THE ROOT DYNAMICS OF MIXED- AND SINGLE-SPECIES STANDS IN THE BOREAL FOREST OF CENTRAL AND EASTERN CANADA

By

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ABSTRACT

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Keywords: atmospheric carbon dioxide concentration, boreal forest, coarse root biomass allometric equations, facilitation, fine root production, mortality, and decomposition, mixed- and single-species stands, niche differentiation, over-yielding hypothesis, plant competition, soil nutrient availability, spatial rooting heterogeneity, species complementarity.

Despite that a substantial proportion of plant resources in forest ecosystems are allocated below-ground, the majority of research on diversity-productivity relationships in this ecosystem type has focused above-ground. Furthermore, relatively little is known about the key mechanisms which drive observed diversity-productivity relationships in terrestrial ecosystems. The objective of this dissertation, therefore, was to improve understanding regarding how the productivity dynamics of roots are influenced by plant diversity and environmental characteristics in forest ecosystems. To achieve this goal, I first conducted a literature synthesis on the effects of abiotic and biotic characteristics on root production and structure and carbon allocation above- and below-ground in northern forests. Next, I examined trends of fine root biomass and necromass in different mixed- and single-species stands within the central and eastern regions of the North American boreal forest to determine how annual fine root production, mortality, and decomposition and seasonal patterns of fine root biomass, necromass, and spatial heterogeneity within the soil profile vary with stand species composition. Lastly, I conducted root excavations in the central region of the North American boreal forest of mature trees of *Abies balsamea* L., *Picea mariana* (Mill.) BSP, *Pinus banksiana* Lamb., and *Populus tremuloides* Michx. to develop allometric equations relating stem diameter at breast-height and height to coarse root biomass.

In the first fine root study, annual fine root production and total fine root biomass in July and October were higher in stands of *P. tremuloides*, *P. mariana*, *Picea glauca* (Moench) Voss, and *A. balsamea* (mixed-species stands) than relatively pure stands of *P. tremuloides* (single-species stands). Furthermore, the mixed-species stands had lower horizontal and higher vertical fine root biomass heterogeneity, respectively, compared to the single-species stands. In the second fine root study, annual fine root production and total fine root biomass for most sampling dates (May to October) were higher in both mixed-species stand types (stands of *P. banksiana*, *P. mariana*, *P. glauca*, and *A. balsamea* (mixed conifer stands) and stands of *P. banksiana* and *P. tremuloides* (mixedwood stands)) than the single-species stands (relatively pure stands of *P. banksiana* (conifer stands)). Furthermore, horizontal fine root biomass heterogeneity was lower in the mixed- than single-species stands in July, August, and September, but similar among the three stand types for the other sampling dates. By contrast, vertical fine root biomass heterogeneity was higher in the mixed conifer than conifer stands from June to September, whereas mixedwood stands differed significantly from conifer stands for only a single sampling date.

There were distinct temporal trends of fine root biomass, necromass, and spatial biomass heterogeneity in the second fine root study. Total fine root biomass followed an inverse U-shaped pattern with sampling date (i.e., highest in the summer and lower in spring and fall), while total fine root necromass followed a U-shaped pattern (i.e., lowest in the summer and higher in spring and fall) in all three stand types, respectively. In the two mixed-species stand types, horizontal fine root biomass heterogeneity followed a U-shaped trend with sampling date, while vertical fine root biomass heterogeneity had an inverse U-shaped trend in mixed conifer stands and a U-shaped trend in mixedwood stands, respectively. However, neither horizontal nor vertical fine root biomass heterogeneity differed with sampling date in the conifer stands. The findings of both fine root studies support the theory that the differences in crown structures and rooting traits between component species in the mixed-species and mixed conifer stands in the first and second fine root studies, respectively (niche differentiation), versus increased nutrient availability resulting from the *P. tremuloides* leaf litter in the mixedwood stands in the second fine root study (facilitation), were promoting greater soil space filling of fine root biomas and fine root productivity in the mixed- than single-species stands for both studies. In particular, the greater ability of the mixed-species stands to fill the soil space with fine roots during the period of the growing season when demands for soil nutrients and water are at their highest (i.e., summer) relative to the single-species stands (so that competition among individual roots for soil resources is minimized), appears to be the key driver for the observed fine root productivity differences between the mixed- and single-species stands in the two studies.

All regressions for coarse root biomass using diameter at breast-height (DBH) or height alone, or both DBH and height as predictors were significant. The DBH – coarse root biomass models had higher R^2 values than the height – coarse root biomass models for all four species, indicating that DBH was a better predictor for coarse root biomass than height. Furthermore, the DBH-height – coarse root biomass models did not have higher R^2 values than the DBH – coarse root biomass models. All but one DBH – coarse root biomass model from the published literature with similar DBH range underestimated or overestimated coarse root biomass using the data from this study. Coarse root biomass allometric equations, therefore, are probably site-specific as above- and below-ground biomass allocation differs with site condition.

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CHAPTER ONE GENERAL INTRODUCTION

Central to ecological theory on intercropping is the premise that a plant community containing two or more species growing in mixture can potentially achieve higher productivity if the functional trait differences between them promote more complete exploitation of site resources than monocultures of the same component species (over-yielding hypothesis) (Vandermeer 1992). Studies from both grassland (Spehn *et al.* 2005; De Boeck *et al.* 2008; Bessler *et al.* 2009; Marquard *et al.* 2009) and forest (Fredericksen and Zedaker 1995; MacPherson *et al.* 2001; Wang *et al.* 2002; Vilà *et al.* 2003) ecosystems have provided support for this theory by showing that plant diversity has positive effects on productivity at the community level. However, most diversity-productivity studies to date have failed to identify the underlying causes of their observed diversity-productivity relationships.

In forest ecosystems, annual production below-ground can often exceed production above-ground (Gower *et al.* 1992; Helmisaari *et al.* 2002). Despite, however, that a substantial proportion of plant resources in forest ecosystems are allocated below-ground, the majority of research on diversity-productivity relationships in this ecosystem type has focused above-ground (e.g., Kelty 1989; Edgar and Burk 2001; MacPherson *et al.* 2001; Chen *et al.* 2003; Vilà *et al.* 2003; Légaré *et al.* 2005; Varga *et al.* 2005; Brassard *et al.* 2008; Cavard *et al.* 2010) (but see studies on diversity and below-ground productivity by Fredericksen and Zedaker (1995), Leuschner *et al.* (2001), and Wang *et al.* (2002)). Therefore, the relationship between plant diversity and below-ground productivity in forest ecosystems can be a key to increase understanding concerning the mechanisms which drive observed diversity-productivity relationships in terrestrial ecosystems.

The objective of this dissertation was to improve understanding regarding how the productivity dynamics of roots are influenced by plant diversity and environmental characteristics in forest ecosystems. To achieve this goal, I first conducted a literature synthesis on the effects of abiotic and biotic characteristics on root production and structure and carbon allocation above- and below-ground in northern forests. Next, I examined trends of fine root biomass and necromass in different mixed- and single-species stands within the central and eastern regions of the North American boreal forest (Appendix I) to determine how annual fine root production, mortality, and decomposition and seasonal patterns of fine root biomass, necromass, and spatial heterogeneity within the soil profile vary with stand species composition. Lastly, I conducted root excavations in the central region of the North American boreal forest of mature trees of *Abies balsamea* L., *Picea mariana* (Mill.) BSP, *Pinus banksiana* Lamb., and *Populus tremuloides* Michx. to develop allometric equations relating stem diameter at breast-height and height to coarse root biomass (these will prove valuable in my future efforts to study total carbon dynamics in the study area). I also tested to what extent these equations would be appropriate for use in other areas of the North American boreal forest by comparing them to equations from the published literature.

Chapters 2 and 3 of this dissertation have already been published (Chapter 2 in Critical Reviews in Plant Sciences (Brassard *et al.* 2009) and Chapter 3 in Functional Ecology (Brassard *et al.* 2010)). Since each chapter has been written as a distinct manuscript to facilitate publication, I have made reference to Chapter 2 in Chapters 3, 4, and 5 and Chapter 3 in Chapter 4, respectively. The work completed in this dissertation represents a component of a larger collaborative project between Lakehead University, The University of Quebec, and the Canadian

Forest Service to investigate the species mixture effect on carbon dynamics in the North American boreal forest.

CHAPTER TWO INFLUENCE OF ENVIRONMENTAL VARIABILITY ON ROOT DYNAMICS IN NORTHERN FORESTS

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 theses 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: (1) 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, (2) 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 (3) investigate how plant inter- and intraspecific competition influences root production, system morphology, and C allocation to plant structures above- and below-ground.

PRODUCTION, STRUCTURE, AND CARBON ALLOCATION DYNAMICS

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 knowledge of general short- and long-term trends of root dynamics is fundamental to enhancing understanding of C allocation and storage in terrestrial ecosystems. Therefore in this section, I will describe the following: (1) the seasonal patterns of root production and mortality and (2) the dynamic changes in root biomass over the extent of stand development, which are generally ubiquitous of most northern forests.

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) (Figure 2.1A). 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.

As the demand for nutrients is reduced in late summer and fall in preparation for leaf senescence and over-wintering, there is a reduction in fine root production and maintenance and

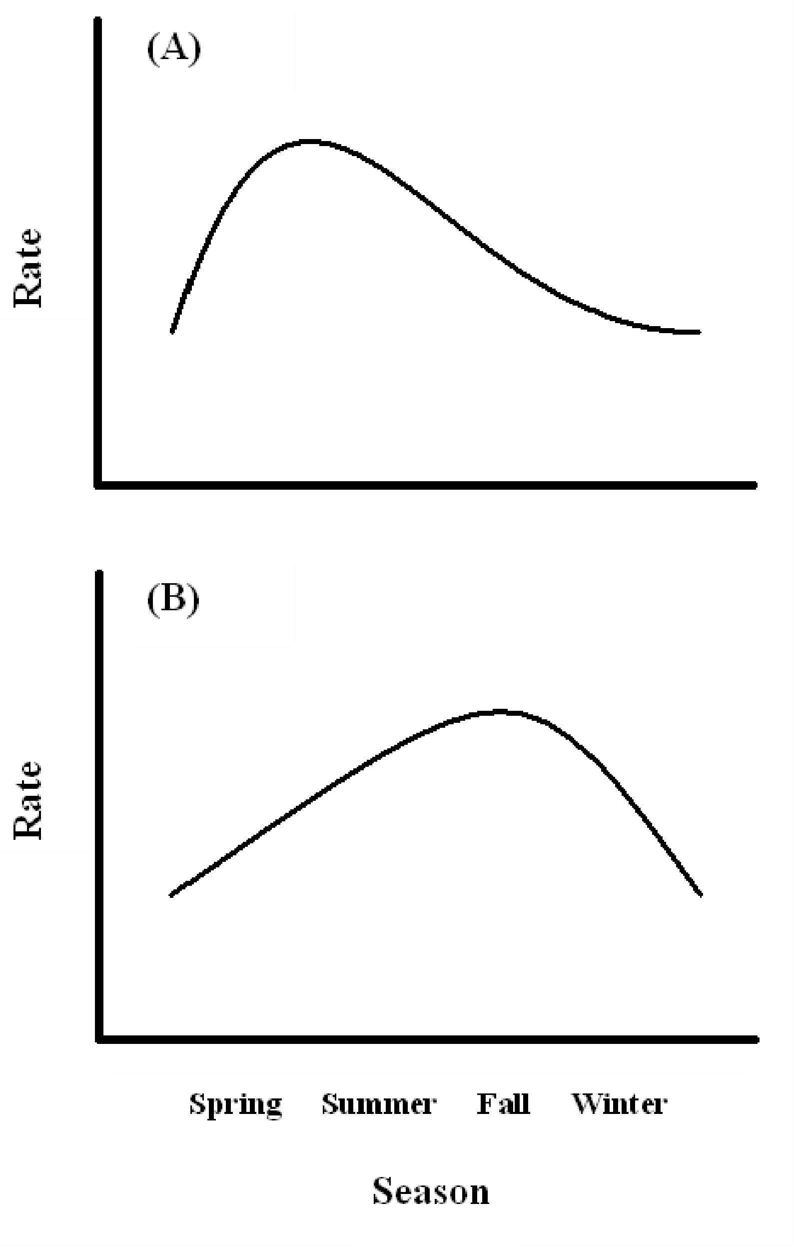

Figure 2.1. Seasonal fluctuations of fine root (A) production and (B) mortality.

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) (Figure 2.1B). 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).

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; 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 (Figure 2.2A). 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.

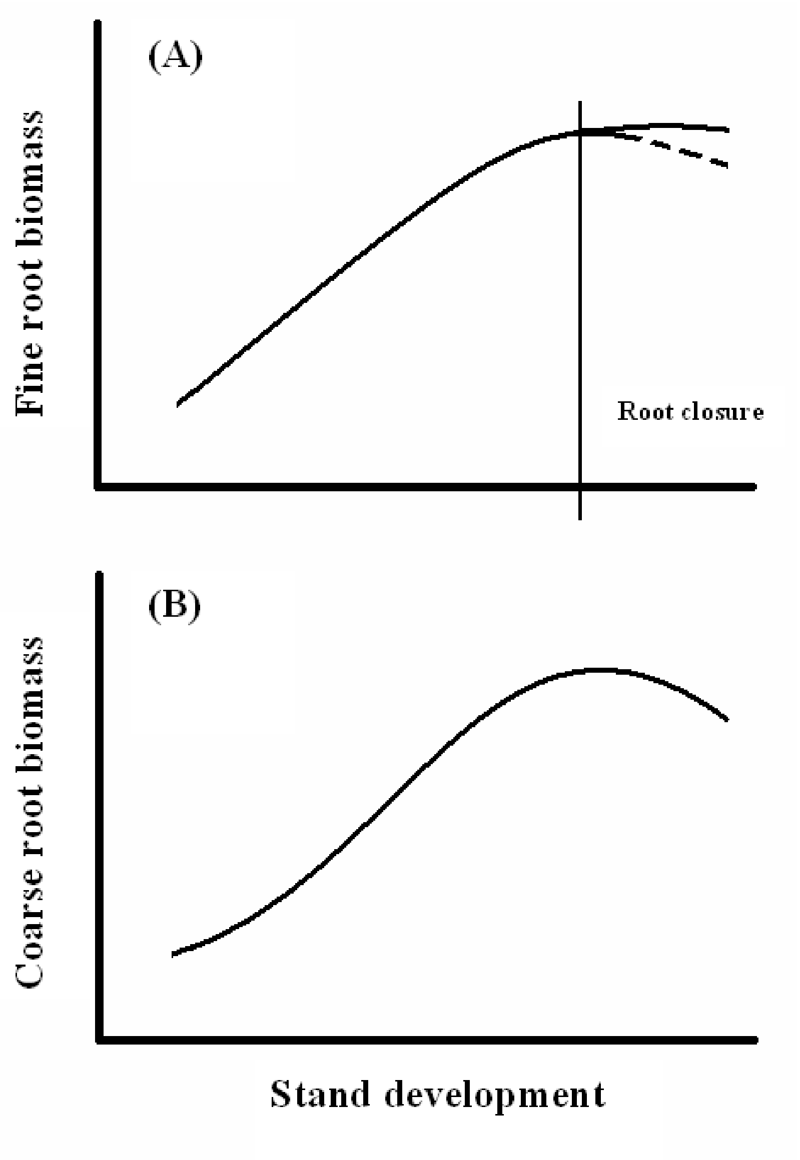

Figure 2.2. Trends of (A) fine and (B) coarse root biomass through stand development.

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; Peichl and Arain 2007) (Figure 2.2B). 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).

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), I have chosen below to describe structural rooting patterns in the vertical and horizontal directions separately.

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 1983b; 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.

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 1983b; 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.

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 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: (1) 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 (2) 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) (Figure 2.3). 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 exceeds annual below-ground biomass production, resulting in a gradual decrease in root/shoot ratio.

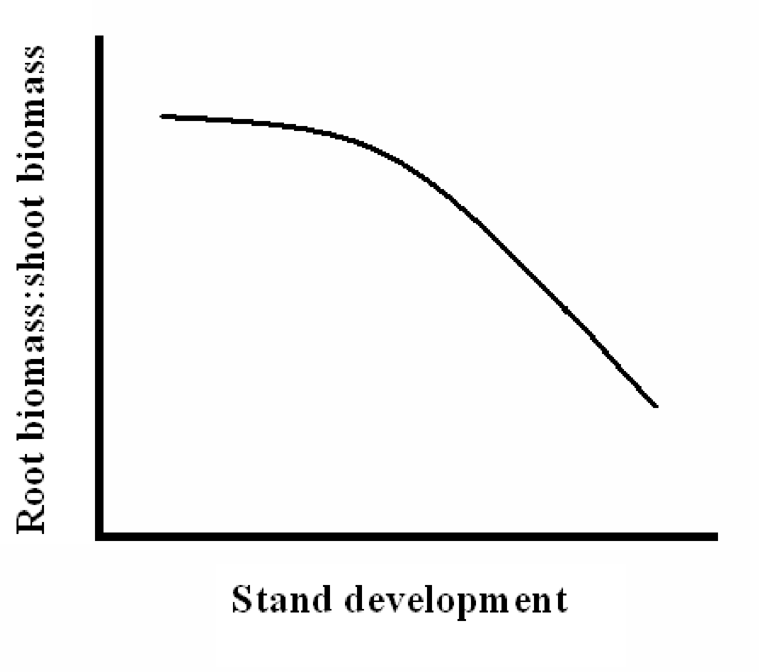

Figure 2.3. Ratio of root biomass to shoot biomass through stand development.

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, I will 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, I 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.

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

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 2.1). 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 I 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.

Table 2.1. 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
Safford (1974)	-	-	Increase
Persson (1980)	-	-	Increase
Grier *et al.* (1981)	Decrease	-	-
Aber *et al.* (1985)	Increase	Increase	Decrease
Nadelhoffer *et al.* (1985)	Increase	Increase	Decrease
Burke *et al.* (1992)	Increase	-	-
Gower *et al.* (1992)	Decrease	-	-
Nadelhoffer and Raich (1992)	Increase	-	Decrease
Hendricks *et al.* (1993)	Increase	Increase	-
Pregitzer *et al.* (1993)	Increase	Decrease	-
Fahey and Hughes (1994)	-	Decrease	-
Ericsson (1995)	Increase	-	-
Haynes and Gower (1995)	Decrease	-	Decrease
Pregitzer *et al.* (1995)	Increase	Increase	-
Ruess *et al.* (1996)	-	Decrease	-
Vogt *et al.* (1996)	Decrease	-	Decrease
Albaugh *et al.* (1998)	Decrease	-	-
Côté *et al.* (1998)	Decrease	-	Decrease
King *et al.* (1999a)	-	-	Decrease
King *et al.* (1999b)	Increase	Increase	-
Burton *et al.* (2000)	Increase	Decrease	-
Pregitzer *et al.* (2000b)	Increase	-	Increase
Curt *et al.* (2001)	-	-	Increase
Majdi (2001)	Increase	-	Increase
King *et al.* (2002)	Increase	-	-
Schmid and Kazda (2002)	-	-	Decrease
Kern *et al.* (2004)	Increase	-	Increase

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 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- 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) (Figure 2.4).

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).

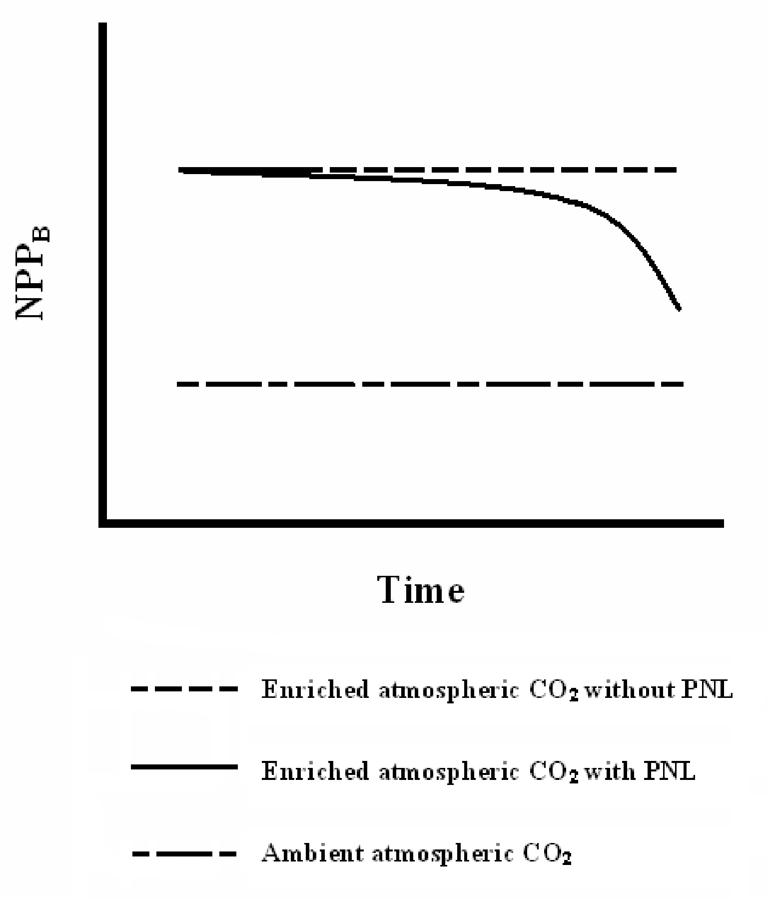

Figure 2.4. Rates of annual below-ground net primary production (NPP$_B$) over time under scenarios of ambient atmospheric CO$_2$, enriched atmospheric CO$_2$ without progressive nitrogen limitation (PNL), and enriched atmospheric CO$_2$ with PNL.

