Although overall input of C to the soil as root detritus would increase, soil C pools may remain largely unchanged, as the quantity of C cycled through the soil should dramatically increase from enhanced microbial activity (Fig. 5A).

(ii) *Scenario II: Decreased root turnover*: Since, in this scenario, root production increases and root turnover decreases, root biomass should also increase. However, we expect soil C pools to decline from an increased dependence of soil microbes on soil C reserves. Some soil C losses may be compensated for if microbial activity is reduced as a consequence of lower root detritus inputs in association with reduced root turnover, or if some soil C is protected from microbial decomposition by sequestration into long-term C pools (Fig. 5B).

(iii) *Scenario III: No change in root turnover*: Root biomass should also increase under this scenario, since root production would increase but root turnover would not significantly change. However, soil C pools should remain largely unchanged since root detritus inputs, and therefore microbial activity and C cycling, should not be significantly enhanced (Fig. 5C).

The above scenarios represent our 'best guesses' of overall C pool flux following predicted future climatic change, where we recognize that the response of root turnover to elevated atmospheric temperatures and concentrations of CO_2 is much less understood than that of root production. As plant responses to predicted future climatic change may be species-specific (Bazzaz *et al.*, 1990; Norby, 1994; King *et al.*, 1996; Norby and Jackson, 2000) and dependent on various abiotic and biotic factors, generalized models may be challenging to develop (Matamala and Schlesinger, 2000; Lal, 2005). Furthermore, we recognize that our above predictions are probably based on too simplified of logic. Northern forests have been reported to store the greatest amount of C below-ground among forest biomes (Dixon *et al.*, 1994; Lal, 2005), and have traditionally been regarded as global C sinks (Ciais *et al.*, 1995; Goulden *et al.*, 1996). However, since these forests are projected to experience the greatest increases in atmospheric temperatures among forest biomes in association with global warming (Pastor and Post, 1988), alteration of C cycling and below-ground C storage through changes in root production and turnover could potentially turn them into a source and further enhance rates of global change.

B. Patterns of Root Placement and Structural Plasticity in Response to Edaphic and Climatic Characteristics

1. *Soil Nutrient Availability*

In order to forage effectively in a heterogeneous environment, plant root systems must show a certain degree of phenotypic plasticity in response to soil nutrient variability (Hutchings and John, 2003; Hutchings and John, 2004) and competitive

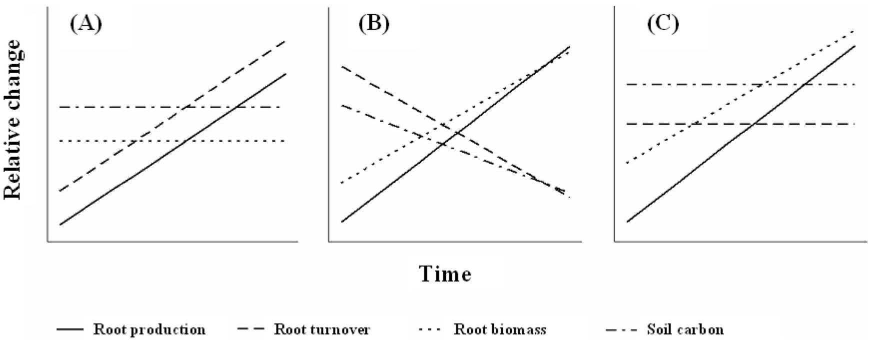

FIG. 5. Hypothetical responses of root biomass and soil carbon to an increase in root production and (A) increased, (B) decreased, and (C) no change in root turnover.

