SOIL CO_2 EFFLUX FROM TEMPERATE AND BOREAL FORESTS IN ONTARIO

SOIL CO_2 EFFLUX FROM TEMPERATE AND BOREAL FORESTS IN ONTARIO, CANADA

By

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ABSTRACT

Forests play an important role in the net ecosystem exchange of CO_2 in terrestrial ecosystems. Soil respiration is often the major source of CO_2 in forests and is greatly influenced by climatic variability and management practices.

Spatial and temporal variations of soil respiration have been examined in a *chronosequence* (60, 30, 15, and 1 year-old) of *temperate*, afforested, white pine (*Pinus strobus*) forest stands in Southern Ontario, Canada, in order to investigate any age related differences.

Spatial and temporal variations of soil respiration in a 74 year-old *boreal*, mixed-wood forest in Central Ontario, was also studied and compared with results from the 60 year-old, temperate, white pine, forest stand, in order to investigate any climate related differences.

Soil CO_2 flux, temperature, and moisture were measured for one year (June 2003 to May 2004, inclusive, for the chronosequence study, and August 2003 to July 2004, inclusive, for the boreal- temperate study). In all stands, *temporal* variability of soil respiration followed the seasonal pattern of soil temperature, reaching a minimum in winter and maximum in summer. Temporal variability of soil temperature was able to explain 80 to 96% of the *temporal* variability in soil respiration at all stands. *Spatial* variability in soil respiration was also observed at all stands and the degree of this variability was seasonal, following the seasonal trend of mean daily soil respiration. Spatial variability of some soil chemical properties was highly correlated with the *spatial* variability of soil respiration, while litter thickness was not. The location of soil

respiration measurement with respect to tree trunks may also help to explain some of the spatial variability in soil respiration.

Across the chronosequence, the highest mean daily CO_2 efflux was observed during the growing season for the 15 year-old-stand (5.2 ± 1.3 to 0.4 ± 0.2 μmol CO_2 m^{-2} s^{-1}), which was comparable to the 60 year-old-stand (4.9 ± 1.3 to 0.2 ± 0.1 μmol CO_2 m^{-2} s^{-1}), but higher than the 30 year (3.8 ± 0.9 to 0.2 ± 0.0 μmol CO_2 m^{-2} s^{-1}) and 1 year (2.9 ± 0.9 to 0.3 ± 0.3 μmol CO_2 m^{-2} s^{-1}) old stands. From boreal-temperate comparison, it was observed that mean daily soil respiration rates for the boreal stand (6.9 ± 1.7 to 0.5 ± 0.1 μmol CO_2 m^{-2} s^{-1}) were higher during the growing season compared to the 60 year-old temperate forest stand.

Understanding temporal and spatial variability of soil respiration and how it is controlled is essential to improving forest ecosystem carbon budget assessments, and subsequently, the global carbon budget. This study will contribute direct observations necessary for improving and validating forest ecosystem CO_2 exchange models.

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Finally, thanks to you – the reader – for actually opening up this thesis and reading some. Enjoy the rest!

[1] "Huge Thank you" – Ukrainian

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CHAPTER 1: INTRODUCTION

1.1 Soils and global climate change

Soil carbon is an important component of the global carbon cycle. Soils store about 1500 Pg [1] of carbon, which is more than the amount stored by the atmosphere and biosphere, combined (Molles, 2002). Soils cycle about 10% of atmospheric carbon dioxide (CO_2) per year (Raich, 2002), emitting about 75 Pg of carbon during the process (Schlesinger et al, 2000). In comparison, the combined estimated CO_2 emissions due to fossil fuel emissions and deforestation is only around 7 Pg of carbon per year (Sundquist, 1993).

CO_2 is one of several gases responsible for the global greenhouse effect, highlighted by potential increases in global surface temperatures and changes in global precipitation patterns (Arhens, 1998). Climate change models show that increased CO_2 concentrations in the atmosphere may increase global temperatures with positive feedback on increases in atmospheric CO_2 concentrations (Schimel et al, 1994; Schlesinger et al, 2000). Raich and Schlesinger (1992) used data from several terrestrial ecosystems to study the effects of climate change on global *soil* CO_2 emissions. They concluded that increased global temperatures will likely increase *soil* CO_2 emissions and feedback positively on the greenhouse effect.

The greatest impact of rising soil temperatures on global soil CO_2 efflux are expected in colder climates (Lloyd and Taylor, 1994), such as found in Canada. Human induced land-use changes, such as afforestation and soil management practices, can have

[1] Pg – peptogram = 10^{15} grams

a significant impact on global soil CO_2 emissions (House et al, 2002; Schlesinger 2000; IPCC, 2000). In light of the concerns regarding global climate change due to increased greenhouse gases, studies of *soil* CO_2 emissions are crucial to gaining a better understanding of what controls terrestrial ecosystems' contributions to atmospheric CO_2 concentrations. Such studies will help us to better predict and mitigate any human-induced adverse effects on our climate.

1.2 Forest Soil Respiration

"Soil respiration" refers to soil emissions of CO_2 gas, produced as a result of the soil's metabolic functions (Singh and Gupta, 1975). These functions include respiration of soil micro-organisms, root respiration and chemical oxidation of carbonate minerals (Singh and Gupta, 1975). Respiration by plant roots provides one major source of soil CO_2 emissions, which can account for as little as 10% and as much as 90% of total CO_2 respired from soils (Hanson et al, 2000). Respiration by soil micro-organisms, especially due to decomposition activity, often makes up the rest of the total (Rustad et al, 2000; Buchmann, 2000). Mineral oxidation tends to be minor, except for soils that are high in carbonate mineral content.

In forest ecosystems, soil respiration can account for up to two thirds of annual ecosystem CO_2 emissions (Valentini, 2000; Law et al, 2001) The magnitude of this respiration was found to correlate with the climate in which the forest is found (Matteucci et al, 2000; Valentini et al., 2000). Others have shown that the greatest positive effect of increasing global surface temperatures on the rates of forest soil respiration were likely to

occur in cold temperate and boreal forests, due to higher rates of soil organic matter accumulation and increased temperature sensitivity of decomposition rates in those ecosystems (Niinistö et al, 2004; Baldocchi et al, 2001; Matteucci et al, 2000; Lindroth et al, 1998; Kicklighter et al, 1994).

1.2.1 Seasonal variability in soil respiration

Temporal changes in soil respiration have been related to annual litter accumulation (Raich et al, 1989), precipitation events (Law et al, 2001, Lee et al 2004), temperature changes (Lloyd et al, 1994; Xu & Qi, 2001), and growth activity of vegetation (Kelliher et al, 1999). Some recent studies have also linked rates of soil respiration with below ground allocation of photosynthates, which can also vary with growing seasons (Janssens et al, 2001; Högberg et al, 2001).

However, temperature and moisture, by far, are the most commonly reported environmental factors that control temporal variability of soil respiration. In an attempt to model the annual trend of soil CO_2 emissions and to calculate annual soil CO_2 -emissions from an ecosystem, various mathematical relationships have been applied relating the rate of soil respiration to these two parameters. There appears to be greater agreement on the relationship with temperature, which tends to be some sort of an exponential function (Qi et al 2002, Davidson et al, 2000 Lloyd and Taylor, 1994). One general form of this relationship is as follows:

$$R_s = ae^{bT_s}, \quad (1)$$

where Rs is soil CO_2 efflux, Ts is soil temperature and *a* and *b* are empirically-fitted, site-specific parameters. A temperature sensitivity factor, called Q_{10}, often accompanies those relationships and can be calculated from the above equation as follows (Xu and Qi, 2001):

$$Q_{10} = e^{10b} \quad , \tag{2}$$

where *b* is a parameter from equation (1). The Q_{10} value describes the sensitivity of soil respiration for every 10°C increase in soil temperature and is often used in global carbon budget models, in simulations of ecosystem respiration (Qi et al, 2002). Higher Q_{10} values denote higher temperature sensitivity. Reported Q_{10} values are usually around 2 to 2.5 (Raich et al, 1992). However, often this is not the case for cool temperate and boreal regions, where Q_{10} values in the range of 4-6 have been reported (Morgenstern et al, 2004; Janssens et al, 2003; Russell and Voroney, 1998; Black et al, 1996). Therefore, despite the numerous studies thus far, there is still considerable debate in the scientific community as to the degree of soil respiration's sensitivity to temperature control, which tend to vary seasonally and regionally (Janssens et al, 2003; Qi et al, 2002). As a result, more long-term continuous data sets are required to help resolve the issue.

Even greater uncertainties and variability exist when an attempt is made to try and generalize the effect of soil moisture on soil respiration, as reviewed by Davidson et al (2002). Although the effects of soil temperature and soil moisture are often confounding, when there is sufficient moisture available to plants and microorganisms, temperature appears to have greater control on soil respiration (Rayment et al, 2000; Russell et al, 1998; Raich and Schlesinger, 1992). Only when moisture falls beyond a critical value, which appears to be site specific, will moisture become more significant in explaining

variability in soil respiration (Scott-Denton et al, 2003; Rey et al, 2002; Irvine, 2002; Law et al, 2001; Xu & Qi, 2001; Davidson et al, 2000; Matteucci et al, 2000).

1.2.2 Spatial variability in soil respiration

Spatial variability in observed rates of soil CO_2 emissions are widely reported in literature (Wiseman and Sieler, 2004; Scott-Denton et al, 2003; Irvine and Law, 2002; Law et al, 2001; Xu and Qi, 2001; Rayment and Jarvis, 2000; Fang et al, 1998). A variety of factors have been used to explain this variability, including spatial variability in litter thickness, root density and microbial population densities. For example, soil respiration was found to be lower above bare soil compared to litter-covered soils in a Ponderosa pine forest in Oregon, USA (Law et al, 2001). Similar correlations were found by Litton et al (2003) in a lodge pole pine forest in Wyoming, USA, where soil respiration was higher for stands with higher stem density. Higher stem density would translate into higher root density and thus higher soil CO_2 efflux. In another study, Wiseman and Seiler (2004) studied soil respiration in a planted loblolly pine forest stand and showed that soil respiration was higher close to the base of trees, compared to inter-row areas.

The density of roots and soil microorganisms can vary spatially and the variability may depend on soil chemical and physical properties (Brunner et al., 1999; Grayson et al., 2001; Morris, 1999; Puhe, 2003). Some soil chemical properties (such as soil pH, nitrogen (N) and carbon (C) contents, to name but a few are important in maintaining soil biological activities (Cotrufo et al, 2000; Taiz and Zeiger, 2002). Thus, spatial variations

of soil chemical properties may be able to explain some of the spatial variability in soil respiration.

Not many studies have been done until recently, which attempt to explain spatial variability of soil respiration with variability of soil chemical properties, other than pH, C:N ratio and organic matter (OM) content. Of the examples that do exists, Xu and Qi (2001) reported that 84% of spatial variability in soil respiration, observed at their ponderosa pine forest study site in California, could be explained by a *combination* of the following parameters: root biomass, microbial C, OM, total N, P, K, Mg, Ca contents, pH, and bulk density. Although one may argue that roots and microbial densities may have explained the majority of the reported 84% variability, the authors also reported that total N, pH, Mg, and OM could *individually* explain 44-55% of the variability. In another study, La Scala et al. (2000) found that cation exchange capacity (CEC) could explain 27 to 39% and Fe could explain 22 to 42% of the spatial variability in soil respiration they observed over bare soils in Brazil. Similarly, Vanhala (2002) reported that in the event of constant soil temperature and moisture, any variations observed in soil respiration may often be explained by soil chemical properties. Keith et al (1997) reported that short-term increases in soil P can reduce soil respiration by reducing root activity.

Furthermore, soil chemical and physical properties are required for coupled carbon and nitrogen terrestrial ecosystem models, which are being developed and tested for the purpose of studying and better predicting the relationships between climate change, land use and terrestrial ecosystems. Measurements of nitrogen, phosphorus, pH, cation exchange capacity and organic carbon are among the parameters sought. Thus, it is of

great interest to investigate further the relationship between soil chemical properties and soil respiration in forest ecosystems.

1.3 Temperate White Pine Forest Chronosequence Study

Eastern white pines (*Pinus Strobus*) have a wide span from northern hardwood to southern boreal forest zones, where they play a key role in the successional sequences from one zone to the other (Richardson and Rundel, 2000). *Pinus strobus* thrives on nutrient-poor, dry, sandy soils, where other tree species tend to fail (Richardson and Rundel, 2000), and are often preferred as afforestation species (Arain et al, 2004). Economically, white pines are widely used in construction lumber, furniture, window sashes, doors and other products (Lancaster and Leak, 1978). Despite their ecological and economical importance, studies of the effects of climate and land-use changes on white pine forest ecosystems in eastern North America are under-represented.

One unique aspect of this particular study was to compare soil respiration across an age chronosequence of afforested white pine stands in southern Ontario. This allowed for an investigation of how soil respiration varies with stand age, which may be of importance to improving future forest management and harvesting practices in accordance with carbon allowances imposed by policies established for regulating global carbon emissions. Furthermore, the white pine research site studied here lies in the temperate broad-leaf deciduous to boreal forest transition zone and thus provided a unique opportunity to add to the ongoing investigation of the strength of the carbon

source or sink capabilities of planted coniferous forests and its sensitivity to seasonal and annual climate variability in the region (Arain et al, 2004).

1.4 Boreal Forests study

Boreal forests occupy about 11% of the earth's terrestrial surface area in a biome that spans right around the earth in the Northern Hemisphere (a band between 50° and 65° N latitude) (Molles, 2002). They are an important economic source of lumber and pulp, which makes them vulnerable to mass deforestation (Molles, 2002). Boreal forests are often dominated by firs (*Abies* spp.) and spruces (*Picea* spp.), but can also include birch (*Betula* spp.) and aspen (*Populus tremuloides* Michx.) (Richardson and Rundel, 2000). Due to the short growing seasons found in those regions, large accumulations of litter occur there (Molles, 2002). This accumulated litter acts as a temporal storage for carbon, unless disturbed by deforestation or climate changes. As was mentioned above, carbon emissions from boreal forests are particularly sensitive to increases in global temperatures, yet so far this sensitivity is not well defined.

In this study, soil CO_2 emissions were measured, throughout the year, from the floor of a boreal forest in central Ontario, at the southern edges of the boreal biome in Ontario. This study provides further data sets necessary to improve models of global carbon and nitrogen cycling used in climate change research. Furthermore, a unique opportunity was available to compare directly soil respiration in the boreal forest to that of the temperate one, measured over the course of the same year. Such comparisons will

help to better identify and understand any similarities and differences in soil respiration and its controlling factors in two different climate zones in Ontario.