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 it is assumed 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, predictions can be made of how below-ground C pools, both root biomass and soil C, may respond to variation in root turnover under future climatic change:

1. <u>Scenario 1: Increased root turnover</u>: 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 (Figure 2.5A).

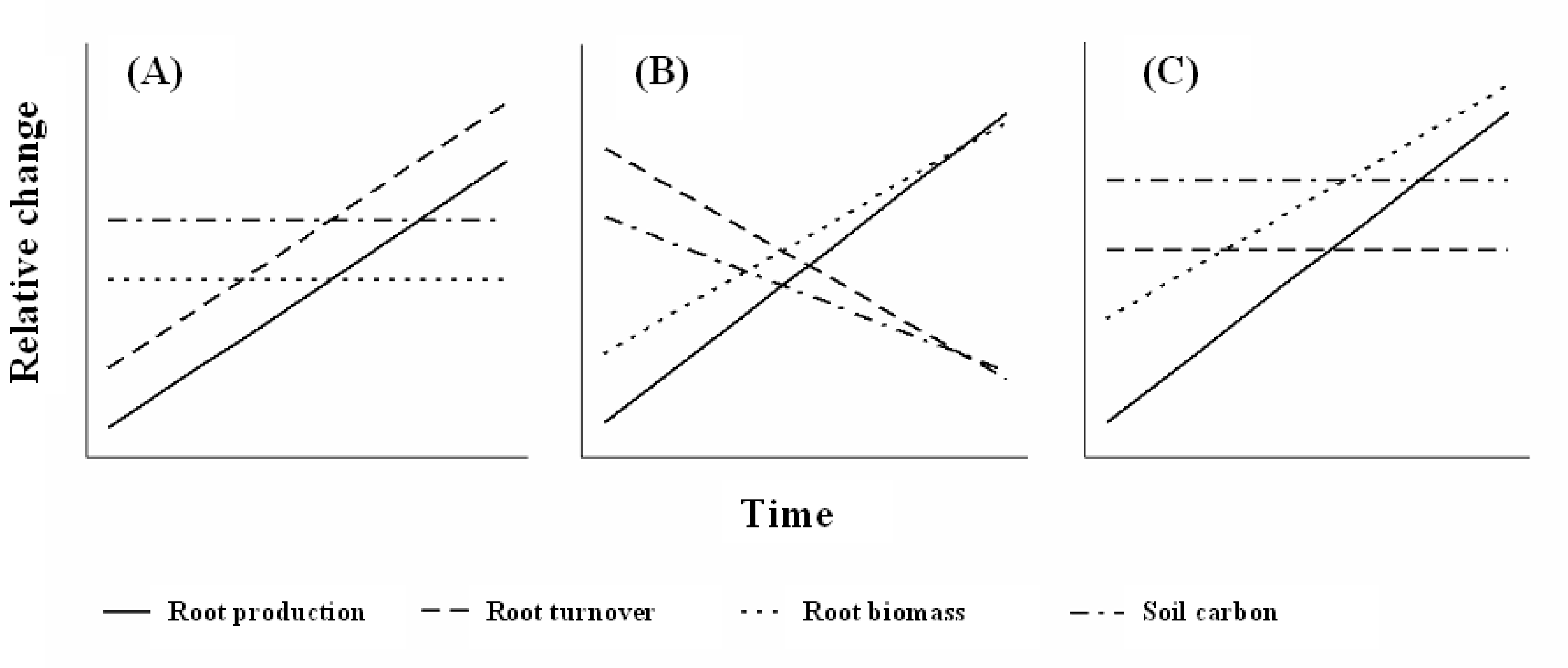

Figure 2.5. Hypothetical responses of root biomass and soil carbon to an increase in root production and (A) increased, (B) decreased, and (C) no change in root turnover.

2. Scenario 2: Decreased root turnover: Since, in this scenario, root production increases and root turnover decreases, root biomass should also increase. However, soil C pools may 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 (Figure 2.5B).
3. Scenario 3: 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 (Figure 2.5C).

The above scenarios represent ‘best guesses’ of overall C pool flux following predicted future climatic change, as it is well recognized that the potential 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; 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, I recognize that the 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.

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

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 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; 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 understanding of the mechanisms coordinating morphological and physiological changes as 'economic tradeoffs' that ultimately impact plant fitness.

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, I 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.

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 2.2). In accordance with this hypothesis, when light and CO_2 levels are low, a plant should favor foliage production, while

Table 2.2. 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	Low	Decrease
dioxide	High	Increase or no change
Soil moisture	Low	Increase
availability	High	Decrease or no change
Soil nitrogen	Low	Increase
availability	High	Decrease or no change
Air and soil	Low	Decrease, increase, or no change
temperature	High	Decrease, increase, or no change

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 above-ground, 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 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).

BIOTIC INFLUENCES

Roots and associated mycorrhizae are the principle organs for below-ground competition among individual plants (Wilson 1988; Casper and Jackson 1997; Leuschner *et al.* 2001). Root competition can be generally divided into two broad categories: (1) scramble or exploitative competition and (2) 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, I 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. I 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.

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: (1) they may increase their competitive ability or (2) 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 (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, I 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, I have first outlined a simplified, conceptual example involving three different tree species growing together in different combinations and separately. Next, I 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.

Applying the Competition Reduction Theorem to Roots – A Hypothetical Example

To better understand how below-ground plant competition influences root dynamics, I 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). I 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, I have compared below-ground production and structure in three conceptual forest stand types: (1) a mixture of two trees species with different successional status (stand A), (2) a mixture of trees species with similar successional status (stand B), and (3) a monoculture (stand C) (Table 2.3). In the hypothetical example, all three stands have similar site conditions. I 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 the 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; Chen *et al.* 2009).

Table 2.3. 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

Evidence from Northern Forests

The postulates formulated above can be tested 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, 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 the 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.

Carbon Allocation between Roots and Shoots – Influence of Interference Competition

Most of the 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. 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. I emphasize that this type of below-ground response to the presence of a competing plant is probably invoked by non-toxic 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 remain poorly understood and largely understudied.

SYNTHESIS AND FUTURE RESEARCH NEEDS

Remarkably little is still known 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:

1. Plants invest a substantial proportion of annual total net primary production to the production and maintenance of roots and associated 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 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 will assist researchers in predicting 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.

CHAPTER THREE DIFFERENCES IN FINE ROOT PRODUCTIVITY BETWEEN MIXED- AND SINGLE-SPECIES STANDS

INTRODUCTION

Ever since Darwin and Wallace (1858) first proposed that higher crop species diversity may be linked to higher crop yields, the question of whether or not plant diversity is related to net primary productivity has remained highly contested amongst the scientific community. During the past two decades, various experimental and observational studies have reported that polycultures can have higher above-ground biomass production than the average above-ground biomass production of monocultures under similar site conditions, i.e., over-yielding. Two hypotheses have been proposed to explain the observed positive diversity effect on productivity. The species complementarity hypothesis predicts that a mixture of two or more species of plants can achieve higher productivity than monocultures of the same component species via either facilitation, i.e., the presence of one species benefits the other by improving growing conditions, or niche differentiation, i.e., coexisting species occupy different ecological niches that results in more complete resource use (Tilman *et al.* 1997; Loreau and Hector 2001; Spehn *et al.* 2005; Marquard *et al.* 2009). Critics of the species complementarity hypothesis, however, argue that a selection effect, i.e., that a more diverse plant community has a higher probability of containing the most productive species, could alternatively explain the observed higher productivity of polycultures than monocultures in some studies (Špaèková and Lepš 2001; Cardinale *et al.* 2006; Schmid *et al.* 2008). A recent meta-analysis by Cardinale *et al.* (2007) has shown that species mixtures are more productive than the average of all monocultures in 79% of 44 diversity-productivity experiments, but achieve higher biomass in only 12% of these experiments, indicating that positive diversity-productivity relationships are likely attributable to both selection and species complementarity effects.

The majority of diversity-productivity studies to date have occurred in grasslands on above-ground components, where parameters can be more easily controlled and measured (e.g., Tilman *et al.* 1996; Hector *et al.* 1999; Loreau and Hector 2001; Hector *et al.* 2002; Flombaum and Sala 2008; Marquard *et al.* 2009). By contrast, diversity-productivity relationships have been less studied in forests, as the complex structure of this ecosystem type, and the relatively long life span of trees, make direct manipulation difficult. Especially lacking are studies that examine this relationship below-ground, despite that below-ground production can account for approximately half of total annual net primary production in forest ecosystems (Gower *et al.* 1992; Helmisaari *et al.* 2002).

The objective of this study was to examine fine root (≤ 2 mm in diameter) productivity and rooting patterns in single-species stands of *Populus tremuloides* Michx. and mixed stands of *P. tremuloides*, *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss, and *Abies balsamea* L. Fine roots are primarily responsible for nutrient and water acquisition from the soil, and their production can account for well over three quarters of annual below-ground production in forest ecosystems (Jackson *et al.* 1997; Brassard *et al.* 2009). I attempted to test: (1) whether *P. tremuloides* – *Picea* spp. – *A. balsamea* mixtures have higher fine root productivity, measured by annual fine root production and total fine root biomass (live roots), than pure *P. tremuloides* stands (over-yielding hypothesis) and (2) the niche differentiation hypothesis, i.e., that the difference in productivity between stand types may be the result of greater soil space filling by the fine roots due to the contrasting rooting traits of the component species in the mixed stands. To avoid a potential selection effect, this study was designed to compare the fine root productivity of the most productive single-species stand type in the North American boreal forest, pure *P. tremuloides* stands, with mixed stands of *P. tremuloides*, *P. mariana*, *P. glauca*, and *A. balsamea*. To test the second hypothesis, I used a heterogeneity index to characterize stand-level horizontal and vertical fine root biomass distributions as an indicator of how fully below-ground growing space is being utilized within a stand. To my knowledge, this study is the first to investigate the link between fine root spatial biomass heterogeneity and below-ground productivity.

This study was conducted in two regions, a drier and warmer central region and a cooler and wetter eastern region of the North American boreal forest. The studied stand types are common on mesic sites in both regions. *Populus tremuloides* is a shade-intolerant broadleaf species that roots deeper than the more shade-tolerant conifers *P. mariana*, *P. glauca*, and *A. balsamea*, while having a higher rate of above- and below-ground growth (Burns and Honkala 1990). All four of these tree species can establish immediately after stand-replacing crown fire, but *P. glauca* and *A. balsamea* can also recruit later in stand development by seeding in from neighboring stands (Galipeau *et al.* 1997; Bergeron 2000; Ilisson and Chen 2009).

MATERIALS AND METHODS

Study Area

One study region was located west of Lake Nipigon in the Upper English River (B.11) Forest Region (Rowe 1972), approximately 150 km north of Thunder Bay, Ontario, Canada (49º 23’ N to 49º 37’ N, 89º 31’ W to 89º 45’ W). The average annual precipitation for Thunder Bay (1971-2000), the location of the closest weather station, is 712 mm, and the average annual temperature is 2.5 ºC (Environment Canada 2010). The second was located east of Lac Turgeon approximately 100 km northeast of La Sarre, Quebec, Canada (49º 08’ N to 49º 12’ N, 89º 46’

W to 89º 54’ W) in the Northern Clay (B.4) Forest Region. The closest weather station is located in La Sarre, where the average annual precipitation and temperature is 823 mm and 0.6 ºC, respectively. Short summers and moderately dry cool climate is common to both study regions, and topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago. Stand-replacing crown fire is the most common natural stand initiating disturbance in both regions (Johnson 1992).

Sampling

I selected, using forest resource inventory maps and random stratified sampling, six mature fire-origin stands in each study region (time since fire: Ontario sites = 85 and Quebec sites = 92 years) that belonged to one of two discrete stand types: (1) stands containing mixtures of *P. tremuloides*, *Picea* spp., and *A. balsamea* (hereafter referred to as ‘mixed-species stands’) and (2) relatively pure stands of *P. tremuloides* (hereafter referred to as ‘single-species stands’). Similar to other studies that investigate the species mixture effect in naturally established mature stands (e.g., Wang *et al.* 2002; Brassard *et al.* 2008; Cavard *et al.* 2010), and in following the definitions for single- and mixed-species stands in the forest resource inventory, criteria for stand selection was that mixed-species stands would contain > 20% stand basal area of *Picea* spp. and *A. balsamea*, while single-species stands would have < 20%. The average percent basal area of *Picea* spp. and *A. balsamea* in the mixed-species stands was 33%, ranging from 24 to 48%, whereas that in the single-species stands was 3% and ranged from 0 to 9% (Table 3.1).

Common understory plant species in the Quebec stands were *Rubus pubescens* Raf., *Diervilla lonicera* Mill., *Viburnum edule* (Michx.) Raf., *Gaultheria hispidula* (L.) Muhl. ex Bigelow, *Alnus* spp., *Cornus canadensis* L., *Viola* spp., *Linnea borealis* L., *Maianthemum canadense* Desf., and *Mitella nuda* L. In the Ontario stands, common understory plants included

Table 3.1. Characteristics (mean and range) of the twelve study stands sampled in northwestern Ontario and northwestern Quebec, Canada. Each stand type was replicated three times in each region.

Study region	Ontario		Quebec	
Stand type	Mixed-species	Single-species	Mixed-species	Single-species
Stand volume (m^3 ha^{-1})*	341.5 (262.8-404.1)	378.6 (222.7-478.9)	413.4 (269.4-501.4)	505.8 (364.6-636.9)
Stand density (trees ha^{-1})	1,600 (1,350-1,850)	734 (675-775)	1,350 (1,100-1,500)	825 (650-1,000)
Shrub, herb, and moss biomass (kg ha^{-1})†	2,413 (1,260-4,709)	25,749 (3,176-43,316)	1,716 (1,251-2,125)	21,860 (14,002-37,460)
Abies balsamea basal area (m^2 ha^{-1})	2.63 (0.71-4.31)	0	0.02 (0-0.06)	0.04 (0-0.12)
Picea glauca basal area (m^2 ha^{-1})	1.86 (0-5.59)	0	0	0
Picea mariana basal area (m^2 ha^{-1})	7.61 (1.80-10.95)	0	14.79 (10.25-17.13)	2.74 (1.04-6.11)
Pinus banksiana basal area (m^2 ha^{-1})	1.59 (0.28-3.24)	1.09 (0.35-1.87)	2.16 (0-3.33)	0.86 (0-2.58)
Populus tremuloides basal area (m^2 ha^{-1})	25.60 (18.39-31.51)	32.50 (20.17-38.75)	25.31 (14.76-33.59)	37.34 (27.57-42.41)

[*] Stand volume was determined using individual tree volumes that were summed to the plot level and scaled up to per ha. Individual tree volumes were estimated using the diameter at breast-height and height measurements and species-specific volume equations developed for tree species of central and eastern Canada (Honer *et al.* 1983).

[†] Shrub, herb, and moss biomass was determined by harvesting all above-ground components of each type in three randomly located 1 m^2 quadrates. All samples were brought back to the laboratory, oven-dried for 48 hours at 65 °C, and weighed. Sample weights were pooled by plot and scaled up to per ha.

Acer spicatum Lam., *R. pubescens*, *Alnus* spp., *Corylus cornuta* Marsh., *D. lonicera*, *C. canadensis*, *Clintonia borealis* (Aiton) Raf., *M. canadense*, *Coptis trifolia* (L.) Salisb., *Viola* spp., and *Aster macrophyllus* L.

To limit site variability, all selected stands were > 1 ha in area, fully stocked, visually homogeneous in structure and composition, and were located on relatively flat, upland, mid-slope positions. Following the procedure described in Taylor *et al.* (2000), a soil pit was dug in each sampled stand to ensure site condition was mesic in Ontario and subhydric in Quebec, the typical site type for boreal mixedwoods in the respective regions. All sampled sites in Quebec belonged to the Luvisolic soil order, while those in Ontario were Brunisolic (Cavard *et al.* 2010).

At each site, a 400 m^2 circular plot was established to represent the stand, where no trees had survived from the last fire. The diameter at breast-height (DBH), taken 1.3 m above the root collar, height, and species of all live trees DBH $\geq$ 2 cm were measured and recorded. Stand basal area by species was summed to the plot level and used for assigning stand type classification.

Within each plot, seven soil cores (6.75 cm diameter) were randomly extracted from the forest floor surface to a mineral soil depth of 30 cm using a power auger in mid July and late October of 2007, which are generally regarded in northern forests as the timings of maximum and minimum fine root biomass, respectively (Steele *et al.* 1997; Wang *et al.* 2003). To facilitate extraction by layers, and to minimize compaction during coring, I extracted the forest floor layer (FF) and two mineral soil sections: MS1 (0-15 cm) and MS2 (15-30 cm) subsequently after removing the upper layer.

Soil core sections were transported in an ice-filled cooler from the field to the laboratory and stored in a freezer for approximately one to two months at -20 °C until processing. Thawed samples were soaked in water to separate roots from soil and gently washed over a 0.5 mm sieve.

Coarse roots (> 2 mm in diameter) and coarse fragments were removed. Remaining root fragments were rinsed with water and sorted according to vitality class, i.e., live versus dead. Roots were considered ‘live’ if they were pale-colored on the exterior, elastic and flexible, and free of decay with a whitish cortex, while roots were classified as ‘dead’ if they were brown or black in color, rigid and inflexible, in various stages of decay, and had a dark colored cortex (Persson 1983; Bennett *et al.* 2002).

Live fine roots were further divided into the following species-based classes: (1) *P. tremuloides*, (2) *Picea* spp. and *A. balsamea*, (3) non-tree (shrubs and herbs), and (4*) P. banksiana* using a combination of morphological characteristics. These included: (1) color (*P. tremuloides* and non-tree roots were more white or yellow in color, while conifer roots were more red or brown in color), (2) size (*Picea* spp. and *A. balsamea* and non-tree roots were generally finer-structured than those of *P. tremuloides* and *P. banksiana*), (3) branching angle (approximately 90° for conifer roots and 45° for *P. tremuloides* and non-tree roots), (4) branching pattern (sections of *Picea* spp. and *A. balsamea* and non-tree roots were more branched than those of *P. tremuloides* and *P. banksiana*), and (5) presence or absence of root hairs (non-tree roots contained small hairs that were not present on tree roots). These criteria were developed previous to root sorting using samples of known origin from the study sites. The fine roots were then oven-dried to a constant mass at 65 °C and weighed.

I also installed ten ingrowth cores (6.75 cm diameter, 30 cm length) at each site to give a second estimate of annual fine root production (Steele *et al.* 1997; Hendricks *et al.* 2006). A power auger was again used to drill holes at each site. A plastic mesh core was then inserted into each hole, filled with root-free soil (medium-textured sand), covered with leaf litter, and marked by a steel rod. All ingrowth cores were installed in October 2007 and removed after one calendar year. Roots were separated from the soil, dried, and weighed as described above, with the exception that roots were not separated by soil layer or species class. No roots > 2 mm in diameter were present in any of the ingrowth cores.

Data Analysis

Total fine root biomass and necromass (dead roots) (kg ha^{-1}) were calculated for each sampling period (July and October) at each site by summing the dry weight of live and dead fine roots, respectively, in each soil core and scaling up to per ha. Annual fine root production (kg ha^{-1} $year^{-1}$) based on the minimum-maximum method was then calculated as the difference between total July and October fine root biomass. Annual fine root production based on the ingrowth core method was calculated at each site by summing the dry weight of live and dead roots in each ingrowth core and scaling up to per ha.