pressures from others plants. When growing on sites with high soil N availability, sufficient concentrations of plant-usable N should be readily available near the plant, and a more localized fine root system should meet the plant's needs, i.e., it would not need to develop as extensive a fine root network for foraging to fulfill N requirements. Under poor soil N conditions, however, the plant may need to develop a fine root system that extends further horizontally from the stem so it can penetrate larger volumes of soil (Persson, 1980; Eissenstat, 1992) and increase the extent of mycorrhizal associations (Grier *et al.*, 1981; Vogt *et al.*, 1982; Johnson and Gehring, 2007) in order to enhance resource uptake. Studies of fine-spatial scale root dynamics reveal that fine root biomass is more abundant in N-rich than N-poor patches of soil (Coutts and Philipson, 1977; St. John *et al.*, 1983; Eissenstat and Caldwell, 1988; Pregitzer *et al.*, 1993; Mou *et al.*, 1995; Bhatti *et al.*, 1998), suggesting an anisotropic response of root growth towards N-rich patches of soil. The results of these studies imply that roots may need to forage greater distances in N-poor environments in order to find elusive N-rich patches of soil.

Roots usually grow deeper under conditions of low soil moisture in order to access reserves of water deeper in the soil profile, while conditions of high soil moisture generally promotes shallower overall rooting (Persson *et al.*, 1995; Hendrick and Pregitzer, 1996; Hutchings and John, 2003). Furthermore, plants may also actively seek out patches of high soil moisture, although it has yet to be determined if roots forage horizontally through the soil profile for patches of high soil moisture similar to how they forage for soil N. Since roots generally focus their efforts where resources are abundant rather than scarce, plants may commonly forage for patches of water in more arid forests, where competition for water among individual plants can be intense.

A highly branched root system is more expensive to construct and maintain than one that is less branched (Eissenstat, 1992; Pregitzer *et al.*, 2002; Hutchings and John, 2003). Smaller-diametered roots have shorter lifespans than larger-diametered roots (Coleman *et al.*, 2000; Kern *et al.*, 2004; Baddeley and Watson, 2005) and are more metabolically active (Nadelhoffer and Raich, 1992; Pregitzer *et al.*, 1998; McDowell *et al.*, 2001), representing a higher C cost to the plant. However, roots of small diameter are also more involved in nutrient absorption, as evidenced by their greater nutrient concentrations (Cox *et al.*, 1978; Joslin and Henderson, 1987; Fahey *et al.*, 1988; Burke and Raynal, 1994). Consequently, in nutrient-rich soils, constructing a greater proportion of smaller-diametered roots, thereby increasing root system 'branchiness,' may be beneficial to the plant if nutrient uptake potential increases enough to offset higher C production and metabolic costs (Eissenstat, 1992; Eissenstat *et al.*, 2000). In nutrient-poor soils, however, plants may choose to invest photosynthate into the production of a greater proportion of more perennial roots to reduce C costs, so long as greater fine root biomass would not necessarily convey substantial nutrient uptake increases. Indeed, evidence from experiments on both annual and perennial plants indicate that plants have significantly greater specific root length, i.e., greater length of roots per given root mass, when growing in nutrient-rich compared to nutrient-poor soils (Eissenstat and Caldwell, 1988; Pregitzer *et al.*, 1993; Mou *et al.*, 1995; Fransen *et al.*, 1998; Majdi *et al.*, 2001).

Plants may instead respond to changes in soil nutrient availability by altering their fine root physiological rate of nutrient acquisition instead of modifying morphology, especially in heterogeneous or nutrient-poor soils, which may be a less C expensive alternative (Schwinning and Weiner, 1998; Hutchings and John, 2003). Hence, physiological adjustment of fine root function can be a critically important adaptation to soil resource heterogeneity that may be equally as crucial to plant success as root morphological plasticity. Some species may be more capable than others of either morphological or physiological plasticity when presented with temporally or spatially patchy nutrient concentrations, conferring a competitive advantage to some individuals and not others depending on environmental conditions. Future studies to identify species-specific root responses to soil resource heterogeneity in northern forests will enhance our understanding of the mechanisms coordinating morphological and physiological changes as 'economic tradeoffs' that ultimately impact plant fitness.