1.5 Objectives

The specific objectives of each study were as follows:

Temperate Chronosequence Study

a) to measure temporal and spatial variability of soil CO_2 efflux across the chronosequence (60, 30, 15, and 1 year old) of temperate, afforested, white pine forest stands in Southern Ontario, Canada
b) to determine environmental variable(s) that exhibit greatest control on soil CO_2 efflux across the chronosequence
c) to investigate causes of spatial variability in soil respiration
d) to compare soil CO_2 efflux across the chronosequence
e) to determine an algorithm describing the relationship between soil CO_2 efflux and any controlling environmental variable(s), for each of the chronosequence stands
f) use the algorithms (from e) to model annual soil CO_2 efflux and estimate annual carbon emissions due to soil respiration at each site.

Boreal Study

a) to measure temporal and spatial variability of soil CO_2 efflux in a 74 year old, boreal, mixed wood forest in central Ontario

b) to determine environmental variable(s) controlling temporal variability in soil CO_2 efflux

c) to investigate causes of spatial variability of soil respiration

d) to determine mathematical relationships between soil CO_2 efflux and its controlling environmental parameters

e) to use these relationships to model annual soil respiration and to estimate annual carbon emissions due to soil respiration for the stand

Comparison between Temperate and Boreal Forest Stands

a) to compare and contrast temporal and spatial variability of soil CO_2 efflux in a boreal and a temperate forest stand

b) to compare and contrast physical and environmental variables controlling temporal and spatial variability in soil CO_2 efflux at the two stands

c) to compare and contrast estimates of annual soil CO_2 -emissions from the two forest stands

CHAPTER 2: STUDY SITES AND METHODOLOGY

2.1 Turkey Point Flux Station (TPFS) – temperate chronosequence sites

The study area is located on the northern shore of Lake Erie, near Turkey Point, in Southern Ontario, Canada (Figure 2.1). The site was established in 2002 by the McMaster Climate Change Research Group (Dr. Altaf Arain), who have been maintaining the site ever since. There are four, primarily white pine, stands located within 20 km of each other, referred to as the Turkey Point Flux Station (**TPFS**). The age of the oldest stand is 60 years, the second oldest one is 30 years and the younger two are 15 and 1 year old (given ages are as of the year 2002). All stands grow on eolian sandy soils (Presant and Acton, 1984). The two oldest forest stands have been initially planted for harvest on cleared crown lands, and have since become conservation areas. The 15 year stand was planted on abandoned land, but is privately owned. The youngest (1yr) stand was planted on former farmland that has been abandoned three years prior to planting. It is also privately owned. The 60 year old site has a well developed understory of white pine seedlings (*Pinus strobus* L.), black cherry (*Prunus serotina* Ehrh.), white oak (*Quercus alba* L.), poison ivy (*Rhus radicans* L. ssp.), bracken ferns (*Pteridium aquilinum* L.) and blackberry (*Rubus allegheniensis* Porter) (*pers. commun.* Altaf Arain and Natalia Restrepo; Newmaster et al, 1998). Litter accumulation at the 60 year old stand is about 5-8 cm deep, consisting of pine needles and cones, leaves and small twigs. Canopy closure at the 60 year stand is about 70%. The 30 year old stand has minimal understory vegetation consisting only of several kinds of mosses (*Phlox subulata* and *Polytrichum spp.*). Litter accumulation at this stand is about 4-5 cm, which

Figure 2.1 : Turkey Point Flux Station (★) is located about 12 km south of the town of Simcoe, on the northern edge of Lake Erie in Southern Ontario, Canada (42° 42' 55'' N and 80° 22' 20'' W)

includes: needles, cones, and small twigs. At the 30 year stand canopy closure is about 30%. The 15 year old stand has no understory growth. Litter accumulation at this stand is about 5 cm, which includes: pine needles and cones. There is a strip of red pines planted along the edge of the 15 year stand (about 3 outer rows). Although the stand has 100% canopy closure, there are a few naturally-generated openings that support weed growth in summer. The youngest site, one year old, has an open canopy and no effective litter accumulation. However, from about May to October, prolific weed growth was observed there. These weeds were mowed twice a year (spring and fall) to reduce competition with white pine seedlings.

TPFS experiences a temperate climate with an annual mean daily air temperature around 8.0°C and mean annual precipitation around 800 mm. Further site characteristics, including weather normals, are given in Table 2.1 and Arain et al, 2004. TPFS is an associated research station of Fluxnet-Canada Research Network. The network is involved in studying how climate change and disturbance influence carbon cycling across forests and peatlands in Canada.

Table 2.1: Site characteristics of the four white pine chronosequence stands in Southern Ontario[1]

	60 year old	30 year old	15 year old	1 year old
Latitude	42.7122N	42.7094N	42.7757N	42.6636N
Longitude	80.3572W	80.3485W	80.459W	80.56W
Elevation (m)	184	184	212	265
Mean annual temperature (°C)[2]	8.1	8.1	7.9	8.1
Mean annual precipitation (mm)[2]	832	832	776	790
Mean annual snowfall (cm)[2]	142	142	137	142
Leaf Area Index	2.5-3.0	2.0	5.0	0.1
Mean Tree Height (m), [ave DBH (cm)]	22 [34.5]	12 [19.5]	6 [16.2]	0.2-0.3 [0.8]
Stem density (stems/ha)	760	1050	1800	2250
Soil density ($g.cm^{-3}$)	1.33	1.14	1.23	1.47

[1] *data courtesy of Altaf Arain and Natalia Restrepo with the exception of mean air T, snowfall and ppt normals*

[2] *mean annual T, snowfall and ppt were taken from Presant and Acton (1984). For the 60 and 30 year old forest stands, data from St. Williams (42°42'N 80°27'W; elev. 213m) weather station is shown; for the 15 year old stand averages from Delhi (42°52'N 80°33'W; elev. 232m) and Simcoe (42°51'N 80°16'W; elev. 240m) weather stations are shown; and for the 1 year old site, averages from St. Wiliams (42°42'N 80°27'W; elev. 213m) and Clear Creek (-) weather stations are shown.*

2.2 Groundhog River Flux Station (GRFS)

Groundhog River Flux Station (**GRFS**) is located about 80 km west of Timmins, Ontario, near the Groundhog River, along highway 101 (Figure 2.2). It is an official site of Fluxnet-Canada Research Network. GRFS was established and began operations in summer 2003, under the lead supervision and care of Queen's University Climatology Group (Dr. Harry McCaughey). The site consists of a 74-year-old (as of 2003) mixed-wood boreal forest, naturally regenerated after logging that took place in 1930's. The trees at the site include trembling aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), white birch (*Betula papyrifera* Marsh.), and balsam fir (*Abies balsamea* L. Mill.) (*pers. commun.* Altaf Harry McCaughey and Valerie Thomas; Newmaster et al, 1998). Smaller seedlings, bushes, herbaceous species, such as bunchberry (*Cornus Canadensis* L.) and a variety of mosses (feather moss (*Ptilium crista-castrensis* (Hedw.) De Not.), sphagnum moss and club moss (*Lycopodium clavatum* L.) compose the understory of the forest. The soil consists of a 12-20 cm thick organic (LFH) layer that overlies a silty very fine sand layer. Mean annual temperature in the area is about 1.5°C and mean annual precipitation is about 814 mm, of which 545 mm falls as rain and 295 cm as snow. Further site characteristics are given in Table 2.1.

Figure 2.2: The boreal mixed-wood forest stand, called Groundhog River Flux Station (★) is located about 80 km west of Timmins in Ontario, Canada (48, 217° N and 82,156° W). The temperate TPFS chronosequence (★) is included for comparison.

Table 2.2: Site characteristics of Groundhog River Flux Station, Ontario.[1]

	GRFS
Latitude[2]	48,217°N
Longitude[2]	82,156°W
Elevation[1] (m)	341
Mean annual temperature (°C) ± st dev	1.5 ± 1.1
Mean annual precipitation (mm)	814
Mean annual rainfall (mm)	545
Mean annual snowfall (cm)	295
Plant Area Index[1]	2.5 ± 0.5
Mean Tree Height (m), [ave DBH (cm)][1]	14 [18]
Canopy height (m)[1]	21.6
Stem density (stems/ha)[1]	937 (with DBH > 9cm)

Above data is courtesy of [1]Valerie Thomas and [2]Dr.Harry McCaughey from Queen's University Climatology Group.
Climate data courtesy of Environment Canada, as appears on Environment Canada website: annual means were calculated from annual averages downloaded for Chapleau Airport (47°49'N 83°20'W; elev. 447m) and Timmins Airport (48°34'N 81°22'W; elev. 295m) weather stations for the 1971 to 2000 time period.

2.3 Methodology

2.3.1 Instrumentation

Soil respiration was measured using a LI-COR 6400 portable photosynthesis system that had a LI-COR 6400-09 soil chamber attachment and a LI-COR 6400-013 soil temperature probe attachment (LI-COR, inc., Lincoln, Nebraska, USA) (Figure 2.3 a). This is an IRGA-based instrument that uses non-steady state, flow through technique to detect CO_2 and H_2O in sampled air (detection limits are about ± 0.2 μmol CO_2 m^{-2} s^{-1}, depending on settings). When in the soil-chamber-measurement mode, the instrument monitors and quantifies increases in CO_2 concentrations inside the chamber's head space.

Measurements were begun by allowing the instrument to equilibrate with ambient air CO_2 at each site. A single measurement involved placing the soil chamber over pre-

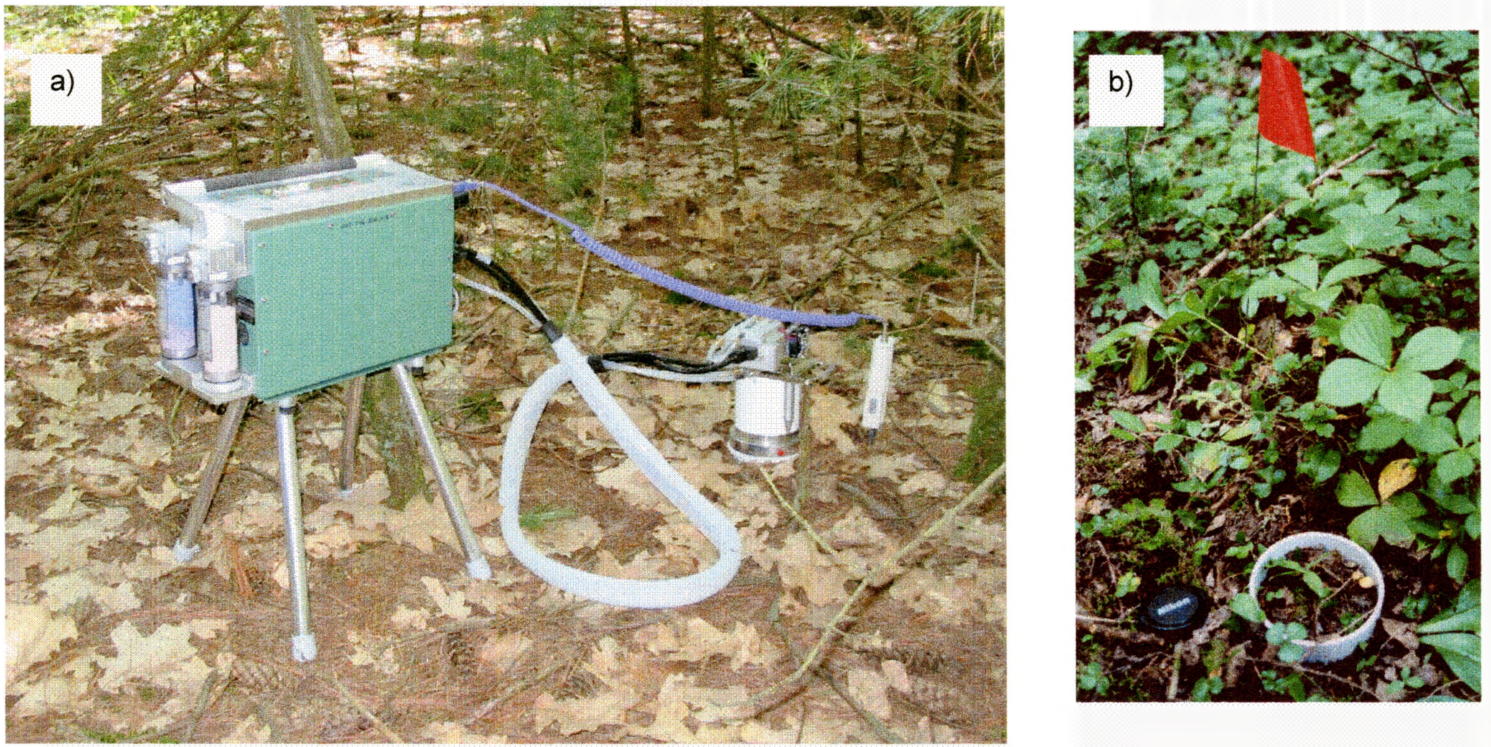


Figure 2.3: a) Above (left) is a photo of the LI-COR 6400 instrument with the 6400-009 soil chamber attachment, used to measure soil respiration during this study. In the photo, the chamber (on the right) is sitting above one of the collars, and the instrument is in the process of measuring soil respiration. Next to the chamber is the soil temperature probe (6400-013), inserted into soil. The green "box" is the console, a computer that controls the instrument. Attached to the left-hand side of the console are soil chemical tubes used to scrub chamber-air of CO_2. The IRGA analyzer is connected directly to the soil chamber (the rectangular block with plumbing, right on top of the chamber). b) (right) Close-up of an installed summer collar used to support the LI-6400 chamber at each measurement point. Using these collars helped to minimize forest floor disturbance due to frequent sampling.

installed soil respiration collars (7.5 cm height, 10.16 cm diameter – 81 cm^2 soil surface area enclosed), which were made at McMaster from PVC sewer pipes (Figure 2.3 b). One edge of each collar was beveled to make it easier to install into the ground. A foam seal ring was placed along the edge of contact between the collar and chamber to minimize air leakage. Chamber height was adjusted between measurement locations so that chamber volume was constant at about 991 cm^3 (zero insertion depth). The instrument was programmed to chemically scrub CO_2 from the air, inside the chamber, until the CO_2 concentration fell by about 10 μmol below ambient. After which, the instrument went into measuring mode. As CO_2 in the chamber air increased, due to soil respiration, the instrument monitored and recorded rising CO_2 concentration in the chamber air with time. Once the CO_2 concentration went up by about 10 μmol above ambient concentration, the instrument stopped measuring and calculated the rate of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) at the ambient concentration, based on linear regression analysis of collected data. Each measurement involved three consecutive replicate measurements of soil respiration at each collar, which lasted for a total of about 4 minutes. Air flow was set at 700 μmol s^{-1} for all measurements, except in winter, when fluxes were low. Then the flow was reduced to 500 μmol s^{-1} to increase the instrument's sensitivity.

