University of Alberta

Soil respiration processes in Canadian boreal forest soils following fire

by

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Abstract

The study examined two aspects of carbon cycling in the post-fire boreal forest: 1) soil respiration and its spatial variation in three post-fire boreal forest sites and 2) ecosystem respiration response to soil temperature and moisture during dry (2003) and wet (2005) years at the same sites. Soil respiration showed 35% within-site spatial variability and was not spatially autocorrelated. Soil respiration was positively and linearly related to fine root biomass ($R^2 = 0.63$ to 0.85; $P < 0.05$). Forest Floor removal reduced the soil respiration by 18 to 38% depending on the site. Ecosystem respiration showed exponential relationships with soil temperature. Older sites showed 2 to 3 times greater sensitivity of ecosystem respiration to soil temperature variation (Q_{10}) compared to the youngest F98 site.

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List of Abbreviations

ANOVA	Analysis of Variance
BERMS	Boreal Ecosystem Research and Monitoring Sites
BOREAS	Boreal Ecosystem-Atmosphere Study
C	Carbon
C.V.	Coefficient of Variation
CWD	Coarse Woody Debris
EC	Eddy Covariance
ER	Ecosystem Respiration
FCRN	Fluxnet Canada Research Network
GEP	Gross Ecosystem Productivity
NEE	Net Ecosystem Exchange
NEP	Net Ecosystem Productivity
PAR	Photosynthetically Active Radiation
PVC	Polyvinyl Chloride
RSS	Residual Sum of Squares
SE	Standard Error

CHAPTER 1

1. INTRODUCTION

1.1. Carbon Cycling and Soil Respiration in Boreal Forest Ecosystems

An important part of the carbon cycle in boreal forest ecosystems is the exchange of carbon (C) between the two main reservoirs: boreal forests and the atmosphere. The flux of carbon from soils to the atmosphere occurs primarily in the form of CO_2, and is the result of soil respiration. Soil respiration represents the combined respiration of roots and soil micro- and macroorganisms and is generally considered as an index of metabolic activity of microbes and plant roots. Estimates of the magnitude of this flux range from 68 Pg C yr^{-1} (Raich & Schlesinger, 1992) to 100 Pg C yr^{-1} on a global basis (Musselman & Fox, 1991). This makes soil respiration one of the largest fluxes in the global C cycle after gross primary productivity, which is estimated to range from 100 to 120 Pg C yr^{-1} (Houghton & Woodwell, 1989).

Almost 10 % of atmospheric CO_2 passes through soil each year (Raich and Potter, 1995); this is more than 10 times the CO_2 released from fossil fuel combustion. Due to the magnitude of the soil CO_2 flux and the large pool of potentially mineralizable C in soils (Eswaran et al., 1995), any increase in soil CO_2 emissions in response to environmental change has the potential to exacerbate the increasing atmospheric CO_2 levels and to provide a positive feedback to global warming (Kirschbaum, 1995). Identifying environmental factors that control soil CO_2 emissions, and their effects on emission rates, is crucial for assessing the potential impacts of environmental change.

Another issue linked to soil respiration processes is the relative contribution of root (autotrophic) versus microbial (heterotrophic) respiration. These two fluxes may react differently to changes in environmental conditions. It is therefore important to get a better insight into both components of soil respiration (Boone et al., 1998). However, under field conditions, the separation of root (including the rhizosphere microorganisms) and microbial respiration of the bulk soil organic matter is a difficult task. Various methods have been used *in situ*, which range from minimum to severe disturbance of a site to separate the plant-soil respiratory components (Hanson et al., 2000). Examples of methods that promote minimum disturbance include the use of isotopes:

(a) Exploitation of the natural stable carbon isotope differences:

  (i) where land use is switched from C_3-vegetation to C_4-vegetation over several years, or vice-versa (Rochette et al., 1999),

  (ii) where ^{13}C-depleted CO_2 from a fossil fuel system is used to label the C flux through a plant-soil-microbial systems after photosynthesis, as is the case in many free-air carbon enrichment experiments (FACE) at several places in the world (Pendall et al., 2003).

(b) Labeling of tree canopy with radioisotope ^{14}C-CO_2 (Howarth et al., 1994).

(c) Application of naturally ^{13}C-labelled simple organic substrates to soil (Hogberg and Ekblad, 1996; Ekblad and Hogberg, 2000).

(d) The combined use of natural ^{13}C and ^{18}O isotopes (Lin et al., 1999).

The other field-based method that causes minimum disturbance includes girdling (also called "ring barking") where bark at breast height of trees is removed to instantaneously stop the supply of recent photosynthates to roots. As a result, soil respiration from plots with girdled trees corresponds to microbial respiration while non-girdled tree plots give total soil respiration (root plus microbial respiration). This separates root and microbial respiration in soil by difference between the total and microbial respiration (Hogberg et al., 2001). Some scientists also have recently used the phloem chilling method to stop the flux of recently-fixed C from the tree canopy to belowground roots and soil (Johnsen et al., 2007).

The methods that cause more severe disturbance to the delicate root-soil-microbial continuum are trenching, where plastic sheets are inserted into the soil covering all sides of the plot to avoid any root growth. The respiration from the trenched plots corresponds to microbial respiration while control plots with no trenching give microbial as well as root respiration. (Boone et al., 1998; Hart and Sollins, 1998), root cuvettes to measure the autotrophic respiration of intact roots in the field (Gansert, 1994) or laboratory measurements using excised roots (Burton et al., 1998). Usually due to the use of a range of methods and any associated artifacts, the ratios between the root and microbial components of soil respiration have been reported to vary between 1 and 9 (Hanson et al., 2000). However, with the recent advancements in the use of methods that cause minimum disturbance, many studies have started to propose a narrower ratio (between 4 and 6) for the root and microbial components of soil respiration in boreal forests under both ambient (e.g. Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003) or elevated CO_2 environments (Pendall et al., 2003).

1.2. Fire Disturbance Impacts on Boreal Forest Ecosystems

Fire in the boreal forest is one of the important disturbances, and recognized as a main stand renewal agent. According to recent estimates, 8000 fires have burned about 2.8 million hectares of forest annually on average in Canada, over the past few decades. This is approximately 0.7% of the Canadian boreal forest (Stocks et al., 2002). The general view is that the Canadian boreal forests act as a static carbon sink (Apps et al., 1993). However, current carbon budget models have challenged this view, and show increasing evidence that the boreal forest has now become a decreased sink or even a C source since the late 20th century (Kurz and Apps, 1999; Chen et. al., 2000). This change in the boreal forest from a C sink to a source is largely caused by fire disturbance events (Kurz and Apps, 1999). These events cause: 1) a direct loss of C from biomass burning, which is approximately 27 Tg C year^{-1} averaged during 1959-1999 (Amiro et al., 2001) and 2) a shift in the ecosystem structure and function through its indirect effects following fire (Harden et al., 2000; Wang et al., 2001). Occurrence of fires in the boreal forest has increased over the last few decades and will likely increase further if global warming occurs (Harden et al., 2000; Flannigan et al., 2005). This projected increase in fire frequency may further accelerate the increase of greenhouse gases by lessening the ecosystem recovery period between fires (Kasischke et al., 1995).

Net ecosystem production (NEP), which is the difference between the gross ecosystem production (GEP) and ecosystem respiration (ER), determines the C source-sink relationships of forest ecosystems. Recently, flux towers have been established at many forest sites across Canada and also at many other places in the world. These towers measure NEP using the eddy covariance method (Margolis et al., 2006). Both GEP and ER are important and are usually determined from NEP using relationships among driving variables such as light, temperature and moisture. The ecosystem respiration (ER) is composed of respiration from plants (autotrophic) and soil macro- and microorganisms (heterotrophic). However, following fire a large amount of coarse woody debris (CWD) can be found in the forest either on the ground or perched. It is generally believed that respiration from soil and CWD dominates ER in the post-fire forest ecosystem. However, the specific contribution of respiration from CWD to ER is largely unknown. Although a few recent studies have provided some good quality data (e.g. Bond-Lamberty et al., 2002; Wang et al., 2002), results may largely depend on site-specific issues. For example, the CWD may not decompose easily until it makes contact with the soil surface. This is especially important at the recently burned sites, where most of the CWD debris remains standing or perched, hence not touching the ground until it eventually falls over during severe wind events. Sander (2003) reported that CWD lying on or close to the soil surface decomposed faster than CWD perched >5 cm above the ground regardless of stand type. Furthermore, CWD should be moist enough and experience sufficient temperature for microbial decomposition. Therefore, due to a large uncertainty in the estimation of CWD respiration, soil respiration is the quantity that can be more thoroughly measured to help get a better understanding of the carbon balance in post-fire ecosystems.

1.3. Post-fire Succession and Soil Respiration Processes

The change in soil respiration with time since fire is an important part of the carbon flux. Fig. 1.1. shows a simplified hypothetical illustration of the changes in soil respiration during forest regeneration. However, these changes could be significantly affected by environmental factors such as soil temperature, moisture and the intensity of fire. In a review by Johnson (1992), soil respiration was little affected by low-intensity burns. On the other hand, Weber (1985) found that soil respiration decreased significantly up to six years after a stand-replacing fire that occurred during the early stages of jack pine stand development. In a boreal aspen stand, burned plots showed decreased soil respiration for the first two years, with a recovery in the third compared to the control unburned plots (Weber, 1990). Burke et al. (1997) found no effect on soil respiration immediately following fire, and decreased respiration two years later in black spruce sites of different ages. Soil respiration then recovered to pre-burn levels after seven years. Recently, Wang et al. (2001) also showed that soil respiration decreased rapidly after wildfires in a boreal black spruce chronosequence.

It is believed that this general decrease in soil respiration can be partially explained by a decrease in root respiration when vegetation is killed by fire (Amiro et al., 2003; Wang et al., 2001). Some other studies found a decrease in total soil respiration yet an increase in microbial respiration following fire (Sawamoto et al., 2000; Richter et al., 2000). However, many other studies have shown a decrease in post-fire microbial respiration (White, 1986; Pietikainen and Fritze, 1993). These experimental results challenge the model of Auclair and Carter (1993), which estimated that 60% of the total release of CO_2 following fire was caused by enhanced soil respiration.

To date, the bulk of respiration studies in the literature suggests that total respiration usually decreases following fire, although the separate effect of root and microbial components on soil respiration is not clear. Moreover, we lack a good understanding of how and why the proportion of each soil respiration component changes with the age of regenerating forests following fire.

1.4. Fluxnet-Canada Research Network (FCRN)

Fluxnet-Canada is a nationwide research network in Canada, whose main objective is to gain a thorough understanding of C cycling in Canadian forest and peatland ecosystems. The network examines the influence of management practices, natural disturbances, and climatic variability on C cycling in forest and peatland ecosystems in Canada. About 40% of Canada's land surface is covered by forests and peatlands and because of such a large cover, these two ecosystem types have the potential to significantly impact the global carbon cycle. However, due to the diverse forest vegetation composition, stand age class structure, disturbances (insects, fire and harvesting) and differences in the environmental conditions, it is difficult for scientists to fully understand the boreal forest carbon cycle and its impact on global climate change (Margolis et al., 2006).

In order to advance our knowledge about the functioning of forests, networks of flux towers have been developed at many places throughout the world to measure and model the CO_2, water and energy exchange in forest ecosystems. Some of these networks are: Ameriflux, Fluxnet-Canada, CarboEurope, and Ozflux (Fluxnet 2001). The collaboration of these regional networks helped to share new insights into the biophysical controls of ecosystem-atmosphere carbon exchange and the role that different forest types play in the global carbon cycle from regional to international scales (Black et al., 2000; Amiro et al., 2001).

In Canada, the network of flux towers in forested areas was first established under the BOREAS (Boreal Ecosystem-Atmosphere Study) experiment during the early 1990's across Canada. The flux towers, also called "Eddy Covariance Towers", measure the exchange of carbon dioxide, water vapor and energy between the biosphere and atmosphere. The measurements are usually calculated for 30 min intervals (Baldocchi, 1997) over the spatial scales ranging from several hundred square meters to a square kilometer (Schuepp et al., 1990). This is the only method currently available for a year long, continuous, long-term measurement of ecosystem level fluxes. During the BOREAS experiment, carbon cycling was studied through measurements in the field, by aircraft and also by meteorological measurements from 1994 to 1996. The study areas were located in Saskatchewan and Manitoba. Almost all measurements of carbon fluxes were made over mature forests (Goulden et al., 1997; Jarvis et al., 1997). After the termination of BOREAS in 1996, some of the towers continued their measurements in northern and southern study areas. The flux towers in the southern area formed the basis of the Boreal Ecosystem Research and Monitoring Sites (BERMS) in 1996.

At present, the BERMS include three mature, three harvested, one clear cut, one fen and three fire disturbed sites in central Saskatchewan. The mature sites range from 70 to 150 years and named as "old aspen" (OA), "old black spruce" (OB) and "old jack pine" (OJP). Harvested sites are jack pine sites harvested in 2002, 1994 and 1975. The fire disturbed sites were burned in 1998, 1989 and 1977.

1.5. Soil Respiration Measurement Methods at the BERMS sites

Soil respiration in the field is usually measured either by using automatic or manual small chamber systems. In both cases, a chamber type is used that encloses a certain area of soil surface, and the rate of increase in CO_2 concentration within the chamber head space is measured. The flux is then assumed to be proportional to the rate of increase. This chamber type is called "flow through, no-steady state type" (Livingston and Hutchinson, 1995) and is most widely used to measure soil respiration. There are also some other chamber types that are occasionally used (for a review, see Livingston and Hutchinson, 1995).

Automated chamber systems currently run at the BERMS mature sites. These systems provide continuous soil respiration measurements. The systems provide a high temporal frequency in the measurements, therefore the temporal variability in soil respiration is well characterized. The high resolution temporal soil respiration measurements are also compared to the eddy covariance estimates of total ecosystem respiration from the "eddy covariance towers" at these sites. This helps to generate more accurate estimates of the contribution of soil respiration to total ecosystem respiration. Another advantage is that the greater area of these chambers as compared to manual systems provide a better spatial sample of measurements. However, automated systems are much more expensive and require greater infrastructure including power and housing facility in order to operate. Due to these constraints, only six to 12 chambers per site currently run at the BERMS mature sites. Therefore, the spatial distribution of soil respiration is not well understood at these sites.

At the fire disturbed sites, a "manual small chamber system" was used. Because this system is portable in nature, and less expensive than the automated chamber system, a large number of measurements can be obtained, which narrows the standard deviation of the mean, therefore increasing the confidence in the site mean estimate with respect to spatial variation (Savage and Davidson, 2003). This helps to better characterize the spatial variability in soil respiration. However, "the manual small chamber system" does not afford good temporal frequency of sampling because of the time constraints of the operator. Although both temporal and spatial variations in soil respiration are important, the main focus at the fire disturbed sites is on the spatial variability aspect of this flux. This is mainly because, unlike the mature sites, the soil surface looks highly patchy and uneven with some areas burned more than others at these sites, especially at the younger F98 site. Therefore, a high spatial variability in soil respiration could be expected. A large number of soil respiration measurements have been taken at each of these sites, which are described in detail in Chapter 2.

1.6. Aims and Objectives

This research is carried out within the Fluxnet-Canada Research Network and is focused on studying soil respiration processes at the BERMS fire chronosequence sites. The last three chapters provide detailed information on various experiments, their results and conclusions, and associated implications of understanding the carbon cycling in boreal forests following fire.

