

THE FINE ROOT DYNAMICS AFTER STAND-REPLACING
FIRE AND CLEARCUTTING IN THE BOREAL FOREST OF
CENTRAL CANADA

by

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A Dissertation submitted to the Faculty of Natural Resources Management

Lakehead University

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy in Forest Sciences

Faculty of Natural Resources Management

Lakehead University

March 2011

Lakehead UNIVERSITY

OFFICE OF GRADUATE STUDIES

NAME OF STUDENT: ZHIYOU YUAN

DEGREE AWARDED: Ph.D

ACADEMIC UNIT: FORESTRY

TITLE OF DISSERTATION: THE FINE ROOT DYNAMICS AFTER
STAND-REPLACING FIRE AND CLEARCUTTING
IN THE BOREAL FOREST OF CENTRAL CANADA

This dissertation has been prepared
under my supervision
and the candidate has complied
with the Doctoral regulations.



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March 5, 2011
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ACKNOWLEDGEMENTS

This dissertation would not have been possible without the assistance and support of dozens of professors, staff, and students at Lakehead University, and friends, family, and colleagues across North America and China.

First, I would like to thank my supervisor Han Chen, who is so organised and well planned, and always quick to get back to me with well thought through comments on manuscripts and other documents. Also thanks for wise advice and tips on writing manuscripts, and support throughout the development of this dissertation.

Thanks to Drs. William Parker, Chander Shahi, and Lense Meyer at Lakehead University for your valuable comments that helped me improve this thesis and achieve it finally.

Thanks to all the people who have helped me in my fieldwork and in my lab work: Yu Zhang, Xinrong Shi, Changyu Wei, Brian W Brassard, and Shuli Wang.

This research was supported by the Natural Sciences and Engineering Research Council of Canada (DG283336-09).

ABSTRACT

Yuan, Z.Y. 2011. The fine root dynamics after stand-replacing fire and clearcutting in the boreal forest of central Canada. 169 pp.

Key words: Biomass, boreal forest, clearcutting, decomposition, disturbance, fine roots, fire, ingrowth soil cores, plant competition, production, sequential soil core, soil nutrients, secondary forest succession, stand origin, turnover rate.

In boreal forest ecosystems, stand age is a key driver of forest ecosystem productivity, carbon storage/sequestration, and other ecosystem functions. The age-related decline of aboveground productivity is well known in secondary forests after stand-replacing disturbances, however, how belowground root system changes with stand age is not well understood.

Both fire and harvesting (mostly mechanical clearcutting) are also well known to be two main disturbances in boreal forests. These two disturbances are two distinct processes in terms of ecological effects, one is a natural disturbance, and the other is an anthropogenic one, resulting in different regeneration substrates, coarse woody debris structures, and understory vegetation communities. However, direct comparisons of belowground root dynamics between these two disturbance types within the same region are not common.

In this present study, a boreal forest chronosequence in northern Ontario that spans over 200 years (3-, 10-, 29-, 94-, 142- and 205-year old for postfire stands and 3-, 10-, and 29-year old for post-clearcutting stands) was used to study how ecosystem functions such as the dynamics of fine roots (≤ 2 mm in diameter) vary with stand ages and disturbances.

Sequential root coring, ingrowth root cores, and root decomposition experiments were used to 1) quantify how fine root biomass, decomposition, production, and turnover rate, changed with stand age, and 2) investigate whether these parameters differed with stand origin (fire clearcutting).

In postfire stands, fine root biomass in forest floor, 0-15 cm and 16-30 cm soil layers from different sampling dates was found to increase in stands from 3-year old, peaked at 29-year-old stands, and leveled off or declined thereafter. Fine root decomposition rates (k values) also differed significantly with stand age, which increased in stands from 3-year old, peaked in 10-year-old stands, and declined thereafter. Fine root production increased in stands from 3-year-old to 10-year old, and leveled off or declined thereafter. Fine root turnover rates, similarly to production, was also higher in 3- and 10-year-old stands, and leveled off thereafter. These age-related patterns of fine root processes (decomposition, production, and turnover rate) were similar to the well-known age-related decline of aboveground net primary productivity. However, the causes for these age-related fine root process patterns were unclear because stand aging was inherently coupled with changes in stand composition and some soil attributes, all of which were difficult to separate their effects from the stand age effect on these fine root processes. It seemed that the physiological, ecological, and phylogenetic changes coupled with stand ageing contributed to the age-related patterns of fine root decomposition, production, and turnover rate processes.

In terms of the effects of stand origin (fire vs. clearcutting), fine root biomass did not significantly differ between stand origins either in 3-, 10-, or 29-year-old stands. However, the fine root decomposition rates, *i.e.*, the k values, were higher in fire-origin stands than in clearcutting-origin stands at 3- and 10-year-old ages, but were similar at 29-year-old age.

Also, fine root production differed significantly between stand origins in 3-, and 10-year-old stands but not in 29-year-old stands. Fine root turnover rates, similar to production, were different significantly between stand origins in 3-, and 10-year-old stands, but were similar in 29-year-old stands. The differences and similarities of fine root biomass, decomposition production, and turnover rates between fire- and clearcutting-origin stands also reflected the differences and similarities in stand composition and soil environments between these two disturbance types.

LIST OF ABBREVIATIONS USED

A: stand age

ANPP: aboveground annual net primary production

B: biomass

BNPP: belowground annual net primary production

D: dead roots

FF: forest floor layer

FR: fine roots

FRB: fine root biomass

FRN: fine root necromass

FRP: fine root production

FRT: fine root turnover rates

M: mortality

MS1: mineral soil 0–15 cm

MS2: mineral soil 16–30 cm

NPP: annual net primary production

O: stand origin

P: production

RB: root biomass

RP: root production

RT: root turnover rates

CHAPTER ONE: GENERAL INTRODUCTION

Comprising one third of the global forest area and containing about 60% of the global forest soil carbon (C) (470 Pg) (Dixon *et al.* 1994), boreal forests at high latitudes play a unique role in the global climate system (Goodale *et al.* 2002; Chapin *et al.* 2006; Hari & Kulmala 2008). However, there is still much uncertainty concerning the impacts of climate change on boreal forest C. Particularly, it remains less well understood for the patterns and functioning of belowground traits, including fine roots (≤ 2 mm in diameter, FR) that are a prominent sink for C acquired in terrestrial net primary production (NPP) and the primary pathway for water and nutrient uptake by plants (Jackson *et al.* 1997; Burton & Adamowicz 2003; Persson & Stadenberg 2009; Brassard *et al.* 2009). Previous studies have showed that primary production allocated to belowground is often greater than that allocated to aboveground, and the annual C and nutrient inputs to the soil from FR frequently equal or exceed those from foliage (Norby & Jackson 2000). A global estimate indicates around 7.2×10^9 Mg of fine root biomass (FRB) in boreal forest ecosystems, similar to tundra ecosystems (Jackson *et al.* 1997). Fine root production (FRP) in the boreal forest based on our regional estimates was 2.8 Gt year^{-1} , accounting for 73% of total root production (Yuan & Chen 2010b) and for 32% of the total boreal forest production (Pregitzer & Euskirchen 2004). Fine roots in the boreal forest also turn over fast and contain high amount of nutrients (Prescott *et al.* 2000a; Pinno *et al.* 2010; Yuan & Chen 2010b). Despite their obvious importance for C fluxes, nutrient cycling, resource capture, and global biogeochemistry, the factors that control FR dynamic processes are still poorly understood (Hendrick & Pregitzer 1996; Brassard *et al.* 2009).

In the boreal forest, both fire and clearcutting are important agents of disturbance for

secondary forest succession (Nepstad *et al.* 1999; Lindenmayer *et al.* 2004; DellaSala *et al.* 2006; Taylor *et al.* 2009; Ilisson & Chen 2009). Previous studies have shown that biodiversity, C storage, and soil nutrients change with both fire and clearcutting disturbance-disturbance-induced stand development (Reich *et al.* 2001b; Deluca *et al.* 2002; Hart & Chen 2008; Shrestha & Chen 2010). However, the crucial belowground processes, such as FRP and turnover rates (FRT) in relation to stand development and disturbances, have received far less attention and are less well understood.

In general, aboveground biomass and production follow predictable patterns during secondary forest succession (Gower *et al.* 1996a; Ryan *et al.* 1997): aboveground net primary production (ANPP) increases with stand development, peaks at intermediate stand age, and declines thereafter. Although the patterns of belowground net primary production (BNPP) and turnover, including FRP and FRT, in relation to stand age, although not well understood, have been assumed to be similar to aboveground (Yuan & Chen 2010b).

A number of reports on stand belowground root biomass have been published during the past decades, but only a few of them examined variation in FRB with stand development, and most of these studies focused on temperate and tropical forests (Ovington 1957; Moir & Bachelard 1969; Santantonio *et al.* 1977; Vanninen *et al.* 1996; Helmisaari & Hallbacken 1999; John *et al.* 2002; Fujimaki *et al.* 2007), reflecting the difficulty of obtaining root biomass data and of comparing results obtained by different methods. The maximum root biomass that a stand is capable of maintaining is likely reached at different ages in stand development, dependent on tree species and environments (Yuan & Chen 2010b). Studies in tropical forests, for example, showed that after only a few years, FRB is only slightly lower than in mature forests (Berish 1982; Berish & Ewel 1988). In temperate forests, FRB of

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands peaks at 46 years old, coinciding with the time of canopy closure (Vogt *et al.* 1983b). Studies in boreal forest types (Claus & George 2005; Borja *et al.* 2008) have suggested that FRB increases until about age 20 and then gradually levels off, which is similar to the timing of the peak in leaf area (Covington & Aber 1980). However, some studies did not find this general pattern. Finer *et al.* (1997), for instance, found no significant differences in total standing root biomass among 48- to 232-232-year-old mixed boreal forests. Ruark and Bockheim's (1987) either found differences in small roots (< 3 mm in diameter) among an age series of young aspen (*Populus tremuloides* Michx.) stands from 10-, 20- to 32-year old in Wisconsin, U.S.A. Persson (1983) found an increase in FRB from 20- to 120-year-old Scots pine (*Pinus Sylvestris* L.) stands in Sweden. Vanninen and Mäkelä (1999) found that in *P. Sylvestris* stands in southern Finland FRB increased with stand age from 23 to 178-year old on a poor sites, whereas on a more fertile sites there were no relationship or the FRB decreased with stand age from 5 to 24-year old. The rate of recovery of FRB following disturbance probably follows complex patterns that depend upon a variety of vegetation, soil and climatic features, and additional systematic study will be necessary to develop a general understanding of this phenomenon.

Compared to FRB, even fewer studies have examined FRP and FRT, and their relationship with stand age is not well understood. In *P. sylvestris* stands, FRP has been found to increase with stand age from 15, 35, to 100-year old, and the FR turned over fastest in the oldest stands (Helmisaari *et al.* 2002). In contrast, Persson (1983) found that FR turned over faster in a 20-year-old *P. sylvestris* stand than in a 120-year-old stand, and FR production was greater in young stands. These contradictory results suggest that more work is needed to investigate the mechanisms that control changes in FRP and FRT with stand development.

Both fire and clearcutting are main disturbances in boreal forests, but do not produce the same effects (McRae *et al.* 2001). In boreal forests, these two disturbances influence stand composition, aboveground biomass, coarse woody debris, and soil fertility in boreal forests. Research examining these disturbances independently suggests similarities and differences between them (Lecomte *et al.* 2006; Brassard & Chen 2008; Ilisson & Chen 2009; Seedre & Chen 2010; Shrestha & Chen 2010). At a stand level, fire and clearcutting have different effects on ecosystem processes and nutrient fluxes. At early stage, fire-origin stands generally have a lower stem density (Nguyen-Xuan *et al.* 2000), less downed woody debris (Brassard & Chen 2008), a thinner forest floor layer (Simard *et al.* 2001; Shrestha & Chen 2010), lower proportions of black spruce (*Picea mariana* [Mill.] B.S.P.) and balsam fir (*Abies balsamea* [L.] Mill.), and higher proportions of paper birch (*Betula papyrifera* Marsh.) (Ilisson & Chen 2009) than clearcutting-origin stands. Fire can cause substantial losses of C, nitrogen (N), and sulfur (S) through volatilization, reduces soil acidity (*i.e.*, increases pH), and generate a plant-available nutrient pulse in the soil that can be taken up by regenerating vegetation. Also, fire may reduce forest floor depth, resulting in a seedbed appropriate for the establishment of early successional species. In contrast, clearcutting can increase soil acidity and the loss of base cations, and leave a large portion of the forest floor undisturbed and may not generate the same nutrient pulse observed with fire (McRae *et al.* 2001). These differences have the potential to impact FR growth and death even in stands of the same age.

To estimate FR changes at various stages of forest development, this study employed a chronosequential approach to investigate forest stands that differed in age but were climatically and geologically similar. This space for time approach allows for a direct comparison of different-aged stands during the same time period, which can yield specific

inferences about the biology and ecology of developing forests (Fukami & Wardle 2005). Here, an age gradient, originating from different disturbances (fire *vs.* clearcutting), was selected to address the effects of disturbance types and stand development on FR biomass, production, decomposition, and turnover rates. Ingrowth cores and sequential soil coring together with FR decomposition measurements were used to study FR dynamics over a 2-2-year period in six postfire age classes and three post-clearcutting age classes, each replicated three times. The objectives were 1) to investigate FR dynamics (biomass, production, and turnover rates) with stand development; and 2) to examine the effects of different disturbance origins (fire *vs.* clearcutting) on FR dynamics in postfire and post-clearcutting stands.

In this dissertation, Chapter 1 provides general information about FR biomass, production, and turnover in relation to fire- (or clearcutting-) induced stand development and stand origins. Chapter 2 reviews a data set of 218 published root studies and examines how FR in boreal forests at a biome scale respond to site and climatic factors. Chapter 3 addresses FRB patterns; Chapter 4 investigates FR decomposition; Chapter 5 addresses FR production based on ingrowth soil cores and sequential soil cores; Chapter 6 addresses FR turnover patterns. Chapter 7 provides a synthesis of how fine roots vary with stand age and between different disturbance types.

CHAPTER TWO: LITERATURE REVIEW AND META- ANALYSES

Introduction

As the second largest forest biome in the world, the boreal forest represents about one third of the global forest area, and contains about 60% of the global forest soil carbon (470 Gt) and 25% of the forest tree carbon (88 Gt) (Dixon *et al.* 1994; Gower *et al.* 2001). In the boreal forest, nutrient availability generally increases with rising soil temperature because the mineralization of organically bound nutrients is directly related to the temperature-dependent metabolic activity of soil microbes (Bonan & VanCleve 1992; Pregitzer & King 2005). The cold climate of the boreal forest ecosystems in northern sites most likely restricts the availability of N and thus fine root growth (Nadelhoffer 2000; Rasse 2002; Cruz-Ramirez *et al.* 2009). However, in part due to these nutrient limitations, the boreal forest requires relatively large root systems (Hari & Kulmala 2008) and tend to have higher root:shoot ratios (0.32 on average) than plants in other biomes (*e.g.*, the corresponding ratio in temperate forest ecosystems is 0.20, estimated by Jackson *et al.* 1996).

Much has been learned about the role of the fine root systems in C and nutrient fluxes of ecosystems. It has been estimated, for example, that up to “76% of annual total net primary production (NPP) by forests [may be] allocated to fine roots” (Gower *et al.* 1996b) although fine root biomass contributes relatively little to total forest biomass (usually < 5%; Vogt *et al.* 1996). Jackson *et al.* (1997) estimated that the production of fine roots accounts for as much as 33% of global annual NPP. Fine root mortality contributes 18 to 58% total N to forest higher than N addition from aboveground litterfall in some ecosystems (Vogt *et al.* 1986).

However, due to difficulties in measuring their activity *in situ*, knowledge of the ecology of fine roots is much more limited than aboveground components of trees.

It is anticipated that climate warming will occur in the future with the greatest warming occurring in boreal and subarctic regions (IPCC 2007). The boreal forest is a key biome to be understood and to be represented accurately in global C models due to its large size, large amount of C contained in the soil, sensitivity of NPP to small climatic variations, and anticipated effects of climate warming (Bonan *et al.* 1992; Goulden *et al.* 1998; Majdi & Ohrvik 2004). Potential changes in fine root-production and turnover, associated with climate changes, may alter nutrient availability in forest soils, and in turn influence overall production and feedback to climate change. Thus, accurate estimates of fine root biomass, production, turnover, and nutrient pools are essential for improving and refining C budget models.

In previous studies, fine root biomass, production, turnover, and nutrient pools have been related to internal factors as the genotype of plant species and several external factors such as soil properties, stand age, and climate (Vogt *et al.* 1986; Jackson *et al.* 1996; Vogt *et al.* 1996; Cairns *et al.* 1997; Joslin *et al.* 2000; Pregitzer *et al.* 2000; Leuschner & Hertel 2003; Block *et al.* 2006; Kalyn & Van Rees 2006; Brassard *et al.* 2009). However, it is still unclear how fine roots change over a large biome scale.

In this paper, fine root biomass, production, turnover, and nutrient data of the boreal forest were collected from the published literature. The objectives were to examine how abiotic factors such as temperature, precipitation, soil chemical parameters (pH, soil fertility), and biotic factors such as stand age, affect fine root biomass, production, turnover, and nutrient pools. Due to the differences in functional groups (Pugnaire & Valladares 2007),

differences between stands dominated by broad-leaved and needle-leaved species, and differences between stands dominated by early- and late-successional species were also examined.

Materials and methods

The literature (from ISI Web of Science, PubMed, Google Scholar, JSTOR, and Scirus) was reviewed for information about fine root biomass, production, turnover rates, and nutrient contents in the boreal forest ecosystems. All sources and data were critically reviewed using the following criteria: 1) the studied forest stands were located in the boreal region of Eurasia and North America ranging between 46° N and 66° N latitude (Wein & MacLean 1983; Engelmark 1999; Jarvis *et al.* 2001); 2) data from boreal wetlands, *i.e.*, bogs and swamps (Walker & Chapin 1986; Rodgers *et al.* 2003; Crawford *et al.* 2007) were not examined; 3) for the paper to be considered for this review, sampling had to be carried out with corers or by the monolith technique yielding volume-based fine root biomass; 4) if fine roots were sampled more than once per growing season, seasonal averages were used; 5) only those studies that sampled in (at least) the uppermost 20 cm of the mineral soil and the forest floor were selected; 6) root data that referred to the forest floor layer only were not included; 7) stands <20 years old were only used in analysis for the effects of stand age, but not for other effects to minimize the influence of stand age; 8) data from fertilized systems were not included, nor those from pot or greenhouse experiments with seedlings.

The total data set represented 182 sites (33 from North America and 149 from Eurasia). Geographic coordinates (latitude and longitude) were taken from original papers. For missing latitude or longitude, data were obtained from other related studies in the same sites or from

the Global Gazetteer web site (www.calle.com/world/index.html). Site elevation ranged from 3 to ≈ 2000 m. Mean annual temperature ranged from -9 to 12°C ; mean annual precipitation ranged from 270 to $1420 \text{ mm year}^{-1}$.

Fine root biomass, production, turnover, and nutrients vary greatly depending on forest type, soil condition, stand age, and sampling method (Nadelhoffer & Raich 1992; Eissenstat & Yanai 1997). Because means of samples are much more likely to be normally distributed than the individuals values (Underwood 1997; Pitcher & Stutchbury 1998; Kirwan *et al.* 2009), we used means for analysis (Middleton & Mckee 2004) by averaging overall estimates of the selected fine root variables that fall within a single unit of latitude (1°), temperature (1°C), and precipitation (100mm), stand age (10 year), to eliminate effects of unidentifiable factors other than environmental variables, *e.g.*, sampling methodologies (Hendricks *et al.* 2006).

Means of root biomass, production, turnover rates, and nutrients were compared by root size (<1, 1~2, 2~5, and >5 mm) using one-way analysis of variance (ANOVA), followed by Duncan's post hoc comparisons when an effect was significant. ANOVA was used to test the differences between broad- and needle-leaved species as well as between early-successional and late-successional species. The early-successional trees included the genera *Populus*, and species *Pinus sylvestris* L. and *P. banksiana* (Lamb.); the late-successional trees included the genera *Abies* and species *Picea abies* L. (Karst), *P. mariana* (Mill.), *P. glauca* L. (Moench), and *Thuja occidentalis* L. (Arborvitae) (Syrjanen *et al.* 1994; Linder *et al.* 1997; Linder Bergeron 2000; Ryan 2002; Chen & Popadiouk 2002). Means of fine root variables were also compared among main species. Multiple regression analysis was conducted to examine the responses of fine root biomass, production, turnover rates, and nutrients to climate variables

(mean annual temperature and precipitation) and soil variables (pH, soil total N, and total P). Temperature was log (50+y)-transformed to reduce the influence of a few sites with exceptionally low temperature. The relationships between fine root biomass and stand age were analyzed using a quadratic regression model. All statistical analyses were performed in R for Windows version 2.10.1 statistical software (R Development Core Team 2010).

Results

Differences among root sizes

At a biome scale, the boreal forest roots differed in biomass, production, turnover rates, and nutrient contents among diameter classes (Table 2.1). The root biomass in the boreal forest was 33.8 Mg ha⁻¹ and increased with root size with most proportions occurring as coarse roots (> 5 mm in diameter). Fine roots (<2 mm in diameter) accounted for about 16% of total root biomass. The total root production in the boreal forest was 3.88 Mg ha⁻¹ year⁻¹ and decreased with root size. The production of fine roots (<2 mm in diameter) was 2.83 Mg ha⁻¹ year⁻¹, accounting for about 73% of total root production. On average, roots in the boreal forest turnover 0.74 times per year. The turnover rates were lower in coarse roots (>5 mm in diameter) (0.30 year⁻¹) than in fine roots (<2 mm in diameter) (1.08 year⁻¹). Totally, root systems in the boreal forest contained 307 and 46 kg ha⁻¹ N and P, respectively. With increasing root size, both N and P contents increased. Fine roots (<2 mm in diameter) contained 17% N and 8% P of entire root total N and total P, respectively.

The root biomass in the boreal forest accounted for 21% of total biomass (including above- and below-ground) (Table 2.1). Fine roots (<2 mm in diameter) constituted a small fraction (\approx 3%) of total vegetation biomass. By contrast, the total root production in the boreal

forest accounted for 44% of total production (including above- and below-ground NPP). The production of fine roots (<2 mm in diameter) in the whole boreal forest was 3.4 Gt year⁻¹, accounting for ≈ 32% of total production. In total, root systems of the boreal forest contained 369 and 58 Mt N and P, respectively. Fine roots (<2 mm in diameter) contained about 5% N and 3% P of total N and total P of the entire boreal vegetation, respectively.

Table 2.1 Root biomass, production, turnover rates, and nutrients in relation to root size in the boreal forest.

Root size	< 1 mm	1–2 mm	2–5 mm	> 5 mm	Overall*
<i>Mean</i>					
Biomass (Mg ha ⁻¹)	2.13 ± 0.17 ^B (246)	3.15 ± 0.11 ^B (519)	3.91 ± 0.24 ^B (206)	24.64 ± 2.79 ^A (128)	33.83 ± 5.41 (1099)
Production (Mg ha ⁻¹ year ⁻¹)	1.35 ± 0.11 ^A (82)	1.48 ± 0.08 ^A (154)	0.63 ± 0.11 ^B (18)	0.43 ± 0.04 ^B (59)	3.88 ± 0.05 (313)
Turnover (year ⁻¹)	1.09 ± 0.09 ^A (70)	1.07 ± 0.09 ^A (42)	0.51 ± 0.11 ^B (17)	0.30 ± 0.08 ^B (20)	0.74 ± 0.20 (149)
Nitrogen (kg ha ⁻¹)	27.34 ± 6.70 ^C (52)	23.60 ± 2.06 ^C (71)	101.28 ± 25.5 ^B (14)	154.85 ± 68.46 ^A (6)	307.08 ± 31.58 (143)
Phosphorus (kg ha ⁻¹)	1.30 ± 0.21 ^C (44)	2.33 ± 0.35 ^C (33)	9.76 ± 2.68 ^B (11)	35.00 ± 11.79 ^A (4)	48.38 ± 5.16 (92)
<i>Total</i> [†]					

Biomass (Gt) ‡	2.56, 1.3%	3.78, 1.9%	4.69, 2.4%	29.57, 15.1%	40.60, 20.8%
Production (Gt year ⁻¹)	1.62, 15.1%	1.77, 16.6%	0.75, 7.0%	0.52, 4.8%	7.14, 43.5%
Nitrogen (Mt)	32.81, 2.5%	28.32, 2.1%	121.54, 9.1%	185.82, 13.9%	368.50, 27.6%
Phosphorus (Mt)	1.56, 0.8%	2.80, 1.5%	11.71, 6.2%	42.00, 22.1%	58.06, 30.6%

Notes: Values are mean \pm 1 S.E. with number of samples in brackets

**The overall data for root turnover rates are average of all root sizes and the rest are sum of different root sizes. Significant differences ($\alpha = 0.05$) among root size classes are indicated by different letters.*

†Total biomass, production, and nutrients in the boreal forest for root diameter size classes and their proportion of boreal vegetation are reported based on 1.2×10^7 km² land area of the boreal forest (Apps et al. 1993; Dixon et al. 1994; Jackson et al. 1997).

‡The proportion of biomass is based on data from Dixon et al. (1994); production based on data from Gower et al. (2001); nitrogen based on data from Potter & Klooster (1997); and phosphorus based on data from Bashkin (2006). The percentage is calculated as biomass, nitrogen and phosphorus contents in this present study divided by the global data in these cited studies.

Influence of species traits on fine roots

Stands dominated by broad-leaved species generally had lower fine root biomass and

production but higher turnover rates than those dominated by needle-leaved species (Table 2.2). Broad-leaved species dominated stands contained more N but similar P to those dominated by needle-leaved species (Table 2.2).

There were no differences in fine root biomass and turnover rates between the stands dominated by early- and late-successional species (Table 2.2). However, fine root production was higher in stands dominated by early-successional species than by those late-successional species. N contents in fine roots were marginally higher ($P = 0.044$) in stands dominated by early-successional species than by those late-successional species. When major genera were analysed separately, *Betula* and *Populus* stands had relatively higher fine root biomass but lower production than *Abies*, *Pinus*, and *Picea* (Table 2.2). The turnover rates of fine roots were higher in *Betula* and *Populus* (Table 2.2). Also, *Betula* and *Populus* stands contained higher N contents in fine roots (Table 2.2).

Table 2.2 Fine root biomass, production, turnover rates, and nutrients in the boreal forest by functional groups.

Life trait	Biomass (Mg ha ⁻¹)	Production (Mg ha ⁻¹ year ⁻¹)	Turnover (year ⁻¹)	Nitrogen (kg ha ⁻¹)	Phosphorus (kg ha ⁻¹)
Broad-leaved	2.12 ^B ± 0.10 (61)	2.01 ^B ± 0.17 (22)	1.15 ^A ± 0.23 (12)	45.32 ^A ± 3.69 (3)	1.32 ^A ± 0.34 (3)
Needle-leaved	2.92 ^A ± 0.36 (637)	2.31 ^A ± 0.12 (168)	0.76 ^B ± 0.06 (71)	21.04 ^B ± 1.56 (98)	1.70 ^A ± 0.21 (59)
Early-successional species	2.91 ^A ± 0.14 (247)	2.62 ^A ± 0.23 (94)	0.86 ^A ± 0.15 (22)	32.1 ^A ± 6.3 (10)	/
Late-successional species	2.81 ^A ± 0.12 (451)	1.94 ^B ± 0.18 (96)	0.80 ^A ± 0.06 (61)	20.6 ^B ± 1.7 (91)	1.70 ± 0.21 (59)
<i>Abies</i>	2.83 ^B ± 0.50 (22)	4.39 ^A ± 0.62 (3)	0.61 ^B ± 0.12 (9)	12.7 ^B ± 3.86 (12)	/
<i>Betula</i>	4.15 ^A ± 0.59 (19)	1.85 ^B ± 0.33 (8)	1.22 ^A ± 0.56 (3)	79.0 ^A ± 9.12 (3)	/
<i>Picea</i>	2.78 ^B ± 0.13 (409)	1.80 ^B ± 0.18 (85)	0.84 ^{AB} ± 0.07	22.0 ^B ± 1.81 (78)	1.70 ± 0.21 (59)
<i>Pinus</i>	2.52 ^B ± 0.13 (199)	2.80 ^A ± 0.27 (75)	0.61 ^B ± 0.17 (11)	26.3 ^B ± 2.58 (8)	/
<i>Populus</i>	4.80 ^A ± 0.55 (29)	1.96 ^B ± 0.47 (11)	1.28 ^A ± 0.26 (9)	46.7 ^A ± 1.0 (3)	/

Notes: Values are means ± 1 S.E with number of samples in brackets. Different capital letters indicate significant difference ($\alpha =$ between leaf habit (broadleaved vs. needle-leaved), between successional groups (pioneer vs. late-successional), and among major genera.

Stands dominated by early-successional species had deeper root systems, whereas those dominated by late-successional species had shallower root systems (Figure 2.1). Vertically, fine root biomass was greatest at the top layer, with half the biomass in the top 10-cm of soil (including forest floor layer). For all groups, 90% of the biomass occurred in the top 30-cm surface layers (Figure 2.2).

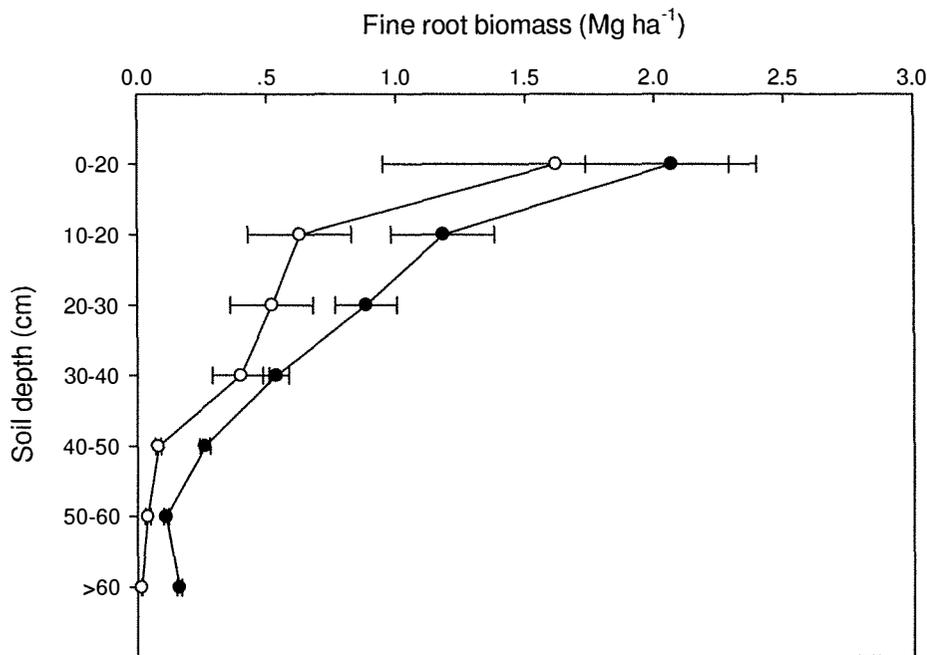


Figure 2.1 Vertical fine root distribution patterns of early-successional and late-successional species in the boreal forest.

Notes: Values are mean \pm 1 S.E. ● = early-successional species, ○ = late successional species.

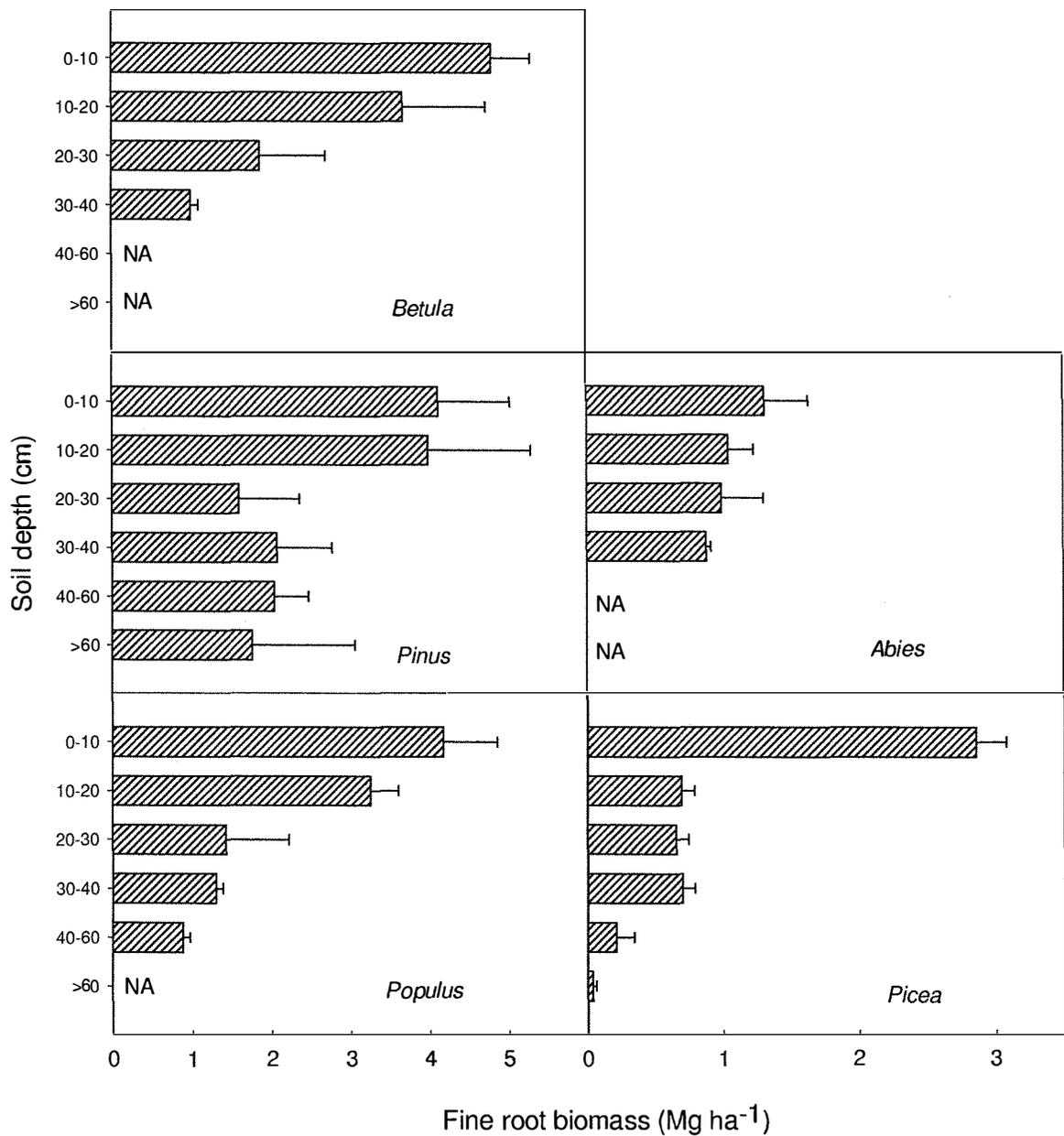


Figure 2.2 Vertical fine root distribution patterns of main dominated genera in the boreal forest.