2. *Increased Atmospheric Temperatures and CO_2 Concentrations*

It is still not fully understood how increased atmospheric CO_2 concentrations and temperatures influence root system morphology, nor is it known if the responses reported for a small set of plant species under controlled conditions are applicable to larger scales under natural field settings, where the relationships between below-ground flora and fauna are much more complex. Since so little is generally known concerning the implications of predicted future climatic change on root system architecture and root foraging ability in northern forests, we pose a critically important broad-scale question (and specific follow-up questions) for future research to address: How will fine root structural patterns be affected by projected future increases in atmospheric temperatures and CO_2 concentrations? If the sharp temperature and nutrient gradients in northern forests are restricting the vertical rooting ability of fine roots, then increases in soil temperature and moisture and nutrient availabilities in association with global warming may facilitate greater rooting depth. If rooting depth does increase under these conditions, will it mark an increase in absolute fine root biomass or just redistribution (i.e., less in upper soil horizons and more in lower layers)? If nutrient availability generally increases in association with elevated atmospheric CO_2 concentrations and temperatures, how will the intensity of fine root competition be affected, and what may be the consequences for mycorrhizal associations? Will global warming, and subsequent increases in soil N availability, increase the 'branchiness' of plant root systems? These questions are clearly challenging to address, but are essential to understanding the implications of CO_2 enrichment and temperature increases on ecosystem function and integrity.

TABLE 2
Influence of environmental factors on biomass allocation patterns between the root and the shoot systems as predicted by the functional equilibrium hypothesis

Variable	Resource availability	Response of root/shoot ratio
Light	Low	Decrease
	High	Increase or no change
Atmospheric carbon dioxide	Low	Decrease
	High	Increase or no change
Soil moisture availability	Low	Increase
	High	Decrease or no change
Soil nitrogen availability	Low	Increase
	High	Decrease or no change
Air and soil temperature	Low	Decrease, increase, or no change
	High	Decrease, increase, or no change

C. Carbon Allocation between Roots and Shoots—Influence of Environmental Factors

Phenotypic plasticity is an important evolutionary achievement that has allowed plants to vary their characteristics in response to different environmental stimuli (Eissenstat, 1992; Kollmann *et al.*, 2004; Weiner, 2004). The biomass allocation strategies of plants to environmental heterogeneity can be best understood by applying the functional equilibrium (balance) hypothesis, which states that plants should respond to stress in their respective above- and below-ground parts by increasing the relative production of a particular absorbing organ to facilitate greater resource capture and reduce stress (Table 2). In accordance with this hypothesis, when light and CO_2 levels are low, a plant should favor foliage production, while root production, specifically fine root production, should be enhanced following shortages of water and N (Axelsson and Axelsson, 1986; Walters *et al.*, 1993; Ericsson, 1995; Ericsson *et al.*, 1996; Albaugh *et al.*, 1998; King *et al.*, 1999a). Since low air and soil temperatures mutually reduce rates of photosynthesis (promoting above-ground growth) and the ability of plants to uptake soil nutrients (promoting root growth), it is not unexpected that plants have been reported to shift biomass allocation from roots to foliage and foliage to roots in low- temperature environments (Ruess *et al.*, 1996; King *et al.*, 1999b; Peng and Dang, 2003; Mokany *et al.*, 2006).

Increased N availability has been commonly reported to decrease the proportional allocation of biomass to roots compared to shoots (Axelsson and Axelsson, 1986; Birk and Vitousek, 1986; Gower *et al.*, 1992; Ericsson, 1995; Pregitzer *et al.*, 1995; Albaugh *et al.*, 1998; Coleman *et al.*, 2004). However, some studies have reported contrasting allocation patterns to that predicted by the functional equilibrium hypothesis. For example, Nadelhoffer *et al.* (1985) reported that N fertilization increased total below-ground C allocation relative to aboveground, while King *et al.* (1999b) found that the relationship between above- and below-ground biomass was not significantly affected by N fertilization. Alternatively, changes in allocation associated with N availability may simply represent accelerated development (Gedroc *et al.*, 1996; King *et al.*, 1999a; Vanninen and Mäkela, 1999; Coleman *et al.*, 2004) instead of an environmentally-induced shift in biomass partitioning irrespective of plant age, or, more plausibly, a combination of both.

