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Carbon dynamics of boreal mixedwoods in central Canada

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CARBON DYNAMICS OF BOREAL MIXEDWOODS IN CENTRAL CANADA

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ABSTRACT

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Key Words: Carbon dynamics, carbon pools, live biomass, dead wood, forest floor, mineral soil, boreal forest, mixedwoods, chronosequence, wildfire, clearcut logging.

Large amount of carbon (C) stored in boreal forest ecosystems plays an important role in the global carbon cycle. Forest ecosystem C is stored in four major pools: live vegetation (above- and belowground), dead woody material (snags, down woody debris, and stumps), organic soil horizons (forest floor), and mineral soil. Carbon cycling among these pools is mainly determined by disturbance. A large portion of previously fire-driven ecosystems in boreal North American forest are now managed. How C cycling of managed stands differs from that of natural stands strongly influences boreal forest carbon balance. In this thesis I first synthesize literature on carbon dynamics in North American boreal forests followed by a study about aboveground biomass C dynamics in boreal mixedwoods after wildfire and clearcut harvest.

Carbon pool dynamics in forest ecosystems after stand replacing wildfire are described and compared with carbon dynamics after clearcut harvesting. Following a stand replacing disturbance, 1) live biomass increases rapidly leading to the maximal biomass stage, then stabilizes at stand maturation; 2) dead woody material carbon generally follows a 'U' or 'S' shaped pattern during succession; 3) Forest floor carbon increases throughout stand development; 4) mineral soil carbon is the largest terrestrial organic carbon pool and is highly variable, but an overall increase over time has been observed. These pools are connected and throughout stand development C allocation from one pool to another takes place. Wildfire and harvesting differ in many ways, fire being more as a chemical and harvesting as a mechanical disturbance. Fire consumes forest floor and small live vegetation and foliage while during logging much of large size biomass is removed and forest floor is mechanically disturbed. Another major difference is the absence of coarse woody debris after logging. Also, regeneration of the new stand is different after wildfire and logging. Fire often destroys advanced regeneration while it is less affected by logging, resulting different species composition and therefore different stand C dynamics. Overall, the manner in which different types of disturbance effect C dynamics in boreal forest is poorly understood. Further studies following wildfire but especially forest harvesting are needed to improve understanding of the effect of disturbance on C dynamics.

Live biomass carbon (C) pool dynamics are central to understanding carbon sequestration of forest ecosystems. Despite its importance, how aboveground live C pools change with stand development of boreal mixedwoods is poorly understood, in particular in relation to different disturbance origins. I quantified above ground live biomass C pools in a postfire chronosequence ranging from 1 to 203 years and a post-logging chronosequence ranging from 1 to 27 years in boreal mixedwood forest in central Canada. Stands were chosen along a successional sequence in boreal mixedwoods. Total live biomass C was significantly affected by time since disturbance and stand origin with time since disturbance explaining most of the variation. The biomass C dynamics was largely determined by overstory tree dynamics as it constituted

most of stand biomass. Biomass in postfire stands reached maximum (109.18 Mg C/ha) at the age of 92 years after fire and then declined in older age classes. Post-logged stands had significantly more biomass C compared to postfire stands with the biggest difference at 27 years after disturbance when post-logged stands had 38.5 Mg C/ha more C than postfire stands.

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NOTE TO THE READER

The two chapters of this thesis have been written as distinct manuscripts to be submitted for publication. Therefore, due to similar subject matter some overlap in introductory material occurs. The review (Chapter 2) deals with all ecosystem C pools while the original study (Chapter 3) only examines aboveground biomass C.

Chapter 2:

Seedre, M., Shrestha, B.M., Chen, H. 2009. Carbon dynamics of boreal forest of North America.

Chapter 3:

Seedre, M. and Chen, H. 2009. Carbon dynamics of aboveground live vegetation of boreal mixedwoods after wildfire and clearcutting.

CHAPTER ONE GENERAL INTRODUCTION

The boreal forest is the largest terrestrial biome in the world (Meillio et al. 1993). Its vast wetlands, forest, and permafrost form nearly a contiguous circumpolar band in the northern hemisphere, containing carbon (C) equaling roughly 50% of that presently in the atmosphere (Chapin et al. 2000; Gower et al. 2001). In North America, the boreal forest covers 34% of all land, totalling 412 million ha (Bourgeau-Chavez et al. 2000) and containing 66.7 Pg of C (Goodale et al. 2002). These large C stores are the result of long days during the growing season, with long cold winters, and poorly drained soils that limit decomposition (Gower et al. 1997). Boreal forest C storage and sequestration is a critical element for global C management and has recently gained attention because of its importance to global warming (Harden et al. 2000; Wang et al. 2003; Howard et al. 2004; Martin et al. 2005).

Disturbance is key to understanding boreal forest dynamics (Banfield et al. 2002; Howard et al. 2004; Bond-Lamberty et al. 2004). Time since disturbance (age of stand) determines many ecosystem functions and its total C content (Pregitzer & Euskirchen 2004; Hart & Chen 2006; Brassard & Chen 2006). Ecosystem C density varies greatly with stand age. Therefore, disturbance driven age class distribution, affected by disturbance patterns, ultimately determines the ecosystem C balance (Bhatti et al. 2002; Pregitzer & Euskirchen 2004; Magnani et al. 2007).

The primary stand replacing disturbance in North American boreal forests is wildfire (Kasischke et al. 1995; Weber & Flannigan 1997). It is the main driver of ecological processes influencing boreal forest structure and function, and a significant factor in determining ecosystem C balance (Bond-Lamberty et al. 2007). Human

activities, such as harvesting, have historically only contributed a small fraction of the overall disturbance affects in boreal forests (Kurz & Apps 1996); however, growing demand for forest products has increased harvest levels. Many areas of the boreal forest, previously subject to uncontrolled wildfires, are now managed through a combination of fire suppression and harvesting (McRae et al. 2001; Bergeron 2004). An understanding of how ecosystem C dynamics is influenced by harvesting relative to wildfire is critical in understanding C budgets.

Forest ecosystems have four major C pools, that respond differently to disturbance; (1) live vegetation (above and below ground), (2) dead vegetation (snags, down woody debris, and stumps), (3) organic soil horizons (forest floor), and (4) mineral soil. Those pools are connected and transfers among pools (C allocation) inside ecosystem occur as a forest matures (Pregitzer & Euskirchen 2004). Different C pools contain varying amounts of C and change uniquely during succession. Changes in C pool during stand development are affected by many biotic and abiotic factors such as species composition, water and nutrient availability, disturbance (e.g. fire, insects, disease, and harvest) and climate (e.g. growing season length, temperature) (Banfield et al. 2002; Hyvönen et al. 2007; Litton et al. 2007).

There are several reviews concerning C dynamics in forest ecosystems. For example, Pregitzer & Euskirchen (2004) study C cycling and storage in world forests, Litton et al. (2007) study C allocation in forest ecosystems and several reviews focus on effects of global warming on C dynamics (e.g. Hyvönen et al. 2007; Millard et al. 2007). Some reviews look at individual C pools, like coarse woody debris (Laiho & Prescott 2004) or soil C (Lal 2005). Also, work has been done to compare the effects of wildfire

and harvesting and their implications in forest management (McRae et al. 2001).

Although variety of studies have been done about different aspects of C cycling in forest ecosystems, no review has examined all major C pools and compared their dynamics after stand replacing disturbance by fire and harvest in the of boreal forest.

Live biomass C accumulation plays an important role in C cycling by controlling the major terrestrial transfer of C between atmosphere and the soil (Hyvönen et al. 2007). Through photosynthesis, plants take CO₂ from the atmosphere and through respiration by vegetation and decomposing organisms (mainly fungi) in the soil (heterotrophic respiration) return it to atmosphere. Biomass dynamics has also received much attention due to use of wood as a renewable resource. Several studies have looked at biomass growth in single species dominated stands (e.g. Gower et al. 1997; Wang et al. 2003) however there are only few studies which examine biomass C in boreal mixedwood forests (Pare & Bergeron 1995; Brassard & Chen 2006). Therefore, our understanding about boreal mixedwood live biomass C dynamics is limited. Furthermore, little is known about harvesting influences on live biomass C compared to wildfire influences. Most studies have compared young plantations with old fire origin stands therefore confounding the effect of stand age with disturbance (Fredeen et al. 2005; Martin et al. 2005; Taylor et al. 2007).

The initial objectives of this thesis are to (1) investigate the dynamics of major ecosystem C pools through stand development after wildfire and (2) examine the effects of different forest types and environment on C dynamics and (3) investigate how clearcut harvesting affects C dynamics compared to wildfire.

This thesis will then: (1) quantify the changes in aboveground live vegetation carbon pools in a boreal mixedwood chronosequence and (2) compare aboveground live vegetation carbon dynamics of mixedwood stands after wildfire and clearcut logging.

CHAPTER TWO CARBON DYNAMICS OF NORTH AMERICAN BOREAL FOREST: A REVIEW

INTRODUCTION

Boreal forest carbon (C) storage and sequestration is a critical element for global C management (Harden et al. 2000; Wang et al. 2003; Howard et al. 2004; Martin et al. 2005). The C dynamics in the boreal forests is largely disturbance driven (Banfield et al. 2002; Howard et al. 2004; Bond-Lamberty et al. 2007) because large quantities of C stored in forest ecosystems can be released to the atmosphere over short time steps following the disturbance (Korner 2003). Boreal forest disturbances vary greatly in intensity and frequency from natural wildfire, insect/pest outbreak, windthrow, and flooding to anthropologic prescribed fire, tree harvesting/logging, and land use change. For example, wildfire can be severe, replacing a stand completely, or less severe, causing only minor disturbances (Certini 2005). Similarly, during logging a full stand or a part of a stand can be removed. Fire initiates secondary succession and is the dominant driver of C dynamics in the boreal forest (Kasischke & Bruhwiler 2002). Harvesting has historically contributed only a small fraction of the overall disturbance affects in boreal forests (Kurz & Apps 1996). However, due to growing demand for forest products the harvest levels have increased in the recent time (Gower 2003; Field et al. 2007).

Forest disturbances differ temporally and spatially, affecting forest stand development in various ways. Temporal scale of disturbance and time since disturbance (TSD) are the main drivers determining many ecosystem functions and its total C content (Pregitzer & Euskirchen 2004; Hart & Chen 2006).

Carbon sequestration capacity increases with stand age at early stages, but declines at later stage of stand development. There is growing concern about the old-growth forests (unmanaged, generally older than 100 years since last stand replacing disturbance): whether they act as sink or source of atmospheric CO₂ (Neilson et al. 2007; Luyssaert et al. 2008). Neilson et al. (2007) reported that trees of age 100-150 years showed a decline in total C in biomass while Luyssaert et al. (2008) showed that old-growth forest are C sinks, continuously accumulating C, thus arguing that old-growth forests should be credited in the C-accounting rules.

Another ongoing debate is about the effect of climate change on the C dynamics of the boreal forest, whether it will become a sink or source of CO₂ in response to increasing temperature and altered precipitation. In the northern hemisphere warming was reported to be nearly 1°C during the last five centuries, half of which occurred in the last 50 years (Beltrami & Bourlon 2004). Eastern and central Canada, have showed continuous warming in the last 150 years (Beltrami & Mareschal 1993). Warming can have various effects on forest C balance. For example, a large quantity of C stored in peat and in humus may be released to the atmosphere due to the positive effects increased temperature may have on decomposing organisms. On the other hand, if a long lasting warming of the climate occurs, production capacity and areal extent of the boreal forest could also increase with shift of tree line northwards. In such case, an increase of C in the biomass would compensate the net release from decomposition of dead organic matter (Kolchugina & Vinson 1993).

There are several syntheses concerning C dynamics in forest ecosystems with focuses on the effects of forest age (Pregitzer & Euskirchen 2004), C allocation in

different components of an ecosystem (Litton et al. 2007), effect of climate change, CO₂ fertilization and N deposition on C dynamics (e.g. Hyvönen et al. 2007; Millard et al. 2007) or individual C pools, like coarse woody debris (Laiho & Prescott 2004) or soil C (Lal 2005). However, to my knowledge no review has examined all major C pools of the boreal forest and compared their dynamics after stand replacement by fire and harvesting. In this review, I will synthesize and discuss the effects of forest disturbances on C storage and sequestration in boreal ecosystems. Specific objectives include reviewing the effects of forest fire and harvesting on (i) above ground and belowground C pools, (ii) C sequestration in vegetation and soils, and (iii) effects of climate change in the C pools and C sequestration in boreal ecosystems. This review will begin by describing trends in vegetation succession following stand-replacing fire. Then it will discuss how species composition, site condition, and regional climate may affect aboveground vegetation C dynamics. A discussion of the implications of forest management, in particular the practices of clear-cutting and site preparation, for C dynamics follows.