Notes: Means with 1 S.E. are reported. NA, data not available.

Influences of environmental factors on fine roots

When all data were pooled, fine root biomass in the boreal forest was related to climate variables (Figure 2.3). It decreased significantly with increasing latitude, by a decline of 0.10 Mg ha⁻¹ per degree latitude (Figure 2.3A). Fine roots biomass increased with increasing mean annual temperature (Figure 2.3B) and precipitation (Figure 2.3C). The linear regression analysis also showed a significant increase of fine root biomass at a rate of 0.18 Mg ha⁻¹ per 1 °C of temperature and 0.43 Mg ha⁻¹ per 100 mm year⁻¹ of precipitation along the entire geographic range of the boreal forest. Climate data (mean annual temperature and precipitation) collectively explained 18% of the variation in fine root biomass (Table 2.3). When means were used in the regression analysis, similar patterns were observed with lower *P* but higher *r*² values (Figures 2.3D–F).

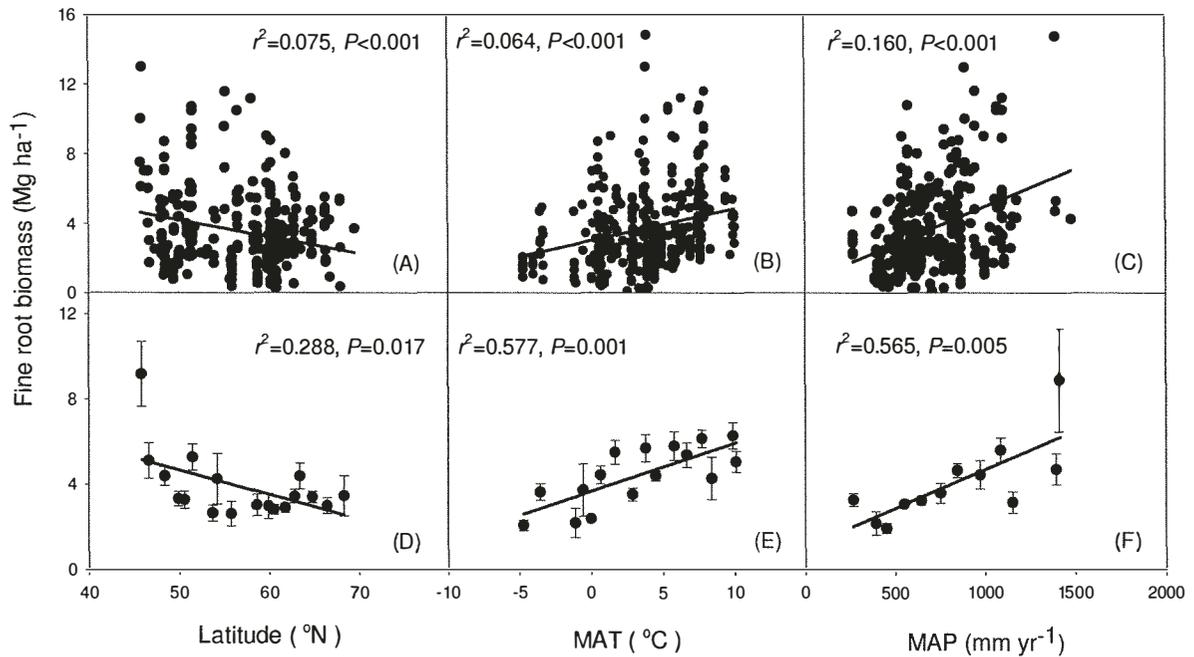


Figure 2.3 Fine root biomass in relation to latitude, mean annual temperature, and mean annual precipitation.

Notes: The top three Figures (A, B, and C) show individual data while the bottom three (D, E, and F) show means with 1 S.E. (see the text). MAT = mean annual temperature (°C), MAP = mean annual precipitation (mm year⁻¹).

When life traits were considered, fine root biomass in stands dominated by broad- and needle-leaved species decreased with latitude. Fine root biomass in two life traits increased with mean annual temperature and precipitation (Figures 2.4A–C). Multiple regression analysis showed that mean annual temperature and precipitation explained 14% and 17% of variability in fine root biomass for these two life history traits, respectively (Table 2.3).

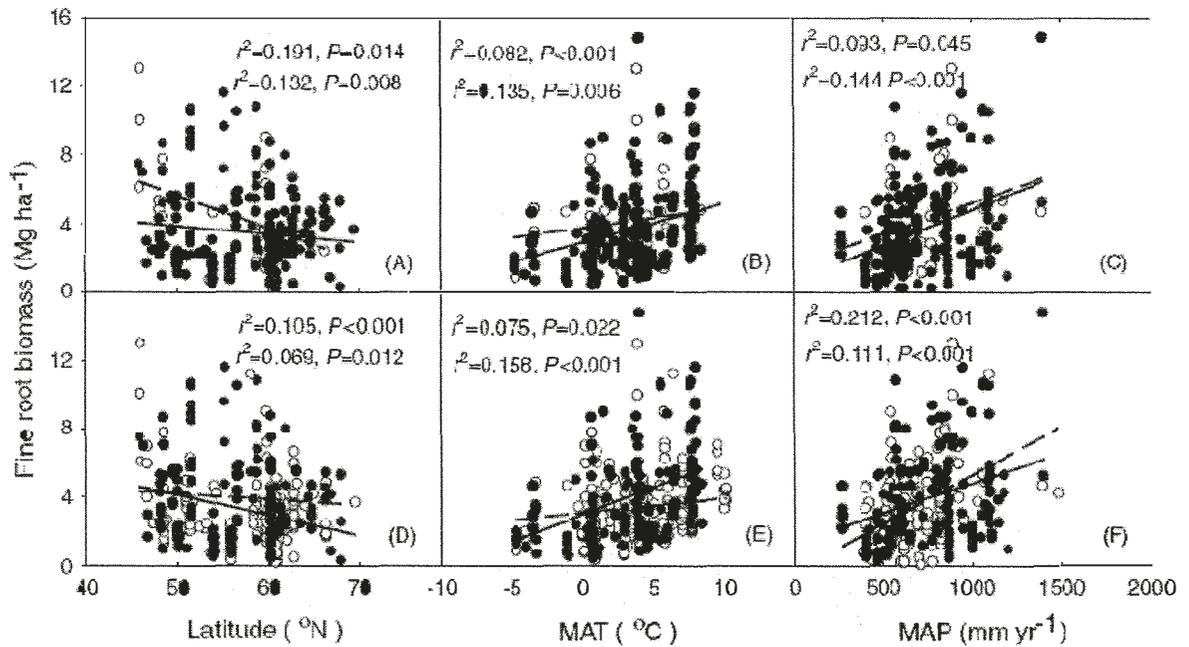


Figure 2.4 The relationship between fine root biomass and latitude, mean annual

temperature and mean annual precipitation in the boreal forest dominated by broad-leaved

vs. needle-leaved species, and in the boreal forest dominated by early- vs. late-successional.

Notes: The coefficients of determination (r^2) and P values are shown in each panel for broad-

leaved (the first line) vs. needle-leaved (the second line) (A, B, and C) and for early- (the first

line) vs. late-successional species (the second line) (D, E, and F). ○ = broad-leaved (dashed

line), ● = needle-leaved (solid line), MAT = mean annual temperature (°C), MAP = mean

annual precipitation (mm year⁻¹).

Table 2.3 Results of multiple regression analyses of fine root biomass, production, turnover rates, and nutrients in relation to mean annual temperature and mean annual precipitation.

Life trait	r^2	MAT	MAP	MAT×MAP
<i>Biomass</i>				
All data	0.179***	28.934***	49.680***	0.5001ns
Broad-leaved	0.142*	2.458*	4.020*	0.716ns
Needle-leaved	0.174***	23.510***	24.492***	1.580ns
Pioneer species	0.183***	3.819*	21.214***	2.085ns
Late-successional species	0.175***	31.639***	3.428ns	0.006ns
<i>Production</i>				
All data	0.070**	11.169**	0.764ns	0.109ns
Broad-leaved	0.481**	17.262***	6.941*	2.631ns
Needle-leaved	0.168*	2.351*	2.248*	2.063*
Pioneer species	0.128*	8.039**	1.683ns	0.149ns
Late-successional species	0.080ns	5.9178	2.067ns	0.455ns
<i>Turnover rates</i>				
All data	0.159ns	4.721*	0.055ns	0.474ns
Broad-leaved	0.307ns	1.323ns	0.526ns	0.056ns
Needle-leaved	0.110ns	1.245ns	0.047ns	0.926ns
Pioneer species	0.286ns	2.657ns	1.630ns	0.265ns
Late-successional species	0.104ns	1.889ns	0.001ns	0.306ns
<i>N contents</i>				
All data	0.183*	2.088*	5.978*	1.208ns

Broad-leaved	/	/	/	/
Needle-leaved	0.175ns	0.043ns	6.745*	0.244ns
Pioneer species	0.421**	66.519***	4.005ns	0.356ns
Late-successional species	0.202ns	0.022ns	5.178*	0.115ns
<i>P contents</i>				
All data	0.355**	109.7***	57.539***	1.590ns
Broad-leaved	/	/	/	/
Needle-leaved	0.286ns	1.205ns	0.424ns	0.502ns
Pioneer species	/	/	/	/
Late-successional species	0.386ns	1.205ns	0.424ns	0.502ns

*Notes: The r^2 values, F ratios, and their significance are shown for each of the dependent variables. ns, $P > 0.05$ (not significant); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. MAT = mean annual temperature ($^{\circ}\text{C}$), MAP = mean annual precipitation (mm year^{-1}).*

Fine root biomass in early-successional species-dominated stands increased with mean annual temperature and precipitation, and decreased with latitude. Fine root biomass in late-successional-species dominated stands showed similar patterns in relation to latitude, mean annual temperature and precipitation (Figures 2.4D–F). Mean annual temperature and precipitation collectively explained $\approx 18\%$ of the variation in fine root biomass for both life history traits (Table 2.3).

When all data were pooled, fine root production increased with mean annual temperature and precipitation, but did not change with latitude (Figures 2.5A–C). Similarly, fine root production for functional groups (broad- vs. needle-leaved, early- vs. late-successional)

associated significantly only with mean annual temperature. Mean annual temperature and precipitation data explained 10–40% of the variation in fine root production (Table 2.3). Fine root turnover, when pooled, increased with mean annual temperature, and decreased with latitude (Figures 2.5 D and E). There were no significant effects of mean annual precipitation on fine root turnover rates (Figure 2.5 F). Fine root turnover rates for most functional groups were not significantly related to mean annual temperature and precipitation but this may be due to small sample sizes (Table 2.3).

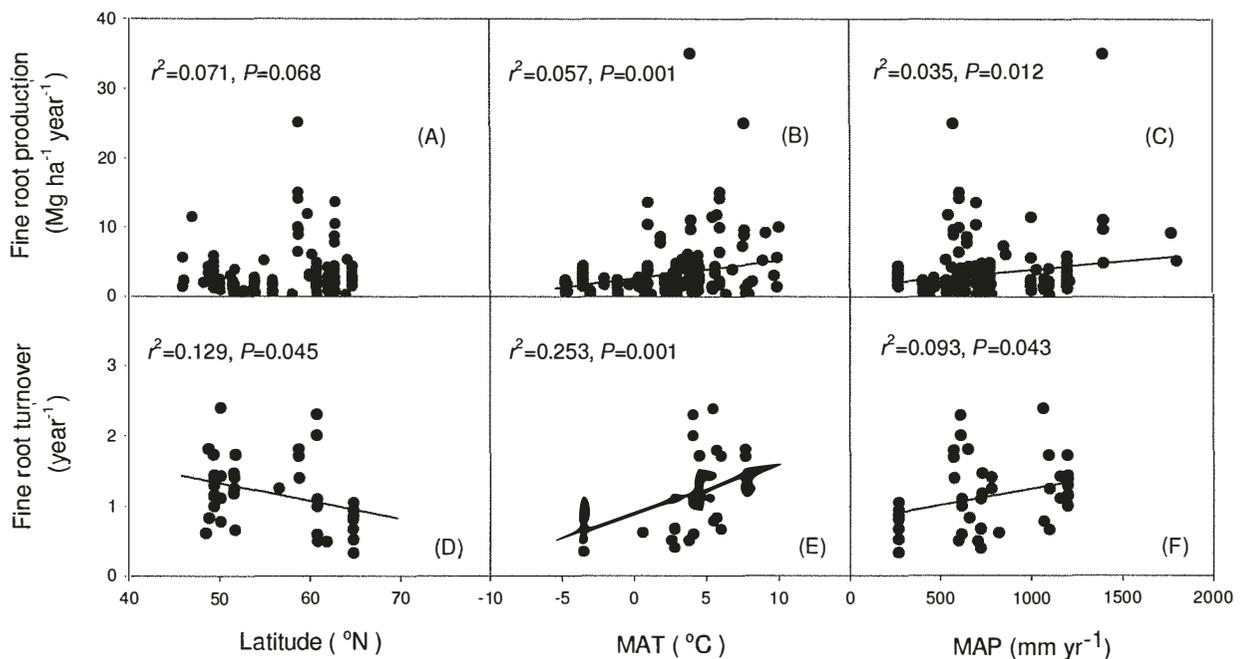


Figure 2.5 Fine root production (A, B, and C) and turnover rates (D, E, and F) in relation to latitude, mean annual temperature, and mean annual precipitation.

Notes: MAT = mean annual temperature (°C), MAP = mean annual precipitation (mm year⁻¹).

When all data were pooled, fine root N and P contents in the boreal forest were also affected by climate variables (Figure 2.6). N contents increased significantly with increasing latitude (Figure 2.6A) while P contents did not change (Figure 2.6D). Both N and P contents decreased with increasing mean annual temperature (Figures 2.6B and 6E) and precipitation (Figures 2.6C and 6F). Mean annual temperature and precipitation explained 18% and 36% of the variation in fine root N and P contents, respectively (Table 2.3).

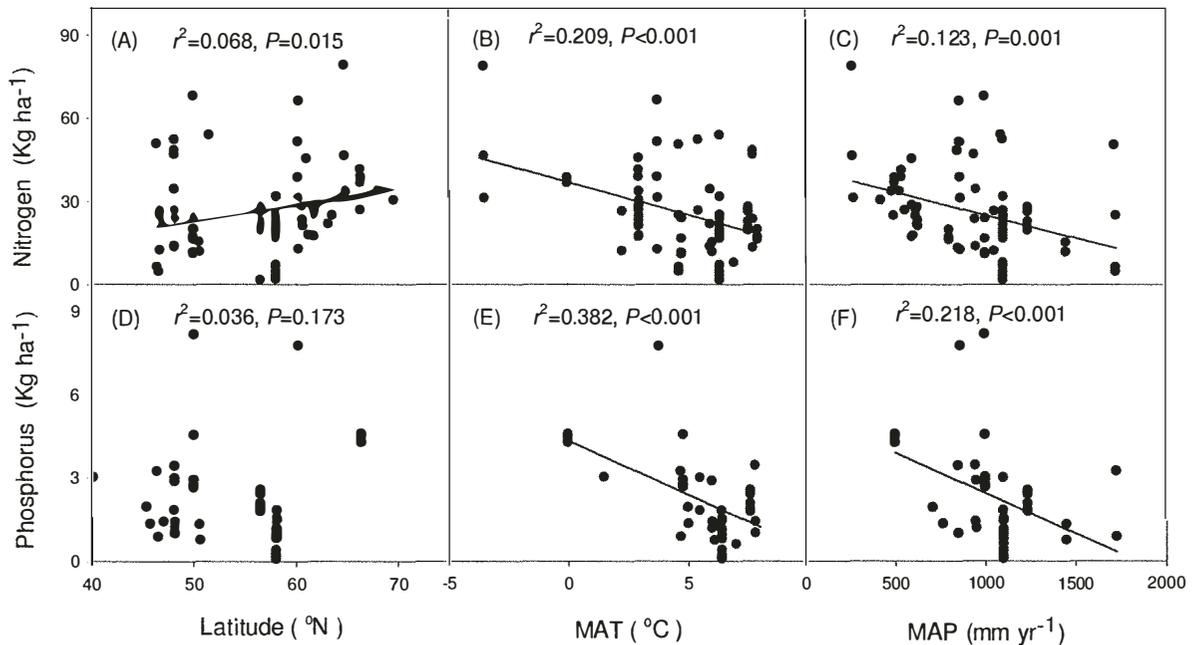


Figure 2.6 Fine root nitrogen (A, B, and C) and phosphorus contents (D, E, and F) in relation to latitude, mean annual temperature, and mean annual precipitation.

Notes: MAT = mean annual temperature (°C), MAP = mean annual precipitation (mm year⁻¹).

When all data were pooled, fine root biomass in the boreal forest increased with respect to soil pH, but decreased with respect to soil total N and P (Figure 2.7).

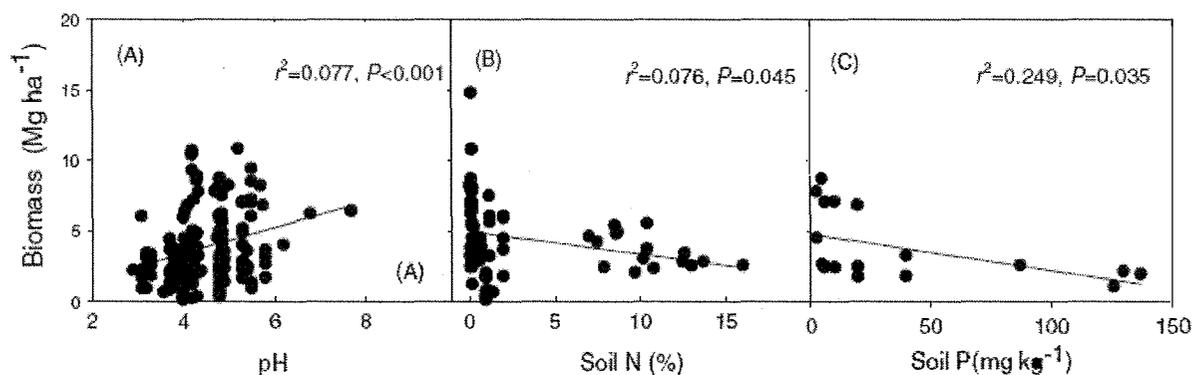


Figure 2.7 Fine root biomass in relation to soil pH (A), soil total nitrogen (B), and soil phosphorus (C).

Fine root biomass changed with stand development (Figure 2.8). Fine root biomass in the broad-leaved stands increased for stands up to 70 years old (Figure 2.8A), whereas in needle-leaved stands, fine root biomass showed a general trend of increase for stands up to 90 years old and declined thereafter (Figure 2.8B). Also, fine root biomass in both early-successional and in late-successional species changed with respect to stand age (Figures 2.8C and D). For the two species having the largest number of data points, fine root biomass of *Picea abies* by quadratic regression analysis showed a significant increase with stand age up to 70 years old (Figure 2.8E), and that of *Pinus sylvestris* increased to 100 years old, thereafter decreasing (Figure 2.8F).

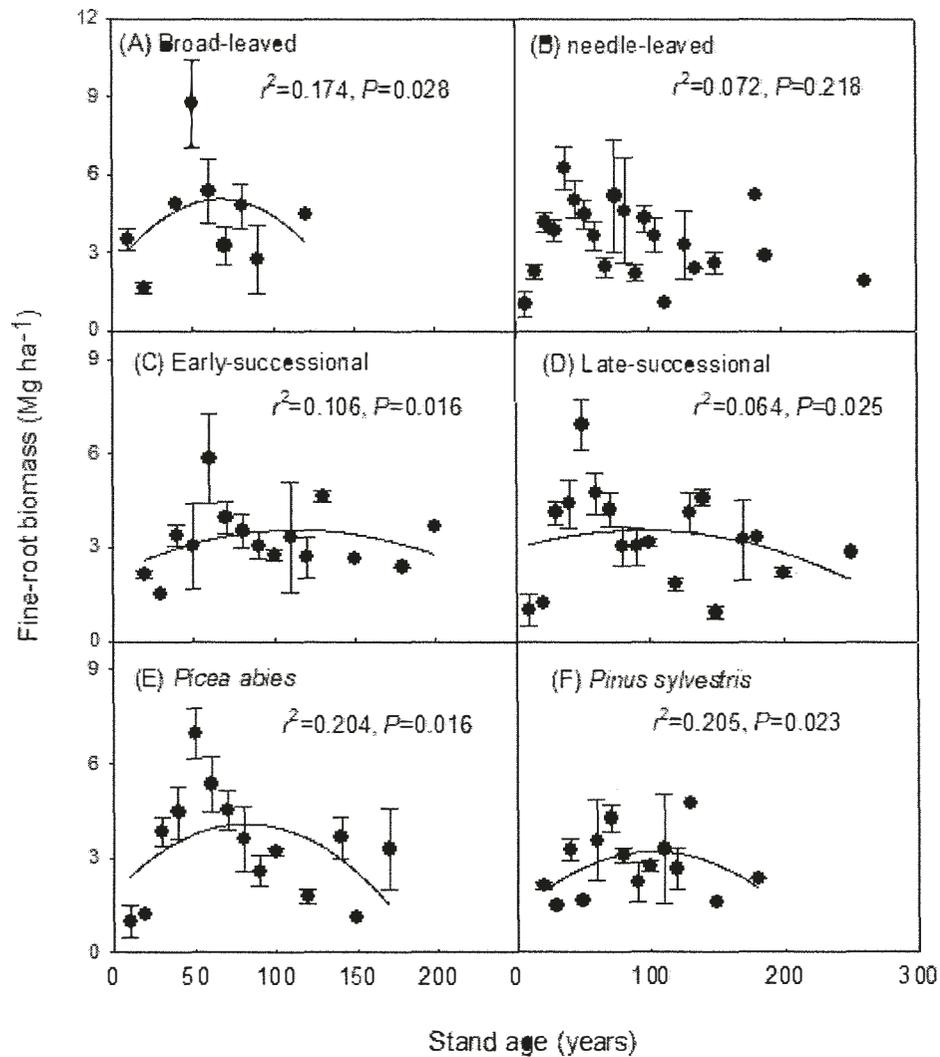


Figure 2.8 Fine root biomass of broad-leaved (A), needle-leaved (B), early-successional (C), late-successional (D), *Picea abies* (E), and *Pinus sylvestris* (F) in relation to stand development.

Discussion

Differences among root sizes

Root biomass in the boreal forest varied with root size: it was higher in coarse roots >5cm in

diameter than in roots of <1, 1-2, 2-5 cm classes, which did not differ from each other (Table 2.1). Similar observations have been reported in boreal (Ruess *et al.* 2006; Persson & Stadenberg 2009), temperate (Fujii & Kasuya 2008) and tropical forests (Sanford 1989; Maycock & Congdon 2000), indicating that the large size classes of roots represent large biomass pools. The average biomass of fine roots <2 mm in diameter was 5.28 Mg ha⁻¹ biomass ($n=765$), similar to the estimate by Jackson *et al.* (1997) who reported a mean of 6 Mg ha⁻¹ from a sample size of 5 stands for boreal forest. On average, fine root biomass constituted 16% of all roots in the boreal forest (Table 2.1).

On average, the production of fine roots was 2.82 Mg ha⁻¹ year⁻¹, accounting for 66% of total root production. Therefore, smaller, younger size classes, while shorter-lived and much faster to decompose, contributed substantially more to total root production and/or the annual C fluxes through the root system (Pregitzer *et al.* 2002; Ruess *et al.* 2003). Both production and turnover rates decreased with root diameter size, resulting in no significant differences in net standing crop biomass among roots <5 mm diameter size classes (Table 2.1). Due to the high amount of biomass, coarse roots >5mm were found to contain more N and P contents than middle (2-5 mm) and fine roots in this present study although nutrient concentrations might be higher in fine roots (Van Rraag *et al.* 1988; Tripathi *et al.* 1999; Gordon & Jackson 2000; Peri & Lasagno 2010).

Combining the land area of 1.2×10^7 km² for the boreal forest (Dixon *et al.* 1994; Jackson *et al.* 1997) with the data for root characteristics (Table 2.1), the boreal forest is estimated to have a total root biomass of 40.6 Gt, amounting to 13.9% of global terrestrial root biomass (Jackson *et al.* 1997) and 20.8% of the total boreal forest vegetation. The fine root biomass was 6.3 Gt, which was 8.1% of global total fine root biomass. Our estimate of fine root

biomass is 12% lower than the estimate by Jackson *et al.* (1997), likely be due to different sampling sizes (765 vs. 5).

The fine root production in the boreal forest was 2.8 Gt year⁻¹, about 73% of total root production and 32% of the total boreal forest production (Marschner & Rengel 2007). Total root production in the boreal forest was 3.9 Gt year⁻¹, about 43.5% of the total boreal forest production and 4% of the total global terrestrial production (Melillo *et al.* 1993). On average, root turnover rate in the boreal forest was 0.74 year⁻¹. Ruess *et al.* (1996) found that roots turn over annually in central Alaska, suggesting that it is possible for the boreal forest root systems to have high turnover rates. However, turnover rates decreased with root size. This finding is consistent with results from previous studies (Gaudinski *et al.* 2001; Matamala *et al.* 2003; Baddeley & Watson 2005).

Influence of species traits on fine roots

We found that broad-leaved and needle-leaved stands had 2.12 and 2.92 Mg ha⁻¹ fine root biomass, respectively. Vogt *et al.*(1996), who included several studies with roots <5 mm ($n=38$ and 21 for broad-leaved and needle-leaved, respectively), yielded much lower means (1.29 and 1.03 Mg ha⁻¹, respectively). Jackson *et al.* (1997) found a similar patterns for these two different leaf-habit types of temperate forest (7.8 vs. 8.2 Mg ha⁻¹). However, stands dominated by broad-leaved species of *Betula* and *Populus* had higher fine root biomass than needle-leaved species such as *Abies*, *Picea*, and *Pinus* (Table 2.2). The average fine root biomass for broad-leaved stands was calculated not only from *Betula* and *Populus*, but also from other broad-leaved species. The same was true for the calculation of needle-leaved stands, which contributed to the differences at genera and species scales. Another reason might due to the stand age effect which will be addressed below. In some other temperate

stands, fine root biomass has been found to be higher in broad-leaved than in needle-leaved species (Farrish 1991; Vogt *et al.* 1996; Leuschner & Hertel 2003; Noguchi *et al.* 2007). The reason for these contradictory observations between boreal and temperate or tropical forests is unclear.

In this present study, fine root biomass of both early- and late-successional species showed a continuous decrease with soil depth (Figure 2.1), in accordance with many studies which indicated that this root profile usually corresponds to a vertical decrease of nutrient and water storage capacity in soil profiles (*e.g.*, Sainju & Good 1993; Curt *et al.* 2001; Soethe *et al.* 2006). The root systems were concentrated in the upper layer of soil, especially in the organic horizons for all dominant species (Figure 2.2), which appears to be a general pattern in northern forest ecosystems (Brandtberg *et al.* 2000; Wang *et al.* 2002; Claus & George 2005; Borja *et al.* 2008; Brassard *et al.* 2009). In northern forests, this vertical distribution pattern emphasizes the importance of the surface layer for the availability of water and nutrients, as well as the activity of microorganisms (Hendrick & Pregitzer 1996).

Although fine root biomass in stands dominated by both early- and late-successional species decreased with soil depth, the vertical fine root distribution patterns were not the same (Figure 2.1). Root systems of early-successional species penetrated to deep soil and were more effective in exploiting an unoccupied and a more homogeneous substrate, resulting from either geologic deposition or nutrient and water redistribution following forest disturbances and through regular, albeit slow soil forming processes such as leaching, *e.g.*, podzolization process. This mechanism could enable these trees to use water and nutrients in deeper layers. Conversely, late-successional species that are typically shallow rooted compete better for nutrients concentrated near the surface as the result of biocycling and accumulation

of a forest floor layer. Gale & Grigal (1987) also found that early-successional or intolerant species had a significantly higher proportion of roots occurring deeper than did late-successional or tolerant species. In fact, maximum rooting depth is usually established during the seedling stage (Lyr & Hoffman 1967). Therefore, young stands, because of their more rapid biomass accumulation, are expected to accumulate nutrients more rapidly than their older counterparts (Yanai *et al.* 2006). By contrast, recycling of nutrients by decomposition is proportionally more important for older stands with relatively more roots near the surface where most mineralization occurs.

Similar vertical patterns occurred among species within each of the two successional species groups (Figure 2.2), suggesting that root vertical patterns are genetically controlled since consistent root distributions for some species are reported across many sites (Holch 1931; Yeager 1935; Bannan 1940). In the boreal forest in Alberta, Canada, for instance, the soil profile has a definite vertical partitioning of bulk density (clay soils have higher bulk density in subsurface which physically limits root growth) and resources that favors growth of shallow *Picea glauca* roots over deeper *Pinus banksiana* roots (Kimmins & Hawkes 1978; Strong & Laroi 1983). The observed high amounts of fine roots in surface layers may reflect the distribution of nutrient uptake despite somewhat species-specific differences (Figure 2.2). In Hubbard Brook Experimental Forest in New Hampshire, owing to the interaction between processes of biological decomposition and tree nutrient uptake, P was tightly regulated within the surface soil (Wood *et al.* 1984), resulting in much root biomass found in the surface soils at the late successional stage.

The differences in vertical root distributions between deep rooted intolerant early-successional species and shallow rooted tolerant late-successional species are

potentially important in nutrient cycling. In secondary succession, the establishment of deep rooted intolerant early-successional species on a disturbed site provides increased nutrients to the forest floor from deeper soil via litterfall and foliar leaching (Kimmins & Hawkes 1978). As a stand ages and early-successional species mature, increased amounts of root detritus and other organic material enrich the soil, making it more favorable for further root growth (Grier *et al.* 1981). While the vertical distribution pattern for individual species dominated stands seems to be apparent, in boreal mixedwoods canopy succession along with understory vegetation takes place through stand development (Wang *et al.* 2002; Hart & Chen 2006; Hart & Chen 2008). The mechanisms of how vertical root distribution changes with stand development and how individual species perform in mixed communities are unclear, but may be partially attributable to difficulties in species sorting of roots (Wang *et al.* 2002).

Quantifying patterns of allocation to fine roots and identifying controls on fine root production is crucial to the understanding of ecosystem structure and function, and in predicting how these ecosystems will respond to disturbance (Clark *et al.* 2001). In this present study, fine root production in the boreal forest averaged $2.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (Table 2.1). Boreal needle-leaved coniferous had higher fine root production than broad-leaved deciduous species (Table 2.2), consistent with the observation that evergreen trees appear to allocate a greater proportion of photosynthate to fine roots than deciduous trees (Vogt *et al.* 1986). In the boreal forest in interior Alaska, Ruess *et al.* (1996) found that fine root production (max-min method) accounted for an average of 32% total stand production for deciduous stands and 49% total stand production for coniferous stands. In the boreal forest in Saskatchewan and Manitoba, Canada, the fraction of NPP allocated to coarse and fine root production is almost twofold greater for evergreen conifers than deciduous (Gower *et al.*

1997; Steele *et al.* 1997; Gower *et al.* 2001). Steele *et al.* (1997) estimated fine root production as 0.59 and 2.35 Mg ha⁻¹ year⁻¹ for aspen and black spruce (*Picea mariana*), respectively, by using minirhizotron tubes, but found significantly lower estimates by using ingrowth cores. In a 38-year-old Scots pine (*Pinus sylvestris*) stand in eastern Finland, fine root production was 7.21 Mg ha⁻¹ year⁻¹ as determined by sequential soil cores and 3.76 Mg ha⁻¹ year⁻¹) as determined by the root ingrowth core method (Makkonen & Helmisaari). The large variation of fine root production estimates among various sampling methods highlights a significant challenge to accurately determine root production.

It is generally considered that fine root turnover is important to the global C budget as well as to nutrient cycling in ecosystems and to the success of individual plants (Hendricks *et al.* 1993; Eissenstat & Yanai 2002). Although data are scarce and root turnover rates vary greatly among different methods, the available data in this present study showed that fine roots of the boreal forest turned over about 1.0 year on average. Our analysis provides, to the best of our knowledge, the first biome-level estimate in the boreal forest for fine root turnover, which could help improve estimates of C cycling in global biogeochemical models. In addition to methodological challenges, the large variation in fine root turnover rates (Table 2.1) is attributable to tree species composition, stand age, and soil characteristics. Fine roots of broad-leaved species turned over faster than needle-leaved species (Table 2.2). Therefore, the higher fine root biomass in needle-leaved stands as mentioned above could be also a result of its lower turnover rates.