Although elevated concentrations of CO_2 in the atmosphere and increased global temperatures may increase annual total net primary production to some extent if soil nutrients are not limiting, it is still highly debated whether this increase will shift the relative allocation of assimilates between below- and above-ground plant parts. Greenhouse experiments on tree seedlings and sapling in containers or open- and closed-top chambers and free-air CO_2 enrichment studies on young stands in the field (Norby *et al.*, 1992; Curtis *et al.*, 1994; Larigauderie *et al.*, 1994; Norby, 1994; King *et al.*, 1996; Berntson and Bazzaz, 1997; Zak *et al.*, 2000; Kozovits *et al.*, 2005) suggest that overall allometry between roots and shoots will not change significantly following CO_2 enrichment, at least in the short-term. However, increases (Gorissen, 1996; Ineson *et al.*, 1996; Jach *et al.*, 2000; Tingey *et al.*, 2000) and decreases (Wan *et al.*, 2004) in root/shoot ratio have also been reported.

Overall root/shoot ratios alone may not provide sufficient information concerning the anatomical and physiological responses of plants to CO_2 enrichment and higher atmospheric temperatures. For example, plants may shift C allocation from one root fraction to another without changing overall root and shoot biomass, by shifting C allocation to more distal (smaller diameter) relative to more proximal (larger diameter) roots, i.e., below-ground transfer from support to absorbing tissues (Larigauderie *et al.*, 1994; King *et al.*, 1996; Norby and Iversen, 2006). As the scenarios in most CO_2 and temperature enrichment experiments do no represent natural conditions per se at most ecological scales, their rational is to provide insight, if not direct prediction, into how plants may behave under predicted future climate change scenarios. It is vital to our understanding to distinguish if natural forests in the long-term will respond similarly to higher CO_2 concentrations in the atmosphere and elevated global temperatures as do plants in short-term greenhouse and field experiments.

Biomass partitioning is likely regulated by both ontogenetic and environment influences to a certain degree (Farrar and Jones, 2000; Hutchings and John, 2004) and variable among plant functional groups (Bond-Lamberty *et al.*, 2002; Li *et al.*, 2003; Peng and Dang, 2003; Niklas, 2005). Ultimately, the priority of genetics or environment at regulating biomass allocation can be best explained by applying the optimal partitioning model. When a resource is limited enough to cause a plant significant stress (i.e., low light levels hindering photosynthesis), it may adapt its morphology or physiology to reduce the stress (i.e., increasing foliage production and modifying foliage architecture) (Gedroc *et al.*, 1996; McConnaughay and Coleman, 1999; Weiner, 2004; Kozovits *et al.*, 2005). More field studies are needed to further understand the influence of environment on allocation patterns. Identifying the prominent environmental regulators of C allocation to above- and below-ground plant parts in forested ecosystems is essential for extrapolating C budgets of stands to scales at the landscape- and ecosystem-levels (Kurz *et al.*, 1996; Li *et al.*, 2003).

IV. BIOTIC INFLUENCES

Roots and associated mycorrhizae are the principle organs for below-ground competition among individual plants (Wilson, 1988; Mou *et al.*, 1995; Casper and Jackson, 1997; Leuschner *et al.*, 2001). Root competition can be generally divided into two broad categories: (*i*) scramble or exploitative competition and (*ii*) contest or interference competition (Schenk *et al.*, 1999; de Kroon *et al.*, 2003; Schenk, 2006). Exploitative competition between plants for limited environmental resources (i.e., soil growing space and nutrients) is based upon unequal acquisition: some plants are better able to uptake and use soil resources (per unit area per unit time) than others, and will consequently enjoy greater overall fitness than competitors. However, this form of root competition does not involve root-to-root interaction, and is simply a response by the plant to soil resource heterogeneity.