Several authors have reviewed various methods for measuring soil respiration using different chamber and micrometeorological (Eddy Covariance –EC) techniques (Liang et al, 2004; Pumpanen et al, 2004; Janssens et al, 2001; Norman et al, 1997; Singh and Gupta, 1977). Each method has some level of uncertainty associated with it and

systematic differences between the methods exist, often requiring adjustment factors before data sets are compared (Norman et al, 1997).

The LI-6400 has been shown to give accurate fluxes against a set reference soil CO_2 efflux in lab experiments, which compared the performances of several chamber-based instruments (Pumpanen, 2004). Nonetheless, for through-flow, non-steady state systems, such as the LI-6400, areas of concern exist and include the following effects: chamber head space CO_2 concentrations, methods of mixing chamber air, pressure gradients created at the soil surfaces enclosed by chambers, and dilution effects of water. The LI-6400 has been designed with those concerns in mind (LI-COR Inc., 2004). For example, if CO_2 concentrations in chamber air are allowed to accumulate, soil CO_2 effluxes can be underestimated. To overcome this effect, LI-6400 has been designed to automatically scrub chamber air just below ambient (by few parts per million (ppm)) and then measure CO_2 until it rises just above ambient, thus keeping the natural CO_2 gradient inside the chamber within a few ppm of its undisturbed value. To deal with the effects of small pressure gradients, that can develop inside the chamber and cause over or underestimation of fluxes, the LI-6400 soil chamber has been fitted with a pressure equilibration valve that helps to control pressure gradients. In order to correctly sample CO_2 concentrations inside the chamber volume, the chamber air must be mixed. This mixing can also create localized pressure gradients or ventilate the surface, which can affect observed fluxes. For that purpose, the LI-6400-09 chamber has a fan that pushes air through a perforated manifold to distribute it through the chamber. Over wet surfaces, CO_2 emissions may be underestimated due to increases in partial water vapor pressure

and accompanying decreases in partial CO_2 pressures inside the chamber. To account for this effect, the LI-6400 system has been designed to automatically measure the rate of increase of chamber water vapor at the same time it monitors increases in chamber CO_2 concentrations, calculate a dilution factor and apply it to CO_2 measurements. Another unique feature of the LI-6400 system is that the IRGA is located right on top of the chamber, which reduces errors due to adsorption and travel time, when the chamber and IRGA are separated.

Finally, portable systems, like the LI-6400, involve manual measurements, which for logistical and financial reasons are often constrained to several hours during a day and only to few days per year. Thus such systems are at a disadvantage when compared to automatic soil chambers and below-canopy EC methods[2], which can also be used for soil CO_2 efflux measurements, but on continuous timescales. Continuous measurements provide more accurate estimates of annual soil CO_2 emissions. The continuous methods are better at capturing finer details of the temporal trends in soil respiration, such as the freeze-thaw cycle, rain events, and any diurnal variability, often missed with periodic manual sampling. On the other hand, these alternative methods are more complicated to install and maintain, and, in the case of EC measurements, tend to be plagued by many assumptions and potential errors in measurements due to lack of turbulence (Janssens et al, 2001; Lavigne et al, 1997; Norman et al, 1997). Automatic soil chambers and EC installations can also be very costly and cumbersome to move around, due to the extensive plumbing and wiring associated with them. In comparison to portable systems,

[2] when stem and understory respiration are excluded

these techniques are not very-effective at capturing spatial variability of soil respiration across the site, which can be quite significant. Thus, capturing spatial variability appears to be the niche of portable systems.

2.3.2 Sampling Design

2.3.2.1 Pilot study

Prior to establishing permanent sampling plots at TPFS forest stands, a pilot study was conducted in order to determine the spatial set-up of measurement locations. The aim was to sample stands in a way that best represented the whole forest floor, yet allowed us to measure all four stands at least once within a single day.

The 60 year old stand was chosen for the pilot study because it was thought to have the most heterogeneity in the forest floor of all four stands. Thus, if a set-up capable of capturing the spatial variability at this stand was determined, this set-up should have been adequate for capturing the "lesser" variability at the other three stands.

Set-up of measurement locations for Pilot Study

On June 13, 2003, one hundred and eleven (111) collars were installed to a depth of about 5.5 cm at the 60 yr TPFS stand (Figure 2.4). Fifty (50) collars were installed about every 2 m along a transect, which consisted of two 50-m-long sub-sections on opposite sides of the square plot.

Sixty one (61) collars were installed in the square plot area. This square area was divided into twenty-five, 5 x 5 m^2 grid squares. Thirty six (36) collars were installed at

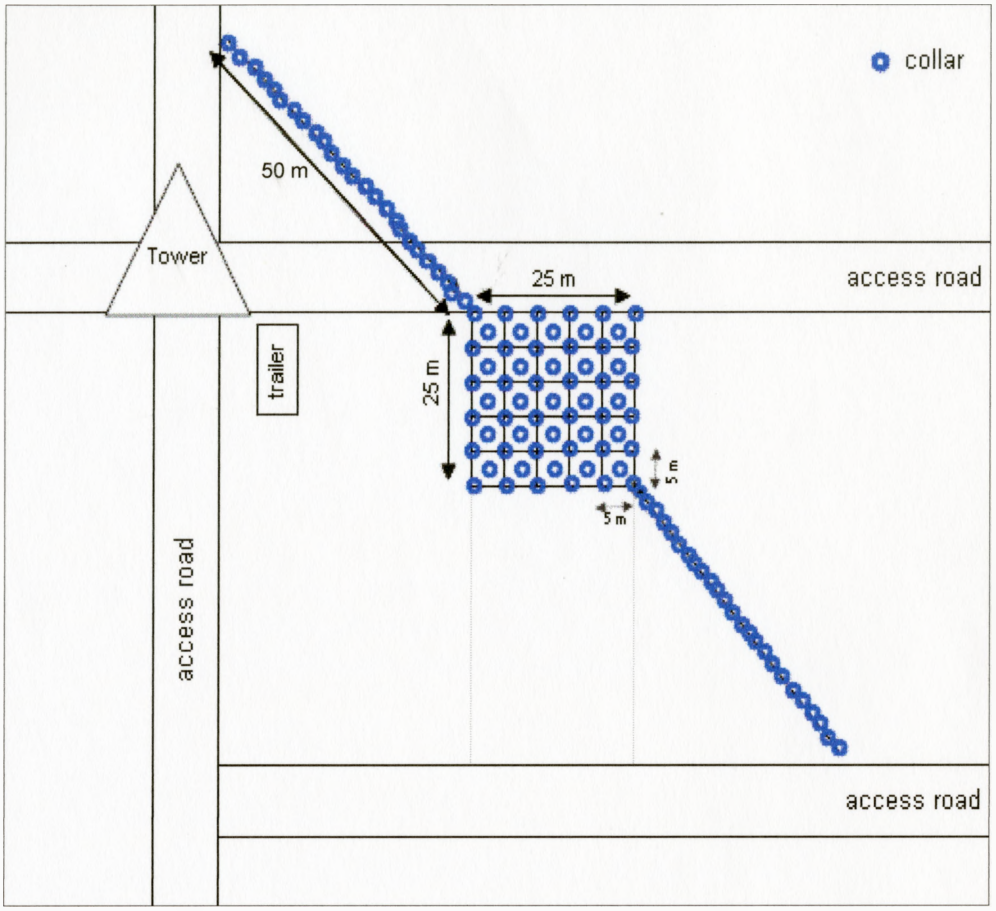


Figure 2.4: The set-up of 111 PVC collars used for soil respiration measurements during the pilot study at the 60 year old stand. The figure is not to scale, but shows the placement of the two 50 m-long transects and the square area (25 m x 25 m) relative to each other and major markers at the site (Flux tower, trailer and forest access roads).

the corners of each of the smaller squares and the rest of the collars (25) were installed at the centres of the smaller grid squares. If there was vegetation inside the collars (mosses, small herbaceous species), those were not removed, but left inside the collars. If a plant was too big to be inserted into the soil chamber, it was trimmed, but not rooted out.

Pilot Study Measurements

On June 16, 2003 soil CO_2 efflux at each collar was measured along the transect. Similarly, on June 17, 2003 soil CO_2 efflux at each collar was measured inside the square plot. Three repeat observations per collar per set of measurements was taken. On both occasions, two sets of measurements were carried out during the day at each site, once in the morning and once in the afternoon. With every soil respiration measurement, soil temperature and soil gravimetric water content (GWC) was also measured (*see section 2.3.2.4*). Soil temperature was measured beside every collar, while soil GWC was measured beside every other collar along the transect and beside collars located at the centres of the 5x5 m^2 sub-squares for the square-set up.

Data Analysis for Pilot Study

The results obtained in the pilot study were analyzed to calculate average soil respiration, standard deviation, average time of measurements per set-up, coefficients of determinations (r^2) and percent coefficients of variation (%CV) for the collected data points along the transect and inside the square. Mean soil respiration at the study site was estimated within 10-20% of the actual value at a 95% confidence level (CL) for each set-

up, using T-test statistics and data collected during the pilot study. The number of collars that would be required to estimate the mean flux within 10 and 20% at 90 and 95 %CL was also calculated following Yim et al (2003). All calculations were performed using Microsoft® Excel Spreadsheets (Standard Office XP, edition).

2.3.2.2 Establishment of permanent measurement locations

TPFS Temperate Chronosequence Sites

Based on results from the Pilot Study, in June 2003, one permanent 50 m long transect was established at each of the four stands at TPFS. Along each transect, 12 soil respiration collars were installed every 4 m to a depth of about 5.5 cm. The installed collars remained in the ground for the entire duration of this study. All installed collars were checked for air leaks, by placing the instrument over the collar and blowing a breath of air around the collar, while checking the CO_2 readings for erratic fluctuations.

The transects were installed within 30 metres of the Flux Towers already present at each of the four stands, where air temperature and whole ecosystem CO_2 and H_2O fluxes were being measured by other members of the McMaster Climate Change Research group. Each transect was also located within 20 m of two soil pits, equipped with instruments that monitored soil temperature and moisture (*see Section 2.3.2.4*). The transects were laid out such that they went across tree rows, on a diagonal, avoiding always sampling respiration at the same proximity to tree trunks.

In January 2004, new "winter collars" were installed along TPFS transects. These collars had the same dimensions as those permanently installed along the transects, except

for their height (35 cm tall). Winter collars were inserted within 20-30 cm of the original permanent collars along the transects. Their insertion depth was about 5-7 cm, leaving about 28-30 cm above surface (Figure 2.5). Taller collars were inserted in anticipation of winter snow accumulation. Plans were made to measure soil respiration in winter, above snow, in a way that would minimize snow disturbance. Thus these winter collars were made and installed.

GRFS Boreal Site

At the end of July 2003, a 100-m-long transect was established at the Groundhog River Flux Station. Fifty (50) collars were installed every 2 m to a depth of about 5.5 cm, along this transect. The collars were of the same dimensions and material as the ones used at TPFS. The transect was located within 20 m of soil pits that measured soil temperature and moisture (*Section 2.3.2.4*). The installed collars remained in the ground for the entire duration of the experiment, with the exception of 12 collars that were removed during soil coring in November 2003. All collars were checked for possible air leaks, as there was concern about the collars sealing well with the extensive porous organic soil layer. No leaks were detected.

In November 2003, 12 winter collars were installed along the transect, within 20 cm of every odd-numbered collar, beginning with collar #1 and ending with collar #23. To account for the higher snow accumulation expected in the region that would persist into early spring, these collars were taller (50 cm) compared to ones used at TPFS. The height of GRFS winter collars was 50 cm, instead of the 35 cm used at TPFS. These

Figure 2.5: Above photo shows two winter collars installed along the transect at the 60 yr TPFS stand. A walking path was made to the side to the transect to use in winter, so as not to disturb snow around collars

winter collars were installed about 5-10 cm into the ground, leaving only 40-45 cm above ground.

2.3.2.3 Diurnal measurements of soil respiration

Some researchers have reported observing diurnal variability in soil respiration (Law et al, 2001; Xu and Qi, 2001). As a result, some suggested that measurements be done at given hours of the day to avoid biased results. Soil respiration measurements for all four sites at TPFS stands were measured on a single day, at different times of day in each stand. Thus as part of the sampling design for this study, it was decided to check the degree of diurnal variability in soil respiration at each TPFS stand, in order to determine the validity of comparing mean soil respiration between stands, calculated from measurements taken at different times of day for each stand.

In August and September 2003 diurnal measurements of soil respiration and soil temperature (at the 15 cm depth) were conducted at the TPFS, along permanently installed transects. One diurnal measurement was carried out per stand in 2003 and an additional diurnal measurement was carried out at the 60 year old stand in 2004. At the oldest site, measurements were conducted over a 24 hour period, with the transect sampled once every hour (August 15-16, 2003 and repeated June 25-26, 2004). Measurements began around 20:00 on day one and finished around 19:00 the following day. The sampling procedure, in terms of the number of replicate measurements taken per collar and the instrument set-up, was the same as described for the Pilot study above (*see section 2.3.2.1*). In 2004, measurements were also taken over the course of 24 hours,

once every hour, with measurement starting at 20:30 on June 25 and ending at 19:30 on June 26.

At the other three stands, diurnal measurements were conducted on an 18 hour basis, with measurements beginning before sunrise at 5:30 and ending after sunset at 23:00. The youngest site (1 yr) was sampled on August 12, 2003. The 30 and 15 year old sites were sampled on August 21 and September 4, 2003, respectively.

No diurnal measurements of soil respiration were conducted at the GRFS during the course of this study.

2.3.2.4 Measurements of environmental variables

Soil temperature and soil moisture

Each time a soil respiration measurement was measured, a soil temperature measurement was also recorded. Soil temperature was measured within 20-30 cm of each collar, with a temperature probe (LI-COR 6400-013) inserted to a 15 cm depth each time. A 15 cm depth was used, which was the full length of the temperature probe.

For gravimetric water content (GWC) analysis of soils near each collar, one soil core was taken, within a 50 cm radius of a collar, to a depth of 15 cm, using a stainless steel corer (1.48 cm internal diameter stainless steel pipe). The extracted sample was placed into a re-sealable plastic bag and transported to McMaster University, where it was analyzed within 24 hours. Pre-weighed, individual soil samples were heated at 110°C for

24 hours before being re-weighed again. Gravimetric Water Content (GWC) for each sample was calculated according to the following equation:

$$GWC = \left(\frac{W_{wet} - W_{dry}}{W_{dry} - W_{container}} \right), \quad (3)$$

where W_{wet} refers to the weight of the fresh sample and crucible; "W_{Dry}" refers to the weight of the dried sample and crucible; "$W_{container}$" is the weight of the crucible in which the sample was held and dried.