Horizontal fine root biomass heterogeneity was calculated as the standard deviation of the fine root biomass values of all soil layers combined among the seven soil cores at each site for both sampling periods. Vertical fine root biomass heterogeneity was calculated for both sampling periods as the standard deviation of the fine root biomass values among the three soil layers averaged from all soil cores. A higher standard deviation value would imply that fine root biomass is less evenly distributed, i.e., more heterogeneous, among the soil cores or soil layers, respectively. Since detailed maps of fine root distributions are currently almost impossible to construct at the stand level, using among soil core fine root biomass heterogeneity to approximate how variable fine roots are distributed horizontally within a stand provides a practical tool for assessing fine rooting patterns in the horizontal dimension.

To determine if annual fine root production, total July and October fine root biomass and necromass, July and October horizontal and vertical fine root biomass heterogeneity, and the biomass of fine roots in July and October by species – soil layer class differed with stand type and study region, I used the following general linear model (eq. 3.1):

$$[3.1] \quad Y_{ijk} = \mu + T_i + R_j + T \times R_{ij} + \varepsilon_{(ij)k}$$

where Y_{ijk} is annual production, biomass or necromass, or biomass heterogeneity, μ is the overall mean, T_i is stand type ($i = 1, 2$), R_j is study region ($j = 1, 2$), $T \times R_{ij}$ is the stand type – study region interaction, and $\varepsilon_{(ij)k}$ is the random error. Simple linear regression analysis was then used to determine if total July and October fine root biomass were related to July and October horizontal or vertical fine root biomass heterogeneity, respectively. Normality and homogeneous variances were confirmed following Kutner *et al.* (2005). Statistical significance was based on $\alpha = 0.05$, and all analyses were performed using SPSS® version 16.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Both the minimum-maximum and ingrowth core methods indicated that annual fine root production was significantly higher in mixed- than single-species stands in both study regions (Table 3.2, Figure 3.1). Total July and October fine root biomass were significantly and marginally significantly ($\alpha = 0.10$) higher in mixed- than single-species stands, respectively, in both study regions. Total July fine root necromass, however, did not differ with stand type or study region, whereas total October fine root necromass was significantly higher in mixed- than single-species stands in both study regions (Table 3.2, Figure 3.2).

The biomass of *P. tremuloides* fine roots did not differ between stand types and study regions for all three soil layers in both sampling periods (Table 3.3, Figure 3.2). The biomass of *Picea* spp. and *A. balsamea* fine roots was significantly higher in mixed- than single-species

Table 3.2. Effects (P-values) of stand type (*T*) and study region (*R*) on annual fine root production, the total biomass and necromass of fine roots in July and October, and horizontal and vertical fine root biomass heterogeneity in July and October.

Characteristic	R^2	Source[*]		
		T	*R*	*T*×*R*
Annual fine root production				
Minimum-maximum method	0.597	**0.011**	0.582	0.401
Ingrowth core method	0.604	**0.008**	0.749	0.988
Total fine root biomass				
July	0.510	**0.022**	0.920	0.630
October	0.427	**0.071**	0.657	0.272
Total fine root necromass				
July	0.124	0.467	0.842	0.495
October	0.419	**0.046**	0.975	0.654
Horizontal fine root biomass heterogeneity				
July	0.554	**0.038**	**0.089**	0.981
October	0.462	0.541	**0.057**	0.250
Vertical fine root biomass heterogeneity				
July	0.446	**0.061**	0.261	0.623
October	0.609	**0.016**	0.667	0.117

[*] Source is explained in eq. 3.1.

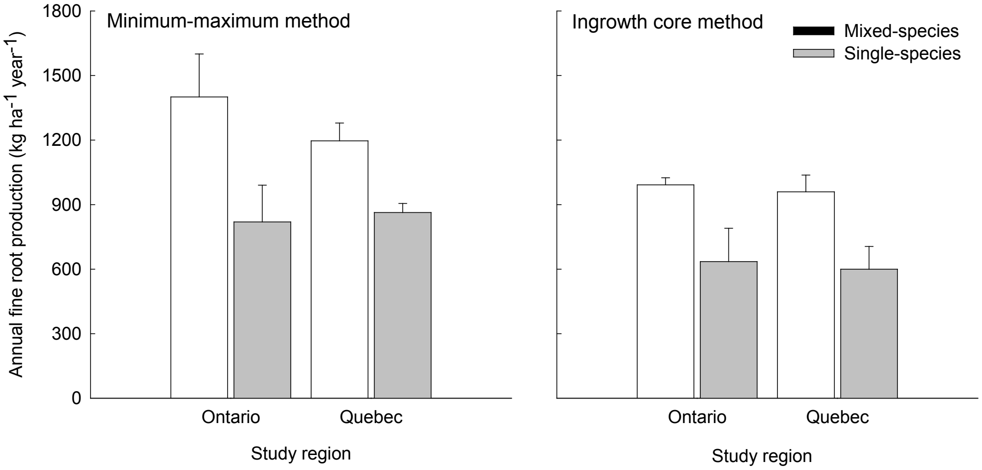

Figure 3.1. Annual fine root production by stand type (mixed-species and single-species), study region (Ontario and Quebec), and method of sampling (minimum-maximum method and ingrowth core method). Error bars represent 1 SEM.

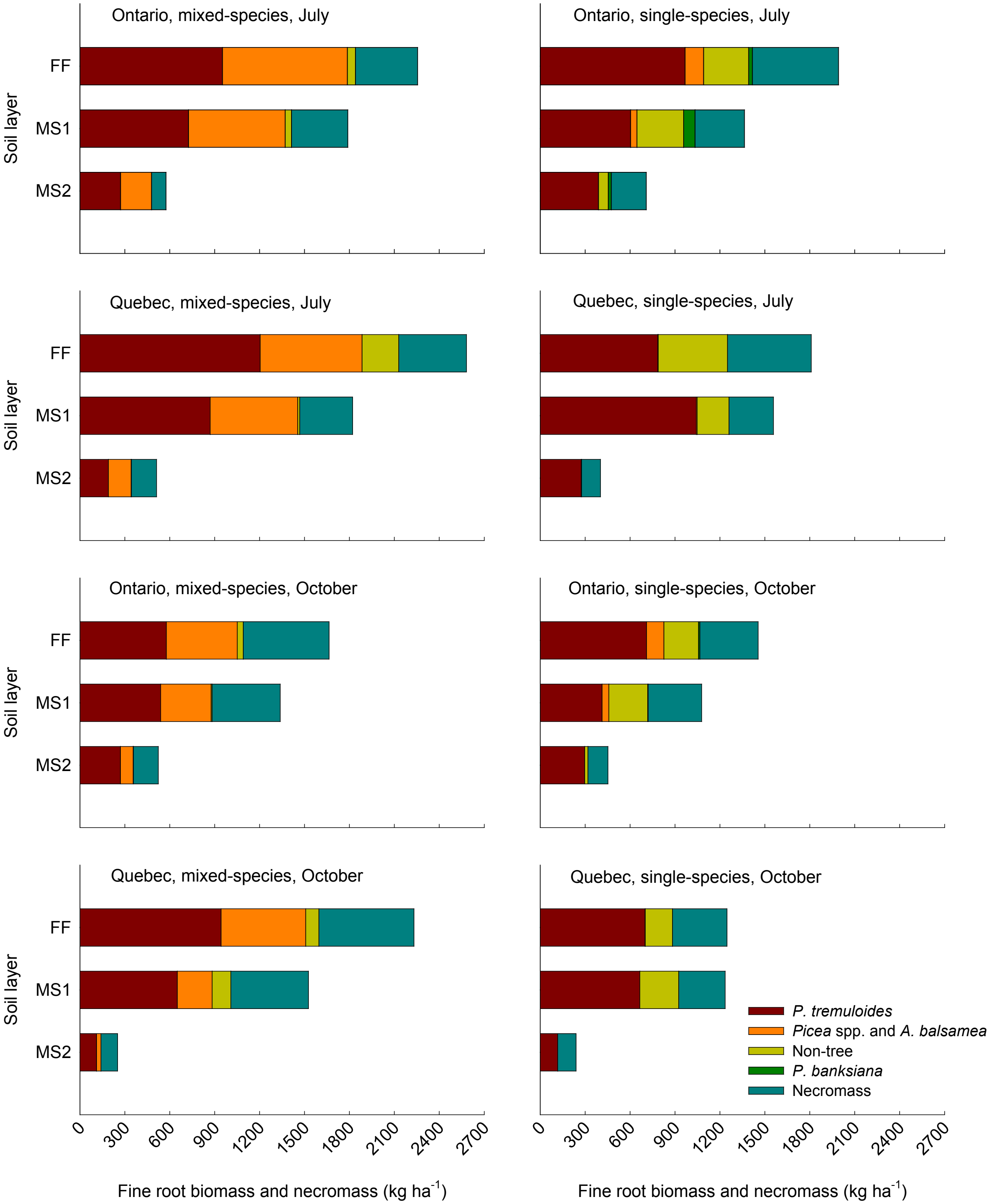

Figure 3.2. The biomass (*Populus tremuloides*, *Picea* spp. and *Abies balsamea*, non-tree, and *Pinus banksiana*) and necromass of fine roots by soil layer (FF, MS1, and MS2), stand type (mixed-species and single-species), study region (Ontario and Quebec), and sampling period (July and October).

Table 3.3. Effects (P-values) of stand type (*T*) and study region (*R*) on the biomass of fine roots in July and October by species – soil layer class.

Species – soil layer class	July				October			
	R^2	Source[*]			R^2	Source[*]		
		T	*R*	*T*×*R*		*T*	*R*	*T*×*R*
Populus tremuloides								
FF layer	0.317	0.229	0.827	0.198	0.384	0.650	0.172	0.152
MS1 layer	0.447	0.650	0.153	0.286	0.281	0.639	0.151	0.559
MS2 layer	0.326	0.201	0.208	0.823	0.399	0.837	0.171	0.492
Picea spp. and *Abies balsamea*								
FF layer	0.925	**<0.001**	**0.090**	0.819	0.844	**<0.001**	0.881	0.188
MS1 layer	0.901	**<0.001**	0.503	0.870	0.856	**<0.001**	**0.095**	0.466
MS2 layer	0.940	**<0.001**	0.133	0.133	0.591	**0.023**	0.210	0.280
Non-tree								
FF layer	0.597	**0.026**	**0.072**	0.867	0.676	**0.005**	0.984	0.216
MS1 layer	0.568	**0.015**	0.426	0.662	0.402	**0.066**	0.531	0.538
MS2 layer	0.437	0.177	0.208	0.183	0.529	0.138	0.106	0.148
All species[†]								
FF layer	0.491	**0.031**	0.812	0.388	0.559	**0.057**	0.361	0.103
MS1 layer	0.328	0.123	0.432	0.626	0.182	0.455	0.326	0.805
MS2 layer	0.330	0.691	**0.093**	0.724	0.527	0.669	**0.018**	0.920

[*] Source is explained in eq. 3.1.

[†] Includes *P. tremuloides*, *Picea* spp. and *A. balsamea*, non-tree, and *Pinus banksiana* fine root biomass.

stands in all three soil layers for both sampling periods. July and October *Picea* spp. and *A. balsamea* fine root biomass were marginally higher in the Ontario than Quebec region in the FF and MS1 layer, respectively, but did not differ between study regions in the MS2 layer for either sampling period (Table 3.3, Figure 3.2). By contrast, non-tree fine root biomass was significantly or marginally higher in single- than mixed-species stands in the FF and MS1 layers, but did not differ between stand types in the MS2 layer, for either sampling period. Non-tree fine root biomass in the FF layer was marginally higher in the Quebec than Ontario region in July, but did not differ between study regions in the other two soil layers in July, or any of the soil layers in October (Table 3.3, Figure 3.2). The fine root biomass of all species combined was higher in mixed- than single-species stands in the FF layer, while both stand types had similar total fine root biomass in the MS1 and MS2 layers, in both sampling periods. Stands in the Ontario region, however, contained higher total fine root biomass in the MS2 layer, but similar biomass in the other two soil layers, compared with those in the Quebec region, in both sampling periods (Table 3.3, Figure 3.2).

July horizontal fine root biomass heterogeneity was significantly higher in single- than mixed-species stands, and marginally higher in stands of the Ontario than Quebec regions (Table 3.2, Figure 3.3). October horizontal fine root biomass heterogeneity, however, did not differ between stand types, but showed a similar regional trend. By contrast, July and October vertical fine root biomass heterogeneity were marginally and significantly higher in mixed- than single-species stands, respectively, but did not differ between study regions (Table 3.2, Figure 3.3). Total July fine root biomass increased with decreasing horizontal fine root biomass heterogeneity and increasing vertical fine root biomass heterogeneity. Total October fine root biomass, however, was not significantly affected by horizontal fine root biomass heterogeneity, but did increase with increasing vertical fine root biomass heterogeneity (Figure 3.4).

DISCUSSION

The data supported my first hypothesis that fine root productivity, measured by annual fine root production and total fine root biomass, is higher in mixed- than single-species stands. Although this study is the first, to my knowledge, to examine fine root production in different stand types of similar age and site conditions, fine root biomass has been compared between mixed- and single-species stands in a limited number of other studies. For example, Fredericksen

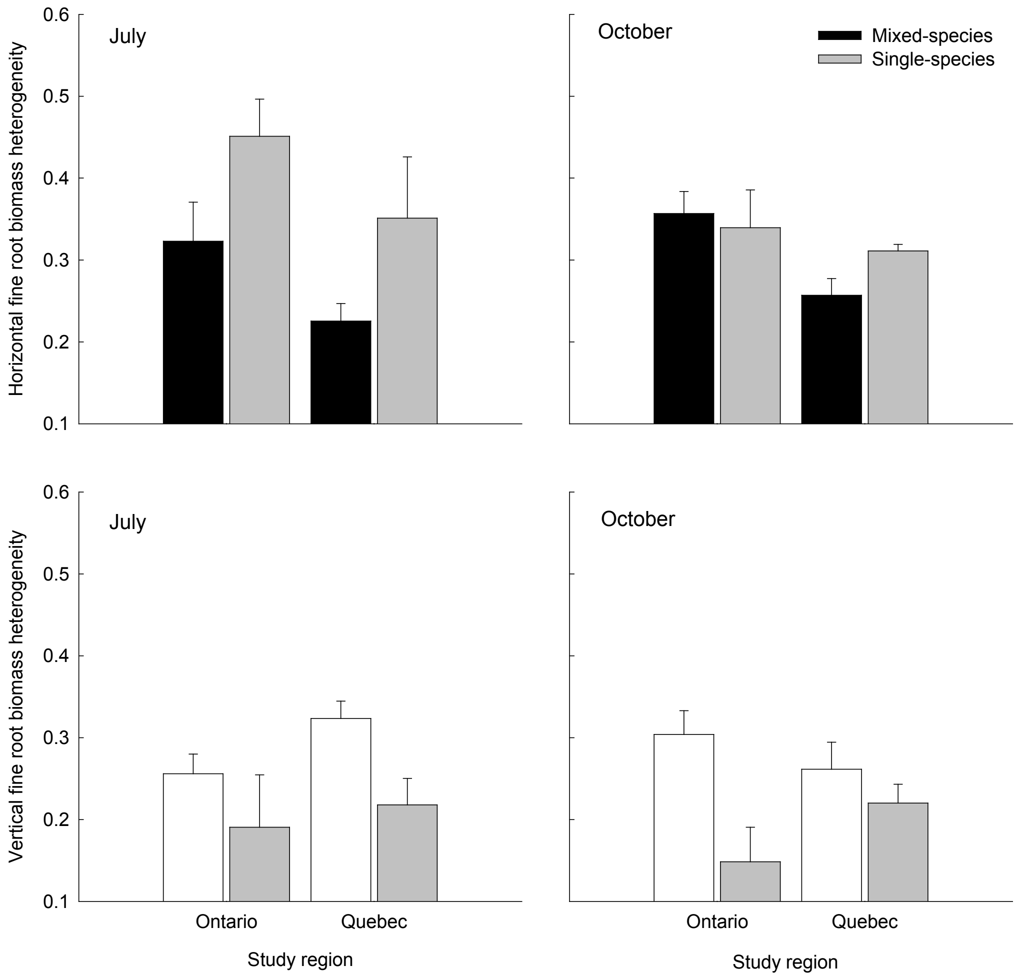

Figure 3.3. Horizontal and vertical fine root biomass heterogeneity (standard deviation of the seven soil cores within a stand and that of the three soil layers, respectively) by stand type (mixed-species and single-species), study region (Ontario and Quebec), and sampling period (July and October). Error bars represent 1 SEM.

and Zedaker (1995) found that *Pinus taeda* L. – *Robinia pseudoacacia* L. mixtures contained higher fine root biomass than relatively pure *P. taeda* stands. Similarly, Wang *et al.* (2002) reported that root biomass in *Tsuga heterophylla* (Raf.) Sarg. – *Thuja plicata* Donn ex D. Don mixtures was almost double that compared with single-species stands of *T. heterophylla* and *T. plicata*. By contrast, Leuschner *et al.* (2001) did not find a difference in fine root biomass

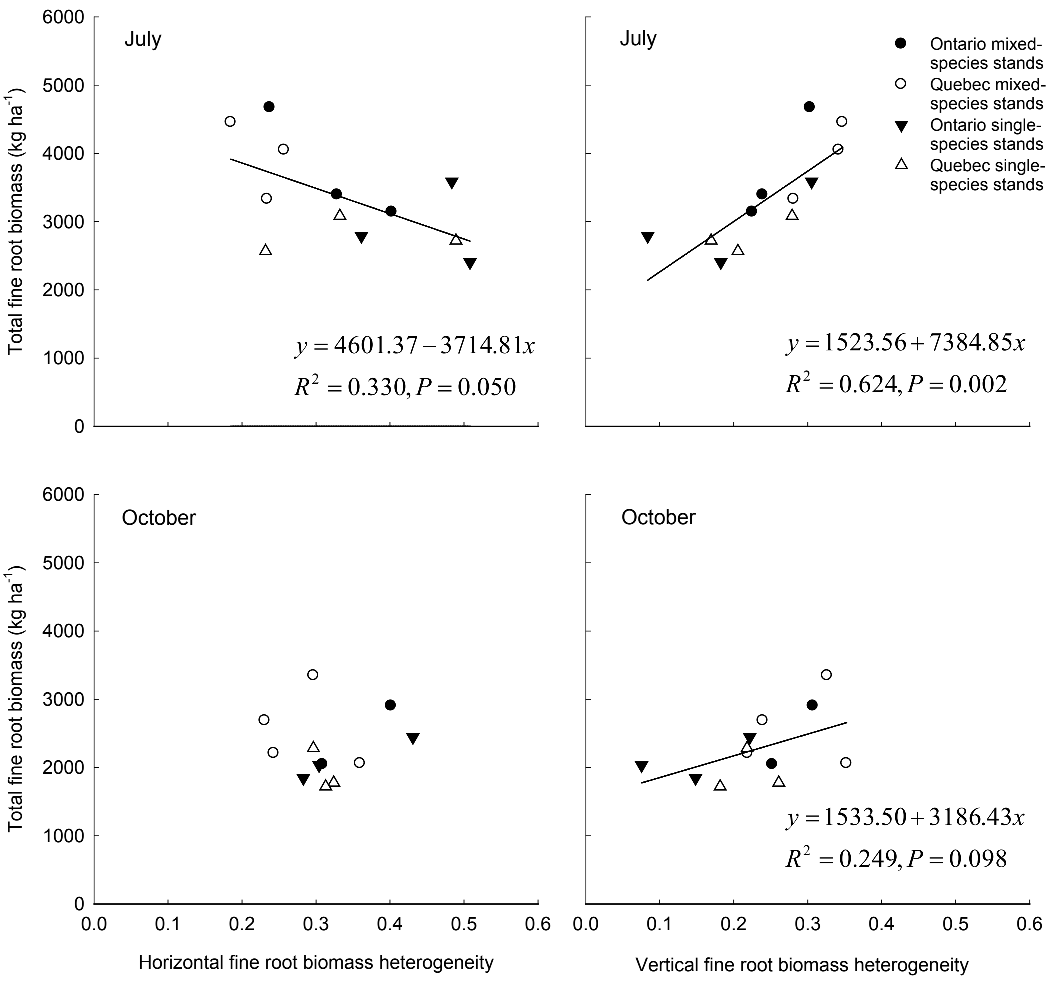

Figure 3.4. Relationship between total fine root biomass and horizontal and vertical fine root biomass heterogeneity (standard deviation of the seven soil cores within a stand and that of the three soil layers, respectively) in July and October, respectively.

between single- and mixed-species stands of *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. Likewise, Meinen *et al.* (2009) did not find a species diversity effect on fine root biomass between single- and mixed-species broadleaf stands. It would appear, therefore, that whether mixed-species stands can yield higher fine root productivity than single-species stands may depend on the presence of contrasting rooting traits among component species in mixture affecting the number of individuals that can occupy a stand and the magnitude to which the soil space and resources of a stand can be filled and used by the fine roots, respectively (Köstler *et al.* 1968; Brassard *et al.* 2009).