The overall goal of this research project is to improve our understanding of post-fire C dynamics in the Canadian boreal forest. The main emphasis is on the assessment of soil respiration and the influence of driving factors along the successional trajectory, which may dictate the net C balance of the forest. This is especially important when the boreal forest fire frequency is expected to increase in the near future (Flannigan et al., 2005). For this study, we have a chronosequence of three post-fire sites in central Saskatchewan. The sites are named as F98, F89 and F77, and were burned in 1998, 1989 and 1977 respectively. These sites had NEP flux tower measurements as part of the Fluxnet-Canada Research Network.

In Chapter 2, the following specific objectives are addressed in detail:

1. To identify the role of soil respiration in boreal forest ecosystems through comparisons of three sites at discrete sampling periods.
2. To establish whether small-chamber measurements can be treated as random on a local scale.
3. To determine if the amount of organic material left after fire affects soil respiration.

In Chapter 3, I attempt to evaluate and compare the ecosystem respiration response to soil temperature and moisture at these post-fire sites in contrasting dry (2003) and wet (2005) years. The objectives of this chapter include:

4. To evaluate and compare the ecosystem respiration response to soil temperature and moisture at the three post-fire sites.
5. To determine whether ecosystem respiration shows any seasonal patterns related to soil moisture, by excluding the effect of soil temperature.
6. To determine whether the Q_{10} value differs among the post-fire sites and how much does it differs in the wet and dry years.

Chapter 4 synthesizes major findings reported in this thesis as this study significantly improves our understanding of the belowground respiration processes following fire in the Canadian boreal forests. The implications of these results on the boreal forest carbon balance are also discussed.

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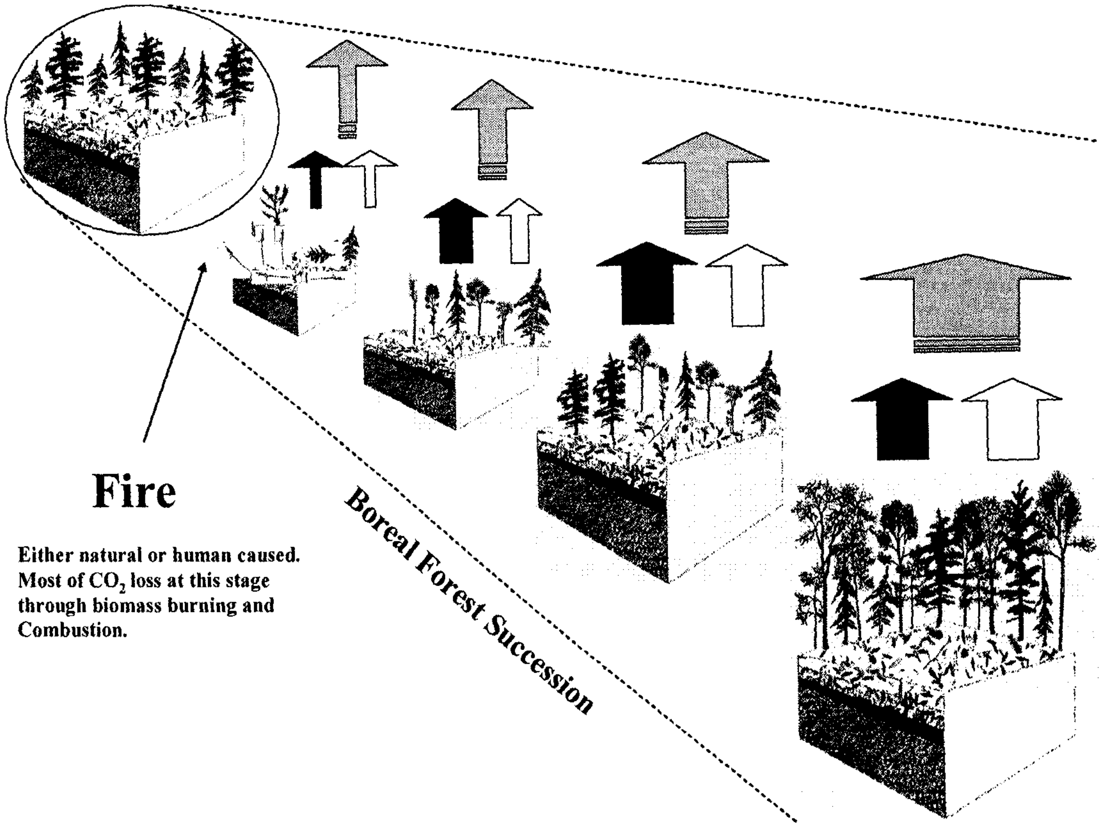
Fig 1.1. A simplified hypothetical illustration of boreal forest dynamics and soil respiration following fire. The grey arrow represents the C loss due to the total soil respiration. Black and white arrows are root (autotrophic) and microbial (heterotrophic) respiration, respectively. The thickness of the arrows indicates the likely magnitude of these fluxes alon the post-fire boreal forest succession.



Either natural or human caused. Most of CO_2 loss at this stage through biomass burning and Combustion.

CHAPTER 2

2. FACTORS AFFECTING THE SPATIAL VARIABILITY OF SOIL RESPIRATION IN CANADIAN BOREAL FOREST SOILS FOLLOWING FIRE

2.1. Introduction

The soils of boreal forest ecosystems contain about one-third of the global soil carbon (Dixon et al., 1994). Global warming is expected to be greatest in the boreal region, which may be accelerated by an increased release of CO_2 from these ecosystems (Raich and Schlesinger, 1992). One of the primary regulators of carbon (C) uptake and emission in the boreal forest is wildfire (Kasischke et al., 1995). Fire has a capacity to alter several soil physical and biochemical properties such as temperature, moisture, and substrate quality that regulate C exchange with the atmosphere.

An important component of C exchange from a terrestrial ecosystem is soil respiration. Large spatial and temporal variability in soil respiration is typically found within and among sites (Buchmann, 2000; Franzluebbers et al., 2002). The variability has been attributed to plant species composition, stand age and management practices (Hanson et al., 1993; Nakane and Lee, 1995). The root biomass, substrate quantity and quality, and soil texture are also important in this context (Shibistova et al., 2002; Boone et al., 1998). Russell and Voroney (1998) found that 29 to 40 soil respiration measurments may be needed to get a representative mean value using a 40 m transect with a 2 m sampling interval in a mature aspen boreal forest. In another study, Xu and Qi, (2001) reported a mean sample size of 7 to

27 is required to estimate mean soil respiration for a 20 × 20 m plot in a young ponderosa pine plantation. These estimates were based on soil respiration measurements taken by individual chambers covering about 86 cm^2 area. However, in boreal ecosystems established following fire disturbance, the spatial variability in soil respiration is not well understood. Following fire, the soil surface often appears as a random mosaic of some areas severely affected by the fire while others are only slightly impacted (Rab, 1996). Therefore, surface organic layers can exhibit large variations in thickness and composition. This may bring changes not only in the soil carbon stocks, but also in carbon fluxes (Schimel et al., 1997), which could result in a higher spatial variability in soil respiration compared to non fire-disturbed boreal forest. Some studies describe the variability in soil respiration at fire-disturbed sites but are limited to either one site (Litton et al., 2003) or several same-aged stands (O'Neill et al., 2002). Thus, the soil respiration variability during the regeneration stages following fire has been less studied. A chronosequence of post-fire sites often exhibits varying degrees of soil development, such as thickness of the forest floor (LFH or duff layer), organic matter quality and quantity, and microbial size and composition (Paré et al., 1993; Brais et al., 1995). During ecosystem recovery, the gradual build up of forest floor may lessen the forest floor patchiness caused by fire disturbance. Therefore, the forest floor would be expected to become more homogenous with stand age. Consequently, soil respiration may be expected to become less spatially variable with increasing stand age. Soil respiration within a given stand can be said to be dependent upon the amount, distribution and activity of fine roots and quantity and quality of soil C pools. Studies have reported that root activity, microbial activity, and soil carbon storage all increase along the regeneration stages

(Peltoniemi et al., 2004; Yu et al., 2002), especially during early succession (5-40 years). Thus, total soil respiration is also expected to increase with stand age.

The objectives of this study were 1) to identify the role of soil respiration in the early stages of post-fire ecosystem through comparisons of three sites at discrete sampling periods, 2) to establish whether small-chamber measurements could be treated as random on a local scale, and 3) to determine if the amount of organic material left after fire affects soil respiration.

These questions are particularly important because the forest floor can be substantially consumed by fire. On average a loss of about 2.1 kg dry biomass m^{-2} from the forest floor organic layer has been reported by Amiro et al. (2001). Moreover, this loss results in a patchy distribution and variable thickness of the forest floor (Miyanishi and Johnson, 2002). These conditions could potentially cause differences in respiration within and among sites. It is also hypothesized that fine root biomass in the top soil layer could influence soil respiration. This study includes identification of factors contributing to differences in soil respiration among sites as well as to the spatial variability at the three post-fire sites.

2.2. Materials and Methods

2.2.1. Study Sites

The study sites are part of BERMS (Boreal Ecosystem Research and Monitoring Sites within the Fluxnet–Canada Research Network), which are located in central Saskatchewan. Three post-fire sites (F98, F89 and F77 referring to the year of the most recent fire: 1998, 1989 and 1977, respectively) were included in our present study, with stand characteristics given by

Coursolle et al. (2006) and Amiro et al. (2006). The soils are classified as Dystric Brunisols with a loamy sand texture (Soil Classification Working Group, 1998). The normal mean annual temperature is 0.4°C and annual precipitation is 467 mm (Environment Canada, 2007). The F98 site (54.083° N, 106.000° W) is located in the east part of Prince Albert National Park, Saskatchewan, within the 1700 ha area burned by a wildfire in July 1998. The pre-fire forest consisted of jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) stands, with some intermixed aspen (*Populus tremuloides*). The fire was severe, consuming much of the top soil organic layer and killing all trees. In our plots, much of the regeneration vegetation consisted of jack pine saplings less than 2 m high and black spruce seedlings that were less than 0.5 m tall. There was an overstorey of dead, leafless jack pine trees and black spruce. Sparse grass and herbs, such as fireweed (*Epilobium angustifolium*) covered the ground. There were a large number of fallen dead trees, mostly perched above the ground that were not decomposing quickly.

Site F89 (54.250° N, 105.867° W) is approximately 25 km northeast of F98. It originated from a human-caused fire that burned an area of about 13,500 ha. Parts of the area had been logged prior to the fire, and slash residues would have been burned in some locations, reducing the amount of coarse woody debris that would be found in a non-harvested area. Parts of the area were aerially seeded with jack pine seeds in 1990. The present tree canopy is composed of jack pine, trembling aspen, balsam poplar (*Populus balsamifera*) and birch (*Betula papyrifera*) with some smaller black spruce. Numerous dead black spruce and jack pine are still standing, although most had fallen over and formed a leaning mix of dry, dead tree boles. At our plot, the dominant trees consisted of jack pine with some trembling aspen and some green alder (*Alnus crispa*). The understorey species included bearberry (*Arctostaphylos uva-ursi*), blueberry (*Vaccinium myrtilloides*), raspberry (*Rubus idaeus*), rose (*Rosa acicularis*), bunchberry (*Cornus canadensis*) and reed grass (*Calamagrostis canadensis*).

The F77 site (54.485° N, 105.817° W) is located approximately 25 km north of F89. The present tree canopy consists of jack pine and shorter black spruce as understorey vegetation. At this site and also in our study plots, most of the dead trees resulting from fire were lying on the ground. The above-ground vegetation in our plot was mostly jack pine and a few aspen trees. The ground cover consisted of black spruce, shrubs, Cladina lichens and blueberry.

2.2.2. Experimental Layout and Soil Respiration Measurements

A square plot of 18 m * 18 m was established at each site in June 2004. The plots were located about 100 m west of the eddy covariance flux tower previously installed at these sites by the Fluxnet–Canada Research Network. At each plot, a grid of 2 m * 2 m was made. Thus, a total of 100 grid points per plot per site were selected, including the outer boundaries of the plot. At each grid point, a PVC collar (10 cm long, 10 cm inside diameter) was inserted to a depth of 5 to 6 cm into the soil. After installing the collars, the forest floor thickness at each grid point was measured to the nearest 0.5 cm. The thickness was recorded in cm using a ruler inserted in the soil outside of each collar. The soil disturbance caused by the collar insertion generally results in initially high fluxes just after the collar installation, but fluxes stabilize after 10-30 min (Norman et al., 1997). Collars were inserted at least 24 h prior to the first measurements. In total, there were 300 collars inserted (100 per site). Soil respiration was measured monthly at each site during the growing season of 2004 (June-August) using a soil respiration chamber connected to a portable photosynthesis system (LI-6400-09; LiCor, Lincoln, Nebraska, USA). Readings were recorded by placing the chamber on the collars. It took 4 to 5 hrs to take 100 respiration measurements along the grid at one site. At the same time, soil temperature at the depth of 4 to 5 cm was measured near each collar with the thermocouple attached to the LI-6400 system. Measurements were usually started about 9:00 am local time. We also took multiple measurements on the same collar at the F98 and F89 sites to check the precision of our measurements. Gravimetric soil water contents for the plots were determined from the soil samples (12-15 per plot) taken randomly from the top 0 to 5 cm including the surface organic layer beside the plots. The wet soil samples were weighed, and then dried at 70°C for 24 hours. Soil moisture is expressed as percent moisture by dry weight.

2.2.3. Forest Floor Removal and Soil Respiration

In June 2005, 30 of the remaining 65 collars were selected randomly and pulled out. The forest floor layer from these points was completely removed with the help of a soil knife and the collars were then reinserted into the soil. The collars were left in the soil for at least 24 h before measurements. Soil respiration on 35 collars with organic and 30 collars without organic layer were measured the next day at each site. Measurements were taken once in June and once in August/early September 2005 at each site. The soil temperature and gravimetric soil water content were determined similarly to the previous year.

2.2.4. Fine Root Biomass Analysis

In August 2004, 35 collars were selected randomly and pulled out at each site. Soil in the top 0 to 5 cm, including the surface organic layer, was collected using a 5-cm-diameter corer. The samples were transferred to polyethylene freezer zip-lock bags, labelled and transported back to the lab in a cooler. At each site, three samples were selected from each of the collars that had shown low, medium and high respiration during the month of August (i.e., three replicates of three respiration classes). Fine roots were collected after sieving the soil samples through a 2-mm sieve and then roots were hand picked. Root samples were dried at 70°C for 24 hrs. Samples were then weighed to calculate fine root dry biomass (< 2 mm).

We also determined the fine root biomass in the forest floor organic layer alone to allow comparisons for respiration measurements with and without the forest floor. The samples were collected from the four corners of a 10 m x 10 m permanent sample plot at each site in July 2005 using a 5-cm diameter corer. The organic layer was removed from the core, oven dried at 70° C for 24 hrs and the dry mass was recorded. The samples were then wetted and fine roots were manually picked with tweezers. The wet roots were oven dried at 70° C for 24 hrs. Samples were then weighed to calculate the root dry biomass.

2.2.5. Geostatistics and Statistical Analysis

We used GS+ software (Gamma Design, 1998) to examine the spatial autocorrelation for soil respiration at all the sites. Semi-variograms were used to evaluate the level of spatial autocorrelation of soil respiration among the 100 grid points. This statistic was calculated using:

$$\gamma(h) = [2N(h)]^{-1} \sum_{i=1}^{N(h)} (Z(x_i) - Z(x_{i+h}))^2 \qquad [2.1]$$

Where $\gamma(h)$ is called semivariance, N(h) is the number of pairs of observations with a separation distance of h, and x_i and x_{i+h} are the observations with the separation distance of h. Thus, we obtained semi-variograms by plotting the semivariance against the separation distance between each pair of samples. The sample variograms were fitted with linear and spherical variogram models based on the smallest set of residual sum of squares (RSS) between model prediction of variance for each lag distance and measured values. The models are defined by equations [2.2] and [2.3], respectively (Deutsch and Journel, 1998).

$$\gamma(h) = C_o + C[(h/Ao)] \qquad [2.2]$$

and

$$\gamma(h) = C_o + C[1.5(h/Ao) - 0.5(h/Ao)^3], h \leqslant Ao$$

$$\gamma(h) = C_o + C, h \geqslant Ao \qquad [2.3]$$

where C_0 is called nugget variance, which is the y intercept of the model, an indication of either variance that exists at a shorter distance than field sampling intervals or measurement error; C is the asymptote of semi-variance γ(h); the sum of C_0 and C is called sill; A_0 is called range, the distance at which the sill is approached (typically near maximum semi-variance). We used the nugget-to-sill fraction as an indicator of "degree of randomness". A nugget-to-sill fraction close to unity indicates that there is little spatial autocorrelation.