MAJOR ECOLOGICAL FEATURES OF BOREAL REGION

The boreal forest zone (Figure 1) is the fourth largest eco-zone of the world covering about 13% of earth's land mass (Schultz 2002). It is the cold eco-zone of the world- temperature remains higher than 5°C for only 3-6 months of a year, annual precipitation ranges from 250 to 500 mm and can be as high as 800 mm. The winter snow cover ranges from 30-100 cm for 6-7 months. Notably the summer solstice ranges from 16-24 hours of daylight from the southern to northerly areas, respectively, that compensates the lower solar radiation. The pedosphere consists of large area of

permafrost soils causing shallow root depth. Soils are highly acidic; podzols are dominant while other soil types found in the region are cambisols and leptosols in the uplands, histosols and luvisols in poorly drained soils (Schultz 2002). Nutrient levels are very low due to slow mineralization rate. As a result, mineral soils are often covered with thick litter-fibric-humic (LFH) layer due to slow decomposition of organic materials (Steele et al. 1997). Coniferous and mixed forests are two of the major forests found in this zone. Spruces (*Picea spp.*), pines (*Pinus spp.*), larches (*Larix spp.*) and firs (*Abies spp.*) cover thousands of square kilometers in single species stands. In mixed forests, deciduous species such as birches (*Betula spp.*), poplars (*Populus spp.*), willows (*Salix spp.*), alders (*Alnus spp.*) and ashes (*Fraxinus spp.*) live with the coniferous species. Different species of shrubs and herbs are also present in the forests.



Figure 1. Map of the Boreal Forest of North America (Natural Resources Canada).

Peat bogs cover almost 10% of the boreal region and have been an important reservoir of C (storing almost 25% of global organic C) in the post ice age time (Gorham 1991; Bond-Lamberty et al. 2007). However in response to increasing global temperature there is possibility of a release of this stored C, which will be discussed in more detail in the later chapter.

FOREST FIRE AND ITS ROLE IN BOREAL FOREST SUCCESSION

Fire is the main trigger in secondary forest succession in the boreal region and a significant factor in determining ecosystem C balance (Auclair & Carter 1993; Kasischke et al. 1995; Weber & Flannigan 1997; Amiro et al. 2001; Boulanger & Sirois 2006; Bond-Lamberty et al. 2007). In contrast to tropical region, where forest fire is usually human caused, the occurrence of forest fire in boreal region is mostly natural, and is mainly due to lightning (Certini 2005). Size and intensity of wildfire is normally higher in the well-drained uplands than in poorly drained lowlands of the boreal forest (Harden et al. 2000). Moist soils transfer thermal energy faster than dry soil. Due to higher latent heat of vaporization of water, temperature in mineral soil subjected to fire may reach a maximum of 150°C in the upper 5 cm soil depth. However, little or no heating occurs below 20-30 cm although this depends on soil thickness, bulk density and moisture of fuel bed (Certini 2005).

Fire can alter the soil's physical, chemical, mineralogical and biological properties temporarily or permanently depending upon the burn intensity, frequency of fires and post-fire climatic conditions. Further loss of fine particles due to post-fire water erosion, small-scale resorting of soil constituents and removal of volatilized nutrients can make a forest floor unsuitable for establishment of pioneer species for

long periods of time (Bormann et al. 2008). In general, nitrogen (N) and available phosphorus (P) concentration increases but micro-organism populations are reduced severely in soil in post-fire period. In case of intense fires, surface soil may be rendered sterile with re-colonization happening later (Certini 2005). In coniferous stands studied by Fritze et al. (1993), up to 12 years were required for microbial biomass to return to pre-fire levels. Intense forest fire may expose loose surface rocks when most of the soil organic matter (SOM) is consumed (Bormann et al. 2008). Thus, forest regeneration in the post-fire stand will be also different depending upon the fire severity. For example in the case of non stand replacing fire, there will be dominance of same tree species as before the disturbance while if the fire is stand replacing, the species composition of the new stand will be different (Hart & Chen 2008).

BOREAL FOREST SUCCESSION

As C cycling is strongly influenced by age of the stand and the stand species composition, it is important to understand boreal forest successional dynamics. Successional trends in the boreal forest depend upon differences in the fire frequency. In many parts of the boreal forest (ca. 75%), fire frequency is generally longer than the life-span of the dominant tree species (Johnson 1992). Therefore, little or no species replacement occurs during stand development, thus, post-fire composition will be similar to pre-fire composition (Horn 1981; Johnson 1992) until the next stand replacing fire (Chen & Popadiouk 2002). In such case there will be dominance of shade-intolerant species such as jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.). In the long run, these species will be replaced by the shade-tolerant species such as white spruce

(*Picea glauca* (Moench)), black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.) and white cedar (*Thuja occidentalis* L.), given long enough time since fire (Brassard & Chen 2006). In stands dominated by one species, structural development independent of changes in species composition may be the key process, affecting indirectly the abundance and distribution of species (Harper et al. 2002) and therefore C dynamics. The successional stages will be different in case of intense stand replacing fire. With highly disturbed forest floors, it will probably take time for pioneer tree species to establish, with the speed of regeneration depending on seed supply from the surrounding stands and below ground viable propagules. Paper birch and trembling aspen, if they are present in the area before fire, usually colonize the fire-disturbed site first as they are adapted to frequent fires and as they can reproduce by stem sprout and suckering respectively or by seeds. In the next stage, shade-tolerant conifer species emerge and forest will become mixed (Brassard & Chen 2006)

In boreal mixedwood stands, clear changes occur in species composition during stand development after forest fire (Hart & Chen 2008) which influence stand C dynamics. These changes can be divided into four stages; stand initiation, stem exclusion, canopy transition and gap dynamics (Chen & Popadiouk 2002). The characteristics of each of these stages on a particular site are determined by tree growth, development, age and species-specific resource requirements (Day & Harvey 1981; Gilmore & Seymour 1997; Whittle et al. 1997). The course of succession is driven by successional mechanisms caused by the interaction between various factors including species longevity, type of regeneration, growth rate, and shade tolerance (Frelich & Reich 1995; Frelich & Reich 1999; Bergeron 2000).

CARBON POOLS AND THEIR INTER-RELATIONSHIP

Forest ecosystem C is typically classified into four pools -(1) live vegetation (above and below ground), (2) dead wood (snags, down woody debris, stumps and dead roots), (3) organic soil horizons (forest floor), and (4) mineral soil (Pregitzer & Euskirchen 2004). These pools are inter-connected and are dynamic during forest growth and succession (Pregitzer & Euskirchen 2004). Through photosynthesis, forests take up CO₂ from the atmosphere. Conversely, respiration by vegetation and decomposing organisms (mainly fungi) in the soil (heterotrophic respiration) return CO₂ to the atmosphere. The difference between the sequestered C and released C through plant respiration is termed as net primary productivity (NPP); if release also includes heterotrophic respiration, then it is termed net ecosystem productivity (NEP). The C captured through photosynthesis will be allocated by plants into their trunks, branches, roots, leaves, etc. The leaf litter including small twigs will be aboveground C input; dead roots (especially the fine roots and root hairs) will be belowground C input for organic and mineral soil. Turnover of C in dead wood will vary depending upon species, stage of decay, biotic and abiotic factors. Finally, the C from different pools will be mixed into the mineral soil as soil organic C (SOC) which binds necessary plant nutrients. Thus there is always a dynamic relationship of different C pools in an ecosystem. Importantly, the C in mineral soil is more stable and has much longer residence time compared to vegetation C (Vogt et al. 1995). Within the SOC itself, the residence time is higher in root-derived C than the shoot-derived C (Rasse et al. 2005). Several studies have reported that there will be no effect of forest fire on mineral soil C pool as the effect is mainly in the upper 5 cm soil layer (Johnson & Curtis 2001; Certini 2005). In contrast, a study by Bormann et al. (2008) reported that there was a

loss of 60% C and 57% N from mineral horizons. They concluded that intense forest fires sharply reduces the mineral soil C and N with major implications for forest succession, productivity and climate and C dynamics.

LIVE BIOMASS C DYNAMICS

Live vegetation is comprised of over-story and under-story trees, shrubs, and ground vegetation, including both their aboveground and belowground (roots) components. The following subheadings will describe how the C dynamics varies in different vegetation forms and their components.

Tree biomass

The C accumulation in live trees can be described using tree biomass accumulation function- the sigmoid growth function (Figure 2a, b) e.g., the Chapman-Richards and Von Bertalanffy function (Pienaar & Turnbull 1973; Bormann & Likens 1979). Following stand replacing disturbance, biomass C accumulates slowly at first then more rapidly before reaching a maximum; after the canopy closure, biomass C slows (Figure 2). The biomass accumulation is dependent on disturbance type. For example, if a stand replacing fire takes place, the biomass accumulation in both root and shoot of vegetation will start from zero level (Figure 2a); in contrast, after clearcut harvesting, the biomass accumulation may be somewhat above the zero level (Figure 2b). After reaching a maximum, C mass remains constant or declines slightly (Sprugel 1985). This type of growth dynamics has been observed over a wide range of forest ecosystems (Sprugel 1985) and is also supported by several C dynamics studies in boreal (Martin et al. 2005) and near boreal (Rothstein et al. 2004) forest regions. The speed of C accumulation is dependent on forest productivity: more productive forests

accumulate C faster and reach production peak earlier than the less productive forests, but also reach a decline phase sooner (Chen et al. 2002).

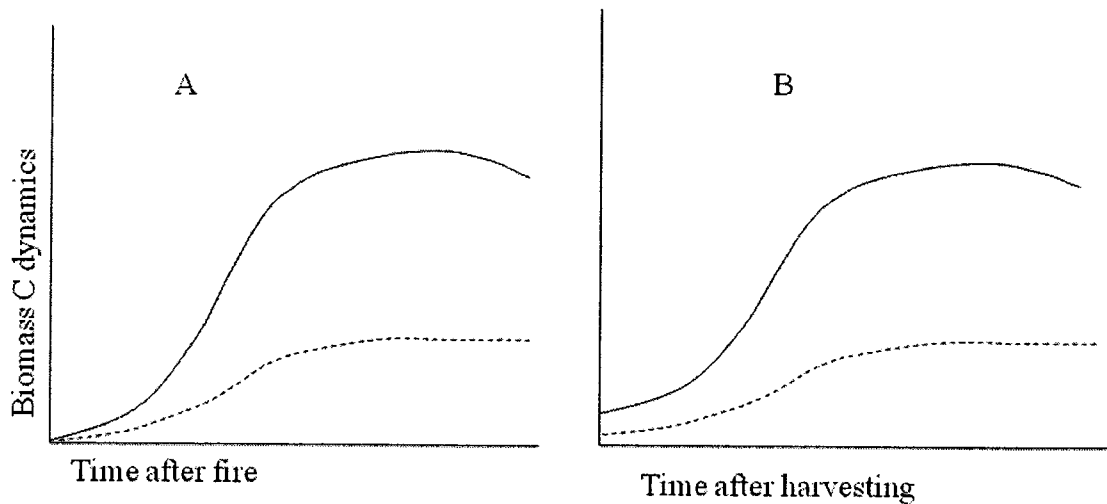


Figure 2 A and B. Conceptual figure showing dynamics of above ground tree biomass (solid line) and belowground root biomass (dotted line) after fire (A) and after clearcut harvest (B).

Major causes of decline in C accumulation after canopy closure in even aged forests (Smith & Long 2001; Ryan et al. 2004) are still unclear. Several mechanisms have been suggested, including the decline in C assimilation and increased respiration (Möller et al. 1954; Kira & Shidei 1967), decreased soil nutrient availability, declining photosynthesis (Gower et al. 1996; Ryan et al. 1997), and successional changes in species composition and increased susceptibility to insect and/or wind damage (Pare & Bergeron 1995). Another possible reason for age-related decline in boreal forests is the accumulation of organic matter in the forest floor (FF) (Gower et al. 1996; Murty et al. 1996; Prescott et al. 2000). A thick FF contributes to soil cooling and restricts nutrient mineralization and uptake by plants (Gower et al. 1996; Murty et al. 1996; Prescott et

al. 2000). Also, large amounts of nutrients in FF are in complex organic molecules and not accessible to plants (Prescott et al. 2000), resulting in reduced productivity. In contrast, Ryan et al. (2004) found that neither nutrient limitation nor decreased photosynthetic capacity is responsible for the declined productivity. They proposed that decline is mostly caused by decreased canopy C gain and shift in partitioning of sequestered C to belowground biomass and foliage respiration. A study by Smith and Long (2001) suggests that the age related decline is a population phenomenon. They reported that even if in some sites the age related decline might be related to nutrient limitations, more often, and more importantly it is due to mechanical abrasion as a result of physical interaction between individual tree crowns. While following a general sigmoidal pattern, C accumulation differs significantly between forest types (Gower et al. 1997). It has been found that annual net primary productivity (ANPP) is greater in deciduous boreal forest compared to evergreen boreal forests (Van Cleve et al. 1983; Ruess et al. 1996; Gower et al. 1997). It is unclear why boreal deciduous forests have higher ANPP. One proposed explanation is the greater light use efficiency of deciduous forests (Hunt & Running 1992; Gower et al. 1997).

Several of the C dynamic studies have been carried out in black spruce (*Picea mariana* (Mill.) BSP) forests as it is the most abundant tree species in the North American boreal forest. Black spruce covers a larger area and contains more C (Gower et al. 1997; Goetz et al. 1999; Gower et al. 2001) than other major boreal ecosystems (fir, jack pine, and aspen forests). Wang et al. (2003) examined C dynamics after fire in well- and poorly- drained black spruce forests of northern Manitoba using a

chronosequence of 3 to 151 years. Their results showed that soil drainage affected C distribution; dry sites accumulated more C than wet sites (Table 1).

Table 1. Carbon pools of boreal forest.