Evidence to support my second hypothesis is manifested by both the heterogeneity analyses and biomass plots. The lower July horizontal fine root biomass heterogeneity in mixed-species stands would appear to indicate that greater horizontal space filling is occurring in this stand type than single-species stands. The higher July and October vertical fine root biomass heterogeneity in mixed-species stands, attributable to the significantly higher fine root biomass in the FF layer in this stand type than single-species stands, suggests that the mixed-species stands allow for greater soil space filling of fine roots in this nutrient-rich layer than the single-species stands. Furthermore, since the biomass of *P. tremuloides* fine roots did not differ between stand types in the FF layer, this among stand type difference is largely the result of the higher *Picea* spp. and *A. balsamea* fine root biomass in the FF layer of the mixed-species stands compared to the non-tree fine root biomass in the FF layer of the single-species stands. These findings support the heterogeneity analyses that a certain amount of growing space is not being utilized by fine roots in single-species stands, so that total soil space filling and soil resource exploitation by fine roots is lower in single- than mixed-species stands.

Three of the four heterogeneity indices indicated a direct link between total fine root biomass and fine root biomass heterogeneity. This result suggests that fine root biomass heterogeneity, as an indicator of the total soil space filling of fine roots within a stand, may be a key driver for the observed below-ground productivity-plant diversity relationships found in this study, supporting the existence of below-ground niche differentiation in the mixed-species stands I studied. Furthermore, above-ground functional trait differences between *P. tremuloides* and *P.*

mariana, *P. glauca*, and *A. balsamea* (e.g., the more shade-tolerant *Picea* spp. and *A. balsamea*, with their narrow, conical-shaped crowns (Burns and Honkala 1990) may position themselves between the larger crowns of *P. tremuloides* despite the relatively closed canopy), in conjunction with their different rooting traits, may also be important for facilitating greater below-ground space filling and higher fine root productivity in the mixed- compared to single-species stands. However, these hypotheses must be tested in other forest and ecosystems types before any broader generalizations can be made.

Based on the results from both forest and grassland studies, it appears that contrasting and similar above- and below-ground diversity-productivity relationships can occur within the same plant communities. Although fine root productivity, for example, was found to be higher in the mixed- than single-species stands, the single-species stands were found to contain higher above-ground biomass than the mixed-species stands (Cavard *et al.* 2010). By contrast, Chen and Klinka (2003) reported that above-ground productivity did not differ between mixed- and single-species stands of *T. heterophylla* and *T. plicata*, whereas Wang *et al.* (2002) found that *T. heterophylla* and *T. plicata* mixtures contained higher root biomass than relatively pure *T. heterophylla* and *T. plicata* stands at the same sites. Furthermore, while Spehn *et al.* (2005), De Boeck *et al.* (2008), and Fornara and Tilman (2008) found that more diverse grassland communities contained greater above- and below-ground biomass than less diverse communities, Bessler *et al.* (2009) and Wacker *et al.* (2009) reported that above-ground biomass production was greater, but below-ground biomass production similar, in more than less diverse grassland communities. However, Hooper (1998) did not find a significant relationship between functional group diversity and above-ground or below-ground biomass production in a serpentine grassland. It is apparent, therefore, that certain functional trait differences between component species in mixture that promote below-ground over-yielding may not necessary do so above-ground, while the same is true regarding the expression of above- but not below-ground over-yielding. What still remains to be determined, however, is what functional trait differences are key to facilitating below-ground over-yielding, and which are important for above-ground over-yielding.

In summary, this study is one of the first to not only demonstrate a positive relationship between plant diversity and below-ground productivity in forest ecosystems that is unrelated to a selection effect, but also to present empirical evidence, through characterization of stand-level fine root biomass distributions, that below-ground niche differentiation is a key driver of higher fine root productivity in species mixtures with contrasting rooting traits in comparison to single-species stands. Given that the biodiversity effect on productivity can vary between natural and artificial systems (Flombaum and Sala 2008), future plant diversity-productivity studies should strive to study this process in natural ecosystems, despite the added challenges of separating selection from species complementarity effects that this approach presents.

CHAPTER FOUR SPECIES COMPLEMENTARITY INFLUENCES THE FINE ROOT DYNAMICS OF FOREST ECOSYSTEMS

INTRODUCTION

Experimental evidence from both grassland (e.g., Spehn *et al.* 2005; De Boeck *et al.* 2008; Fornara and Tilman 2008; Bessler *et al.* 2009; Marquard *et al.* 2009) and forest ecosystems (e.g., MacPherson *et al.* 2001; Wang *et al.* 2002; Vilà *et al.* 2003; Brassard *et al.* 2010; Varga *et al.* 2005) has shown that plant diversity has a positive effect on community productivity. Despite, however, the growing body of evidence linking plant diversity to productivity in terrestrial ecosystems, understanding the underlying causes of this relationship is still tenuous. Selection effects, where the probability of a plant community containing the most productive species increases with increasing diversity (Špaèková and Lepš 2001; Cardinale *et al.* 2006; Schmid *et al.* 2008), and ecological effects, have both been proposed as drivers for observed positive diversity-productivity relationships. In support of the second conjecture, the species complementarity hypothesis proposes that species mixtures can achieve higher productivity than monocultures if functional trait differences between the component species cause the growing environment to be more fully utilized by the plant community as a whole via either niche differentiation (where differences between species allow for differential use of resources in space or time) or facilitation (where certain characteristics of one or more species improve the conditions for growth of the others) (Tilman *et al.* 1997; Loreau and Hector 2001; Spehn *et al.* 2005; Marquard *et al.* 2009).

In the central boreal forest of North America, *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss, and *Abies balsamea* L. are all widespread in distribution on mesic sites (Rowe 1972). *Pinus banksiana* and

P. tremuloides are shade-intolerant coniferous and broadleaf species, respectively, and are both deep rooting with large, broadly-shaped crowns (Burns and Honkala 1990). By comparison, *P. mariana*, *P. glauca*, and *A. balsamea* are shade-tolerant conifers that are relatively shallow rooting and have narrow, conical-shaped crowns. *Pinus banksiana* and *P. tremuloides* also have higher rates of above- and below-ground growth than *P. mariana*, *P. glauca*, and *A. balsamea* (Burns and Honkala 1990).

As was first theorized by myself and my colleagues in our review on the dynamics of roots in northern forests (Brassard *et al.* 2009), and experimentally verified in our study on the productivity differences between single-species stands of *P. tremuloides* and mixed-species stands of *P. tremuloides*, *P. mariana*, *P. glauca*, and *A. balsamea* (Brassard *et al.* 2010), horizontal and vertical soil space filling of fine roots (≤ 2 mm in diameter) are key drivers for over-yielding in certain species mixtures compared to single-species stands of their component species. Therefore, the objective of this study was to further explore the link between fine root soil space filling and fine root productivity by examining in detail the seasonal patterns of fine root productivity and rooting distributions in relatively pure stands of *P. banksiana* and mixed stands of *P. banksiana* and *P. tremuloides* versus *P. banksiana*, *P. mariana*, *P. glauca*, and *A. balsamea*. I attempted to test: (1) whether the two mixed-species stand types had higher fine root productivity, measured by annual fine root production and total fine root biomass (live roots), than the single-species stands, i.e., over-yielding hypothesis and (2) the species complementarity hypothesis, i.e., that the differences in productivity between the mixed- and single-species stands was the result of greater soil space filling of fine roots due to the inherent functional trait differences between the component species in the two mixed-species stand types, i.e., differential rooting traits and crown structures in the stands of *P. banksiana*, *P. mariana*, *P. glauca*, and *A.*

balsamea (niche differentiation) versus increased nutrient availability as a result of greater annual litterfall of more nutrient-rich, easily-decomposable litter in the stands of *P. banksiana* and *P. tremuloides* (facilitation).

In this study, I took two approaches to avoid a potential selection effect in the stand type comparisons. First, by comparing the fine root productivity of single-species stands of the productive species *P. banksiana* with mixed stands of *P. banksiana* and the less productive species *P. mariana*, *P. glauca*, and *A. balsamea*, increases in the fine root productivity of the mixed stands would be attributable to the additive effects of the *P. mariana*, *P. glauca*, and *A. balsamea*. Secondly, by comparing the fine root productivity of mixed stands of two productive species, *P. banksiana* and *P. tremuloides*, to single-species stands of *P. banksiana*, a higher fine root productivity for the mixed stands in this case would indicate that the mixed stands are achieving higher fine root productivity than the single-species stands despite the similar productivities of the component species.

MATERIALS AND METHODS

Study Area

The study was conducted in the boreal forest north of Lake Superior and west of Lake Nipigon in the Upper English River (B. 11) Forest Region (Rowe 1972) approximately 150 km north of Thunder Bay, Ontario, Canada between 49º27’ N to 49º38’ N and 89º29’ W to 89º54’ W. The closest meteorological station is located in Thunder Bay, Ontario (48º 22’ N, 89º 19’ W, 199 m elevation). The study area has a moderately dry, cool climate with short summers. The average annual precipitation for Thunder Bay (1971-2000) is 712 mm and the average annual temperature is 2.5 ºC (Environment Canada 2010). Topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago. The natural stand-initiating disturbance of the area is predominately stand-replacing crown fire, which is the most common stand-replacing mechanism in the North American boreal forest (Johnson 1992).

Sampling

I selected, using forest resource inventory maps and random stratified sampling, nine mature, fire-origin stands (time since fire = 85 years) that belonged to one of three stand types: (1) relatively pure stands of *P. banksiana* (hereafter referred to as conifer stands) (n = 3), (2) stands containing mixtures of *P. banksiana* and *P. tremuloides* (hereafter referred to as mixedwood stands) (n = 3), and (3) stands containing mixtures of *P. banksiana*, *P. mariana, P. glauca*, and *A. balsamea* (hereafter referred to as mixed conifer stands) (n = 3). Mixedwood stands were selected to have relatively equal proportions by stand basal area of *P. banksiana* and *P. tremuloides*, while mixed conifer stands were selected to have relatively equal proportions of *P. banksiana* and *Picea* spp. + *A. balsamea* by stand basal area. By comparison, conifer stands were to have > 90% of *P. banksiana* by stand basal area. In mixedwood stands, the average percent basal area of *P. banksiana* and *P. tremuloides* was 49.2 and 47.1, respectively. In mixed conifer stands, the average percent basal area of *P. banksiana* and *Picea* spp. + *A. balsamea* was 59.6 and 40.4, respectively, while the average percent basal area of *P. banksiana* in conifer stands was 95.8 (Table 4.1).

To limit site variability, all stands were mesic and allocated on flat midslope positions, with no slope exceeding 5%, on well drained glacial moraines greater than 50 cm in thickness, which is the prevailing site type in the region. In the field, site condition was determined by topographic characteristics, and soil order and texture determined from a soil pit dug in the center of the plot. For all sites, soil order was Brunisolic and soil texture either sandy loam or

Table 4.1. Characteristics (mean and range) of study stands in northwestern Ontario, Canada. Each stand type was replicated three times.

Characteristic	Stand type		
	Conifer	Mixedwood	Mixed conifer
Stand volume (m^3 ha^{-1})*	304.9 (242.6-418.3)	332.1 (275.5-375.6)	328.0 (275.9-435.6)
Stand density (trees ha^{-1})	1,837 (1,525-2,400)	1,797 (1,300-2,375)	2,308 (1,700-2,625)
Shrub, herb, and moss biomass (kg ha^{-1})†	3,327 (1,138-5,060)	2,828 (1,366-3,901)	1,135 (239-2,243)
Annual litterfall (kg ha^{-1} $year^{-1}$)‡	2,273 (2,080-2,801)	2,574 (2,054-3,358)	2,239 (2,081-2,520)
Abies balsamea basal area (m^2 ha^{-1})	0.50 (0-1.49)	0	2.84 (0.75-4.93)
Picea glauca basal area (m^2 ha^{-1})	0	0	1.02 (0-3.06)
Picea mariana basal area (m^2 ha^{-1})	1.06 (0.64-1.37)	1.26 (0.84-2.05)	14.47 (11.41-17.92)
Pinus banksiana basal area (m^2 ha^{-1})	35.70 (28.79-41.75)	16.84 (13.41-23.22)	27.05 (23.95-30.54)
Populus tremuloides basal area (m^2 ha^{-1})	0	16.14 (9.65-21.88)	0

*Stand volume was determined using individual tree volumes that were summed to the plot level and scaled up to per ha. Individual tree volumes were estimated using the diameter at breast-height and height measurements and species-specific volume equations developed for tree species of central and eastern Canada (Honer *et al.* 1983).

†Shrub, herb, and moss biomass was determined by harvesting all above-ground components of each type in three randomly located 1 m^2 quadrates. All samples were then brought back to the laboratory, oven-dried for 48 hours at 65 °C, and weighed. Sample weights were pooled by plot and scaled up to per ha.

‡Annual litterfall was determined at each site by collecting litter (e.g., foliage, bark, twigs < 2 cm diameter) from four mesh-covered rectangular litter traps (0.94 m^2) from May 2006 to May 2008. All samples were brought back to the laboratory, oven-dried for 48 hours at 65 °C, and weighed. Sample weights were then pooled by plot, scaled up to per ha, and divided by two (since sampling occurred over a two-year period).

sandy clay loam (Sims *et al.* 1997). All selected stands were > 1 ha in area and were visually homogeneous in structure and composition.

Within each stand, stand type classification was verified by measuring overstory characteristics in a randomly allocated 400 m^2 circular plot, where no trees had survived from the last fire. The diameter at breast-height (DBH) (1.3 m above the root collar), height, and species of all trees (DBH ≥ 2 cm) within the plot were measured and recorded. Stand basal area by species was summed to plot level and scaled up to per ha. Stand density was lower in the conifer and mixedwood stands than the mixed conifer stands, whereas annual litterfall was higher in the mixedwood stands than the other two stand types (Table 4.1).

Within each plot, seven soil cores (6.75 cm diameter) were randomly extracted from the forest floor surface to a mineral soil depth of 30 cm using a power auger each month during the 2007 growing season (early May to late October). Fine root production during the non-growing season was assumed to be negligible (Burke and Raynal 1994; Haynes and Gower 1995; Steele *et al.* 1997). To facilitate extraction by layers, and to minimize compaction during coring, I extracted the forest floor layer (FF) and two mineral soil sections: MS1 (0-15 cm) and MS2 (15-30 cm), subsequently after removing the upper layer.

Soil core sections were transported in an ice-filled cooler from the field to the laboratory and stored in a deep freeze until processing. Thawed samples were soaked in water to separate roots from soil, and then hand sorted to remove visible roots and coarse fragments. Roots > 2 mm, determined using calipers, and coarse fragments were discarded. The remaining material was then gently washed over a 0.5 mm sieve to remove remaining root fragments. Roots < 0.5 mm that were not identified during hand sorting were considered a component of the soil and were not included. Remaining root fragments were rinsed with water and sorted according to vitality class, i.e., live versus dead. Roots were considered ‘live’ if they were pale-colored on the exterior, elastic and flexible, and free of decay with a whitish cortex, while roots were classified as ‘dead’ if they were brown or black in color, rigid and inflexible, in various stages of decay, and had a dark colored cortex (Persson 1983; Bennett *et al.* 2002).

Live fine roots were further divided into the following species classes: (1) *P. banksiana*, (2) *P. tremuloides*, (3) *Picea* spp. and *A. balsamea*, and (4) non-tree (shrubs and herbs) using a combination of morphological characteristics. These included: (1) color (*P. tremuloides* and non-tree roots were more white or yellow in color, while conifer roots were more red or brown in color), (2) size (*Picea* spp. and *A. balsamea* and non-tree roots were generally finer structured than those of *P. tremuloides* and *P. banksiana*), (3) branching angle (approximately 90° for conifer roots and 45° for *P. tremuloides* and non-tree roots), (4) branching pattern (sections of *Picea* spp. and *A. balsamea* and non-tree roots were more highly branched than those of *P. tremuloides* and *P. banksiana*), and (5) presence or absence of root hairs (non-tree roots contained small hairs that were not present on tree roots). These criteria were developed previous to root sorting using samples of known origin from the study sites. The fine roots were then oven-dried to a constant mass at 65 °C and weighed.

I also installed ten ingrowth cores (6.75 cm diameter, 30 cm length) at each site (Steele *et al.* 1997; Hendricks *et al.* 2006). A power auger was again used to drill holes at each site. A plastic mesh core (hole size = 3 mm) was then inserted into each hole, filled with root-free soil (medium-textured sand), covered with leaf litter, and marked by a steel rod. All ingrowth cores were installed in October 2007 and removed after one calendar year. Roots were separated from the soil, dried, and weighed as described above, with the exception that roots were not separated by soil layer or species class. No roots > 2 mm in diameter were present in any of the ingrowth cores.

Ten decomposition bags (15 cm × 15 cm) were also installed at each site in October 2008. Bags were constructed of nylon mesh and had a hole size of 1 mm. Each bag was filled with approximately 3 g of fine roots (mean = 3.10 g, standard deviation = 0.04 g) that had been dried to constant mass at 65 °C. The root material used to fill the bags was a mixture of *P. banksiana*, *P. tremuloides*, *Picea* spp. and *A. balsamea*, and non-tree fine roots that had been extracted during soil coring. To bury a bag, I sliced down through the soil at a 45° angle to a depth of 15 cm using a sharp knife, and slid the bag into the incision. Because the incision was narrow, bags would have had relatively good contact with the soil. The location of each bag was then marked by a steel rod. All bags were removed after one calendar year, and the remaining root material in each bag was then separated from any soil that may have adhered to the roots as described above, dried to constant mass at 65 °C, and weighed.

Soil characteristics were determined at each site by excavating four randomly located volumetric soil samples from the FF layer and four from the MS1 layer (approximately 450 cm^3 each) in June 2007. Total nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) ($mg\ g^{-1}$) were determined using the methods described in Laganière *et al.* (2009). Available P, K, Ca, and Mg ($mg\ kg^{-1}$) were determined following extraction with 0.1 M barium chloride ($BaCl_2$) and atomic absorption spectro-photometry (Perkin Elmer 5100 PC) (Carter 1993). Moisture content (%) was found by taking the difference in sample weight before and after drying to constant mass at 65 °C.

Data Analysis

Total fine root biomass and necromass (dead roots) (kg ha^{-1}) was calculated for each sampling date (May, June, July, August, September, and October) at each site by summing the dry weight of live and dead fine roots, respectively, in each soil core and scaling up to per ha. Annual fine root production (kg ha^{-1} $year^{-1}$) was then calculated by (1) determining all changes in total fine root biomass and necromass between sampling dates, whether or not significantly different, using a decision matrix (decision matrix method) (Mcclaugherty *et al.* 1982; Hendricks *et al.* 2006) and (2) calculating the difference between total July and October fine root biomass (minimum-maximum method). These two sampling dates were found to generally be the timings of maximum and minimum fine root biomass, respectively (cf., section three of the results). Annual fine root production based on the ingrowth core method was calculated at each site by summing the dry weight of live and dead roots in each ingrowth core and scaling up to per ha. Annual fine root mortality (kg ha^{-1} $year^{-1}$) was also determined by calculating changes in total fine root biomass and necromass between sampling dates using the same decisions matrix for calculating annual fine root production. The annual percent mass loss of fine roots at each site, as an estimate of annual fine root decomposition, was found by taking the difference between the average initial and average final mass of fine roots among the ten decomposition bags and dividing by the average initial mass.