Gravimetric water content at each TPFS site was sampled only six times during the course of study (five times in 2003 and once in 2004). At GRFS, soil samples for GWC analysis were collected on all occasions, with the exception of November 2003, when soil coring (for chemical analysis) was performed, and also with the exception of March and April 2004, when there was still snow on ground. Samples for GWC analysis taken at GRFS were deeper (24 cm) compared to the ones at TPFS (15 cm) and took an extra traveling day to get to our lab before being analyzed (48 hours after collection).

Meteorological Stations at Turkey Point Flux Station

At each of the TPFS chronosequence stands, a permanent meteorological station has been established back in 2002. Data at the stations are being collected ever since by the McMaster Climate Change Research group. Air temperature, soil temperature and moisture are among the many weather and ecosystem parameters being monitored (Arain et al, 2004). During the study period, air temperature was measured using a temperature probe (model HMP45C, Vaisala Oyj, Helsinki, Finland). Soil temperature was monitored

in two soil pits at depths of 2, 5, 10, 20, 50 and 100 cm, using soil temperature probes (model 107B; Campbell Scientific, Inc., Canada), while soil moisture was monitored at 5, 10 , 20, 50 and 100cm depths, using water content reflectometers (model CS615; Campbell Scientific, Inc., Canada). All meteorological and soil data were recorded at half-hour intervals using data loggers (model CR23X; Campbell Scientific, Inc., Canada). Further details regarding meteorological and soil data collection or gap-filling are found in Arain et al (2004).

Meteorological Stations at Groundhog River Flux Station

Meteorological and soil data at Groundhog River Flux Station began to be recorded in August 2003 by Queens University Climatology Group, upon the installation of a permanent meteorological station that same year. Similar to the measurements done at TPFS, air temperature, soil temperature and moisture, at several soil depths, are being monitored at the site. Air temperature is measured using temperature probe (model HMP45C, Helsinki, Finland). Soil temperature and moisture is being measured in two soil pits. Soil temperature is monitored at depths of 2, 5, 10, 20, 50 and 100 cm, using thermocouples, while soil moisture is monitored every four hours, at 15, 30 , 45, 60, 80 and 100 cm depths, using water content reflectometers (model CS616; Campbell Scientific, Inc., Canada). All meteorological and soil data were recorded using data loggers (model CR23X; Campbell Scientific, Inc., Canada). (*pers. commun. Elizabeth Wells, Queen's University Climatology Group*).

2.3.3 Seasonal Measurements of Soil Respiration

Seasonal measurements at TPFS

Seasonal soil respiration measurements at TPFS stands began on June 26, 2003. Throughout the study, measurements were carried out about every two to three weeks (weather permitting). Soil respiration was measured with the LI-COR 6400 system, following the same procedure as was used for the pilot study, with the exception of winter measurements. In winter, soil respiration measurements were reduced to a single set of measurements per day per stand, due to reduced day-light and spatial variability of observed fluxes. Soil temperature and moisture measurements accompanied each soil respiration measurement, as per discussion above (Section 2.3.2.4) with the exception of winter when the soil was snow covered and frozen.

Seasonal measurements at GRFS

The sampling procedure and instrument set up for GRFS was the same as the one employed at TPFS, with the following exceptions. The first soil respiration measurement was taken 1 day after collar installation, on July 31, 2003. Measurements were carried out on a *monthly* basis (Jul'03 to Nov'03 and then Mar'04 till present). No soil respiration measurements were carried out in December 2003 through February 2004, due to site access restrictions in winter and also due to the inoperability of LI-6400 instrument below -10^{o}C temperatures. When measurements resumed in March 2004, there was still a significant amount of snow on the ground (about 60-80 cm deep accumulation along the

transect), so in the end the height of our winter collars was grossly underestimated for this site!

2.3.4 Annual Litter Accumulation Estimates at TPFS

Annual litter fall estimates at TPFS stands were carried out to help explain age related patterns of soil respiration observed at TPFS stands. In November 2003, after all leaf-fall in Southern Ontario, three rectangular sampling plots along the transects at three TPFS stands were set-up. The youngest site (1 yr) had no litter to be collected. In each plot, all fresh leaf-needle litter (differentiated based on colour) was collected into resealable plastic bags. The samples were taken to McMaster University where they were analyzed as follows: all of the samples were pre-weighed, dried in a 110°C oven for 24 hours, and then reweighed after drying. The mass of dry litter (grams) was divided by the area (m^2) of the sampling plot from which it was collected. The obtained values were averaged per stand and used as estimates of annual litter accumulation for their respective stands. This analysis assumed that all of the fresh litter that was collected in November was a good representative of the annual litter fall.

2.3.5 Investigation of spatial variability

Spatial variability in soil respiration was observed at all sites during the course of this study, which prompted us to investigate some possible causes of this variability. Inferred tree root density below each soil respiration measurement location, spatial

variability of soil chemical properties, and spatial variability in the thickness of the litter-organic layer along the transect were considered.

2.3.5.1 Effects of tree root density below measurement location

For this to work, it was important to select a site where the majority of roots that will be detected will come from a single tree (the one along the transect) with little interference from neighbouring trees, shrubs or other understory vegetation. Such conditions were found at the 30 year old forest and so it was chosen for this experiment.

In May and June 2004, two tree transects were installed. One of the established tree transects was 3.5 m long (transect A). Eight collars (same construction as for seasonal measurements) were installed along this transect, at 50 cm intervals, starting at the tree's trunk and moving out into the open area. A second tree transect (transect B) was established beside a different tree. This transect was 3.5 m long and had 15 collars installed along it, at 25 cm spacing, going from the tree trunk out into the open area. Where moss was present inside the collars along the tree transects, it was removed. Measurements were done at least 24 hours after transect installation, using the same measuring procedure as for seasonal measurements, except that a single measurement along the transect was taken per day.

2.3.5.2 Spatial variability of soil nutrient contents

Soil Chemical Analysis at TPFS Chronosequence Sites

On December 31, 2003, soil respiration was measured once along the 50 m long transects, at each TPFS stand. After the soil respiration measurement, soil cores were collected within 20-30 cm of the collar. All twelve collars were sampled at the 60 year old site and only six collars (every second one, odd numbers) at the other three stands (1, 15, and 30 year old). Three samples per collar were collected: one sample of the litter-organic (LFH) soil layer (about 2-5 cm in depth), and two samples of the mineral layer (20 and 15 cm deep). At the youngest site, no litter layer was collected, because none was present. As well, only a single mineral soil core (20 cm deep) was taken at the 1 year old site, since most of the seedling roots were expected to be within the upper 20 cm of the soil, and thus, any chemical effects on soil respiration were also expected to be limited mostly to this depth.

Soil samples were collected, following National Forest Inventory (NFI) Soil Sampling Guidelines (Fluxnet-Canada Research Network, 2003). At first the litter layer (20 x 20 cm^2 area centered about the collar) was removed all the way down to the mineral layer. The thickness of the litter layer was recorded. Then two mineral soil cores were taken using a corer (AMS Basic Soil Sampling Kit, AMS Inc., ID, USA: 2" (5.08cm) diameter corer) from 0-20 cm and 20-35 cm in length at each sampling location. When the second core was taken, the top 1cm of the core was discarded to eliminate contamination by falling soil and debris that occurred when the first core was taken-out. The soil was removed from the corer by gentle tapping on the sides of the corer with a

hammer. All sample handling was done above a ply-wood board surface to prevent spilling and loss of samples. The working surface and tools were wiped clean with a clean cloth after each core was sampled to avoid cross-contamination. All collected samples were placed into individual, labeled, heavy re-sealable plastic bags and transported to a soil testing lab for analysis, within 48 hours of collection. During transportation the soils were kept at temperatures ranging from 0-9 °C.

All mineral soil samples and the litter samples from the 60 year old site were sent for soil chemical analysis to A & L Canada Laboratories Inc., London, ON. All soil samples were analyzed for organic matter, phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), sodium (Na), soil pH, aluminum (Al), total carbon (C) and nitrogen (N). C:N ratios were reported by the lab, where applicable.

Soil Chemical Analysis at GRFS

On November 22, 2003, soil respiration was measured once along the 100 m long transect. After the soil respiration measurement, twelve of the fifty collars (#1-23, all odd-numbered ones) were relocated to within 20-30 cm of their original location, so that soil could be cored below the original collar locations. Four samples per collar were collected using the same equipment and methods described above for TPFS site, except that three mineral soil depths were sampled, instead of just two as was done at TPFS. In total, the mineral soil was sampled to a depth of about 50 cm. All GRFS samples were

analyzed at A & L Canada Laboratories Inc., London, ON for the same soil chemicals as described for TPFS soil samples above.

2.3.5.3 Litter thickness

Litter thickness at each stand was recorded during soil sampling campaigns, when soils were cored for soil chemical analysis. Litter thicknesses collected at that time were correlated to observed soil respirations for each collar. Additionally, at GRFS, four collars were randomly established near existing collars along the 50 m transect, and had the soil organic (LFH) layer removed, all the way to the mineral soil layer. These collars, and their adjacent collars along the transect, which had the organic soil layer intact, were measured in late spring and summer 2004 for comparison.

2.3.6 Data analysis and gap-filling

Data Analysis

Once all of the chamber and associated measurements were obtained, the numbers were analyzed using Excel spreadsheets (Standard Microsoft® Office XP). For each site, for every day of sampling, a mean of morning and afternoon measurements was calculated. A daily mean, which included all measurements, was also calculated, as were standard deviation and coefficients of variability. Linear and exponential regression analysis was performed on daily mean soil respiration measurements and daily mean soil temperature and moisture measurements to see if there was a correlation between respiration and environmental parameters.

The "Analysis ToolPak" package, available with the Excel XP software was used to statistically analyze data. Correlations (r-value) between spatial variability of soil nutrients and litter-thickness to spatial variability of soil respiration were determined using the package, following Qi and Xu (2001). Absolute values of the correlation coefficient above 0.5 were considered to represent a significant correlation. The sign of r told what sort of a correlation existed. A positive r value meant that the correlation was positive - as the nutrient content increased, so did the rate of soil respiration. A negative r-value indicated a negative correlation, whereby if the nutrient concentration increased, then soil respiration decreased.

One major underlying *assumption* in this comparison is that the concentrations of soil chemicals detected from cores collected in November (GRFS) and December (TPFS) remained unchanged throughout the year and were good representatives of soil conditions for each stand.

Filling Missing Data

On several occasions (4 times for 60 yr, 15 yr and 1 yr sites, 6 times for 30 yr site, and 1 time for GRFS), soil temperature values were missing due to equipment failure or frozen soils (in winter). Missing data was filled using continuous data collected in the nearby soil pits. Temperature gaps were filled by taking an average of soil temperatures at 10 and 20 cm depths from both pits, for the hour(s) during which soil respiration was measured at the site on the given day.

Soil moisture (m^3/m^3) measurements from soil pits were used to fill-in missing GWC moisture data, after proper unit conversions. Mean soil moisture for a given day was calculated as an average of either 10 and 20 cm (TPFS) or 15 and 30 cm (GRFS) measurements, collected at the nearby soil pits, for the hours during which respiration was measured at each site.

2.3.7 Modeling annual soil CO_2 -emission estimates

Since actual soil respiration measurements were only periodic, in order to estimate annual soil CO_2 -emissions for each forest stand studied here, a model was required to simulate daily soil respiration, with a reasonably good fit to observed data. Two models were considered in this study. One was a simple temperature-based exponential model that was empirically derived from observed data sets. The other one was taken from literature and fitted with our own site-specific parameters. This second model included temperature, moisture and C:N ratio sensitivity of soil respiration.

Exponential Model

An exponential relationship relating soil temperature (15 cm depth) to soil respiration was fitted to measurements collected during this study, individually for each stand. The general form of the equation describing the relationship was:

$$R_s = a \times e^{bT_{15\,cm}}, \quad (4)$$

where Rs represents soil CO_2 efflux in μmol CO_2 m^{-2} s^{-1}; *a* and *b* are site specific parameters, derived empirically; and Ts is soil temperature at 15 cm depth.

Table 2.3 lists all of the empirically derived exponential equations, their corresponding r^2-values and Q_{10}-values.

Table 2.3: List of equations derived empirically during this study that related seasonal soil respiration variability to seasonal soil temperature and were used to model annual daily soil respiration at TPFS forest stands.

Stand	Empirical Model	r^2	Q_{10}
60 yr TPFS	$R = 0.350e^{0.140T_{15cm}}$	0.93	4.1
30 yr TPFS	$R = 0.333e^{0.128T_{15cm}}$	0.90	3.6
15 yr TPFS	$R = 0.428e^{0.138T_{15cm}}$	0.96	4.0
1 yr TPFS	$R = 0.424e^{0.074T_{15cm}}$	0.80	2.1
GRFS	$R = 0.451e^{0.210T_{15cm}}$	0.95	8.2

Soil Moisture and C:N ratio Sensitive Model

Law et al (2000) used several models to simulate soil respiration in a Ponderosa pine forest in Central Oregon, USA, and compared their simulations to actual observed results from the site. They found the best fit to a model that contained soil temperature, moisture, and C:N ratio. The following generalized equation from Law et al (1999), their equation (2), was used:

$$R = (a \times CN) + (-b \times \theta) + \exp(c \times Ts), \quad (5)$$

where R refers to soil CO_2 efflux in μmol CO_2 m^{-2} s^{-1}; Ts is soil temperature in °C (15 cm was used); θ is soil volumetric water content (Law et al used 0-100 cm depths, but here an average of 0-20 cm depths was used for TPFS stands, and 0-30 cm average for GRFS);

C:N is carbon to nitrogen ratio of soil. Variables, a, b and c, are site specific parameters, that were fitted to data at TPFS and GRFS, separately for each stand. The parameters that were used are listed in APPENDIX B.

For GRFS and the 60 year old TPFS stand, C:N ratios for the organic (LFH) soil layers were used. For the 30 and 15 year old stands, the model was applied using C:N ratios from the 60-year-old stand, since no C:N ratio's were available for the younger sites. For the 1 year old stand, the model was used without the C:N component (i.e. C:N = 0) since there was no litter layer at the site.