Reference	Location of the study	Forest type	Moisture regime	Age	Origin	C pool range (Mg C ha ⁻¹)			
						Live biomass	Dead wood	Forest floor	Mineral soil
Bond-Lamberty et al. (2003)	Manitoba	Black spruce	Dry site	2 - 130	Fire	5.0 - 177.6			
Boulanger & Sirois (2006)	Quebec	Black spruce	Wet site	2 - 130	Fire	1.4 - 94.1			
Fleming & Freedman (1998)	New Brunswick	Hardwood	Dry site	4 - 29	Fire ²	2.9 - 13.8			
				55 - 60	Fire ²	74.9 - 92.7	7.8 - 11.2	12.1 - 23.2	
		Mixedwood	Dry site	105	Fire	73.2	14.1	18.1	
		Coniferous	Dry site	75 - 95	Fire	57.1 - 71.0	23.7 - 36.9	22.9	
		Black spruce	Dry site	3 - 21	Harvest	0.33 - 29.9	0.14 - 16.9	15.4 - 31.1	
Fredeen et al. (2005) ¹	British Columbia	Coniferous	Dry site	0 - 20	Harvest	42	13	27	112
				0 - 20	Harvest	49	9	29	106
				151 - 250	Harvest	195	35	78	115
				151 - 250	Harvest	149	31	35	110
Gower et al. (1997)	Saskatchewan	Trembling aspen		67		93.3 [†]			36.0
		Black spruce		115		49.2			390.4
		Jack pine		25 - 65	Fire	12.3 - 34.6			20.2 - 14.2
	Manitoba	Trembling aspen		53		57.0			97.2
		Black spruce		155		57.2			418.4
		Jack pine		25 - 63	Fire	7.8 - 29.0			25.8 - 28.4
Howard et al. (2004)	Saskatchewan	Jack pine		0 - 29	Harvest	1.2 - 24.4*	2.0 - 7.1	10.9 - 26.9	22.0 - 32.1
				79	Fire	38.7	3.2	8.6	20.9

Table 1. Continued.

Manies et al. (2005)	Manitoba	Black spruce	5 - 53	Fire	7.0 - 14.8	
Martin et al (2005)	Manitoba	Mixedwood	11 - 30	Harvest	16.0 - 32.7	31.0 - 15.6 31.0 - 43.8 46.2 - 51.5
Nalder & Wein (1999)	Saskatchewan	Jack pine	65	Fire	60.2	9.1 24.9 53.0
	Alberta / Northwest Territories	Jack pine	16 - 111	Fire	8.1 - 84.4†	7 - 21
	Manitoba	Jack pine	16 - 135	Fire	14.0 - 77.4	10 - 24
	Saskatchewan	Trembling aspen	30 - 82	Fire	21.1 - 39.2	8 - 18
	Alberta / Northwest Territories	Trembling aspen	36 - 132	Fire	20.1 - 117.3	22 - 37
	Manitoba	Trembling aspen	14 - 149	Fire	5.0 - 83.1	14 - 46
O'Connell et al. (2003a)	Manitoba	Trembling aspen	28 - 112	Fire	15.0 - 82.4	15 - 31
Rapalee et al. (1998)	Manitoba	Jack pine	13 - 90+	Fire		0 - 9 0 - 37
		Black spruce	13 - 90+	Fire		10 - 44 96 - 127
		Black spruce	13 - 90+	Fire		8 - 48 153 - 197
		Black spruce	13 - 90+	Fire		7 - 42 117 - 143
Taylor et al. (2008)	Nova Scotia	Red spruce	1 - 140	Harvest	8.31 - 120.7	8.1 - 32.0 18.9 - 47.1 51.4
Wang et al. (2003)	Manitoba	Black spruce	3 - 151	Fire	1.3 - 83.3	10.3 - 96.0
		Wet site	3 - 151	Fire	0.6 - 37.4	12.6 - 77.4

Carbon cycling in black spruce forest is also strongly affected by ground cover type (Bisbee et al. 2001; O'Connell et al. 2003a). Black spruce FF is often covered by two types of bryophytes, feather moss (different boreal upland mosses branched with feathery manner) and *Sphagnum* spp.. Bryophytes affect soil temperature, water regime, nutrient availability (Van Cleve et al. 1983) and therefore stand C dynamics. O'Connell et al. (2003a) reported that stands with feather moss ground cover are significantly greater C pool than stands with *Sphagnum* ground cover.

Topographical conditions of the forest stands affect soil water, temperature and nutrient availability and ultimately forest C accumulation. A study by Grant (2004) in boreal black spruce forests found that boreal upslope stands had accumulated almost three times more wood C compared to stands in low basin areas. Higher productivity was attributed to decreased soil moisture conditions, higher soil temperatures and improved soil nutrient status (Grant 2004). In contrast, a study from north-eastern Ontario found that total live tree C was not significantly different with respect to slope positions despite large variations within upland and riparian forests where there were significantly different species composition and different C allocation (Hazlett et al. 2005).

It has been hypothesized that mixedwood stands have higher productivity compared to single species stands (Vandermeer 1989; Chen & Popadiouk 2002). Results of some studies have either fully supported this hypothesis (MacPherson et al. 2001; Martin et al. 2005), or partially supported it (Brassard et al. 2008). Fleming and Freedman (1998) reported that natural hardwood dominated stands (55 – 60 years) have more C in live woody biomass than mixed-species (105 years) or conifer

dominated stands (75-95 years) (Table 1). However, the conifer dominated stands might have less C in live tree biomass due to the increased mortality of balsam fir and black spruce due to an infestation of spruce budworm (Fleming & Freedman 1998).

Understory vegetation biomass

In the Boreal forest, the understory vegetation (dwarf shrubs, herbs and grasses, mosses, lichens) and understory tree (shrubs, seedlings, saplings) biomass is usually small immediately after stand replacing fire. Following fire, the biomass of understory components starts to increase rapidly (Hart & Chen 2006). Depending upon the disturbance type, the proportion of biomass in understory may be considerable in the early stages of forest succession when it is the major living vegetation component of forest ecosystem (Figure 3). Later in succession, the understory share of overall biomass decreases eventually forming only a minor part in mature forests. Although a small fraction of total biomass, bryophyte production rates can equal or exceed overstorey production (Gower et al. 1997; 2001; O'Connell et al. 2003 b).

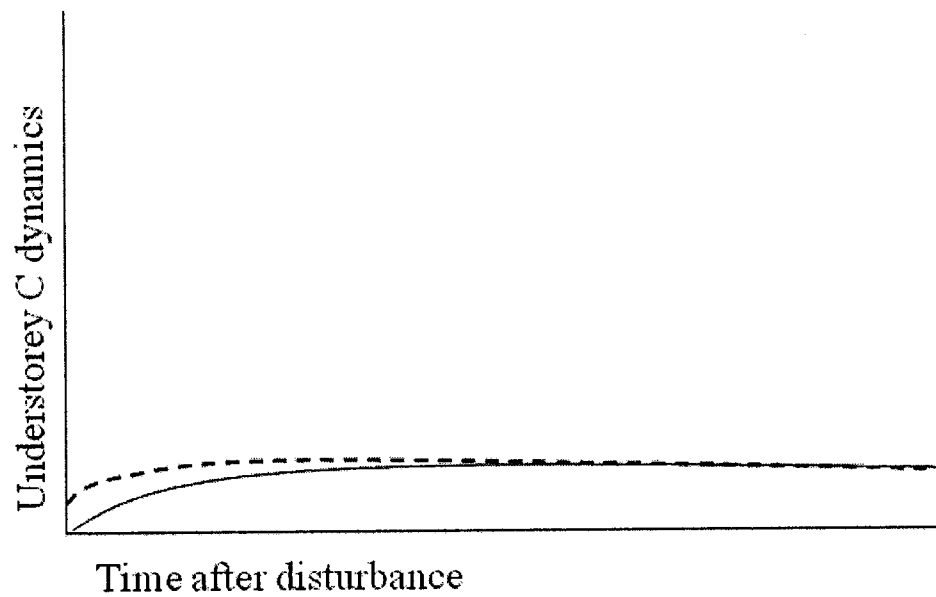


Figure 3. Conceptual figure showing biomass dynamics in forest understorey after fire (solid line) and after harvest (dotted line).

Only few studies of the boreal forest quantify C pool in both the understorey vegetation and tree biomass (Fleming & Freedman 1998; Nalder & Wein 1999; Fredeen et al. 2005; Nalder & Wein 2006) and comprehensive data about these pools is lacking. The C dynamics of understorey vegetation is largely influenced by climate, soil type, stand age and compositions (Nalder & Wein 1999; Hart & Chen 2006). Fredeen et al. (2005) found that small tree biomass C was higher in stands growing on coarse textured soils compared to fine textured soils and that herb and shrub biomass C was higher in younger forests than in matured forests in both soil types (Fredeen et al. 2005). Small trees of natural mixed forests stored less than 3% of total live biomass C (Fleming & Freedman 1998), while in the single species forests the biomass C in moss

and lichen and shrubs was significantly lower in aspen stands compared to pine stands (Nalder & Wein 1999).

Root biomass

Roots can be divided into two classes- coarse and fine roots depending on their size and function (Ouimet et al. 2008). The largest fraction of labile C (C turning over relatively rapidly, < 2 years) in boreal forest ecosystems is in roots and root derived products (Ruess et al. 2003). Some studies have found that broadleaved trees allocate greater fraction of C to root production compared to conifers (Gower et al. 1997).

Coarse roots are an important part of the ecosystem C pool. Jenkins et al. (2003) compiled diameter-based allometric regression equations for estimating tree biomass and reported that roots represent 8 – 37% of aboveground biomass of the tree species found in North America. Fine roots, often classified as roots < 5 mm in diameter (Vogt et al. 1996a), are roots responsible for nutrient and water uptake (Ruess et al. 2003).

Litton et al. (2003) and Mokany et al. (2006) proposed that higher tree density and increasingly coarse soil texture were related to greater C allocation to roots, likely due to competition for nutrients and water. As trees grow bigger in size, they allocate significantly more C to aboveground parts than to roots (Litton et al. 2003; Mokany et al. 2006). Moreover, increasing precipitation resulted in a decrease of root biomass C relative to aboveground C (Gower et al. 1992; Schenk & Jackson 2002). Notably, limitations of nutrients and water were found to influence root biomass C to increase (Chen et al. 2002; Campbell et al. 2004). Plants adjust to nutrient and water limitations

by allocating new biomass to organs that are responsible for obtaining the limiting resources (Marschner 1995; Hermans et al. 2006).

Coarse roots

Coarse roots provide structural support for aboveground components of trees and are highly important for nutrient storage and transport (Steele et al. 1997; Ouimet et al. 2008). Coarse root C accumulation closely follows aboveground C accumulation- it increases with time and slows at stand maturity, peaks and thereafter remains relatively constant or declines slightly (Bray 1963; Cairns et al. 1997; Li et al. 2003; Bond-Lamberty et al. 2004; Peichl & Arain 2006; Ouimet et al. 2008). Coarse roots have small net primary productivity (NPP) compared to fine roots. In the boreal forest coarse root NPP may be only 6% of total ecosystem NPP (Li et al. 2003) whereas their biomass is often more than 18% of total ecosystem biomass (Vogt et al. 1996).

Mostly due to the difficulties of sampling, knowledge of root C accumulation and distribution is limited and root C dynamics data are scarce compared to aboveground C pool data. Due to the strong relationship between tree aboveground and belowground components, root C mass is mostly estimated using root : shoot ratios (Mokany et al. 2006). A review by Cairns et al. (1997) found that aboveground biomass explains 83% of variation in root biomass. It is also possible to estimate root biomass from breast height diameter (dbh) or shoot biomass of a tree using allometric equations (Kurz et al. 1996; Vogt et al. 1996; Cairns et al. 1997; Vogt et al. 1998) but these methods appear to be less accurate than using root : shoot ratios (Mokany et al. 2006). Root : shoot ratio is dynamic (Bray 1963) and is affected by various biotic and abiotic factors that vary spatially and temporally (Ryan et al. 1997; Gower et al. 2001).

Fine roots

Carbon dynamics in fine roots is the least understood aspect of plant C dynamics. The C dynamics in fine roots differ from that of other tree components, with the exception of foliage (Cannell & Dewar 1994; Litton et al. 2003). The majority of fine roots in the boreal forests are found above the mineral soil in the LFH layers (Steele et al. 1997). Fine roots contribute mainly to SOC due to root hair senescence (Bloomfield et al. 1996). Fine roots remain in constant flux; dying, replacing, and decomposing continuously throughout the growing season (Bloomfield et al. 1996; Trumbore & Gaudinski 2003). Different studies have reported different fine root accumulation patterns in boreal forest stands. The majority of the literature suggests that fine root biomass increases rapidly after stand initiation and slows at canopy closure or stand maturity (Bond-Lamberty et al. 2004; Claus & George 2005; Yanai et al. 2006; Peichl & Arain 2006). Whether fine root biomass decreases or stabilizes thereafter is largely unknown. A study by Campbell et al. (2004) suggested that fine root biomass reaches maximum early in stand development (much earlier than maximum foliage mass) and then remains stable throughout the stand growth.

It has been found that coniferous forests allocate greater proportion of biomass to fine root production than deciduous forests, especially in boreal forests where low soil fertility and soil temperature limit tree growth (Ruess et al. 1996; Gower et al. 1997; Steele et al. 1997). Lower nutrient availability in conifer stands makes trees allocate more resources belowground to better access nutrients (Ruess et al. 1996; Hermans et al. 2006). This is also supported by Chen et al. (2002) who reported that on

more productive sites, trees allocated more C to woody components, whereas more C is allocated to fine roots and foliage on less productive sites.