For statistical analyses, an F-test was used to test the difference in variance among sites for each month. The variance difference could result in different sample sizes required for each site, therefore a statistical analysis was used to estimate the sample size required for the mean population within 10% or 20%, at the 95% probability level according to Petersen and Calvin (1986). The 2004 soil respiration data were power transformed (to 1.25) to meet the ANOVA assumptions. A repeated measure analysis of variance (ANOVA) with time as a repeated factor was used to test for significant differences in soil respiration, soil temperature and soil moisture within and among sites. A Tukey's honestly significant difference (HSD) *a posteriori* test ($\alpha = 0.05$) was used to separate the means. A linear regression analysis was used to test the relationship between the thickness of the organic layer, fine root biomass and soil respiration. For this test, the effect of soil temperature on respiration was removed with a Q_{10} function, using a base of the mean soil temperature of the site and a $Q_{10} = 2$. The use of $Q_{10} = 3$ or 4 did not alter the statistical conclusions.

The 2005 data did not meet ANOVA assumptions for normality and equal variance even with the data transformation. Thus, we tested for the effect of the removal of the organic layer using a non- parametric Mann Whitney *U* test for significant differences with and without organic layer respiration at all three sites during two sampling events. Because six tests were done, individual α -values were tested according to the Bonferroni method. All the statistical analyses were done with SAS statistical software (SAS Institute Inc., 2003).

2.2.6. Methodological Issues during 2004 Field Measurements

The respiration measurements were taken with a chamber connected with the LI6400 system. While taking the measurements in 2004, the O-ring/seal ring was not included, therefore the missing O-ring might have caused some uncertainties with the 2004 data. The 2005 respiration measurements included the O-ring. To test for the effect of the missing O-ring, we took with-ring and without-ring soil respiration measurements on 18-20 collars at each site during the June 2005 sampling event to determine the error and whether this contributed to additional variance. We tested for significant differences in the mean soil respiration and the variance between with-and without-ring measurements using a paired t-test at each site. Regression analysis between with-and without-ring was used to estimate the difference. We derived a correction factor from the regression analysis to correct the mean soil respiration for 2004 sampling events.

2.3 Results

2.3.1. Data Corrections

The mean soil respiration was significantly lower for the without-ring measurements at all three sites. Fig. 2.1 shows the regression analyses between with- and without-ring measurements for all sites. The regression analysis was significant ($P < 0.05$) and $r^2 = 0.95$. We used the regression slope as a correction factor (1.15) forcing the intercept through zero for the combined soil respiration (with and without ring) data from all sites.

The important thing to note is that there was no significant difference in the variance between with-and without-ring measurements (paired T-test, $P<0.05$) despite the significantly higher mean soil respiration with-ring measurements. Furthermore, the coefficient of variation was less than 2% higher for without-ring soil respiration measurement at any given site. Multiple measurements on the same collars were also taken during one occasion. At each site, five measurements per collar on 4-5 collars were taken at the interval of 7-8 minutes for about 35-45 minutes at the F98 and F89 sites. The coefficient of variation of the multiple measurements on the same collar without ring (during 2004) was less than 0.05, indicating a high precision between the measurements even without the ring. Therefore, we have presented the data uncorrected for the missing O-ring in Table 2.1 and Fig. 2.2 to preserve the actual measurements in any given year. However, we also present our best estimate of respiration in Fig. 2.4 to include the 14% O-ring correction.

2.3.2. Mean Soil Respiration, Temperature and Moisture among Sites

There were significant differences in the mean soil respiration among sites in both years. The F89 site had significantly higher mean soil respiration in 2005 whereas in 2004 it was only significantly higher in July compared to the other sites (Fig. 2.2). The youngest F98 site always had a significantly lower soil respiration except in June 2004 when it was similar to the older F89 and F77 sites (Fig. 2.2).

The soil temperature was significantly higher in July at all the sites during 2004. The F98 site always showed a significantly higher soil temperature in any given month, whereas the F77 site always had a significantly lower soil temperature. There was no significant difference between the soil moisture at F98 and F89 sites during 2004 except in August where F98 was significantly higher in soil moisture (Fig. 2.2). However, F98 was wetter than the other sites in 2005.

2.3.3. Spatial Variation in Soil Respiration

The within-site spatial coefficients of variation (C.V.) vary between 26 and 61%, averaging about 35% (Table 2.1). In general, site F98 was the most variable among sites. However, at any given site, the highest within-site variability (C.V.) was seen during different months, e.g. site F98 during July 2004, site F89 during June 2004 and site F77 during August.

We tested for spatial autocorrelation to assess the range of within-site spatial variation in soil respiration. Variogram model parameters fitted based on the lowest residual sum of squares (RSS) varied from site to site (Table. 2.1). The nugget-to-sill fraction was high (0.5 to 1.0) during all sampling events, indicating that the semivariance did not change much with distance between grid sampling points. This indicates that soil respiration was randomly distributed over the entire lag distance at scales between 2 and 20 m.

There was no significant difference in the variance between the F98 and F89 sites during all sampling dates ($P > 0.05$) while F77 showed significantly lower variance except in August. We calculated the sample size required for characterizing the variability in soil respiration using Peterson and Calvin (1986) statistics. The average number of sampling locations required to estimate the population mean for soil respiration at the 95% probability within 10% of the true mean was 99, 39 and 47 for the F98, F89 and F77 sites respectively. However, sample size of 25, 10, and 12 would estimate it within 20%. Similarly for 100 samples, the average C.V. values were 49, 32 and 34 (Table 2.1). Note that despite similar variance, the estimated sample size varies at the F98 and F89 sites. This is because the sample size was estimated by scaling with the mean soil respiration value of the sites at any given month (see Petersen and Calvin, 1986).

2.3.4. Relationship between Soil Respiration and the Thickness of the Forest Floor

We had measured soil respiration and thickness of the forest floor at 100 points per site. Figure. 2.3 shows the relationship between the soil respiration and thickness of the forest floor at 100 points at each of the three sites during the June sampling. There was no significant relationship between the soil respiration and thickness of the forest floor ($r^2 = 0.009$, $P > 0.05$). Similar patterns were observed during July and August samplings at all sites with no significant relationship. Hence, there was no effect caused by the amount of forest floor, either left behind from the fire (F98 site) or developed since the last fire (F77 site).We do not have measurements of the forest floor mass but the thickness should scale linearly with mass based on geometry.

2.3.5. Effect of Forest Floor Removal on Soil Respiration

Removal of the forest floor caused a reduction in soil respiration of 17 to 38%, depending upon the site (Table 2.2). The F77 site showed the greatest reduction (34-38%) among sites whereas the F98 site had the lowest (17-18%). The reduction was essentially the same in both June and August at all sites. The F98 and F89 sites showed no significant difference in mean forest floor thickness, but estimated respiration from the forest floor was 2 to 3 times smaller at the F98 site (Table 2.2, mean difference). In contrast, although the mean forest floor organic layer thickness at the F77 site was significantly greater than at the F89 site ($P <$

0.015), the respiration from the forest floor was quite similar between these sites (Table 2.2, mean difference).

2.3.6. Relationship between Soil Respiration and Fine Root Biomass

Soil respiration was positively and linearly related to fine root biomass in the top 5 cm of soil (including the forest floor organic layer) at all sites with R^2 values of about 0.7 or greater (Fig. 2.4). The non-site-specific regression R^2 value was 0.7. Among sites, an important observation is that similar soil respiration was observed at sites with different root biomass. Note that the respiration values were corrected for soil temperature using a Q_{10} value of 2 and a base temperature of the mean soil temperature for measurements on that day. This removed the temperature effect to help determine the effect of root biomass.

The amounts of mean fine root biomass in the forest floor organic layer were 0.28 and 0.34 kg m^{-3} at the F98 and F89 sites, respectively. The concentrations were not significantly different between the sites ($P = 0.33$). We also compared the fine root biomass between the mineral horizon and forest floor organic layer at each site. The forest floor organic layer at the F98 and F89 sites contributed approximately 15% of the total fine root biomass in the top 30 cm of soil profile at these sites. According to the recent inventory, the top 10 cm of these soils contains approximately half of the fine root total biomass (Fluxnet Canada, 2007).

2.4. Discussion

Fire induces both biotic and abiotic changes in the ecosystem properties, which could strongly influence soil C pools and fluxes (Burke et. al., 1997). There is an immediate release of stored soil carbon during combustion and subsequent reduction in carbon inputs from primary production. These changes could potentially influence the net exchange of C with the atmosphere more than the direct emission of CO_2 during biomass combustion (Auclair and Carter, 1993; Amiro et. al., 2003). Generally, soil temperature can increase after fire with overstorey removal and soil moisture can increase with the reduction in transpiration rates. Litter input can also be greatly altered, with a decline in fine litter, loss of rhizosphere exudation and a large initial increase in inputs of coarse woody debris. Furthermore, the organic layer can be severely reduced by fire. Depending upon its intensity, organic layers can be unevenly burned and become charred (Dyrness and Norum, 1983; Miyanishi and Johnson, 2002). All of these changes are hypothesized to affect the post-fire soil respiration processes. A review by Johnson (1992) concluded that low intensity burns had very little effect on soil respiration. However, a stand-replacing fire that occurred during early stages of stand development significantly lowered the soil respiration six years after the burn in jack pine stands (Weber, 1985). Also, in a boreal aspen stand, burned plots had decreased soil respiration compared to control plots for the first two years with recovery in the third (Weber, 1990). In another study in black spruce sites of different ages in northern Manitoba, Burke et al. (1997) found no effect immediately after fire, decreased soil respiration two years later, and a recovery to pre-burn levels after seven years. A review of several studies concluded that soil respiration generally decreases following fire (Amiro et al., 2003). The study suggested that in addition to the decrease in root respiration, decomposition also decreases, which is likely caused by a decrease in soil microbial population and less available carbon substrate.

Our results for a chronosequence of 7-, 17- and 27-year-old post-fire stands showed that the F89 site (17-year-old) had the highest soil respiration during the growing season of 2004 and 2005. The mean soil temperature did not explain the differences in soil respiration among sites. The vegetation at the F89 site is composed of a mix of jack pine, trembling aspen, and birch and several authors have suggested that the rate of organic matter decomposition in mixed forests is higher than in pure coniferous forests (Weber, 1985, 1990; Gordon et al., 1987). Therefore, the higher level of soil respiration at the F89 site could be attributed to higher litter inputs, decomposition and root activity in mixed stands (Sims et al., 1989).

The soil respiration peaked in July corresponding to higher soil temperature and moisture at all sites. Similar seasonal temperature and moisture related patterns for soil respiration were observed in a mature boreal aspen stand (Gaumont-Guay et al., 2006) and black spruce stand (Jassal and Black, 2006) located within the BERMS area. However, the soil respiration was 2-3 times higher at these sites compared to our fire-disturbed sites. Several other studies have also reported similar soil respiration patterns for boreal (Hogberg et al., 2001) and temperate forests (Lee et al., 2003). Apart from the dependence of microbial respiration on soil temperature, the dependence of root respiration on soil temperature has also been reported (Boone et al., 1998). Recently, root respiration was found to be more closely connected with the supply of current photosynthates from the tree canopy than with soil temperature (Hogberg et al., 2001). In boreal forests of central Saskatchewan, photosynthesis peaks in the middle of summer (Barr et al., 2002), and the concurrently fixed photosynthetic C gets transported from the tree canopy to the roots within a few days (Bhupinderpal-Singh et al., 2003). The soil respiration at our sites did not decrease with the decrease in soil temperature and moisture during August. At this time of the year, it appears that either the microbial activity and/or the root activity was enhanced. Thus, more likely it is a combination of environmental and physiological factors that resulted in the higher soil respiration during the July-August months as compared to June.

The spatial variation in soil respiration was about 49, 32 and 34 % at the F98, F89 and F77 sites respectively (C.V., Table 2.1). Hanson et al. (1993) found a C.V. for daytime forest floor respiration of between 28% and 42% in a deciduous oak forest similar to this study, although no indication of the spatial scale of this variability was given. Goulden et al. (1996) described extensive heterogeneity in soil respiration rate at the Harvard forest, with rates varying between 3.8 and 7.5 μmol m^{-2} s^{-1}, although the area over which this variation occurred was not reported.

Although the coefficient of variation may be a useful indicator of spatial variation for soil respiration, it may be of little use to simply compare the coefficients of variation between the different studies because of the lack of standard design for experiments, such as the size and shape of a plot. However, our comparison of coefficient of variation among sites with similar experimental design showed that the F98 site was more variable than the F89 and F77 sites. Also, the differences in the absolute variances (regardless of the mean) in soil respiration showed that the F98 and F89 sites were significantly more variable compared to the F77 site ($P< 0.05$). Since the F98 site was more variable in soil respiration both in absolute and relative terms, the average required sample size was greater at this site. The average sample size of 99, 39 and 47 could estimate the population mean soil respiration within 10% at F98, F89 and F77 respectively. However, a sample size of 25, 10 and 12 would estimate it within 20%. This compares with the sample size estimates from the other researchers of 40 (Russell and Voroney, 1998) and 27 (Xu and Qi, 2001), using the same-sized collars as in our study.

Some studies suggest that it may also be necessary to examine the effects of separation distance (distance between the sampling points) to adequately describe the spatial autocorrelation. In the present study, no spatial autocorrelation in soil respiration was observed at any of the sites, thus indicating that the soil respiration was randomly distributed among the sampling points, at least on a local scale of about 400 m^2. Nakayama (1990) also reported no spatial autocorrelation at locations 1 m apart, which are even closer, compared to 2 m of separation distance in this study. In contrast, Rayment and Jarvis (2000) found a high degree of autocorrelation between the soil respiration measurements at locations separated by less than 1 m in a black spruce dominated stand. However, the spatial heterogeneity increased at distances greater than 1 m. Also, the variations in soil respiration rates were correlated with the thickness of the dead moss layer in their study.

Fire disturbance causes uneven patches of thick or thin, partially or fully burnt organic layers. Thus, our spatial variability in soil respiration could be the result of the degree of forest floor development as measured by its thickness. However, in contrast to this hypothesis, no significant relationship was observed between the soil respiration and forest floor thickness at any of the sites (Fig. 2.3). These results clearly show that the forest floor thickness or the degree of forest floor development is not a good indicator of spatial variability in soil respiration at our sites. The removal of forest floor organic layer experiment further indicated that forest floor organic layer contributed only 17 to 38 % of the total respiration (Table 2.2). Similar results have been reported from Norway spruce stands in Germany (Buchmann, 2000), where the majority of respiration originates from the mineral horizon (>60%) as well as in boreal Canadian (Mallik and Hu, 1997) and Japanese forests (Nakane et al., 1996). Since the respiration contribution of forest floor organic layer to the total soil respiration was small, the thickness of the forest floor organic layer was not a good parameter to account for the spatial variability in soil respiration at our sites. The F98 site had two to three times less respiration from its forest floor than the F89 site (Table 2.2, mean difference) although there was no significant difference in their mean forest floor thicknesses. The F89 and F77 sites showed similar respiration from their forest floors but the F77 site had a significantly higher mean forest floor organic layer thickness. These data suggest two things: (i) at the F89 site, a significantly higher mean respiration from the mineral soil horizons was largely responsible for the overall differences in soil respiration when compared to the F77 site (Table 2.2); and (ii) at the F98 site, a significantly lower respiration from both forest floor and mineral horizons was likely the cause of overall differences in soil respiration when compared to the F89 site.