Interference competition, however, involves recognition and interaction between individual roots independent of soil resource conditions, either by one root impacting another by means of direct contact or the release of growth hormones (i.e., self/non-self discrimination) or through the secretion of root exudates by one plant that significantly reduces the overall fitness of another (i.e., allelopathy). Although some plant species in more southern forests and grasslands have been shown to release root exudates that significantly reduce the vigor of rival plants, e.g., Sorghum (*Sorghum bicolor* (L.) Moench), creosote bush (*Larrea tridentata* (DC.) Coville), and black walnut (*Juglans nigra* L.) (Inderjit and Weston, 2003), allelopathy is generally not an important mechanism of root competition in more northern forests. While the general objective of exploitative competition is to deplete resources before a competitor, interference competition is based on reducing a competitor's ability to uptake or use resources.

Although the relationships between root competition, architectural design, and above- and below-ground production and carbon allocation have been extensively studied in agricultural and grassland systems (Wilson, 1988; Vandermeer, 1992), they have only recently been given attention in forests. In this section, we will first describe how plant competition, from the individual root- to the community-level, affects root production, morphology, and carbon allocation to plant structures above and below ground in northern forests, and review strategies by which roots can adapt their form and function to reduce competitive pressures from other plants. We will then demonstrate how and why certain plant species in particular mixtures may alternatively alter their exploitative abilities in the presence of a competitor irrespective of soil resource conditions.

A. Consequences of Spatial Root Segregation for Exploitative Competition and Stand-Level Root Production

Plants choose to proliferate roots in soil free of other roots and higher in available nutrients if all other factors are equal (Gersani *et al.*, 2001; O'Brien *et al.*, 2005). Intense root competition between individual plants for similar, locally finite soil nutrients and growing space can significantly reduce overall plant fitness (Mou *et al.*, 1995; Cahill, 2002; Callaway, 2002; Schenk, 2006). Consequently, plants over time have evolved two independent, but not mutually exclusive, responses to resource competition from other plants: (*i*) they may increase their competitive ability or (*ii*) they may reduce competitive interactions with other plants (Falik *et al.*, 2003). Depending on species-specific morphological and physiological attributes and edaphic and climatic characteristics, either response may be evolutionarily advantageous (Schenk *et al.*, 1999).

According to the competition reduction theorem, in order to reduce exploitative competition below ground, a particular plant species which coevolved in the same growing space as other species may have developed unique functional traits, most prominently as different soil resource requirements or rooting morphology, which allow them to partially or completely segregate niches below ground with coexisting species (Vandermeer, 1992; Büttner and Leuschner, 1994; Man and Lieffers, 1999; Bennett *et al.*, 2002). A mixture of two or more species of plants with differential functional traits may collectively attain higher root production through more efficient and complete usage of soil resources than a community of a single plant species (monoculture) or a mixture with similar functional traits. While the premise of niche separation has been applied to the above-ground component of forested ecosystems to explain patterns of stand-level production and structural complexity, i.e., analysis of above-ground growing space and light efficiency (Kelty, 1989; MacPherson *et al.*, 2001; Chen and Klinka, 2003; Chen *et al.*, 2003; Légaré *et al.*, 2005; Brassard *et al.*, 2008), it has been less studied below ground.

Extending the tenants of the competition reduction theorem below ground to the stand-level, we hypothesize that mixed-species stands, where component species have differential rooting characteristics, could attain higher root biomass and architectural complexity through a reduction in interspecific exploitative competition than single-species stands or mixtures where component species have similar rooting characteristics. To test this theory, we have first outlined a simplified, conceptual example involving three different tree species growing together in different combinations and separately. Next, we present evidence from the literature that demonstrates indirectly that greater root spatial segregation can facilitate a reduction in exploitative root competition in some species mixtures, leading to enhanced overall above- and below-ground plant production.