Estimates of annual soil CO_2 - emissions

Annual CO_2 - emissions for all stands were calculated using results from both models that used half hour soil temperature (10 and 20 cm averages) and soil moisture (0-20 cm averages for TPFS stands and 0-30 cm average for GRFS) data available from each site for one full year of the study (June 2003 to May 2004, inclusive for TPFS and August 9, 2003 to August 8, 2004 for GRFS). For GRFS soil moisture data was linearly extrapolated from the four hour measurements to half-hour measurements before being used in soil CO_2 - emission simulations. The total and seasonal estimates were calculated and are discussed below, with the following ***break down of months per season*: winter** was taken as December to March, **spring** as April and May, **summer** as June to September, and **fall** as October and November.

2.3.8 Uncertainty in Measurements

Uncertainties in soil respiration measurements included the possibility of slight overestimation due to the presence of vegetation in some of the collars, which also respires above ground and may have added to the observed soil flux. Vegetation protruding up above the collar into the soil chamber can affect calculated rates by changing chamber volume.

Diurnal variability in soil temperatures, especially for the youngest stand, may have biased the calculated average, especially in the spring and summer when diurnal fluctuations in air temperatures were more profound. However, this effect was not too great and to compensate for it, morning and afternoon measurements were taken at each site during measurement campaigns (more in *Section 3.2*).

Winter measurements had several problems associated with them. Instrument performance was one of them. LI-6400 instruments have been designed to work in the temperature range of 0° to +50 °C. However, in the past, researchers have successfully used the LI-6400 to measure soil respiration in temperatures around or below 0°C (McDowell et al 2000; Shibistova et al, 2002; Elberling et al, 2003). From personal communications with some of the authors of those studies, they reported experiencing some operational difficulties with the instrument which they resolved by insulating the instrument, bringing it inside to warm-up in between measurements and not using it below -10°C (*per. comm.* O. Shibitstova and B. Elberling). The same approaches were also applied in this study. Neither the IRGA nor the console ever shut-down during our winter measurements. However, at air temperatures of about -5°C, the screen on the

console (which was not insulated) blacked-out on several occasions, making it impossible to program the instrument or read what was being logged. A more important issue was also the fact that winter respiration at TPFS was often near the detection limits of the instrument, thus winter respiration values must be viewed with caution.

A greater problem was experienced with measurements done above winter collars. During February measurements at TPFS, the snow inside the collars, especially at the youngest two sites was quite low (only about 5-10 cm deep). When winter collars (30 cm tall) were used, the chamber was sitting about 20-25 cm above the soil surface (insertion depth of about 20-25 cm). Later in the lab, after analyzing collected data, it was noticed that when "insertion depth" was above 10 cm above ground, the total volume calculated by the instrument was negative and all associated fluxes were also negative. During subsequent measurements over snow, it was determined that placing the collar directly on snow was the best option for winter measurements. Use of winter collars was abandoned. Measuring winter respiration directly over snow was further supported by reasonable results obtained at GRFS during March, when all winter collars were lost below snow-cover and the only way to complete the measurements was by placing the chamber directly over snow.

CHAPTER 3: JUSTIFICATION OF SAMPLING DESIGN

3.1 Results and discussion of pilot study

Table 3.1 compares the results obtained from the pilot study for the square and transect collar set-ups. For the transect, the mean soil respiration observed was 4.0 ± 1.4 μmol CO_2 m^{-2} s^{-1}, while for the square set-up it was 3.7 ± 1.0 μmol CO_2 m^{-2} s^{-1}. Coefficient of variation (%), a representative of soil respiration's spatial variability, was higher for the transect set-up (35%) compared to the square set-up (28%). Thus, the transect was better at capturing greater degree of spatial variability of soil respiration along the forest floor, compared to the square set-up.

Table 3.1: Comparison of soil respiration and its variability between the square and transect collar set-ups

	Transect	Square set-up
land cover	100 m line	625 m^2
# of collars measured	50	61
Average Respiration (μmol CO_2 $m^{-2}s^{-1}$)	4.0	3.7
Standard Deviation	1.4	1.0
%CV (coefficient of variation)	35	28

Following Yim et al (2003), an analysis was done to determine how many collars would need to be installed per stand, such that measured mean soil respiration was within 10% or 20% of its value at 95% and 90% confidence levels. Table 3.2 shows the results of this analysis. Yim et al. analyzed 50 sampling points in a 900 m^2 plot. They found that they would need 27 to 33 collars to estimate mean soil respiration within 10% and only 7 to 8 collars to estimate mean soil respiration within 20% of its actual value at the 95 % confidence level. The coefficient of variation (%CV) Yim et al got for their square

set up was 26 to 29%, which was comparable to the results of our pilot study using a square set-up (i.e. 28% for a 625 m^2 area).

From our pilot study, it was determined that for a transect, 49 collars would be required in order to estimate soil respiration within 10% of the actual value at 95% CL, while to be within 20% at the same confidence level, only 12 collars would suffice (Table 3.2). For comparison, 31 collars inside a square plot would be required to estimate soil respiration within 10% and only 8 within 20% of the actual value at the 95% CL.

Table 3.2: Number of collars that would be needed to estimate mean soil respiration to within 10% and 20% of its actual value at the 90% and 95% confidence levels (CL).

			# of collars needed to be at			
			90% CL		95% CL	
Measurement set up	# of collars measured in Pilot Study	Measured average soil respiration	Within 10%	Within 20%	Within 10%	**Within 20%**
Square (625 m^2)	61	3.7 ± 1.0 μmol $CO_2m^{-2}s^{-1}$	22	5	31	**8**
Transect (100 m long)	50	4.0 ± 1.4 μmol $CO_2m^{-2}s^{-1}$	34	8	49	**12**

For completeness, Table 3.2 also gives the estimated number of collars that would be required to measure soil respiration for each set-up, such that the mean was within 10% and 20% of the actual at a 90% CL. For the 90% CL, less collars would do the job compared to the 95% CL.

In *conclusion*, a transect was chosen over a square, since it better captured spatial variability in soil respiration and 12 collars per TPFS stand were installed (good enough to be within 20% at 95% CL and still manageable, in terms of time,to complete morning and afternoon measurements at all four sites in a *single* day).

3.2 Results and discussion of diurnal measurements

If a valid comparison between soil respiration across the chronosequence was to be made using measurements carried out at different times of day, it should be shown that the measurements were indeed comparable and no diurnal variability was biasing the results. In other words, minimal diurnal variability was required to justify our sampling scheme.

Diurnal variability

Figures 3.1 (a-d) show diurnal trends in soil respiration across the chronosequence sites measured in 2003 and 2004. At the 60 year old stand, in August 2003, soil respiration seemed to increase after sunset and peaked before dawn, but upon sunrise, around 7 am, respiration began decreasing once more. As an interesting aside, during this diurnal measurement, we were very fortunate to capture an event that very often evades those in our community who measure soil respiration only periodically. Between 13:00 and 14:00 there was a brief and heavy thunderstorm at the site. A sudden and short-lasting peak in soil respiration, after the rain event, was observed. This peak corresponded to rising soil moisture content, as detected in nearby soil pits (Figure 3.2). Other research groups have also observed increased soil respiration following rain events (Lee et al, 2004; Irvine et al, 2002) It was suggested that heavy rain could cause a short-term burst of CO_2 gas from soil pores, as rain water percolates down initially displacing gas from soil pores (Lee et al, 2004). Now back to diurnal measurements…

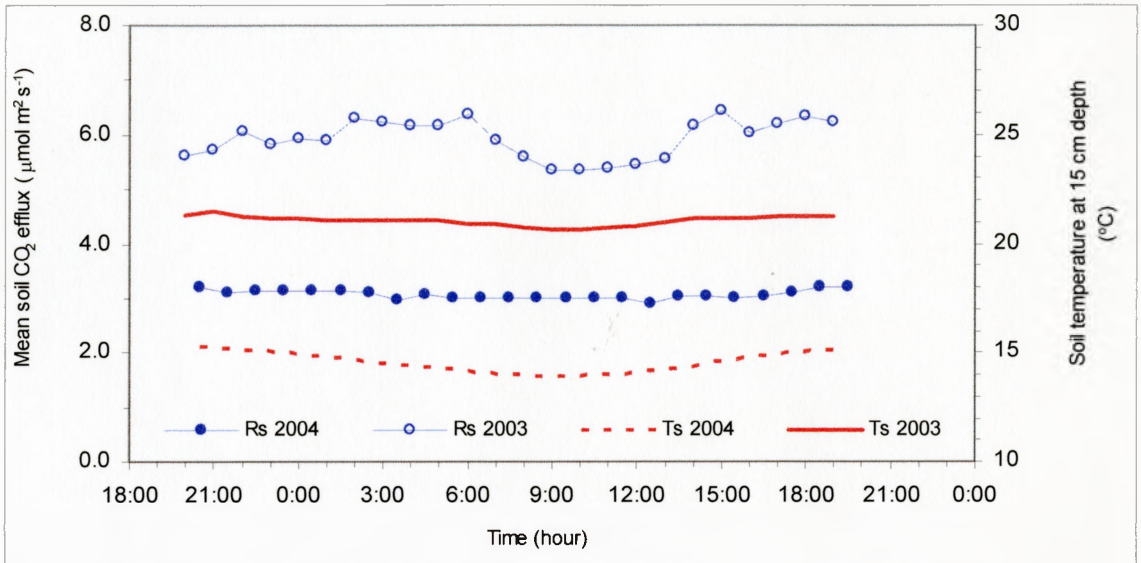


Figure 3.1 a) Mean diurnal soil CO_2 efflux, Rs, and soil temperaure (15 cm depth), Ts, at the 60 year old stand, calculated from measurements taken at 12 collars along a 50 m transect on Aug 15-16, 2003 and Jun 25-26 2004.

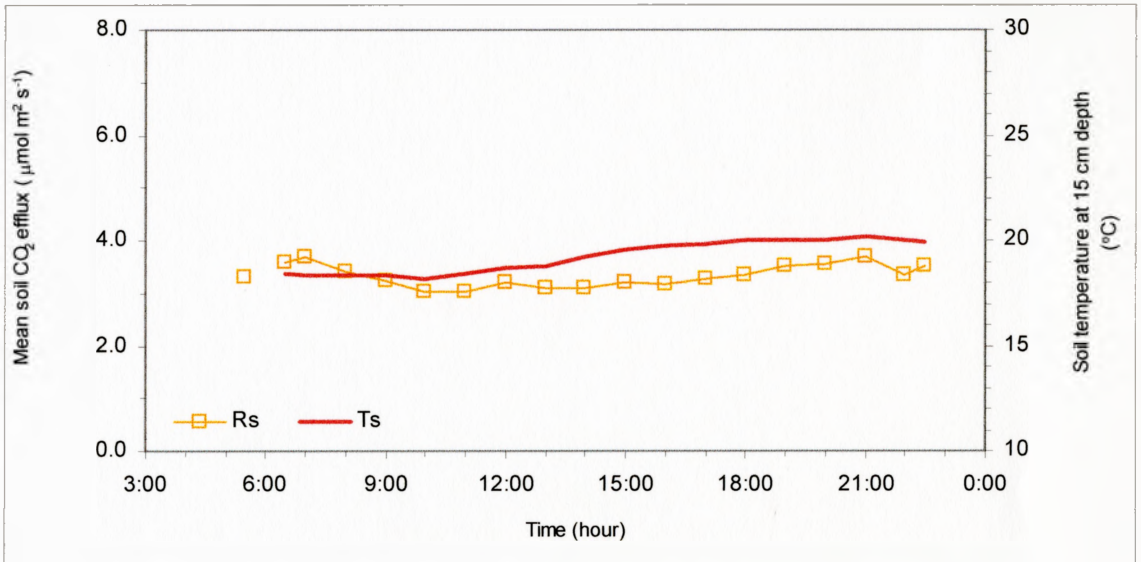


Figure 3.1 b) Mean diurnal soil CO_2 efflux, Rs, and soil temperaure (15 cm depth), Ts, at the 30 year old stand, calculated from measurements taken at 12 collars along a 50 m transect on Aug 21, 2003.

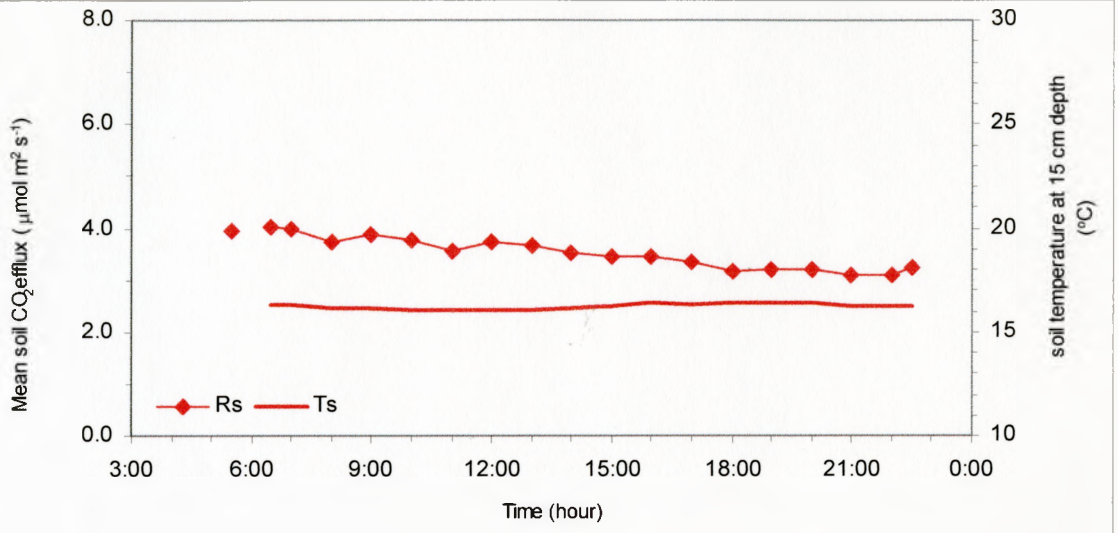


Figure 3.1 c) Mean diurnal soil CO_2 efflux, Rs, and soil temperaure (15 cm depth), Ts, at the 15 year old stand, calculated from measurements taken at 12 collars along a 50 m transect on Sep 4, 2003.