The percentage of fine root biomass in the forest floor organic layer was 16 and 13 % at the F98 and F89 sites, respectively. At the F98 site, the reduction of 17 to 18% in soil respiration due to forest floor removal (Table 2.2) could be largely due to the removal of fine roots in the forest floor. This means the majority of respiration from the forest floor at the F98 site was due to roots. Although litter quantity and quality is important for microbial activity/respiration, it may contribute only a small fraction to the organic layer respiration at the F98 site. In contrast, at the F89 site, the soil organic matter (SOM) in the forest floor seems to be the more important factor compared to roots for forest floor respiration. There would have been a gradual build up of SOM with stand age and many studies have shown a positive relationship between SOM quantity and stand age while SOM quality depends on the type of litter (Eijsackers and Zehnder, 1990; Prescott et al., 2000). Although we did not have data on SOM characteristics in the forest floor organic layers, there could be differences in SOM quality at the F89 and also F77 sites when compared to the F98 site.

The soil respiration was positively and linearly related to the fine root biomass at all the sites (Fig. 2.4.). These relationships indicate that the spatial variability could be attributed to spatial distribution of fine root biomass. Our finding is consistent with studies of Fang et al. (1998) and Shibistova et al. (2002) where the fine root biomass was an important controlling factor of spatial heterogeneity in soil respiration. Similarly, Widen and Majdi (2001) found that more than 60% of the spatial variation in soil respiration could be caused by the effect of differences in root density and organic matter content and quality. Although soil temperature and soil water content are often dominant factors (Fang and Moncrieff, 2001), their effects with time are usually much higher than their spatial variation effects. It has been assumed that root respiration is positively and linearly related to fine root biomass (Behera et. al., 1990). Our results are in support of such an assumption given the strong linear relationships between fine root biomass and soil respiration. Therefore, at any given site, root respiration appears to be controlling respiration spatial patterns. Root respiration, however failed to explain differences among sites, i.e. the sites differ in the amount of fine root biomass but show similar soil respiration (Fig. 2.4).

2.5. Methodological Limitations

We had some concerns about the missing-ring during our 2004 field measurements. Due to the missing ring, there was a slight outward CO_2 leak from the chamber, possibly due to wind effects. Since we took measurements in mainly calm forested sites surrounded by tall jack pine, black spruce and some aspen seedlings, the likely magnitude of this leak was small. The other argument is that the top round edge of the collars was made uniformly smooth on the electrically operated "sander" at the Canadian Forest Service Laboratory in Edmonton, before setting up in the field. Also, the rounded metal ring of the LI6400 instrument was uniformly smooth and the method of placing the chamber on the collar to take measurements was the same throughout the study. Hence, it is unlikely to have large uneven leakages from the individual collars. However, we tackled this issue by taking soil respiration measurements with and without ring to assess the possible magnitude of error. A correction factor was derived from these measurements to correct the 2004 mean soil respiration. Therefore, we can reasonably compare the mean soil respiration among sites and our relationships with the fine root biomass during the 2004 growing season. However, even if we assume some uncertainty, we still can reasonably explain that the missing ring did not significantly affect the variance and the coefficient of variation based on with- and without-ring measurements in the 2005 field samplings. Hence, our calculated number of collars at the given site could be reasonable enough to explain the variability in the soil respiration. The ideal solution would be to repeat this experiment to estimate and compare more accurately the mean soil respiration rates among sites.

The study provided useful information on characterizing the variability in soil respiration and its relationship with fine root biomass, which has been corroborated by several other studies (discussed above). Furthermore, our forest floor removal experiments in 2005 provided important information on the contribution of respiration from the forest floor vs. the mineral soil during the successional stages following fire. This contribution was further pinned down to the source of respiration (roots vs. microbial) from the organic layer and mineral soil.

2.6. Conclusions and Implications

Fire, through its effects on the surface organic layers and stand age, plays an important role in the flux of C from soils in boreal ecosystems. Considerable spatial variability in soil respiration was observed at the sites, however the older sites (F89 and F77) tend to be less variable compared to the younger F98 site. Fire researchers often characterize fire severity by the depth of burn (Van Wagner, 1972; Wells et al., 1979; Alexander, 1982), which likely results in variation in the organic layer thickness. However, the variability in the organic layer thickness did not explain the spatial variability in soil respiration at any of the sites, which is likely because only 17 to 38% of respiration is from the forest floor organic layer. The reduction in forest floor organic layer respiration was largely due to the removal of roots in the organic layer at the F98 site and due to organic matter at the F89 and F77 sites. Strong linear relationships of soil respiration with fine root biomass at all sites indicate that the spatial variability in soil respiration may be largely attributed to the amount of fine root biomass, with 70 to 85 % of the variation explained. Therefore, much of the post-fire respiration during the early succession is apparently due to the root respiration of actively growing early succession. Heterotrophic respiration, even in the younger F98 site, seems to be much less important.

Our findings provide a significant contribution in understanding post-fire soil respiration processes, its sources and relationships with soil and plant factors. However, a better understanding of C cycling and post-fire soil processes is crucial for predicting how the changes in climate and disturbance will affect the exchange of C between the forest and the atmosphere. Fire causes heterogeneous landscape characteristics where the carbon stocks and physical soil parameters have been altered to a different degree. These changes in the soil environment are important in driving post-fire soil respiration processes in boreal forest soils, especially during the early regeneration stages. Many studies have used models or equations with abiotic factors, mainly temperature and soil moisture, to predict soil respiration. However, it is also important to consider biotic factors such as fine root biomass as well as the relative contribution of the organic layer and mineral soil respiration to the total soil respiration in the carbon models. This is particularly important in the light of predictions that forest fire will increase in Canada with the projected changes in climate (Flannigan et al., 2005; Stocks et al., 1998).

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Table 2.1. The descriptive statistics and spatial structure of soil respiration rates at the three post-fire sites for 100 sample points in 2004.

			Descriptive Statistics (μmol m^{-2} s^{-1})				Variogram Model Parameters				
Study sites	Mean	CV (%)	Variance**	Minimum	Maximum	Skewness	Nugget	Sill	Range (m)	Nugget to Sill fraction	RSS*
June 2004											
F98 site	1.65	38	0.42^a	0.08	3.73	0.36	0.22	0.28	20.7	0.8	0.0047
F89 site	1.79	33	0.34^a	0.70	3.14	0.28	0.06	0.13	13.0	0.5	0.0036
F77 site	1.47	31	0.20^b	0.61	3.37	1.32	0.08	0.08	24.4	1.0	0.0018
July 2004											
F98 site	1.92	61	1.38^c	0.26	11.40	5.42	0.20	0.23	20.7	0.9	0.0028
F89 site	3.92	32	1.59^c	1.54	7.70	0.44	0.10	0.12	24.4	0.9	0.0027
F77 site	3.47	26	0.78^d	1.22	6.35	0.42	0.06	0.09	24.4	0.6	0.0008
August 2004											
F98 site	2.77	48	1.75^e	0.29	8.39	1.53	0.20	0.26	22.7	0.8	0.0037
F89 site	3.96	31	1.33^e	1.98	7.95	0.87	0.08	0.11	22.7	0.7	0.0005
F77 site	3.79	44	2.90^f	1.62	11.10	2.53	0.12	0.12	24.4	1.0	0.0023

* Residual Sum of Squares of the model fitted

** Different letters denote significantly different variance (F-test, $\alpha = 0.05$) within each month.

Table 2.2. Effect of removal of the forest floor on soil respiration. The bracketed terms indicate ± 1 standard error.

Site	Mean Thickness of Forest Floor Removed (cm)	Soil Respiration (μmol $m^{-2}s^{-1}$)			% Decrease in Soil Respiration
		With Forest Floor	Without Forest Floor	Mean Difference	
June 2005					
F98	2.16 (0.20)[a]	4.26 (0.11)	3.51 (0.12)	0.75	17
F89	2.11 (0.23)[a]	7.16 (0.59)	5.22 (0.30)	1.94	27
F77	2.52 (0.18)[b]	5.55 (0.22)	3.42 (0.14)	2.13	38
August 2005					
F98		3.87 (0.11)	3.16 (0.12)	0.71	18
F89		6.66 (0.56)	4.86 (0.29)	1.80	27
F77		5.33 (0.19)	3.51 (0.16)	1.82	34

[a,b] same symbols denote no significant difference at P=0.05.

Fig 2.1. Regression analyses for with and without ring soil respiration combined for the F98, F89 and F77 sites. Regression equation is: $y = 1.14x$ (forced through zero), $R^2 = 0.94$, $P < 0.05$.

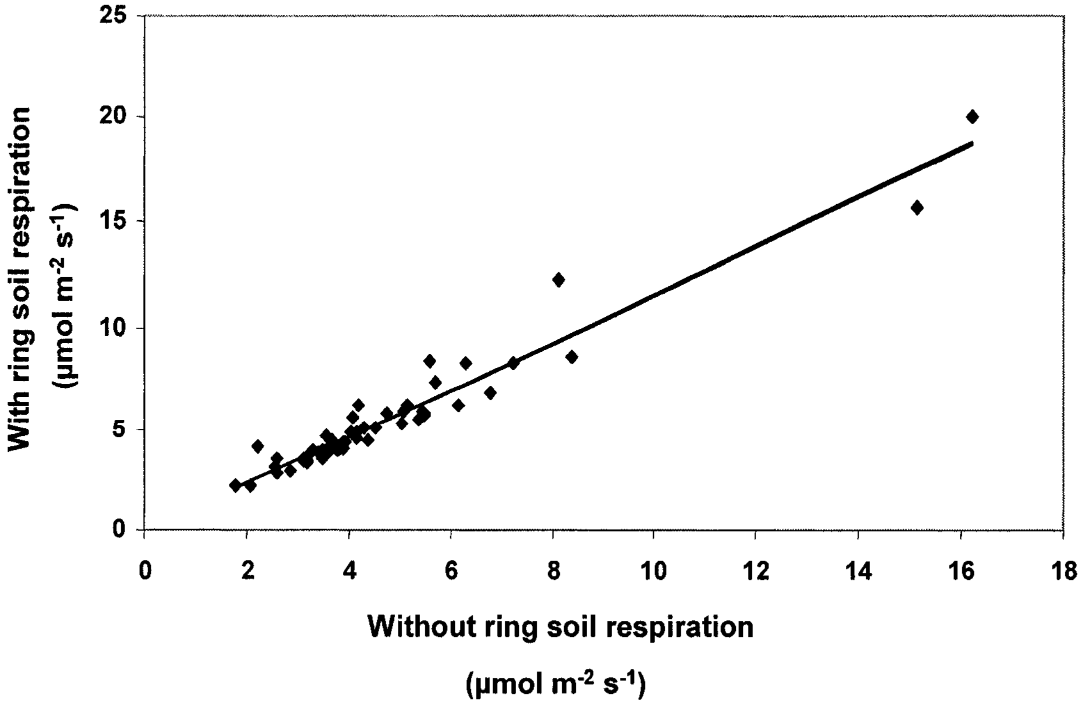


Fig 2.2. Soil respiration, soil temperature and soil moisture during the growing season of 2004 and 2005 at the three post-fire sites. Means (± SE) are given. For soil respiration and soil temperature, n =100 in 2004 and n =35 in 2005 and for soil moisture n =12 to 15. Different letters indicate a significant difference (P<0.05) among sites and sampling periods within a given year only.

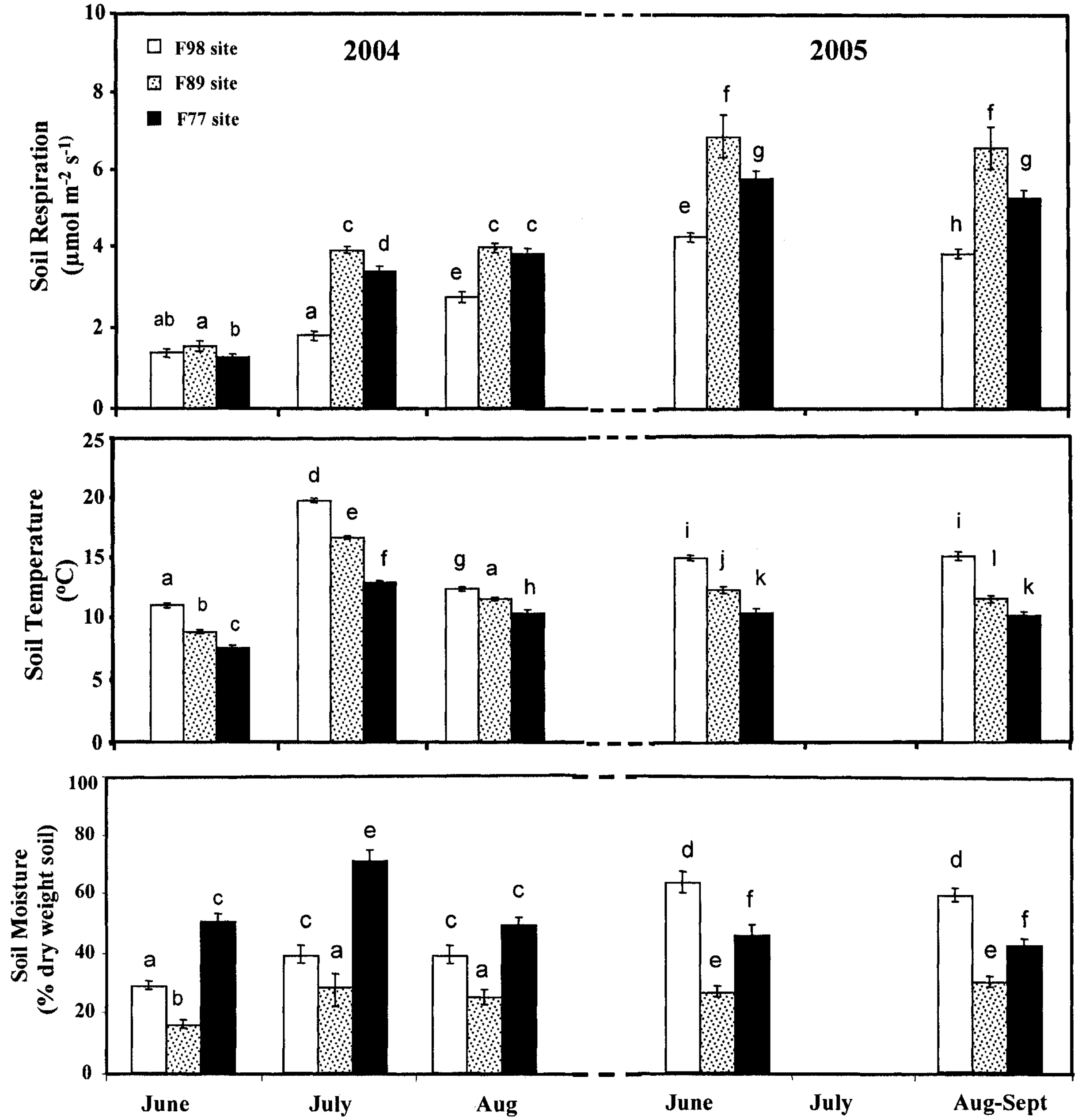


Fig 2.3. Relationship between soil respiration and the organic layer thickness in June 2004. Relationships were not statistically different for any of the sites. The data were corrected to a base temperature using a Q_{10} of 2 (see text for details).