The share of fine root biomass of overall live biomass is small (often <3%) but fine roots are biologically very active and their share of total forest NPP is large (Vogt et al. 1996; Cairns et al. 1997). Jackson et al. (1997) found that as much as 33% of global ANPP is used for fine root production. Similarly, Li et al. (2003) showed that fine root NPP in the boreal forest of Canadian Prairie Provinces is 40% of total ecosystem NPP. Ruess et al. (2003) found that annual fine root production in interior Alaska constitutes as much as 56% of total stand production. However, Strand et al. (2008) reported that fine root biomass turnover is systematically overestimated as short term minirhizotron studies underestimate the residence time of fine root biomass. Therefore, fine roots might not comprise such a large share from overall NPP.

Accurate estimation of total fine root biomass is complicated as large proportion of fine roots are very fine with diameters smaller than 0.35 mm, and adequate sampling of these very fine roots is difficult (Ruess et al. 2003; Ruess et al. 2006). Therefore, many previous studies on fine roots might have underestimated total fine root biomass. For example, Ruess et al. (2003) carefully re-estimated fine root biomass in area earlier sampled and found fine root biomass to be five times greater than previously reported.

DEAD BIOMASS C DYNAMICS

Dead biomass is comprised of leaf litter, dead wood and dead roots. The C dynamics in dead biomass is directly related to its decomposition process.

Decomposition rate of dead biomass is strongly influenced by its chemical and

physical characteristics that vary greatly with plant species and are influenced by several other factors, such as temperature, moisture and aeration (Harmon et al. 1986; Laiho & Prescott 2004) proximity to ground and position of the dead material (Vogt et al. 1996b). The wood decomposition tends to decrease with decreasing mean annual temperature (Yatskov et al. 2003) and elevation (Brown et al. 1998). Decomposition of dead biomass is greater in moist and warm sites compared to dry and cold sites and vertically standing deadwood (snag) decompose slower than fallen poles. Generally broad-leaved species decomposes faster than conifer species. Boreal forests have low mean annual temperature and short growing seasons. Therefore, heterotrophic activity is reduced, causing reduced rate of C and nutrient cycling from dead biomass (Trofymow et al. 2002). The total C pool in the forest system is influenced by the presence of dead wood and its decomposition rates. More importantly they determine the fuel load for the forest fires- the higher the mass of dead biomass, the more likelihood of a more intense fire.

Dead wood

Coarse woody debris (CWD) includes sound and rotting logs, snags, and stumps generally greater than 10 cm in diameter (Harmon & Sexton 1996). The role of CWD in C cycling is well recognized due to the appreciation of the values of CWD as a long lasting C stock (Krankina & Harmon 1995; Harden et al. 2000; Krankina et al. 2002; Yatskov et al. 2003; Wang et al. 2003; Manies et al. 2005). Due to its low surface area and high lignin content, CWD plays an important role in the long term C storage (Harmon et al. 1986), especially in the boreal forest (Manies et al. 2005).

Accumulation of C in CWD in the boreal forest is significantly affected by TSD and can follow several different pathways that are largely influenced by stand species composition (Hély et al. 2000; Arseneault 2001): a continuous increase with age (Hély et al. 2000), an inverse U-shaped curve (Brown & See 1981) or a U- or S-shaped curve (Sturtevant et al. 1997; Clark et al. 1998; Pedlar et al. 2002; Brais et al. 2005; Martin et al. 2005). The most common of these in the boreal forest is the U-shaped CWD accumulation curve (Figure 4). The biomass of the dead wood will be significantly higher in the sites disturbed by fire than in the sites disturbed by harvesting. During the early stages of forest development in post-fire stands, the pre-disturbance debris, disturbance generated debris, and residual standing trees influence the CWD structure and C pool size and CWD mass is high (Lee et al. 1997). Over time the residual mass of CWD declines logarithmically determined by decomposition. There will be little new input of CWD from young stands, but additional dead woody materials from regenerating stands begin to accumulate and CWD levels rise again in somewhat older stands (Figure 4). This input can begin earlier in the harvested sites than fire-disturbed sites. As mortality increases due to self thinning during stem exclusion, the CWD mass continues to increase exponentially. This type of U- or S-shaped pattern has been observed in single-species stands (Sturtevant et al. 1997; Pedlar et al. 2002; Brais et al. 2005) as well as in younger (11-65 years) logging origin mixedwood stands (Martin et al. 2005). However, Hély et al. (2000) found that in fire origin boreal mixedwoods, the CWD did not follow a traditional 'U-shaped' pattern probably due to the lack of initial decrease of residual pre-disturbance debris. Inverse U-shaped curve can occur when tree mortality is particularly high due to high tree

density, windthrow, insects, or disease during the mid-age of stand (Harmon et al. 1986; Feller 2003).

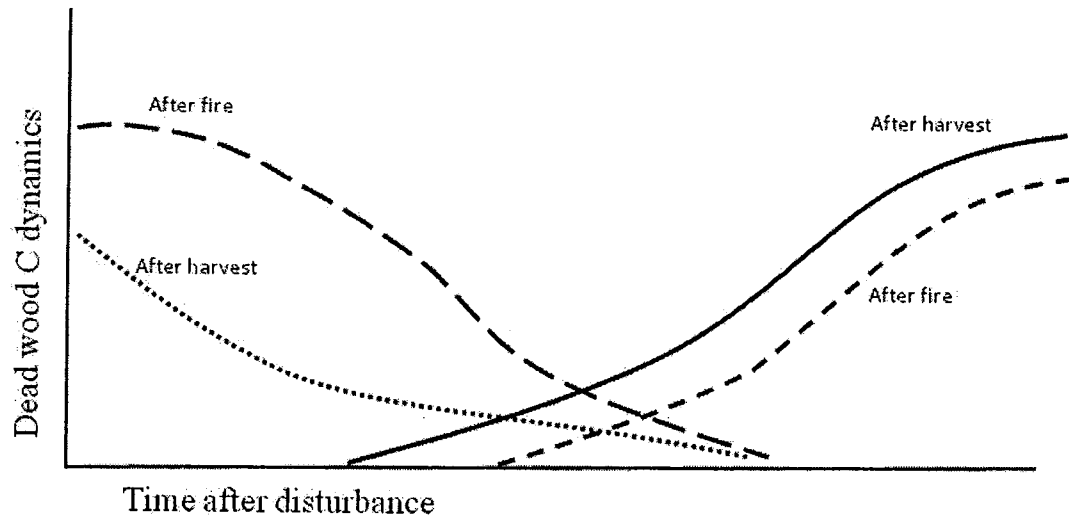


Figure 4. Conceptual figure showing dead wood C dynamics after forest fire (broken line), forest harvesting (dotted line) and after self-thinning in clearcut harvested sites (solid line) and in burnt sites (square dotted line).

The CWD dynamics after maturity in old growth forest is poorly understood. Studies in temperate Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests showed that CWD levels can rise up to age of 500 years and then decline (Spies et al. 1988). This decline resulted from a stand species composition change to faster decaying species like Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Pacific silver fir (*Abies amabilis* Douglas ex Forbes). Steady state of CWD would probably not occur until 1200 – 1500 yrs after stand establishment (Spies et al. 1988). Due to high disturbance frequency in the boreal forest, CWD would not reach a steady state and will always fluctuate due to disturbances and succession.

Although volume dynamics of CWD are now well generalized (Brassard & Chen 2006), mass and C dynamics of CWD still need further investigation to

generalize since CWD wood densities differ with stand development, CWD size, species composition, and decay status (Laiho & Prescott 2004). Changes in decay class roughly representing density are related to changes in C and N concentration, (Creed et al. 2004b). During decomposition, biomass and C in CWD are lost by leaching and decomposition (Harmon & Sexton 1996; Krankina et al. 1999; Creed et al. 2004a). Increasing decay leads to considerable decline in wood density and there is a small increase in C (also in N and P) concentration probably due to the loss of carbohydrate and relative increase in lignin, alkyl, and carbonyl C (Preston et al. 1998; Sandstrom et al. 2007). The structural integrity of the CWD is retained as some of the more recalcitrant portions remain undecomposed, resulting in a reduction of total wood density and C density (Harmon et al. 1986).

Dead wood studies are often focused on CWD and visible dead material. Due to sampling difficulties, fine – sized debris, buried material, and dead roots (both fine and coarse) are often not studied, hindering full characterization of CWD and its contribution to C cycling (Manies et al. 2005). Partially and completely buried wood can compose up to 26% of the total woody debris in older stands and small size debris (<5 cm) can comprise up to 43% of the total dead wood biomass (Hély et al. 2000; Manies et al. 2005).

Dead roots

Coarse roots

Coarse roots are as old as the tree and do not have consistent growth and senescence pattern compared to fine roots. Very little information is available on the senescence rate of coarse roots. Vogt et al.(1985) suggested that the turnover of woody

roots might be related to the amount of carbohydrate reserve. When there is insufficient carbohydrate to maintain the root function, woody coarse root will die in the process analogous to mortality of lower branches of trees.

Fine roots

In contrast to coarse root, fine root senescence is widely studied to determine their role in nutrient and C cycling in local, regional and global scales (Vogt et al. 1985; Ruess et al. 1996; Jackson et al. 1997; Tufekcioglu et al. 1998; Ruess et al. 2003; Ruess et al. 2006). Some models assume that the life span of fine roots is predetermined when it is formed. This is based on a finite supply of C as carbohydrate which will cause the root to die when the carbohydrate has been depleted (Marshall & Waring 1985). Some data from field studies do not support this assumption particularly in those sites which do not have regular fine root senescence but have an association of mycorrhiza (Vogt et al. 1991).

Many biotic and abiotic factors cause senescence of fine roots including soil temperature, moisture, nutrients, insects, bacteria and other soil organisms (Bloomfield et al. 1996; Vogt et al. 1998). Considerable variation exists in the longevity of fine roots of different plant species (0.02 -8 years); fine roots of deciduous tree species have shorter life span than fine roots of evergreen species (Bloomfield et al. 1996). The residence time of C in soil from the fine root is normally longer than shoot derived C due to physico-chemical protection, physical protection through mycorrhiza, and chemical interactions with metal ions (Rasse et al. 2005).

FOREST FLOOR C DYNAMICS

Many boreal forests have thick organic LFH layers above the mineral soil which is often referred to as forest floor (FF) or organic soil layer. As mentioned above, the FF is comprised of foliage, root, fine woody litter, partially decomposed organic matter and may also contain substantial amounts of mineral particles that are mixed in from below by animals or other agents (Yanai et al. 2003). Limited decomposition rate of organic matter in the boreal region results in an accumulation of organic layers above the mineral soil (Harden et al. 1997). The FF is a major nutrient pool and is the most biologically active portion of the boreal forest soil (Krause 1998). Compared to mineral soil, FF is more sensitive to temperature and soil moisture changes (Khomik et al. 2006) as it is more exposed.

Humus formation takes place in FF, which is made up of the recalcitrant products of decomposition (Prescott et al. 2000). Humus formation is thought to involve microbial modification of lignin and condensation of proteins into humus precursors (Prescott et al. 2000). That is followed by the complexation of those precursors into humus (Prescott et al. 2000). Although vegetation is unable to uptake nutrients tied up in complex humus molecules, these nutrients are released and made available after a fire (Lecomte et al. 2006). Incorporation of humus in soil binds C for thousands of years (Dec & Bollag 1997).

Large portions of surface organic material of FF is consumed during a wildfire (Neff et al. 2005). The proportion of FF consumed by forest fire varies greatly (15 - 100%) depending on fire intensity (DeBano et al. 1998; Kasischke & Bruhwiler 2002; Neff et al. 2005). Stand replacing fires are often high intensity fires that consume most of the FF (Yanai et al. 2003; Certini 2005). After fire, with regeneration, the FF starts

to accumulate and increases throughout the life of a stand (Rapalee et al. 1998; Nalder & Wein 1999)(Figure 5). However in the harvested site, the biomass C in FF can slightly increase with decomposition of debris in first few years after harvest but will begin decline until it gets input from established new stands (Figure 5).

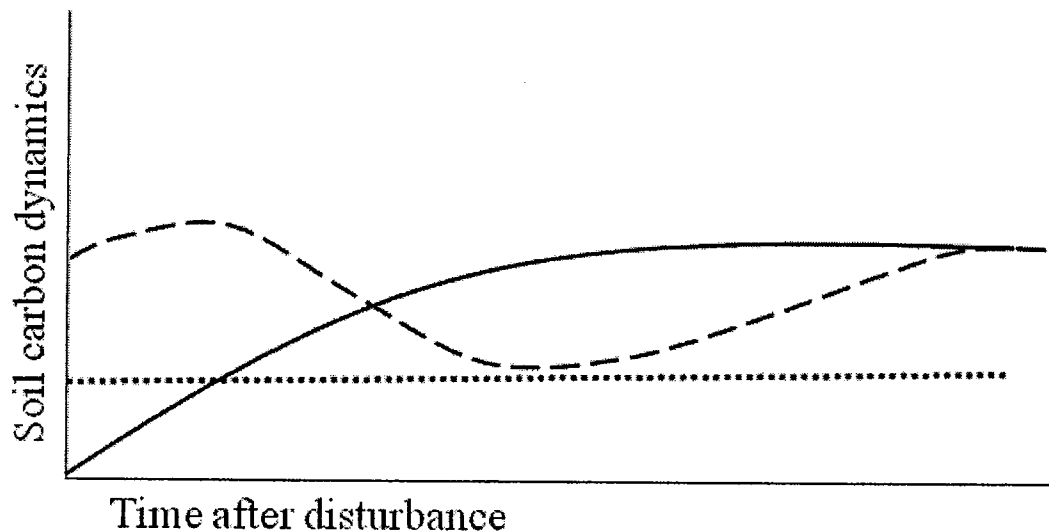


Figure 5. Conceptual figure showing carbon dynamics in organic soil layer (FF) after fire (solid line) and after harvesting (broken line) and in mineral soil (dotted line).