Similar to Brassard *et al.* (2010), I used a heterogeneity index to characterize stand-level horizontal and vertical fine root biomass distributions as an indicator of how fully below-ground growing space was being utilized within each stand. Horizontal fine root biomass heterogeneity was calculated as the standard deviation of the fine root biomass values of all soil layers combined among the seven soil cores at each site for all sampling dates. Vertical fine root biomass heterogeneity was calculated for all sampling dates as the standard deviation of the fine root biomass values among the three soil layers averaged from all soil cores. A higher standard deviation value would imply that fine root biomass is less evenly distributed, i.e., more heterogeneous, among the soil cores or soil layers, respectively.

To determine if soil characteristics, annual fine root production and mortality, and the percent annual loss of fine root mass differed with stand type, I used the following general linear model (eq. 4.1):

$$[4.1] \quad Y_{ij} = \mu + T_i + \varepsilon_{(i)j}$$

where Y_{ij} is the dependent variable of interest, μ is the overall mean, T_i is stand type (i = 1, 2, 3), and $\varepsilon_{(i)j}$ is the random error. The following general linear model, however, was used to determine if total fine root biomass and necromass, the biomass of fine roots by soil layer, and horizontal and vertical fine root biomass heterogeneity differed with stand type and sampling date (eq. 4.2):

$$[4.2] \quad Y_{ijk} = \mu + T_i + D_j + T \times D_{ij} + \varepsilon_{(ij)k}$$

where Y_{ijk} is the dependent variable of interest, μ is the overall mean, T_i is stand type (i = 1, 2, 3), D_j is sampling date (j = 1, 2, 3, 4, 5, 6), $T{\times}D_{ij}$ is the stand type – sampling date interaction, and $\varepsilon_{(ij)k}$ is the random error. Tukey's contrasts were performed following eq. 4.1 and 4.2 tests when effects were significant ($\alpha = 0.05$).

To determine how total fine root biomass and necromass and horizontal and vertical fine root biomass heterogeneity for each stand type differed with sampling date, polynomial regression analyses were conducted using the following model (eq. 4.3):

$$[4.3] \quad I' = b_o + b_1 D + b_2 D^2 + b_3 D^3 + b_4 D^4$$

where I' is the dependent variable of interest, b_i are coefficients, and D is the sampling date in months. To facilitate the regression analyses, each sampling date was assigned a numerical value

(May = 1, June = 2, July = 3, August = 4, September = 5, and October = 6) so that sampling date could be treated as a continuous variable. Insignificant predictor variables were removed from eq. 4.3 using a backward stepwise procedure with a critical $\alpha = 0.10$. Normality and homogeneous variances were confirmed following Kutner *et al.* (2005), and all analyses were performed using SPSS® version 16.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Soil Characteristics

Total Ca and Mg in the FF layer were significantly affected by stand type, while total N and moisture content were marginally affected ($\alpha = 0.10$) (Table 4.2). Total N, Ca, and Mg were lower in mixed conifer and conifer stands than mixedwood stands, whereas moisture content was highest in mixed conifer and lowest in conifer stands with mixedwood stands intermediate (Figure 4.1). Neither total P nor K differed significantly with stand type (Table 4.2, Figure 4.1). Available Ca and Mg, however, were the only soil characteristics that differed significantly or marginally significantly between stand types in the MS1 layer (Table 4.2). Both exchangeable Ca and Mg were lower in mixed conifer and conifer stands than mixedwood stands (Figure 4.1). Total N, available P and K, and moisture content, by contrast, were similar among the three stand types (Table 4.2, Figure 4.1).

Fine Root Production, Mortality, and Decomposition

All three sampling methods, i.e., decision matrix, minimum-maximum, and ingrowth core methods, indicated that annual fine root production differed significantly or marginally significantly with stand type (Table 4.3). According to the decision matrix method, annual fine root production was highest in the mixedwood stands, lowest in the conifer stands, and intermediate in the mixed conifer stands, whereas the minimum-maximum and ingrowth core

Table 4.2. The effects of stand type on soil characteristics in the FF and MS1 layers.

Soil characteristic*	R^2	*df*	MS	F	P
FF layer					
Total N	0.557	2, 6	14.248, 3.781	3.769	**0.087**
Total P	0.255	2, 6	0.027, 0.026	1.025	0.414
Total K	0.202	2, 6	0.029, 0.039	0.761	0.508
Total Ca	0.893	2, 6	31.422, 1.249	25.163	**0.001**
Total Mg	0.867	2, 6	0.530, 0.027	19.476	**0.002**
Moisture content	0.600	2, 6	126.805, 28.133	4.507	**0.064**
MS1 layer					
Total N	0.347	2, 6	0.136, 0.085	1.593	0.279
Available P	0.185	2, 6	27.283, 40.144	0.680	0.542
Available K	0.508	2, 6	172.718, 55.665	3.103	0.119
Available Ca	0.689	2, 6	32,352.8, 4,858.2	6.659	**0.030**
Available Mg	0.856	2, 6	1,798.3, 100.7	17.857	**0.003**
Moisture content	0.377	2, 6	19.763, 10.903	1.813	0.242

*Abbreviations: N = nitrogen, P = phosphorus, K = potassium, Ca = calcium, and Mg = magnesium.

methods both indicated that annual fine root production was lower in conifer stands than the other two stand types (Figure 4.2). Both annual fine root mortality and the annual percent mass loss of fine roots, however, was highest in the mixedwood stands followed by the conifer than mixed conifer stands (Table 4.3, Figure 4.2).

Fine Root Biomass and Necromass

Total fine root biomass and necromass both differed significantly with stand type and sampling date (Table 4.3). July and September total fine root biomass were higher in mixed conifer and mixedwood stands than conifer stands, while August and October total fine root biomass were highest in mixed conifer stands, intermediate in mixedwood stands, and lowest in conifer stands (Figure 4.3). Mixedwood stands, however, had the highest June total fine root biomass, followed by mixed conifer than conifer stands, whereas total fine root biomass was

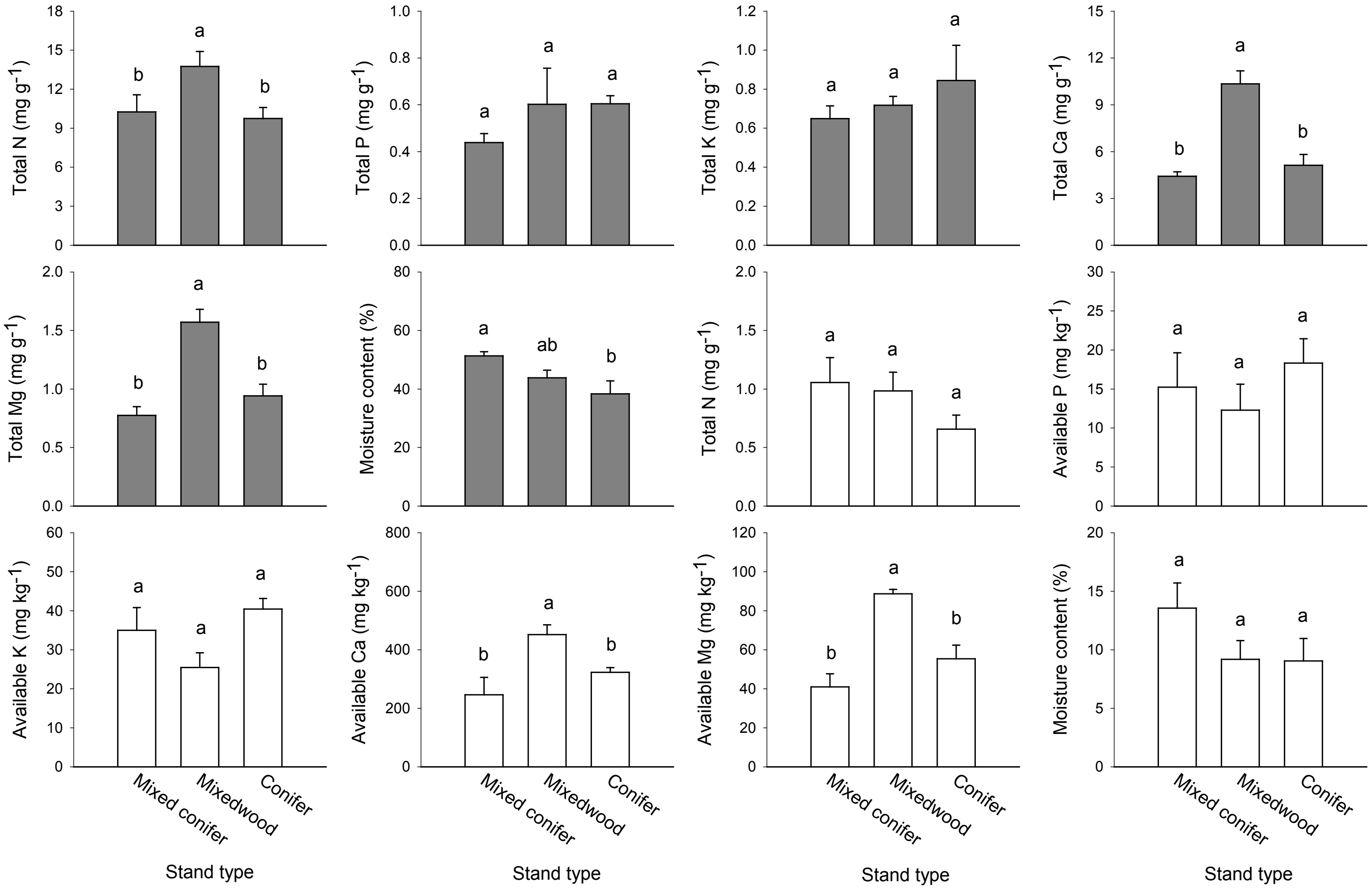

Figure 4.1. Soil characteristics by stand type (mixed conifer, mixedwood, and conifer) and soil layer (FF = filled bars and MS1 = empty bars). Abbreviations are N = nitrogen, P = phosphorus, K = potassium, Ca = calcium, and Mg = magnesium. Error bars represent 1 SEM.

Table 4.3. The effects (P-values) of stand type (*T*) on annual fine root production, mortality, and percent mass loss and stand type and sampling date (*D*) on the total biomass and necromass of fine roots, the biomass of fine roots by soil layer, and horizontal and vertical fine root biomass heterogeneity, respectively. See Appendix II for the *df*, MS, and F values.

Characteristic	R^2	Source*		
		T	*D*	*T*×*D*
Annual fine root production				
Decision matrix method	0.585	**0.072**		
Minimum-maximum method	0.720	**0.022**		
Ingrowth core method	0.645	**0.045**		
Annual fine root mortality	0.560	**0.085**		
Percent annual fine root mass loss	0.660	**0.039**		
Total fine root biomass	0.778	**<0.001**	**<0.001**	0.304
Fine roots biomass in FF layer	0.769	**<0.001**	**<0.001**	**0.017**
Fine root biomass in MS1 layer	0.670	**<0.001**	**<0.001**	0.227
Fine root biomass in MS2 layer	0.686	**<0.001**	**<0.001**	0.352
Total fine root necromass	0.667	**<0.001**	**<0.001**	0.468
Horizontal fine root biomass heterogeneity	0.636	**<0.001**	**<0.001**	0.349
Vertical fine root biomass heterogeneity	0.641	**<0.001**	**0.047**	**0.012**

*Source is explained in eqs. 4.1 and 4.2.

similar between the three stand types in May. Total fine root necromass in June, September, and October were lower in conifer stands than the other two stand types, while total fine root necromass in May was highest in mixed conifer stands, intermediate in mixedwood stands, and lowest in conifer stands (Figure 4.3). However, all three stand types had similar total fine root necromass in July and August. Regardless of stand type, total fine root biomass and necromass followed inverse U- and U-shaped trends with sampling date, respectively (Table 4.4, Figure 4.4).

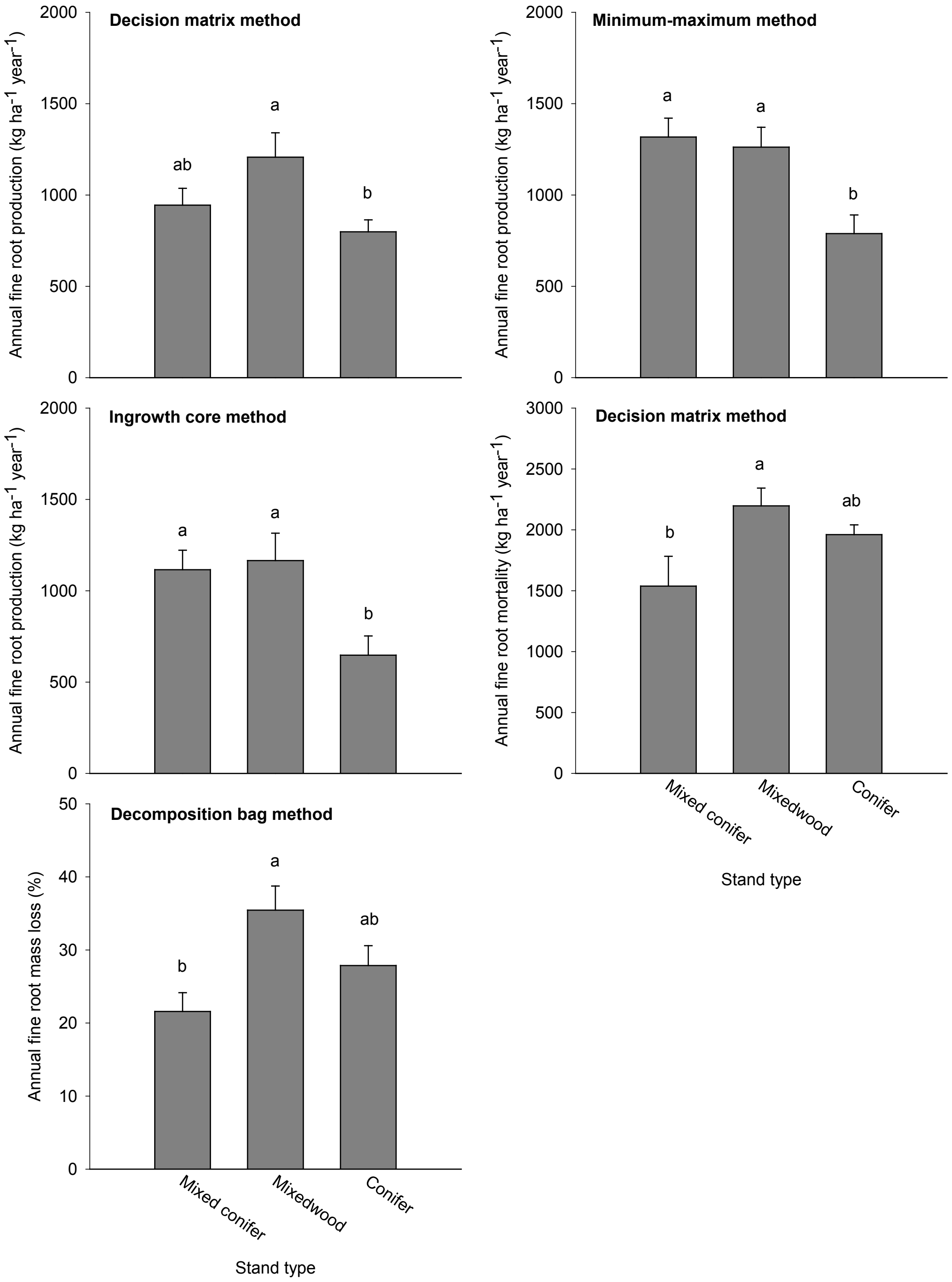

Figure 4.2. Annual fine root production, mortality, and percent mass loss by stand type (mixed conifer, mixedwood, and conifer) and sampling method (decision matrix method, minimum-maximum method, ingrowth core method, and decomposition bag method). Error bars represent 1 SEM.

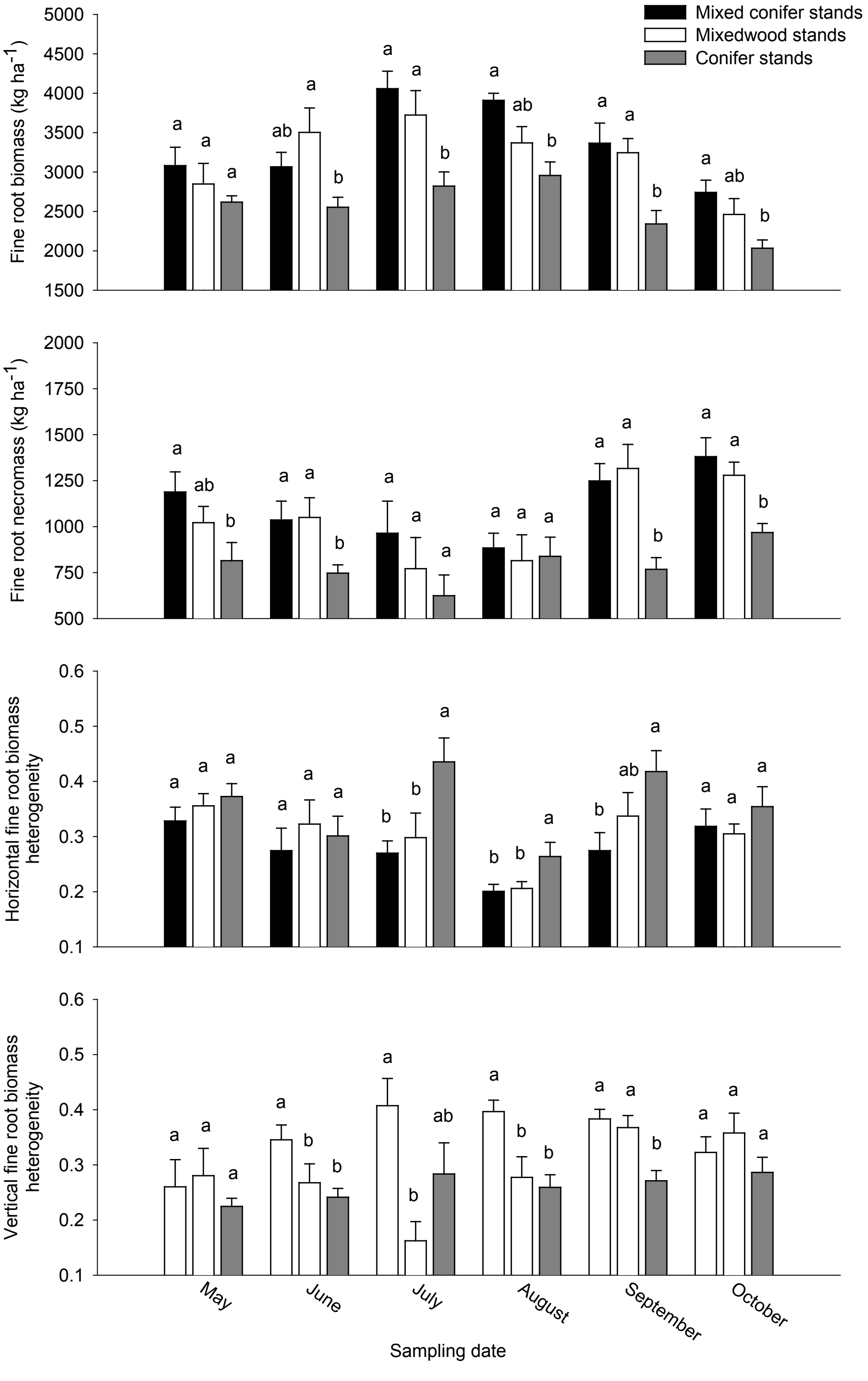

Figure 4.3. The biomass and necromass of fine roots and horizontal and vertical fine root biomass heterogeneity (standard deviation of the seven cores within a stand and that of the three layers, respectively) by stand type (mixed conifer stands, mixedwood stands, and conifer stands) and sampling date (May, June, July, August, September, and October). Tukey's contrasts were performed independently for each sampling date. Error bars represent 1 SEM.

Table 4.4. The effects of sampling date (*D*) on total fine root biomass and necromass and horizontal and vertical fine root biomass heterogeneity in mixed conifer, mixedwood, and conifer stands.