In this present study, fine roots of the boreal forest on average contained 51 kg ha⁻¹ for N and 3.6 kg ha⁻¹ for P (Table 2.1). The boreal forest region is estimated to cover 1200 Mha (Dixon *et al.* 1994); using this figure, the N and P pools of fine roots in the boreal forest was

estimated to be 61 Mt N and 4.4 Mt P, about 12.7% and 9.9% of global fine root N and P, respectively (Jackson *et al.* 1997). These estimates were lower than those by that used the average of global fine root [N] and [P] data from Jackson *et al.* (1997) (the corresponding estimates for N and P pools in the boreal forest using the global average from Jackson *et al.* (1997), were 84 and 7.9 Mt, respectively). The higher fine root N and P concentrations and biomass from Jackson *et al.* (1997) may be a result of their small sample sizes ($n=24$ for N and 14 for P, respectively) that were available fourteen years ago. Based on the estimated total N and P in the global terrestrial biota (Pierrou 1976; Soderlund & Svensson 1976; Schlesinger 1997; Reeburgh 1997), the root N and P pools in the boreal forest would be 2.9% and 3.2% of global terrestrial vegetation. Furthermore, stands dominated by broad-leaved species had higher N content in fine roots than by needle-leaved species, likely attributable to higher N concentration in fine roots of broad-leaved species. However, physiological reasons for this observed difference is unclear; needle-leaved species appear to have a higher N-N-resorption and use efficiency, and the needle-leaved habit is an adaptation to habitats with low nutrient availability (Givnish 2002; Yuan *et al.* 2006; Yuan & Chen 2009b).

Influences of environmental factors on fine roots

Discerning how climatic patterns and soil processes influence fine root growth is important given current and projected future climate and vegetation changes. Climatic variables are important regulators that affect fine root growth (Vogt *et al.* 1996; Gill & Jackson 2000; Norby & Jackson 2000; Silver & Miya 2001), as well as green and senesced leaves (Yuan & Chen 2009a). Previous studies have demonstrated that soil temperature, moisture, and nutrient availability control, at least in part, the timing and duration of root growth (Pregitzer *et al.* 2000; Norby & Jackson 2000). In this present study, the fine root biomass, production,

turnover rates, and nutrient contents in the boreal forest were weakly but significantly associated with the selected environmental factors (Figures 2.3–8), confirming the importance of abiotic regulation on fine roots.

It has been found that fine root biomass is higher in temperate forests than in boreal forests (Vogt *et al.* 1996; Jackson *et al.* 1997; Finer *et al.* 2007). In a warming experiment in boreal forest, Majdi and Öhrvik (2004) reported that soil warming led to increased root production and mortality. In our data set, fine root biomass increased with mean annual temperature (Figure 2.3). However, different forest types appeared to be influenced by different climatic variables. For example, maximum monthly temperature explained 65% of the variation in fine root biomass for needle-leaved stands, but not for broad-leaved stands (Vogt *et al.* 1986). Although stands dominated by both needle- vs. broad-leaved and early- vs. late-successional species showed significant associations with mean annual temperature, the slopes differed (Figure 2.4). At the species (genus) level, *Picea* and *Pinus* showed significant increases of fine root biomass with mean annual temperature and precipitation. In contrast, fine root biomass of *Populus* was not significantly related with any of climatic factors. The reasons for the species-specific differences were unclear. With all data pooled, fine root production in the boreal forest increased with increased mean annual temperature (Figure 2.5). This positive relationship appears, at least partly, to be a result of the increase of mineralization with rising temperature, which improves N availability and stimulates fine root growth (Pregitzer *et al.* 2000).

Root turnover appears to be generally slower in species from cold environments (Eissenstat & Yanai 1997). It has been suggested that higher soil temperatures might increase plant root turnover. Hendrick and Pregitzer (1993), for example, examined fine root turnover

in two northern hardwood stands in Michigan and found roots turned over faster at the southern site and speculated that warmer soil temperatures at the southern site might be the cause. In this present study, we found that fine root turnover rates increased with mean annual temperature (Figure 2.5), suggesting that temperature is important in regulating fine root turnover in the boreal forest. If soils warm as a result of global climate change, this could lead to higher nutrient availability, which could in turn result in higher rates of root turnover (Ryser 1996). The exponential increase in maintenance respiration with temperature (Eissenstat & Yanai 1997) can be another potential cause for the increase in turnover with higher temperatures. The increases in microbial activity and root-feeding herbivores with soil temperature can also contribute to these turnover patterns and might result in higher nutrient availability (Boone *et al.* 1998). Although contradictory evidence still exists (Burton *et al.* 2000), our study geographically expanded previous work (Gill & Jackson 2000) in quantifying fine root demography along a latitudinal temperature gradient.

In this meta analysis, fine root biomass in the boreal forest was found to increase with mean annual precipitation (Figure 2.3, Table 2.3). Previous studies in temperate forests (Leuschner & Hertel 2003; Meier & Leuschner 2008) and tropical forests (Sanford 1989; Sanchez-Gallen & Alvarez-Sanchez 1996; McGroddy & Silver 2000) also showed a positive relationship between fine root biomass and precipitation. In greenhouse and garden experiments with boreal tree saplings, irrigation treatment was found to stimulate fine root growth (Fort *et al.* 1997). These findings suggest that root growth the boreal forest is sensitive to drought although these ecosystems are limited by temperature and soil nutrients. It has also been found that *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris* are drought-drought-sensitive species (Backes & Leuschner 2000; Dreyer *et al.* 2001), which contributed

to the observed relationship between fine root biomass and precipitation.

Our findings also illustrate the importance of soil moisture in determining patterns of root growth in boreal forest. Low precipitation generally causes a soil moisture deficit and reduces soil nutrient transport via mass flow and diffusion from soil surface to the roots, resulting in decreased nutrient availability at the root surface and a reduction in cell division and expansion (North & Nobel 1997).

Previous studies have reported that fine root production are higher during the wet years and seasons (*e.g.*, Yavitt & Wright 2001). Our findings also showed that fine root production and turnover in the boreal forest increased with increasing precipitation (Figure 2.5), but again, reasons remain unclear. At a global scale, it is believed that root turnover is not related to precipitation across different ecosystems (Gill & Jackson 2000). This suggests potentially different primary climatic factors in regulating root turnover at the regional and global scales. Eissenstat *et al.* (2000) suggested that increasing N concentration in fine roots reduced longevity (*i.e.*, stimulated turnover rates due to increasing respiration costs with higher N levels). We also found that fine root turnover rates were positively related to N concentration ($r^2=0.21$, $P<0.05$, data not shown), which generally increases with rainfall.

In this present study, fine root biomass in the boreal forest was found to be positively related to soil pH (Figure 2.7A). Several studies appear to support our findings. For example, Leuschner *et al.* (2003) and Helmisaari *et al.* (2009) have studied the effect of soil acidity on fine root density in Norway spruce (*Picea abies*) and reported that on the most acidic sites fine root density was lower than on the least acidic sites. This was attributed to the sensitivity of spruce fine roots to hydrogen or aluminium ions. In southern Germany, acid irrigation depressed root growth rate, while liming increased root growth in 80-year old *Picea abies*

stands (Hahn & Marschner 1998). In acidic soils, microbial activity is inhibited, whereas soils with a higher pH can potentially stimulate the growth of fine roots (Haynes 1982; Francis 1986). $[Al^{3+}]$ in soil solution has been found to be high in soils with pH <5.5, which can inhibit root elongation and reduce the capacity of roots to explore soil for moisture and nutrients (Valle *et al.* 2009). The concentration of Al^{3+} also affects the P uptake of roots by complexing P so it is no longer soluble and may actually form precipitates within the root, physically ‘clogging’ nutrient pathways inside the cell (Kochian 1995; Mimmo *et al.* 2009). Jentschke *et al.* (2001) reported that soil acidity alters the vertical pattern of fine roots in *Picea abies* stands by increasing biomass in the humus layer and decreasing biomass in the mineral soil. However, despite lower fine root production, plants may allocate more production to fine root growth at acidic nutrient-poor sites as a response to high N and P residence times in biologically inactive soils (Vogt *et al.* 1996).

Soil resource availability greatly impacts plant growth but its effects on fine roots are still unclear (Nadelhoffer 2000). Fine root biomass has been reported to be lower in more fertile sites in both needle-leaved and deciduous stands in the Oregon Cascade Mountains (Keyes & Grier 1981). In 13 deciduous and needle-leaved forest stands in Wisconsin and Massachusetts, fine root biomass significantly decreased as nitrification increased (Aber *et al.* 1985). In this present study, we found that fine root biomass in the boreal forest was negatively related to soil fertility (Figures 2.7B and C), consistent with previous studies (*e.g.*, Keyes & Grier 1981; Helmisaari *et al.* 2009). Soil fertility may, however, be less important in the boreal forest where N deposition from precipitation may be high enough in many areas. It may be temperature, rather than soil N as a growth-limiting factor. Our observed inverse relationships between fine root biomass and soil nutrients do not necessarily mean that fine

root production and turnover rates follow the same patterns, because fine roots may grow fast (high production) and also turnover fast (high mortality) as soil available nutrients increase, resulting in a decline of net standing biomass.

Fine root biomass showed an increase with stand age (Figure 2.8). This appears to be a result of rapid above- and belowground biomass accumulation associated with stand development (Odum 1969; Wang *et al.* 2002) coupled with an increased nutrient concentration during stand development (Vogt *et al.* 1981; Ehrenfeld *et al.* 1992; Finer *et al.* 1997; Yuan & Chen 2010a). Leaf litter of early-successional species comprised of broad-broad-leaved deciduous species, appears to improve soil nutrient availability in humus and top mineral layers (Tamm 1951; Pare & Bergeron 1995; Prescott *et al.* 2000c). With increasing aboveground production (*e.g.*, at canopy closure), leaf litter accumulates at the forest floor, resulting in a higher nutrient input. For young stands, the deep soil layers therefore might be proportionally more exploited by roots to meet the nutrient requirement of the rapid aboveground growth. This was exhibited by the early-successional species which had deeper roots than the late-successional species (Figure 2.2). Because fine root biomass was found to decline with increasing total N and P (Figure 7, also see Nadelhoffer 2000), the slightly elevated total N contents in soil in the old stands may indicate that soil nutrient status has negatively affected fine root biomass. It should be noted that although total N reflects the local humus content and is often positively associated with soil N availability (Keeney & Nelson 1982), much of the total N may be tied up in organic matter and simply unavailable to plant roots (Tiedemann & Klemmedson 1973); hence it is necessary to study how available soil nutrients impact root dynamics during stand development. However, the effect of stand age and nutrient availability on root biomass may not be separated. Canopy composition

tends to have a pronounced influence on root biomass and vertical structure (Wang *et al.* 2002). However, this review study design does not permit us to distinguish the effects of species composition from stand age in explaining variation in root distributions among stands of different ages.

Coile (1937) found that although root density increases with age, the horizontal and vertical extent of roots is reached at a certain tree age (\approx 30-year old), resulting in differences with stand development. The significant relationship between the fine root biomass and stand age in the boreal forest (Figure 2.8) suggests that fine root biomass increases until the canopy transition stage of stand development (Chen & Popadiouk 2002), and levels off or decreases at gap dynamics or at the old growth stage. Previous studies have reported similar stand age-related patterns (Vanninen & Makela 1999; Helmisaari *et al.* 2002; Claus & George 2005; Tang *et al.* 2009).

The maximum root biomass that a stand is capable of maintaining varies among tree species and environments and be reached at different ages in stand development. For example, Finer *et al.* (1997) found no significant differences in total standing root biomass among 48-232 year-old mixed boreal stands. There was no significant difference along an age series of young aspen stands (10-, 20, and 30-year-old) in Wisconsin, USA (Ruark & Bockheim 1987) and from 13- to 160-year-old Douglas-fir stands in western Washington, USA (Vogt *et al.* 1983b; Vogt *et al.* 1987). However, consistent with our findings (Figure Grier *et al.* (1981) found an increase in fine root biomass from 23- to 180-year-old *Abies amabilis* stands in Washington, USA; Persson (1983) reported that fine root biomass increased from 20- to 120-year-old *Pinus sylvestris* stands in Sweden. In a *Picea abies* chronosequence, stand age had an effect on standing fine root biomass with highest values in

young stands (Claus & George 2005). Along a spruce forest chronosequence in central Europe, fine- (<2mm), small- (2-5mm), and medium root (6-100 mm) biomass increased from 16- to 112-year-old stands and levelled off at an age of 142 years (Mund *et al.* 2002). In a chronosequence of four white pine (*Pinus strobus*) plantation stands (2-, 15-, 30-, and 65-65-years-old) in Southern Ontario, Canada, fine root biomass increased with stand age from 0.2 t ha⁻¹ in the 2-year-old stand to a peak of 6.2 t ha⁻¹ in the 30-year-old stand, after which it decreased to 3.5 t ha⁻¹ in the 65-year-old stand (Peichl & Arain 2007). At late-successional stages, production and the relative amount of tree foliage biomass decreases (Pare & Bergeron 1995; Ryan *et al.* 2004), consequently reducing the demand for nutrient and water supply from fine roots. Therefore, how fine root biomass changes with stand development and when it reaches its peak are likely dependent upon ecosystem types. However, total biomass production may be more partitioned to belowground in old-growth stands (Vanninen *et al.* 1996; Ryan *et al.* 2004; Vogel *et al.* 2008). Overall, our review is in agreement with most of the literature that shows fine root biomass decreasing with age in old-growth stands.

Summary

Our analyses showed that the fine root biomass, production, turnover rates, and nutrient contents in the boreal forest are likely affected by climatic and site variables. Fine root biomass, production, turnover rates, and nutrient contents in the boreal forest were strongly affected by latitude, temperature, and precipitation and varied with life-history traits of tree species. In addition, soil conditions (that appear to be coupled with climate conditions) also contributed to the dynamics of fine root biomass, production, and turnover. In the disturbance driven boreal forest, stand age appears to be a strong predictor for fine root dynamics; however, the influence of stand age is inherently coupled with soil nutrient availability and/or

canopy succession, especially for boreal mixedwoods. To gain a better mechanistic understanding of the controls of fine root dynamics, future studies will emphasize decoupling the influences of individual environmental factors, tree species traits, and stand development on fine root dynamics.

CHAPTER THREE: FINE ROOT BIOMASS

Introduction

In northern forest ecosystems, stand age is a key driver of forest ecosystem productivity, C storage/sequestration, and other ecosystem functions (Gower 2003). As a stand ages, a decline in forest aboveground net primary productivity (ANPP) is commonly observed in plantations and in natural forests (Kira & Shidei 1967; Gower *et al.* 1996a; Ryan *et al.* 2004), but the cause of reduced ANPP in aging forest stands remains enigmatic. The age-related ANPP decline observed has been hypothesized to be associated with 1) increasing (eco-) physiological constraints like hydraulic limitation to photosynthesis (Yoder *et al.* 1994), 2) natural resource limitations (*e.g.*, light and nutrients) (Schulze *et al.* 1995), 3) stand density and structure differentiations due to neighbourhood competition (Binkley *et al.* 2002), and 4) changes in intrinsic, genetically-regulated maturation (Day *et al.* 2002). However, these hypotheses have now been largely discredited (Peltzer *et al.* 2010).

Previous work on forest stand development focused on aboveground productivity. It remains unknown whether the commonly observed age-related decline in ANPP is applicable to the belowground root system. In particular, there are relatively few data on how fine root (*i.e.*, roots smaller than 2 mm in diameter, FR) biomass changes with forest stand age. This uncertainty reflects the difficulty of obtaining root biomass data and the difficulty of comparing different methods used to assess root biomass. Because fine root biomass (FRB) is a significant component of C stocks in terrestrial ecosystems, it is important to understand FRB dynamics for measuring and predicting ecosystem dynamics and ecosystem function (Jackson *et al.* 1996; Mokany *et al.* 2006; Brassard *et al.* 2009; Yuan & Chen 2010b).

Detailed studies of FRB in relation to stand age are still sparse because measuring root biomass is labour-intensive and time consuming (Bohm 1979; Atkinson 1991; Smit 2000; de Kroon & Visser 2003; Lambers 2005).

Both fire and harvesting (mostly mechanical clearcutting) are well known main disturbances in boreal forests (Engelmark 1999; McRae *et al.* 2001). These two disturbances have distinct processes in terms of ecological effects, one is a natural disturbance, whereas harvesting is anthropogenic. Each results in different regeneration substrates, coarse woody debris structures, and understory vegetation communities (Brassard & Chen 2008; Nilsson & Chen 2009; Shrestha & Chen 2010). Although the influences of both forest fire and clearcutting on forest ecosystems have been widely studied, direct comparisons of FRB between these two disturbance origins within the same region are not common. The relationships between forest productivity, especially belowground productivity, and the type of disturbance from which a forest stand originates are largely unknown. Aboveground biomass production (using diameter at breast height, specific volume, height increment, or site index) has been found to be higher in stands originating from clearcutting (Lussier *et al.* 2002), from fire (Ruel *et al.* 2004), or even independent of stand origin (Pare *et al.* 2001) in the boreal forest. These findings allow no generalization on the pattern of production in relation to stand origins. Again, previous studies have exclusively focused on comparisons of aboveground between stand origins, generally neglecting belowground parts. In particular, since fine roots are distributed mainly at the upper soil horizons and represent the most dynamic part of the root system (Borken *et al.* 2007), the growth and death of these post-disturbance roots might be strongly affected by forest disturbance origins.

In this chapter, FRB dynamics in relation to stand age and disturbance origin was

examined. The objectives were to determine 1) how FRB changed with stand development in the boreal forest; and 2) whether FRB in stands originating from clearcutting differed from those originating from fire. Two hypotheses were tested in this chapter. First, FRB was hypothesized to increase rapidly after a stand replacing disturbance, peak at an intermediate stage of stand development, and then decline and stabilize in old stands. The reasons for this pattern related to physiological, ecological, and species composition consequences of stand age were elaborated:

- 1) If above- and below-ground traits are functionally coordinated (Roumet *et al.* 2006), the variation in plant FRB which serves as an organ to uptake nutrients and water, will mirror somewhat its aboveground production, which increases after disturbance, peaks at immediate stand age, and then decline in older stands (Gower *et al.* 1996a).
- 2) Based on the sink-source hypothesis (Paul & Foyer 2001), reduced photosynthetic rates (source) in old trees (Hubbard *et al.* 1999), which occur because of increasing hydraulic (Ryan *et al.* 2006; Drake *et al.* 2010) or nutrient limitations (Gower *et al.* 1996a), could have a bottom-up effect on root growth (sink) by carbohydrate feedback inhibition, resulting a FRB decline in old forest stands. Furthermore, the decline in stand density and leaf area index with stand age (Wirth *et al.* 2009; Deroose & Seymour 2010) can reduce photosynthesis and thus root growth in old stands.
- 3) After a stand-replacing disturbance, rapid nutrient uptake by plants results in increased nutrient storage in plant biomass (sink), and thus a decreasing demand subsequently for root (source) penetration and exploitation through time (Kaitaniemi & Honkanen 1996) as a top-top-down effect. Eventually, forest stands reach a stage at which mortality equals net primary production, and there is no net increase or even a decline in tree biomass (Attiwill 1979),

including FRB.

4) Although nutrient shortage can cause a high root:shoot ratio according to the nitrogen-carbon balance concept (Ericsson 1995), the absolute magnitude of root biomass is likely be greater in high resource environments (Lambers *et al.* 2008a); thus FRB is expected to decline due to nutrient limitation in old stands.

5) The shift of canopy tree succession from productive early successional species to less-productive late successional species (Pare & Bergeron 1995; Leuschner & Hertel 2003; Yuan & Chen 2010b) can lead to a reduced FRB in old stands.

6) The accumulation of a thick organic layer that contributes to soil cooling, and thus restricts nutrient mineralization and uptake by plants (Simard *et al.* 2007), would cause FRB to decline in old stands.

Second, because the fire- and clearcutting-induced disturbances in boreal forest stands show differences in the short term, FRB was hypothesized to be higher in postfire stands than in post-clearcutting stands for the following reasons. At the stand scale, there are short-term significant differences between young postfire stands and young post-clearcutting stands, particularly with respect to coarse woody debris (Brassard & Chen 2008) and soil conditions (Shrestha & Chen 2010). Recently clearcut stands generally have a greater stem density (Nguyen-Xuan *et al.* 2000) and higher proportions of black spruce (*Picea mariana* [Mill.] B.S.P.) and balsam fir (*Abies balsamea* [L.] Mill.), but lower proportions of paper birch (*Betula papyrifera* Marsh.) as compared to recent burns of 6-12 years after stand replacing disturbances (Ilisson & Chen 2009). Higher proportions of jack pine (*Pinus banksiana* and deciduous species like trembling aspen (*Populus tremuloides* Michx.) were observed in 1-year-old post-clearcutting stands than in similarly aged postfire stands (27% vs. 0% for *P.*

banksiana and 73% vs. 0% for *P. tremuloides*, respectively) (Seedre & Chen 2010; Shrestha & Chen 2010). However, fire consumes more soil organic matter, creating conditions in mineral seedbeds that better favor seed germination and survival (Whittle *et al.* 1997; Greene *et al.* 1999). Post-clearcutting young sites tend to have fewer snags and more downed woody debris than postfire sites (Brassard & Chen 2008), which would potentially impact nutrient cycling and stand productivity. The forest floor layer, which is not removed by conventional clearcutting techniques, is generally thicker in post-clearcutting sites than postfire sites (Simard *et al.* 2001), exposing regenerating vegetation in post-clearcutting sites usually to a greater mass of soil and forest floor nutrients that may influence fine root growth and death. Compared with clearcutting, the direct and short term effects of fire on boreal forest soil are generally similar, but often stronger, with thinner humus layers, lower mass of organic C, more exchangeable base cations (notably Ca, which help indirectly, increase soil pH), and higher nutrients (Simard *et al.* 2001). Fire may remove substantial quantities of C, N and S by volatilization and later via leaching, whereas clearcutting might increase soil acidity and might not generate the same intensity of nutrient pulse, that is often observed with fire (Lecomte *et al.* 2006).

Materials and Methods

Study area and sites

A postfire boreal forest chronosequence in northern Ontario that spans over 200 years was used in this present study. The system involves a series of six age classes of fire origin and three age classes of clearcutting origin. The chronosequence provides an opportunity for studying how differences in stand ages and disturbances can affect ecosystem functions such

as FRB dynamics. The chronosequence is in the Spruce River Forest and Black Sturgeon Forest, ca. 150 km north of Thunder Bay, Ontario, Canada between 49°27' N to 49°38' N and 89°29' W to 89°54' W (Appendix I, Figure AI.1). This region is characterized by warm summers and cold, snowy winters. The mean annual temperature is ~2.5°C. The mean summer temperature is 14°C and the mean winter temperature is –13°C. The mean annual precipitation is ~710 mm. The study area is dominated by trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* B.S.P), paper birch (*Betula papyrifera* Marsh.). Few white spruce (*Picea glauca* [Moench] Voss) and balsam fir (*Abies balsamea* [L.] Mill.) are also present (Hart & Chen 2008; Brassard & Chen 2008; Shrestha & Chen 2010). Common understory plant species are mountain maple (*Acer spicatum* Lam.), dwarf raspberry (*Rubus pubescens* Raf.), alder (*Alnus* spp.), beaked hazel (*Corylus cornuta* Marsh.), bush honeysuckles (*Diervilla lonicera* Mill.), bluejoint reedgrass (*Calamagrostis canadensis* Michx.), blue-bead lily (*Clintonia borealis* Raf.), Canadian mayflower (*Maianthemum canadense* Desf.), three-leaf goldthread (*Coptis trifolia* Salisb.), violet (*Viola* spp.), and large-leaved aster (*Aster macrophyllus* L.). The average fire return interval is approximately 100 years for the past century (Senici *et al.* 2010).

Sampling design

To determine the effect of time since the last stand-replacing disturbance, fire-origin stands were selected using stand-development stages according to Chen and Popadiouk (2002) to ensure a wide range of stands were sampled. As a result of available fires in the study area, six age classes were selected, each representing stand initiation, canopy closure, stem exclusion, early canopy transition, late canopy transition, and gap dynamics stages,

respectively. Clearcutting-origin stands were sampled only for stand initiation, canopy closure, and stem exclusion stages as commercial harvesting of the study area did not begin until the early 1970s. Therefore, fire- and clearcutting-origin stands ranged in age from 3 to 205 years and 3–29 years time since disturbance, respectively (Table 1). Six fire-origin age classes and three clearcutting-origin age classes (each replicated three times as spatially interspersed as possible) were selected, resulting in a total of 27 sample stands. The young and intermediate stands were dominated by *P. tremuloides* and *P. banksiana*. The oldest postfire stands were dominated by *B. papyrifera* and late-successional conifers including *P. mariana*, *P. glauca*, and *A. balsamea* (Hart & Chen 2008; Shrestha & Chen 2010). Soil varied in pH, CEC, N along the chronosequence (Table 3.1).

Table 3.1 Summary of stand characteristics.

Origin	Fire						Clearcutting			
	Stand age (years)	3	10	29	94	142	205	3	10	29
SC	Bf	0	3	0	4	29	21	0	0	2
	Bw	0	9	1	3	2	42	0	27	22
	Pj	0	26	61	28	8	0	27	22	36
	Po	0	60	26	40	26	1	73	41	30
	Sb	0	2	12	20	35	5	0	10	9
	Sw	0	0	0	4	0	31	0	0	2
SD/BA	0	17446±536	52.0±2.0	35.7±2.0	38.1±4.5	31.2±2.6	0	10100±616	10.8±0.2	
FFLD	1.12±0.33	4.61±0.37	8.34±0.50	7.81±0.43	7.61±0.32	7.59±0.35	5.62±0.43	5.24±0.68	7.42±0.38	
BD	0.95±0.02	0.80±0.01	0.81±0.02	0.70±0.04	0.75±0.05	0.77±0.01	0.87±0.03	0.87±0.06	0.79±0.03	
pH	5.86±0.06	4.91±0.06	4.77±0.07	5.16±0.19	4.80±0.08	5.27±0.10	4.85±0.05	4.82±0.02	4.86±0.09	
CEC	6.49±0.63	7.44±0.63	4.24±0.20	10.1±2.39	5.81±0.28	10.8±2.14	3.46±0.72	4.59±1.17	6.18±1.13	
C%	15.1±1.77	65.2±7.34	65.6±12.4	87.4±2.62	63.5±9.75	61.0±6.49	63.8±12.5	51.4±17.9	66.0±17.7	
N%	0.69±0.17	1.83±0.20	1.91±0.32	3.13±0.15	1.99±0.31	2.51±0.43	1.69±0.25	1.60±0.65	2.45±0.59	
P‰	0.48±0.03	0.41±0.05	0.41±0.01	0.47±0.06	0.34±0.01	0.46±0.01	0.33±0.01	0.32±0.02	0.37±0.06	
K‰	0.78±0.05	0.52±0.01	0.38±0.01	0.67±0.11	0.45±0.02	0.97±0.15	0.42±0.07	0.60±0.03	0.73±0.05	

Note: Each stand age class and stand origin was replicated three times. SC= Species composition (%); Bf= balsam fir; Sw=white spruce; Sb=black spruce; Pj=jack pine; Bw=paper birch; Po=trembling aspen; SD= Stand density (stems ha⁻¹); BA= basal area (m² ha⁻¹); FFLD=forest floor layer depth (cm); BD=Bulk density (g cm⁻³); CEC=cation exchange capacity (meq 100g⁻¹). Stand composition was determined based on stand density for 3- and 10-year-old stands and on basal area for older stands. Stand density (stems ha⁻¹) was determined for 3- and 10-year-old stands, and stand basal area (m² ha⁻¹) for older stands. All stands selected were ha in area and were visually homogeneous in structure and composition. Soil data are from the forest floor layer. Values are means±SE (n=3). Species composition from Hart and Chen (2008) and soil properties from Shrestha and Chen (2010).

Similar to the studies in stand structure, understory vegetation, and forest floor C (Brassard *et al.* 2008; Brassard & Chen 2008; Hart & Chen 2008; Shrestha & Chen 2010; Seedre & Chen 2010), mesic sites on flat mid-slope positions (with no slope exceeding 5%) and on well-drained glacial moraines (>50 cm in thickness), which is the prevailing site type in the region, were deliberately selected to minimize the effect of site condition on fine root dynamics. To ensure that each selected site met the selection criteria, a soil pit was dug in each sampled stand to verify whether the site was mesic following the procedure described in Taylor *et al.* (2000). All stands selected were one ha in area and were visually homogeneous in structure and composition. For old stands, time since the last stand-replacing fire/clearcutting was estimated using tree rings.

To minimize the impact of spatial structure (Legendre & Legendre 1998; Okland 2007), every effort was made to intersperse stands sampled to avoid sampling stands of the same class in close proximity to one another. Interspersion was achieved by selecting stands of the same age and disturbance origin from different road accesses, which resulted in several kilometers between selected stands. A complete interspersion of different stand ages was, however, impossible due to fire history and fire size in the study area. For example, there was only one 29-year-old fire of 120,000 ha and one 205-year-old fire of 2,000 ha in size.

Field measurements

In each stand, a sample plot of $\approx 20 \times 20$ m² was established for fine root sampling. Within each sampling plot, samples were collected from five random points following an elongated ‘S’ pattern every month: July-October in 2008 and May-June 2009 with six sampling times in total. Soil cores were extracted with a soil corer (6.6 cm in inner diameter) from the forest floor surface to 30 cm depth in the mineral soil using a power auger. The extracted soils were

separated into forest floor layer (FF) and two mineral soil sections: MS1 (0–15 cm) and MS2 (16–30 cm), put in root bags in an ice-filled cooler, and then stored in a freezer at -18°C until processing (Brassard *et al.* 2011).

In the laboratory, thawed FF and MS layer samples were soaked overnight, poured into trays, rubbed gently, and roots floating on top of the water were sieved (0.5 mm mesh). This procedure was repeated until only coarse fragments were left in the soil sample. Fine roots (≤ 2 mm in diameter) were sorted according to vitality (live or dead) and functional (broadleaved and coniferous) classes. Fine roots were considered ‘live’ if they were pale-coloured on the exterior, elastic and flexible, and free of decay with a whitish cortex, while fine roots were classified as ‘dead’ if they were brown or black in colour, rigid and inflexible, in various stages of decay, and had a dark coloured cortex (Brassard *et al.* 2011). Fine roots were further divided into broadleaved and coniferous classes based on a combination of morphological characteristics including colour, size, branching angle, branching pattern, and presence or absence of root hairs (Brassard *et al.* 2011): These criteria included 1) colour (broadleaved roots were more white or yellow in colour, while coniferous roots were more red or brown in colour), 2) size (broadleaved roots were generally finer-structured than coniferous roots), 3) branching angle (approximately 90° for coniferous roots and 45° for broadleaved species), 4) branching pattern (broadleaved roots were less branched than coniferous), and 5) presence or absence of root hairs (broadleaved roots contained small hairs that were not present on coniferous roots). These criteria were developed previous to root sorting using samples of known origin from our study sites. Then fine roots were oven-dried to a constant mass at 65°C and weighed.

Data analyses

Because of the difference in age range between stands of fire origin and those of clearcutting origin, analyses were conducted in two steps. First, with time after fire disturbance, changes in fine root variables (biomass and necromass in this chapter, decomposition, production, and turnover rates in latter chapters) were determined for postfire stands from 3- to 205-year old using one-way analysis of variance. Second, the interactive effects of stand age and stand origin were tested with two-way analysis of variance by choosing all stands ≤ 29 -year old, *i.e.*, three age classes from postfire stands and all sampled post-clearcutting stands. Since the monthly samples, taken from the same stand, were not independent, the sampling date was treated as a repeated measure in analysis (Hicks & Turner 1993; Giardina & Ryan 2000; Paul 2007). Models were fitted and analyzed using the *describe.by*, *aov*, *lm*, and *TukeyHSP* functions within R version 2.11.1 statistical software (R Development Core Team 2010). Log_{10} transformations were used for data of fine root biomass and necromass to meet assumptions of normality and homogeneity of variance with the *shapiro.test* and *bartlett.test* functions in R.

Results

Seasonal patterns

During the study period, the total fine root biomass (FRB) in the FF and MS layers tended to increase over the growing season from July to October in 2008 (Figure 3.1). In 2009, FRB was greater in May than in June; but the values in both months were greater than in 2008. During the two-year sampling period, FRB was generally greatest in May 2009 but lowest in July 2008. A second and smaller peak in FRB was detected in the September 2008, especially

in old postfire stands. The FF layer had greater FRB and variation than the two MS layers. The total fine root necromass (FRN), with lower values than FRB, did not show the same clear seasonal patterns as FRB (Figure 3.2). FRN tended to peak in May 2009 for young postfire stands but in October 2008 for old postfire stands. A second and smaller peak of FRN was detected in June/July 2008.