Nalder and Wein (1999) found that there is a positive and highly significant relationship between C in FF and stand age. Synthesis of all available published C data by Pregitzer & Euskirchen (2004) reported that in the boreal forest C in FF accumulates until ca. 70 years of stand development and remains relatively constant or increases slowly with age. Fire cycles are relatively short in central and western Canada (Johnson 1992) and stands do not reach very old age. Therefore, nutrients bound in FF are regularly released by fire and become available for plants. Conversely, as a result of an extended absence of fire (>300 years), in eastern Canada (Bergeron et al. 2004), FF often becomes thicker and denser and accumulates C for many centuries

(>700 years) after fire (Lecomte et al. 2006). Prolonged absence of fire regulates biomass partitioning between live biomass and FF. In stands younger than 200 years, 60% of the biomass is stored in live biomass, but in older stands (>200 years) most of the biomass (80%) will be in FF (Xing et al. 2005).

The C accumulation in FF is strongly influenced by stand species composition, its productivity and regional climate (Nalder & Wein 1999). For example, the C in FF was significantly higher in aspen stands compared to pine stands in western boreal forest (Nalder & Wein 1999). But whether broadleaf stands store generally more or less C in FF than conifers is unknown. It is proposed that biomass of FF is lower in broadleaf stands due to highly decomposable litters. However, it is not always true as Thomas & Prescott (2000) reported smaller while Binkley et al., (1992) reported greater FF biomass under broadleaf species compared to conifers, although these differences might be due to differences in species composition and stand age. Also, drainage class affects FF biomass and C stock, poorly drained soils have higher C stocks in FF compared to FF in well drained soils (Rapalee et al. 1998).

SOIL CARBON

Soil organic carbon

Because of its large size, any levels of changes in soil C pools are important for total forest C storage (Medlyn et al. 2005). Even a small change in soil C pool could have considerable impacts on atmospheric CO₂ concentration and other greenhouse gases and therefore, also on climate (Hossain et al. 2007). Due to slow decomposition rate in boreal region it has been reported that there will be almost constant level of carbon in mineral soil compared to LFH layer (Figure 5).

Soil C pool size is regulated by the balance between C inputs from litterfall and rhizodeposition on one hand and C released from decomposition on other hand (Jandl et al. 2007). Soil pool Carbon is also a function of bulk density, thickness of the soil layer and coarse fragment content. Fine roots contribute substantially more to soil C and nutrient pools than aboveground litter (Ruess et al. 1996) and C accumulation in boreal forest soils can be explained by difference between fine root NPP and fine root turnover (Steele et al. 1997). Even in low nutrient, permafrost-dominated, late successional ecosystems, C and presumably other nutrients are cycling through fine roots at rate of several orders of magnitude faster than through aboveground tissue (Ruess et al. 2003). Therefore, factors influencing stand species composition and growth also affect soil C storage. Total amount of soil organic C (SOC) stock is also influenced by time since disturbance, disturbance intensity, climate (temperature and precipitation), soil texture and topography (Johnson & Curtis 2001; Bhatti et al. 2002).

Forest fires can affect physical, chemical, mineralogical and biological properties of mineral soil and the effects are dependent on peak temperatures and duration of fire, i.e. burn severity (Certini 2005). Approximately 10 – 15% of heat is transferred downward into the mineral soil during wildfire (Raison et al. 1986). Therefore, a direct effect of fire on SOC pool is largely dependent on fire intensity (DeBano et al. 1998). However, Neff et al. (2005) reported that the immediate fire impacts are mostly limited to surface dead moss and fibric horizons, with no change in the mineral soil.

Although fire affects forest soil in various ways, there is no clear understanding of how it influences SOC. Results from different studies are variable. Johnson and

Curtis (2001) reviewed 13 studies reporting soil C after fire and used meta analysis to determine overall effects of fire on soil C. They find no significant overall effect of fire on C in the A horizon nor total on soil C (TOC). However, the C pool increased significantly after 10 years. Also, they found that, although counterintuitive, prescribed fire decreased and wildfire increased soil C. They attributed the soil C increase after forest fire to sequestration of charcoal and recalcitrant, hydrophobic organic matter. Certini (2005) reported that despite common perceptions, most forest soil properties like amount of organic N, available P and SOM can be recovered and even enhanced if plants promptly recolonize the area after fire. Contrary to Johnson and Curtis (2001) a comprehensive synthesis of the literature by Pregitzer and Euskirchen (2004) reported that although soil C pool of the boreal forest is highly variable, an overall trend of increasing C pool size with increasing time since fire can be observed.

Commonly mineral soil C studies sample soil to a one meter depth. Few studies have also quantified C in deeper soil layers (Huang & Schoenau 1996) although quantifying deep horizons C might be largely irrelevant in C cycling calculations (Houghton 1995). Huang and Schoenau (1996) calculated that the soils below 1m (1 – 3.2 m) in BOREAS Saskatchewan sites had an average of 60,6 Mg ha⁻¹ organic C. Jobbagy & Jackson (2000) studied SOC down to 3m depth using different databases and found that boreal forests (648 samples) soils had 125, 93, 24 and 8 Mg C ha⁻¹ in soil depths of 0 – 3, 0 – 1, 1 – 2 and 2 – 3m, respectively. They found that SOC content increased with precipitation and soil clay content and decreased with temperature. Plant types and plant functional groups (forests, shrubs, grasses), through differences in

C allocation, controlled SOC distribution with depth in the soil (Jobbagy & Jackson 2000).

Soil inorganic carbon

Soil inorganic C (SIC) is often not considered in detail in C studies, although it is a large C pool and potential source of CO₂ emissions (Adams & Post 1999; Lettens et al. 2004). The SIC (pedogenic Calcium carbonate, CaCO₃) often occurs in layers or nodules (calcrete- made up mostly of CaCO₃) in petrocalcic and calcic soil horizons, which develop extensively in arid and semi-arid ecosystems (Kern & Schlesinger 1992; Adams & Post 1999). Deeper soil horizons often contain more SIC than horizons closer to the surface (Lettens et al. 2004), which is related to downward migration of calcium carbonate (CaCO₃) and might be influenced by soil management or acidification caused by increased N and S inputs (Batjes & Sombroek 1997). Kern and Schlesinger (1992) suggest that since the last ice age the SIC and SOC pools have moved in opposite directions, resulting in an offset of global C storage.

Information about boreal forests SIC is very limited. Landi et al. (2003) show that prairie and forest soils in Saskatchewan have sequestered 1.4 times more C in the form of pedogenic carbonates than as SOM. They found on average 110.3 to 164.5 kg m⁻² of pedogenic carbonates in 120 cm deep soil profile. A study from aspen stands of Saskatchewan showed that the average SIC mass in mineral soil was 64% of the total mineral soil C while its share in FF of the boreal forest was very small (0.4%- 1.4% of total FF C) compared to the mineral soil (Huang & Schoenau 1996; Nalder & Wein 1999).

IMPLICATIONS OF FOREST MANAGEMENT IN CARBON DYNAMICS

Effect of forest fire and clear cut harvesting in C dynamics

Harvesting, has contributed only a small fraction of the total area of disturbance in the boreal forest in the past century (Kurz & Apps 1996). There are only few studies conducted in the boreal North American forest directly comparing the effects of fire and logging on C dynamics of live vegetation, CWD (Pedlar et al. 2002) and soil (e.g. Smith et al. 2000; Simard et al. 2001; Leduc & Rothstein 2007). Some studies compared C dynamics of older natural forests formed after fire with younger managed forest regenerated after logging (e.g. Fleming & Freedman 1998; Howard et al. 2004; Fredeen et al. 2005; Martin et al. 2005)

Fire consumes litter, small live branches, foliage, and organic soil horizons. During a fire, an immediate transfer by combustion of a portion of ecosystem C to the atmosphere takes place (Harden et al. 2000). However, the fire consumes only about 8% of dead wood at the time of fire and another 8% is converted to charcoal (Tinker & Knight 2001). The charcoal is the stable form of C that can last in forest soils for thousands of years (DeLuca & Aplet 2008). Annual C emissions during wildfires are equivalent to ca. 18% of the C emissions from the Canadian energy sector (Amiro et al. 2001).

Harvesting transfers live biomass out of the forest and into forest products, and may mechanically disturb the forest floor and may also mix forest floor with mineral soil. Harvested biomass is turned into wood and paper products and will be in use, recycled, burned (usually for energy), or placed in landfills. Only a small fraction of C from landfills will eventually be released back to the atmosphere and landfills can serve as significant C stocks (Micales & Skog 1997). Emissions from harvest,

transportation of wood to processing plants, mill emissions, and transport of the products to distributors and consumers need to be evaluated to determine net C budgets for harvested stands (Gower 2003). Wood products store large amounts of C and increased use of wood can help to sequester additional C from atmosphere, especially if wood is used for products with long life span (IPCC 2007). Eriksson et al. (2007) found that management practices like fertilization, harvesting of slash and stumps, and wood usage as construction material could greatly reduce net C emissions from forest harvesting.

The absence of CWD is one of the most obvious differences between wildfire and clearcut origin stands (Harmon et al. 1990; Sippola et al. 1998; Fridman & Walheim 2000; Siitonen et al. 2000). A study by Pedlar et al. (2002) after fire and clear-cutting in boreal Canadian mixedwood forests reported that clearcuts and burns were different with respect to the amount, size, and type of CWD. Recent burns consisted mostly of standing dead wood of various sizes, while recent clearcuts consisted of logs and stumps relatively small in size (Pedlar et al. 2002). They also found that the amount and type of CWD in both clearcut and fire origin stands was highly dependent on time since disturbance.

Although stand replacing fires typically kill live trees, they only consume a fraction of the biomass (Kashian et al. 2006). Fires mostly consume litter and FF (Simard et al. 2001). After an immediate large pulse of C released to the atmosphere during the fire, C is later lost through decomposition of dead vegetation (Kasischke et al. 1995). The speed of decomposition of standing dead trees is slow until the trees fall and makes contact with the soil. At this stage, its moisture content will increase and

wood will become colonized by heterotrophs (Harmon et al. 1986; Wang et al. 2002). Dead vegetation decomposition causes even greater C release than fire itself (Kashian et al. 2006). As much as three times more CO₂ can be released to the atmosphere via decomposition of dead roots and boles for the several decades following fire than during fire (Auclair & Carter 1993). In contrast to stands that have burned, after clear-cutting most tree stems have been removed for processing into forest products and only decomposition of the material left on site will contribute to CO₂ emissions.

Various results with respect to C pools sizes between logging and wildfire on different ecosystems have been reported. Pumpanen et al. (2004) found that the SOC pool may increase in the long run as a result of intensive forest management. Leduc and Rothstein (2007) compared soil C and N dynamics after wildfire and clear cutting in Michigan jack pine stands and found no difference on total or labile soil C pools. However, significantly lower total and labile soil N pool and nitrification was present after wildfire, with potentially important consequences on plant nutrition and risk of leaching. A study from Quebec's boreal forest by Simard et al. (2001) showed that clear-cutting and wildfire could have different effects on soil nutrient status, but no conclusion about the effects on long-term productivity were made.

A meta analysis by Johnson & Curtis (2001) showed that both fire and harvesting had little or no effect on soil C and N. Significant effects were related to harvest type, with saw log harvesting causing an 18% increase and whole-tree harvesting causing a 6% decrease on soil C and N pools (Johnson & Curtis 2001). For unknown reasons the positive effect of saw log harvesting seemed to be restricted to conifer stands.

A review of forest management effects on mineral soil C by Jandl et al. (2007) clearly showed that forest management directly influenced C flux in the soil, with the overall effect of harvesting on soil C dependent on the degree of soil disturbance during harvesting, thinning or the degree of stability against disintegration of the stand structure. Smith et al. (2000) found that fire and reduced-impact harvesting affected soil processes of upland black spruce stands in similar ways. Despite long-term differences in stand stocking and fine root biomass, soil C, N, and P stocks and dynamics recovered to similar levels several decades after disturbance. Smith et al. (2000) highlighted the need for future studies in stands that have experienced more than one biomass removal to determine if C and nutrient stocks return to similar levels after repeated harvesting.

Several studies have evaluated the effects of converting old-growth forest to plantations and generally found that such conversion resulted in a loss of C. Fleming and Freedman (1998) found that converting mature old-growth forests to plantations will result in a substantial reduction of C storage in some biomass compartments. Martin et al. (2005) studied young harvest-origin mixedwood stands and older fire-origin stands. They found that tree C pool was greatest in the older stands and dead wood C was greatest in young stands. Fredeen et al. (2005) studied old-growth and young second-growth sub-boreal forests over much of the central interior plateau system of British Columbia. They found that large-tree and total aboveground biomass C was significantly higher in old-growth than in young second-growth stands. Both aboveground live tree C and woody debris C were significantly reduced following conversion of old-growth forests to young plantations. Harvesting of those old-growth

forests lowered total C stocks by 41 - 54%, but had no effect on soil C (Fredeen et al. 2005; Martin et al. 2005).