Characteristic	R^2	*df*	MS	F	P	Source*				Regression equation
						D		D^2		
						t	P	t	P	
Total fine root biomass										
Mixed conifer stands	0.563	2, 15	1,525,831.0, 157,661.6	9.678	0.002	4.178	**0.001**	-4.371	**0.001**	$I'=1934.38+1120.86D-164.01D^2$
Mixedwood stands	0.554	2, 15	1,514,087.2, 162,686.7	9.307	0.002	3.612	**0.003**	-4.018	**0.001**	$I'=2067.66+984.52D-153.14D^2$
Conifer stands	0.544	2, 15	654,874.6, 73,319.8	8.932	0.003	2.711	**0.016**	-3.316	**0.005**	$I'=2104.04+495.98D-84.85D^2$
Total fine root necromass										
Mixed conifer stands	0.458	2, 15	228,451.0, 36,119.0	6.325	0.010	-2.744	**0.015**	3.148	**0.007**	$I'=1492.48-352.35D+56.54D^2$
Mixedwood stands	0.361	2, 15	236,031.7, 55,710.8	4.237	0.035	-1.805	**0.091**	2.233	**0.041**	$I'=1294.10-287.88D+49.81D^2$
Conifer stands	0.296	2, 15	65,942.9, 20,880.7	3.158	0.072	-1.674	0.115	2.022	**0.061**	$I'=946.42-163.48D+27.61D^2$
Horizontal fine root biomass heterogeneity										
Mixed conifer stands	0.394	2, 15	0.012, 0.002	4.876	0.023	-3.120	**0.007**	3.083	**0.008**	$I'=0.423-0.104D+0.014D^2$
Mixedwood stands	0.220	2, 15	0.009, 0.004	2.121	0.154	-1.979	**0.066**	1.821	**0.089**	$I'=0.439-0.087D+0.011D^2$
Conifer stands	0.003	2, 15	0.001, 0.007	0.047	0.830	0.218	0.830			$I'=0.349+0.002D$
Vertical fine root biomass heterogeneity										
Mixed conifer stands	0.511	2, 15	0.023, 0.003	7.827	0.005	3.871	**0.002**	-3.621	**0.003**	$I'=0.139+0.141D-0.018D^2$
Mixedwood stands	0.384	2, 15	0.025, 0.005	4.676	0.026	-1.548	0.143	2.054	**0.058**	$I'=0.338-0.077D+0.014D^2$
Conifer stands	0.147	2, 15	0.006, 0.002	2.761	0.116	1.662	0.116			$I'=0.224+0.011D$

*Source is explained in eq. 4.3.

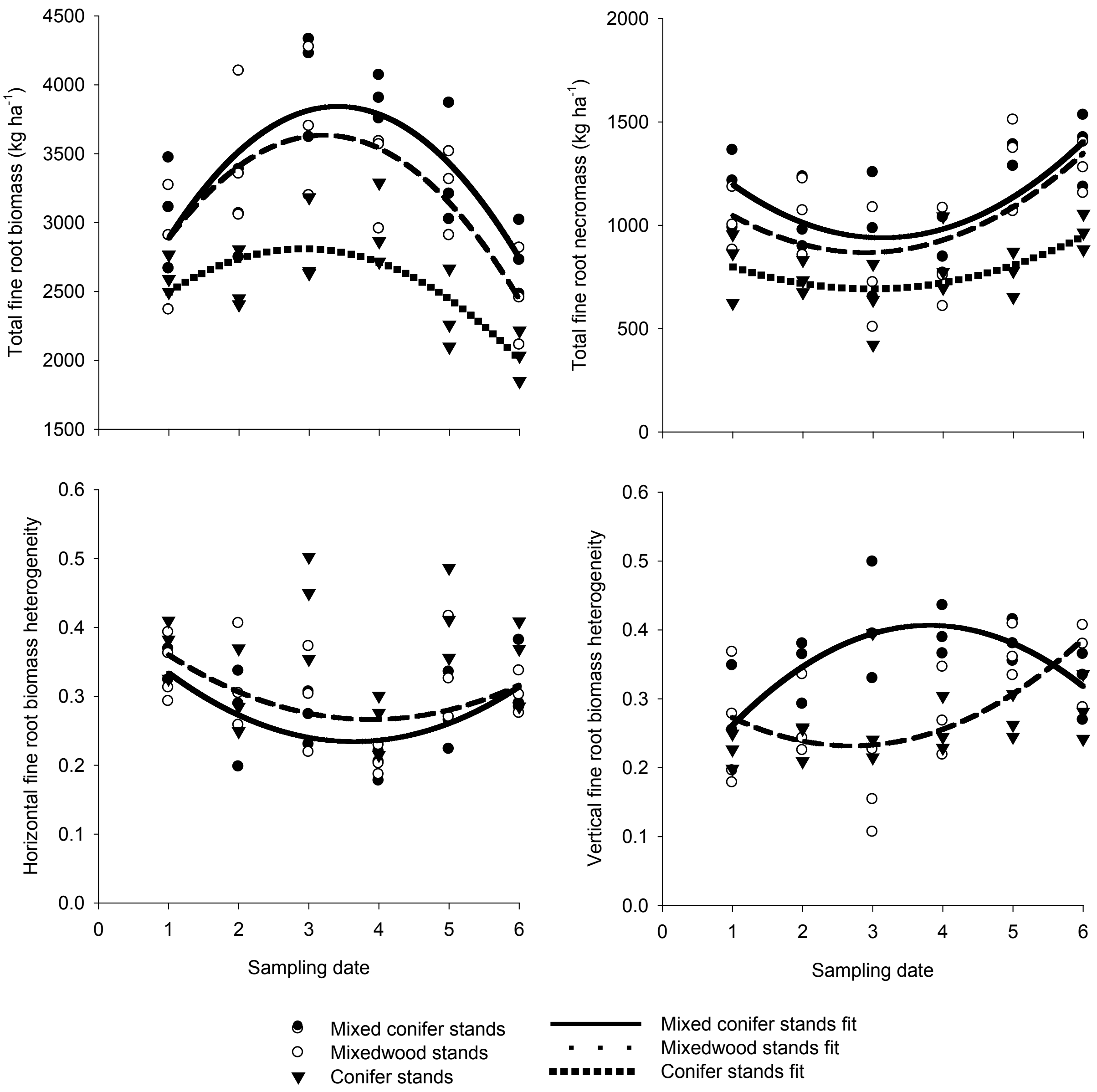

Figure 4.4. Relationship between sampling date (1 = May, 2 = June, 3 = July, 4 = August, 5 = September, and 6 = October) and total fine root biomass, total fine root necromass, horizontal fine root biomass heterogeneity (standard deviation of the seven cores within a stand) and vertical fine root biomass heterogeneity (standard deviation of the three soil layers within a stand) in mixed conifer, mixedwood, and conifer stands. See Table 4.4 for the regression equations.

Fine root biomass differed significantly with stand type and sampling date in the FF, MS1, and MS2 layer (Table 4.3). In May, July, and September, fine root biomass in the FF layer was highest in mixed conifer stands, intermediate in mixedwood stands, and lowest in conifer stands (Figure 4.5). By comparison, mixed conifer and mixedwood stands had higher fine root biomass in the FF layer in June than conifer stands, while fine root biomass in the FF layer in August was higher in mixed conifer stands than the other two stand types. However, fine root biomass was similar among the three stand types in October. In the MS1 layer, fine root biomass in July, August, and September was higher in mixed conifer and mixedwood stands than conifer stands, whereas fine root biomass in June was highest in mixedwood stands, followed by mixed conifer than conifer stands. Fine root biomass in the MS1 layer in October, however, was higher in mixed conifer than mixedwood and conifer stands, while all three stand types had similar fine root biomass in May (Figure 4.5). Although mixedwood stands had higher fine root biomass in the MS2 layer in July, August, September, and October than mixed conifer and conifer stands, mixed conifer stands had similar fine root biomass as conifer stands in July and August, lower fine root biomass in September, and higher fine root biomass in October. By contrast, all three stand types had similar fine root biomass in the MS2 layer in May and June (Figure 4.5).

Fine Root Spatial Biomass Heterogeneity

Both horizontal and vertical fine root biomass heterogeneity differed significantly with stand type and sampling date (Table 4.3). July and August horizontal fine root biomass heterogeneity were similar in mixed conifer and mixedwood stands but higher in conifer stands, while September horizontal fine root biomass heterogeneity was highest in conifer stands, lowest in mixed conifer stands, and intermediate in mixedwood stands (Figure 4.3). Vertical fine root biomass heterogeneity in June and August were similar in mixedwood and conifer stands but

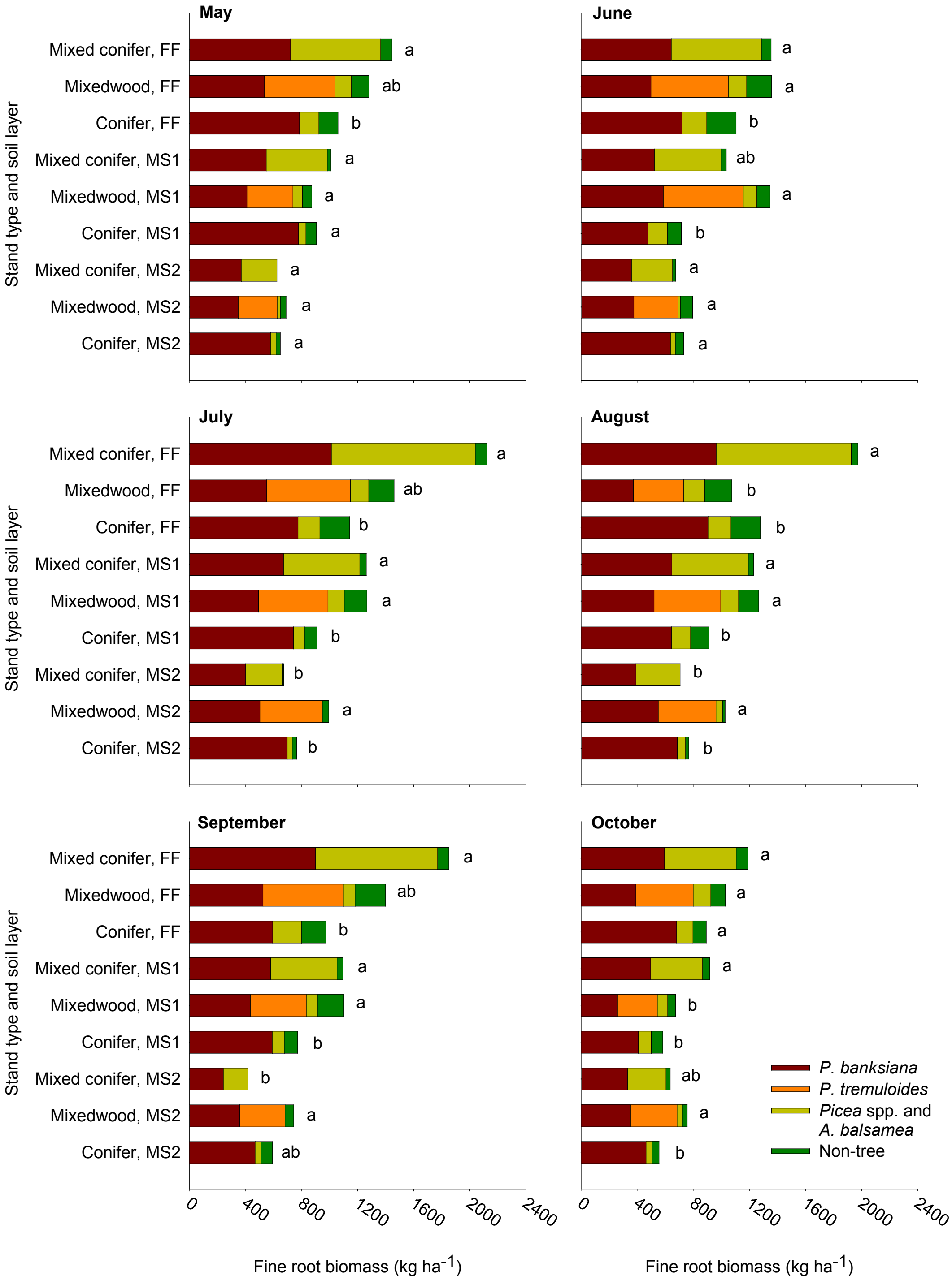

Figure 4.5. The biomass of fine roots by species class (*Pinus banksiana*, *Populus tremuloides*, *Picea* spp. and *Abies balsamea*, and non-tree), stand type (mixed conifer, mixedwood, and conifer), soil layer (FF, MS1, and MS2), and sampling date (May, June, July, August, September, and October). Tukey's contrasts were performed independently for the sum of fine root biomass of all species classes in each soil layer for each sampling date.

higher in mixed conifer stands (Figure 4.3). July vertical fine root biomass heterogeneity was highest in mixed conifer stands, followed by conifer than mixedwood stands, whereas September vertical fine root biomass heterogeneity was lower in conifer stands than the other two stand types. Horizontal fine root biomass heterogeneity in May, June, and October, and vertical fine root biomass heterogeneity in May and October, by contrast, were similar among the three stand types, respectively (Figure 4.3).

In mixed conifer and mixedwood stands, horizontal fine root biomass heterogeneity followed a U-shaped trend with sampling date, but did not differ with sampling date in the conifer stands (Table 4.4, Figure 4.4). By contrast, vertical fine root biomass heterogeneity in the mixed conifer stands followed an inverse U-shaped trend with sampling date, a U-shaped trend with sampling date in the mixedwood stands, and did not differ with sampling date in the conifer stands (Table 4.4, Figure 4.4).

DISCUSSION

Stand Type Effect on Fine Root Dynamics

In support of my first hypothesis, fine root productivity, measured by annual fine root production and total fine root biomass, was higher in both mixed-species stand types than the single-species stand type (except in May, where all three stand types had similar total fine root biomass). In support of my second hypothesis, the differences in fine root productivity between the mixed- and single-species stands appear to be driven by functional trait differences between the component species of the two mixed-species stand types promoting greater soil space filling of fine roots than the single-species stands. Furthermore, the results of the soil analysis, heterogeneity analysis, and biomass plots strongly suggest that different species complementarity mechanisms are driving below-ground over-yielding in the mixed conifer and mixedwood stands than the conifer stands.

Compared to the conifer stands, mixed conifer stands had lower horizontal fine root biomass heterogeneity in July, August, and September, and greater vertical fine root biomass heterogeneity for all sampling dates besides May and October. Furthermore, fine root biomass was higher in mixed conifer than conifer stands in the FF and MS1 layers for all sampling dates but October and May, respectively, whereas mixed conifer stands in the MS2 layer had marginally lower fine root biomass than conifer stands in September, marginally higher fine root biomass in October, and similar fine root biomass for all other sampling dates. Therefore, the heterogeneity and biomass differences between these two stand types appear to be attributable to the greater ability of the *P. banksiana*, *Picea* spp., and *A. balsamea* fine roots to collectively fill the upper soils layers in the mixed conifer stands than the *P. banksiana* and non-tree fine roots in the conifer stands. This strongly suggests that the differences in rooting traits and crown structures between the *P. banksiana* and *P. mariana*, *P. glauca*, and *A. balsamea*, as a form of niche differentiation (allowing the *P. mariana*, *P. glauca*, and *A. balsamea* to ‘fit’ between the *P. banksiana* in the mixed conifer stands and increase tree density relative to the conifer stands), has resulted in soil space being more fully occupied by fine roots, and higher fine root productivity, in the mixed conifer than conifer stands. Similarly, Brassard *et al.* (2010) found that *P. tremuloides* – *Picea* spp. – *A. balsamea* stands had higher fine root productivity, lower horizontal fine root biomass heterogeneity, and higher vertical fine root biomass heterogeneity than relatively pure *P. tremuloides* stands in the study area. They also attributed this to greater fine root space filling in the upper soil layers among the mixed- than single-species stands due to the contrasting rooting traits and crown structures of *P. tremuloides* versus *P. mariana*, *P. glauca*, and *A. balsamea*.

Mixedwood stands, by contrast, had higher horizontal fine root biomass heterogeneity in July, August, and September than conifer stands (while other sampling dates were similar), whereas vertical fine root biomass heterogeneity did not differ significantly between the two stand types for any sampling date except September (where conifer stands were lower than mixedwood stands). Similar to the mixed conifer stands, these results suggest that the mixedwood stands also had greater space filling of fine roots compared to the conifer stands. However, as vertical fine root biomass heterogeneity, stand density, and the distribution of fine root biomass by soil layer were relatively similar between the mixedwood and conifer stands, and since *P. banksiana* and *P. tremuloides* have comparable rooting traits, growth rates, and crown structures, it is doubtful that the higher fine root productivity of the mixedwood stands is attributable to niche differentiation via rooting trait and crown structural differences between the component species. Instead, I suggest that the rapidly-decomposable, nutrient-rich, deciduous foliage of *P. tremuloides*, relative to the more slowly-decomposable, nutrient-poor, longer-lived foliage of *P. banksiana*, has caused mixedwood stands to have greater nutrient availability than conifer stands (facilitated by greater soil microbial and arthropod activity), a fact which was confirmed by the soil analysis. This in turn, may have resulted in a greater density of nutrient-rich soil patches and a greater availability of nutrients at greater soil depths, in the mixedwood than conifer stands, which would have promoted greater soil space filling of fine roots throughout the stand and contributed to the fine root productivity differences between these two stand types.

Further evidence that the activity of soil microbes and arthropods was higher in mixedwood than conifer stands comes from the observed higher fine root decomposition rates, measured by the percent mass loss of fine roots in the decomposition bags, in the mixedwood than conifer stands. Higher fine root decomposition rates in broadleaf-dominated and mixed broadleaf-conifer stands than conifer-dominated stands have also been documented in other boreal studies (Finér *et al.* 1997). Additionally, the fact that mixedwood stands had higher annual fine root mortality than conifer stands suggests that fine roots were overall more shorter-lived in the mixedwood than conifer stands (either because broadleaf species like *P. tremuloides* have shorter overall fine root life spans than conifers such as *P. banksiana* (Black *et al.* 1998; Coleman *et al.* 2000), or because herbivory-related losses of fine roots may have been greater in the mixedwood than conifer stands). Therefore facilitation, via higher nutrient availability resulting from the *P. tremuloides* litterfall and overall shorter fine root life spans appear to be responsible for the greater space filling of fine roots and fine root productivities in the mixedwood than conifer stands. Similarly, Fornara and Tilman (2008) reported that mixtures of legumes and C4 grasses in a grassland experiment had higher fine root productivity than legume and C4 grass monocultures because of higher N availability.

Seasonal Patterns of Fine Root Dynamics

Similar to other studies of temperate forests with distinct growing and non-growing seasons (e.g., Steele *et al.* 1997; Burton *et al.* 2000; Tierney and Fahey 2001; Konôpka *et al.* 2005), total fine root biomass followed an inverse U-shaped pattern with sampling date (i.e., highest in the summer and lower in spring and fall), while total fine root necromass followed a U-shaped pattern (i.e., lowest in the summer and higher in spring and fall) in all three stand types, respectively. These findings support the generally accepted theory that maximum standing fine root biomass occurs during the summer when temperatures are optimal for growth and the plant's demand for nutrients and water is at its greatest (Brassard *et al.* 2009). Furthermore, as maintaining a large network of fine roots over the winter would be a large carbon and nutrient cost for the plant (as the low temperatures restrict its ability to photosynthesize and offset the costs of maintaining roots over the winter), standing fine root biomass is expected to be low in the fall (as a large proportion of fine roots are shed in preparation for the non-growing season) and the following spring (until the growth of new fine roots commences in preparation for the growing season). This in turn, inputs a large pulse in the fall of fine root necromass to the soil, which appears to persist into the spring. By the summer, however, a large proportion of this input seems to have decomposed or been consumed by soil herbivores, resulting in the low observed fine root necromass values among all the stand types.

An unexpected result of this study was that fine root biomass was higher, and fine root necromass lower, in May than October in all three stand types, respectively. This result suggests that some fine root production may be occurring over the winter or early spring at these sites so that a network for nutrient and water acquisition is partially in place to meet the needs of the plant for nutrients and water when growth recommences in the spring as temperatures begin to rise. This is also supported by Hendrick and Pregitzer (1993a) who have shown that the production of fine roots can begin in early spring in the northern hardwood forests of Michigan, USA. The finding that fine root necromass was lower in May than October may be an indication that some decomposition of fine root necromass by soil microbes, or consumption of fine root necromass by soil arthropods, is occurring over the non-growing season, despite that the cold soil temperatures during this period should be restricting the activity of these organisms.

Alternatively, this result may be just a reflection of inter-annual variation, e.g., higher fine root biomass in the preceding May than the May which was sampled.