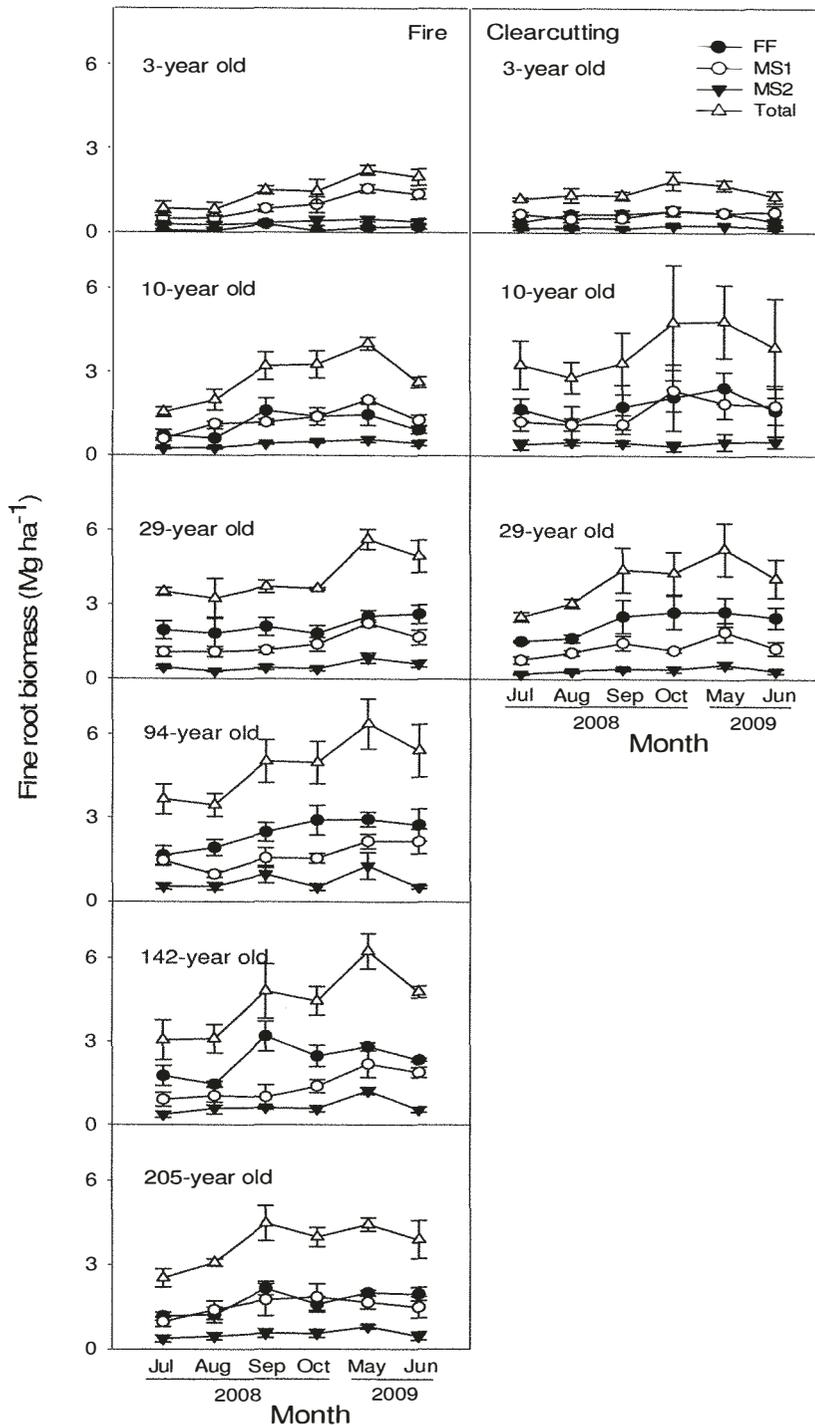


Figure 3.1 Seasonal variations in fine root biomass.

Values are means \pm SE ($n=3$). FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer, Total= FRB of all layers (FF+MS1+MS2).

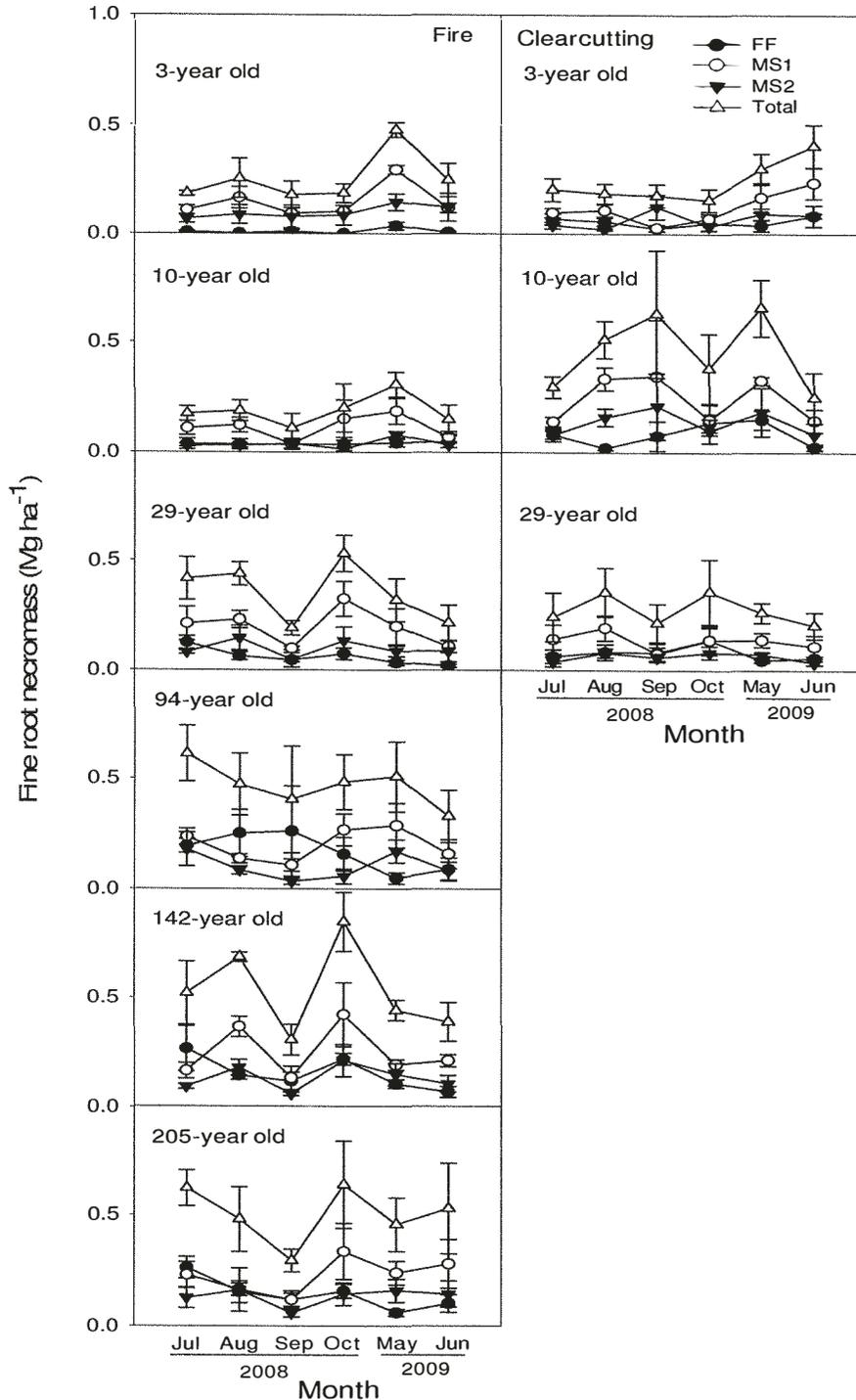


Figure 3.2 Seasonal variations in fine root necromass.

Values are means \pm SE ($n=3$). FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer, Total= FRB of all layers (FF+MS1+MS2). Influence of time since fire

FRB in postfire stands varied significantly with stand age for all sampling dates (Table 3.2). FRB generally increased in stands from 3-year old until 29-year old, and then levelled off or declined (Figure 3.3). FRN varied with stand age and upon sampling time. There were significant differences in FRN which tended to increase in stands from 3-year old until 29-29-year old, and levelled off or declined thereafter (Table 3.2, Figure 3.3). The total fine root mass, *i.e.*, the sum of biomass and necromass, showed similar trends to FRB. For all sampling dates, the total FR mass changed significantly with stand age (Table 3.2), which generally increased from in stands from 3-year old until 29-year old,, and then levelled off or declined (Figure 3.3).

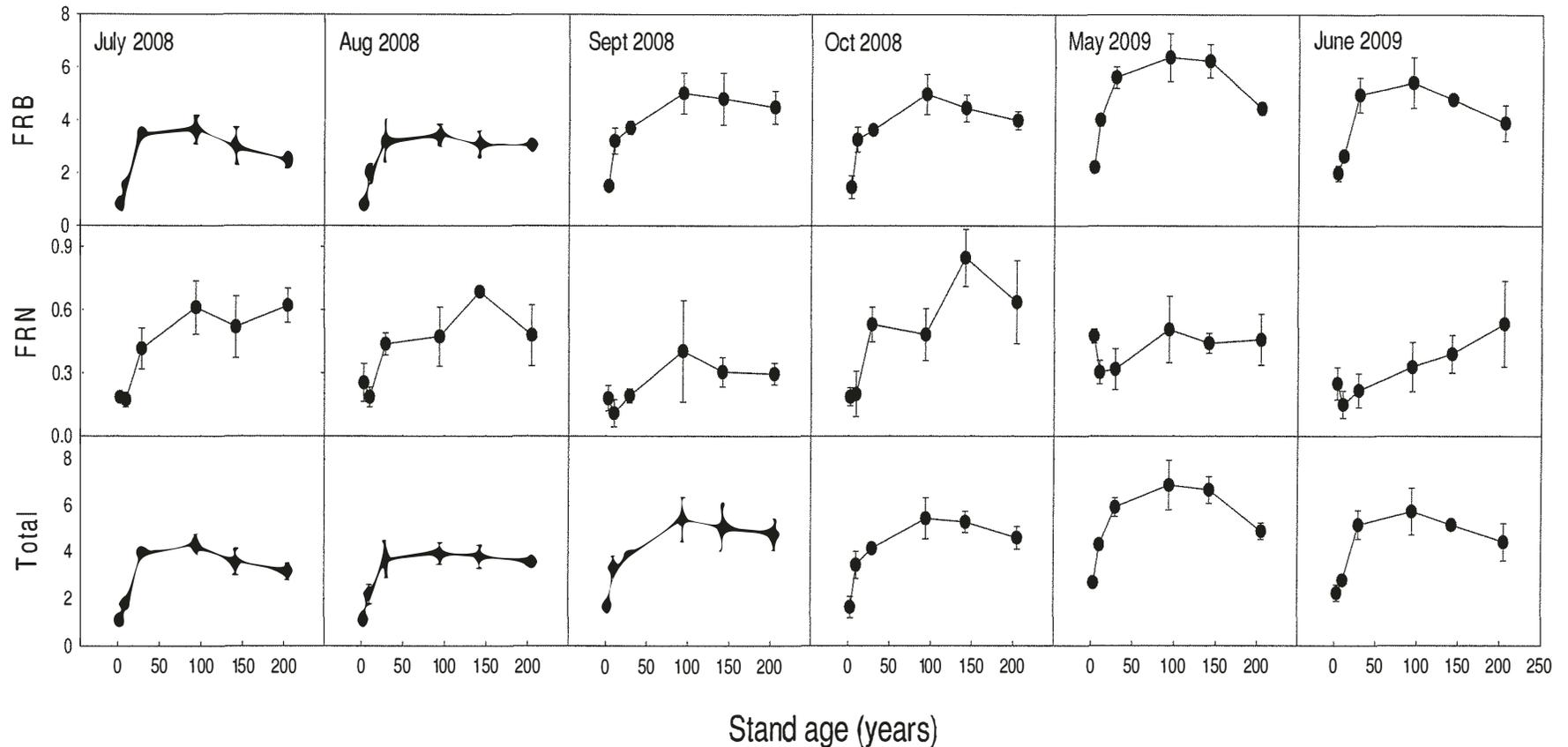


Figure 3.3 Changes in fine root biomass, necromass, and total mass with stand age in fire-origin stands.

Notes: Values are means \pm SE ($n=3$). FRB = biomass, FRN = necromass, total mass = biomass + necromass. Units for FRB and FRN are $Mg\ ha^{-1}$.

Table 3.2 *P-values of repeated measures analysis of variance for the effects of stand age and sampling date on fine root biomass, necromass, and total mass in postfire stands.*

Source	Between subject	Within subject	
	Stand age (A)	Sampling date (D)	A×D
FRB			
FF	<0.001	<0.001	0.036
MS1	<0.001	<0.001	0.209
MS2	<0.001	<0.001	0.179
Total	0.001	<0.001	0.109
FRN			
FF	<0.001	0.004	0.277
MS1	<0.001	<0.001	0.112
MS2	<0.001	0.014	0.483
Total	<0.001	<0.001	0.132
Total mass			
FF	<0.001	<0.001	0.153
MS1	<0.001	<0.001	0.288
MS2	<0.001	<0.001	0.249
Total	<0.001	<0.001	0.331

Notes: Bold indicates significant effects. FRB= biomass, FRN=necromass, total mass

=biomass+necromass, FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer

Effects of stand origin

FRB in 3-, 10-, and 29-year-old stands did not significantly differ between stands of fire and clearcutting origins for all layers, but in FF and MS1 layers FRB differed with stand age, increasing in stands from 3-year old until 29-year old (Figure 3.4, Table 3.3). In FF layer, FRN was greater in clearcutting-origin stands than in fire-origin stands. However, stand origin did not show significant effects on FRN in MS1 and MS2 layers. As a result, there were no significant differences in the total FR mass (FRB+FRN) between stands of fire and clearcutting origins (Table 3.3).

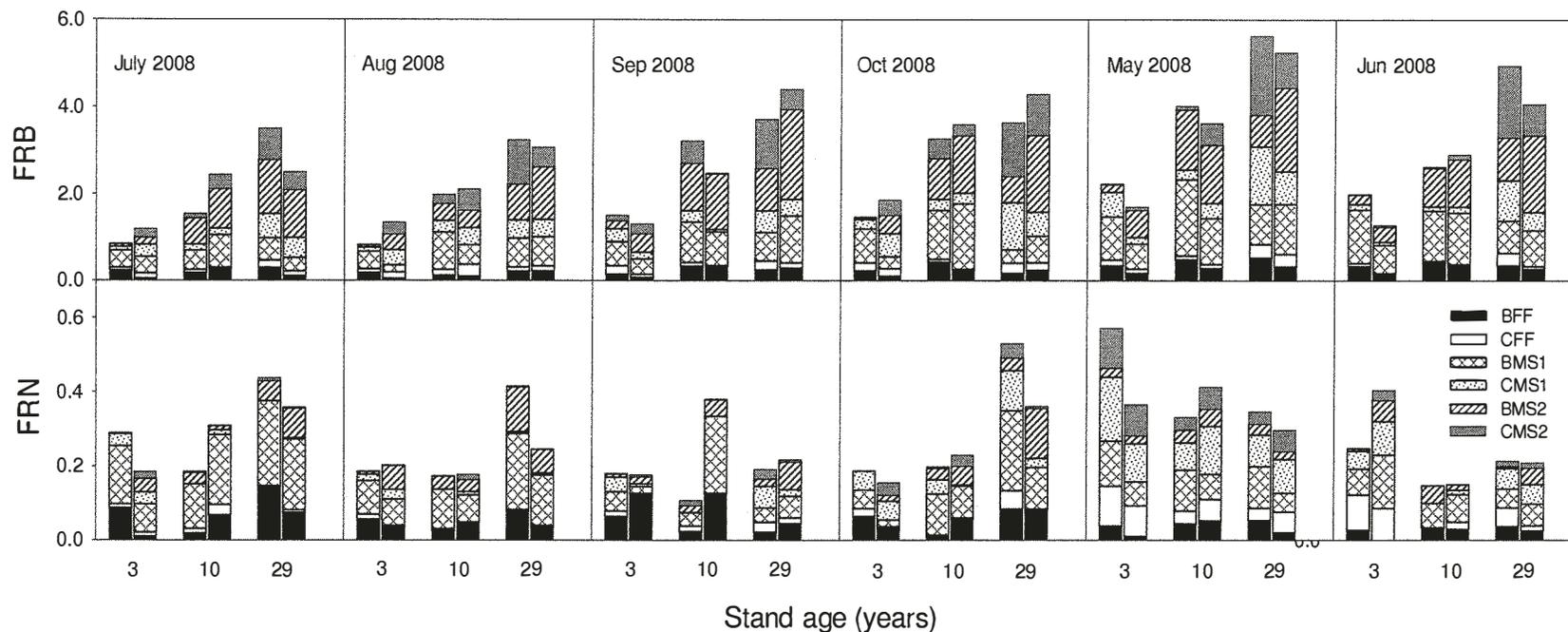


Figure 3.4 Effects of stand origin (fire vs. clearcutting) on fine root biomass and necromass.

Notes: Fire-origin stands on the left and clearcutting-origin stands on the right. FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer, B=broadleaved, C=coniferous, FRB= biomass, FRN=necromass, BFF=broadleaved FRB in FF layer, CFF= coniferous FRB in FF layer, BMS1= broadleaved FRB in MS1 layer, CMS1= coniferous FRB in MS1 layer, BMS2= broadleaved FRB MS2 layer, CMS2= coniferous FRB in MS2 layer. Units for FRB and FRN are Mg ha⁻¹.

Table 3.3 *P-values of repeated measures analysis of variance for the effects of stand ages, disturbance origin (fire vs. clearcutting), and sampling dates on fine root biomass, necromass, and total mass in younger stands (3- to 29-year-old).*

Source	Between subject			Within subject			
	A	O	A×O	D	D×A	D×O	A×O×D
FRB							
FF	<0.001	0.306	0.865	<0.001	0.198	0.540	0.486
MS1	0.014	0.193	0.782	<0.001	0.157	0.025	0.114
MS2	0.100	0.056	0.788	<0.001	0.299	0.096	0.505
Total	0.001	0.922	0.964	<0.001	0.127	0.254	0.208
FRN							
FF	0.007	0.012	0.262	0.468	0.314	0.686	0.374
MS1	0.405	0.441	0.297	0.003	0.039	0.105	0.375
MS2	0.525	0.692	0.161	0.431	0.290	0.466	0.789
Total	0.249	0.968	0.302	0.010	0.001	0.251	0.474
Total mass							
FF	<0.001	0.276	0.849	<0.001	0.253	0.484	0.468
MS1	0.022	0.200	0.726	<0.001	0.366	0.046	0.239
MS2	0.174	0.079	0.553	<0.001	0.822	0.147	0.739
Total	0.001	0.924	0.920	<0.001	0.382	0.380	0.329

Notes: Bold indicates significant effects (P<0.05). A=stand age, O=disturbance,

D=sampling date, FRB= biomass, FRN=necromass, total mass =biomass+necromass,

FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer.

Discussion

In postfire stands, FRB generally increased in stands from 3-year old, peaked at 29-year-old stands, and leveled off or declined thereafter (Figure 3.2). These findings support the first hypothesis that FRB changes with stand development, *i.e.*, FRB culminates early and declines thereafter. However, FRB did not significantly differ between stand origin in either 3-, 10-, or 29-year-old stands, rejecting the second hypothesis that FRB differs between postfire and clearcut stands.

Seasonal patterns

Seasonal variations were found for both FRB and FRN (Figures 3.1 and 3.2), suggesting that fine roots in the boreal forest grow and senesce rapidly within a year, probably influenced by the seasonal variations in soil temperature and moisture. FRB peaked in late spring, followed by a rapid decrease in the summer and fall (Figure 3.1), which has been observed in other northern forest ecosystems (Grier *et al.* 1981; McLaugherty *et al.* 1982; Hendrick & Pregitzer 1993; Steele *et al.* 1997; Borja *et al.* 2008; McDonald 2010). The peak of FRB in May 2009 could be associated with the onset of water percolating into the soil from the snow pack and increasing nutrient availability in early spring. In addition, the temporal FRB changes might correspond to the aboveground phenology in boreal forests, such as bud break/leaf expansion in early summer and leaf senescence in fall, both of which can regulate root growth (Reich *et al.* 1980; Tryon & Chapin 1983; Willaume & Pages 2006). Shoot elongation in summer, for example, requires greater C by the aboveground canopy, reducing carbohydrate translocation to the roots and depressing root growth (Konopka *et al.* 2005). The second peak of FRB in September could be linked to the decreasing activity of the aboveground parts of the trees at the end of growth

season, as predicted by the optimal partitioning theory (Bloom *et al.* 1985). Furthermore, FRB appeared to peak earlier in the FF layer than in the MS layer, but the results were difficult to interpret. The possible reason could be that FF layer gets warmer earlier than the deeper layer.

In 2008, FRB increased from July to October (Figure 3.1). In the boreal forest of northern Saskatchewan, Canada, FRB was also found to increase from June to October in 2005, but it peaked in August or September and declined thereafter in other studied years (McDonald 2010). The opposite patterns of FRB in July and October in the same sites at different years have been found in other northern forests (Santantonio & Hermann 1985; Fahey & Hughes 1994; Makkonen & Helmisaari 1998; Lopez *et al.* 2001; Iivonen *et al.* 2001). The FRB trends in 2008 in this present study were contrary to the findings of Brassard *et al.* (2011), who found greater FRB in July than in October 2007 in 94-year-94-year-old stands. These different findings probably result from the different precipitation patterns in these two years. In 2007, July's total rainfall was similar to the average, but October's total rainfall amounted to a record 111.5 mm, 62% higher than the normal values of 69.0 mm (Appendix I, Table AI.1). Furthermore, in June 2007, the total rainfall was also similar to the average; but September's rainfall was 66% higher than the normal value. The previous month's rainfall that was held within the soil would make the current month's soil wetter, especially in October when the temperature turned cold. The much greater rainfall throughout September and October in 2007 could have an influence on soil conditions and thus FRB. An increase in soil moisture content may have a cooling effect on boreal soils (Bond-Lamberty *et al.* 2006b). In October 2007, the wetness encountered in many boreal forests (Environmental Canada, <http://www.on.ec.gc.ca/announce.cfm?ID=779&Lang=e>), generally associated with

colder soil temperature (Van Cleve & Yarie 1986; Bisbee *et al.* 2001), might be a major factor contributing the reduction of FRB in October compared to July 2007. Therefore, lower FRB in October than in July 2007 (Brassard *et al.* 2011) was probably related to higher September-October precipitation, resulting in high soil water content and a lack of nutrient pulses. The FRB in July 2008 (Figure 3.4) was similar to the same month in 2007 (Brassard *et al.* 2011), which was probably attributed to the similarity of the June and July rainfall in 2007 and 2008 (210 mm vs. 217 mm). The greater FRB in the 94-year-old postfire stands in October 2008 (4.97 Mg ha^{-1}) than the same month in 2007 ($\approx 2.597 \text{ Mg ha}^{-1}$) (Brassard *et al.* 2011) could be due to the much higher June and July rainfall in which was 253 mm, 1.6 times the average and 2.3 times the rainfall in the same period in 2008 (Appendix I, Table AI.1). In fact, the regression analysis showed that FRB in 94-94-year-old postfire stands was positively associated with the monthly rainfall, but high rainfall in the growth season could lead to FRB reductions in these stands (Figure 3.5).

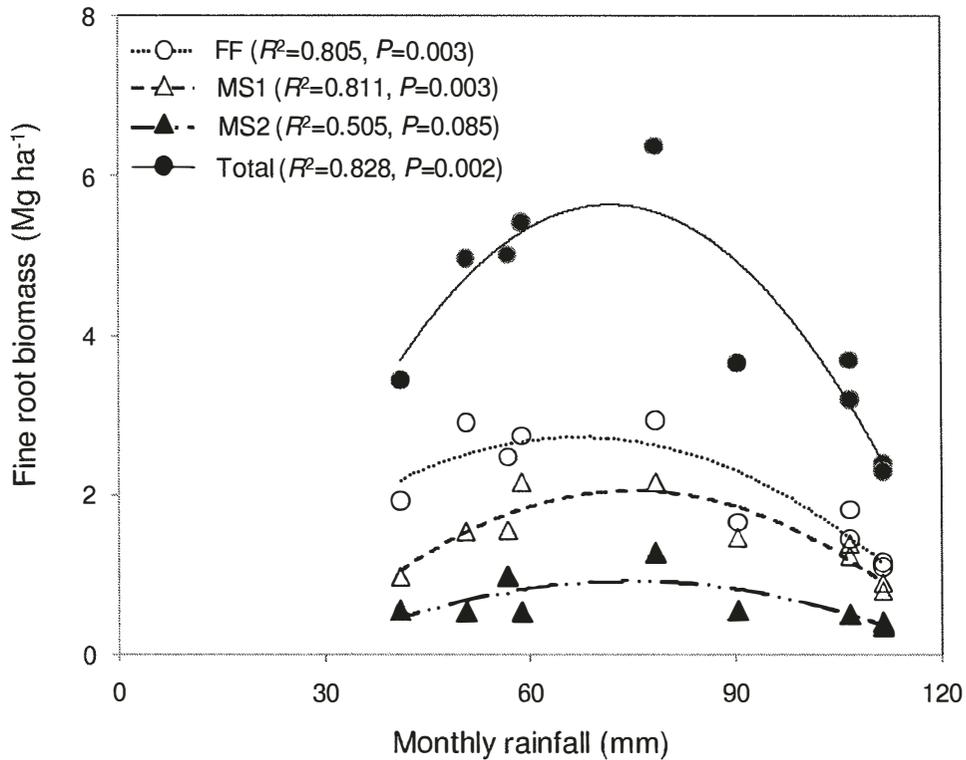


Figure 3.5 Fine root biomass in relation to monthly rainfall in the 94-year-old postfire stands.

Notes: Data from this study and Brassard *et al.* (2011). FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer, Total=FF+MS1+MS2.

Seasonal FRB patterns reveal little about the dynamics of FR production and mortality, because changes in FRB reflect only the net effect of these two processes. In fact, FR growth, mortality, and decay occur simultaneously, but are not necessarily constant through time (Figures 3.1 and 2) (Kurz & Kimmins 1987; Steele *et al.* 1997). FR production in boreal forests generally increases in early spring and peaks in late spring to mid-summer before decreasing in the fall, while FR mortality is generally highest in later summer and fall and lowest in spring and winter (Brassard *et al.* 2009). However, FR

production and mortality might not reach their peaks at the same time in different years, resulting in delaying or advancing the peak of FRB (Figure 3.6): When FR production peaks in late spring to mid-summer, the peak of FR mortality in early fall (Steele *et al.* 1997) reflected by a higher FRB in July than in October (Figure 3.6A) as found by Brassard *et al.* (2011), but a delayed peak of FR mortality in late fall (Ruess *et al.* 1998) can lead to a lower FRB occurring in July than in October (Figure 3.6B) as found in this present study. Even with the same patterns of FR production and mortality, a reduced mortality can also lead to a delayed peak of FRB and a probably higher FRB in October than in July. The often observed bimodal patterns of FR production and mortality (Grier *et al.* 1981; Symbula & Day 1988) indicate that temporal FRB patterns depend on the intra- and inter-annual sampling times. In fact, previous studies showed different FRB seasonal patterns, ranging from stands with no distinct peak (Persson 1978) to those with one peak (Keyes & Grier 1981; Mcclaugherty *et al.* 1982) or two peaks (Alexander & Fairley 1983; Dress & Boerner 2001). The seasonality of FRB seems to be regulated by both external and internal factors such as climates, species, management systems, soil conditions, and the growth of the aboveground biomass.

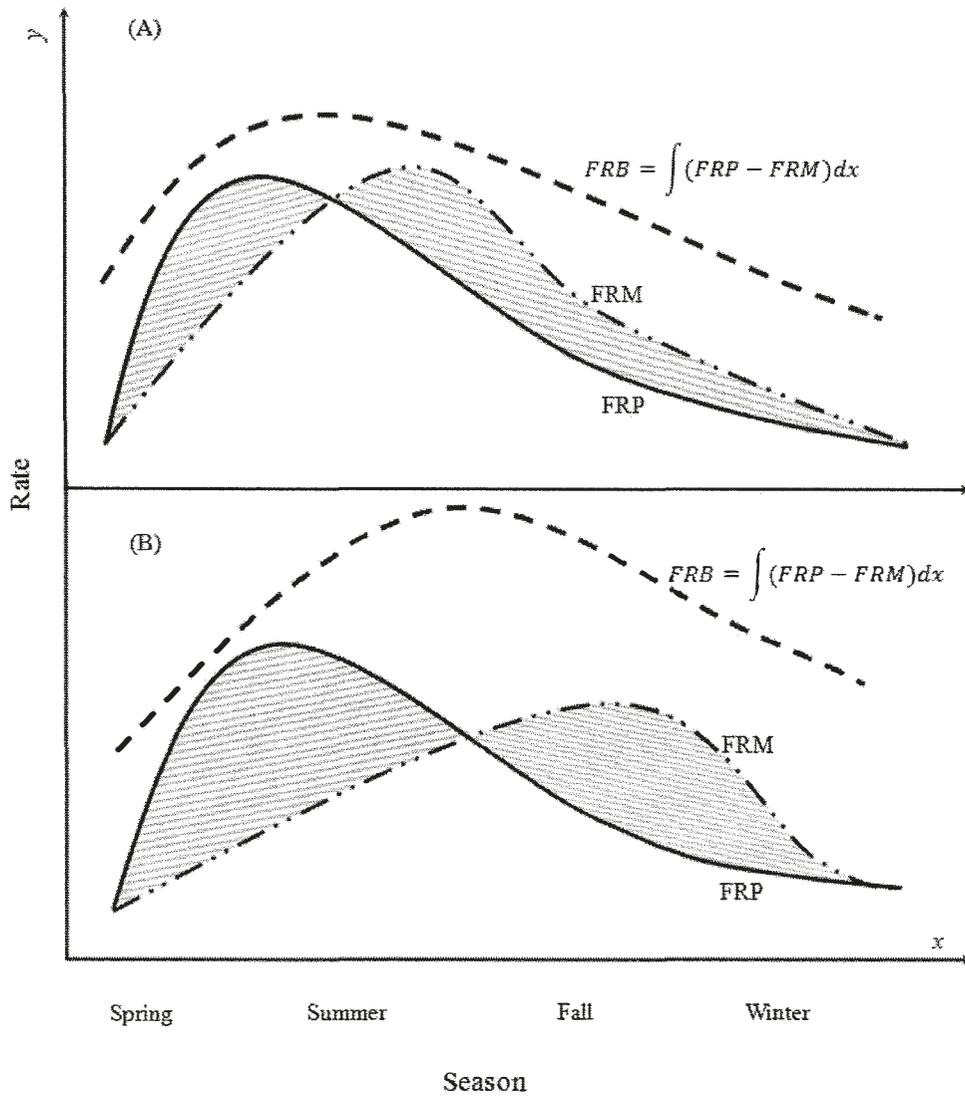


Figure 3.6 A conceptual model depicting different seasonal patterns of fine root production and mortality that result in delaying/advancing peak of fine root biomass.

Notes: FRB= fine root biomass, FRP=fine root production, FRM= fine root mortality.

Stand age effects

There are a number of studies on aboveground biomass changes with respect to stand development, including the collecting chronosequence data (Gower *et al.* 1996a; Ryan *et*

al. 2004). However, only a few studies examine variation in FRB with stand age, and how roots vary during secondary forest succession is still open to debate since reports are scarce and results are sometimes contradictory. FRB, for example, has been suggested to peak within a large range from 5 to 80 years of stand initiation in forests dominated by Khasi pine (*Pinus kesiya* Royle ex Gordon) (John *et al.* 2002), Japanese cedar (*Cryptomeria japonica* D. Don) (Karizumi 1968; Fujimaki *et al.* 2007), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Vogt *et al.* 1983b; Vogt *et al.* 1987), Norway spruce (*Picea abies* [L.] Karst) (Borja *et al.* 2008), red pine (*Pinus resinosa* Ait.) (McLaugherty *et al.* 1982), Scots pine (*Pinus sylvestris* L.) (Makkonen & Helmisaari 2001; Helmisaari *et al.* 2002), white pine (*Pinus strobes* L.) (Peichl & Arain 2006), and beech (*Fagus sylvatica* L.) and Turkey oak (*Quercus cerris* L.) (Claus & George 2005). Also in *P. sylvestris* stands, FRB was found to be independent of stand age on a poor CT (*Calluna* type) site, but FRB decreased with stand age on a more fertile MT (*Myrtillus* type) site (Vanninen & Makela 1999). Among 48-232 year-old mixed boreal conifer-conifer-broadleaved forests, no significant differences in FRB were found (Finer *et al.* 1997), in accordance with observations from a chronosequence of young *P. tremuloides* stands (10-, 20-, and 32-year-old) in Wisconsin, USA (Ruark & Bockheim 1987). Vogt *et al.* (1987) found that FRB decreased significantly in highly productive *P. menziesii* stands once the canopy closed, whereas FRB remained relatively constant in stands of low productivity.

In this present study, FRB in postfire stands changed with stand development (Figure 3.1): it increased in stands from 3-year old and peaked at 29-year-old stands and gradually levelled off thereafter. Therefore, stand age clearly showed a significant effect on FRB, supporting the first hypothesis that FRB initially increases rapidly, reaches the maximum,

and then declines with increasing stand age. The FRB dynamics seen in this present study are in accordance with the general pattern of aboveground biomass accumulation observed in eastern (Pare & Bergeron 1995) and central (Brassard *et al.* 2008) boreal mixedwoods (Seedre & Chen 2010), and other forest ecosystems (Gower *et al.* 1996a; Ryan *et al.* 1997). However, the aboveground biomass in the same sites peaked in 94-94-year-old stands (Seedre & Chen 2010), suggesting that maximum FRB occurs much earlier than maximum aboveground biomass.

The FRB patterns with respect to stand age most likely resulted from two processes: fine root productivity (input) and mortality (output). However, the underlying mechanisms are complex, and which process contributed most to the FRB patterns with stand development remains unclear. The FRB pattern of low values in an early stand stage, peaking at a middle stage, and then leveling off at a old stage, may be attributed to both physiological and ecological factors. First, internal factors such as growth rhythm of root aging and senescence, regulate growth and death processes that determine root biomass. The development of trees and shrubs in the stands tends to follow phases of establishment, rapid growth and maturation. During the early stage, young plants allocate more resources to FRB in order to maximize water and nutrient uptake that support rapid growth of their crowns, securing their survival. As trees mature following canopy closure, more and more nutrients are bound in the litter and humus (Shrestha & Chen 2010), which decreases nutrient availability and leads to production declines, consequently reducing the demand for nutrient and water supply from fine roots, and thus decreasing FRB allocation in mature stands.

Second, successional changes in species composition (Hart & Chen 2008) and increased probabilities of insect and/or wind damage (Chen & Popadiouk 2002) may also

contribute to the age-related FRB decline. From previous studies conducted on the same sites as the present study, the abundance of *P. tremuloides*, a species with potential high above- and belowground productivity (Pare & Bergeron 1995; Block *et al.* 2006), was found to decline from 40% of the total aboveground biomass in 94-year-old stands, to in 142-year-old stands, and to only 1% in 205-year-old stands (Seedre & Chen 2010). Low tree density (Litton *et al.* 2003; Borja *et al.* 2008) and sparse understory (Wirth *et al.* 2009) may also have accounted for the low FRB in old stands. Although not as severe as in eastern boreal mixedwoods (Chen & Popadiouk 2002), the studied old stands also experienced some spruce budworm outbreaks which can reduce aboveground biomass (Seedre & Chen 2010) and possibly belowground biomass.