Howard et al. (2004) studied C pools of young (0 – ca. 29 years) harvested jack pine stands and older (ca. 79 years) wildfire origin stands and reported that harvested forest had a significant annual net source of C for two years following harvest. These results were not specific to conversion of old-growth forest to plantations, as ecosystem C balance was generally negative after wildfire and harvest (Wirth et al. 2002). In harvested sites, disturbance generated material decomposed faster than new vegetation could accumulate C in young stands up to 40 years; thereafter growth usually exceeded decomposition and ecosystems accumulated C (Wirth et al. 2002).

Land use changes and C dynamics

Another important change in ecosystem C pools occurs during land use change, mainly from conversion of forest land to agriculture. Immediate effect of land use change is biomass harvesting but it more importantly influences forest soil properties, especially soil C pool (Walker & Steffen 1999; Muller et al. 2007). Land use change is critically important in the boreal region where losses of soil C may be greater than in other biomes due to its large size and very large soil C stores (Grünzweig et al. 2004). Possibly due to increased temperature at high latitudes, there has been an intensification of agricultural, forestry and mining activities in Canada's mid-north and even arctic areas, which has resulted in increased population in these areas (McCarthy et al. 2001). Grünzweig et al. (2004) reported that this has been leading to additional forest land conversion to agricultural land and that further rise in temperature increases the potential of additional land use change.

Shifts from forest to arable agriculture generally decrease soil C (Ellert & Gregorich 1996; Carter et al. 1998). Carter et al. (1998) compared cultivated and forest soils in Prince Edward Island and Quebec. They found that cultivation decreased the SOC mass in Podzolic soils by 35% but increased SOC mass in Brunisolic and Gleysolic soils by 25%. Ellert and Gregorich (1996) found that surface layers of cultivated soils of southern Ontario have 34% less C than adjacent forest soils surface layers. Another study from central and eastern Canada shows much larger (60 – 70%) C losses due to cultivation (Dumanski et al. 1986). Further studies are needed to specify the effects of land use change to soil C pool.

Effect of climate change on C pool dynamics and sequestration and future implications

Climate plays an important role in vegetation succession pathways (Chen & Popadiouk 2002), stand dynamics and fire regimes (Brassard & Chen 2006) that influence directly ecosystem C dynamics. Human induced climate change has a large influence on forest C balance (Hyvönen et al. 2007; Millard et al. 2007). There has been a temporal increase in fire cycle in Northern American boreal forest since the little ice age along with a continuous temperature increase. A study based on General Circulation Models (GCMs) by Stock et al (1998) predicted that there will be earlier starts of fire seasons and significant increases in fire danger areas in Russia and Canada. There will likely be an increase in fire frequency with future climate change but Bond-Lamberty et al. (2007) concluded that the direct ecophysiological changes resulting from global climate change have not yet been experienced in the boreal region. The variations in C balance and vegetation dominance are so far largely a result

of increased fire frequency, but the mean C balance in landscape level has yet to be affected.

Shift or vegetation habitat expansion with warmer climate could cause the northward migration of the boreal forest species, which would in turn result in further warming (Plochl & Cramer 1995). While boreal species may move northward, it is likely that southern tree species will also move northward into the current boreal range causing a decrease in abundance of northern temperate deciduous and boreal tree species, and an increase southern temperate species (He et al. 2002). However, a greater proportion of the landscape being occupied by early successional species could be the consequence of global warming (Overpeck et al. 1990). The boreal species will be benefitted by CO₂ fertilization effects and ANPP will be increased resulting higher accumulation of biomass C (Hyvonen et al. 2007). On the other hand thawing of permafrost and the resulting microbial decomposition of previously frozen organic C is one of the most significant potential feedbacks from terrestrial ecosystems to the atmosphere in a changing climate (Schuur et al. 2008).

CONCLUSIONS

Conclusions are provided in the end of the thesis in chapter four.

CHAPTER THREE CARBON DYNAMICS OF ABOVEGROUND LIVE VEGETATION OF BOREAL MIXEDWOODS AFTER WILDFIRE AND CLEARCUTTING

INTRODUCTION

Carbon (C) dynamics of the northern forest are largely driven by disturbances and subsequent stand development (Pregitzer & Euskirchen, 2004; Bond-Lamberty *et al.*, 2007; Magnani *et al.*, 2007; Luysaert *et al.*, 2008). Live vegetation C yield after wildfire in single-species stands is documented as following a sigmoidal pattern (Gower *et al.*, 2001; Wang *et al.*, 2003; Taylor *et al.*, 2007), i.e., vegetation C initially increases rapidly, and after reaching its maximum, remains unchanged. However, few studies have examined C dynamics of boreal mixedwoods, despite that they are the most productive and diverse boreal ecosystems in North America (Chen & Popadiouk, 2002), covering approximately one to two quarters of the boreal forests (Steyaert *et al.*, 1997). A post-fire chronosequence (27 - 230 years since fire) of boreal mixedwoods (Pare & Bergeron, 1995) indicates that long-term biomass accumulation, similar to single species stands, initially increases rapidly with stand age, but declines through succession, attributed to diminishing role of trembling aspen (*Populus tremuloides* Michx.), the most productive species in boreal forest, and spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks at the late stages of stand development.

Along with forest fires that affects several millions ha of the Canada's boreal forest, timber harvesting, mostly mechanical clearcutting, has been an important stand replacing disturbance and continues at approximately 900,000 ha per year (CCFM, 2005). Several studies have compared vegetation C between young post-logged and

older fire-origin boreal mixedwood stands (e.g., Fleming & Freedman, 1998; Lee *et al.*, 2002; Howard *et al.*, 2004; Martin *et al.*, 2005; Fredeen *et al.*, 2005; Taylor *et al.*, 2007), thus confounding the effect of stand ageing with disturbance origins (Chen & Popadiouk, 2002; Pregitzer & Euskirchen, 2004; Brassard & Chen, 2006). The effect of clearcutting on post-disturbance vegetation C accumulation may be different from fire (Pinard & Cropper, 2000; Ruel *et al.*, 2004; Gough *et al.*, 2007).

To adequately compare how natural and anthropogenic disturbances influence vegetation growth, it is necessary to compare stands with similar age, species composition and soil type affected by different disturbances. The objectives of this study were to: (1) quantify the changes in aboveground live vegetation C pools in a postfire chronosequence of boreal mixedwoods and (2) compare aboveground live vegetation C dynamics of mixedwood stands after wildfire and clearcutting. I hypothesize that after reaching maximum biomass during stand development there is a decline in total tree C because of species replacement from more productive pioneer tree species to late-successional species during succession. I also hypothesize that postlogged sites have more live tree aboveground C compared to postfire sites because of presence of advanced regeneration after clearcutting and subsequent silvicultural treatments that foster establishment and growth of trees.

MATERIALS AND METHODS

Study area

The study was conducted in the boreal mixedwood forest region approximately 150 km north of Thunder Bay, Ontario between 49°27' N to 49°38' N and 89°29' W to 89°54' W. The study area belongs to the Lake Nipigon ecoregion and Moist Mid-Boreal

(MBx) ecoclimatic region (Ecological Stratification Working Group, 1996). This ecoregion surrounds Lake Nipigon and extends westward from the north shore of Lake Superior to Lake St. Joseph in northwestern Ontario. The ecoregion is characterized by warm summers and cold, snowy winters. The average annual temperature is 2.5° C and average annual precipitation 712 mm (559 mm rain and 188 mm snow), recorded at the closest meteorological station to study area, Thunder Bay, Ontario (48°22' N, 89°19' W, 199 m elevation) (Environment Canada, 2008). Topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago. The soil type on upland sites is relatively deep glacial till of the Brunisolic order (Soil Classification Working Group, 1996).

Stand replacing crown fire is the main natural stand initiating disturbance in the study area. Average fire return interval of the region is unknown, but is likely between shorter fire cycles of the western boreal forest (75 years) and longer fire cycles of the eastern boreal forest (100 years) (Bergeron, 1991; Weir *et al.*, 2000). The dominant tree species in the study area are jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench)), and balsam fir (*Abies balsamea* (L.) Mill.), occurring in mixed dominance. Detailed information on understory vegetation abundance, diversity and composition can be found in Hart and Chen (2008).

Changes occur in species composition during stand development in boreal forests (Chen & Popadiouk, 2002). Although multiple successional pathways can occur depending on site characteristics, surrounding stands, and minor disturbances, shifts

from shade-intolerant species to mixed coniferous-deciduous or coniferous species in post-fire stands are predominant pathways in the central boreal mixedwood region (Brassard & Chen, 2008; Brassard *et al.*, 2008). In this study, I sampled the stands dominated by trembling aspen and jack pine at early stages to the stands dominated by black spruce, balsam fir, and paper birch at the later stages of stand development (Table 1).

To limit site condition effects on aboveground live biomass accumulation, I deliberately selected mesic sites on flat midslope positions (with no slope exceeding 5%), on well-drained glacial moraines more than 50 cm in thickness, which is the prevailing site type in the region. To ensure that each selected site met our selection criteria, I used topographic characteristics and soil profiles determined from a soil pit dug in the center of the plot for measurements. All stands selected were 1 ha in area and were visually homogeneous in structure and composition.

Data collection

It is difficult to have a well-balanced design to study the effects of disturbances (Turner *et al.*, 1997; Parker & Wiens, 2005). I used post facto and before-after control-impact designs recommended by Parker and Wiens (2005). Every effort was made to intersperse sample stands to minimize the effect of spatial structure (Legendre & Legendre, 1998). The interspersion was achieved by selecting stands of the same stand age and disturbance origin from different road accesses, resulting in several kilometers between the stands of the same age and disturbance origin. A totally spatially interspersed sample was, however, impossible due to fire history and fire size in the study area. For example, there was only one 27 year-old fire of 120,000 ha in size.

Field work took place in summer 2007. To study the effects of time since disturbance (TSD), fire-origin stands were selected to represent all developmental phases of mixedwood succession: stand initiation, stem exclusion, canopy transition, and gap dynamics stage (Chen & Popadiouk, 2002). Determined by the fire history of the area, six TSD classes were selected for the postfire chronosequence with stand age ranging from 1 to 203 years (Table 1, Appendix 1). The postfire sites were naturally regenerated without any subsequent anthropogenic disturbances.

Table 1. Stand characteristics (mean and 1 SEM) of 27 stands sampled in northwestern Ontario.

Origin	TSD (yrs)	n	Stand density (stems/ha) or basal area (m ² /ha)*	Stand composition (%)†						
				<i>Abies balsamea</i>	<i>Betula papyrifera</i>	<i>Picea glauca</i>	<i>Picea mariana</i>	<i>Pinus banksiana</i>	<i>Populus tremuloides</i>	
Fire	1	3	0	0	0	0	0	0	0	0
	9	3	21917 (3619)	3	9	0	2	26	60	
	27	3	7.06 (0.6)	0	1	0	12	61	26	
	92	3	45.30 (6.0)	4	3	4	20	28	40	
	140	3	31.56 (7.5)	29	2	0	35	8	26	
	203	3	31.28 (2.4)	21	42	31	5	0	1	
Logging	1	3	833 (83)	0	0	0	0	27	73	
	9	3	21050 (2344)	0	27	0	10	22	41	
	27	3	27.95 (1.5)	2	22	2	9	36	30	

*Stand density (stems/ha) was determined for 1 and 9 year old stands and stand basal area (m²/ha) for older stands.

†Stand composition was determined based on stand density for 1 and 9 year old stands and on basal area for older stands.

Large scale commercial logging began in early 1970s in the study area. I sampled logging-origin stands aged 1, 9, and 27 years. All postlogged sites were clearcutting-origin, but differed somewhat in the logging method. For the 1- and 27-year-old postlogged sites, trees were felled, topped, and delimbed at the stump before being dragged to roadside. For the 9-year-old postlogged sites, trees were felled and dragged to roadside for processing. After logging, all postlogged sites were artificially regenerated (aerial seeding with jack pine) to achieve desirable species composition. Each stand origin and stand age class was replicated three times, resulting in 27 sampled stands.

Time since last disturbance was determined for each stand sampled. For stands younger than 70 years, time since last stand-replacing disturbance was determined by using detailed fire and harvesting records. For older postfire stands, time since disturbance was previously determined using cores from breast height or disks cut at the base from at least three postfire *P. banksiana* or *P. tremuloides* trees per stand (see Brassard & Chen, 2008). For each selected tree, a core or disk at breast height was taken and brought to the laboratory. In the laboratory, the cores were mounted on constructed core strips and disks were cut transversely and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. If cores were taken from breast-height (1.3 m above the ground), tree ages were corrected to time since fire by adding seven years using the model developed by Vasiliauskas and Chen (2002). For the oldest burned area (i.e., 203-year-old stands), one live jack pine tree and seven jack pine snags were sampled and disks were cut at the

base of stems. The ring count of the live tree was 201 years and that of snags ranged from 140 to 180 years in 2005. I used the live tree age as time since fire for the area.