In the two mixed-species stand types, horizontal fine root biomass heterogeneity followed a U-shaped trend with sampling date, while vertical fine root biomass heterogeneity had an inverse U-shaped trend in mixed conifer stands and a U-shaped trend in mixedwood stands, respectively. These findings suggest that as the growing season progressed from spring to summer, and the intensity of below-ground competition and demand for soil nutrients and water increased (reflecting patterns of above- and below-ground production), the species complementary mechanisms operating in each of the respective stand types (i.e., niche differentiation in the mixed conifer stands versus facilitation in the mixedwood stands) became important for reducing competition between the fine roots through the promotion of greater fine root space filling. The lack of a difference in horizontal or vertical fine root biomass heterogeneity with sampling date in the conifer stands, by contrast, implies that unlike their mixed-species counterparts, space filling of fine roots in this stand type remained relatively unchanged throughout the growing season. Therefore, the greater ability of the two mixed-species stand types to fill soil space with fine roots during the period of the growing seasons when the demand for soil nutrients and water is at it highest (so that competition among individual roots for soil resources is minimized) in comparison to the single-species stands, appears to be the key driver for the observed fine root productivity differences between the mixed- and single-species stands at the study sites.

CONCLUSION

While Brassard *et al.* (2010) was one of the first studies to make the link between the ability of a stand to occupy its soil space with fine roots and its fine root productivity (by examining the relationship between fine root spatial biomass heterogeneity and below-ground productivity), this study advances the current state of knowledge by more directly linking fine root soil space filling to stand-level fine root productivity. Through the collection of monthly data on the spatial biomass heterogeneity of fine roots from May to October (instead of just July and October, as in Brassard *et al.* (2010)), I have shown that seasonal patterns of fine root soil space filling are highly synchronous with total fine root biomass in the mixed-species stands, where the greatest space filling of fine roots occurs in the summer when competition for soil resources within the stand and stand productivity is highest. Furthermore, the differences in functional traits between component species in the mixed conifer and mixedwood stands that promote the respective below-ground species complementarity appear to be critical for the mixed-species stands filling soil space with fine roots more completely during the late spring, summer, and early fall than the conifer stands, and in the process, achieving higher fine root productivity.

CHAPTER FIVE COARSE ROOT BIOMASS ALLOMETRIC EQUATIONS FOR *ABIES BALSAMEA*, *PICEA MARIANA*, *PINUS BANKSIANA*, AND *POPULUS TREMULOIDES* IN THE BOREAL FOREST OF CENTRAL CANADA

INTRODUCTION

Accurate quantification of below-ground carbon stocks in forest ecosystems is critical for effectively predicting how future climatic change will impact global carbon dynamics (Brassard *et al.* 2009). However, the development of forest carbon budget models has historically been plagued by the lack of species- and site-specific estimates of root biomass, so that existing models rely heavily on the use of non-species-specific and -site-specific data for deriving larger scale below-ground carbon estimates (Kurz *et al.* 1996; Li *et al.* 2003). As the relative allocation of carbon a plant makes above- and below-ground can vary depending on environmental conditions and its specific life history characteristics (Keyes and Grier 1981; Haynes and Gower 1995; King *et al.* 1999a; Pregitzer *et al.* 2000b), the use of non-species-specific and -site-specific data can introduce large errors into a model and compromise its predictive power.

Complete and partial tree harvests have shown that above-ground attributes such as stem diameter and height can be strong predictors of coarse root (diameter > 1 cm) biomass (e.g., Young *et al.* 1964; Rencz and Auclair 1980; Foster 1985; Ruark and Bockheim 1987; Bond-Lamberty *et al.* 2002; Xing *et al.* 2005; Miller *et al.* 2006; Lavigne and Krasowski 2007; Ouimet *et al.* 2008), due to the fact that the development of below- and above-ground structures is highly synchronous in higher plants (Gedroc *et al.* 1996; Niklas 2005). The coarse root component is comprised of larger, structural roots which provide support for the above-ground portion (Brassard *et al.* 2009), and can account for approximately 30% of total biomass in forest ecosystems (Gower *et al.* 1992; Wang *et al.* 2001; Helmisaari *et al.* 2002; Miller *et al.* 2006). While some stem diameter – coarse root and stem height – coarse root biomass allometric equations have been produced for North American boreal tree species of relatively small diameter and height (e.g., Rencz and Auclair 1980; Foster 1985; Ruark and Bockheim 1987; Bond-Lamberty *et al.* 2002; Ouimet *et al.* 2008), few equations are available for larger individuals (but see Young *et al.* (1964), Ruark and Bockheim (1987), Lavigne and Krasowski (2007), Xing *et al.* (2005), and Ouimet *et al.* (2008)), attributable in part, to the difficulty associated with excavating the entire root systems of larger trees. The objectives of this study were: (1) to develop diameter at breast-height (DBH) – , height – , and DBH-height – coarse root biomass equations for large size *Abies balsamea* L., *Picea mariana* (Mill.) BSP, *Pinus banksiana* Lamb., and *Populus tremuloides* Michx. trees (DBH > 10 cm) in the central Canadian boreal mixedwood forest and (2) to compare the equations for these four tree species with previously published equations.

Abies balsamea, *P. mariana*, *P. banksiana*, and *P. tremuloides* are all widely distributed in the central region of the Canadian boreal forest (Rowe 1972), and are commercially important to Canada's forest industry. *Pinus banksiana* and *P. tremuloides* are shade intolerant and fast growing, whereas *A. balsamea* and *P. mariana* are shade tolerant and slower growing (Burns and Honkala 1990). Since forest resource inventories in Canada commonly contain detailed information at the stand level on many above-ground attributes, including stem diameter and height, the equations developed in this study would allow biomass and carbon budget models to more accurately characterize below-ground dynamics using readily available above-ground metrics.

MATERIALS AND METHODS

Study Area

The study was conducted in the boreal forest north of Lake Superior and west of Lake Nipigon in the Upper English River (B. 11) Forest Region (Rowe 1972) approximately 150 km north of Thunder Bay, Ontario, Canada between 49º27' N to 49º38' N and 89º29' W to 89º54' W. The closest meteorological station is located in Thunder Bay, Ontario (48º 22' N, 89º 19' W, 199 m elevation). The study area has a moderately dry, cool climate with short summers. The average annual precipitation for Thunder Bay (1971-2000) is 712 mm and the average annual temperature is 2.5 ºC (Environment Canada 2010). Topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago. The prevailing site type of the region is well drained glacial moraines > 50 cm in thickness.

The natural stand-initiating disturbance of the area is predominately stand-replacing crown fire, which is the most common stand-replacing mechanism in the Canadian boreal forest (Johnson 1992). The forests of this region are characterized by a mosaic of stands dominated by *A. balsamea*, *P. mariana*, *P. banksiana*, *P. tremuloides*, *Picea glauca* (Moench) Voss, and *Betula papyrifera* Marsh. in various proportion on upland mesic sites (Rowe 1972).

Sampling

Using forest resource inventory maps and following ground-based verification, I allocated a study plot approximately 1 ha in size that met the following criteria: (1) mature forest that established naturally after stand-replacing fire, (2) located on an upland, mesic site with a relatively flat, midslope position, (3) contained a mixture of *P. tremuloides*, *P. banksiana*, *P. mariana*, and *A. balsamea* with limited presence of *P. glauca* and *B. papyrifera*, and (4) adequate road access to facilitate felling and coarse root extraction using a feller-buncher and back-hoe excavator, respectively. Trees were selected for excavation using a systematic random encounter technique, modified from Gower *et al.* (1992). I selected only healthy, undamaged trees with a minimum 10 cm of DBH (taken 1.3 m above the root collar). Twelve to sixteen trees of each species were sampled (*A. balsamea*, *P. mariana*, *P. banksiana*, and *P. tremuloides*). Trees were selected among species to represent the range of sizes available in the sample stand. In total, 58 trees were sampled.

The DBH, height, and species of each sampled tree was measured and recorded, and a marking system was used to ensure that tree stems could be paired with their respective root systems after felling. A feller-buncher was used to fell all trees, and a chainsaw, when needed, was used to remove stemwood which extended above the root collar. A back-hoe excavator was then used for whole root system extraction, exercising care to retain lateral roots. Height was initially estimated for each selected tree using a clinometer (PM-5/1520, Suunto Instrument Co.) with the intention of measuring actual heights following felling. However, the felling process extensively destroyed the tops of many trees so that height was based on the estimate from the clinometer measurement. Root systems were washed free of soil using high pressure water, and the entire root system was weighed on site.

The weight of lateral roots that broke off during excavation was approximated using intact lateral roots. This was done by measuring the diameter at the point of breakage, removing a randomly selected intact lateral root from the same tree at an equivalent diameter, and adding the weight of this section to the measured weight for the entire root system. Roots ≤ 1 cm, which are generally regarded as fine and medium roots, were largely lost during the excavation and washing processes, and any roots ≤ 1 cm that were retained after processing were judged to contribute relatively inconsequentially to the total coarse root biomass among individuals of these sizes.

To determine the dry weight of each tree root system, fifteen randomly selected fresh root samples were taken for each tree species and weighed in the field. The samples were then transported from the field back to the laboratory, dried to a constant mass at 70 °C, and weighed. The species-specific fresh to dry weight ratios were then used to derive dry weight for each tree root system.

Data Analysis

Single power regression models that related coarse root biomass to DBH and height were developed for each species (eq. 5.1):

[5.1] $Y = b_1 \times X^{b_2}$

where Y is coarse root biomass (kg), X is DBH (cm) or height (m), and b_1 and b_2 are coefficients (Lavigne and Krasowski 2007; Ouimet *et al.* 2008). To relate coarse root biomass to both DBH and height, I followed the procedure described in Lambert *et al.* (2005) for above-ground biomass components by developing multiple power regression models for each species (eq. 5.2):

[5.2] $Y = b_1 \times X_1^{b_2} \times X_2^{b_3}$

where X_1 is DBH, X_2 is height, b_3 is a coefficient, and Y, b_1, and b_2 are previously defined. In order to perform standard least squares regression analysis, both models were linearized by applying a natural logarithmic ($\log_n$) transformation. Therefore, a correction factor (*CF*) was applied to the models in eqs. 5.1 and 5.2 to account for the bias of converting from logarithmic to arithmetic units (Sprugel 1983), so that these models had the final forms (eqs. 5.3 and 5.4):

[5.3] $Y = b_1 \times CF \times X^{b_2}$

[5.4] $Y = b_1 \times CF \times X_1^{b_2} \times X_2^{b_3}$

To test if the DBH – coarse root biomass models developed in this study were biased in comparison with other published models for a similar DBH range, I measured the deviation of the residuals of each of the previously published DBH – coarse root biomass models using a one sample t-test, similar to that used by Chen *et al.* (1998). Published models whose mean residuals differed significantly ($\alpha = 0.05$) from zero were considered to be biased in estimating coarse root biomass for the trees I studied. The residuals of each model were derived by taking the difference between the actual values of the present study and the predicted values from the previously published DBH – coarse root biomass models. Normality and homogeneous variances were confirmed following Kutner *et al.* (2005), and all analyses were performed using SYSTAT® version 10.0 (SPSS Inc., Chicago, IL, USA).

RESULTS AND DISCUSSION

All DBH – coarse root and height – coarse root biomass regressions were highly significant ($P < 0.001$), with correlation coefficients ranging from 0.796 to 0.959 (Tables 5.1 and 5.2, Figures 5.1 and 5.2). Diameter at breast-height – coarse root biomass models had consistently higher R^2 than height – coarse root biomass models for all four species, indicating that DBH was a better predictor of coarse root biomass than height. This is further confirmed by the fact that height was only a significant factor in a single DBH-height – coarse root biomass model, and in all other cases, DBH was a much more significant factor than height (Table 5.3). I suspect that the better fit (higher R^2) of the DBH – than height – coarse root biomass models may be the result of the higher accuracy and precision related to measuring DBH directly with a diameter tape versus estimating height with a climometer.

Table 5.1. Regression coefficients for allometric equations relating coarse root biomass to diameter at breast-height (DBH) for *Abies balsamea*, *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides*. Values in parentheses are the coefficient standard errors.

Species	DBH range (cm)	$\log_n(b_1)$	b_2	R^2	P	MSE[*]	SEE[†]	CF[‡]
A. balsamea	13.2 – 28.1	-3.495	2.351	0.922	**<0.001**	0.031	0.177	1.016
(n = 12)		(0.662)	(0.217)					
P. mariana	12.2 – 25.9	-4.081	2.498	0.941	**<0.001**	0.028	0.167	1.014
(n = 15)		(0.502)	(0.174)					
P. banksiana	15.2 – 31.2	-4.593	2.791	0.959	**<0.001**	0.016	0.128	1.008
(n = 15)		(0.498)	(0.159)					
P. tremuloides	11.1 – 33.1	-2.941	2.204	0.862	**<0.001**	0.080	0.282	1.041
(n = 16)		(0.729)	(0.236)					

Note: Transformed regression equations had the form $\log_n Y = \log_n b_1 + b_2 \times \log_n X$, where Y is coarse root biomass (kg), X is DBH (cm), and b_1 and b_2 are coefficients.

[*] MSE = mean square of the error.

[†] SEE = standard error of the estimate of the regression in logarithm units.

[‡] $CF = e^{(SEE^2/2)}$. CF is a correction factor to account for the bias of converting from logarithmic to arithmetic units.

Table 5.2. Regression coefficients for allometric equations relating coarse root biomass to height for *Abies balsamea*, *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides*. Values in parentheses are the coefficient standard errors.

Species	Height range (m)	$\log_n(b_1)$	b_2	R^2	P	MSE[*]	SEE[†]	CF[‡]
A. balsamea	12.0 – 22.5	-3.601	2.578	0.796	**<0.001**	0.082	0.286	1.042
(n = 12)		(1.166)	(0.413)					
P. mariana	10.5 – 22.0	-5.283	3.044	0.876	**<0.001**	0.058	0.242	1.030
(n = 15)		(0.876)	(0.318)					
P. banksiana	13.5 – 26.0	-5.927	3.336	0.824	**<0.001**	0.071	0.267	1.036
(n = 15)		(1.288)	(0.428)					
P. tremuloides	15.0 – 28.0	-5.941	3.148	0.805	**<0.001**	0.113	0.336	1.058
(n = 16)		(1.290)	(0.414)					

Note: Transformed regression equations had the form $\log_n Y = \log_n b_1 + b_2 \times \log_n X$, where Y is coarse root biomass (kg), X is height (m), and b_1 and b_2 are coefficients.

[*] MSE = mean square of the error.

[†] SEE = standard error of the estimate of the regression in logarithm units.

[‡] $CF = e^{(SEE^2/2)}$. CF is a correction factor to account for the bias of converting from logarithmic to arithmetic units.

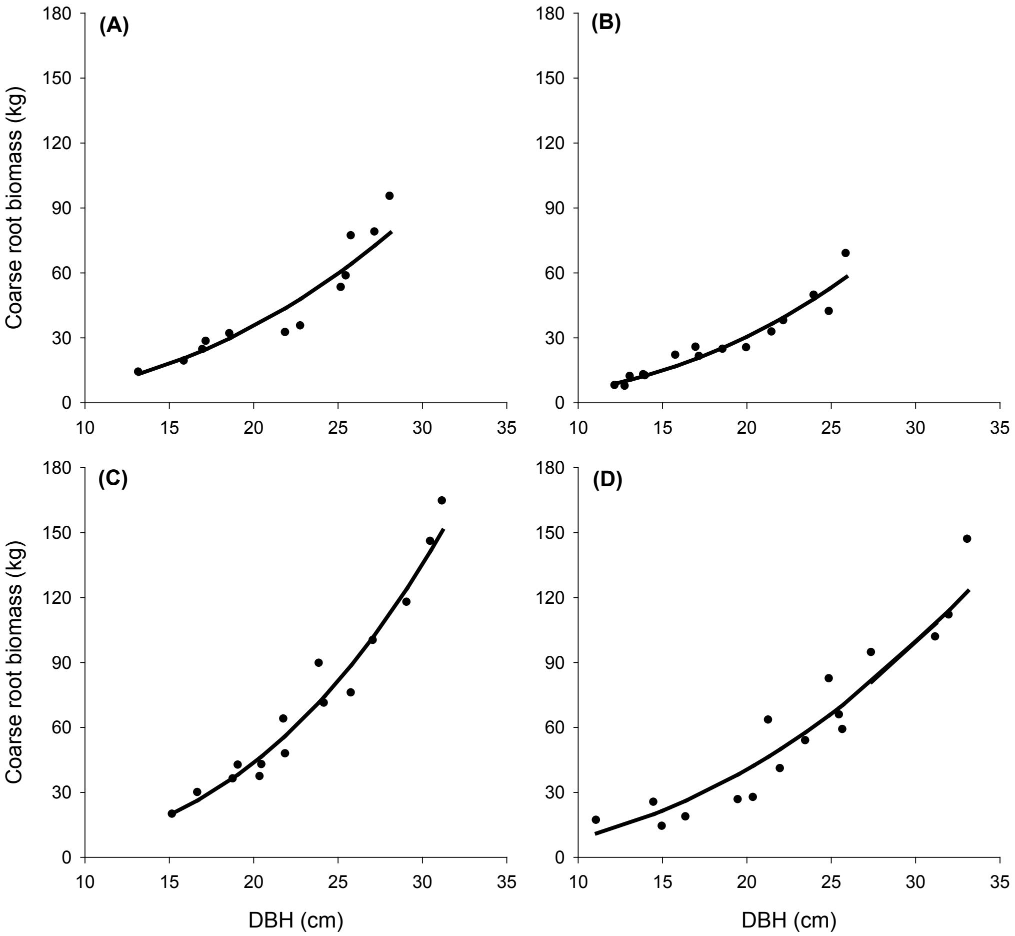

Figure 5.1. Relationship between diameter at breast-height (DBH) and coarse root biomass for (A) *Abies balsamea*, (B) *Picea mariana*, (C) *Pinus banksiana*, and (D) *Populus tremuloides*. Fitted equations have the form $Y = b_1 \times CF \times X^{b_2}$, where Y is coarse root biomass (kg), X is DBH (cm), b_1 and b_2 are coefficients, and CF is a correction factor. The regression coefficients and CF for each model are reported in Table 5.1.

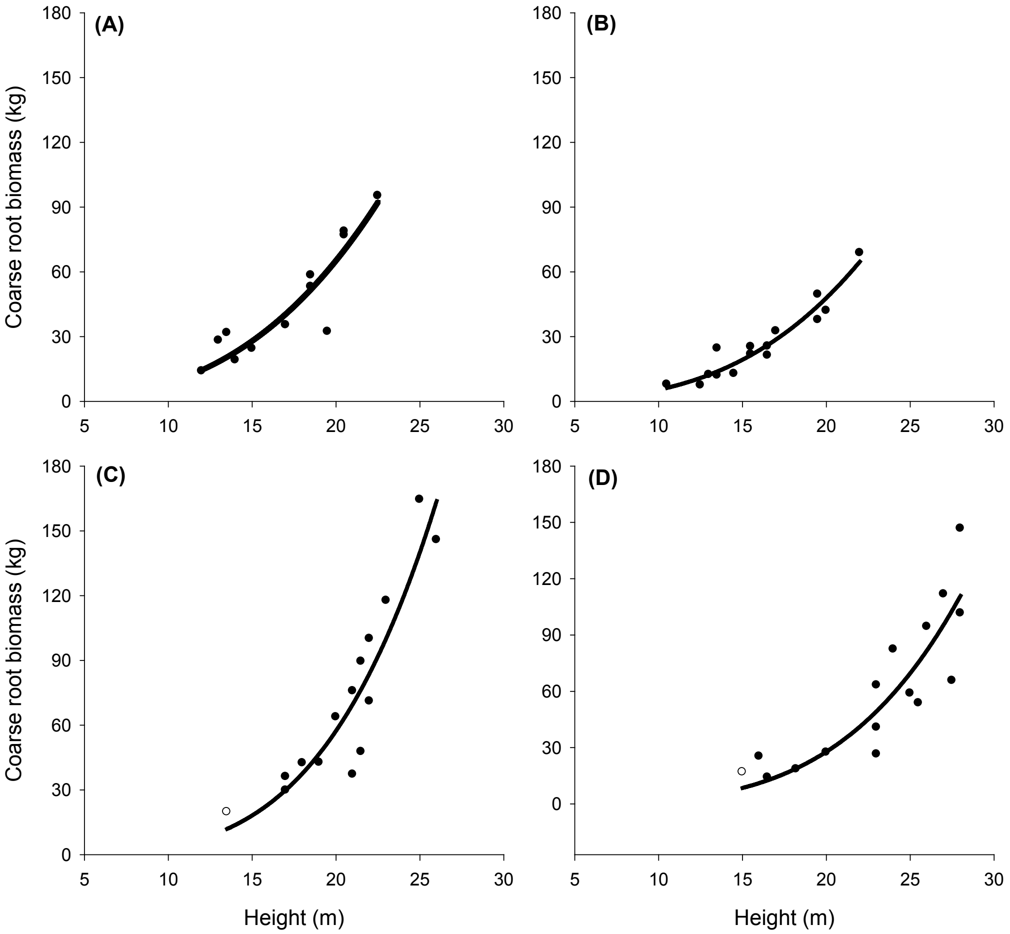

Figure 5.2. Relationship between height and coarse root biomass for (A) *Abies balsamea*, (B) *Picea mariana*, (C) *Pinus banksiana*, and (D) *Populus tremuloides*. Fitted equations have the form $Y = b_1 \times CF \times X^{b_2}$, where Y is coarse root biomass (kg), X is height (m), b_1 and b_2 are coefficients, and CF is a correction factor. The regression coefficients and CF for each model are reported in Table 5.2.