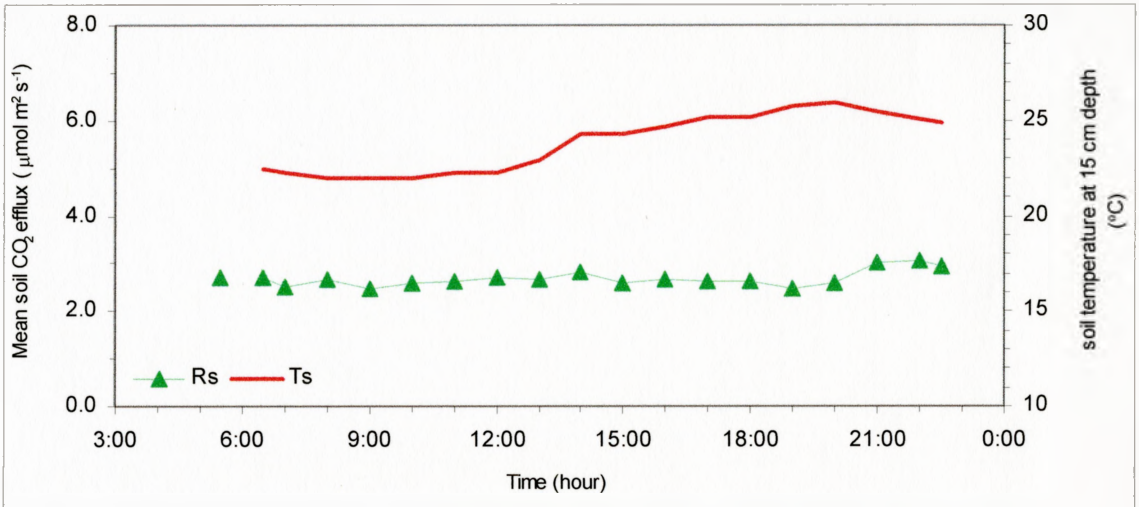


Figure 3.1 d) Mean diurnal soil CO_2 efflux, Rs, and soil temperaure (15 cm depth), Ts, at the 1 year old stand, calculated from measurements taken at 12 collars along a 50 m transect on Aug 12, 2003.

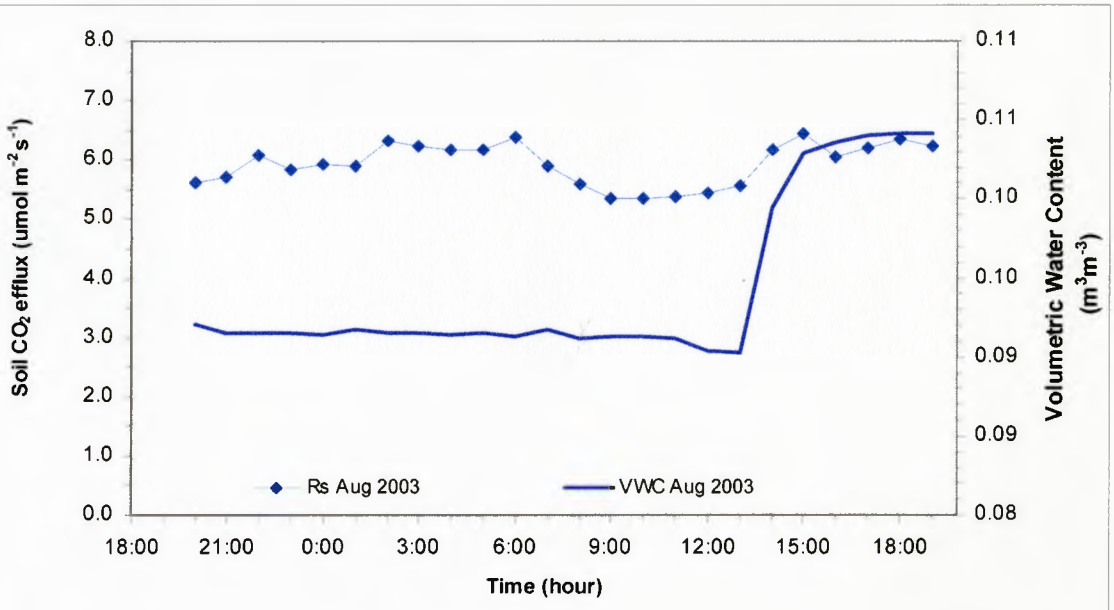


Figure 3.2 : Diurnal measurement of soil respiration at the 60 yr site, showing a correlation between an intense rain event (13:00-14:00) and short-term increase in soil respiration (Rs).

For all sites, diurnal fluctuation of mean soil respiration was about 1μmol CO_2 m^{-2} s^{-1} over the course of 24 hours (or 18 hours). This was comparable to the diurnal fluctuation reported by Xu and Qi (2001) in a ponderosa pine forest in California.

However, the degree of diurnal variability may vary with season. When the two diurnal measurements of soil respiration at the 60 year old site are compared, there appears to be less variability in observed respiration during early growing season (June 2004) compared to the respiration observed during late growing season (August 2003). This was despite greater variability in soil temperatures in 2004 compared to 2003. The increased variability may be due to some physiological changes that the forest undergoes over the course of the growing season. Law et al (1999) also reported seasonal variability in diurnal course of soil respiration in their ponderosa pine forest in Central Oregon. They observed lower variability in spring compared to summer time, when soil respiration rates tend to be at their maximum.

Morning vs Afternoon Measurements

Figure 3.3 (a) compares morning and afternoon soil respiration measurements at all four TPFS stands carried out throughout the study period. The correlation between the two sets of measurements for all, but the youngest site, was high (r^2= 0.97-0.98). At the youngest site, the correlation was lower (r^2 = 0.75), most likely due to the much larger diurnal variability in soil temperature that was also observed there. This diurnal variability appears to be seasonal, with the largest variability observed in the early and late growing seasons, which also corresponds to larger diurnal variability in soil

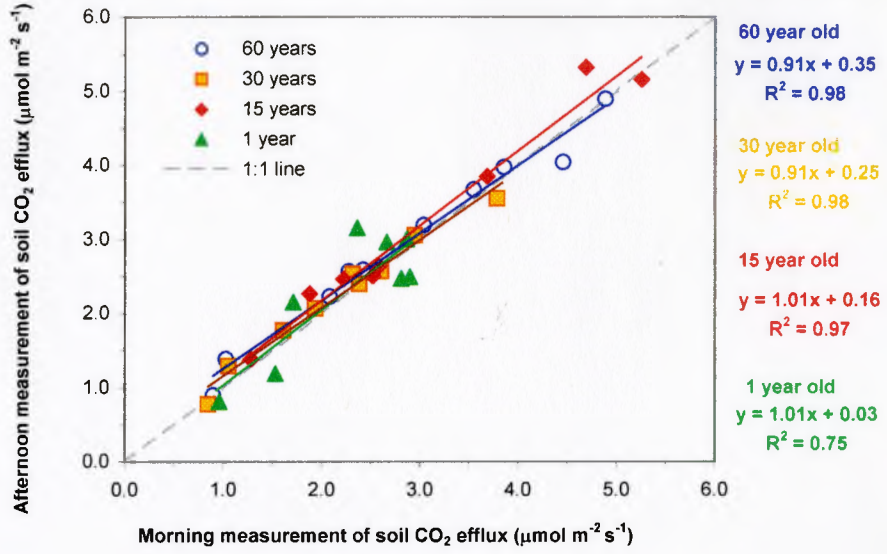


Figure 3.3 a: Comparison of morning and afternoon soil respiration measurements at the four chronosequence sites. Each point represents a mean calculated from measurements done at 12 collars along the transect.

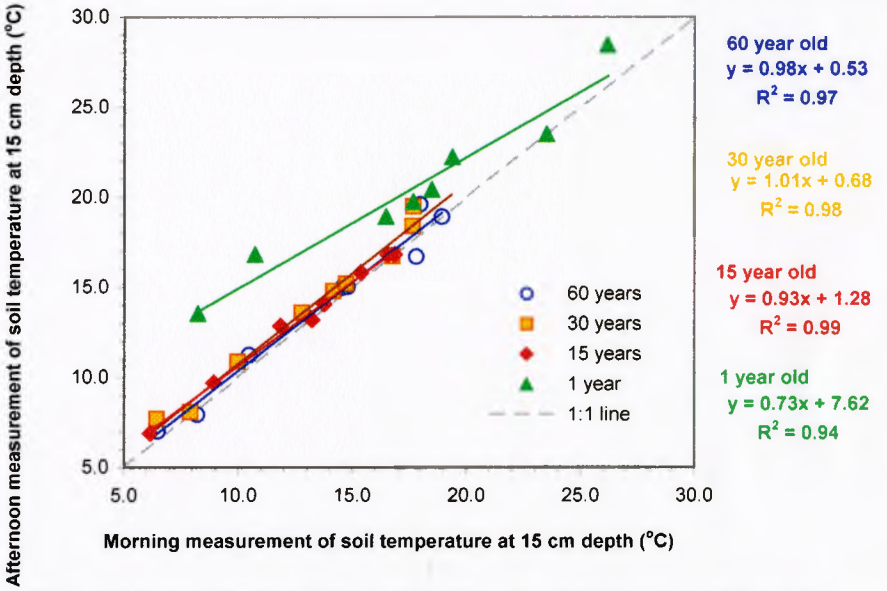


Figure 3.3 b: Comparison of morning and afternoon soil temperatures taken during soil respiration measurements at the four chronosequence sites. Each point represents a mean calculated from measurements done at 12 collars along the transect.

temperatures at the site (Figure 3.3 (b)). The one year old stand has very little canopy and no litter-cover to help regulate its diurnal soil temperature regime and so its soil temperature is more prone to diurnal fluctuations of air temperature. The two outliers in figure 3.3.b correspond to spring and fall measurements, when day-night air temperature fluctuations tend to be high.

In *conclusion,* results from diurnal measurements and comparison of morning and afternoon measurements of respiration at TPFS stands justified our sampling strategy, whereby we could compare daily soil respiration among the four stands, even though the stands were not measured concurrently. This was especially true for the three older stands. The only discrepancy may be at the 1 year stand during spring and fall, when larger ranges in diurnal air temperatures may cause increased diurnal variability in soil temperatures and consequently in soil respiration. Another problem may arise on rainy days, when soil respiration may be overestimated immediately following rain. However, during the course of this study, rainy days were avoided for measurements, as best as was possible (since the electronics of an exposed LI-6400 are not very fond of water).

CHAPTER 4: TEMPERATE FOREST CHRONOSEQUENCE STUDY

4.1 Results

4.1.1 Environmental conditions during study

Table 4.1 compares the minimum and maximum values of average daily air and soil temperatures and soil moisture. The month(s), when the maxima or minima were observed, are also listed in the table as are the yearly averages of all the variables. Figures 4.1 (a_i-d_i) show the course of average daily air and soil temperatures (average of 10 & 20 cm depths for soils) at each of the TPFS sites for the year of the study. Included in the figures are soil temperature measurements taken during soil respiration measurements with the LI-COR 6400-013 soil-temperature probe. Figures 4.1 (a_{ii}-d_{ii}) show the trends in daily average soil moisture at the four sites during the course of the study period. The figures also show point-measurements of soil moisture, calculated from gravimetric water content measurements performed occasionally throughout the study period in conjunction with soil respiration measurements.

Air and Soil Temperatures

Over the course of the study period, the mean yearly (Jun'03 to May'04, inclusive) air temperatures at all four sites (8.6 °C, 9.1 °C, 9.0 °C, 9.2 °C for the 60, 30 ,15 and 1 year old site, respectively) were comparable among each other. The values were slightly higher, by about 0.5 to 1 °C, than the normals reported for the areas (Table 2.1, page 13). During this study period, maximum average daily air temperatures were observed at the

Table 4.1: Comparison of environmental conditions at the four TPFS sites during the course of the study period. Shown are air and soil temperatures and soil moisture, their average daily maximum and minimum values, the months during which those values where observed, and the yearly average.

	Air temperature			**Soil temperature**			**Soil moisture**		
	Max	**Min**	**Ave**	**Max**	**Min**	**Ave**	**Max**	**Min**	**Ave**
60 yr site	23.7	-18.1	8.6	21.9	-0.4	9.8	0.19	0.06	0.11
month	*Jul-03*	*Jan-04*		*Aug-03*	*Feb-04*		*Mar-04*	*Jul, Aug, Sept -03*	
30 yr site	24.5	-17	9.1	20.9	-0.5	9.7	0.19	0.06	0.12
month	*Jun-03*	*Jan-04*		*Aug-03*	*Jan, Feb-04*		*Mar-04*	*Jul, Aug, Sept -03*	
15 yr site	24.4	-18.2	9.0	15.7	-3.9	6.8	0.21	0.06	0.11
month	*Jun-03*	*Jan-04*		*Sep-03*	*Jan-04*		*Mar-04*	*Aug, Sep-03*	
1 yr site	24.2	-17.9	9.2	27.3	-3.1	12.1	0.18	0.07	0.12
month	*Jul-03*	*Jan-04*		*Aug-03*	*Jan-04*		*Oct-03*	*Jan, Jun -04*	

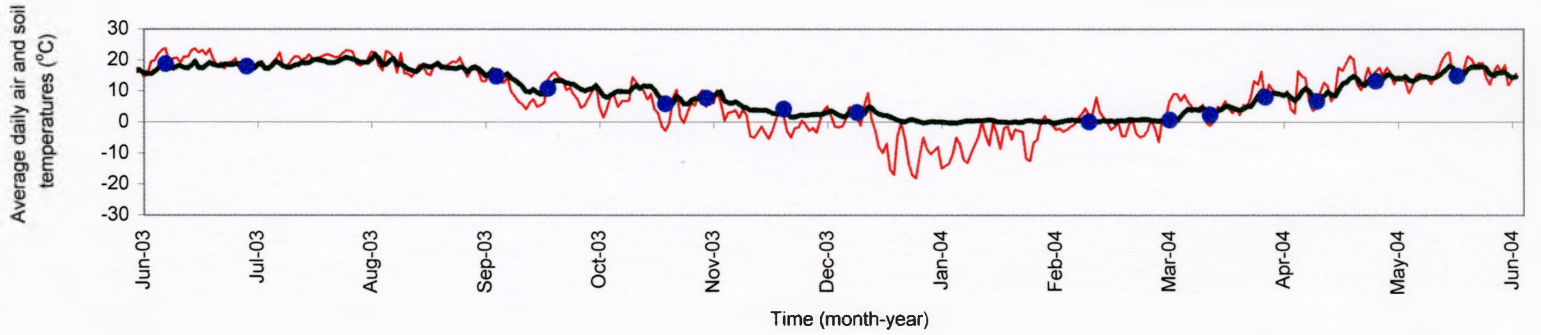


Figure 4.1 a $_{i}$): Trends in daily average air, Tair, and soil, Ts, (average of 10 and 20 cm depths from both soil pits) temperatures at the 60-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements. Symbols represent average soil temperature measurements taken along the transect with the LI-6400-013 soil T-probe.