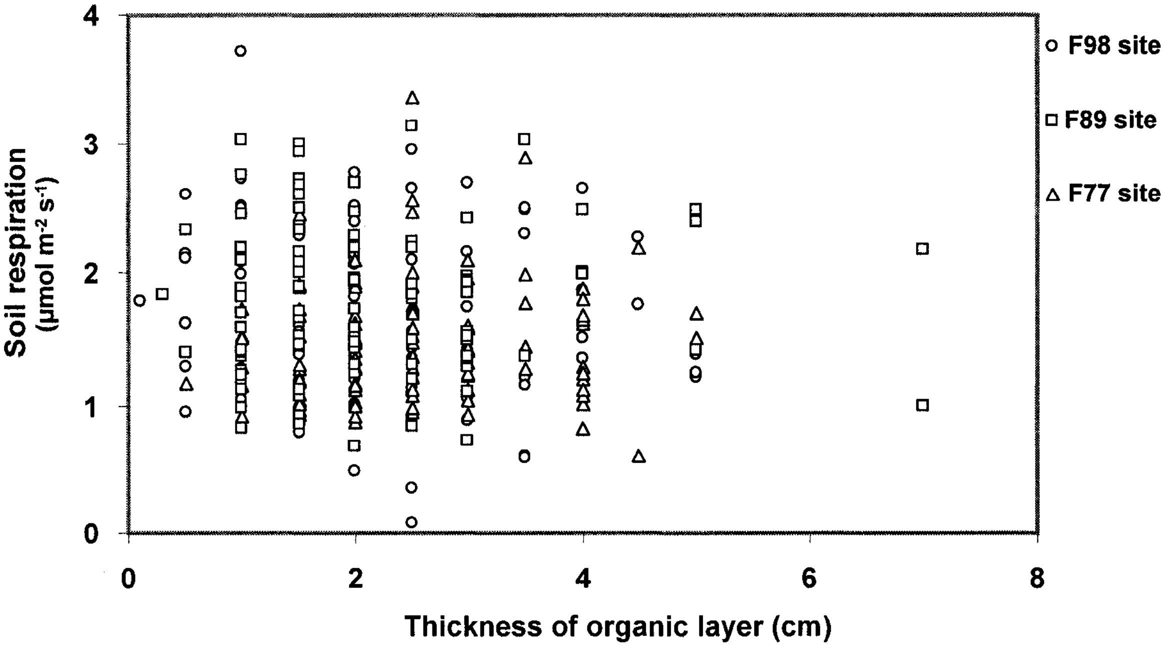
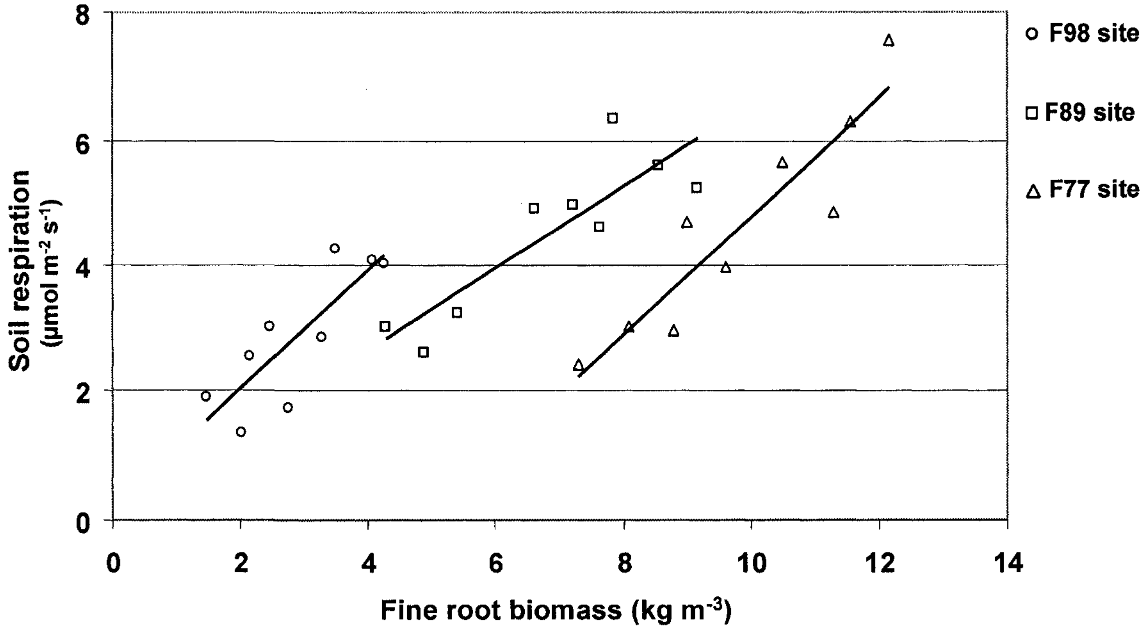


Fig 2.4. Relationship between soil respiration and dry fine root biomass (0 to 5 cm depth) at the three post-fire sites in August 2004. Regression equations are F98 site: $y = 0.83x + 0.10$ ($R^2 = 0.68$), F89 site: $y = 0.58x - 0.02$ ($R^2 = 0.76$), F77 site: $y = 0.82x - 4.09$ ($R^2 = 0.85$), where $n = 9$ and $P < 0.005$ in all cases. The data were corrected for a missing O-ring by an increase of 14% and were adjusted to a base temperature using a Q_{10} of 2 (see text for details).



CHAPTER 3

3. RESPONSES OF ECOSYSTEM RESPIRATION IN POST-FIRE BOREAL FORESTS TO SOIL TEMPERATURE AND MOISTURE VARIATIONS IN CONTRASTING WET AND DRY YEARS

3.1. Introduction

Ecosystem respiration (ER) has recently been suggested as the main determinant of the carbon balance (Valentini et al., 2000; Janssens et al., 2001). ER is a process whereby CO_2 is released via aboveground plant respiration, soil respiration that includes microbial and plant root respiration and woody debris respiration. Each of these ER components is important; however soil respiration is generally considered a dominant ER process, which accounts for more than two-thirds of ER on an annual basis (Bolstad et al., 2004; Griffis et al., 2004; Lavigne et al., 1997). Ecosystem respiration is generally measured either through separate chamber measurements of each ER component or through night-time eddy covariance flux (EC) measurements. Night-time EC measurements are best suited to measure ER, when photosynthetic fixation of CO_2 is not a factor. Despite physiological differences between the night-time and day-time ER, studies have tried to extrapolate the night-time ER to calculate day-time ER using temperature response functions (Griffis et al., 2003; Falge et al., 2002). These studies have reported good agreements between the day-time and night-time ER for a variety of ecosystem types.

To predict climate change, we require a thorough understanding of environmental controls on ER. Since soil respiration is a component of the bulk ER, therefore factors controlling soil respiration may help in better understanding the environmental controls on ER. Moreover, the night-time ER measured by EC is sometimes referred to as "soil respiration" (Lavigne et al., 1997).

Variations in soil respiration are usually correlated with change in soil temperature (Lloyd and Taylor, 1994). Many studies have reported a high correlation between soil respiration and temperature when water is not limiting, especially at the seasonal time scale (Drewitt et al., 2002; Curiel Yuste et al., 2003). At low soil water content, a strong reduction in soil respiration has been observed (Griffis et al., 2004), which is mainly attributed to the reduction of microbial decomposition of organic matter. At high soil water content, a slight reduction in soil respiration may also occur due to diffusional constraints to the transport of CO_2 and oxygen (O_2) within the soil matrix (Bunnell et al., 1977). However, there are only limited studies to fully understand and support this hypothesis (Drewitt et al., 2002). Generally, the seasonal dependence of soil respiration on soil water content is often confounded with its relation to soil temperature and it is difficult to identify the independent effect of each variable. While there is no general agreement on the mathematical model of the relationship between soil respiration and soil water content (Davidson et al., 2000), the relationship between soil respiration and temperature is usually modeled by a simple exponential function (Lloyd and Taylor, 1994; Qi et al., 2002). This is generally described by the following equation:

$$R_s = ae^{bT} \quad [3.1]$$

where R_s is soil CO_2 efflux, and a and b are site-specific, empirical, fitted parameters. A temperature sensitivity factor called Q_{10} (= e^{10b}), describes the sensitivity of soil respiration to every 10°C increase in soil temperature. A higher Q_{10} value corresponds to higher temperature sensitivity, irrespective of soil moisture content. Reported Q_{10} values are usually around 2 to 2.5 (Raich and Schlesinger, 1992), but higher Q_{10} values between 4 and 6 have also been reported for cool temperate and boreal regions (Morgenstern et al., 2004; Russell and Voroney, 1998).

The Q_{10} value is often used in carbon budget models to simulate the response of soil respiration or ER to temperature fluctuations (Lloyd and Taylor, 1994; Qi et al., 2002). The use of this simple Q_{10} relationship in the models has been criticized, because the relationship itself depends both on temperature and moisture (Lloyd and Taylor, 1994; Davidson et al., 2000; Qi et al., 2002). However, an empirical relationship often provides a better fit compared to process based models, where moisture effects are also incorporated (Drewitt et al., 2002).

There is increasing evidence that the temperature sensitivity of soil respiration decreases with increasing soil temperature within and among stands (Reichstein et al., 2003, Kirschbaum, 1995). A similar response has been shown under low soil moisture or drought conditions (Curiel Yuste et al., 2003, Flanagan and Johnson, 2005, Lavigne et al., 2004). Although the exact mechanism for these responses is not clear, it could be due to the physiological acclimation of roots (Atkin et al., 2000) or there could be rapid exhaustion of labile organic substrates at higher temperature and subsequent decrease in heterotrophic respiration. There could be also a shift in microbial community structure (Janssens and Pilegaard, 2003) under water stress conditions, which in turn switches the microbial decomposition from labile to recalcitrant substrates, or vice versa.

Recently, some comprehensive studies have been carried out to better understand of the soil respiration response to the environmental variables in natural ecosystems. For example, Griffis et al. (2004) reported that soil temperature was the primary variable accounting for seasonal variations in soil respiration but that a drought resulted in strong reduction in soil respiration late in the growing season. Gaumont-Guay et al. (2006) indicated only a short-term reduction in the temperature sensitivity of soil respiration with increasing soil water limitation in a mature boreal aspen stand. Their calculated daily Q_{10} values showed strong seasonality and had a lower Q_{10} (2.8) than those derived from the seasonal relationships. However, in post-fire ecosystems, the soil respiration processes show small to large variations depending upon the intensity of fire. Singh et al. (2008) reported that much of the post-fire respiration during the early forest succession is mainly due to the root respiration of actively growing early succession, and that microbial (heterotrophic) respiration seemed to be less important. This means that the root (autotrophic) response to variations in soil temperature and moisture may contribute more compared to microbial component in predicting the Q_{10} relationships in the younger post-fire boreal forest sites.

The objectives of this study were 1) to evaluate and compare the night-time ER response to variations in soil temperature and moisture at three post-fire sites (F98, F89 and F77 site) burned in 1998, 1989 and 1977 respectively during dry (2003) and wet (2005) years; and 2) to determine whether ER shows any seasonal patterns related to soil moisture, by excluding the effect of soil temperature. In addition, we also attempted to calculate Q_{10} from the night-time ER and soil temperature relationships and compare among sites and years, wherever possible.

3.2. Materials and Methods

3.2.1. Study Sites

A detailed description of study sites is given in Chapter 2, section 2.2.1.

3.2.2. Flux Measurements

The flux towers or eddy covariance towers at our sites were run as a part of the Fluxnet-Canada Research Network (FCRN). The towers measure half hourly ecosystem exchange of CO_2 between the forest and atmosphere. Towers were triangular with a height of 5.2 and 7.4 m at the F89 and F77 sites, respectively. However, at the F98 site, a 20 m tall scaffold tower has been established since August 2002. The meteorological and flux measurements were taken at the top of the tower by site-specific instruments.

The site specific instrumentation, meteorological and flux measurements are fully described by Sass (2007). Briefly, the flux measurements used the eddy covariance technique, which used a sonic anemometer coupled with an infra-red gas analyser (IRGA). High frequency (10

Hz) data were processed on-line to calculate the covariance at 30-min intervals. Coordinate rotations were done following the method of Tanner and Thurtell (1969). Mass storage was included in the fluxes, although this becomes very small as daily totals. Down-welling photosynthetically-active radiation (PAR) was measured with quantum sensors (Licor Inc. LI190, Lincoln, NE, USA).

The yearly meteorological and flux data sets for our sites and many other sites across Canada get uploaded by the Fluxnet-Canada Research Network on their website – www.fluxnet-canada.ca at the end of a given year. The fluxnet data archive is only available to the research and student participants. The data were downloaded from the fluxnet data archive for the year 2003 and 2005 for our sites. A quality control and comprehensive analysis was performed on each data set. These are described in the following sections.

3.2.3. Data Quality Control

Quality control included removal of periods of clearly bad half-hour data (e.g., caused by precipitation or malfunctions). Data below a specified u* (friction velocity) threshold were also removed. Night-time measurements were defined when PAR was less than 0 μmol $m^{-2}s^{-1}$ and were separated from the data. The night-time data were then bin-averaged for 10 bins with an equal number of measurements. The 80% of the average CO_2 flux was then calculated for the last three bins, which defined the u* threshold value. The threshold value is rounded up to the nearest 0.05 m s^{-1} value (Amiro et al., 2006). A range of threshold values were found between 0.2 m s^{-1} and 0.3 m s^{-1} when calculated for each site per year. For the data analysis, we used a threshold of 0.30 m s^{-1} for the F98 and F77 sites and 0.25 m s^{-1} for the F89 site as our best estimate.

3.2.4. Soil Temperature and Moisture Measurements

Soil temperature and moisture data were used from the archived meteorological data files from the FCRN website. The data contained half-hourly soil temperature measurements at a depth of 5 cm and half-hourly soil volumetric moisture measurements over a depth of 0-30 cm. The half-hourly soil temperature and volumetric soil moisture were measured using thermocouples and CS616 soil moisture probes (Campbell Scientific Inc., Logan, UT, USA), respectively.

3.2.5. Ecosystem Respiration (ER) Measurements from Tower Data

Generally, the night-time forest-atmosphere CO_2 exchange (NEE) measured with eddy covariance techniques provides a measure of ER (Barr et al., 2002; Griffis et al., 2003). We only considered the raw NEE values (not gap-filled) in our analysis. A number of steps in the data analysis were performed to obtain night-time NEE measurements. The first step in our analysis was data filtration for the u* threshold. This is described in section 3.2.3 (see above). In the second step, the data were filtered and rejected when PAR > 10 μmol $m^{-2}s^{-1}$.The last step included data filtering for upper and lower limits of NEE as $-30 < \text{NEE} < 30$ μmol $m^{-2}s^{-1}$.

When all the quality control and data filtration were done, we created data sets for half hourly ER and soil temperature for the 2003 and 2005 years at our three post-fire sites.

Therefore, to better analyse the ER and temperature relationships, the average ER values were binned for the corresponding soil temperature at the depth of 5 cm over the range of 0 to 20°C with a bin size of 1°C.

3.2.6. Statistical Analyses

Regression analyses were used to analyse ER and soil temperature relationships at each site during the wet (2005) and dry (2003) years. Data were compared by fitting exponential and empirical logistic relationships over each year. The fitted equations for an exponential and an empirical logistic model are given below by (3) and (4) respectively.

$$ER = \beta_o . e^{(\beta_1 . T)} \qquad [3.2]$$

$$ER = r_1 / (1+ \exp [r_2(r_3 - T)]) \qquad [3.3]$$

where, T represents soil temperature, β_1 in equation (3) is the slope of the exponential model while r_1, r_2, and r_3 in (4) are empirical constants for the logistic model. The exponential model represented by equation (3) is the standard model given in various statistical packages. However, the empirical logistic model given in equation (4) is the standard model used by the FCRN to gap fill the missing NEE data. A detailed algorithm is described by Sass (2007) and Amiro et al. (2006).