Thirdly, during secondary forest succession, not only does the species composition change, but the chemical and physical environments of soils change (Table 3.1), resulting in FRB variations with stand development. Therefore, soil environments could contribute to FRB variations with respect to stand stage of stand development. Canopy tree succession from N-rich early successional species to N-poor late successional species (Pare & Bergeron 1995) can lead to a decrease in litter nutrient input and a decline of soil total N in old stands (Smith *et al.* 2000; Welke & Hope 2005; Shrestha & Chen 2010). As a stand ages, more N is bound to organic matter, causing an increased soil total N in the forest floor (Shrestha & Chen 2010) but a decreased N availability that can lead to FRB reduction. The idea that nutrient limitation is responsible for age-related ANPP decline is, at least partly, applicable to observed trends of FRB. Under the closed canopy of old-growth forests, an attenuating quantity of light, coupled with thick forest floor layer (Wirth *et al.* 2009), may indirectly reduce root biomass by decreasing soil temperature, microbial activities and mycorrhizal colonization (Zak *et al.* 1990). Therefore, the rate of

recovery of FRB following large-scale forest fire/clearcutting disturbances probably follows complex patterns that depend upon changes with stand age that couples internal changes (*e.g.*, vegetation composition) and external changes (*e.g.*, soil features).

Additional systematic studies are necessary to develop a general understanding of this phenomenon and to determine the primary factors that affect age-related FRB dynamics.

Stand origin effects

FRB did not significantly differ between stand origins in 3-, 10- or 29-year-old stands (Figure 3.4), which did not support the second hypothesis that FRB differs between these two disturbance types. The FRB findings were also partly consistent with findings (Seedre & Chen 2010) that the aboveground live C pools that were higher in post-clearcutting stands than in postfire stands 3 and 27 years after disturbance, but similar in 10-year-old stands. Seedre & Chen (2010) speculated that the differences in aboveground C pools in the youngest stands may be due to the residual live trees left after clearcutting that were not present after wildfire. However, such a difference would not immediately contribute to FRB. Three years after a stand-replacing disturbance, both *P. tremuloides* and *P. banksiana* regenerated in postfire/clearcutting stands (personal observation), differing from the first years after disturbances (both 0% of stand composition for these 2 species in the first year) (Seedre & Chen 2010). The understory herbs also did not differ between fire and clearcutting origins in the youngest stands, likely contributing to the similarity of FRB between the two post-disturbance stands (Figure 3.4, Table 3.3). The rapid stand establishment and fast capture of site resources by vegetations might result in no differences in soil conditions (Shrestha & Chen 2010); and be the reason for no significant differences in FRB found in 10- and 29-year-old stands. If *B. papyrifera* was more productive than *P. banksiana*, the 29-year-old postfire stands had

a greater *P. banksiana* component and less *B. papyrifera* (Seedre & Chen 2010), probably resulting in a high C pool in post-clearcutting stands. However, FRB did not significantly differ between fire and clearcutting origins at this stage. A possible reason may be the presence of more understory plants in postfire stands than in post-clearcutting stands (Seedre & Chen 2010) offset the deciduous-evergreen effects. Another reason might be that the thicker organic layer (Shrestha & Chen 2010) in post-clearcutting stands were more important than the species-specific effects. Because the accumulation of live fine root biomass is the net result of production and mortality, the similarity of FRB (Table indicates differences in fine root production and mortality between the two disturbance types. The differences in fine root necromass between disturbances (Figure 3.2) also might be the result of mortality (input) and decomposition (output) processes (to be addressed in the next chapters).

Summary

Similar to the well-known decline of aboveground net primary productivity with stand development (Gower *et al.* 1996a; Ryan *et al.* 1997), along the chronosequence of boreal forests spanning over 200 years, both biomass and necromass of fine roots increased with stand age in postfire stands from 3-year old until 29-year old, and levelled off thereafter (Figure 3.3). However, the causes for the FRB patterns were not clear because stand aging is inherently coupled with changes in tree age, species composition, and soil attributes, and it is difficult to separate the effects of these factors from the effect of stand age which drive FRB patterns. FRB did not significantly differ between fire- and clearcutting-origin stands from 3- to 29-year old. The FR biomass and necromass dynamics with stand age and stand origin could be attributed to the dynamics of productivity, mortality, and decomposition, three important processes for fine root growth and disappearance.

CHAPTER FOUR: FINE ROOT DECOMPOSITION

Introduction

Fine root (FR) decomposition is an important nutrient source in boreal forests (Majdi 2004; Johnson & Hale 2008), despite slow rates that are mainly related to cold temperatures (Parton *et al.* 2007) and limited N availability for microbial and plant growth (Cruz-Ramirez *et al.* 2009) in these ecosystems. Compared with woody components and foliar litter, FR with small diameter, relatively short life span, high nutrient concentrations, and low C:N ratio, has a rapid turnover and decomposition rates (McClougherty *et al.* 1984; Fahey *et al.* 1988; Lehmann *et al.* 1995; Yuan & Chen 2010b). In the boreal forest, FR decomposition contributed up to 30% of total organic detritus mass, similar in magnitude to that from aboveground foliage (Persson 1979; Joslin & Henderson 1987). Direct observations in boreal forests have found faster rates of FR growth and decomposition relative to aboveground tissues (Ruess *et al.* 1998); more N is returned to the soil via FR decomposition than by decomposition of aboveground litterfall (Vogt *et al.* 1996). However, compared with the amount of data on aboveground foliar litter decomposition, the process of FR decomposition remains poorly quantified.

On a broad scale, FR chemistry is the primary determinant of FR decomposition with climate and other environmental factors also playing a role (Silver & Miya 2001). On a local scale, however, soil attributes and plant community composition exert their influence on FR growth and death by modifying the microclimate and regulating the FR decomposition process. FR decomposition rates are positively correlated to soil temperature and nutrient availability (Chen *et al.* 2008; Berg & McClougherty 2008). In some cases, broadleaf roots decompose much faster than conifer roots (Berg &

McClagherty 2008).

In boreal forests, both fire and clearcutting are important agents of disturbance for secondary forest succession (Nepstad *et al.* 1999; Lindenmayer *et al.* 2004; DellaSala *et al.* 2006). With stand development after a stand replacing disturbance, both plant species composition and soil characteristics change (Bergeron & Dubuc 1989; Chen & Popadiouk 2002; Hart & Chen 2008; Taylor & Chen 2010). In boreal mixedwood forests, FR decomposition tends to decrease with stand development because of the change in species composition from trembling aspen to balsam fir and cedar (Finer *et al.* 1997). Coupled with the change in species composition, soil chemical and physical environments also change (Turner *et al.* 1998). With increasing stand age, soil bulk density, forest floor depth, total organic C, N and the cation exchange capacity increase in boreal forests, but pH, P and K decrease. All these soil factors may affect FR decomposition during stand development after a stand-replacing disturbance (Shrestha & Chen 2010).

Fire and clearcutting may differ in their influence on ecosystem processes such as coarse woody debris, tree composition, structure, and soil nutrient fluxes (McRae *et al.* 2001; Haeussler & Bergeron 2004; Lecomte *et al.* 2006). Fire can cause substantial losses of C, N, and sulphur (S) through volatilisation, whereas clearcutting may increase soil acidity and the loss of base cations (Shrestha & Chen 2010). The differences in impacts of fire and clearcutting on chemical characteristics of organic matter could have potential effects on the FR decomposition process. On the other hand, similarities also exist between fire and clearcutting-induced disturbances both at stand scale and landscape scale (Nitschke 2005; Lecomte *et al.* 2006). But overall, the patterns of FR decomposition in boreal forest ecosystems have not yet been compared between fire- and clearcutting-origin stands of similar ages.

In this chapter, the patterns of FR decomposition rates along a secondary boreal forest successional gradient originating from fire and clearcutting were studied during a 2-year period. The research questions included 1) how FR decomposition rates varied with stand development after stand replacing disturbances? and 2) whether FR decomposition was similar between fire- and clearcutting-induced stands of similar ages? Because plant roots buried in the underground are more buffered from climatic conditions, their decompositions at a local scale are expected to be regulated more by their chemical composition than by climate. Therefore, the differences at stand levels were expected to affect the age-related FR decomposition pattern and the stand-origin pattern. First, because the litterfall of broadleaved and deciduous species generally decomposes faster than needle-leaved and evergreen species (Berg & McClaugherty 2008), FR decomposition rates were hypothesized to be higher in young stands than in old stands because young stands tend to have higher broadleaved tree species (*e.g.*, *Populus tremuloides* Michx. and herbaceous plants) (Hart & Chen 2008; Ilisson & Chen 2009) that account for a large amount of FR biomass (Figure 3.1 in Chapter 3), Furthermore, as a stand ages, the forest floor layer becomes thicker, lowering soil temperature and its variation (Foster 1985; Prescott *et al.* 2000b; Shrestha & Chen 2010). Consequently, FR decomposition rates decrease as a stand ages. However, the increasing soil nutrients by N fixing and atmospheric deposition with stand development could override these effects. Second, fire-origin stands tend to contain more broadleaved species (*e.g.*, *Betula papyrifera* Marsh. And herbs) and fewer coniferous (*e.g.*, *Picea mariana* [Mill.] B.S.P. and *Abies balsamea* [L.] Mill.) than clearcutting-origin stands. Fine roots were hypothesized to decompose faster in fire-origin stands than in clearcutting-origin stands.

Materials and Methods

Study area and sites

Description in Chapter 3.

Sampling design

Description in Chapter 3.

Field measurements

FR decomposition rates were determined by using standard mesh bag techniques (Mcclaugherty *et al.* 1982). Because it was impossible to separate roots by species in the soil cores, the data presented are for the entire plant community of the sampled stand. Roots were collected in late May 2008 (together with ingrowth cores, see Chapter 5) from the top 30 cm of surface using a power soil auger. After washing, roots were dried at 65°C for 48 hrs, and cut into 2~5 cm lengths. Approximately 0.5 g of root material was placed into each mesh bag (10 × 20 cm size with 0.3 mm mesh). These bags were then returned to their original stands with fifteen bags in each stand. To bury the bags, the soil was sliced down at a 45° angle to a depth of 20 cm by a shovel and then the mesh bag was slipped into the incision. The incision was made to be narrow so that bags had good soil contact with minimum soil disturbance. Four bags from each plot were collected at intervals of 4, 13, and 15 months, and the roots remaining in the bags after washing were dried at 65°C and weighed. The root mesh bags within a plot were pooled, so that all mass values represented a plot average.

Data analyses

Growing degree days (GDD) were estimated as an average of maximum and minimum

temperatures above 5°C (Chapin *et al.* 2006). The decomposition rate constant (k) was calculated for each stand and was examined using an exponential model based on the relationship between mass remaining and time (Wieder & Lang 1982):

$$\frac{M_t}{M_0} = e^{-kt} \quad (4.1)$$

where M_0 is the dry mass at the beginning of decomposition, M_t is the mass remaining at time t , expressed in years; decomposition rate constants k is expressed in year⁻¹. When $M_t = \frac{M_0}{2}$, the half decay time

$$t_{50\%} = \frac{\ln 2}{k} = \frac{0.693}{k} \quad (4.2)$$

When $M_t = 5\%M_0$, the time to 95% mass loss

$$t_{95\%} = -\frac{\ln 0.05}{k} = \frac{2.996}{k} \quad (4.3)$$

The turnover time (or mean residence time) is given by $\frac{1}{k}$ (Giardina & Ryan 2000; Paul 2007). In that case, k was turnover rates for the root system with output (decomposition) but without input (mortality), similar to the first-order kinetics of the radioactive decay process. Therefore, the turnover rates in this chapter referred to dead root system, which differ from the live root turnover process in Chapter 6.

Since the samples after 4, 13, and 15 months were taken from the same stand, they were not independent. The sampling date was treated as a repeated measure in analysis (Hicks & Turner 1993), which was conducted with the repeated ANOVA by *aov* function within R version 2.11.1 statistical software (R Development Core Team 2010). Log transformations were used for the fine root mass remaining to meet assumptions of normality and homogeneity of variance with the *shapiro.test* and *bartlett.test* functions in R.

Results

The remaining FR mass after 15 months across all ages and origins ranged from 46% (10-year-old fire-origin stands) to 72% (205-year-old fire-origin stands) for the *in situ* litter (Figure 4.1). The remaining FR mass differed significantly among postfire stands (Table 4.1), and generally increased from young to old stands (Figure 1).

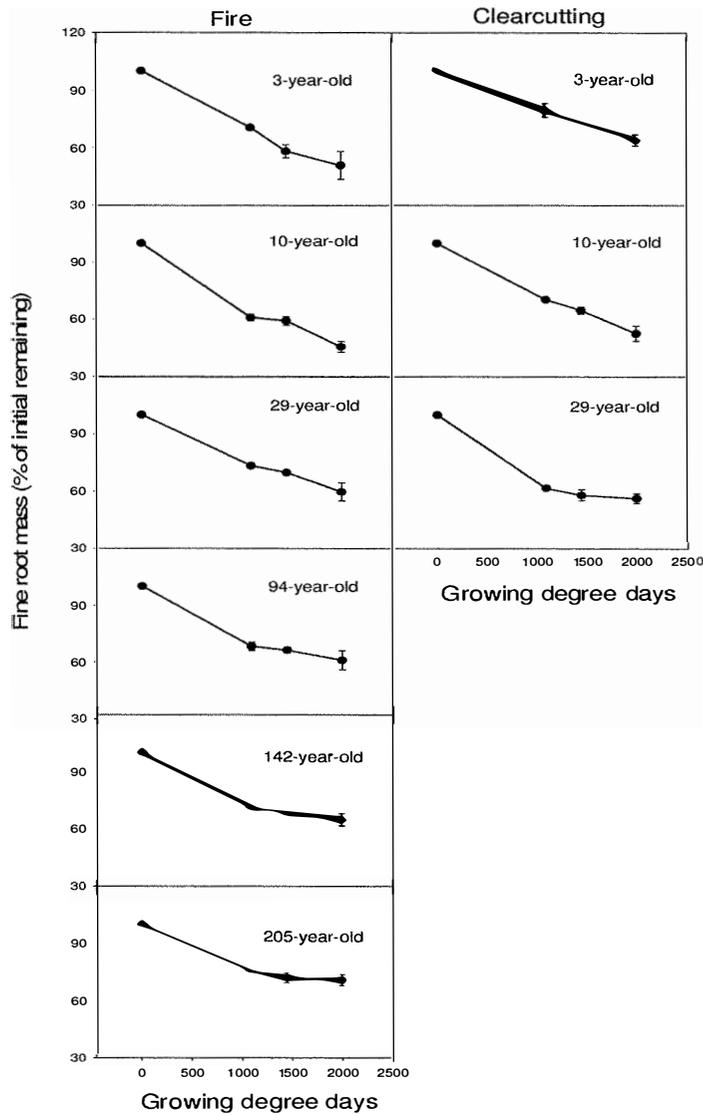


Figure 4.1 Changes in percent of initial mass remaining in fine root litterbags with growing degree days.

Notes: Dotted data values are means with 1 SE error bars. Growing degree days were estimated as average of maximum and minimum temperatures above 5°C (Chapin *et al.* 2006).

FR decomposition rates (*k*-values) also differed significantly with stand age in fire-

fire-origin stands (Table 4.2), which increased in stands from 3-year old, peaked in 10-10-year-old stands, and declined thereafter (Table 4.3). Similarly, $t_{50\%}$ and $t_{95\%}$ values (representing the time required for 50% and 95% loss of dry weight, respectively) were higher in 3-year-old stands, lowest in 10-year-old stands, and increased thereafter from 29-year-old to 205-year-old fire-origin stands.

Table 4.1 Repeated measures analysis of variance for the effects of stand age and sampling date on % fine root mass remaining in postfire stands.

Source	Df	MS	F	P-value
Between subject (stand age)				
Stand age (A)	5	288.230	7.842	0.002
Within subject (stand age)				
Sampling date (D)	3	727.885	235.5	<0.001
D×A	15	135.090	4.210	0.019

Notes: Significant effects at $P < 0.05$ are in bold. Data are \log_{10} transformed before analysis.

Table 4.2 One-way ANOVA for the effects of stand ages on decomposition constant k of fine roots in fire-origin stands.

Source	SS	df	MS	F	P
Between groups	0.188	5	0.038	4.535	0.015
Within groups	0.100	12	0.008		

Notes: Data have been \log_{10} -transformed. Significant effects at $P < 0.05$ are in bold.

Table 4.3 *Decomposition rate constants of fine roots.*

Origin	Stand age (years)	k (year ⁻¹)	r^2	$t_{50\%}$ (year ⁻¹)	$t_{95\%}$ (year ⁻¹)	Mean residence time (year)
Fire	3	0.213±0.029	0.792***	3.249	14.048	4.689
	10	0.505±0.020	0.731***	1.371	5.928	1.979
	29	0.343±0.015	0.737***	2.020	8.732	2.915
	94	0.352±0.110	0.640**	1.967	8.504	2.838
	142	0.315±0.035	0.679**	2.199	9.505	3.173
	205	0.237±0.038	0.648**	2.927	12.656	4.224
Clearcutting	3	0.189±0.016	0.800***	3.661	15.827	5.283
	10	0.334±0.084	0.796***	2.077	8.979	2.997
	29	0.371±0.068	0.620**	1.869	8.081	2.697

*Notes: k values were calculated for each age-class using an exponential decay model, $t_{50\%}$ and $t_{95\%}$ values represent the time required for a 50% and a 95% loss of dry weight (years). r^2 values represent fit of the model, with ns: not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.*

Among stands ≤ 29 years old, the FR mass remaining also differed between stands with fire- and clearcutting-origin (Table 4.4). Higher values were observed in clearcutting-origin stands than in fire-origin stands at 3- and 10-year-old ages, but similar values at 29-year-old age. The k -values tended to be higher in fire-origin stands than in clearcutting-origin stands at 3- and 10-year-old ages, but similar at 29-year-old age (Table 4.3). However, the effects of disturbance origins on k -values did not differ significantly (Table 4.5). Similarly, $t_{50\%}$ and $t_{95\%}$ values, calculated from k -values, tended to be lower in 3- and 10-year-old fire-origin stands than in the same age clearcutting-origin stands, but similar in 29-year-old stands. The mean residence time, *i.e.*, the inverse of k -values, showed a pattern similar to the k -values between stand origins of fire and clearcutting (Table 4.3 and 4.5).

Table 4.4 Repeated measures analysis of variance for the effects of stand ages, disturbance origin (fire vs clearcutting), and sampling times on total % fine root mass remaining in 3-, 10-, and 29-year-old stands.

Source	df	MS	F	P value
Between subject				
Stand age (A)	2	195.594	8.148	0.006
Disturbance (O)	1	149.980	6.248	0.028
A×O	2	446.328	18.592	<0.001
Within subject				
Sampling date (D)	3	6866.511	362.371	<0.001
D×A	6	49.635	2.605	0.034
D×O	3	26.786	1.414	0.255
O×A×D	6	63.279	3.339	0.010

Notes: Data have been \log_{10} -transformed. Significant effects at $P < 0.05$ are in bold.

Table 4.5 Two-way ANOVA results for the responses of k-constant for fine roots to disturbance types (fire or clearcutting) and stand ages in 3-, 10-, and 29-year-old stands.

Source	SS	df	MS	F	P-value
Stand age (A)	0.152	2	0.076	11.255	0.002
Disturbance (O)	0.014	1	0.014	2.097	0.173
A×O	0.032	2	0.016	2.386	0.134
Error	0.081	12	0.007		

Discussion

Stand age effects

There were significant effects of stand age on FR decomposition rates (Table 4.2), supporting the first hypothesis that FR would decompose faster in young stands than in old stands. A previous study found that in the southern boreal forest of Quebec, *P. tremuloides* roots (≤ 10 mm in diameter) were found to decompose faster in younger stands (48-year old) than in older forest stands (232-year old) (Finer *et al.* 1997). In Pacific silver fir (*Abies amabilis* Dougl.), foliar litterfall also decomposed faster in young stands (23-year old) than in old stands (180-year old) (Vogt *et al.* 1983b), again suggesting that FR decomposition also follows the suit because both decomposition processes are mostly regulated by the same factors (Berg & McClaugherty 2008).

First, the age-related patterns of FR decomposition rates may reflect ecological effects that regulate FR decomposition process. As a stand ages, a change in tree species composition from *P. tremuloides* to *P. mariana* (Hart & Chen 2008) may cause a root chemical composition that is less favorable for root decay. Therefore, the decline of the FR decomposition rate with stand development could be attributed to younger having more broadleaved species (such as *P. tremuloides* and herbs) (Figure 3.1 in Chapter 3) whose root litter decomposes faster than conifer roots. Therefore, the results support the conclusion that FR decomposes faster in boreal forest stands dominated by broad-leaved, deciduous species than in those dominated by coniferous, evergreen species (Finer *et al.* 1997). These results may also support the conclusion that at a local scale FR decomposition is primarily regulated by FR chemical composition rather than climate factors (Berg & McClaugherty 2008).

As foliar litterfall tends to increase over time beneath late successional conifer-

conifer-dominated stands, the slow decomposition rates also results in thicker humus layer (Table 3.1 in Chapter 3) (Van Cleve *et al.* 1983; Pare *et al.* 1993; Brais *et al.* 1995; Shrestha & Chen 2010). An increasingly thick humus layer, coupled with low soil temperature but high moisture conditions (Yermakov & Rothstein 2006; Bond-Lamberty *et al.* 2006a) could strongly affect FR decomposition rates as a stand develops. Decomposition rates have been observed to increase 50%–100% when soil temperatures increase 5°C–10°C (O'Neill *et al.* 2002).

In general, N mineralization and nitrification rates decline during both primary and secondary succession of forests (Vitousek *et al.* 1989; Lambers *et al.* 2008b; Peltzer *et al.* 2010) and is strongly correlated with litter decomposition. In turn, slow decomposition rates generally result in N accumulating in the forest floor, reducing nutrient availability because of low mineralization rates (Gower *et al.* 1996a). However, nutrient contents in soils generally increase with these age-chronosequences (Shrestha & Chen 2010; Yuan & Chen 2010a), indicating that nutrient supplies were not associated with the decline of FR decomposition rates with stand age. However, due to more coniferous roots in old stands than in young stands (Figure 3.1 in Chapter 3), the average nutrient concentrations in FR could decrease with stand age, resulting in a decline of FR decomposition rates in old stands. Therefore, the findings in this present study suggest that it is not soil nutrients but the mean FR quality (*i.e.*, the ratio of broadleaved and coniferous roots) that mainly regulates FR decomposition at a local scale and stand level. Additionally, the more rapid decomposition of fine roots observed in younger fire-origin stands compared to older fire-origin stands (Table 4.1), may be explained by the higher pH values and higher base saturation of the soil in these younger stands (Table 3.1 in Chapter 3), which should favor root decomposition (King *et al.* 1997). Both 3-year old postfire and post-clearcutting

stands had a low k -value in (Table 4.4), suggesting that low soil nutrients in these sites might contribute more to fine root decomposition than other factors. The 10-year-old sites did not have a closed canopy, and had the highest k -value, suggesting that this successional stage provided better microsites for decay (Table 4.4).

The effects of fire vs. clearcutting origins

In this present study, stand origins showed no significant effects on the k constant (Table 4.5), non-supporting the hypothesis that FR decomposes faster in fire-origin stands than in clearcutting-origin stands. These similarities might be explained by the FR composition that regulates FR decomposition. 1) In 3-year-old stands, herbs accounted for similar fractions of FR biomass for the two disturbance types. The 3-year-old clearcutting-origin stands contained more FR biomass of broadleaved species *P. tremuloides* than fire-origin stands. In addition, there was more FR biomass made up of coniferous species *P. banksiana* in clearcutting-origin stands than in fire-origin stands, which could contribute to similarities of FR decomposition rates between these disturbance types at this age. 2) Although fire-origin stands had more *B. Papyrifera* and fewer *P. mariana* and *A. balsamea* than clearcutting-origin stands in 10-year-old stands, the densities of *P. tremuloides* and *P. banksiana* did not differ between disturbance types (Ilisson & Chen 2009), resulting in no significant differences in FR biomass and decomposition rates between these two disturbances at this age either. 3) Stand composition of *P. tremuloides* did not differ between stand origins in 29-year-old stands. This may be due to the increasing presence of broadleaved species *B. papyriferea*, the coniferous species *P. banksiana*, *Abies balsamea*, and *Picea* spp. occurring in clearcutting-origin stands, thereby creating similarities of FR biomass and decomposition rates to those two disturbance

types. So this study indicated that the proposition that root substrate quality has a major control on root decomposition at a local scale. The similarities of FR decomposition rates between these fire- and clearcutting-origin disturbances were most likely due to the non-significant differences in soil environments such as humus layer depth, soil temperature, soil moisture and nutrients (Shrestha & Chen 2010).

Seasonal patterns

Most FR in the study area decomposed slowly; after 12 months the mass loss was only 32% (Figure 4.1). These results were within the range reported for FR decomposition in other forest ecosystems. In Norway spruce (*Picea abies* L.) (Gaul *et al.* 2008), sugar maple (*Acer saccharum* Marsh.) and white pine (*Pinus strobes* L.) (Mcclaugherty *et al.* 1984), FR have been found to decompose with mass losses of 12–26% per year. In boreal forests of northern Europe, first-year root mass loss (2-3 mm in diameter) ranged from 17 to 41%. Much of this variability was explained by climate (Berg *et al.* 1998). In a meta analysis based on a 176 stand dataset, Silver and Miya (2001) concluded that, on a broad scale, root decomposition is determined by root chemistry, climate and environmental factors. In this present study, it was assumed that all stands had a similar climate, and it believed that the variability was most likely due to differences in disturbances and stand development as discussed above.

After the first year, decay rates remained constant (Figure 4.1), suggesting that FR decomposition relies on first-year mass-loss rates, *i.e.*, the early stage of root decomposition was controlled by nutrient concentrations and readily available solutes. These seasonal patterns of FR mass loss again supported the conclusion that the initial stage of rapid mass loss could be attributed to simple leaching processes and that the second stage of slower mass loss was more dependent upon microbial activity for the

decomposition of remaining recalcitrant substrates after the initial loss of more labile substrates through leaching.

FR decomposed slowly from September to July (Figure 4.1), which could be attributed to the cold soil environments which were less suitable for microbial decomposition. Burke and Raynal (1994) found that the intermediate size roots (0.5-1.5 mm in diameter) did not decompose between 5 and 12 months in a northern hardwood forest ecosystem. McClaugherty *et al.* (1982) reported no change or even an increase in the remaining FR mass after five months in two hardwood stands in north-central Massachusetts. In this present study, the remaining FR mass decreased by 20-42% from the June to the October sampling date (Figure 4.1), pointing to a rapid FR decomposition at the beginning stage.

Summary

The process of FR decomposition is controlled by both internal and external factors. The shift in tree species composition from broadleaved species with high N in FR to coniferous species with low N in FR as a stand ages can result in a FR chemical composition less favorable for root decay, contributing the slower FR decomposition rates in older stands. Therefore, internal factors like FR substrate quality could be the major regulator for FR decomposition process at a local scale. Soil temperature, water content and chemical characteristics, are expected to influence the nature of the decomposer populations, their activity and their distribution in the soil (Joslin & Henderson 1987). In this present study, the increasing humus layer thickness with respect to increasing stand age can cause a decreasing soil temperature, probably another reason for the slow FR decomposition rates in old fire-origin stands. Therefore, at a local scale, FR decomposition is related to the variations in FR litter quality due itself to the changes in

FR composition with stand development. However, microclimates (unqualified) that may varied greatly different along this chronosequence, could also exert some degree of control over FR decomposition, resulting in different k values (Table 4.3). Between fire- and clearcut-origin stands, the similarities in both aboveground biomass (Ilisson & Chen 2009; Seedre & Chen 2010) and belowground FR biomass composition may have helped cause the similarities in FR chemical composition that can result in similar decomposition rates between these two disturbance types. The similarities in soil attributes between stand origins (Ilisson & Chen 2009; Seedre & Chen 2010) also contribute to similarities in FR decomposition between fire- and clearcutting-origin stands.

CHAPTER FIVE: FINE ROOT PRODUCTION

Introduction

Root production is a major regulator of C and nutrient fluxes in terrestrial ecosystems (Mcclaugherty *et al.* 1982; Nadelhoffer *et al.* 1985; Fahey & Hughes 1994; Brassard *et al.* 2009). On average, it has been estimated that 44% of annual net primary production (NPP) is allocated to belowground in boreal forest ecosystems (Vogt *et al.* 1996; Yuan & Chen 2010b). Also, 18 to 58% of N is added to the soil by root mortality, which is greater than that added by aboveground litterfall (Vogt *et al.* 1986). In particular, the dynamics of fine roots (≤ 2 mm in diameter) can represent a substantial C and nutrient input into the soil despite the fact that fine root biomass (FRB) constitutes only a small fraction of total stand biomass. Fine root production (FRP) has been estimated to account for about 30–76% of the C being cycled annually through forest ecosystems (Vogt *et al.* 1996; Gower *et al.* 1996b; Jackson *et al.* 1997). In the boreal forest, FRP was 3.4 Gt year⁻¹, accounting for 73% of total root production and 32% of the total boreal forest production (Yuan & Chen 2010b). Accurate data on root production is important for improving terrestrial ecosystem models and estimates of C cycling. However, despite its importance in nutrient cycling and resource acquisition, FRP, compared with that of aboveground, is seldom measured directly mainly due to methodological difficulties in collecting FR data.

Age-related changes in the aboveground production of secondary forest stands after fire/clearcutting disturbances are well known to ecologists (Gower *et al.* 1996a; Ryan *et al.* 2004); however, studies on belowground production in relation to stand development are limited, especially regarding boreal forests. The existing studies conducted in boreal forests often reveal contradictory results, and how root production changes with stand

development is still unclear (Table 5.1). FRP of black spruce (*Picea mariana* [Mill.] B.S.P.) based on allometric equations has been found to range from 0 to 79 g C m⁻². FRP was highest in 71-year-old stands and 50–70% lower than in 151-year-old stands (Bond-Lamberty *et al.* 2004). Black *et al.* (2009) found that root (<5 mm in diameter) production of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) based on regression models increased until stands reach 30-year old and declined thereafter. Based on sequential soil cores, FRP in Scots pine (*Pinus sylvestris* L.) stands in eastern Finland was found to increase with stand age from 15-, 35-, to 100-year-old stands and occurred beyond canopy closure (Makkonen & Helmisaari 2001; Helmisaari *et al.* 2002). However, in *P. sylvestris* stands in southern Finland, FRP was found to decrease in stands from 7- to 20-year old, and then increased slightly in 85- and 105-year-old stands (Messier & Puttonen 1993). In the southern boreal forest of Quebec, FRP decreased with forest age from 48-, 122- to 232-year-old stands, but this effect was not significant (Finer *et al.* 1997). FR length production in ponderosa pine (*Pinus ponderosa* Laws.) stands in Oregon based on minirhizotron observation was higher in young stands (15-20 years old) than older stands (50-60 and >250 years old) (Andersen *et al.* 2008). However, in Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) stands, FRP was found to be greater in mature (180-year-old) than in young (23-year-old) stands (Grier *et al.* 1981). These studies on root production with stand age allow no generalization of trends, suggesting the difficulties in comparison among studies. If leaf and root traits are functionally coordinated (Roumet *et al.* 2006), root production will mirror somewhat its aboveground production, which increases after disturbance, peaks at immediate stand age, and then declines in older stands.

Table 5.1 Studies on FR patterns with stands age in boreal forests

Location	Dominated species	Age chronosequence	Methods	FR pattern	References
Canada	<i>Picea mariana</i>	3, 6, 12, 20, 37, 151 years	Allometric equations	Increased in stands from 3-, 6-, 12- and 20-year old, peaked at 37-year old, and decreased in 151-year old.	Bond-Lamberty <i>et al.</i> (2004)
Ireland	<i>Picea sitchensis</i>	9, 14, 16, 22, 30, 45, 47 years	Regression models	Increased in young stands, peaked at 30-years old, and decreased thereafter.	Black <i>et al.</i> (2009)
Finland	<i>Pinus sylvestris</i>	15, 30, 100 years	Sequential soil cores	Increased with stand age from 15-, 35-, to 100-yr old.	Makkonen & Helmisaari (2001); Helmisaari <i>et al.</i> (2002)
Finland	<i>Pinus sylvestris</i>	7, 11, 13, 20, 85, 105 years	Ingrowth soil cores	Decrease from 7- to 20-yr-old stands, and then increased slightly in 85- and 105-yr-old stands.	Messier & Puttonen (1993)
Canada	<i>Populus tremuloides</i> , <i>Abies balsamea</i> , <i>Picea glauca</i>	48, 122, 232 years	Ingrowth soil cores	Increased but not significantly different.	Finer <i>et al.</i> (1997)
Oregon	<i>Pinus ponderosa</i>	18, 50, >250 years	Minirhizotron	Higher in young stands than older stands (50 and >250 years old)	Andersen <i>et al.</i> (2008)
Seattle, WA	<i>Abies amabilis</i>	23, 280 years	Regression models	Greater in mature than in young stands	Grier <i>et al.</i> (1981)

As two important disturbances, fire and clearcutting have potential impacts on ecosystem processes such as nutrient fluxes (Lecomte *et al.* 2006; Thiffault *et al.* 2007) and probably on FRP as well. Both similar and different effects have been found comparing fire- and clearcutting-induced disturbances on boreal forests at landscape and stand scales (Lecomte *et al.* 2006). However, how the root production process varies between these disturbances is not well understood and no study has yet addressed this question.