Within each sampled stand, one 400 m² circular plot was established. The diameter at breast height (DBH; 1.3 m above the root collar) of all overstory trees (DBH \geq 10 cm) were measured in the plot. Heights of at least 3 randomly chosen trees of each species per plot were measured using a TruPulse™ 200 laser range finder. To estimate the heights of remaining trees, a height-diameter curve was developed for each tree species of all sampled stands. For understory trees (DBH <10 cm, but height > 4 m), heights and DBHs were measured in a 100 m² plot located inside the 400 m² plot. Heights and DBHs of saplings and tall shrubs (1.3-4 m in height) were measured in ten 2 by 2 m randomly located subplots inside the 400 m² plot. Stand characteristics are summarized based on tree measurements (Table 1). For stands older than 27 years, stand basal area was summed by to plot level and scaled up to per hectare level. Due to the small size of trees, for 1 and 9 year old stands, tree density (stems/ha) is reported.

Understory vascular plant biomass (trees and shrubs <1.3 m in height and herbaceous plants) was estimated by harvesting ten 1 x 1 m subplots located inside the 400 m² circular plot. Plants were clipped at the base and stored in airtight bags and transported daily to the laboratory for determination of biomass. Samples were oven-dried at 70° C for 48-72 hours to a constant mass and weighed. Bryophyte biomass was estimated by harvesting five 25 x 25 cm subplots located inside 400 m² circular plot.

Aboveground tree biomass was estimated as the sum of stem, branch and foliage biomass for each tree using published allometric equations (i.e., Lambert *et al.*, 2005). The biomass of tree components was converted to C based on the estimation that C

content is 50% of oven dry wood tissue and 45% of foliage tissue (Bisbee *et al.*, 2001; IPCC, 2003). C content of vascular plants and bryophytes was calculated as 45% of dry biomass (Bisbee *et al.*, 2001; IPCC, 2003).

Data analysis

With an exception of sapling and shrub C, data were not normally distributed according to Shapiro-Wilk test and the variance was not homogeneous according to Levene's Statistic. To meet these assumptions, square root transformation (suggested by power estimation provided by spread vs. level plot) was required and applied to data.

The following general linear model was used to test the effect of time since disturbance (T; $i = 1, 2, \dots, 6$) and stand origin (O; $j = 1, 2$).

$$Y_{ijk} = \mu + T_i + O_j + T \times O_{ij} + \varepsilon_{(ijk)} \quad (1)$$

where Y_{ijk} is C content of live trees, saplings and shrubs, understory vascular plants, bryophytes, or total live vegetation. Time since disturbance was treated as a categorical variable. Due to unbalanced study design (i.e. missing cells) type IV sum of squares was used. To estimate the proportion of total variance explained by an effect, I present Eta squared (Eta^2) values in percentages. LSD post hoc test was performed to determine critical difference ($\alpha = 0.05$) among means. Statistical analyses were conducted using SPSS version 11 software (SPSS, 2001).

RESULTS

Live tree C

The C pool of trees differed significantly with TSD and stand origin with a significant interaction between TSD and stand origin, while 84% of the C pool was

accounted by TSD (Table 2, Figure 1). After fire, all trees were dead. The tree C pool increased to 0.8 Mg/ha in 9-year-old stands, 10.3 Mg/ha in 27-year-old stand, 109.2 Mg/ha in the 92 year old stand, and then declined to approximately 70 Mg/ha in both 140- and 203-year-old stands (Figure 1, Appendix 2).

Logging-origin stands had more live tree C than fire-origin stands in 1- and 27-year-old stands, but not in 9-year-old stands (Table 2, Figure 1). Live tree C pool was 8.4 Mg/ha in one-year-old postlogged stands, and 40.5 Mg/ha more in 27-year-old postlogged than postfire stands, while the C pool was approximately 0.8 Mg/ha in 9-year-old stands of both origins.

Table 2. The effects of time since disturbance (TSD) and stand origin on C of trees, saplings and shrubs, understory vascular plants, and bryophytes.

C pool	Source	df	MS	F	P	Eta ² (%)
Trees	TSD	5	57.55	55.45	<0.001	84
	Origin	1	23.35	22.503	<0.001	7
	TSD x Origin	2	6.00	5.78	0.012	4
	Error	18	1.04			
Saplings and shrubs	TSD	5	3.77	7.16	0.001	54
	Origin	1	3.55	6.74	0.018	10
	TSD x Origin	2	1.62	3.08	0.071	9
	Error	18	0.53			
Understory vascular plants	TSD	5	0.0617	11.94	0.001	65
	Origin	1	0.0003	0.038	0.848	0
	TSD x Origin	2	0.0061	0.71	0.505	3
	Error	18	0.0086			
Bryophytes	TSD	5	0.29	2.14	0.108	24
	Origin	1	0.10	0.74	0.403	2
	TSD x Origin	2	0.99	7.21	0.005	33
	Error	18	0.14			
Total live C	TSD	5	50.53	50.37	<0.001	85
	Origin	1	18.94	18.88	<0.001	6
	TSD x Origin	2	4.44	4.43	0.027	3
	Error	18	1.00			

Note: Eta squared (Eta²) values are in percentage.

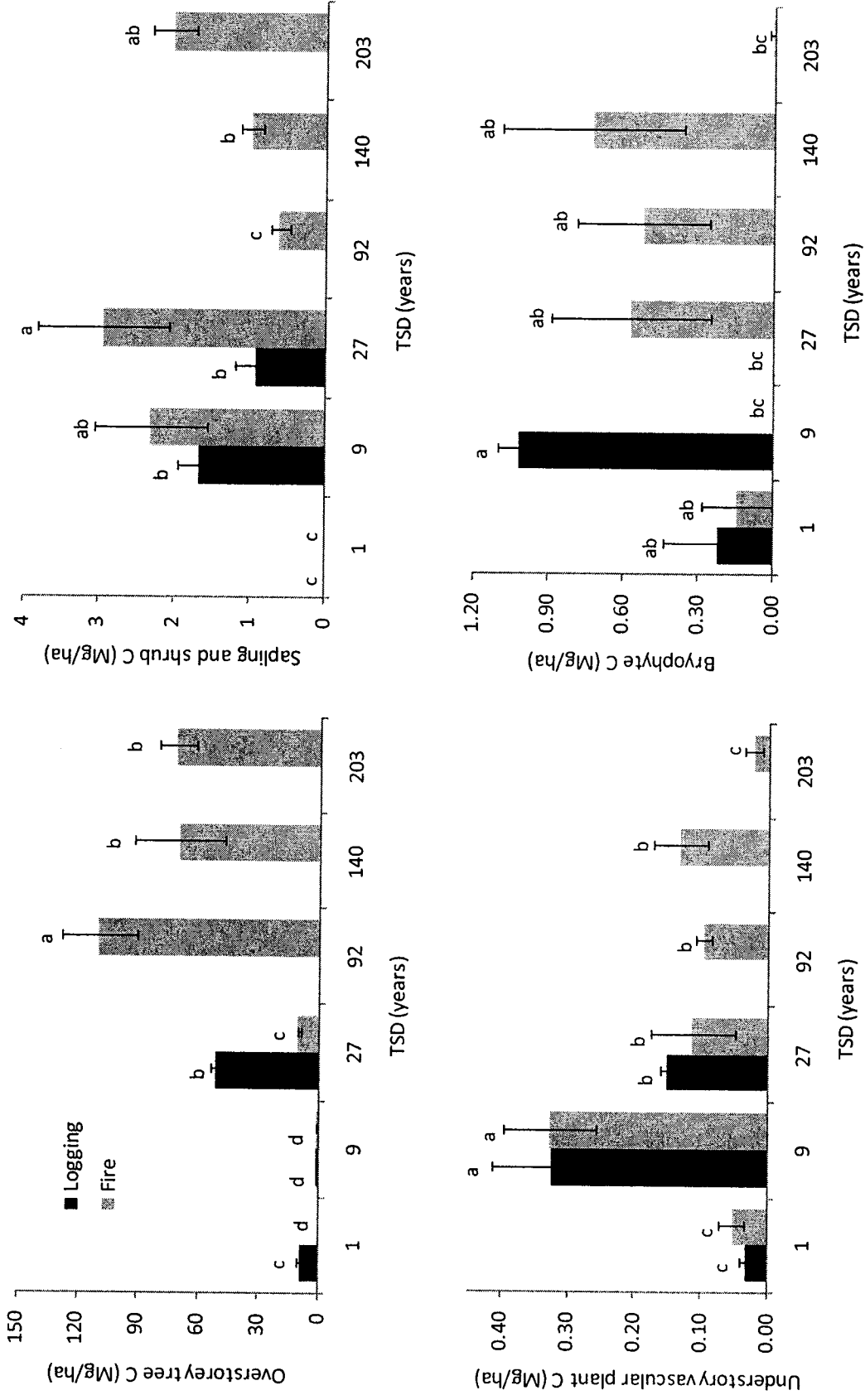


Figure 1. Aboveground live carbon pools in relation to time since disturbance (years) and stand origin (fire and logging): (a) trees (> 4 m in height), (b) saplings and shrubs (1.3-4 m in height), (c) understorey vascular plants (<1.3 m in height), and (d) bryophytes. Error bars represent 1 SEM. Means topped by the same letter are not significantly different ($P < 0.05$).

Sapling and shrub C

The sapling and shrub C pool also differed significantly with TSD and stand origin with TSD explaining 54% of the variation (Table 2). No saplings or shrubs were present one year after either disturbance. In postfire stands, the pool increased to 1.7 Mg/ha in 9-year-old, 3 Mg/ha in 27 year-old, decreased in 92- and 140-year-old stands, and then increased to approximately 2 Mg/ha in 203-year-old stands (Figure 1). In comparison with postfire stands of the same age, the C pool was smaller in 9- and 27-year-old postlogged stands (Figure 1).

The C pool accounted for a small proportion of live vegetation C in all ages except 9-year-old stands (Figure 2). In 9-year-old stands, they constituted 68% and 73% of total live tree C in post-logged and postfire stands, respectively (Figure 2). Their share was 22% in 27 year old postfire sites with 3 Mg/ha, which was the highest among all sites. Their share was < 3% of total live vegetation C in all other cases.

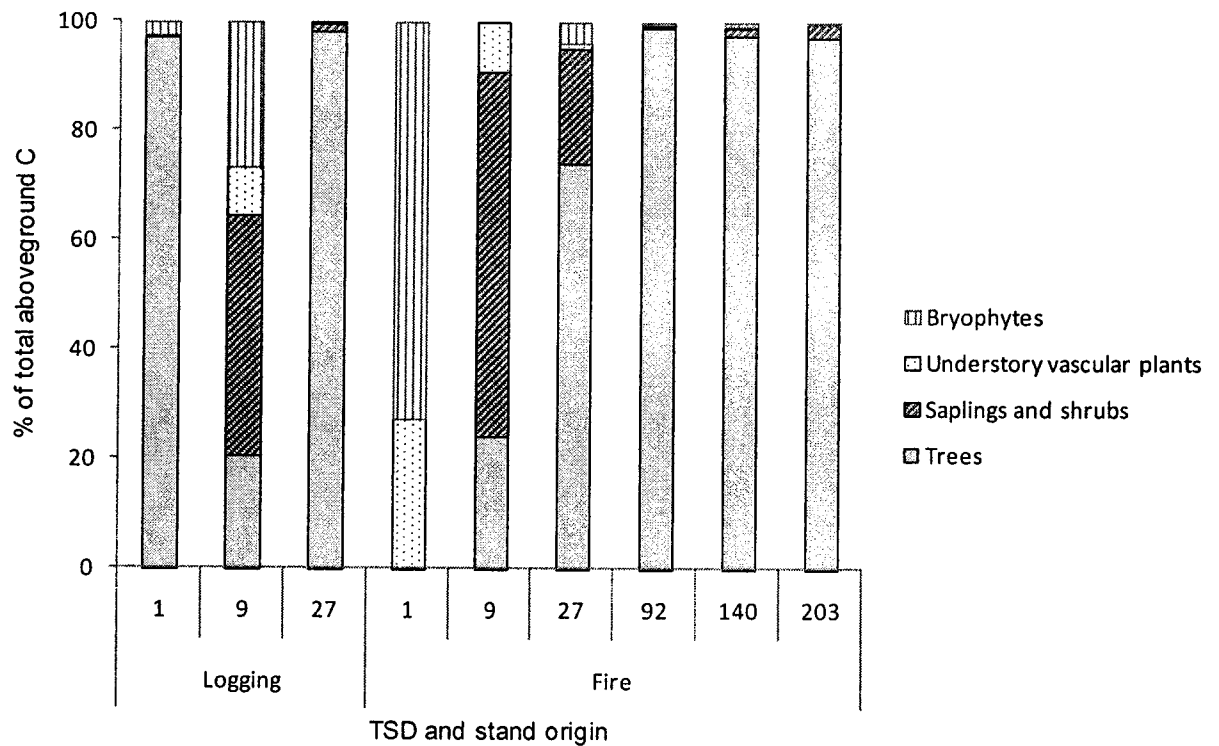


Figure 2. Relative carbon content of trees (> 4 m in height), saplings and shrubs (1.3-4 m in height), understory vascular plants (<1.3 m in height), and bryophytes.

Understory vascular plant C

The C pool of understory vascular plants differed with TSD that explained 65% of the variation, but the pool was not affected by stand origin (Table 2, Figure 1). The C pool peaked 9 years after disturbance at approximately 0.3 Mg/ha, whereas it was the smallest (0.02 Mg/ha) in 203-year-old postfire stands. Understory vascular plants were the only living plants one year after fire (Figure 2). They also constituted a large share of total live C 9 years after logging (12%) and fire (9%), while in other stands, their share of total live C was < 1%.