1. *Applying the Competition Reduction Theorem to Roots—A Hypothetical Example*

To better understand how below-ground plant competition influences root dynamics, we have illustrated below a hypothetical example using trees that vary in successional status. Late and early successional tree species have many different physiological and morphological characteristics (Finegan, 1984; Burns and Honkala, 1990). Particularly in the boreal forest, tree species of early successional status, which colonize shortly after catastrophic disturbance, e.g., stand-replacing crown fire (Johnson, 1992; Weber and Stocks, 1998) and spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks (Bergeron *et al.*, 1995; Bouchard *et al.*, 2005), generally have root systems that are deeper, larger, and extent further horizontally than those of later successional tree species, which have a greater proportion of fibrous roots (Strong and La Roi, 1983a; Strong and La Roi, 1983b; Gale and Grigal, 1987; Finér *et al.*, 1997).

Plants with larger-sized root systems often have competitive advantages with respect to soil resource acquisition than plants with smaller-sized root systems (Wilson, 1988; Schwinning and Weiner, 1998; Schenk, 2006). We would argue that early successional species may have evolved rooting strategies to maximize below-ground resource acquisition rather than reducing interspecific root competition. Since following catastrophic disturbance, soils are generally free from intense root competition, early successional species should strive to exploit soil space and nutrients rapidly and as fully as possible. However, for later successional species, which generally begin to establish later during stand development, and subdominant species, such as herbs and shrubs, the ability to share available nutrients and growing space through spatial root segregation may be a more common evolutionary adaptation that permits them to successfully coexist on a site with colonizers. For example, their shallower rooting tendencies and greater proportion of fibrous roots may allow them to compete more efficiently for nutrients near the surface, where root competition from early successional species may not be as intense.

Spatial root segregation between individual plants can therefore be extremely beneficial for plant community diversity by permitting individual plants to control completely or partially the growing space they occupy (Schenk *et al.*, 1999; Gersani *et al.*, 2001). In order to illustrate how spatial root segregation could enhance root production at the stand-level in northern forests, we have compared below-ground production and structure in three conceptual forest stand types: (*i*) a mixture of two trees species with different successional status (stand A), (*ii*) a mixture of trees species with similar successional status (stand B), and (*iii*) a monoculture (stand C) (Table 3). In our hypothetical example, all three stands have similar site conditions. We theorize that stand A will attain higher below-ground (and above-ground) stand biomass compared to stands B or C, attributed to the species in stand A collectively being able to exploit soil resources more fully than the species in stands B or C by accessing resources in different soil horizons or by accessing different resources through greater intermingling that reduces overlap of depletion zones. If the species in stand B have similar rooting characteristics, then stand B should attain similar below-ground biomass as stand C. Obviously in nature, the situation is more complex than our simplified example, as both naturally and artificially regenerated stands often have many more species co-existing on the same site (Chen and Popadiouk, 2002; Brassard and Chen, 2006; Hart and Chen, 2006; Hart and Chen, 2008; Chen *et al.*, 2009).

TABLE 3
Tree species composition of three conceptual stands and hypothetical stand-level root production, expressed as relative to stand B

Stand	Tree species composition	Root production
A	Early successional species (species 1) + later successional species (species 2)	Higher
B	Early successional species (species 1) + early successional species (species 3)	/
C	Early successional species (species 1)	Similar

2. *Evidence from Northern Forests*

We can test the postulates formulated above by reviewing studies from the literature where root biomass was compared in single- and mixed-species stands. Wang *et al.* (2002) reported that western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) – western redcedar (*Thuja plicata* Donn. ex D. Don) mixtures had higher fine root biomass compared to pure western hemlock (an early successional species) and western redcedar (a later successional species) stands. In contrast, however, Frederickson and Zedaker (1995) found that pure stands of loblolly pine (*Pinus taeda* L.) (an early successional species) and red maple (*Acer rubrum* L.) (an early to mid successional species) had similar fine root biomass as mixed stands of the component species. Leuschner *et al.* (2001) also reported no significant difference in fine root biomass between old-growth single- and mixed-species stands of sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.), both of which are later successional species.

With empirical evidence supporting our above hypothesis that certain mixed-species stands (where component species have different rooting characteristics) could potentially yield higher below- and above-ground biomass production and structural and species diversity compared to single-species stands, forest management practices that favor mixtures of trees and understory vegetation with different functional traits may promote higher stemwood production and more diverse stands over a rotation, which could have significant economical ramifications, habitat quality implications, and be beneficial from a climate change perspective.