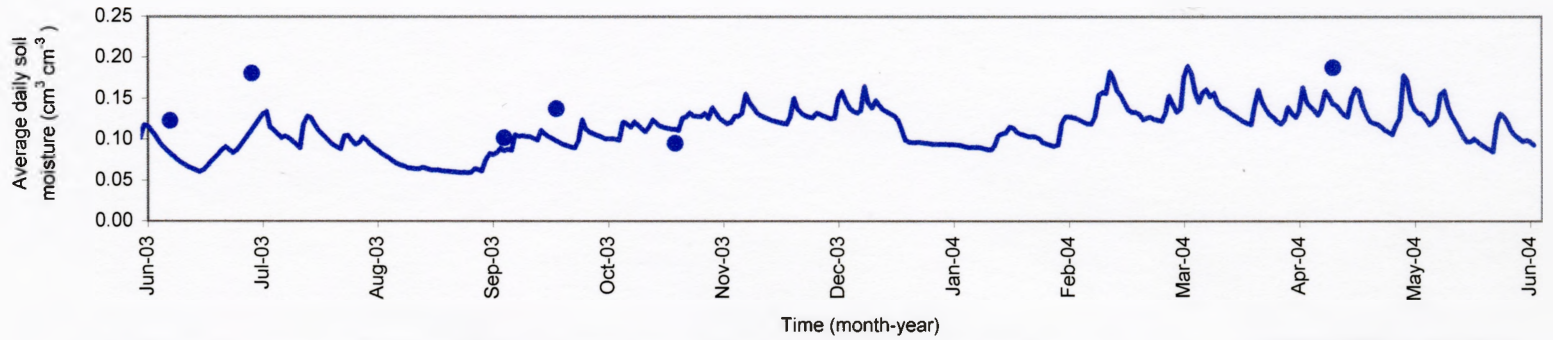


Figure 4.1 a $_{ii}$): Trends in daily average soil moisture at the 60-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements, collected at 5, 10 & 20 cm depths in both soil pits: A and B. Symbols represent average GWC measurements (multiplied by bulk density to give VWC) occasionally done along the transect at the site.

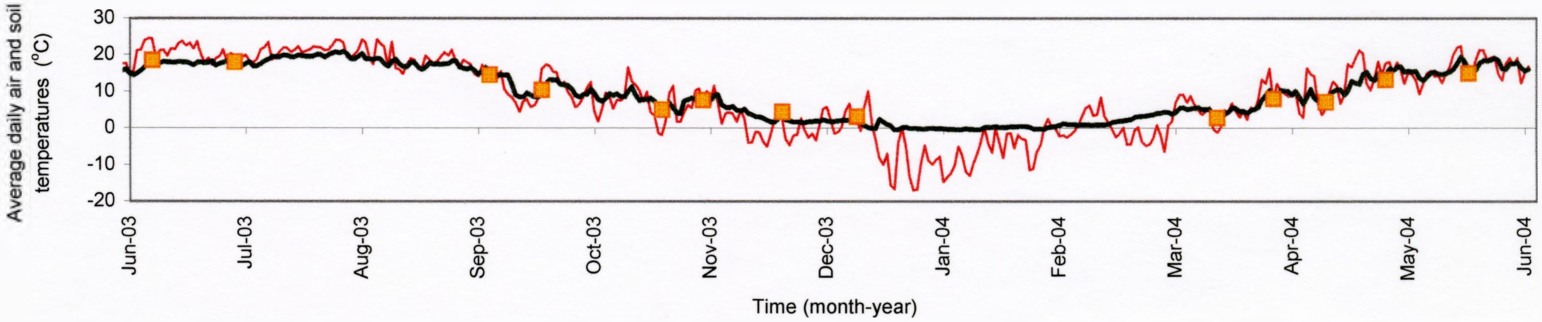


Figure 4.1 b $_{i}$): Trends in daily average air, Tair, and soil, Ts, (average of 10 and 20 cm depths from both soil pits) temperatures at the 30-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements. Symbols represent average soil temperature measurements taken along the transect with the LI-6400-013 soil T-probe.

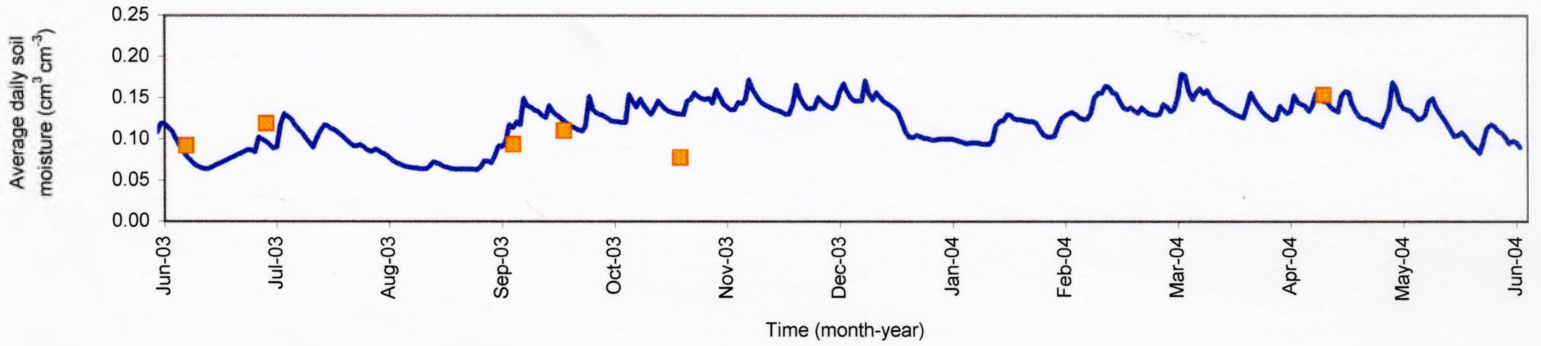


Figure 4.1 b $_{ii}$): Trends in daily average soil moisture at the 30-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements, collected at 5, 10 & 20 cm depths in both soil pits: A and B. Symbols represent average GWC measurements (multiplied by bulk density to give VWC) occasionally done along the transect at the site.

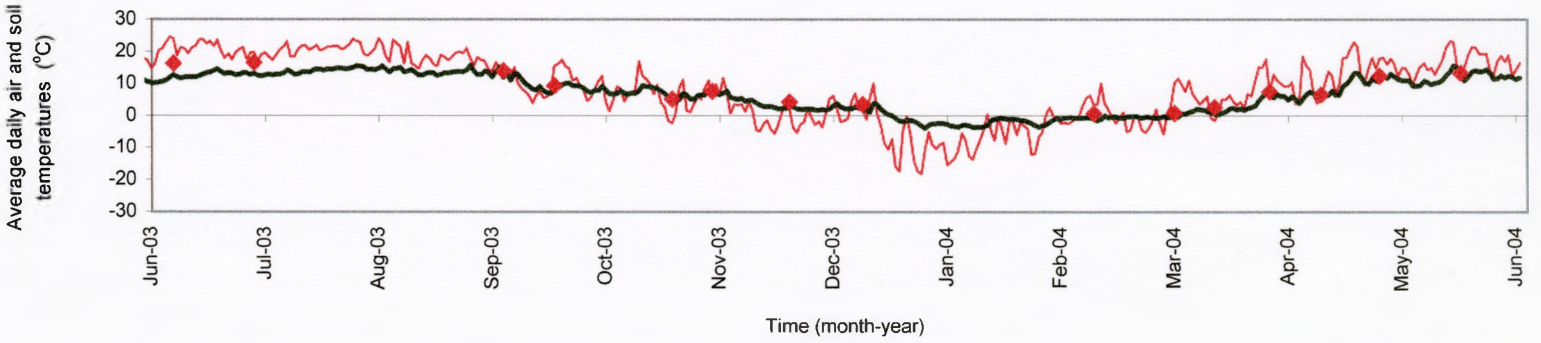


Figure 4.1 c $_{i}$): Trends in daily average air, Tair, and soil, Ts, (average of 10 and 20 cm depths from both soil pits) temperatures at the 15-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements. Symbols represent average soil temperature measurements taken along the transect with the LI-6400-013 soil T-probe.

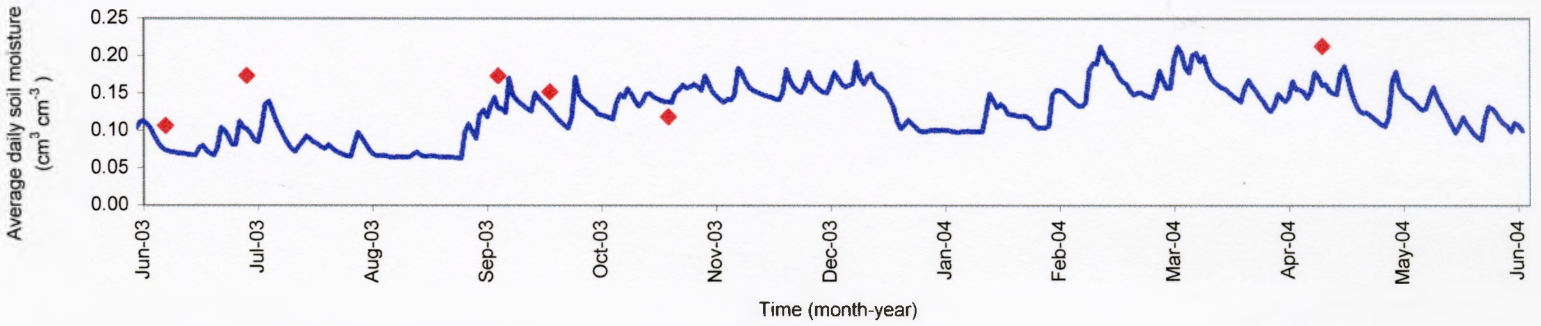


Figure 4.1 c $_{ii}$): Trends in daily average soil moisture at the 15-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements, collected at 5, 10 & 20 cm depths in both soil pits: A and B. Symbols represent average GWC measurements (multiplied by bulk density to give VWC) occasionally done along the transect at the site.

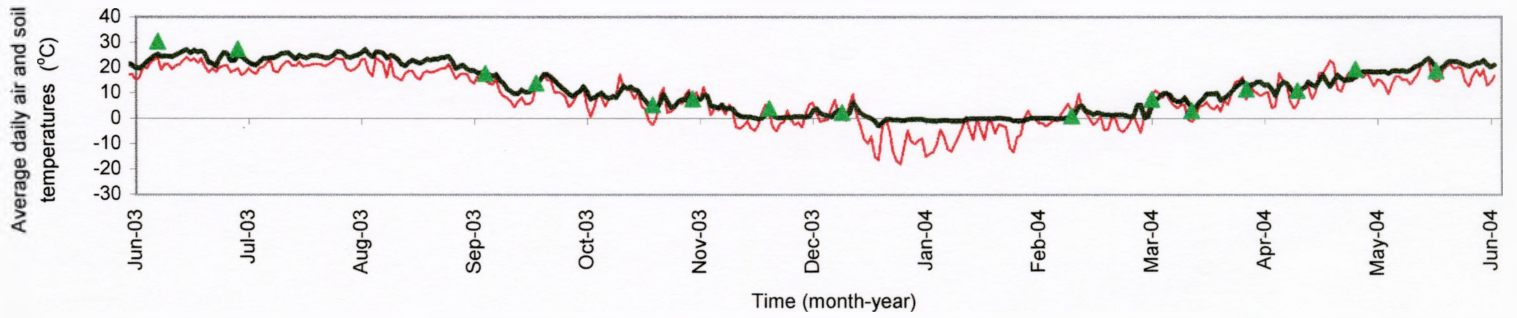


Figure 4.1 d $_{i}$) Trends in daily average air, Tair, and soil, Ts, (average of 10 and 20 cm depths from both soil pits) temperatures at the 1-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements. Symbols represent average soil temperature measurements taken along the transect with the LI-6400-013 soil T-probe.

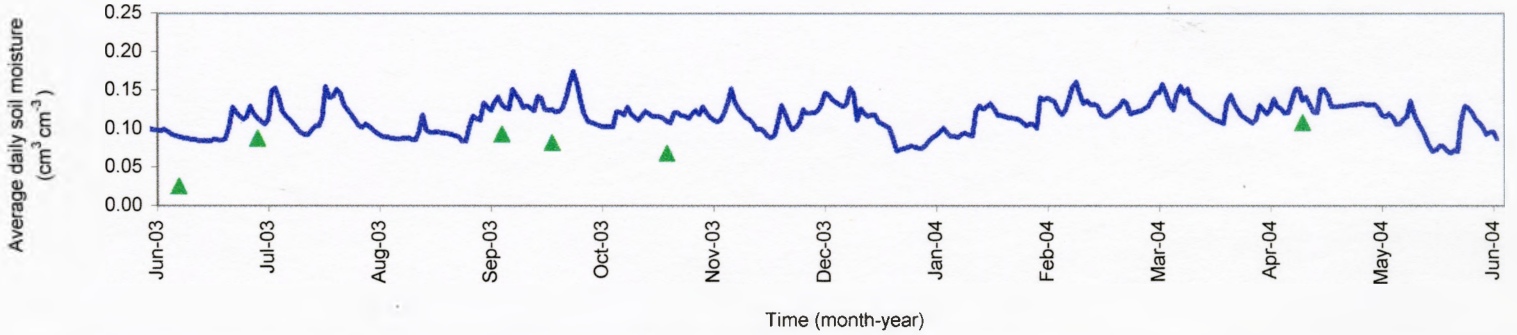


Figure 4.1 d $_{ii}$): Trends in daily average soil moisture at the 1-year-old TPFS stand over the course of the study period. Daily averages were calculated from half-hour measurements, collected at 5, 10 & 20 cm depths in both soil pits: A and B. Symbols represent average GWC measurements (multiplied by bulk density to give VWC) occasionally done along the transect at the site.

end of June, beginning of July 2003 for all four forest stands. The minimum average daily air temperatures were observed in January 2004.

Greater variability among sites was observed when soil temperatures were considered. The 60 and 30 year old sites were comparable in terms of their maximum and minimum daily averages of soil temperature. At the 60 year old stand, maximum average daily soil temperature was observed at the end of August 2003 (21.9 °C), while the minimum was observed at the end of February 2004 (-0.4°C). Similarly, the maximum daily average soil temperature at the 30 year old site was observed in mid August 2003 (20.9 °C), while the minimum was observed throughout January until February 2004 (-0.5 °C). The yearly averages were also comparable between those two sites (9.8°C and 9.7°C for the 60 and 30 year old stands, respectively). In contrast, soil temperature at the 15 year old site appeared to be the coolest, with a yearly average of 6.8°C, while the youngest site was the warmest, with the yearly average of 12.1°C. The maximum daily average soil temperature at the 15 year old stand was recorded in mid September 2003 (15.7°C), which was about 5°C cooler than the maximums observed at the oldest two sites and about 12°C cooler compared to the maximum at the youngest site. The minimum daily average soil temperature at the 15 year old stand was observed in January (-3.9°C) and was the lowest one recorded across the chronosequence during this study period. On the other hand, the youngest stand attained the highest daily average soil temperature of all sites (27.3°C), at the end of August 2003. The minimum daily average temperature at the 1-year-old stand was observed in January 2004 (-3.1°C).