At sites F98 and F77 an exponential relationship between ER and soil temperature was a better fit based on higher R^2 value during both wet and dry years. Therefore, these data were transformed into the logarithmic form. This was done to approach homogeneity in variances for each set of data. Linear regression analysis was then performed to test the relationships. The slopes or rates of increase in ER among sites were compared using a dummy variable procedure in the regression analysis followed by a contrast test for regression coefficients (SAS Institute Inc., 2003). We accepted the test to be significant at $P \leq 0.05$. A Q_{10} value for these sites was calculated using equation (5) below.

$$Q_{10} = e^{10 \cdot \beta_1} \tag{5}$$

where β_1 is from equation [3.2].

The ER and moisture relationships were tested using linear regression analyses. The empirical logistic models were fitted and parameters estimated using the "Solver" feature in the Microsoft Excel software. All other analyses were done with SAS statistical software (SAS Institute Inc., 2003).

3.3. Results

3.3.1. Dry (2003) and wet (2005) years. Table 3.1 shows the annual precipitation values at our post-fire sites. The years 2003 and 2005 were characterized as dry and wet years respectively. The total yearly rainfall during 2003 was about 63% of that in 2005.

3.3.2. Relationship between Ecosystem Respiration (ER) and Soil Temperature.

A comparison of exponential and empirical logistic relationships between ER and soil temperature at any given site during the dry and wet years is shown in Fig. 3.1. The F98 and

F77 sites tend to follow an exponential model rather than an empirical logistic model. Although both models show significant relationships ($P<0.05$), R^2 values were generally higher for the exponential model compared to the logistic model (for site specific R^2 values see Fig. 3.1). Note that the F77 site during the dry year had only five data points within the soil temperature range of 7 to 10°C, therefore it was difficult to accurately predict the relationship between ER and soil respiration at this site. The F89 site seems to be different during both dry and wet years compared to the other sites (Fig 3.1). Clearly, the F89 site showed a significant empirical logistic relationship between ER and soil respiration at least during the dry year. However, the relationship during the wet year could also be viewed as exponential because of only a slight difference (0.04 lower) in R^2 compared to the empirical logistic model. The important thing to note is that ER did not show an increase with increasing soil temperature above 7-8 °C during the dry year whereas this trend is not as obvious during the wet year.

Fig. 3.2. shows the comparison of the ER and soil temperature relationships among the three sites during the dry and wet years separately. Only the best fit models based on higher R^2 are considered here. The model parameters and equations are given in Table 3.2. For the F77 and F98 sites, there was a significant difference ($P< 0.05$) in the slope of the exponential regression curves between the sites during both dry and wet years. The F77 site showed a significantly higher slope or rate of increase ($P<0.05$) in ER with increasing soil temperature compared to the F98 site during the wet year. However, during the wet year, the F89 site showed the highest rate of increase (slope) in ER with increasing soil temperature but not significantly different than the F77 site.

3.3.3. Q_{10} Calculation

We calculated the Q_{10} values from the exponential relationships between ER and soil temperature at the F98 and F77 sites during both dry and wet years (Fig. 3.2.). The calculated Q_{10} values at the F98 and F77 sites were 2.8 and 2.9 for the dry year and 2.7 and 4.1 for the wet year respectively. Note that the F77 site during the dry year showed a lower Q_{10} compared to the wet year. However, we consider the wet year's value to be more realistic because of the limited data during the dry year at this site. For the F89 site, a Q_{10} of 5.6 was calculated for the wet year.

3.3.4. Normalized Ecosystem Respiration (ER) and Soil Moisture Patterns

The ER was normalized for the change in soil temperature at all the sites using their respective Q_{10} values and a 15°C base temperature (see equations 3 and 5). We used the biweekly average of the 'normalized ER' to clearly observe the changes. Fig. 3.3a and 3.4a show the ER at all the sites during both the dry and wet years. Similarly, we calculated biweekly average soil moisture patterns for both years (Fig. 3.3b. and 3.4b.). From these graphs, we tried to evaluate changes in the ER corresponding to changes in the soil moisture. In general, there was no pattern in the ER with changes in soil moisture (Fig 3.3. and 3.4. $R^2 < 0.1$, $P < 0.05$). The volumetric soil moisture showed a two-fold decline from day 100 to day 250 and remained stable afterwards at the F98 site and slightly increased at the F89 site during the dry year. The wet year also experienced a similar decrease but over the period of day 141 to day 211 after which soil moisture rose almost to the previous level within few days. The ER however showed no pattern at the F98 and F77 sites during both years. The F89 site showed a two-to-three fold increase in ER from day 100 to day 170, which declined afterwards during the dry year. The wet year ER however, decreased from the day 141 to 210 and increased afterwards until the end of the year.

Overall, ER was significantly lower ($P<0.05$) at the F98 site during both the dry and wet years while soil moisture was significantly lower only during the wet year. The ER and soil moisture did not differ significantly between the F89 and F77 sites during the wet (2005) year. We did not have enough data points for the F77 site during the dry year, therefore we could only compare the F77 site with the two other sites during the wet year.

3.4. Discussion

3.4.1. Environmental Controls on Ecosystem Respiration (ER) in Post-fire Boreal Forests

ER was highly correlated ($R^2 > 0.75$) with soil temperature at all sites during both dry and wet years. An exponential model best described the relationship between ER and soil temperature at the F89 and F77 sites while an empirical logistic model provided a better fit at the F89 site during both years (Fig. 3.1. and 3.2.). This indicates that ER response to soil temperature is quite different at the F89 site. Even for the F98 and F77 sites, the significant differences in the slope of the exponential curves indicates that ER responds to soil temperature at a much faster rate at the older F77 site compared to the younger F98 site. These differences in the ER rate of response to soil temperature could be attributed to differences in levels of autotrophic (root) and heterotrophic (microbial) activities among sites. Manipulation experiments including warming of post-fire plots in Alaska have demonstrated that soil respiration increases with increasing soil temperature; however, root biomass significantly decreased (Bergner et al. 2004). Hence, increased microbial activity could likely be the reason. But some studies indicate that soil warming only has a short-term effect on heterotrophic respiration (e.g., Melillo et al., 2002) and that root response and net ecosystem production is often more important (Lavigne et al., 2003), especially considering their contribution to the total CO_2 flux across the atmosphere-plant-soil interface. Several authors (e.g. Boone et al., 1998; Epron et al., 2001) previously believed that root respiration responds more strongly to variations in soil temperature than does microbial respiration. However, many recent studies have changed this view and showed that microbial activity is more sensitive to change in soil temperature compared to root respiration, which in fact is more sensitive to current supply of photosynthates from above ground tree canopy (Hogberg et al. 2001, Bhupinderpal-Singh et al. 2003).

In the present study, we speculate that the increase in ER with increasing soil temperature at our post-fire sites could be largely due to an increase in root activity. This is because of the much lower microbial (heterotrophic) contribution to soil respiration compared to root component. The microbial component contributed less than 17, 27 and 38% to total respiration at the F98, F89 and F77 sites respectively (Chapter 2). Moreover, recent studies have reported greater temperature sensitivity for microbial respiration compared to root respiration as discussed above (Bhupinderpal-Singh et al., 2003; Olsson et al., 2005). Therefore, it is not clear whether increases in ER with increasing soil temperature at our post-fire sites could be attributed to greater temperature sensitivity of root respiration (Boone et al., 1998; Epron et al., 2001) or microbial respiration (Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003) or both.

When comparing the ER response to increasing soil temperatures among the three study sites, the youngest F98 site had a significantly lower ER rate of increase compared to the older F77 sites. Note that the F98 site showed the lowest soil respiration and root biomass compared to the older F89 and F77 sites (Chapter 2). Therefore, the lower ER rate of increase at the F98 site could be attributed to its lower root component although there was also some difference in its microbial component, which was <10% (<27 minus 17%) and <21%(<38 minus 17%) (see Table 2.2, Chapter 2) lower compared to the F89 and F77 sites respectively. The F89 and F77 sites showed no significant difference in their ER rate of response during the wet year. Note that the F89 had a lower root biomass than the F77 site, but had a greater total soil respiration. This greater soil respiration was attributed to the presence of broad-leaved trees and their associated greater root activity at the F89 site (Chapter 2). Thus, the differences in this root activity likely explain the differences in the ER rate of response to soil temperature between the F89 and F77 sites. However, in this case microbial component was <11% (38 minus 27% see Table 2.2, Chapter 2) higher at the F77 site. If the microbial component significantly contributes to differences in ER response to soil temperature among sites, F77 site should have the highest ER rate of response to soil temperature. However, this is not the case here, therefore we conclude that differences in root activity among sites largely explain the differences in the ER rate of response to soil temperature.

It is also important to note that ER at the F89 site followed an empirical logistic relationship with soil temperature and tends to stabilize at higher temperature (see Fig. 3.1. and 3.2.). Thus, the rate of ER increase seems to be limited by some factor (other than soil temperature) at higher soil temperature. Soil moisture could be the factor because this trend appears to be more pronounced during the dry year.

The wet and dry years did not affect the exponential relationships between the ER and soil temperature at the F98 site and possibly at the F77 sites as well. Similarly an empirical logistic relationship did not seem to change between the dry and wet years at the F89 site. The wet year may have caused the ER to follow an exponential relationship with soil temperature however it was not detected due to a lack of data points at higher soil temperature. Laboratory studies have clearly demonstrated the importance of water content as a factor influencing respiration. In the field studies, however, the temperature effect is often more pronounced than the water effect, especially in temperate and boreal regions. In general, sites with wet and cool conditions tend to have higher Q_{10} values (Lloyd and Taylor, 1994; Davidson et al., 1998). Similarly, Khomik et al. (2006) reported that their sites in northern Ontario experiencing wet and cool conditions tend to have more sensitive soil respiration-temperature relationships. However, our results seem to contradict these findings because Q_{10} values were quite similar between the wet and dry years at our F98 site. This inconsistency could result from the differences in the contribution and sensitivity of the soil respiratory components of ER, especially root vs microbial respiration, to soil factors such as soil temperature and moisture. Soil respiration at our sites was mainly driven by the root component as discussed above (also see chapter 2) and studies have shown that the root component of soil respiration tends to be less sensitive to moisture changes (Borken et al., 2006). The lower soil moisture sensitivity of root respiration is largely due to the greater rooting depth of trees (Russell and Voroney, 1998; Broken at al., 2006). Thus, it is possible that root-dominated respiration at our sites shows similar Q_{10} values both in wet and dry years.

3.4.2. Q_{10} Values at the Post-fire Sites and its Implications

The temperature dependence of respiration, expressed through the Q_{10} value, has been a focus of many studies recently, for example: Jassal et al. (2007), Gaumont-Guay et al., (2006), Khomik et al. (2006), Wang et al. (2002), Xu and Qi (2001), Bhupinderpal-Singh et al. (2003), Buchmann (2000). However, there are still uncertainties in understanding and modeling the temperature dependence of soil respiration or ER under different environmental conditions. While in some situations, linear regression gives good relationships between soil respiration and temperature (Raich and Schlesinger, 1992), the majority of studies support exponential regression equations (e.g. Wang et al., 2007; Khomik et al., 2006; Lavigne et al., 2004; Boone et al., 1998; Davidson et al., 1998; Burton et al., 1998; Buchmann, 2000). Although we measured ER in this study rather than soil respiration, we observed exponential relationships between ER and soil temperature at the F98 and F77 sites. Some authors strongly recommend an Arrhenius type equation especially where the effective activation energy changes inversely with temperature. This results in evenly distributed residual variances across the entire temperature range (Lloyd and Taylor, 1994). They also argue that over a wide range of temperature, soil microbial populations responsible for soil respiration in part might change, therefore, Q_{10} values, which indicate temperature sensitivity, might also change. However, the temperature range in Lloyd and Taylor (1994) was about 40°C, more than twice the range found in our study. Buchmann (2000) discussed that for a relatively small temperature range (e.g., 0-20°C), an exponential function provides a better fit and similar residual variances compared to the Arrhenius function. The F89 site ER however showed an empirical logistic relationship with soil temperature especially during the dry year. Barr et al. (2002) used a similar equation to describe ER and soil temperature relationship at the Old Aspen site close to our sites and the Camp Borden site in southern Ontario.

The Q_{10} value of ER at our post-fire sites varied between 2.7 and 5.6. The recently burned F98 site showed the lowest Q_{10} values followed by the oldest F77 site and F89 sites. The Q_{10} values were almost one and a half and two fold higher at the F77 and F89 sites compared to the F98 site during the wet and dry year, respectively. These differences in Q_{10} or ER response to soil temperature are discussed in section 3.4.1. In general, these values are comparable to previously reported values by Russell and Voroney (1998) of between 3.9 and 5.1 for their boreal forest study. More recently, Wang et al. (2006) reported Q_{10} values ranging from 1.8 to 5.4 for their different aged stands in northern Manitoba. Other authors have reported Q_{10} values of approximately 2.0 for forest ecosystems across North America and Europe (Falge et al., 2002; Buchmann, 2000). However, Lloyd and Taylor (1994) and Qi et al. (2002) indicate that Q_{10} values themselves are temperature dependent.

3.4.3. Ecosystem Respiration and Moisture Relationships

Laboratories studies have clearly demonstrated the importance of moisture as a factor influencing soil respiration. In the field studies, the temperature effect is often more pronounced, especially in temperate and boreal regions. Numerous studies have discussed the soil respiration and temperature relationship using different models, of which the exponential model has been widely accepted. However, the effect of soil moisture on respiration has not been clearly understood. Unlike soil respiration and temperature relation studies, there is no general agreement on soil respiration and soil moisture relationships. Davidson et al. (1998) noted that the effect of temperature and moisture were confounded in the forest soils of New England, where the summers are warm and winters are cool and wet. They noticed an increase in soil respiration from winter to early summer. This was not only due to warmer soil temperature in early summer, but also to a decline in soil moisture from saturated conditions in the winter to near optimal in early summer.

One way to study the effects of soil water content in the field without the confounding effect of temperature would be to choose a field site where temperature is nearly uniform throughout the year. However, it may be difficult to find such conditions. In this study, we normalized the ER for the change in soil temperature at all our post-fire sites using the site-specific Q_{10} values. This allowed us to observe the soil moisture-related changes in ER. Our youngest F98 and oldest F77 sites did not show any moisture-related changes in soil respiration at any given year. The decreasing soil moisture during the summer and relatively stable ER indicate that soil moisture is not the factor influencing soil respiration at these sites. Fang and Moncrieff (2001) reported no influence of soil moisture on CO_2 efflux or on the Q_{10} values among three moisture treatments in their laboratory study. However, in field conditions, the influence of soil moisture on soil CO_2 flux becomes complicated through its effect on respiratory activity of roots and microbes and on the gas transport through soil.

The F89 site showed a temporal pattern in soil respiration over the summer during the dry and wet years (Fig 3.3 and 3.4). The decline in ER during mid to late summer seems to be related to a similar decline in soil moisture at any given year. Although there is a lag for the decline in ER during the dry year, it was more obvious during the wet year, where the dip in soil moisture corresponds to the dip in ER at Day 210. Studies dealing with soil respiration find a similar trend, where soil respiration decreased with decreasing soil water content (Davidson et al., 2000; Orchard and Cook, 1983; Irvine and Law, 2002).