Table 5.3. Regression coefficients for allometric equations relating coarse root biomass to both diameter at breast-height (DBH) and height for *Abies balsamea*, *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides*. Values in parentheses are the coefficient standard errors.

Species	DBH range (cm)	Height range (m)	$\log_n(b_1)$	b_2	b_3	R^2	$P_{(DBH)}$	$P_{(height)}$	MSE[*]	SEE[†]	*CF*[‡]
A. balsamea	13.2 – 28.1	12.0 – 22.5	-3.407	2.528	-0.222	0.922	**0.004**	0.782	0.034	0.186	1.017
(*n* = 12)			(0.760)	(0.660)	(0.779)						
P. mariana	12.2 – 25.9	10.5 – 22.0	-4.795	1.755	1.035	0.959	**<0.001**	**0.041**	0.021	0.145	1.011
(*n* = 15)			(0.536)	(0.358)	(0.452)						
P. banksiana	15.2 – 31.2	13.5 – 26.0	-4.416	2.962	-0.236	0.960	**<0.001**	0.700	0.018	0.133	1.009
(*n* = 15)			(0.682)	(0.464)	(0.599)						
P. tremuloides	11.1 – 33.1	15.0 – 28.0	-3.240	2.028	0.270	0.863	**0.037**	0.837	0.086	0.293	1.044
(*n* = 16)			(1.615)	(0.871)	(1.288)						

Note: Transformed regression equations had the form $\log_n Y = \log_n b_1 + b_2 \times \log_n X_1 + b_3 \times \log_n X_2$, where *Y* is coarse root biomass (kg), X_1 is DBH (cm), X_2 is height (m), and b_1, b_2, and b_3 are coefficients.

[*] MSE = mean square of the error.

[†] SEE = standard error of the estimate of the regression in logarithm units.

[‡] $CF = e^{(SEE^2/2)}$. *CF* is a correction factor to account for the bias of converting from logarithmic to arithmetic units.

With the exception of the Xing *et al.* (2005) model for *A. balsamea*, the DBH – coarse root biomass models among the previously published studies, according to the residual analyses, either underestimated or overestimated coarse root biomass using the data from this study (Tables 5.4 and 5.5, Figure 5.3). Both Young *et al.* (1964) and Lavigne and Krasowski (2007) underestimated the coarse root biomass of *A. balsamea* on average by 51.9% and 30.1%, respectively, while Ouimet *et al.* (2008) overestimated the coarse root biomass of *P. mariana* by an average of 55.3%. Moreover, the coarse root biomass of *P. tremuloides* was underestimated by both Young *et al.* (1964) and Ruark and Bockheim (1987) by an average of 46.2% and 51.7%, respectively. By contrast, Xing *et al.* (2005) effectively predicted the coarse root biomass of *A. balsamea*. These findings imply that most of the previously published DBH – coarse root biomass allometric equations for a similar DBH range do not accurately estimate coarse root biomass using the data from this study, and therefore, may not be suitable for use in the central region of the North American boreal mixedwood forest. However, the extent that the models developed in this study, and those of the other published studies are site-specific may depend on whether among study differences are predominantly the result of variation in site conditions affecting biomass partitioning above- and below-ground or differences in sampling methodologies, and needs to be investigated further.

Several methods have been developed for extracting the coarse root system of trees. These include the use of water pressure (DesRochers and Lieffers 2001), compressed air (Samuelson *et al.* 2004; Lavigne and Krasowski 2007), hand tools (Rencz and Auclair 1980; Foster 1985; Ruark and Bockheim 1987; Ouimet *et al.* 2008), and heavy equipment (Millikin and Bledsoe 1999; Xing *et al.* 2005). In this study, I used a back-hoe excavator to excavate the root

Table 5.4. Regression coefficients for allometric equations relating coarse root biomass to diameter at breast-height (DBH) for *Abies balsamea*, *Picea mariana*, and *Populus tremuloides* from other published studies.

Species	Study[*]	Study location	*n*	DBH range (cm)	b_1	b_2	R^2	*CF*	Model used in Figure 5.3[†]
A. balsamea	Young *et al.* (1964)	Maine, USA	23	15.2 – 35.6	0.008643	2.518	0.997	1.001	$Y = b_1 \times CF \times X^{b_2}$
	Xing *et al.* (2005)	New Brunswick, Canada	12	2.4 – 27.0	0.030869	2.279	0.907	1.203	$Y = b_1 \times CF \times X^{b_2}$
	Lavigne and Krasowski (2007)	New Brunswick, Canada	31	2 – 30 (approx.)	0.0230	2.32	0.95	/	$Y = b_1 \times X^{b_2}$
P. mariana	Ouimet *et al.* (2008)	Quebec, Canada	8	3.8 – 19.4	0.008566	2.87	0.97	1.036	$Y = b_1 \times CF \times X^{b_2}$
P. tremuloides	Young *et al.* (1964)	Maine, USA	13	15.2 – 27.9	0.005940	2.677	0.711	1.071	$Y = b_1 \times CF \times X^{b_2}$
	Ruark and Bockheim (1987)	Wisconsin, USA	38	4.0 – 20.0	0.0421	2.03	0.964	/	$Y = b_1 \times X^{b_2}$

[*] The above-ground limit of the root system was ground level or root collar.

[†] *Y* is coarse root biomass (kg), *X* is DBH (cm), b_1, and b_2 are coefficients, and *CF* is a correction factor to account for the bias of converting from logarithmic to arithmetic units.

Note: The regression coefficients, correlation coefficient, and *CF* for the Young *et al.* (1964) and Xing *et al.* (2005) studies were calculated by regressing $\log_n$ transformed DBH and coarse root biomass data presented in table and graphical form, respectively. Data presented in graphical form was extracted using SigmaScan® Pro version 5 (Systat Software Inc., Point Richmond, CA, USA). Since Ruark and Bockheim (1987) and Lavigne and Krasowski (2007) regressed untransformed DBH and coarse root biomass data directly using eq. 5.1, a *CF* was not required for these two studies.

Table 5.5. Comparison of the residuals derived from the difference between the actual values in the present study and the predicted values from the models listed below. See Tables 5.1 and 5.4 for details on the models used to calculate the predicted values for the present and other published studies, respectively.

Species	Study	*df*	t	*P*	Mean of the residuals (kg)	Variance of the residuals
Abies balsamea	Present study	11	0.136	0.894	0.35	78.4
	Young *et al.* (1964)	11	5.171	**<0.001**	24.09	260.5
	Xing *et al.* (2005)	11	0.791	0.446	2.16	89.6
	Lavigne and Krasowski (2007)	11	3.941	**0.002**	14.98	173.5
Picea mariana	Present study	14	-0.116	0.909	-0.15	24.0
	Ouimet *et al.* (2008)	14	-4.362	**0.001**	-16.14	205.5
Pinus banksiana	Present study	14	0.085	0.934	0.19	71.9
Populus tremuloides	Present study	15	0.048	0.963	0.14	141.9
	Young *et al.* (1964)	15	5.651	**<0.001**	27.38	695.0
	Ruark and Bockheim (1987)	15	5.085	**<0.001**	33.51	375.7

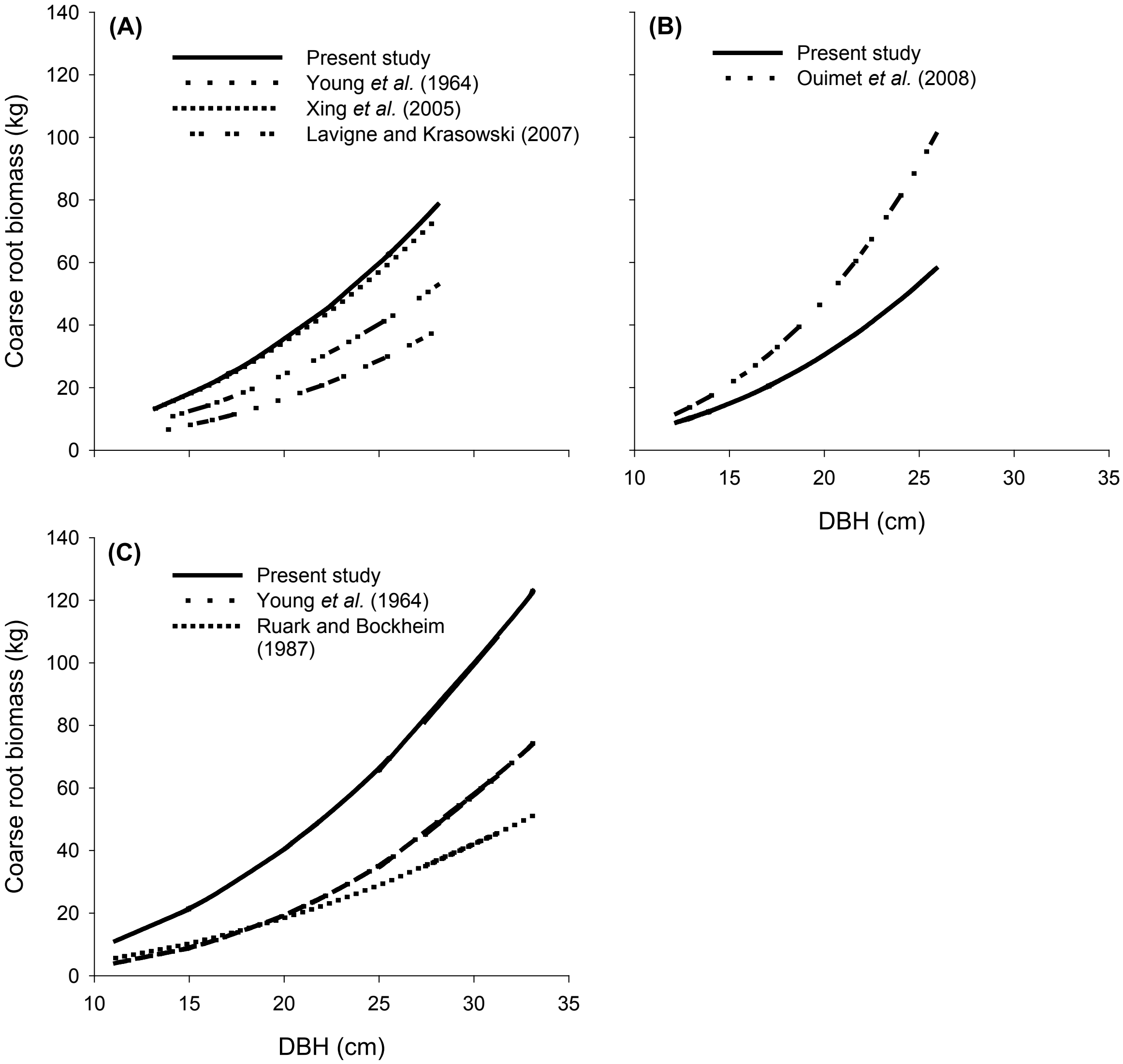

Figure 5.3. Comparisons between the diameter at breast-height (DBH) – coarse root biomass relationships for (A) *Abies balsamea*, (B) *Picea mariana*, and (C) *Populus tremuloides* from the present study and the previously published studies reported in Table 5.4. Fitted equations from the present study have the form $Y = b_1 \times CF \times X^{b_2}$, where Y is coarse root biomass (kg), X is DBH (cm), b_1 and b_2 are coefficients, and CF is a correction factor. Those from the other published studies have either the form $Y = b_1 \times X^{b_2}$ or $Y = b_1 \times CF \times X^{b_2}$, depending on if the regression coefficients were produced by regressing untransformed or transformed DBH and coarse root biomass data using a power or linear function, respectively (see Table 5.4 for further details). The regression coefficients and CF (when applicable) for each model from the present and other published studies are presented in Tables 5.1 and 5.4, respectively.

systems of large sized *A. balsamea*, *P. mariana*, *P. banksiana*, and *P. tremuloides* trees. The major benefit of the back-hoe excavation technique over other methods is that a larger number of trees can be sampled in a shorter period of time with less effort, although some lateral roots can break off during the excavation process. For example, I found that 16.1% of laterals ≤ 3 cm in diameter broke off during excavation. Therefore, unless broken off laterals are excised by hand after stump extraction, or intact laterals are used to approximate the mass of broken off laterals as I did in this study, underestimation of coarse root biomass would result using this method. However, while the back-hoe excavation technique may be appropriate for use in this study region, where soils are dominated by sands and silts on upland mesic sites (Brassard *et al.* 2008), this technique may not be appropriate for regions where soils are dominated by clays or organics, since many more laterals would likely be lost during the excavation process (making it more difficult to determine the biomass of broken off laterals), or the heavy machinery would be prevented from operating, respectively.

Although *P. banksiana* and *P. tremuloides* generally root deeper than *A. balsamea* and *P. mariana* (Burns and Honkala 1990), there was not a large difference between species in the percentage of lateral roots ≤ 3 cm in diameter that broke off during excavation (*A. balsamea* = 14.9%, *P. mariana* = 14.6%, *P. banksiana* = 16.6%, and *P. tremuloides* = 17.0%). This suggests that the deeper rooting species had similar levels of root breakage as the more shallow rooting species at this site. However, *P. banksiana* and *P. tremuloides* may show significantly higher root breakage than *A. balsamea* and *P. mariana* in clay dominated soils because deeper lateral roots would have a higher propensity to break off during back-hoe excavation than at this site.

In summary, this paper presents some of the first coarse root biomass allometric equations for large size trees of *A. balsamea*, *P. mariana*, *P. banksiana*, and *P. tremuloides*, and as expected, stem DBH and height were highly correlated with coarse root biomass. These four species are some of the most commonly found and widely distributed tree species within the North American boreal forest. The addition of these equations to the previously published equations will allow scientists to develop more accurate biomass and carbon budget models for the North American boreal forest by enabling more accurate quantification of below-ground biomass.

CHAPTER SIX GENERAL CONCLUSION

The findings of this dissertation confirm that plant diversity has a positive effect on below-ground productivity in forest ecosystems. Moreover, the extent to which the mixed-species stands in this study, due to functional trait differences between component species, more greatly fill soil space with fine roots compared to the single-species stands appears to be the key driver for the observed diversity-productivity relationships. A summary of the key findings of this dissertation are as follows:

1. The abiotic (e.g., nutrient and water availability, temperature, and carbon dioxide concentration) and biotic (e.g., resource- and non-resource-based plant competition) characteristics of the environment play significant roles in affecting patterns of root production and structure and carbon allocation above- and below-ground in northern forests.
2. In the first fine root study, annual fine root production and total fine root biomass in July and October were higher in stands of *Populus tremuloides* Michx., *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss, and *Abies balsamea* L. (mixed-species stands) than relatively pure stands of *P. tremuloides* (single-species stands). Furthermore, the mixed-species stands had lower and higher horizontal and vertical fine root biomass heterogeneity, respectively, compared to the single-species stands.
3. In the second fine root study, annual fine root production and total fine root biomass for most sampling dates (May to October) were higher in both mixed-species stand types (stands of *Pinus banksiana* Lamb., *P. mariana*, *P. glauca*, and *A. balsamea* (mixed conifer stands) and stands of *P. banksiana* and *P. tremuloides* (mixedwood stands)) than the single-species stands (relatively pure stands of *P. banksiana* (conifer stands)).

Furthermore, horizontal fine root biomass heterogeneity was lower in the mixed- than single-species stands in July, August, and September, but similar between the three stand types for the other sampling dates. By contrast, vertical fine root biomass heterogeneity was higher in the mixed conifer than conifer stands from June to September, whereas mixedwood stands differed significantly from conifer stands for only a single sampling date.

4. There were distinct temporal trends of fine root biomass, necromass, and spatial biomass heterogeneity in the second fine root study. Total fine root biomass followed an inverse U-shaped pattern with sampling date (i.e., highest in the summer and lower in spring and fall), while total fine root necromass followed a U-shaped pattern (i.e., lowest in the summer and higher in spring and fall) in all three stand types, respectively. In the two mixed-species stand types, horizontal fine root biomass heterogeneity followed a U-shaped trend with sampling date, while vertical fine root biomass heterogeneity had an inverse U-shaped trend in mixed conifer stands and a U-shaped trend in mixedwood stands, respectively. However, neither horizontal nor vertical fine root biomass heterogeneity differed with sampling date in the conifer stands.
5. The findings of both fine root studies support the theory that the differences in crown structures and rooting traits between component species in the mixed-species and mixed conifer stands in the first and second fine root studies, respectively (niche differentiation), versus increased nutrient availability resulting from the *P. tremuloides* leaf litter in the mixedwood stands in the second fine root study (facilitation), were promoting greater soil space filling of fine roots and fine root productivity in the mixed- than single-species stands for both studies. In particular, the greater ability of the mixed-species stands to fill

the soil space with fine roots during the period of the growing season when demands for soil nutrients and water are at their highest (i.e., summer) relative to the single-species stands (so that competition among individual roots for soil resources is minimized), appears to be the key driver for the observed fine root productivity differences between the mixed- and single-species stands of the two studies.

6. All regressions (*A. balsamea*, *P. mariana*, *P. banksiana*, and *P. tremuloides*) for coarse root biomass using diameter at breast-height (DBH) or height alone, or both DBH and height as predictors were significant. The DBH – coarse root biomass models had higher R^2 values than the height – coarse root biomass models for all four species, indicating that DBH was a better predictor of coarse root biomass than height. Furthermore, the DBH-height – coarse root biomass models did not have higher R^2 values than the DBH – coarse root biomass models.
7. All but one DBH – coarse root biomass model from the published literature with similar DBH range underestimated or overestimated coarse root biomass using the data from this study. Coarse root biomass allometric equations, therefore, are probably site-specific as above- and below-ground biomass allocation differs with site condition.

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APPENDICES

APPENDIX I. MAP SHOWING THE LOCATION OF THE STUDY PLOTS IN NORTHWESTERN ONTARIO AND NORTHWESTERN QUEBEC, CANADA.

APPENDIX II. THE *DF*, MS, AND F VALUES FOR TABLE 4.3.

Characteristic	*df*	MS	F
Annual fine root production			
Decision matrix method	2, 6	128,478.9, 30,418.8	4.224
Minimum-maximum method	2, 6	253,326.9, 32,838.2	7.714
Ingrowth core method	2, 6	244,551.8, 44,836.7	5.454
Annual fine root mortality	2, 6	334,439.1, 87,532.0	3.821
Percent annual fine root mass loss	2, 6	144.487, 24.829	5.819
Total fine root biomass	2, 5, 10, 36	3,317,229.9, 1,470,039.5, 151,645.4, 122,998.8	26.970, 11.952, 1.233
Fine root biomass in FF layer	2, 5, 10, 36	1,569,351.3, 310,578.2, 131,763.1, 50,272.8	31.217, 6.178, 2.621
Fine root biomass in MS1 layer	2, 5, 10, 36	503,194.3, 219,835.8, 49,152.7, 35,513.1	14.169, 6.190, 1.384
Fine root biomass in MS2 layer	2, 5, 10, 36	219,672.6, 86,406.3, 15,005.5, 12,997.7	16.901, 6.648, 1.154
Total fine root necromass	2, 5, 10, 36	517,349.2, 228,426.3, 34,780.3, 35,043.7	14.763, 6.518, 0.992
Horizontal fine root biomass heterogeneity	2, 5, 10, 36	0.030, 0.020, 0.004, 0.003	9.494, 6.481, 1.159
Vertical fine root biomass heterogeneity	2, 5, 10, 36	0.040, 0.009, 0.009, 0.003	11.901, 2.521, 2.791