Although useful for studying root biomass, destructive samples of root tissue using sequence soil core method cannot be used to measure root production. Therefore, a combination of direct estimation (*e.g.*, ingrowth cores) and destructive sampling (*e.g.*, sequence soil cores) can capitalize on the strengths of both approaches (Hendrick & Pregitzer 1992), and can provide a more comprehensive understanding of the fine root production.

The main purposes of this chapter were to determine the differences in FRP dynamics associated with stand development and between fire- and clearcutting-origin stands using sequential and ingrowth approaches. The first hypothesis tested on these sites was that FRP increases rapidly after disturbance, peaks at intermediate stand ages, and then decreases slowly until it reaches equilibrium in the oldest stands (see description in Chapter 3). The second hypothesis was that FRP was hypothesized to be higher in clearcutting-origin stands than fire-origin stands.

Materials and Methods

Study area and sites

Description in Chapter 3.

Sampling design

Description in Chapter 3.

Field measurements

In this present study, both ingrowth core and sequential core-based methods were used to estimate FRP, so that direct and indirect FRP results could be compared by these two commonly used methods.

1) Ingrowth cores

Root ingrowth cores were established in June 2008, together with decay root-litter bags (see Chapter 4). Sixteen root ingrowth cores were randomly placed within each plot. Four cores were removed from each plot on three periods of the year: October 2008 (before snow), July 2009, and September 2009.

Root ingrowth cores were made of fiberglass mesh (1.5×1.5 mm), and formed into 6.6 cm diameter cylinders with 30 cm depth. After a soil column was removed, the cylinder was placed in the forest floor (H horizon) and through the mineral soil (because most fine roots were located within the first 30 cm of the mineral soil and forest floor (see Chapter 3)). Ingrowth cores were gradually filled with root-free soil of local origin. Root ingrowth cores were removed by carefully digging the soil away from the cylinder and cutting roots that had grown into the bag with a knife and/or scissors. Root bags were stored at -18°C until processing. The cores were separated into two layers: 0-15 and 16-30 cm layers.

2) Sequential soil cores

See Chapter 3.

Data analyses

To estimate FRP from the root ingrowth cores, data from cores extracted over three time intervals were used. Root ingrowth data spanning 2008 to 2009 and annual FRP was calculated for each plot. During the period of ingrowth, roots grow into the cores (live roots) and some of those roots also die (dead roots). As a result, root production from the ingrowth core method was the sum of the live and dead roots. Individual soil cores at each plot were treated as subsamples and were averaged by plot for statistical analysis.

Production based on ingrowth cores was calculated from root biomass divided by the period of growth time (year). Production on a sequential coring basis was estimated by summing the positive increments over all sampling intervals within the year (Fairley & Alexander 1985).

Because of the difference in age range between stands of fire origin and those of clearcutting origin, analyses were conducted in two steps. First, changes in fine root attributes (production, mortality, and decomposition) with time after fire were determined for postfire stands using one-way analysis of variance. Second, the interactive effects of stand age and stand origin were tested with two-way analysis of variance by choosing all stands ≤ 29 years old, *i.e.*, three age classes from postfire stands and all sampled post-clearcutting stands. Models were fitted and analyzed using the *aov* and *lm* functions within R version 2.11.1 statistical software (R Development Core Team 2010). Log transformations were used for data of fine root attributes to meet assumptions of normality and homogeneity of variance with the *shapiro.test* and *bartlett.test* functions in R.

Results

Fine root biomass in ingrowth cores

Fine roots in the 0-15 cm layer grew fast from June to October 2008, stagnated until July 2009, then grew rapidly from July to September 2009. By contrast, fine roots in the 16-30 cm layer increased steadily over the two years period (Figure 5.1).

The total fine root biomass found in the ingrowth cores in the top 30 cm surface differed significantly with respect to stand age (Table 5.2). After 4 months growth, the biomass in 0-15 cm and in 16-30 cm layers did not significantly differ among postfire stands, but the total fine root biomass in the top 30 cm surface began to increase in 3-year-old postfire stands, peaked in 10-year-old stands, and declined thereafter in postfire stands. After 13 months growth, the biomass in the first 15 cm layer did not differ among stand ages, but the biomass in the second layer increased until 10-year-old stands. After 15 months growth, the biomass patterns in both layers were clear with a unimodal peak that peaked in 10-year-old postfire stands (Figure 5.2).

Table 5.2 *Effect of stand age on root biomass in ingrowth cores.*

Sampling date	0-15 cm		15-60 cm		Total mass	
	<i>F</i>	<i>P</i> -value	<i>F</i>	<i>P</i> -value	<i>F</i>	<i>P</i> -value
2008						
October	1.981	0.154	2.489	0.091	4.017	0.023
2009						
July	1.631	0.231	8.445	0.001	4.143	0.020
September	5.505	0.007	3.825	0.026	7.906	0.002

Notes: Significant effects at $P < 0.05$ are in bold.

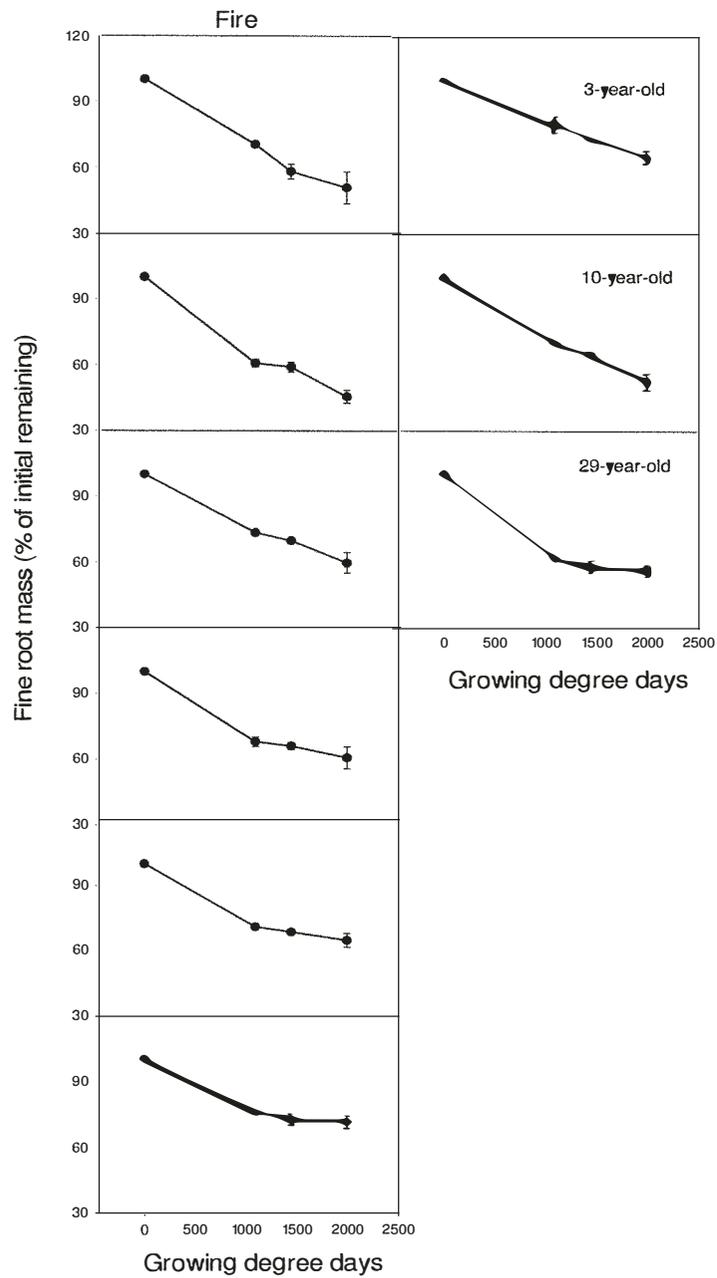


Figure 5.1 Seasonal changes in root biomass in ingrowth cores in postfire and post-clearcutting stands.

Notes: Dotted data are means with 1 S.E. error bars.

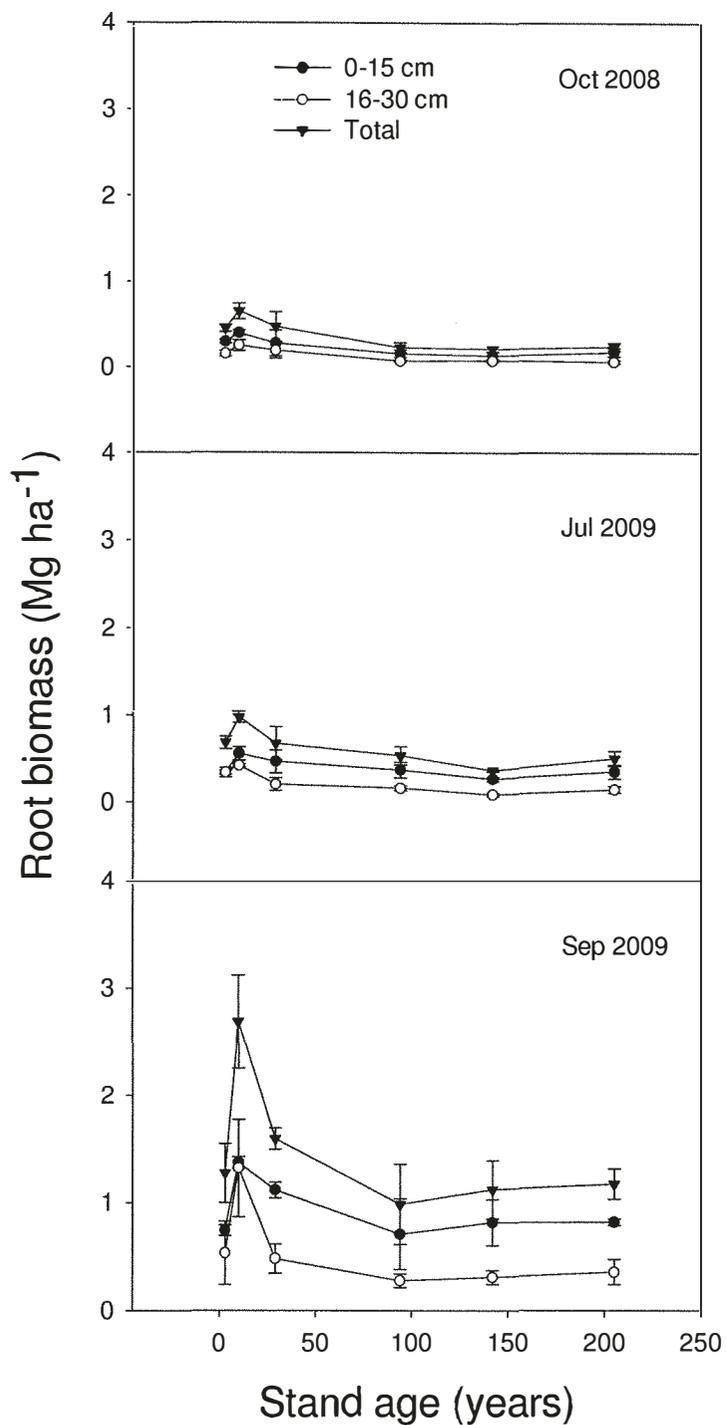


Figure 5.2 Changes in fine root biomass in ingrowth cores in postfire stands.

Notes: dotted data are means with 1 S.E. error bars.

The root biomass in ingrowth cores in the top 0-30 cm layer differed between stand origins (Table 5.3). After 4 months growth, the biomass both in 0-15 cm and in 16-30 cm layers did not significantly differ between postfire and post-clearcutting stands. After 13 months growth, postfire stands tended to have greater biomass in the first 15 cm layer than in post-clearcutting stands, but similar biomass in the second layer. After 15 months growth, the biomass was greater in 3- and -9-year-old postfire stands than in post-clearcutting stands; but similar in 29-year-old stands (Figure 5.3).

Table 5.3 P-values of two-way ANOVA results for the effects of stand age (A) and stand origin types (O) in younger stands (3- to 29-year-old) on root biomass in ingrowth cores.

Sampling date	0-15 cm			16-30 cm			Total mass		
	A	O	A×O	A	O	A×O	A	O	A×O
2008									
Oct.	0.481	0.079	0.166	0.134	0.605	0.192	0.081	0.096	0.040
2009									
July	0.045	0.024	0.237	0.718	0.113	0.025	0.137	0.026	0.040
Sept.	0.001	0.017	0.003	0.093	0.016	0.046	0.005	0.001	0.001

Notes: Bold indicates significant or marginally significant effects.

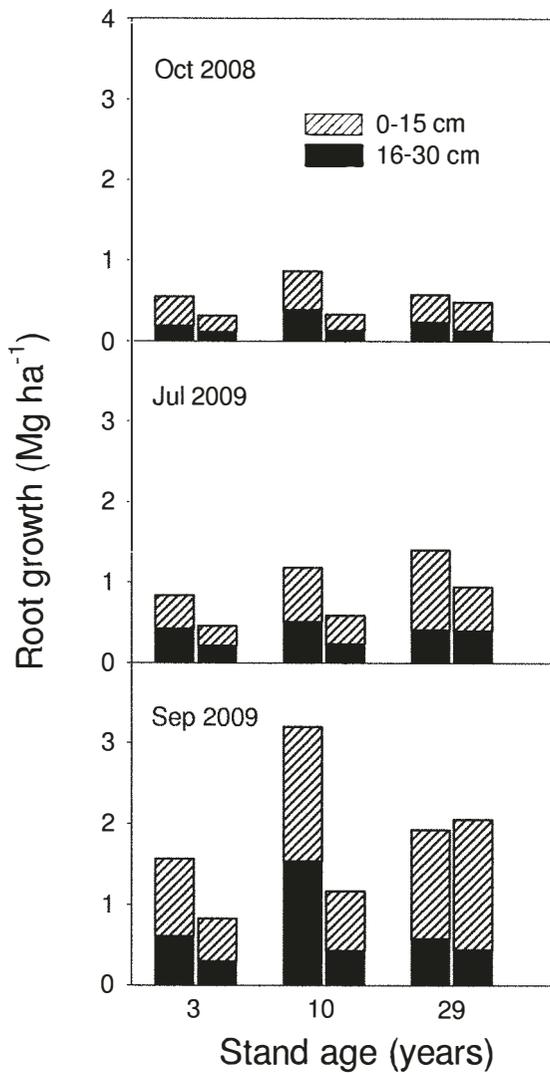


Figure 5.3 Effects of stand origin (fire vs. clearcutting) on root biomass in ingrowth cores.

Notes: Fire-origin stands on the left and clearcutting-origin stands on the right.

Fine root production (FRP)

Both ingrowth and sequential core methods indicated that fine root production varied with stand age in postfire stands (Table 5.4), with greater values in the five older stands than

the youngest stands (Figure 5.4). FRP based on the ingrowth core method in the top 15 cm layer increased from 0.60 Mg ha⁻¹ year⁻¹ in 3-year-old stands to 0.94 Mg ha⁻¹ year⁻¹ in 10-year-old stands and then decreased thereafter in 29-, 94-, 142-, and 205-year-old stands (Figure 5.4). FRP in the second 15 cm layer showed a similar pattern that increased in stands from 3- to 10-year old, then declined in stands from the 29-year old to the 205-205-year old. Based on sequential core methods, FRP in forest floor and MS1 layers also increased in stands from 3- to 10-year old, then declined thereafter in old stands. FRP in MS2 layer did not differ significantly among stands with different ages. Based on ingrowth and sequential core methods, the age-related total FRP had similar patterns that increased in stands from 3- to 10-year old, then declined in old stands (Figure 5.4)

Table 5.4 *Effect of stand age on fine root production.*

Layer	<i>F</i>	<i>P</i> -value
Ingrowth		
0-15 cm	3.871	0.025
15-30 cm	8.724	0.001
Total	9.079	0.001
Sequential		
FF	3.100	0.036
MS1	2.992	0.054
MS2	1.061	0.428
Total	10.941	<0.001

Notes: Significant ($P < 0.05$) or marginally significant ($0.05 < P < 0.10$) effects are in bold.

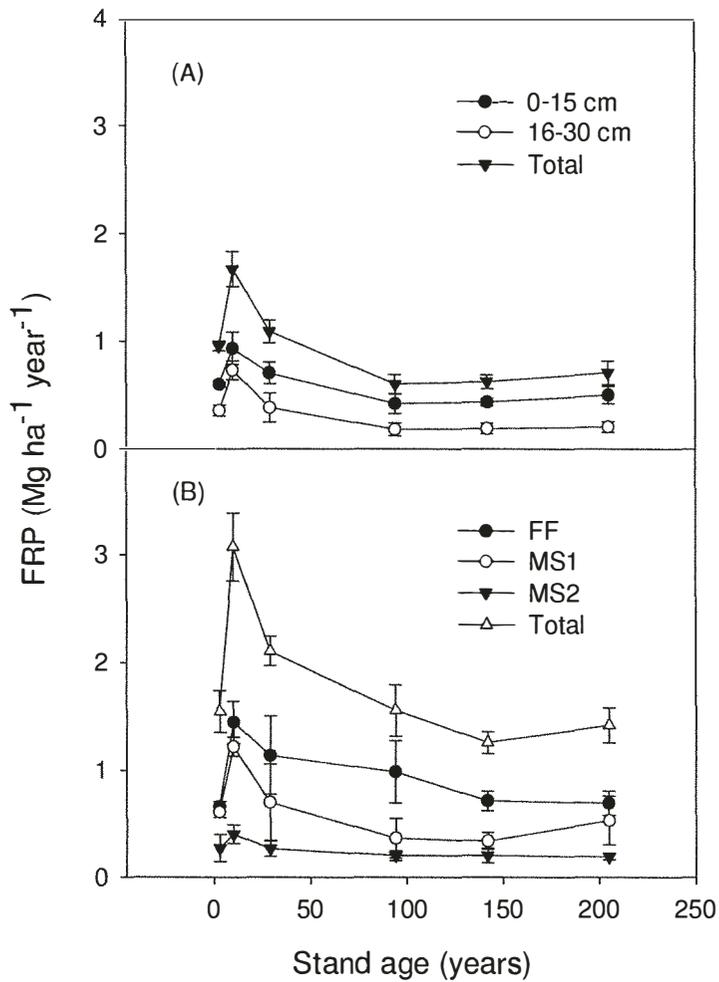


Figure 5.4 Fine root production in postfire stands by ingrowth core (A) and sequential core (B) methods.

Notes: Data in (A) are means for the ingrowth cores of three sampling dates. Error bars represent 1 S.E. FRP = fine root production, FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer.

FRP was significantly different between stand origins (Figure 5.4). Fire-origin stands had greater FRP than clearcutting-origin stands in 3- and 10-year-old stands but not in 29-year-old stands (Figure 5.5). Ingrowth core-based FRP was 0.95, 1.67, and 1.09 Mg ha⁻¹ year⁻¹ in 3-, 10-, 29-year-old postfire stands, respectively; while it was 0.48, 0.65, and 1.35 Mg ha⁻¹ year⁻¹ in 3-, 10-, 29-year-old post-clearcutting stands, respectively. Sequential core-based FRP was greater in fire-origin stands than in clearcutting-origin stands in 3- and 10-year-old stands (1.55 vs. 0.87 and 3.08 vs. 1.68 Mg ha⁻¹ year⁻¹, respectively), whereas it did not differ significantly in 10-year-old stands of both origins (2.11 vs. 1.84 Mg ha⁻¹ year⁻¹) (Table 5.5).

Table 5.5 P-values of two-way ANOVA results for the effects of stand age (A) and stand origin types (O) in younger stands (3- to 29-year-old) on fine root production.

Layer	Source		
	A	O	A×O
Ingrowth			
0-15 cm	0.021	0.012	0.017
15-30 cm	0.031	0.017	0.007
Total	0.008	0.004	0.003
Sequential			
FF	0.048	0.047	0.820
MS1	0.090	0.038	0.450
MS2	0.952	0.171	0.323
Total	<0.001	<0.001	<0.001

Notes: Bold indicates significant or marginally significant effects.

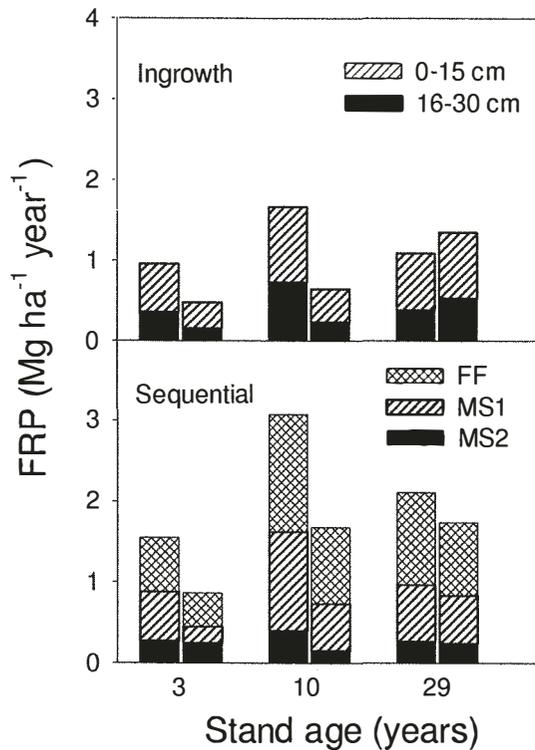


Figure 5.5 Effects of stand origin (fire vs. clearcutting) on fine root production.

Notes: Fire-origin stands on the left and clearcutting-origin stands on the right. Error bars represent 1 SEM. FRP= fine root production, FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer.

Discussion

The results of this present study showed that FRP increased in stands from 3-year old to 10-year old, and leveled off or declined thereafter in 29-, 94, 142, and 205-year-old stands (Figures 5.2 and 5.4), and these findings support the first hypothesis that FRP changes with stand development. The second hypothesis (*i.e.*, FRP differs between fire-

and clearcutting-origin stands) was partly supported in this present study in that FRP differed significantly between stand origins in 3-, and 10-year-old stands but not in 29-29-year-old stands.

Stand age effects

In this present study, FRP (measured with the ingrowth and sequential core methods) increased in stands from 3-year old, reached its peak in 10-year-old stands, and then declined with increasing stand age. These findings suggested that the processes of fine root productivity and turnover rates (Chapter 6) are more substantial in early successional stages dominated by herbs, grasses and woody deciduous species than in late successional stages with more coniferous shrubs and trees (Seedre & Chen 2010). The FRP patterns were consistent with FRB patterns in relation to stand age (Chapter 3), which was not surprising because FRB was defined as the net accumulation of fine root production and mortality. The FRP patterns were also similar to the general pattern of aboveground biomass accumulation observed in eastern (Pare & Bergeron 1995) and central (Seedre & Chen 2010) boreal mixedwoods, and other forest ecosystems (Gower *et al.* 1996a; Ryan *et al.* 1997). However, it appears that the peak ANPP of boreal coniferous *P. abies* stands occurred around 60 years (Gower *et al.* 1996a; Ryan *et al.* 1997), suggesting that maximum belowground productivity is reached at younger ages than maximum aboveground productivity.

But, the factors that cause and maintain these age-related FRP trends remain unclear. Internal factors (*e.g.*, growth rhythm, root aging, and senescence) might be the primary reason for the FRP patterns with respect to stand age. In addition, the ecological effects that occur with stand age could also contribute to the observed FRP patterns. In early

stages, young plants allocate more resources to their root system to maximize water and nutrient uptake that support rapid growth of their aboveground crowns, securing their survival. The age-related decline of FRP might also be related to the successional changes in species composition (Hart & Chen 2008).. The abundance of *P. tremuloides* with potential high above- and belowground productivity (Pare & Bergeron 1995; Block *et al.* 2006) has been found to decline in old stands (Seedre & Chen 2010). Low tree density (Litton *et al.* 2003; Borja *et al.* 2008) and sparse understory (Wirth *et al.* 2009) may account for the low FRP in old stands. Moreover, the increased probabilities of insect and/or wind damage (Chen & Popadiouk 2002; Seedre & Chen 2010) might be another reason for age-related FRP decline. It has been found that most colonizing plants in young stands are non-mycorrhizal, whereas in mature stands, the dominant herbaceous plants tend to have a facultative requirement for arbuscular mycorrhizal fungi. However, in old stands, trees and shrubs, which typically dominate the vegetation, have an obligate need for ectomycorrhizae (Read 1993). The mycorrhizal changes with respect to stand age can affect fine root growth and mortality processes, also one reason responsible for the age-related FRP and FRT patterns found in this present study.

With a stand ages, soil characteristics also vary (Shrestha & Chen 2010). FRP has been found to be positively correlated to soil N availability across a primary successional forest chronosequence spanning over 850 years at Mt. Shasta, California (Uselman *et al.* 2007). Therefore, soil environments could likely contribute to FRP variations with stand development. Canopy tree succession from N-rich early successional species to N-poor late successional species (Pare & Bergeron 1995) can lead to a change in litter nutrient input and a decline of soil N in old stands (Smith *et al.* 2000; Welke & Hope 2005;

Shrestha & Chen 2010). However, FRP was not significantly associated with soil total N in this study ($F=0.027$, $P>0.05$). As a stand ages, more N is bound to organic matter, causing an increase in soil total N in the forest floor (Shrestha & Chen 2010) but a decrease in N availability that can lead to a FRP reduction. Thus it is not total but available N that is associated with FRP, and the idea that nutrient limitation is responsible for age-related ANPP decline is, at least partly, applicable to observed trends of FRP. Under the closed canopy of old-growth forests, the attenuating quantity of light, coupled with a thick forest floor layer (Wirth *et al.* 2009), may indirectly reduce root productivity by decreasing soil temperature, microbial activities and mycorrhizal colonization (Zak *et al.* 1990).

Therefore, the age-related slowing FRP may reflect coupling changes with stand age, including internal (like tree maturity and vegetation composition) and external (*e.g.*, canopy closure, aboveground changes, and site quality) changes. Additional systematic study will be necessary to develop a general understanding of this phenomenon and to determine what primary factors affect age-related FRP dynamics.

Stand origin effects

The present study partly support the second hypothesis in that FRP differs significantly between fire- and clearcutting-origin stands: FRP is higher in postfire stands than in post-clearcutting stands at 3- and 10-year old ages, but similar at 29-year-old age (Figure 5.5). These findings indicate that more differences in internal and external factors that drive fine root growth at an early stage compared to a late stage. These findings were also partly in contrast with the results the aboveground C pools which were higher in 3- and 29-year-old clearcutting-origin stands than in the same years old fire-origin stands, but

were similar in 10-year-old stands (Seedre & Chen 2010). This observation indicates that fire disturbance may result in more available nutrients (Scott Chang, personal communication), therefore supporting more fine root production. However, the aboveground production process may not follow the same pattern as the aboveground live C pools (*i.e.*, biomass resulting from production and mortality) between stand origins. In this present study, FRP patterns also differed from FR biomass which did not significantly differ between stand origins in 3-, 10- or 29-year-old stands (Chapter 3), indicating that the processes of both fine root production and mortality regulate the standing crop of fine root biomass (Raich *et al.* 2009).

Seedre and Chen (2010) speculated that the differences in aboveground live C pools in the youngest stands may be the result of residual live trees left after clearcutting that were not present after wildfire. However, such a difference in aboveground presses could not contribute to belowground FRP process. Young postfire stands tended to have higher densities of deciduous *B. papyrifera* but fewer evergreen *P. mariana* and *A. balsamea* (Ilisson & Chen 2009). Therefore, the FRP differences in young stands, first, could be attributed to changes in stand composition. Another reason for the FRP differences in 3-3-year-old stands could be due to the forest floor depth, which was thicker in post-post-clearcutting stands than in postfire stands (Shrestha & Chen 2010). Thick forest floors insulate the mineral soil and can lower soil temperature and be detrimental to forest productivity at ecosystem and landscape scales (Lecomte *et al.* 2006). The rapid stand establishment and fast capture of site resources by trees in 10- and 29-year-old stands might be a reflection of little or no differences in soil conditions (Shrestha & Chen 2010). As such, no significant differences in FRP were found in 10- and 29-year-old stands.

Because broadleaved species are generally more productive than needleleaved species (Yuan & Chen 2010), a greater *P. banksiana* component and fewer *B. papyrifera* in the 29-year-old postfire stands (Shrestha & Chen 2010) probably results in a higher aboveground live C pool in post-clearcutting stands. However, FRP did not significantly differ between fire and clearcutting origins at this stage. One possible reason may be due to the more understory plants in postfire stands than in post-clearcutting stands (Seedre & Chen 2010), which could have offset the deciduous-evergreen effects.

Summary

Across the boreal chronosequence, fine root production was found to increase rapidly in the initial stage of stand development to allow for the rapid absorption of water and nutrients to meet the requirements of fast growing plants. As the stand progressed, more FR was converted into the coarse roots to provide better structural support to the trees in the older stands, and FRP leveled off or even declined in stands from 10-year old. The age-related FRP variation could be attributed to the coupling changes in stand composition and site quality during secondary forest development. FRP significantly differed with respect to stand origins with greater values in fire-origin stands than in clearcutting-origin stands that grew in similar soil and climatic conditions at a young age. However, the fire- and clearcutting-induced FRP differences diminished with stand age.

CHAPTER SIX: FINE ROOT TURNOVER

Introduction

Plant root turnover generally refers to the fraction of a root system that is renovated during a certain time period (commonly a year) through the replacement by new root growth and the death of old roots (Eissenstat & Yanai 2002; de Kroon & Visser 2003). However, the definition of root turnover rates varies greatly in published papers. In this chapter, root turnover rates referred to live root system, and are measured by the production relative to the size of the standing crop of roots (Notes: this differed from the dead roots as described in Chapter 4. See more details in Appendix II). Similar to production, root turnover, especially fine root turnover (FRT), is an important process responsible for carbon C and nutrient input from plants to soil (Fogel 1983; Vogt *et al.* 1986; Gill & Jackson 2000; Brassard *et al.* 2009). So far, few published data are available on FRT in boreal forests due to inherent difficulties of measurement. Also, the role that fine roots play in the C and nutrient budgets of boreal forests has not been well determined. Thus, information about how major biotic and abiotic factors (*e.g.*, plant attributes, stand development, disturbance types, soil processes, and climatic factors) influence FRT, and how fine roots contribute to the C budget of boreal forests is needed given current and projected future climate and vegetation changes (Jackson 2000).

At a global scale, FRT is primarily influenced by regional climate (Gill & Jackson 2000; Yuan & Chen 2010b), but at a local scale it is regulated by soil conditions, such as temperature, moisture and nutrients that affect root growth, mortality, and decomposition (Norby & Jackson 2000). Stand development after fire- or clearcutting-induced

disturbances in secondary boreal forests results in changes in stand composition (Hart & Chen 2008; Seedre & Chen 2010) and soil environments (Shrestha & Chen 2010), and are coupled with autogenetic drivers (*e.g.*, tree/stand ages) which potentially influence fine root growth, mortality, and decomposition patterns, and thus the turnover process. However, the relationship between stand age and fine root turnover is not well understood. To date no study addressed the age-related FRT patterns during secondary forest succession.

Although the differences and similarities of the effects of forest fire and clearcutting on ecosystem processes and biodiversity have been widely studied for decades (Simard *et al.* 2001; Reich *et al.* 2001a; Lecomte *et al.* 2006), direct comparisons of these disturbance types within the same region are not common. Previous studies in the same sites have shown differences in stand composition (Hart & Chen 2008; Ilisson & Chen 2009), aboveground C pools (Seedre & Chen 2010), and soil nutrients (Seedre & Chen 2010). FRT at a local scale is generally higher for young than old trees (Ruess *et al.* 1998), and higher for deciduous than for evergreen species (Konopka *et al.* 2005; Yuan & Chen 2010b), and increase with soil nutrients (Pritchard *et al.* 2010). The coupling differences in stand composition and soil environments between stand origins are anticipated to affect fine root growth, mortality, and thus the turnover process.

The purposes of this chapter were 1) to examine the pattern of FRT with stand development; and 2) to determine whether FRT differed between the postfire and post-clearcutting stands. Based on the discussion and conclusions in Chapter 3, FRT was hypothesized to increase from young stands and then keep steady or even decline in old stands. Second, FRT between stand origins were hypothesized to differ significantly.

Materials and Methods

Study area and sites

Description in Chapter 3.

Sampling design

Description in Chapters 3 and 5.

Field measurements

Description in Chapters 3 and 5.

Data analyses

FRT (year^{-1}) was defined as the ratio of the total amount of live fine roots produced in 1 year ($\text{Mg ha}^{-1} \text{ year}^{-1}$) over the mean standing biomass (Mg ha^{-1}) of fine roots (Aber *et al.* 1985). Mean live fine root biomass was estimated as the average of live fine root biomass from July to October 2008 (Chapter 3). Live fine root production was estimated from ingrowth and sequential cores (Chapter 5).

As describe in former chapters, analyses were conducted in two steps because of the difference in age range between stands of fire origin and those of clearcutting origin. changes in FRT with time after fire disturbance were determined for postfire stands from 3- to 205-year old using one-way analysis of variance. Second, the interactive effects of stand age and stand origin were tested with two-way analysis of variance by choosing all stands ≤ 29 -year old, *i.e.*, three age classes from postfire stands and all sampled post-post-clearcutting stands. Models were fitted and analyzed using the *aov* and *TukeyHSP* funtions within R version 2.11.1 statistical software (R Development Core Team 2010).

Square root or log transformations were used for data of fine root biomass, production, and turnover rates to meet assumptions of normality and homogeneity of variance with the *shapiro.test* and *bartlett.test* functions in R.

Results

Variation with stand age

FRT based on both ingrowth and sequential core methods varied significantly with stand age in postfire stands (Table 6.1). From ingrowth cores, fine roots turned over fastest from 0.66 year⁻¹ in 3- and 0.62 year⁻¹ in 10-year-old stands, and declined in old stands thereafter. FRT did not change significantly from 29- to 205-year-old stands. Sequential core method yielded a greater FRT than ingrowth core based values, but exhibited a similar age-related FRT pattern. This was also higher in 3- and 10-year-old stands than in old stands (Figure 6.1).

Table 6.1 *Effect of stand age on fine root turnover rates.*

		df	MS	F	P
Ingrowth	Between Groups	5	0.168	18.034	<0.001
	Within Groups	12	0.009		
	Total	17			
Sequential	Between Groups	5	0.420	13.448	<0.001
	Within Groups	12	0.031		
	Total	17			

Notes: Significant effects at P<0.05 are in bold.