B. Carbon Allocation between Roots and Shoots—Influence of Interference Competition

Most of our understanding concerning the influence of root competition on carbon allocation to above- and below-ground plant structures is derived from simplified, short-run pot studies and their derivatives using short-lived herbaceous species (Gersani *et al.*, 2001; Callaway, 2002; Falik *et al.*, 2003; Gruntman and Novoplansky, 2004; O'Brien *et al.*, 2005; Schenk, 2006; Hess and de Kroon, 2007). Although these experiments take place under extremely controlled and artificial circumstances that are unlike natural field conditions, they benefit by allowing the isolation of inter-root competition effects on plant biomass partitioning from those of soil and climatic characteristics, thereby providing valuable insight into plant responses at the individual root-level to competition from other plants irrespective of confounding factors. The results of these studies suggest that a plant may produce greater root biomass in the presence of a competing plant than when growing alone (Fig. 6). However, the extent that root/shoot ratio increases is quite variable, as some studies have reported marginal increases in shoot biomass in addition to root biomass. Greater root production in certain species mixtures was attributed by these authors to self/non-self root discrimination at the individual root-level, where plants growing alone yielded lower root biomass than when growing with a companion to avoid wasteful allocation of resources to competition with its own roots. Consequently, increased inter-, and to a lesser extent intraspecific competition between plants can elicit increased root production and shift the relative allocation of photosynthate below ground. We emphasize that this type of below-ground response to the presence of a competing plant is probably invoked by nontoxic signaling between the roots of different individual plants instead of by soil resource availability (Schenk *et al.*, 1999; Schenk, 2006).

It remains to be tested how applicable the results of the above studies are, however, for explaining patterns of below-ground plant competition in forested ecosystems. By most accounts, mechanisms of competition and facilitation (Vandermeer, 1992; Man and Lieffers, 1999; Brooker *et al.*, 2008) likely interact in the field to collectively structure plant species assemblages at various spatial and temporal scales. However, the importance of these mechanisms for shaping and maintaining forest ecosystem structure and function remains poorly understood and largely understudied.

V. SYNTHESIS AND FUTURE RESEARCH NEEDS

We still know remarkably little about the dynamics of roots in northern forests, particularly how they will respond to a changing climate involving elevated atmospheric CO_2 concentrations and global temperatures and alteration of soil nutrient status. Below are the key conclusions of this review:

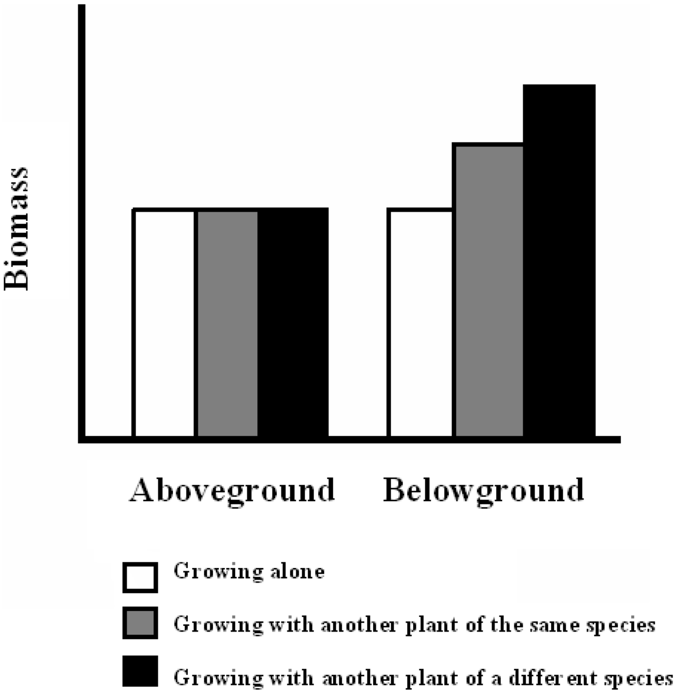

FIG. 6. Variation in below-ground biomass of a hypothetical perennial plant growing alone or with another plant of the same or a different species.