Recently, Gaumont-Guay et al. (2006) reported a decrease in soil respiration during late summer when the soil moisture was below the soil water field capacity. They reasoned that the decline in soil respiration was due to inhibition of microbial activity rather than to root activity. In our case, it was difficult to identify whether the decrease in ER was due to microbial or root inhibition. However, it is speculated that the decline in ER is due to inhibition of both root and microbial activity at our F89 site, although there could be differences in the level of inhibition between the two. At this site, the microbial component contributes less than 27% to ER and is generally more sensitive to the variation in soil moisture than does the root component. Therefore, a greater decline in microbial respiration could be expected.

3.5. Conclusions and Implications

An accurate understanding and interpretation of soil and plant factors influencing ER remains a challenging task. Fire, through its direct and indirect effects on these factors further complicates the belowground processes, which are hypothesized to change during the forest succession following fire (Singh et al., 2008). Comparison of post-fire ER response to soil temperature and moisture between the contrasting dry and wet years provided a better understanding into the control of ER by these variables at our sites.

In our study we found significant exponential relationships between the ER and soil temperature (5-cm depth) at the F98 and F77 sites. The F89 site had an empirical logistic relationship because ER tended to stabilize at higher temperature especially during the dry year. The wet year relationship however was closer to exponential. There was a higher ER rate of response to increasing soil temperature at the older F89 followed by the F77 and F98 sites. Since the root component was the dominant source of soil respiration at these sites (Chapter 2), these differences may therefore be ascribed to the greater root sensitivity to soil temperature at the older F89 and F77 sites. We could not separately examine the soil temperature sensitivity of root and microbial activity. The microbial contribution to ER is quite small (less than 17 to 38%) compared to the root contribution at our post-fire sites. However, the microbial sensitivity to soil temperature should not be underestimated. This is because some recent studies propose that root activity is less sensitive to variations in soil temperature than is microbial activity (Bhupinderpal-Singh et al., 2003). They further argue that root activity in fact is more sensitive to recently fixed carbohydrate supply from the aboveground canopy. Therefore, more thorough studies are definitely needed to better understand the relative contribution and the sensitivity aspects of these two components of ER. It was also noticed that Q_{10}, the temperature sensitivity of the dominating root-driven ER especially at the younger F98 post-fire site, did not differ between the wet and dry years, thus indicating less dependency of root respiration on soil moisture variations.

Since respiration from the whole ecosystem (ER) was measured it is also important to consider respiration from the components other than soil such as coarse woody debris respiration (CWD), stem and leaf respiration. Although most studies agree that the majority of ER comes from the soil component, some studies have reported a wide range of soil respiration to ER ratio varying between 0.3 and 0.9 due to differences in vegetation type and stand age (Davidson et al., 2006; Yuste et al., 2005; Jassal et al., 2007). This means respiration from the components such as stem, leaves or CWD could contribute an appreciable amount (Xu et al., 2000). In post-fire ecosystems, a large amount of CWD debris left following fire could play a significant role in contributing to ER. At our younger post-fire F98 site, CWD is standing or just perched over 1 m above the soil surface. Therefore, respiration from the CWD at this site is expected to be small and should not significantly affect ER. However, at the older F89 site, the CWD debris are on the ground and partially rotten, while they are decomposing quickly at the F77 site. Amiro et al. (2006) reported a large negative NEP (net ecosystem productivity) due to enhanced ER following a period of rain at the F89 site. They hypothesized that wetter conditions may have enhanced CWD decomposition. It is believed that respiration from CWD at the older F89 and F77 sites may contribute significantly to ER. Therefore, to better understand the environmental controls of ER in post-fire ecosystems, we first need to determine the contribution of CWD respiration to ER, and secondly we need to understand the CWD response to environmental factors such as temperature and moisture.

3.6. References

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Table 3.1. Annual precipitation values for the three post-fire boreal forest study sites in central Saskatchewan. Measurements from Waskesiu Lake Town were obtained from Environment Canada archives (Adapted from Sass, 2007).

	Site	2003	2005
Yearly Rainfall (mm) Waskesiu Town		284.8	450.4
Precipitation (mm) Waskesiu Town**		329.6	528.4*
Total Yearly Rainfall (mm)	F98	276.7	423.5
	F89	236.6	490.7
	F77	--	559.2

* Data for January and February 2005 unavailable

** Precipitation includes snow

Table 3.2. Best fit model equations and parameters for ecosystem respiration (ER) and soil temperature relationship at the three post-fire study sites during the dry (2003) and wet (2005) years.

Study sites	Model	Equation	Parameters				
			β_o	β_1	r_1	r_2	r_3
Dry Year (2003)							
F98	Exponential	$y = \beta_o . e^{(\beta_1 . T)}$	0.56	0.11	--	--	--
F89	Logistic	$y = r_1 / (1+ \exp [r_2(r_3-T)])$	--	--	7.4	0.74	3.99
F77	Exponential	$y = \beta_o . e^{(\beta_1 . T)}$	--	--	--	--	--
Wet Year (2005)							
F98	Exponential	$y = \beta_o . e^{(\beta_1 . T)}$	0.92	0.1	--	--	--
F89	Logistic	$y = r_1 / (1+ \exp [r_2(r_3-T)])$	--	--	10.53	0.28	9.62
F77	Exponential	$y = \beta_o . e^{(\beta_1 . T)}$	1.51		--	--	--

Fig 3.1. Relationship between ecosystem respiration (ER) and soil temperature at the three post-fire sites during the dry (2003) and wet (2005) year. Means (± SE) are given. The equations are described in the text. The "dotted" and "solid" line represents the empirical logistic and exponential fitted model respectively (not shown for F77 for wet year). Exponential model R^2 for dry and wet years were for the F98 site: 0.85 and 0.77, F89 site: 0.70 and 0.83 respectively and F77site: 0.93 for wet year. Empirical logistic R^2 were for the F98 site: 0.81 and 0.75, F89 site: 0.91 and 0.87 respectively and F77 site: 0.84 for wet year. N varies from 4 to 120 and $P < 0.05$ in all cases.

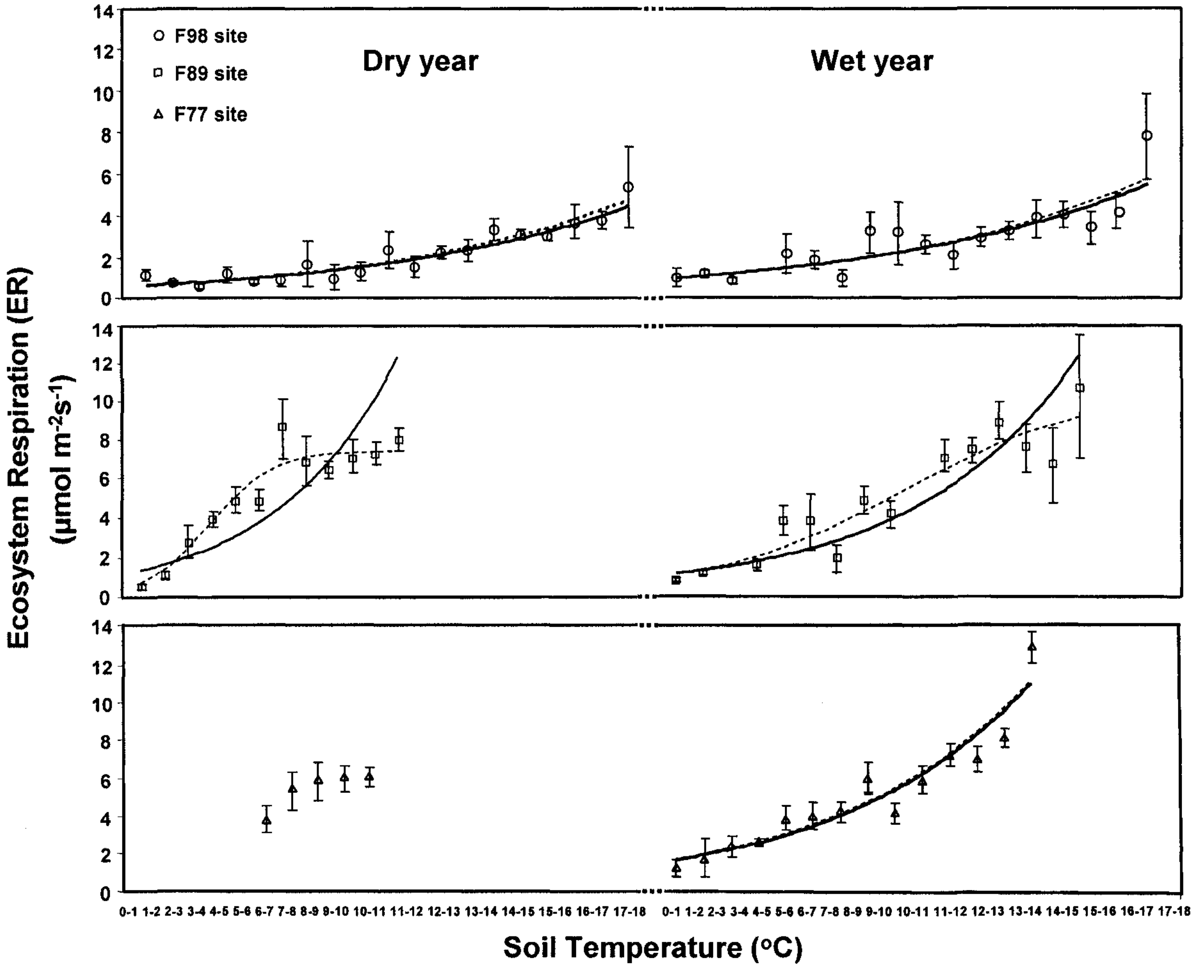


Fig 3.2 (a and b). Comparison of ecosystem respiration (ER) and soil temperature among the three post-fire sites during the dry (2003) and wet (2005) years except F77 for dry year. Means (± SE) are given. Only best fit models are shown i.e. exponential at the F77 and F98 sites and empirical logistic at the F89 site during both dry and wet years. For specific R^2 see fig 3.1.

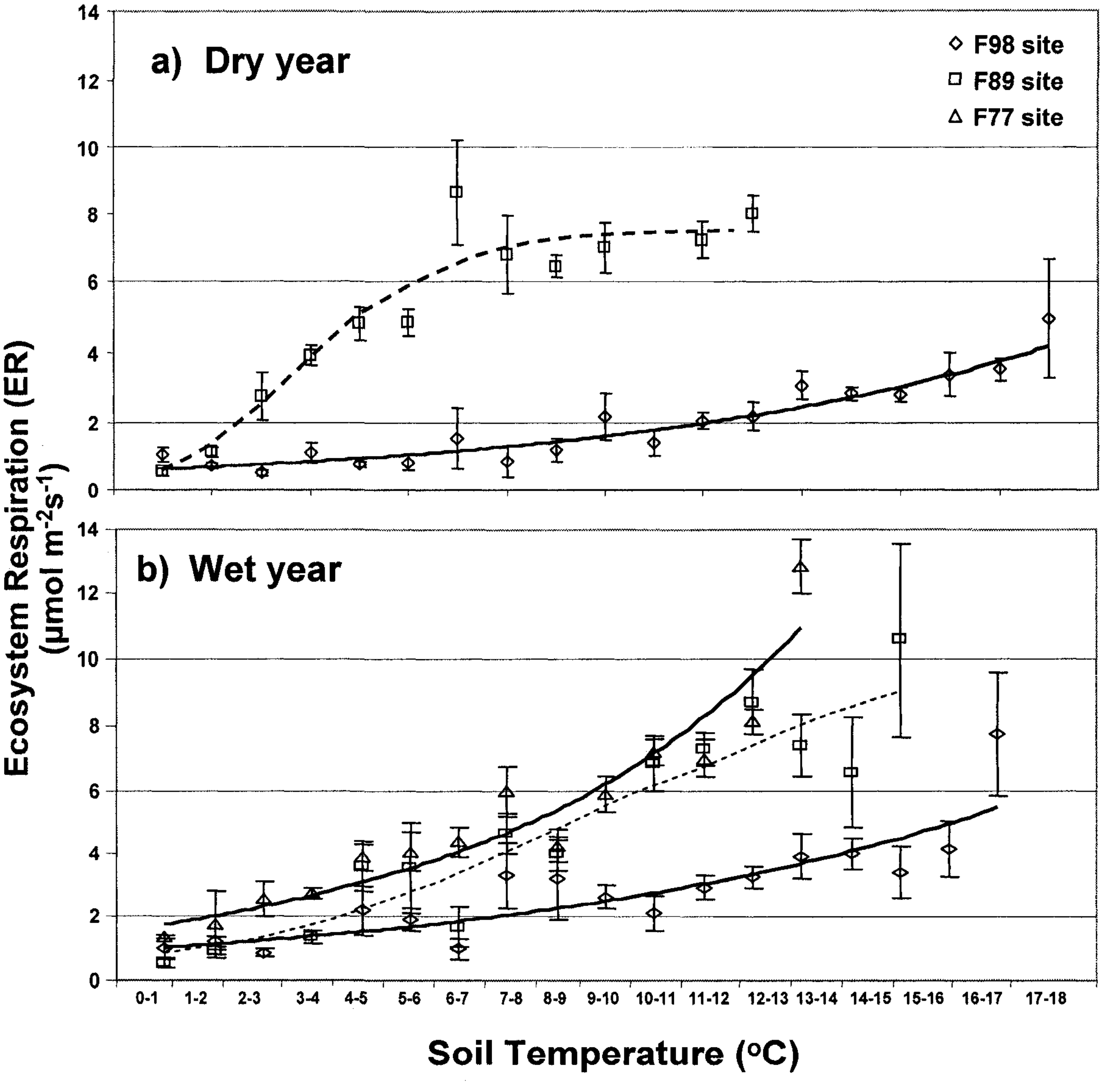


Fig 3.3. (a and b). Soil respiration and moisture patterns at the F98 and F89 sites during the dry (2003) year. Biweekly means (±SE) are given.