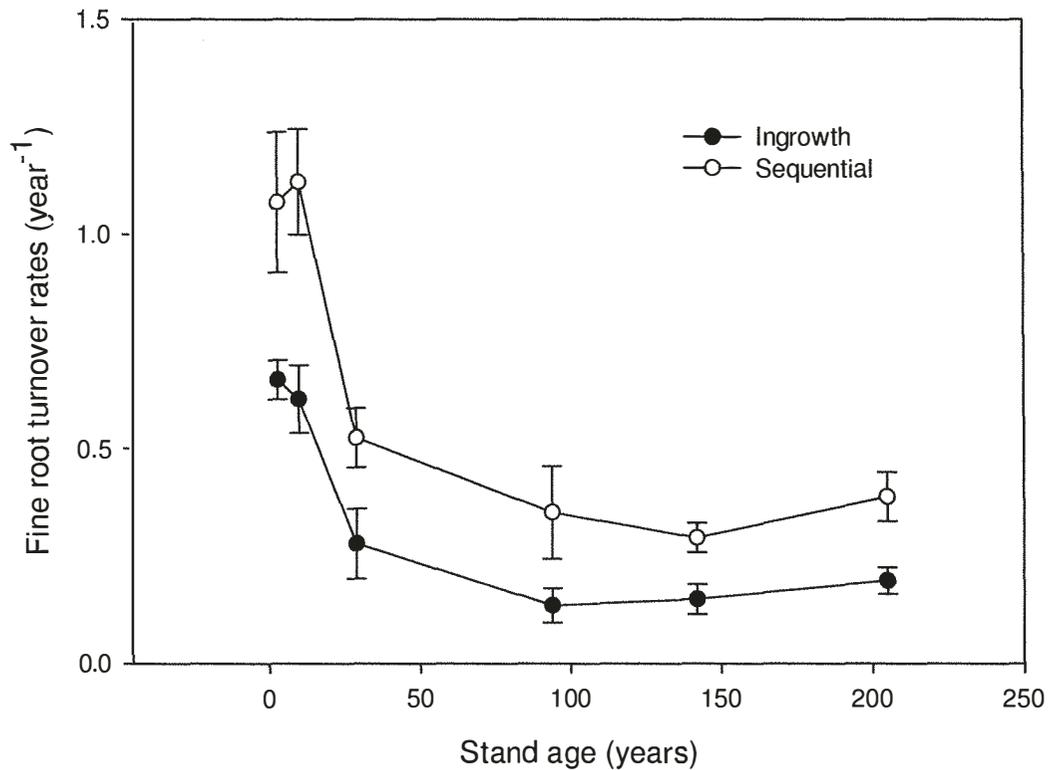


Figure 6.1 Fine root turnover rates in postfire stands by ingrowth core and sequential core methods.

Notes: Error bars represent 1 SEM.

Effects of stand origins

Stand origins showed significant effects on FRT in ≤ 29 -year-old stands (Table. 6.2).

Based on both ingrowth and sequential core methods, FRT was higher in fire-origin stands than in clearcutting-origin stands at 3- and 10-year old, but be similar in stands at the 29-year old (Figure 6.2).

Table 6.2 P-values of two-way ANOVA results for the effects of stand age (A) and stand origin types (O) in younger stands (3- to 29-year-old) on fine root turnover rates.

Source	df	MS	F	P
Ingrowth				
A	2	0.044	2.824	0.099
O	1	0.169	10.749	0.007
A×O	2	0.093	5.941	0.016
Error	12	0.016		
Sequential				
A	2	0.294	6.921	0.010
O	1	0.472	11.105	0.006
A×O	2	0.077	1.815	0.205
Error	12	0.043		

Notes: Bold indicates significant or marginally significant effects.

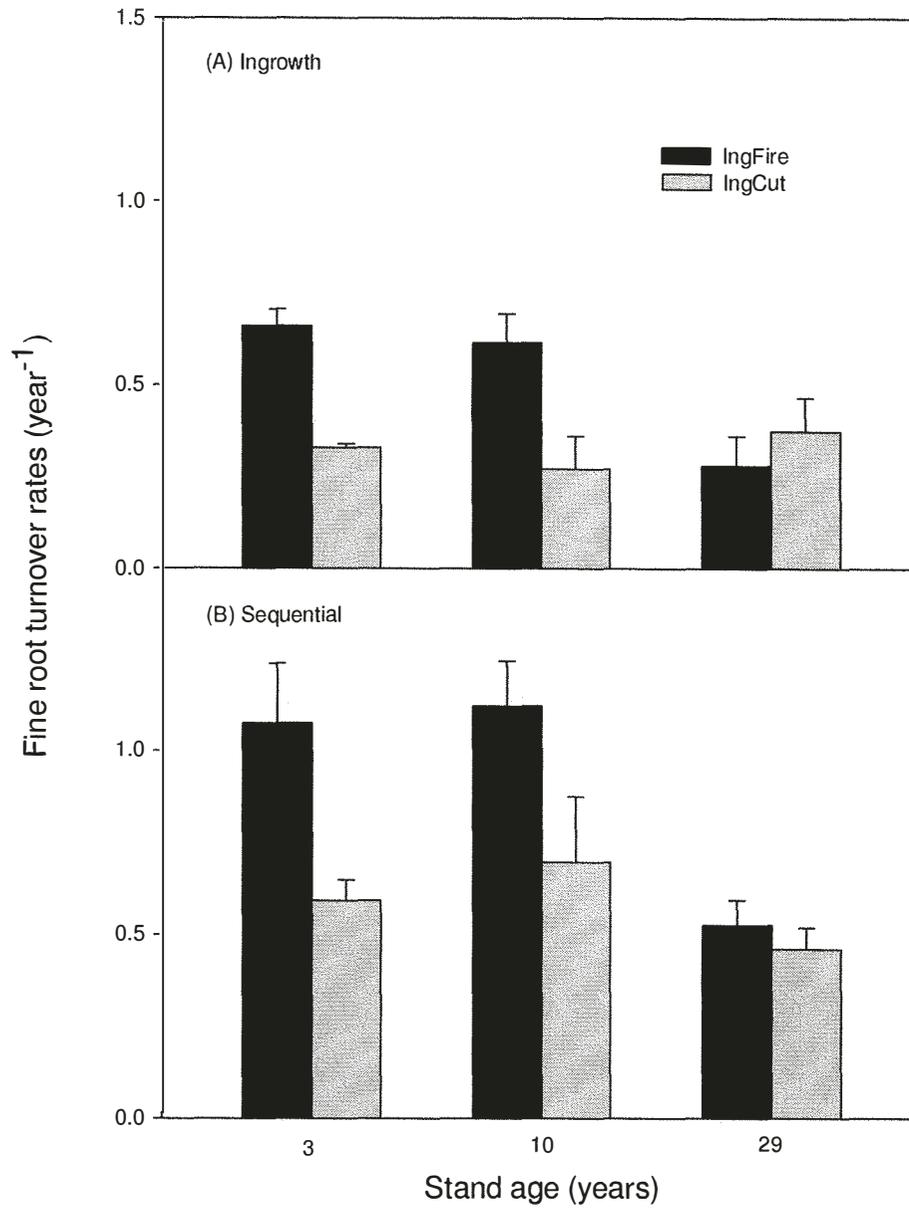


Figure 6.2 Effects of stand origin (fire vs. clearcutting) on fine root turnover rates.

Notes: Fire-origin stands on the left and clearcutting-origin stands on the right. Error bars represent 1 SEM.

Discussion

In postfire stands, FRT was higher in 3- and 10-year-old stands, and leveled off thereafter in 29, 94, 142, and 205-year-old stands (Figure 6.1), supporting the first hypothesis that FRT varies with stand development, *i.e.*, FRT culminates early and declines thereafter. The second hypothesis, *i.e.*, FRT differs between postfire and clearcut stands, was partly supported by the results based on both ingrowth and sequential methods, *i.e.*, FRT was significantly different between stand origins in 3-, and 10-year-old stands, but similar in 29-year-old stands (Figure 6.2).

Stand age effects

In this present study, the age-related FRT patterns in postfire stands (Figure 6.1) suggest that fine root growth and turnover is generally higher in the younger forest stands. The FRT patterns were consistent with the patterns of fine root production (Figure 5.4 in Chapter 5). To date, no study addresses how FRT varies with stand age, allowing no direct data available for comparison. However, Helmisaari *et al.* (2002) reported that increase of fine root production (determined by the decision matrix method) in Scots pine (*Pinus sylvestris* L.) stands in eastern Finland was faster than biomass increase with stand age, indicating increasing ratios of fine-root production/biomass with stand age (0.8, 2.2, and 3.3 for 15-, 35-, and 100-year-old stands, respectively). In contrast, Persson (1983), by summing the positive increments for fine root biomass and necromass, showed that the ratios of fine root production to average fine root standing crop were higher in young than old *P. sylvestris* stands (2.0 vs. 0.7 in a 20- and 120-year-old stands respectively).

What caused the age-related FRT patterns in postfire stands? First, it may be due to

the intrinsic changes of plant ageing and senescence, a highly regulated process (at the molecular, biochemical and physiological levels) could occur (Munne-Bosch 2007), thereby leading to a decreasing growth and turnover rates of fine roots. In young stands, seedlings experience high new growth and mortality due to shading and competition, but after a relatively low threshold size, they escape these influences and growth and mortality tends to decrease or remain constant (Harcombe 1987). Root turnover refers to the fraction of a root system that is renovated during a certain time period (commonly a year) through the replacement by new root growth and the death of old roots. Therefore, FRT is generally estimated as the production divided by biomass, indicating that the highest turnover rate occurs in stands with the highest growth rate. Also, the mortality rates of fine root matched their production (Wells *et al.* 2002; Norby *et al.* 2004), as found by comparing the mortality *vs.* birth rates of all most plant species (spanning from the tiniest phototrophs to the largest trees) (Marba *et al.* 2007), thereby helping to maintain plant communities in equilibrium. In fact, the active fine root senescing process might already be underway during the seeds like embryo stage for animals, with its entire life history genetically programmed, resulting in reduced FRT in old stands dominated by old trees.

Second, the age-related patterns could be related to ecological effects. At a local scale FRT is related to species composition and soil environments (Norby & Jackson 2000). Therefore, the observed age-related FRT patterns could be attributed to changes in stand composition and site quality coupled with stand development. In this age chronosequence, postfire stands were dominated by the deciduous tree species *P. tremuloides* and herbs in young stands, but by the evergreen species *P. banksiana*, *A.*

balsamea, and *Picea* spp. in old stands (Hart & Chen 2008), as found in other boreal forests (Finer *et al.* 1997). Therefore, deciduous aspen made up a greater proportion of the standing root biomass in young stands than in old stands (Chapter 3), certainly changing the average root production, nutrient quality, mortality and thus the turnover process. Because the roots of deciduous, broad-leaved species have higher nutrient concentration and contents, and turnover faster than evergreen, coniferous species (Silver & Miya 2001; Yuan & Chen 2010b), the greater composition of fast-growing *P. tremuloides* roots in young stands might result in faster turnover rates of fine roots (Figure 6.1). Although the nutrients in *P. tremuloides* fine roots may increase with stand age, similar to their aboveground analogue of foliages (Yuan & Chen 2010a), the nutrient levels in fine roots could lessen and result in low turnover rates in old stands (Figure 6.1). Although there were probably species-specific FRT differences, the mean FRT in relation to stand age was mainly controlled by the portion of the root system that accounts for most of the biomass. Therefore, the fast turnover of the largest proportion of fine roots may have a great influence on the turnover process and C cycling because fine roots account for such a great amount of material.

The decline of FRT may be partly attributed to the age-related patterns of soil fertility which increased with stand age and peaked at 94-year-stands (Table 3.1 in Chapter 3) (Shrestha & Chen 2010). The decline might also be due to the fact that soil N in these studied boreal stands was not the main limiting factor for tree growth. However, it should be noted that the soil supply patterns did not necessarily mean that average fine root quality followed the same pattern due to the changes in root composition with stand development. The nutrient supply effect on FRT may have been overridden by the effects

of root composition.

Aside from soil supply, the increasing forest floor depth with stand age found in these studied sites (Shrestha & Chen 2010) and other boreal forests (Wirth *et al.* 2009) could contribute to soil cooling and induce a rise in the water moisture that creates water-logged conditions (Simard *et al.* 2007), reducing root growth activity and causing a FRT decline at old stands.

Therefore, both genetic and environmental factors may contribute to FRT decline with stand development. The combination of internal (genetic, biochemical, and physiological) and external (ecological) factors undoubtedly regulates fine root production, mortality, and the turnover process.

Effects of stand origin

The FRT (based on both ingrowth and sequential core methods) differed between fire- and clearcutting stands in 3- and 10-year-old stands, but there were no significant differences in 29-year-old stands (Figure 6.2), reflecting fine root biomass and production patterns between these two disturbance types (Chapters 3 and 5). These findings indicate that fine roots in postfire stands turn over faster than in post-clearcutting stands at an early stage than at a late stage. Between stand origins, post-disturbance regeneration densities of deciduous *B. papyrifera* were higher after fire, and those of evergreen *P. mariana* and *A. balsamea* were higher after clearcutting (Ilisson & Chen 2009). Because there were no significant differences in soil nutrients between the origins of stands (Shrestha & Chen 2010), thus, the FRP differences could be attributed to other changes (*e.g.*, stand composition which might suppress the soil nutrient effect). Another reason for the FRP differences in 3- and 10-year-old stands could be due to the forest floor depth,

which was thicker in post-clearcutting stands than in postfire stands (Shrestha & Chen 2010). Thick forest floors insulate the mineral soil that can lower soil temperature and reduce forest productivity (Lecomte *et al.* 2006). The rapid stand establishment and fast capture of site resources by trees in old stands irregardless of origins might result in creation of uniform soil conditions (Shrestha & Chen 2010), and may be why no significant differences in FRT were found in the 29-year-old stands. The 29-year-old postfire stands had a greater *P. banksiana* component and less *B. papyrifera* (Seedre & Chen 2010), and may help explain the different turnover rates. However, FRT did not significantly differ between fire and clearcutting origins at this stage. One possible reason was due to more understory plants being present in postfire stands than in post-post-clearcutting stands (Seedre & Chen 2010), and which could offset the deciduous-deciduous-evergreen effects.

Summary

Fine root turnover rates remain quite variable at stand level, resulting in an age-related decline as is often observed for the aboveground productivity (Gower *et al.* 1996a; Ryan *et al.* 1997; Peltzer *et al.* 2010). FRT was higher in young stands than in old stands, likely relating to tree age, stem density, tree species, and soil environments. The FRT differences between fire- and clearcutting-origin stands were significant in the 3- and 10-year-old stands but similar in the 29-year-old stands, reflecting differences and similarities in stand composition and soil environments between these two disturbance types.

CHAPTER SEVEN: CONCLUSIONS

The results of this dissertation confirmed that stand age had impacts on fine root system in secondary boreal forests. Moreover, there were differences and similarities in fine roots between fire- and clearcutting-origin stands. A summary of the key findings of this dissertation was as follows:

Fine root dynamics with stand age in boreal forests

In conclusion, there is a general tendency for growth rates of fine roots to change over the course of succession. Across the boreal chronosequence spanning over 200 years, age-related declines of both fine root production (FRP) and turnover (FRT) rates were found. FRP increased from 3-year-old stands to 10-year-old stands, and leveled off or declined thereafter in 29-, 94, 142, and 205-year-old postfire stands. FRT was also higher in young stands than in old stands. Considering the age-related patterns of fine root mortality (FRM) which generally peak later compared to FRP (Brassard *et al.* 2009; Quan *et al.* 2010), fine root biomass (FRB), the result of FRP and FRT processes, increased with stand age from 3-year-old until 29-year-old postfire stands, and levelled off thereafter. Therefore, because $FRB = \int_0^x (FRP - FRM)dx = \int_0^x (f(x) - g(x))dx$, the peak of FRB occurred between the peaks of FRP and FRM (Figure 7.1).

The age-related variations in FRP and FRT were consistent with the well-known age-related decline of aboveground production during forest secondary succession after stand-replacing disturbances (Gower *et al.* 1996a; Ryan *et al.* 1997; Peltzer *et al.* 2010). However, the reasons for aboveground production decline, still an ongoing debate, are not applicable to belowground. Hydraulic limitations, for instance, are a major cause of

the age-related declines in aboveground net primary productivity (Ryan *et al.* 2006; Drake *et al.* 2010). However, hydraulic limitations cannot contribute directly to the belowground FRP and FRT declines with stand age. The reasons that may contribute to the age-related belowground FRP and FRT declines may include both changes of stand composition and site quality during secondary forest development (*e.g.*, changes in tree age, stem density, tree species, and soil environments) (Figure 7.2): 1) With a stand trees also grow up from young to old, involving every cell, organ, and tissue in the tree body. This genetic-controlled process can cause old stands to have a reduced production, including above-belowground production. Similarly, root turnover rates are slow in old stands. 2) With stand development, changes in species composition occur from nutrient-rich species (*e.g.*, *P. tremuloides*) to nutrient-poor species (*e.g.*, *P. abies* and *A. balsamea*), leading to a slow litterfall decomposition and thus nutrient limitation which can reduce fine root production and turnover rates. 3) Old stands tend to have more tree density and biomass that can increase nutrient demand, again resulting in nutrient limitation. 4) With stand development, the hydraulic limitation-induced closure of stomatal conductance can cause suppress canopy photosynthesis but increase respiration, resulting in an age-related ANPP decline which can reduce the allocation of photosynthetic products to root system and then decrease root production and turnover rates. 5) A thicker forest floor layer in old stands can lower the soil temperature, decrease microbial activity and soil N mineralization, leading to a decline of fine root production and turnover rates. However, the primary cause was not clear because the effects of these factors coupled with stand aging are difficult to separate from the effect of stand age. One thing is certain: The tendency of age-related declines of FRP and FRT may be modified,

at least partly, by physiological and ecological effects (*e.g.*, soil environments). This present study proposed some general fine root trends in temporal patterns of succession rate and identified some of the potential mechanisms that may shape them, which could improve our understanding in terrestrial ecosystem models and their estimates of C cycling.

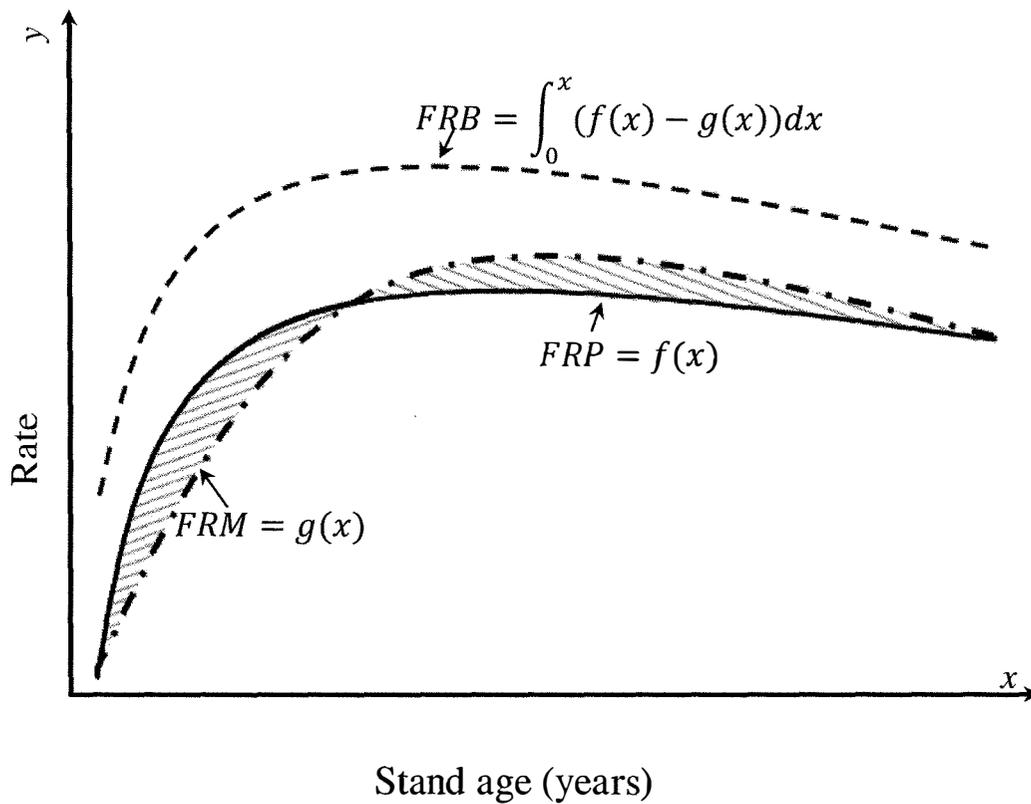


Figure 7.1 Age-related production (FRP) and mortality (FRM) of fine roots and the resulting pattern in fine root biomass (FRB).

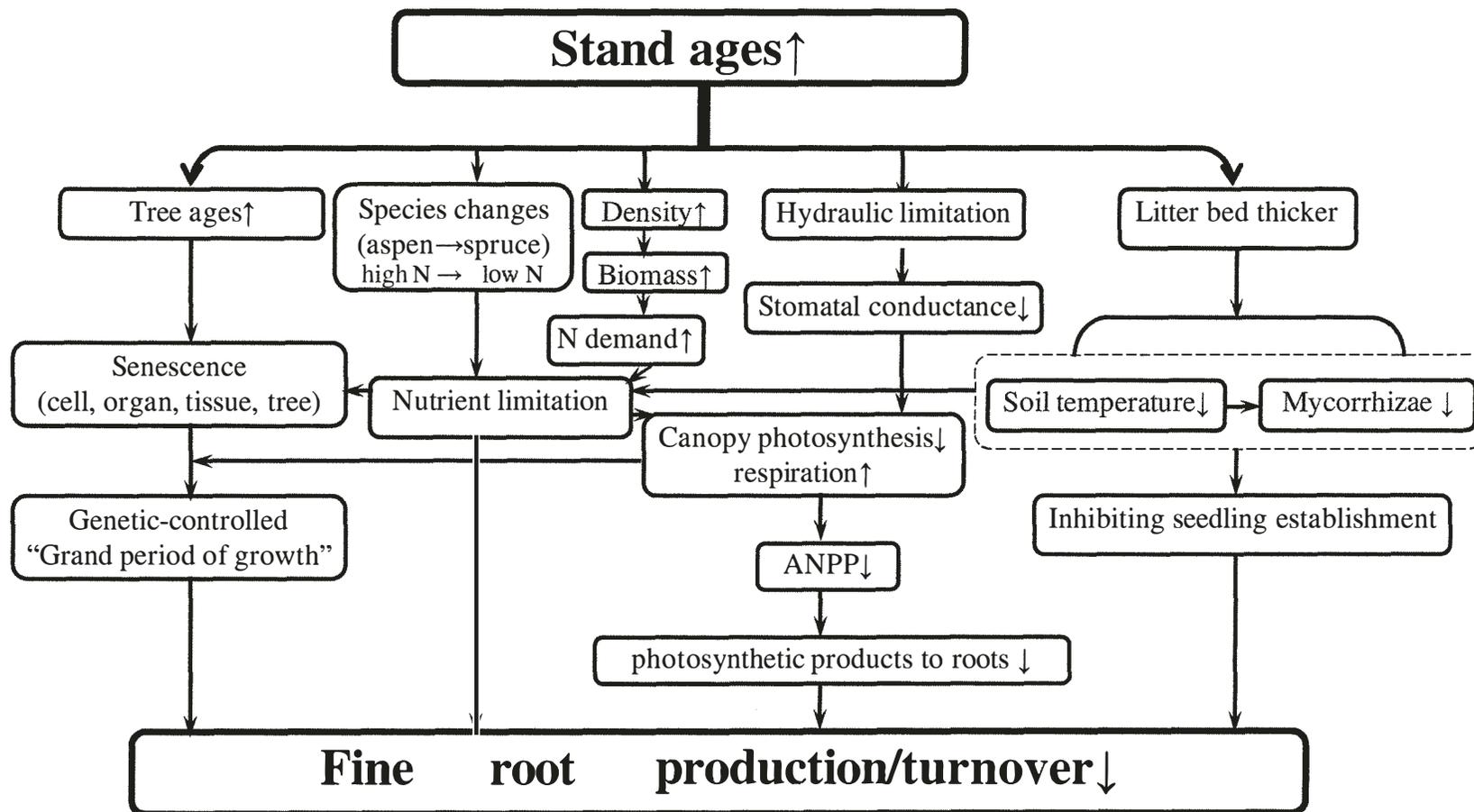


Figure 7.2 A conceptual model depicting how stand age affects fine root production (or turnover).

Effect of stand origin on fine roots in boreal forests

Stand origin generally showed significant effects on processes of fine root production, mortality, and decomposition. FRP significantly differ between stand origins, with greater values in fire-origin stands than clearcutting-origin stands. However, the fire- and clearcutting-induced FRP differences in the very young stands only persist for decades and diminished later. Similarly, FRT between fire- and clearcutting-origin stands were significant different in the very young stands but these differences disappeared a few decades after fire or clearcutting disturbances, reflecting differences and similarities in stand composition and soil environments between these two disturbance types. However, FRB did not significantly differ between fire- and clearcutting-origin stands from 3- to 29-year old.

The differences and similarities of fine roots between stand origins may be attributed to various ecological effects on fine roots. The short-term significant differences between very young postfire stands and very young post-clearcutting stands, particularly with respect to coarse woody debris (Brassard & Chen 2008), stem density (Nguyen-Xuan *et al.* 2000), stand composition (Ilisson & Chen 2009), aboveground C pools (Seedre & Chen 2010) and soil conditions (Simard *et al.* 2001; Shrestha & Chen 2010), can cause differences in FRP, FRM, and FRT. However, in the prolonged absence of disturbance, the effects of fire- and clearcutting-induced disturbances on coarse wood debris (Sturtevant *et al.* 1997; Brassard & Chen 2006; Brassard & Chen 2008), on litterfall attributes (Reich *et al.* 2001a), and on various soil properties (Lecomte *et al.* 2006; Shrestha & Chen 2010) tend to converge, resulting in the similarities of FRP, FRM, and FRT between fire- and clearcutting-origin stands. Fire and clearcutting disturbances

showed different effects on stand composition, humus layer depth, and soil environments, and thus on fine root growth, death, and decay processes, all of which would result in greater fine root production, mortality, and decomposition processes, and thus stand crop of fine root biomass in fire-origin stands than in clearcutting-origin stands at early stage (Figure 7.3): At very young age, postfire stands have more proportion of broad-leaved species *B. papyrifera* but fewer needle-leaved species *P. mariana* and *A. balsamea*, producing nutrient-richer litterfall than post-clearcutting stands. The differences in litterfall quality can result in differences in soil nutrients which could contribute to the greater FRP and FRT in young postfire stands than in post-clearcutting stands. In more coarse woody debris, thinner forest floor layer, and lower stem density in young postfire stands than in post-clearcutting stands, also directly or indirectly affect FRP and FRT through soil process, resulting in higher FRP and FRT in very young postfire stands than in post-clearcutting stands. However, these effects may diminish with time, resulting in similarities of fine roots dynamics in the 29-year-old stands between these two stand origin types (Figure 7.3).

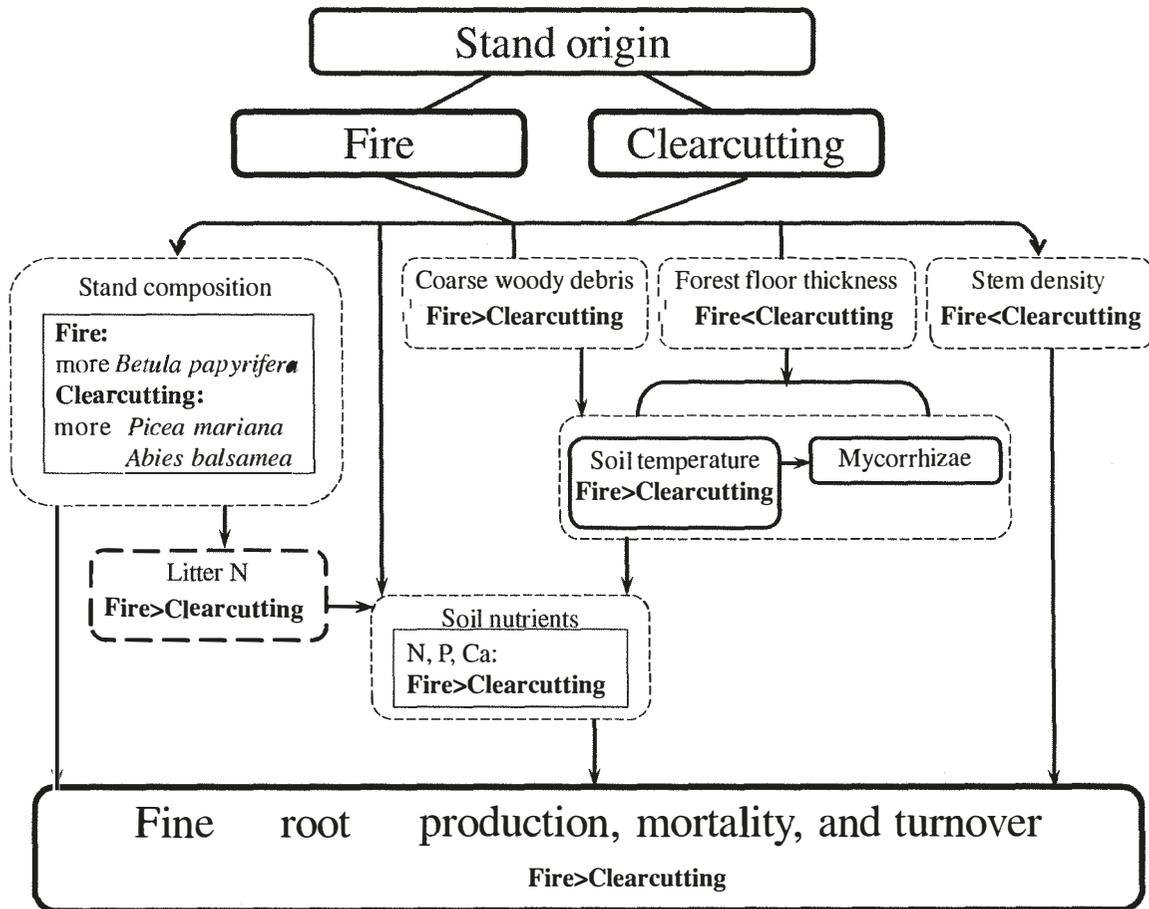


Figure 7.3 A conceptual model depicting the response of fine root production, mortality, and turnover to fire- and clearcutting-induced disturbances.

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APPENDIX I: STUDY SITES AND WEATHER INFORMATION

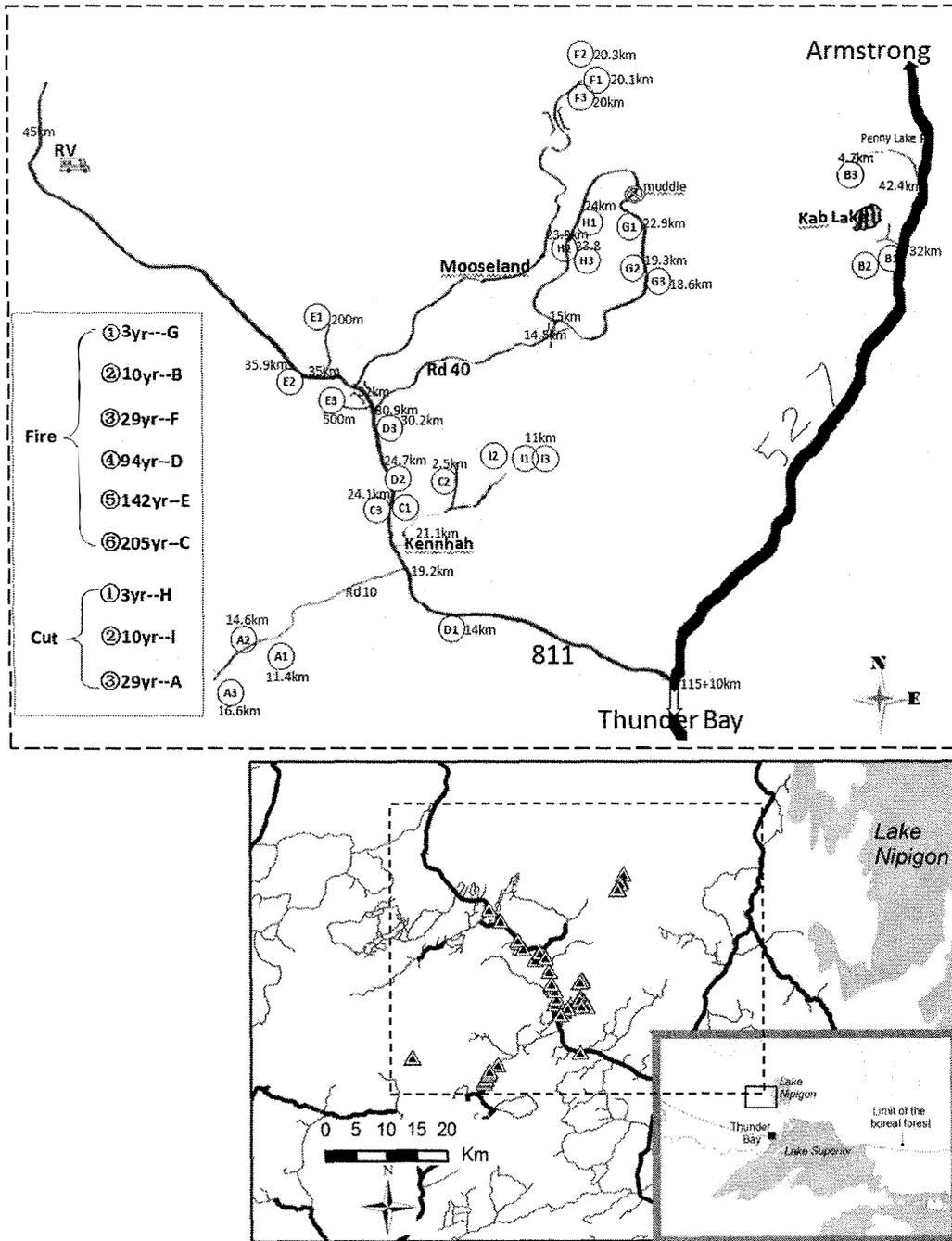


Figure AI. 1 Map of the study area and sampling sites.