Bryophyte C

The C pool of bryophytes was also affected by TSD and stand origin (Table 2). In postfire stands, the pool was bigger in intermediate-aged stands, whereas in postlogged stands, the pool was highest in 9-year-old stands (Figure 1). Overall, bryophytes constituted a small proportion of total live vegetation C pool (Figure 2).

Total live biomass C

The C pool of all live vegetation followed a pattern similar to the pool of trees as this pool constituted the largest share of live vegetation C (Figure 2). Both C pools were significantly affected by TSD and stand origin with a significant interaction of TSD and stand origin (Table 2). In postfire stands, total live vegetation C increased 0.2, 3.5, 13.9, to 110.4, and then declined to 71.5 and 72.7 Mg/ha with increasing stand age from 1, 9, 27, 92, 140, to 203 years since fire. In postlogged stands, total live vegetation C was 8.7, 3.8, and 51.8 Mg/ha for 1-, 9-, and 27-year-old stands, respectively.

DISCUSSION

Our results support the hypothesis that long-term live vegetation through stand development after fire initially increases rapidly, reaches the maximum stand C, and then declines. This decline was accompanied by a successional change from productive pioneer tree species to late-successional species (Table 1). The C dynamics seen in this study are similar to the general pattern of biomass accumulation described by Sprugel (1985) and those observed in eastern (Pare & Bergeron, 1995) and central (Brassard & Chen, 2006) boreal mixedwoods.

Although the decline in growth and C accumulation is common in many forest ecosystems (Ryan *et al.*, 1997), the underlying causes are still unclear. Nutrient

limitation and decreased photosynthetic capacity (reviewed in Ryan *et al.*, 1997) are often thought to result in growth and biomass decline. Ryan *et al.* (2004), studied tropical forests, found that neither of those is responsible for the decline, but the decline of aboveground production with stand age is a result of increased allocations of primary production to belowground biomass and foliage respiration.

In northern forest ecosystems, while biomass allocation and nutrient limitations may also be accountable for biomass decline, successional changes in species composition (Bormann & Sidle, 1990) and increased susceptibility to insect and/or wind damage (Pare & Bergeron, 1995) are also likely contributors to the decline. In our stands, trembling aspen abundance declined from 40% in maximum vegetation C stage at 92-year-old stands to 26% in 140-year-old stands and there was only 1% aspen in 203-year-old stands (Figure 3). The decreasing share of trembling aspen is shown to have a significant negative influence on stand biomass (Pare & Bergeron, 1995). The decline in stand biomass reported by Pare and Bergeron (1995) was largely attributed to spruce budworm outbreak. Our stands also experienced some spruce budworm damages, but likely at a lesser extent than those stands Pare and Bergeron (1995) studied since spruce budworm outbreaks tend to be more severe in eastern than central boreal mixedwoods (Chen & Popadiouk, 2002). The understory regeneration during species replacement also affects stand biomass. When young trees rapidly replace dying trees, the decline phase is moderated. In our stands, sapling and shrub biomass increased after total aboveground biomass peaked.

While tree C accounted for majority of total aboveground C in older stands, understory vegetation C was significant in early stages of stand development.

Understory C pool changed with stand development, following a commonly observed pattern (Hart & Chen, 2006). Understory plant C was low one year after disturbance, peaked at 9 year old stands, decreased thereafter and then remained stable (Figure 1). Stand replacing wildfire consumes most of forest floor and vegetation, resulting in low understory C immediately after disturbance. After fire resources and suitable growing spaces become available and plants rapidly colonize the site; at this stage understory C constitutes a large share of overall stand C (Figure 2). When overstory trees grow, light availability in understory decreases, leading to understory C decline accompanied with a shift in understory species composition (De Grandperé *et al.*, 1993).

Understory vascular plant C was not different in logged and burnt stands. The influence of different disturbances on understory vegetation C depends on disturbance intensity. Generally, more forest floor and understory organic matter is removed during fire compared to logging (Rees & Juday, 2002). Presence of residual species can result in higher understory C of postlogged stands compared to postfire stands, especially when postfire stands experienced very intense fires that destroy seedbeds and vegetatively reproducing plants. However, when residual species after logging are not physiologically suited to grow in abundant light conditions, they will die out and understory biomass will decline. Later in stand development understory species growing in post fire sites benefit from nutrients released during wildfire. In postlogged stands nutrients remain in forest floor and are not accessible for plants which could result in lower understory C compared to burnt sites.

Aboveground tree C was different after wildfire and clearcutting (Table 2). Postlogged stands generally had more aboveground live C than postfire stands. The

difference in stands one year after disturbance was attributed to residual live trees left after logging that were not present after wildfire. There was no difference between postfire and postlogged stands nine years after disturbance, but there was significantly more biomass C 27 years after logging than fire. This large difference (38.49 Mg C/ha) could not be explained by presence of advanced regeneration after logging since there was no regeneration one year after disturbance and no difference was found in the sapling and shrub C pool between postfire and postlogged stand nine years after disturbance. The difference in species composition may be accountable for the difference of biomass C between postfire and postlogged stands at 27 years disturbance (Table 1). At this age, the postfire stands had a larger jack pine component but a lesser paper birch (Figure 3). As hardwoods have higher productivity (Gower *et al.*, 1997) and relative wood density, the presence of paper birch in postlogged stands affects their C mass positively. As there are no other data available to validate our findings, future studies are needed to generalize our findings of the stand biomass C differences between postfire and postlogged stands. Although logging is often seen to influence stand C stores negatively (Fleming & Freedman, 1998; Howard *et al.*, 2004; Fredeen *et al.*, 2005), results from this study suggest that logged mixedwood stands growing in similar soil and climatic conditions can have significantly more aboveground biomass C compared to natural stands at the same age.

Lack of suitable stands with desired similarity in factors other than stand composition and stand age has often limited possibilities to study long term dynamics of boreal forest. I was able to sample a wide range of different age natural stands on similar sites. It would enhance our abilities to study stand dynamics if some age classes between

27 and 92 year old stands were available. Also, I was limited with post-logged age classes due to short history of clearcutting in the area. Furthermore, aboveground biomass C, although constituting a large and active share, is only a part of the total stand C pool. To better understand ecosystem C dynamics, all C pools (i.e., root biomass, dead wood, organic soil, mineral soil) should to be studied. Therefore, future studies focusing on different C pools and their dynamics are needed to better understand the overall C dynamics of boreal mixedwoods.

CHAPTER FOUR GENERAL CONCLUSIONS

The Boreal forest is a very large terrestrial C pool and it is crucial to accurately understand its C dynamics as it has large influence on global C balance. Live biomass and FF C pools increase with stand development, former will remain stable or decline in the later stage. Dead wood C pool experiences a decline immediately after disturbance and starts to increase later with stand development. Soil C pool remains stable throughout stand development.

Large scale logging has been carried out in boreal forest only a few decades and its effects on C dynamics are not well known. Future research should focus on comparing the effects of wildfire and harvesting stands. It is especially important to enhance the understanding of possible management effects on C cycling as boreal forest could act as a C sink and mitigate climate change by sequestering C.

Time since disturbance and stand origin significantly affect boreal mixedwood biomass growth. Results from chapter three show that aboveground live biomass C dynamics of boreal mixedwoods are similar to generally observed dynamics of biomass growth in natural forest ecosystems. After fire, stand biomass C increased rapidly, reached a maximum, and then declined.

Understory vegetation biomass followed a common growth pattern. Understory plant biomass increased faster than overstory biomass, constituting a large share of overall biomass in early stand development, subsequently peaked and declined thereafter. There was a significant difference between biomass C after wildfire and clearcutting; postlogged stands generally had more biomass C than postfire stands.

These results improve our understanding about boreal mixedwood C dynamic. However, to fully understand mixedwood C dynamics other C pools also need to be studied.

There are several critical knowledge gaps that need to be filled in order to better understand boreal forest C dynamics. These include better estimates of different C pools: (I) tree belowground components, especially fine roots that are the least understood aspect of plant dynamics, (II) understorey and bryophyte dynamics which comprise a minor C pool but represent large portion of production, (III) coarse woody debris C dynamics as it differs from generally well known volume dynamics, (IV) fine woody debris and partially and completely buried woody debris and (V) forest floor and mineral soil C dynamics. Overall, studies looking at stand C dynamics should include all C pools as it would largely advance our understanding of C allocation throughout stand development.

Lack of suitable stands with desired similarity in factors other than stand composition and stand age has often limited possibilities to study long term dynamics of boreal forest. I was able to sample a wide range of different age natural stands on similar sites. It would enhance our abilities to study stand dynamics if some age classes between 27 and 92 year old stands were available. Also, I was limited with post-logged age classes due to short history of clearcutting in the area. Furthermore, aboveground biomass C, although constituting a large and active share, is only a part of the total stand C pool. To better understand ecosystem C dynamics, all C pools (i.e., root biomass, dead wood, organic soil, mineral soil) should to be studied. Therefore, future studies focusing on different C pools and their dynamics are needed to better understand the overall C dynamics of boreal mixedwoods.

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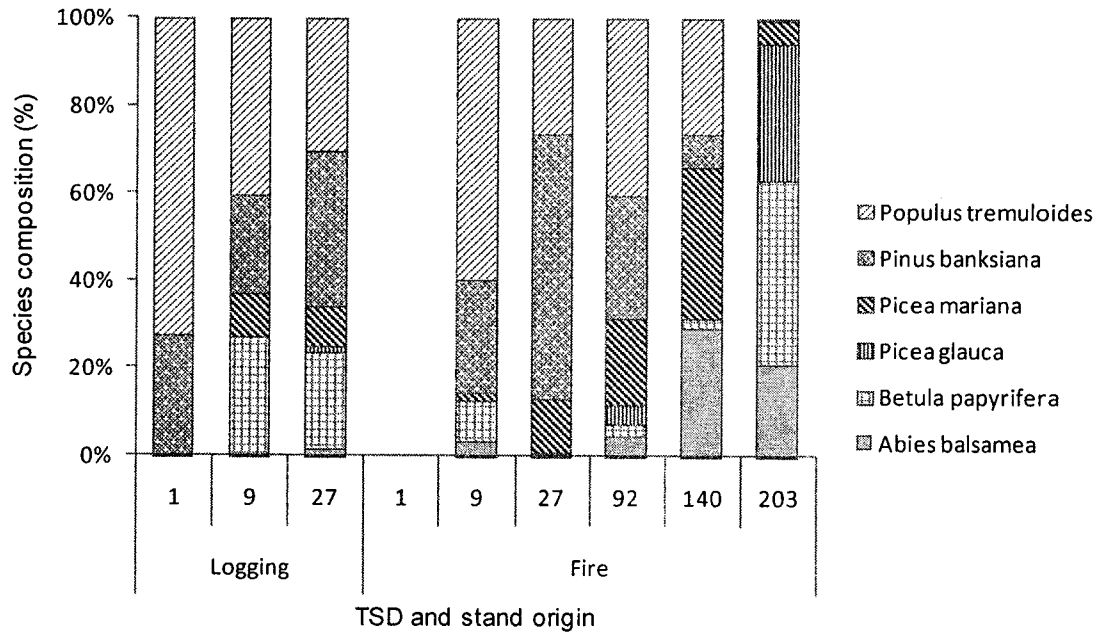
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APPENDICES

Appendix 1.

Relative change in species composition during stand development.



Appendix 2.

Mean values (\pm one standard error) of different live biomass C pools along stand development after clearcut logging and wildfire in northwestern Ontario.

TSD	Overstory trees		Saplings and shrubs		Total tree C	
Cut						
1	8.41	\pm 2.07	0.00	\pm 0.00	8.41	\pm 2.07
9	0.77	\pm 0.26	1.66	\pm 0.28	2.43	\pm 0.03
27	50.77	\pm 2.72	0.91	\pm 0.28	51.69	\pm 2.87
Fire						
1	0.00	\pm 0.00	0.00	\pm 0.00	0.00	\pm 0.00
9	0.83	\pm 0.62	2.30	\pm 0.74	3.13	\pm 1.34
27	10.25	\pm 0.76	2.95	\pm 0.87	13.20	\pm 1.46
92	109.18	\pm 18.43	0.61	\pm 0.13	109.79	\pm 18.40
140	69.65	\pm 22.19	0.98	\pm 0.15	70.63	\pm 22.32
203	70.69	\pm 8.96	2.01	\pm 0.29	72.71	\pm 8.72
TSD	Understory vascular plants		Bryophytes		Total live biomass	
Cut						
1	0.03	\pm 0.01	0.22	\pm 0.22	8.67	\pm 2.29
9	0.32	\pm 0.09	1.02	\pm 0.08	3.77	\pm 0.16
27	0.15	\pm 0.01	0.00	\pm 0.00	51.84	\pm 2.87
Fire						
1	0.05	\pm 0.02	0.14	\pm 0.14	0.20	\pm 0.16
9	0.33	\pm 0.07	0.00	\pm 0.00	3.46	\pm 1.29
27	0.11	\pm 0.06	0.57	\pm 0.32	13.88	\pm 1.64
92	0.10	\pm 0.01	0.52	\pm 0.27	110.41	\pm 18.22
140	0.13	\pm 0.04	0.72	\pm 0.36	71.48	\pm 21.70
203	0.02	\pm 0.02	0.01	\pm 0.01	72.74	\pm 8.73