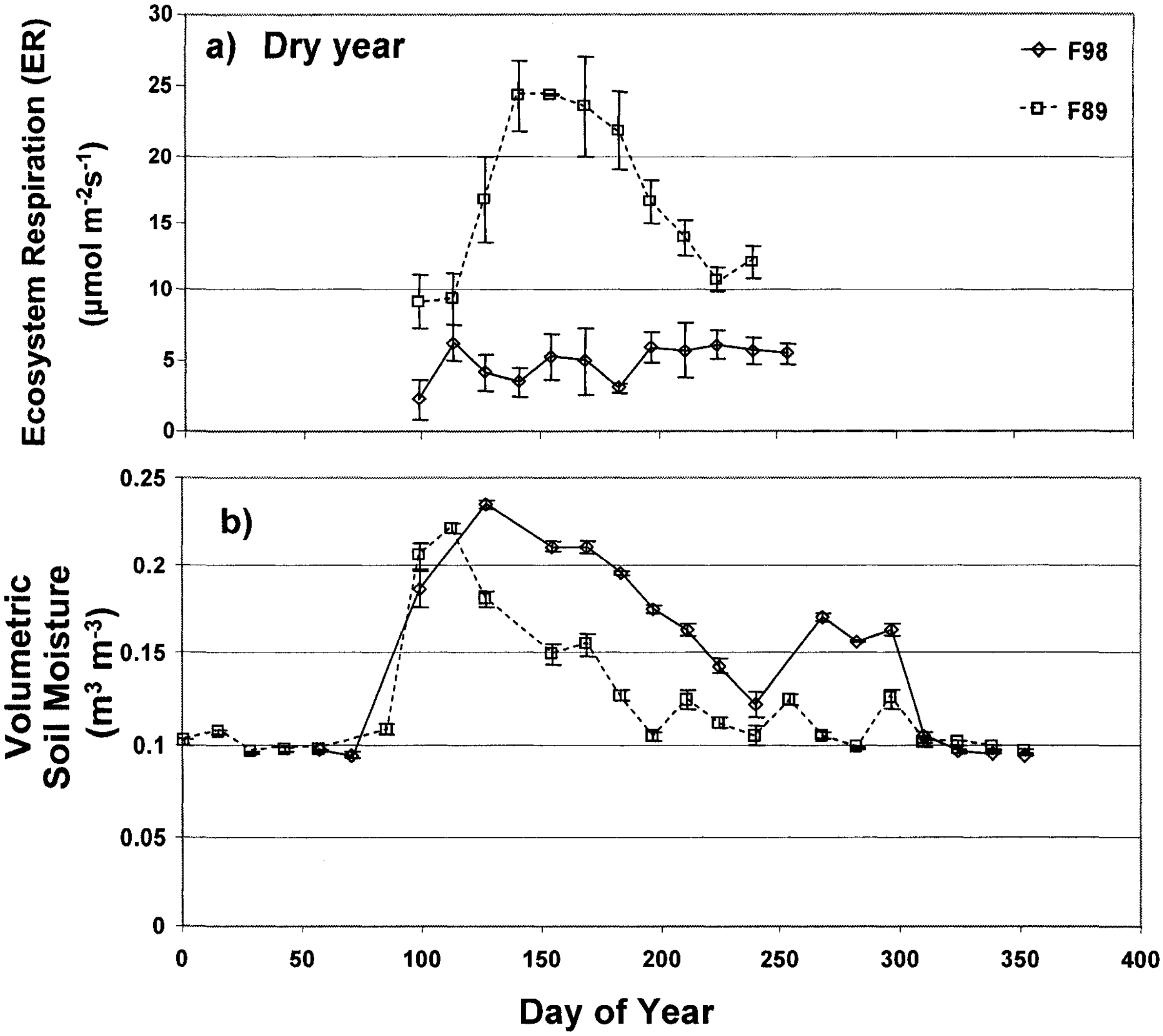
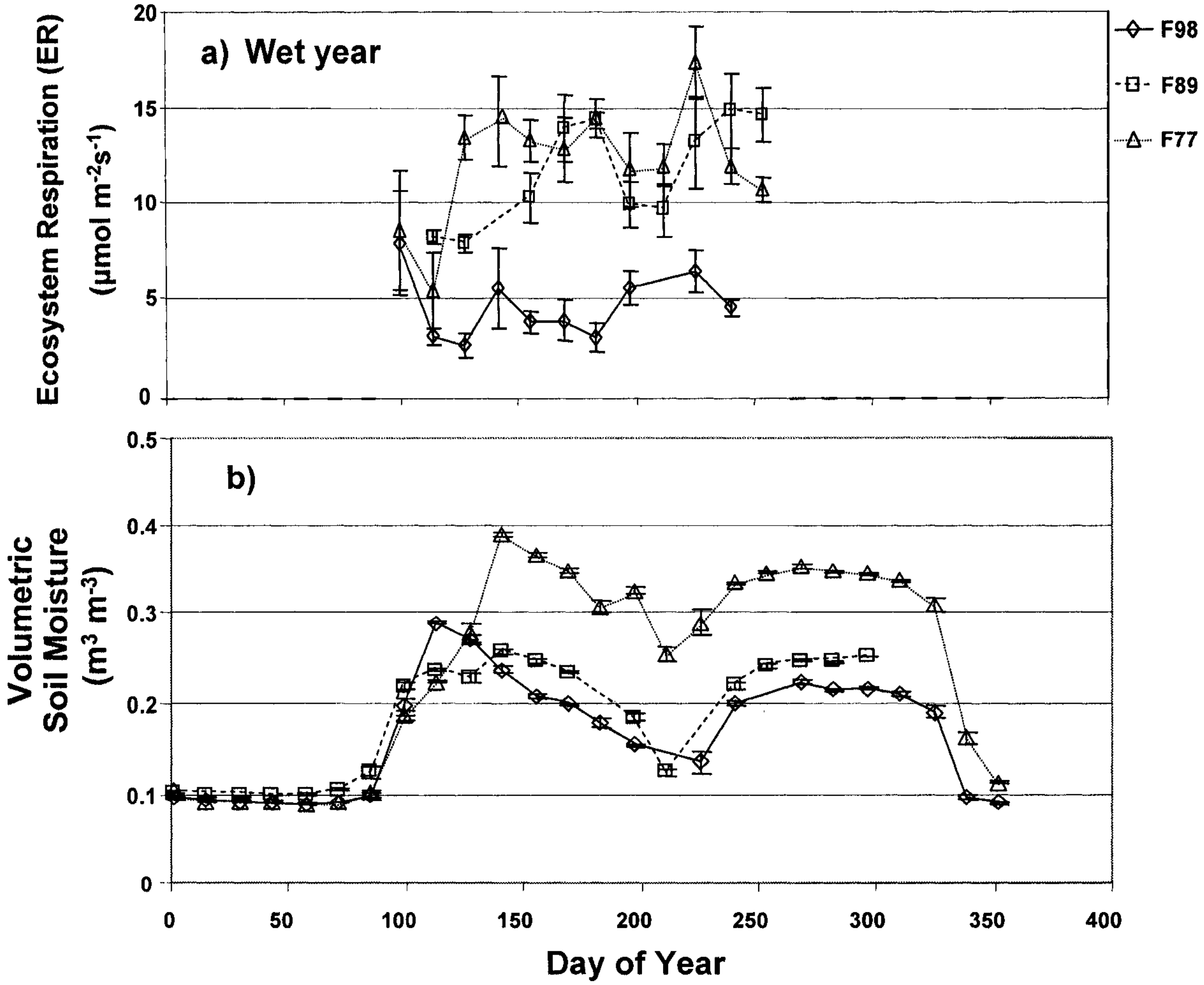


Fig 3.4. (a and b). Soil respiration and moisture patterns at the F98, F89 and F77 sites during the wet (2005) year. Biweekly means (± SE) are given.



CHAPTER 4

4. OVERALL CONCLUSIONS, SYNTHESIS AND IMPLICATION

4.1. Soil Respiration in the Post-fire Forest

Forest fire, through its burning of forest stands as well as of the forest floor organic layer, plays an important role in altering the flux of carbon from soils in boreal forest ecosystems. In this thesis, considerable spatial variability in soil respiration was observed at the post-fire sites, but the older sites (F89 and F77) tended to be less variable than the younger F98 site. Researchers often characterize fire severity by the depth of burn (Van Wagner, 1972; Wells et al., 1979; Alexander, 1982). However, we found that the variability in the forest floor thickness did not explain the spatial variability in soil respiration at any of the studied sites. This is likely because only 17 to 38% of total soil respiration was estimated to be contributed from the forest floor following a manipulative experiment that removed forest floor. The reduction in forest floor organic layer respiration was largely due to the removal of roots in the organic layer at the F98 site and due to removal of organic matter at the F89 and F77 sites (see Chapter 2). Strong linear relationships of soil respiration with fine root biomass at all the sites indicated that the spatial variability in soil respiration may be largely attributed to the amount of fine root biomass, explaining 70 to 85 % of the variation in soil respiration. Therefore, much of the post-fire respiration during the early succession is apparently due to the root respiration of actively growing early succession. Microbial respiration, even in the younger post-fire sites, seems to be much less important.

Fire removes deep organic layers from the boreal forest floor, and in many cases, can expose mineral soil. This removal tends to be patchy with drier areas burning more than wetter areas, although even extensive wetlands can dry out and burn (Turetsky et al., 2004). Thus, fire disturbance often results in heterogeneous landscape characteristics where the carbon stocks and physical soil parameters have been altered. These changes in the soil environment are important in driving post-fire soil respiration processes in boreal forest soils, especially during the early regeneration stages. Many studies have used models or equations with abiotic factors, mainly temperature and soil moisture, to predict soil respiration. However, biotic factors such as fine root biomass and successional vegetation characteristics and their carbon allocation pattern are some of the other important features that need to be considered in the development of post-fire soil respiration models.

4.2. Impacts of Fire on the Carbon Balance

Direct C emissions from fire combustion are reasonably well known for forest ecosystems (Kasischke and Penner, 2004). For the Canadian forests, the estimated direct C losses from fire is about 1.3 kg C m^{-2} (Amiro et al., 2001). Some models estimate that direct emissions only cause about 50 percent of the C loss and the remaining loss occurs through decomposition processes over time (Auclair and Carter, 1993; Kasischke et al., 1995). However, the current best estimates of the carbon stocks in above-ground biomass and soil organic matter is about 20 kg C m^{-2} (Kurz and Apps, 1999). This is far higher than the actual C loss by direct emissions, therefore these model estimates for the post-fire C loss due to decomposition may be much higher than through direct emissions. This is because the decomposition of C is a highly complex process, especially in post-fire forest ecosystems, and the magnitude of post-fire C losses is not well known. Forest fires, especially stand replacing fires cause much of the above-ground vegetation to enter into the decomposition pool and help accelerate the organic matter decomposition due to high soil temperature following fire. Therefore, in order to determine the total efflux of C released over time, the C dynamics in the post-fire environment are even more crucial than the losses of C through the combustion process.

The annual estimates of NEP (g C m^{-2} y^{-1}) measured from eddy covariance towers at the three study sites were -17, 113 and -40 for 2004 and -52, 88 and -79 for 2005 at the F98, F89 and F77 sites respectively (Sass, 2007). Since the NEP is the difference between GEP and ER, the estimated annual GEP and ER (g C m^{-2} y^{-1}) averaged for these two years corresponding to our manual soil chamber measurements was 420 and 454 at F98, 916 and 815 at F89, 825 and 885 at F77 respectively.

This clearly shows that the youngest F98 site respired less compared to the older F89 and F77sites. This corroborates well with our manual soil chamber measurements, where the youngest F98 site had the lowest soil respiration. However, soil respiration is only one component of ER. The other components include measurements of above-ground plant respiration and respiration from coarse woody debris (CWD). The CWD could be a significant source of respiration under favorable moisture and temperature conditions. There are only few studies measuring CWD respiration and its contribution to ER is not well understood. The CWD could be an important source of respiration depending upon its decomposition. The issue is linked with stage when the CWD fall on the ground and makes contact with soil during the post-fire succession.

During the early stages, a large amount of CWD is mostly perched above the ground and will not enter the decomposing pool until it falls on the ground. This is especially true at the F98 site, where the fire-killed trees are mostly dry and perched about 1m above the ground. Therefore, the CWD respiration may only contribute little to the total ecosystem respiration at this stage (Wang et al., 2002; Bond-Lamberty et al., 2002). However, during the late stages of post-fire succession, when the CWD eventually lies on the ground, soil microorganisms start to decompose the material. The soil environment further provides favorable moisture conditions to help accelerate the decomposition process. This is observed at the F77 site and to some extent at the F89 site, where CWD is visibly lying on the ground and rotting. Thus, it is likely that the negative NEP in 2004 and 2005 at the F77 site was partly caused by greater respiration from coarse woody debris. However, the negative NEP at the F98 site does not imply greater CWD respiration because the GEP was about half of that of the other two sites. Similarly, positive NEP at the F89 site is due to greater GEP, while ER is also slightly lower compared to the F77 site (see above). Although we speculate greater contribution of CWD respiration to ER at the F77 site compared to the other sites, manual field measurements of CWD respiration are certainly needed to help better understand the role of CWD in determining the net C budget of the post-fire forest succession.

Our study indicates that roots are a more important component of the total soil respiration in post-fire situations than the amount of organic material on the soil surface. This could be partly related to the quality of organic material left after the fire. A high content of charcoal or black carbon is usually seen on the soil surface following fire and the uptake of this black carbon by microorganisms is generally small (Preston and Schmidt, 2006). Therefore, we still need to determine the post-fire decomposition or cycling rate of organic material in the forest floor. This is especially important for carbon modeling because of uncertainty on the decomposition rate of the post-fire organic material.

4.3. Post-fire Environmental Controls on Ecosystem Respiration

As discussed above, fire is a dominant disturbance and can severely alter the physical, chemical and biological properties of boreal forest ecosystems. This, in turn, significantly affects the soil and plant factors that control the magnitude of CO_2 flux from the ecosystem. The data at F98 and F77 during both wet and dry years and F89 only during the wet year, showed a significant exponential relationship between ER and soil temperature. However, the older F89 and F77 sites responded more rapidly to the changes in soil temperature. The ER rate of response and Q_{10} values were greater at the older sites, especially at the F89 site compared to the younger F98 site. It is however not clear whether these differences in the temperature sensitivity of ER are due to the root or microbial components. According to some studies, root respiration is more sensitive to variations in temperature than microbial respiration (Boone et al., 1998). Since root respiration is shown to be contributing significantly (more than 60 to 80 % depending upon the site) to ER (Chapter 3), the Q_{10} differences among sites could be due to the greater response of root respiration to temperature fluctuations. However, an increasing number of studies have emphasized that microbial respiration is more sensitive to temperature variations compared to root respiration

(Bhupinderpal-Singh et al., 2003, Hogberg et al. 2001). They further showed that root respiration, in fact, is more dependent on the photosynthetic supply of C to roots. Considering their first argument of greater microbial sensitivity to temperature, we however still believe that differences in the ER rate of response to soil temperature were largely due to the root component at our sites. There are two reasons: first, the microbial component contributed less than 17 to 38% to total soil respiration (highest at the oldest F77 site) and secondly, that the F89 site showed a higher ER rate of response to soil temperature than the F77 site, which has a higher microbial contribution. However, the root respiration response to the physiological factors such as photosynthetic supply of C to roots is unknown at our sites and could be a dominating factor governing root respiration (Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003).

In boreal forest ecosystems, we know that the contribution of root respiration to total soil respiration starts later, but decreases to minimum earlier, at the end of the growing season (May to September) in contrast to microbial respiration (Bhupinderpal-Singh et al., 2003). As a result of this, root respiration can show rapid changes in response to changes in tree phenology in a short period of time, but the concurrent changes in soil temperature may be small. It is important to note that the F89 site had the highest GPP (Sass, 2007), and also showed the highest (i) soil respiration largely contributed by root respiration (Chapter 2) and (ii) ER rate of response as well as Q_{10} value (Chapter 3). Therefore, it is also possible that differences in GPP or photosynthetic supply of C from aboveground canopy to roots could be driving the ER rate of response at our post-fire sites rather than temperature. There may also be a strong interaction between soil temperature, plant phenology and seasonality of photosynthates supply to roots. However, distribution and allocation pattern of the photosynthetic C to the aboveground plant parts and belowground roots also remains to be determined at our sites.

Another issue is the CWD component of ER, which is not well known. Although CWD debris respiration may contribute significantly at the older sites, this is largely unknown for boreal forest ecosystems. Furthermore, the environmental controls on CWD component have not been well studied despite a few recent studies (Bond-Lamberty et al., 2002; Wang et al., 2002). Hence, more studies are needed to exactly determine the mechanisms controlling the ER in post-fire ecosystems.

Our study in Chapter 3 provided a snapshot of post-fire ER processes during the early regeneration stages indicating that these ecosystems are highly complex. There could be a complex interaction between the environmental and physiological control of ER components. Therefore, in order to fully understand post-fire ER processes, each component of ER should be thoroughly studied. First, we need to determine the relative contribution of root, microbial and CWD components to ER. Secondly, environmental and physiological factors controlling respiration from these components should be studied separately. These may be challenging at our post-fire sites especially with regards to separating root and microbial contributions given a high spatial variability in fluxes (Chapter 2). However, laboratory experiments in combination with field measurements could help in providing a better insight into the ER processes following fire. This is particularly important in the light of predictions that forest fire will increase in Canada with the projected changes in climate (Flannigan et al., 2005).

4.4. References

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