1. Plants invest a substantial proportion of annual total net primary production to the production and maintenance of roots and assiociated mycorrhizae in northern forests.
2. Fine roots show distinct seasonal trends in production and mortality. Over the extent of stand development, coarse root biomass increases until maturity, while the response of fine roots remains unclear.
3. Roots are generally restricted to the upper soil horizons, and spatial variability of roots in the horizontal direction generally decreases with decreasing root size.
4. For the perennial plant species that dominate northern forests, root/shoot ratio gradually decreases over time, as annual relative increases to stem increment eventually exceed annual below-ground biomass production.
5. Both increases and decreases in root production, turnover, and biomass have been reported following enhanced soil N availability. While root production is projected to increase, providing nutrients are not limiting, under predicted future climatic change, below-ground C pools could increase, decrease, or remain unchanged depending on how root turnover responds.
6. On nutrient-rich sites, roots are often more concentrated around respective stems and root systems can be more branched than on nutrient-poor sites. Global patterns of root distributions show that plants root deeper under low soil

moisture conditions. Roots may also show some tendency towards growth into N-rich rather than N-poor patches of soil.

7. Plants can adapt their particular biomass allocation strategies in response to various edaphic and climatic conditions. However, whether increased global CO_2 concentrations and temperatures may shift the relative allocation of assimilates between below- and above-ground structures remain uncertain.
8. In response to competition from other plants for soil resources, plants can increase their competitive ability or reduce competitive interactions with other plants. Due to a reduction in exploitative competition, stands composed of species with different rooting characteristics could possibly attain higher root production than single-species stands or mixtures of species with similar rooting characteristics as a consequence of enhanced root niche separation and greater total soil exploitation.
9. Plants can produce greater root biomass in the presence of a competing plant than when growing alone, attributed to self/non-self root discrimination at the individual root-level that reduces wasteful allocation of resources to competition with self.

The overall purpose of this review was to enhance understanding of the dynamic nature of roots in northern forests, while identifying critical knowledge gaps. Addressing the following questions is paramount to enhancing our understanding of the role of root systems in ecosystem function in current and future environmental conditions:

1. Are temporal patterns of fine root production and mortality affected by differences in stand species composition and environmental characteristics? If so, how might these differences affect C storage potential and C inputs to the atmosphere?
2. How will increases in atmospheric CO_2 concentrations and associated changes in nutrient availability affect the drivers of root production and turnover, and what types of feedbacks will there be on below-ground biomass pools with stand aging?
3. Will an increase in atmospheric temperature and CO_2 concentrations as a consequence of climate change increase overall rooting depth? If rooting depth does increase, will it lead to an increase in absolute fine root biomass or just redistribution? What are the links between stand age, horizontal rooting patterns, and localized nutrient distributions?
4. How important is the intensity of inter- and intraspecific competition on root production and turnover and below-ground biomass pools, and how might competition among roots at all levels of organization be affected by predicted future climatic change? Could silvicultural techniques that manipulate stand composition be used to enhance above and below-ground production and structural complexity?
5. To what extent are the root and shoot development patterns of northern forest plant species generalized or specific, and to what extent can altered environmental conditions elicit a shift in photosynthate allocation to different plant parts?
6. How will other below-ground plant functions, besides production and mortality, be altered by a changing climate, e.g., resistance to windthrow, mineral nutrition, defense against soil pathogens and insect herbivory, rhizodeposition, and C sequestration?
7. Will plants in ‘natural’ forests behave similarly to elevated global temperatures and concentrations of atmospheric CO_2 as those growing in short-term, controlled greenhouse and field experiments?

A better understanding of the current situation can help predict how environment change will impact below-ground ecology and validate predictive models at the landscape, ecosystem, and global scales. Information obtained by addressing these questions will also allow us to develop effective mitigation policies and procedures for predicted ecosystem responses to environment change.

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