Table AI. 1 Historical weather at the nearby Armstrong Station (50.30Lat, -89.03Long, 351Alt) which is close to the studied sites.
 Monthly weather from 2007 to 2009.

Year	Month	T _{mean}	T _{aver}	+/- (%)	T _{max}	T _{min}	H	P	P _{aver}	+/- (%)
2007	Jan	-15.2	-21.8	30.3	-8.4	-21	77.5	16.26	32	-49.2
	Feb	-19.3	-18.3	-5.5	-12.1	-26	72.4	19.06	30	-36.5
	Mar	-6.5	-11	40.9	1.5	-14.7	68.9	19.55	46	-57.5
	Apr	0.5	-1.4	135.7	8.1	-6.6	61.2	28.45	36	-21.0
	May	9.5	8	18.8	18.3	0.7	29.6	236.23	57	314.4
	Jun	14.6	12.5	16.8	22	7.3	81.2	103.4	88	17.5
	Jul	17.4	16.1	8.1	25.8	9.3	72.2	106.68	89	19.9
	Aug	15.6	14	11.4	22.9	8.9	72.3	83.32	91	-8.4
	Sept	10.6	8.2	29.3	17.6	5.1	83	140.95	85	65.8
	Oct	5.2	2.4	116.7	10.3	1	81.3	111.51	69	61.6
	Nov	-6.6	-6.7	1.5	-1.3	-11.9	82.6	26.42	50	-47.2
	Dec	-16.2	-17.4	6.9	-10.1	-22.7	83.4	49.01	32	53.2
2008	Jan	-15.8	-21.8	27.5	-9.4	-22	80.3	67.06	32	109.6
	Feb	-18	-18.3	1.6	-9.8	-25.6	71.7	28.2	30	-6.0
	Mar	-11.7	-11	-6.4	-2.4	-20	65.6	11.69	46	-74.6
	Apr	0.1	-1.4	107.1	7.3	-5.9	61.9	17.02	36	-52.7
	May	5.2	8	-35.0	13	-2.1	62.9	175.49	57	207.9
	Jun	12.5	12.5	0.0	20.1	5.3	71.7	126.99	88	44.3
	Jul	15.9	16.1	-1.2	22.6	9.1	72.1	90.41	89	1.6
	Aug	15.9	14	13.6	24.5	7.5	69.1	41.15	91	-54.8
	Sept	10.1	8.2	23.2	17.7	3.5	80.6	56.89	85	-33.1
	Oct	3.7	2.4	54.2	9.1	-0.7	83.2	50.8	69	-26.4
	Nov	-4.8	-6.7	28.4	-1.3	-8.3	86.9	0	50	-100.0
	Dec	-19.9	-17.4	-14.4	-13.6	-25.4	79.1	0	32	-100.0
2009	Jan	-20.9	-21.8	4.1	-13.9	-27	77.2	0.51	32	-98.4

Feb	-15.6	-18.3	14.8	-8.3	-23.2	79	20.07	30	-33.1
Mar	-10.1	-11	8.2	-1.7	-17.4	68.6	50.3	46	9.3
Apr	0.1	-1.4	107.1	6.2	-6.3	62.9	34.55	36	-4.0
May	4.6	8	-42.5	12.8	-3.1	66	78.49	57	37.7
Jun	13	12.5	4.0	20.7	5.1	70.9	58.93	88	-33.0
Jul	13.1	16.1	-18.6	20	6.7	76.3	66.54	89	-25.2
Aug	14.1	14	0.7	20.4	7.3	78.9	82.83	91	-9.0
Sept	13.4	8.2	63.4	21.5	7	79.2	59.69	85	-29.8
Oct	0.5	2.4	-79.2	5.6	-4.2	85	47	69	-31.9
Nov	-0.3	-6.7	95.5	4.2	-5.1	83.9	45.97	50	-8.1
Dec	-16.4	-17.4	5.7	-10.5	-21.4	81.1	41.65	32	30.2

(A) Daily weather in from June to October in 2007 and 2008

Year	Date	Jun		Jul		Aug		Sep		Oct	
		T _{mean}	P	T _{mean}	P	T _{mean}	P	T _{mean}	P	T _{mean}	P
2008	1	14.4	8.13	10.8	0	25.1	0	10.6	0.25	11.5	0.76
	2	12.7	0	11.9	0.76	19.6	0	19.1	10.92	11.1	0
	3	14.6	2.29	16.3	7.11	17.1	0	13.1	0	12.3	43.18
	4	11.3	4.83	19.2	0.51	15.1	0	9.9	0	13.4	0
	5	7.7	0	18.7	0.51	20.7	0	12.7	0	6.4	0
	6	5.9	0	16.7	0.25	17.1	5.84	18.2	28.96	4.7	9.65
	7	9.5	18.29	16.7	2.54	14.8	4.32	12.4	12.95	7.7	23.88
	8	12.9	0	18.4	7.11	14.8	5.08	9.3	6.86	5.9	0
	9	17.1	0.51	16.1	0	18.4	0.51	8.1	0	5.1	21.59
	10	15	0.51	12.7	2.29	18.8	0.25	9.2	0	4.5	5.59
	11	19.2	0	13.6	40.39	20.2	19.3	8.7	7.87	2.2	0
	12	19.9	0	12.2	4.83	19.1	0	3.6	0.51	1.2	0
	13	22.5	0	12	0	13.6	0	7.1	3.05	-1.2	0
	14	22.6	0	13.6	8.64	16.2	5.59	3.2	0	-	-
	15	22	0	14.1	0.76	11.7	0	6.1	1.52	-	-
	16	19.1	0	16.4	0.51	12.6	8.13	11.2	0.25	-	-
	17	15.2	0	19.3	0	10.4	3.05	12.7	0	-	-
	18	15.4	14.48	16.3	1.52	11	0	14.7	17.02	-	-
	19	14.2	0	13.4	10.92	10.1	0	13.5	5.33	-	-
	20	12.6	0.76	14.4	0	11.7	0	5.2	4.32	-	-
	21	13.2	0.51	17.7	0	14.4	7.87	11.8	14.22	-	-
	22	10.6	0.25	19.7	0	18.1	6.1	11.9	18.54	-	-
	23	13	5.59	23.9	0	18.9	1.27	9.4	0.25	2.2	3.05
	24	14.6	8.89	24.7	0	15.1	0	19.3	0	0.6	0
	25	18.7	36.07	26.5	0	14.3	0	10.8	6.1	2.9	0

	26	15.6	0	22.9	8.89	13.4	0	6.6	0.51	7.6	0
	27	13.7	1.27	19.5	0.76	20.1	0	10.4	0.25	3.1	0
	28	10.4	0	17.7	0	-	-	9.4	0	-0.8	0
	29	13.7	1.02	21.3	0	12.1	1.02	7.4	1.27	4	0
	30	10.6	0	19.9	8.13	11.2	2.29	13.9	0	5.2	0
	31			24.3	0.25	10.8	12.7			4.3	3.81
2009	1	14.3	0.25	19.4	0.51	15.1	0	22.2	0	4.2	0
	2	9.9	1.52	13.7	8.13	16.7	0.25	22.1	0	3.4	0.51
	3	8.7	0	13.5	0.25	19.2	0	12.8	6.1	2.2	0
	4	8.9	0	16.4	0.25	19.8	0.51	6.6	0	1	0
	5	11.2	15.75	21.8	0	19.3	0	9.1	3.3	1.2	0
	6	9.6	21.84	21.7	0	16.8	0	9	3.56	2.5	0
	7	16.7	1.52	11.3	0	15.1	3.05	8.2	0.76	10.1	0
	8	15.7	0	13	2.29	14.8	0	7.3	8.64	9.4	16.51
	9	9.6	9.91	12.2	0	12.3	0	6.7	0	8.2	2.54
	10	4.2	3.05	12.2	7.87	13.3	0	9.5	0	5.7	0
	11	8.8	0	11.1	0	15.3	0	12.4	0	4.6	5.08
	12	9.2	0	15.3	31.24	16.1	0	11.1	0	6.7	3.05
	13	11.9	1.78	13.2	5.59	17.5	0	14.7	0	13.5	11.94
	14	14	0.25	14.9	3.3	14.7	0	8.4	2.03	6.2	2.79
	15	13.2	0.51	16.9	2.79	15.1	0	6.1	0	3.4	0
	16	8.7	0	15.8	0	22.2	0	10.8	0	3.4	0
	17	9.2	1.27	16.8	0	20.1	0	5.9	0.25	1.7	0
	18	11.2	1.02	17.1	14.22	-	-	2.3	0	2.3	0
	19	13.7	0	15.1	4.06	10.1	0.25	16.6	11.68	7.6	0
	20	15.2	0	17.1	0	16.3	0	6.4	0	0.8	0
	21	16.3	0.25	16.6	0.51	21.2	0	2.1	0	-0.7	0
	22	15.6	0	16.1	0	20.1	0	11.4	0	0.4	0

23	13.8	0	16.4	0	16.5	2.03	14	0	4.7	2.79
24	13.3	0	16.4	0	11.6	2.29	14.3	7.87	3	0
25	13.3	4.83	20.8	0	10.2	0	10.3	1.52	5.3	2.29
26	17	0.76	18	0.25	14.8	0	13.4	0	3.1	2.54
27	17.3	0.25	16.4	0.51	16.6	0	10.8	0.51	-1.6	0.76
28	14.2	52.58	15.3	0	13.6	31.5	3.2	0	-1.3	0
29	16.5	9.65	15.1	6.1	11.3	0	8	10.16	-5.4	0
30	14.4	0	16.3	2.29	14.2	1.02	6	0.51	5.2	0
31			17.3	0.25	18	0.25			4.9	0

Notes: T_{mean} = current monthly mean temperature (°C), T_{aver} = average temperature for the past 30 years (°C), T_{max} = maximum temperature (°C), T_{min} = minimum temperature (°C), H = Mean humidity (%), P = current precipitation amount (mm), P_{aver} = average precipitation amount for the past 30 years (mm). \pm (%) = percentage variation in temperature or precipitation (estimated as $(\text{mean-aver})/\text{aver} \times 100\%$). From <http://www.tutiempo.net/en/Climate> and <http://www.theweathernetwork.com/>. No soil temperature, moisture records are available for the studied sites. The monthly averages from a nearby weather station should reflect those in the studied sites and then is used in this study.

Table AI. 2 P-values for effect of stand age on fine root biomass (FRB), necromass (FRN), and total mass in fire-origin stands.

Sampling date	Layer	FRB		FRN		Total mass	
		B	C	B	C	B	C
2008							
Jul	FF	0.132	0.015	0.059	0.231	0.086	0.016
	MS1	0.077	0.010	0.324	0.004	0.047	0.006
	MS2	0.196	0.222	0.098	0.011	0.028	0.111
	Total	0.078	0.005	0.077	0.026	0.027	0.004
Aug	FF	0.018	0.105	0.078	0.407	0.017	0.095
	MS1	0.420	0.032	0.007	0.003	0.326	0.017
	MS2	0.187	0.059	0.212	0.392	0.173	0.046
	Total	0.080	0.017	0.036	0.081	0.059	0.015
Sep	FF	0.120	0.007	0.133	0.615	0.116	0.010
	MS1	0.502	0.174	0.738	0.146	0.576	0.177
	MS2	0.027	0.089	0.882	0.619	0.054	0.104
	Total	0.103	0.021	0.744	0.669	0.133	0.028
Oct	FF	0.027	0.083	0.030	0.085	0.029	0.083
	MS1	0.347	0.121	0.311	0.689	0.607	0.127
	MS2	0.575	0.292	0.415	0.256	0.848	0.261
	Total	0.122	0.013	0.107	0.034	0.173	0.009
2009							
May	FF	0.025	<0.001	0.953	0.029	0.027	<0.001
	MS1	0.156	0.061	0.638	0.078	0.189	0.066
	MS2	0.262	0.087	0.487	0.134	0.219	0.089
	Total	0.024	0.001	0.503	0.068	0.030	0.001
Jun	FF	0.080	<0.001	0.136	0.295	0.070	<0.001
	MS1	0.361	0.015	0.547	0.110	0.393	0.019
	MS2	0.906	0.049	0.595	0.524	0.955	0.114
	Total	0.408	<0.001	0.435	0.205	0.390	<0.001

Notes: Bold indicates significant effects. B=broadleaved, C=coniferous, FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer.

Table AI. 3 P-values of two-way ANOVA results for the effects of stand age (A) and stand origin types (O) in younger stands (3- to 29-year-old) on fine root biomass (FRB), necromass (FRN), and total mass (biomass + necromass).

Layer	Mass	Source	2008								2009			
			Jul		Aug		Sep		Oct		May		June	
			B	C	B	C	B	C	B	C	B	C	B	C
FF	FRB	A	0.002	0.001	0.001	0.117	0.026	0.035	0.186	0.017	<0.001	<0.001	0.024	<0.001
		O	0.635	0.602	0.092	0.997	0.144	0.081	0.169	0.843	0.006	0.170	0.203	0.022
		A×O	0.650	0.025	0.463	0.210	0.460	0.231	0.715	0.502	0.032	0.001	0.594	0.002
	FRN	A	0.035	0.232	0.044	0.157	0.453	0.457	0.097	0.950	0.434	0.462	0.965	0.424
		O	0.971	0.162	0.395	0.217	0.170	0.257	0.108	0.600	0.938	0.015	0.396	0.388
		A×O	0.066	0.104	0.331	0.018	0.696	0.512	0.376	0.236	0.773	0.265	0.274	0.432
	B+N	A	0.002	0.001	<0.001	0.124	0.021	0.031	0.179	0.024	0.005	<0.001	0.026	<0.001
		O	0.642	0.565	0.074	0.988	0.120	0.073	0.161	0.880	0.031	0.240	0.187	0.028
		A×O	0.574	0.023	0.368	0.209	0.427	0.211	0.690	0.485	0.115	0.001	0.574	0.003
MS1	FRB	A	0.484	0.011	0.011	0.155	0.247	0.101	0.023	0.011	0.045	0.004	0.435	<0.001
		O	0.857	0.667	0.049	0.142	0.900	0.151	0.790	0.563	0.146	0.089	0.519	0.056
		A×O	0.400	0.443	0.268	0.420	0.451	0.940	0.283	0.070	0.128	0.212	0.489	0.049
	FRN	A	0.122	0.191	0.141	0.025	0.420	0.030	0.047	0.112	0.938	0.373	0.545	0.080
		O	0.288	0.493	0.656	0.625	0.354	0.031	0.192	0.033	0.080	0.926	0.449	0.454
		A×O	0.850	0.873	0.276	0.775	0.325	0.249	0.662	0.171	0.965	0.230	0.721	0.695
	B+N	A	0.552	0.013	0.010	0.274	0.260	0.087	0.037	0.010	0.055	0.006	0.468	<0.001
		O	0.938	0.628	0.066	0.139	0.752	0.126	0.959	0.414	0.093	0.088	0.630	0.087
		A×O	0.402	0.438	0.504	0.446	0.550	0.987	0.356	0.058	0.155	0.155	0.612	0.045
MS2	FRB	A	0.520	0.093	0.066	0.138	0.020	0.077	0.202	0.015	0.463	0.001	0.466	0.042
		O	0.078	0.841	0.226	0.107	0.942	0.025	0.356	0.290	0.114	0.534	0.283	0.048
		A×O	0.117	0.315	0.320	0.507	0.732	0.869	0.415	0.840	0.997	0.789	0.852	0.221
	FRN	A	0.420	0.351	0.119	0.421	0.509	0.334	0.221	0.518	0.430	0.094	0.430	0.673
		O	0.277	0.290	0.230	0.421	0.166	0.137	0.850	0.184	0.253	0.712	0.378	0.682
		A×O	0.118	0.641	0.134	0.769	0.740	0.981	0.359	0.522	0.476	0.522	0.772	0.617

	B+N	A	0.539	0.095	0.006	0.134	0.089	0.090	0.399	0.020	0.422	0.003	0.395	0.085
		O	0.057	0.721	0.062	0.114	0.434	0.027	0.460	0.188	0.099	0.672	0.241	0.067
		A×O	0.063	0.385	0.094	0.526	0.819	0.902	0.568	0.776	0.993	0.639	0.806	0.203
Total	FRB	A	0.030	0.002	0.001	0.061	0.022	0.022	0.140	<0.001	0.015	<0.001	0.257	<0.001
		O	0.967	0.667	0.887	0.424	0.295	0.038	0.386	0.488	0.897	0.051	0.838	0.003
		A×O	0.329	0.119	0.296	0.113	0.344	0.504	0.593	0.070	0.140	0.007	0.613	0.001
	FRN	A	0.053	0.216	0.033	0.191	0.551	0.038	0.049	0.077	0.618	0.120	0.886	0.016
		O	0.334	0.604	0.547	0.370	0.086	0.016	0.971	0.045	0.063	0.504	0.574	0.707
		A×O	0.357	0.675	0.313	0.899	0.386	0.594	0.874	0.023	0.620	0.106	0.725	0.565
	B+N	A	0.024	0.003	<0.001	0.086	0.030	0.021	0.156	0.001	0.015	<0.001	0.300	<0.001
		O	0.906	0.649	0.748	0.398	0.217	0.033	0.426	0.396	0.973	0.072	0.796	0.005
		A×O	0.295	0.121	0.423	0.118	0.412	0.518	0.629	0.058	0.166	0.007	0.663	0.001

Notes: Bold indicates significant or marginally significant effects. B=broadleaved, C=coniferous, FF=forest floor layer, MS1= 0-15 cm soil layer, MS2= 16-30 cm soil layer.

APPENDIX II: DEFINITION AND CALCULATION OF FINE ROOT TURNOVER RATES

In effect, our ability to accurately assess the magnitude of this important process has been hindered by current difficulties with measuring root turnover rates at least due to the various definition and thus the various estimates used in the literature and in discussion. In a systems science approach, turnover, is typically defined as a process, the replacement of old stuff (from cell, tissue, plant, to system) with newly generated ones, and often calculated as flux rate divided by pool size (see details as bellow). For plant root system, root turnover is a specific process of root dynamics referring to the fraction of a root system that is renovated during a certain time period (commonly a year) through the replacement by new root growth and the death of some roots. Therefore, root turnover rates could be defined as the proportion of the root pool (including biomass and necromass) that replaced per unit of time (year). For live roots, turnover is a process of both production and mortality; but for dead roots, it is a process of mortality and decomposition.

In some studies, plant root turnover rates have been named ‘turnover coefficients’ (de Kroon & Visser 2003; Park *et al.* 2008), the inverse of longevity (or turnover time). Unfortunately, both the pool and flux for plant root studies are somewhat ambiguous. Some studies have used the term ‘turnover’ as annual root production (Vogt *et al.* 1983a), or annual root mortality plus annual decomposition for the same period (Persson 1979; DeLucia *et al.* 1999), as discussed in Chapter 4. Some researchers also used the term ‘turnover index’, which refers to annual root mortality as absolute turnover in contrast to relative turnover

(Tingey *et al.* 2000; Andersen *et al.* 2008). The absolute turnover rate (which could be called annual root mortality), as discussed in Chapter 5, may be most useful if the primary research interest is in rates of C and nutrient fluxes from roots to soil. By contrast, the relative turnover is the appropriate metric for studies of plant root demography or to link with ecosystem models (Tingey *et al.* 2000; Norby & Jackson 2000). Chapter 6 in this thesis discussed about the latter. However, even for the relative turnover, it has been estimated by different variables in previous studies, making it difficult to compare among results.

The relative turnover rates can be estimated by direct methods like sequential coring, ingrowth cores, isotope, and (mini-)rhizotron, and indirect methods like N budget, C flux, and regression model. In this present thesis, direct methods on ingrowth cores and sequential coring basis were used to estimate root turnover rates. However, even for ingrowth cores and sequential coring methods, the calculation of relative root turnover rates varies greatly in published papers due to at least partly the confusion of FRT definition:

- 1) $\frac{\text{root production}}{\text{maximum standing pool of live roots}}$ (Dahlman & Kucera 1965; Gill & Jackson 2000);
- 2) $\frac{\text{root production}}{\text{mean standing pool of live roots}}$ (Aber *et al.* 1985; Jha & Mohapatra 2010);
- 3) $\frac{\text{root mortality}}{\text{mean standing pool of live roots}}$ (Burton *et al.* 2000; West *et al.* 2004).
- 4) $\frac{\text{root mortality}}{\text{maximum standing pool of live roots}}$ (Andersen *et al.* 2008; Pritchard *et al.* 2010)

Thus relative root turnover rates are generally measured by the production and/or mortality of roots relative to the size of the standing crop of roots (average and/or maximum). The various estimates of FRT in fact mixed some hidden assumptions.

Before turning to the details of the variability method, it was important to survey the

definitions of root turnover rates. Similar to a water reservoir, the total root mass is determined by its initial mass and fluxes in mass entering (influx) and leaving (outflux) the reservoir.

1) A single pool system

Annual root turnover rates on root coring basis could be described by a pool-flux model in a single pool system. This pool-flux model for the studied system could be viewed as a reservoir (or pools) with volume X and fluxes of input and output. In this system, root turnover rates can be defined as flux divided by pool size:

$$k_{in} = \frac{\text{input}}{X} \quad (\text{Appendix II.1})$$

$$k_{out} = \frac{\text{output}}{X} \quad (\text{Appendix II.2})$$

where input and output were the rates at which matter entered (construction) and left (deconstruction) the system, respectively. The pool could be live or dead root system. Due the similar models for live and dead roots, here, live root system was firstly considered, but the deduction process for live roots was also applied to dead roots.

(a) When input=0

That is to say, annual net root production is zero, which was applicable to dead roots (also like radio-isotope or a first-order chemical reaction, Chapter 4). The remaining weight of roots will depend on overall mass weight of roots, W , and also on the length of the brief period of time of t . In other words, the more roots there are the more will decay, and the longer the time period the more roots will decay. Therefore, in a small time interval of dt , the weight of dW will decay:

$$-dW \propto Wdt \quad (\text{Appendix II.3})$$

If the decay constant is k , then the rate of change of substrate W of roots with time is:

$$-dW = kWdt \quad (\text{Appendix II.4})$$

$$-\frac{dW}{W} = kdt \quad (\text{Appendix II.5})$$

When integrating this equation:

$$-\int \frac{dW}{dt} = k \int dt \quad (\text{Appendix II.6})$$

$$\ln W = -kt + C \quad (\text{Appendix II.7})$$

$$W = e^{-kt} \cdot e^C \quad (\text{Appendix II.8})$$

While $t=0$,

$$W_0 = e^C \quad (\text{Appendix II.9})$$

$$W = W_0 \cdot e^{-kt} \quad (\text{Appendix II.10})$$

When $W_t = \frac{W_0}{2}$, the half decay time, *i.e.*, the turnover rates

$$t_{\frac{1}{2}} = \frac{\ln 2}{k} = \frac{0.693}{k} \quad (\text{Appendix II.11})$$

When $W_t = 95\% M_0$, the 95% time

$$t_{95\%} = -\frac{\ln 0.05}{k} = \frac{2.996}{k} \quad (\text{Appendix II.12})$$

The turnover time (or mean residence time) is the time required to transform a quantity of material equal to the starting amount M_0 (*i.e.*, $W_t = W_0$) at steady state and is given by $\frac{1}{k}$ (Chapter 4).

From these formulas, the root turnover rates k could be calculated for live roots (biomass) or dead roots (necromass).

(b) When input=output (*i.e.*, steady state)

That is to say, annual net root mass (annual increment) is zero, as might be expected in a fully developed perennial system or in an annual system in which all roots die at the end of the season, then mortality is equal to production (for dead roots, decomposition is equal to mortality). Then W remains constant. The fraction of the pool being replaced per unit time, *i.e.*, turnover rate

$$T = \frac{\text{output}}{W} \quad (\text{Appendix II.13})$$

This value was often called the rate constant for the system (k).

2) Systems with two or more pools

For plant root systems, they consist of 2 pools (live and dead roots) and 3 fluxes (production, mortality, and decomposition). In this case, root systems could be illustrated as a simple two compartment system: L and D were supposed to be live and dead roots, respectively.

Consider plant live root compartment containing a quantity L_t at time t with material flowing into and out of it at the rates P_t and M_t respectively.

Therefore, this complex model can be viewed as an aggregation of several simple models. Here, the root systems comprise 3 different sorts of turnover rates: k_P , k_M , and k_C (Figure AII.1):

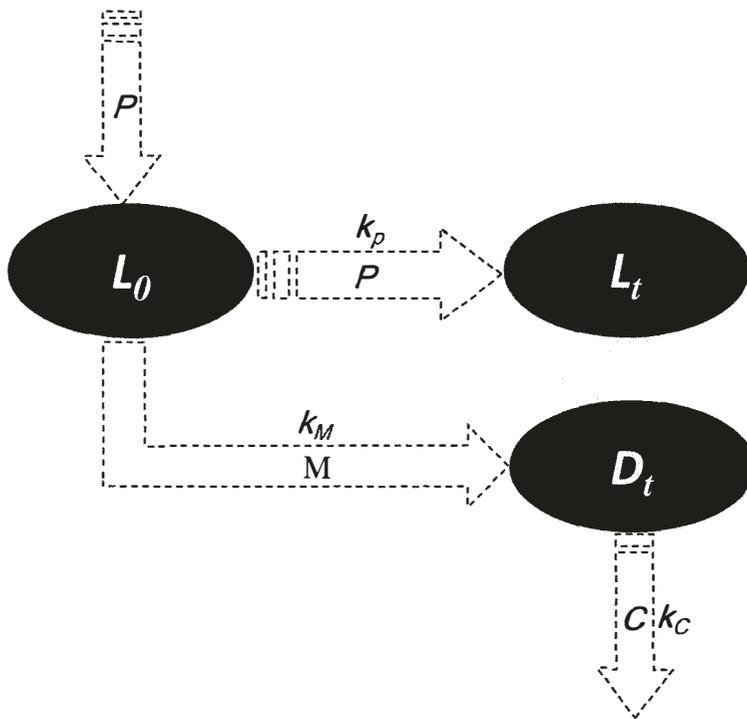


Figure AII. 1 Conceptual diagram of compartment model for the estimates of turnover rates for live and dead roots.

Notes: Pools are represented by boxes; fluxes by dark dashed lines. L =Live mass, D =dead mass, P =production, M =mortality, C =decomposition, k =turnover rates, 0 and t represent time.

$$k_P = \frac{P}{L} \quad (\text{Appendix II.14})$$

$$k_M = \frac{M}{L} \quad (\text{Appendix II.15})$$

$$k_C = \frac{C}{D} \quad (\text{Appendix II.16})$$

Generally, k_M is the turnover rate of live roots, while k_C is the turnover rates of dead roots. k_P , k_M , and k_C could be estimated from ingrowth, max-min, sum of positive changes, matrix decision, or compartment flow model methods. Moreover, for k_C , it is better to be estimated directly from litterbag-decay methods (Chapter 4). However, most published studies mixed them and only turnover rate k_P is presented, even in some highly cited papers (*e.g.*, Gill & Jackson 2000). In that case by Gill and Jackson (2000), the assumption in their paper is that the studied system is at a steady state (flux $P=M$ for pool L):

$$k_M = \frac{M}{L} = \frac{P}{L} = k_P \quad (\text{Appendix II.17})$$

A non-steady-state within the L (live roots) or D (dead roots) pool may have an effect on these kinetic measurements. Root production is the total entry rate of newly roots into the L pool (presumably representing construction or appearance), whereas mortality is the total exit rate of roots from the L pool (presumably representing destruction, damage, or disappearance). Similarly, root mortality is the total entry rate of dead roots into the D pool (presumably representing construction or appearance), whereas decomposition is the total exit rate of roots from the D pool (presumably representing destruction or disappearance). Thus,

$$\text{root production} = \text{replacement rate} + \text{accumulation rate} = \text{removal rate} + \text{accumulation rate} \\ = \text{mortality} + \Delta L \quad (\text{Appendix II.18})$$

where the ΔL can be a positive or negative number. Thus, at a non-steady-state (that is, an increase or decrease in the L pool size), root production does not equal removal rate (mortality). In that case, the live root turnover rate

$$k_L = \frac{P+M}{\alpha_L L} \quad (\text{Appendix II.19})$$

where k_L is the turnover rate of live roots, α_L is a corrected coefficient. At a steady state, the influx rate equals to the efflux rate (*i.e.*, $P=M$), thus $\alpha_L=2$. Therefore, equations AII.13 and

AII.17 were specific cases of equation AII.19. So the turnover rates of live roots could be theoretically estimated from the generalized equation AII.19. However, how could the α_L , the corrected coefficient, be calculated?

Again, considering the pool-flux model as show in Figure II.1, the change in live root biomass:

$$\frac{dL}{dt} = P - M \quad (\text{Appendix II.20})$$

To make the calculation simple and easy, assume that

$$\mu_L = \beta_L L \quad (\text{Appendix II.21})$$

where μ_L is the disappeared biomass at time t that comes from early time; β_L is the ratio of accumulative disappeared biomass to initial biomass. In specific, $\mu_{L0} = \beta_{L0} L_0$, where $\beta_{L0} = 1$.

Because μ_L is mainly driven by the change in efflux, *i.e.*, live root mortality, the rate of change of substrate L of live roots with time can be written as:

$$\frac{d\mu_L}{dt} = \frac{d(\beta_L L)}{dt} = -\beta_L M \quad (\text{Appendix II.22})$$

Differentiate this equation:

$$\frac{d(\beta_L L)}{dt} = \frac{d\beta_L}{dt} L + \beta_L \frac{dL}{dt} = -\beta_L M \quad (\text{Appendix II.23})$$

Substitute equation AII.20 into equation AII.22:

$$\frac{d\beta_L}{dt} L + \beta_L (P - M) = -\beta_L M \quad (\text{Appendix II.24})$$

Simplifying this equation and eliminating the $-\beta_L M$ from the equation:

$$\frac{d\beta_L}{dt} L = -\beta_L P \quad (\text{Appendix II.25})$$

This equation can be changed to:

$$\frac{d\beta_L}{\beta_L} = -\frac{P}{L} dt \quad (\text{Appendix II.26})$$

Integrating both sides of this equation:

$$\int_0^t \frac{d\beta_L}{\beta_L} = - \int_0^t \frac{P}{L} dt \quad (\text{Appendix II.27})$$

Expanding and rearranging this equation:

$$\beta_L = \beta_{L0} e^{-\int_0^t \frac{P}{L} dt} = e^{-\int_0^t \frac{P}{L} dt} \quad (\text{Appendix II.28})$$

Therefore, based on equation AII.22, the rate of change of substrate L of live roots with time is:

$$q_t = \frac{d\mu_L}{dt} = -\beta_L M = -M e^{-\int_0^t \frac{P}{L} dt} \quad (\text{Appendix II.29})$$

At steady state, $P = M = Q$, then

$$q_t = -M e^{-\int_0^t \frac{P}{L} dt} = -Q e^{-\int_0^t \frac{Q}{L_0} dt} = -Q e^{-\frac{Qt}{L_0}} \quad (\text{Appendix II.30})$$

The change of substrate L of live roots is:

$$\int_0^t q_t dt = - \int_0^t Q e^{-\frac{Qt}{L_0}} dt = L_0 e^{-\frac{Qt}{L_0}} \Big|_0^t = -L_0 (1 - e^{-\frac{Qt}{L_0}}) \quad (\text{Appendix II.31})$$

Assume that γ_L is the change ratio of live roots, then

$$\gamma_L = \left| \frac{\int_0^t q_t dt}{L_0} \right| = \frac{1}{L_0} \int_0^t Q e^{-\frac{Qt}{L_0}} dt = 1 - e^{-\frac{Qt}{L_0}} \quad (\text{Appendix II.32})$$

From this equation, the turnover time of t_L for live roots can be calculated:

$$t_L = - \frac{L_0}{Q} \ln(1 - \gamma_L) \quad (\text{Appendix II.33})$$

Therefore, the turnover rates of live roots is:

$$k_L = \frac{1}{t_L} = - \frac{Q}{L_0} \frac{1}{\ln(1 - \gamma_L)} = \frac{Q}{L_0} \frac{1}{\ln \frac{1}{1 - \gamma_L}} \quad (\text{Appendix II.34})$$

According to equation AII.19, the theoretical live roots turnover rate k_L is:

$$k_L = \frac{P+M}{2L} \frac{1}{\ln \frac{1}{1 - \gamma_L}} \quad (\text{Appendix II.35})$$

The γ_L can be calculated from:

$$\gamma_L = \frac{1}{L_0} \int_0^t Q e^{-\frac{Qt}{L_0}} dt = \frac{1}{L_0} \sum_0^t (Q e^{-\sum_0^t (\frac{Q}{L} \Delta L)}) \quad (\text{Appendix II.36})$$

Similarly, the dead root turnover rate can be calculated by:

$$k_D = \frac{M+C}{2D} \frac{1}{\ln \frac{1}{1-\gamma_D}} \quad (\text{Appendix II.37})$$

Therefore, it is in effect complicated to estimate turnover rates of a changing system (including plant fine roots) with influx and outflux. Varied methodologies used in published papers to estimate a system's turnover rate have many underlying assumptions in order to make it easy and practicable for calculation. Since this present thesis focused not on methodology but on the effects of stand age and disturbance type, FRT was calculated with the commonly used methods, *i.e.*, the production divided by the biomass of live roots. By this way, FRT could be compare to that in other published papers. More details of definition and calculation of fine root turnover rates were provided here as an appendix for the readers to read and to get a better understanding for Chapters Four and Six in this thesis.