There did not appear to be much lag between air and soil temperatures across the chronosequence, with the exception of springtime at the three oldest stands, when soil temperatures were somewhat slow in responding to rising air temperatures. Overall, air temperature was more variable than soil temperature. At all sites, both air and soil temperatures peaked over the summer months, fell during autumn, reached a minimum in winter months, and rose again in spring. There was a brief rise in soil temperature in November 2003, due to a heat wave, which was captured during seasonal soil respiration measurements. Below freezing air temperatures were not observed until end of December 2003. Soils began freezing shortly thereafter, beginning in mid January 2004, and remained near 0°C until about March 2004. In early March 2004, there was a brief warm spell, characterized in the figures with a peak in air temperatures. Soil temperature at the three oldest stands did not respond quickly to that warm spell and remained near freezing till end of March, beginning of April. In contrast, soil at the 1 year old site responded much faster to the rising air temperatures in spring, including the warm spell in March, and began warming-up much earlier than the rest of the stands.

The seasonal trend of soil temperature measured with the LI-COR probe closely followed the seasonal trend of daily average soil temperature measured in soil pits at all four sites. The only discrepancies were observed for the two youngest sites at the start of the study period (June, July 2003 measurements), when the LI-COR probe overestimated soil pit temperatures by about 2-5°C.

Soil Moisture

Table 4.1 shows that the average maximum, minimum and yearly soil moisture (cm^3/cm^3) among the four TPFS sites was quite similar. At the three oldest sites, maximum soil moisture (0.18-0.19) was achieved in March 2004, after snowmelt. In contrast, at the 1 year old site, maximum soil moisture was achieved in October 2003. The minimum daily average soil moisture at the oldest three sites (0.06) was observed at the beginning of July 2003 and then again at the end of August 2003 until early September 2003. For the youngest site, minimum soil moisture (0.07) was observed in January and June 2004.

Overall, soil moisture was very variable (Figures 4.1 a_{ii}-d_{ii}). The general trend in soil moisture at all four sites was similar during the study period: soil moisture was low at the start of July 2003, increased somewhat over the month, before plummeting again in late August through September 2003. During the fall months, soil moisture increased, but fell again in January 2004, with the onset of freezing. In early spring 2004, soil moisture increased once again, but has been steadily decreasing towards June 2004, as soil temperatures increased. The manual soil moisture measurements, from gravimetric water content analysis, did match soil pit data well, except for the youngest stand and a few points for the older stands. For the oldest three sites, manual measurements tended to slightly overestimate soil pit measurements by about 0.05 cm^3/cm^3, while for the youngest site they underestimated soil pit measurements by a similar amount.

4.1.2 Seasonal variability in soil respiration

Seasonal Cycle of Respiration

The seasonal cycle of observed mean soil respiration across the chronosequence, from June 2003 through June 2004, is shown in Figure 4.2. All sites followed a similar seasonal pattern of soil respiration over the course of the study period. Soil respiration increased from June 2003 until August 2003, when the highest mean soil respiration was observed (4.9 ± 1.3 μmol CO_2 $m^{-2}s^{-1}$, 3.8 ± 0.9 μmol CO_2 $m^{-2}s^{-1}$, 5.2 ± 1.3 μmol CO_2 $m^{-2}s^{-1}$, 2.9 ± 0.9 μmol CO_2 $m^{-2}s^{-1}$, for 60, 30, 15, and 1 year old sites, respectively). After August's high, mean respiration at all sites decreased, converging in winter. The exception to the declining trend, over the fall months, was a peak in November 2003. In January and February 2004, soil respiration hit a low of 0.2-0.4 μmol CO_2 $m^{-2}s^{-1}$ across the chronosequence. After a winter's low, as soils began to warm-up, respiration began to increase and differentiate once more between the sites. In 2004, the pattern of soil respiration observed during the growing season in 2003 was beginning to reappear, as respiration increased into June 2004.

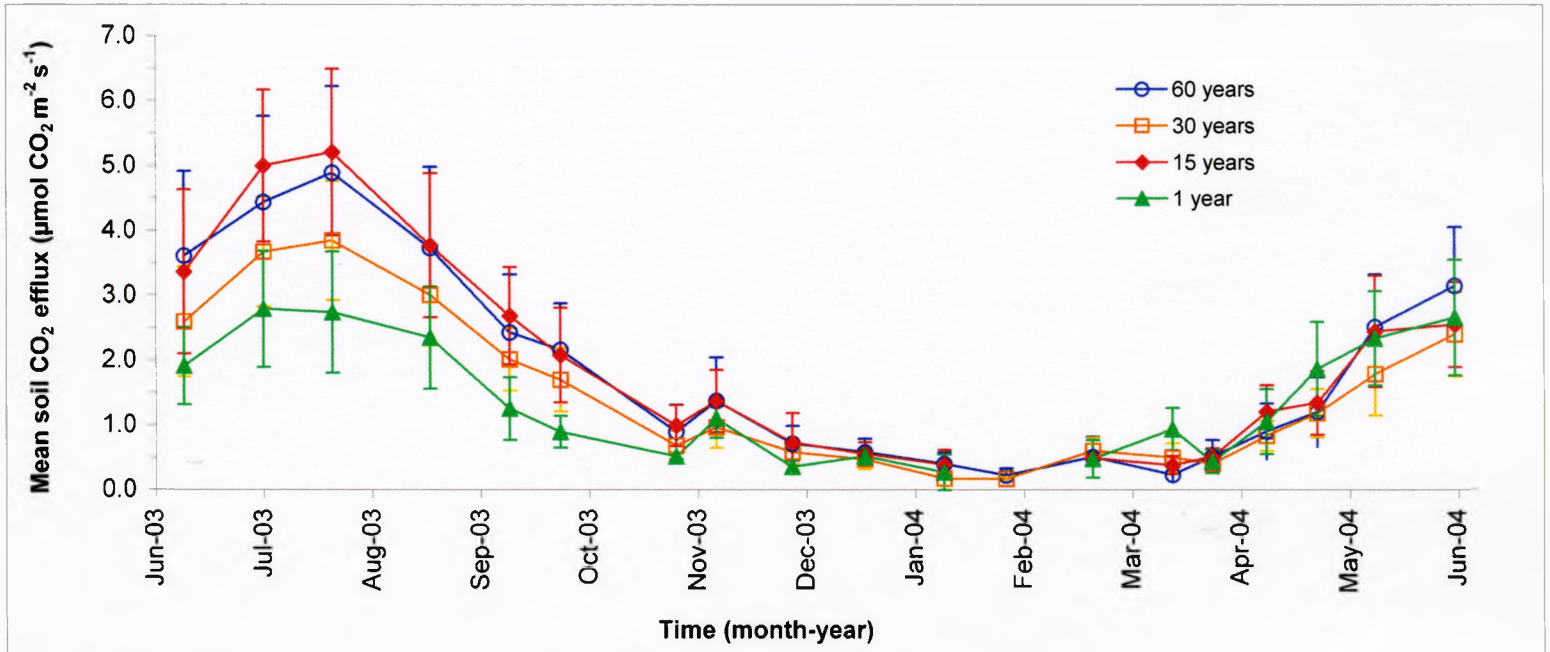


Figure 4.2: Comparison of seasonal variability in soil CO_2 efflux at the four chronosequence sites. Plot shows mean soil CO_2 efflux rates measured on 19 days throughout the year along the transect at each site. Error bars represent ± 1std.dev. February measurements for 1 and 15 year old sites were not included, but should follow closely the trends for the 60- and 30-year-old stands.

Soil respiration and soil temperature

In general, the seasonal variability of mean soil respiration followed closely the seasonal variability of soil temperature. For example, on November 20, soil respiration suddenly increased, which correlated well with a sudden increase in soil temperature at the time. There was a vivid peak in soil respiration at the 1 year old site on March 25, which was not observed at the other three sites. This peak correlated well with increase in soil temperature at the site, which, in turn, corresponded to a warm spell denoted by a peak in air temperature at the same time (Figure 4.1 (a_i-d_i)). The rise of soil respiration in March was not observed at the older three stands. That day, the upper 15 cm of soil at the 1 year old site were already unfrozen and warmed up to 7.5 ± 0.6 °C, while the soil at the other three sites was around 0°C and only beginning to thaw. On several occasions, especially in June 2003 and again in June 2004, soil respiration did not increase, despite increases in soil temperature.

Overall the seasonal variability in soil CO_2 emissions at all TPFS stands was related positively and exponentially to seasonal variability in soil temperatures (Figure 4.3), based on an empirical fit. This relationship was the strongest for the 60 and 15 year old stands (r^2 = 0.93 and 0.96, respectively), followed closely by the 30 year old stand (r^2 = 0.90), but was the weakest for the 1 year old stand (r^2 = 0.80).

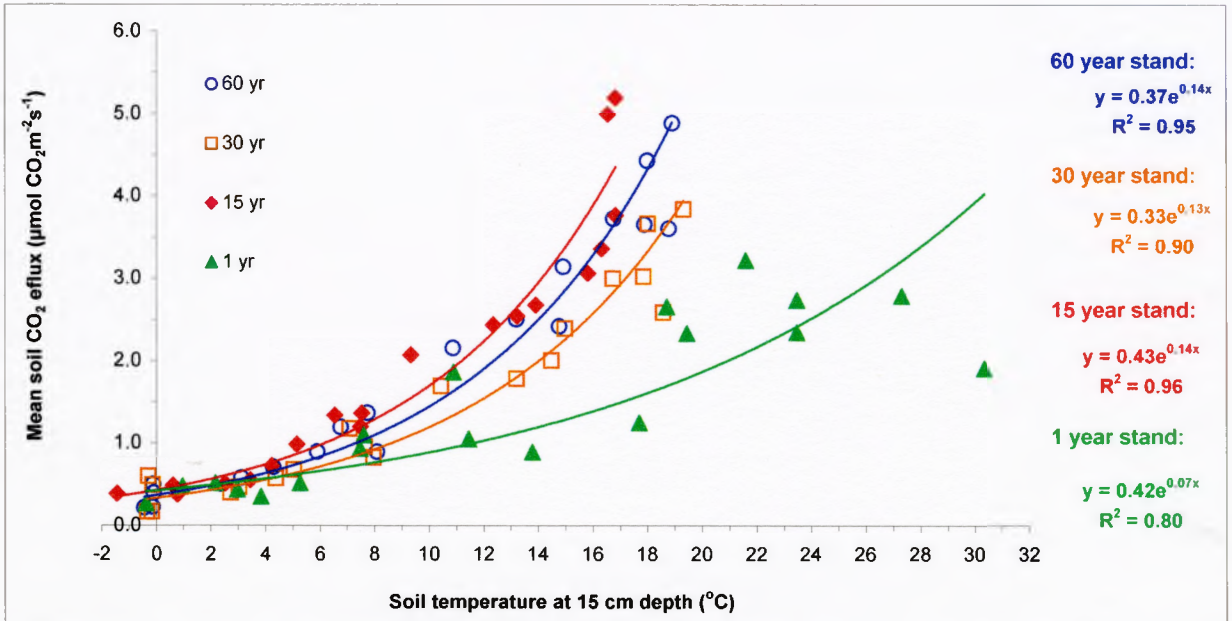


Figure 4.3: Exponential, emprically-derived relationships between mean daily soil respiration and soil temperature (15 cm depth) across the chronosequence. Each data point represents a daily average of measurements at 12 collars along the transect. Measurements from June 2003 to June 2004 are shown.

The Q_{10} values from the relationships were as follows, based on full year's data: 4.1, 3.6, 4.0 and 2.1 for the 60, 30, 15 and 1 year old stands, respectively. The following mean temperature ranges where used to derive the full year's Q_{10}-values: -0.4 to 18.9 °C, -0.3 to 19.3 °C, -1.4 to 16.8 °C, and -0.4 to 30.3 °C for the 60, 30, 15 and 1 year old stands, respectively. When the winter season was excluded (December to March), then the Q_{10} values went down to 3.5, 3.3, 3.6 and 1.9 for the 60, 30, 15 and 1 year old forest stands, respectively, while the r^2 values of the relationships became 0.95, 0.94, 0.94 and 0.70, respectively.

Relationship between Soil Moisture and Soil Respiration

Overall, soil moisture was rather low at all TPFS stands (0.06 to 0.21 VWC) throughout the study period without any significant variability between dry and wet periods. One reason is that the sandy soils at TPFS sites have low soil moisture holding capacities and will drain quickly after any rain event. The lack of seasonal variability in soil moisture may have caused a lack of correlation between this environmental parameter and seasonal variability in soil respiration at TPFS stands. However, when soil temperatures were near their annual high for the study period, low soil moisture may have prevented further increases in soil respiration with increasing temperatures. This was evident for all four stands in June 2003, and especially for the youngest site in June 2004. On those occasions, measured soil temperatures were at or near their observed maximums (for the days of soil respiration measurements), yet soil respiration was not. However, large scatter was observed when volumetric water content from soil pits (for the day and

time of soil respiration measurements) was correlated to observed soil respiration for the entire study period (Figure 4.4 (a-d)).

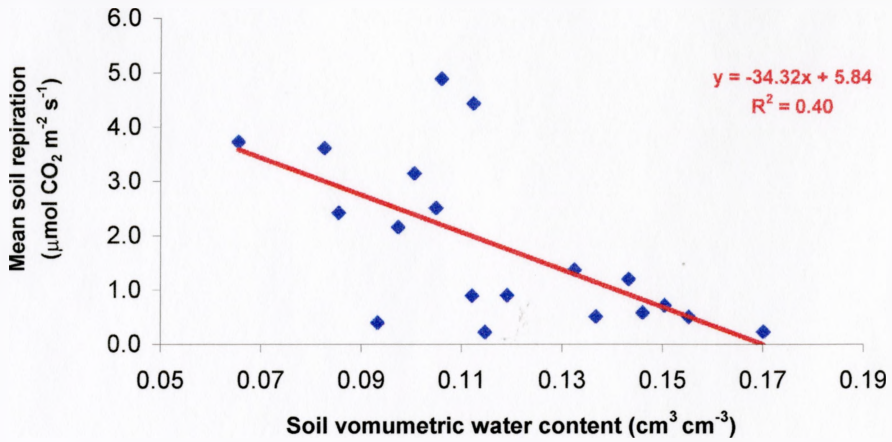


Figure 4.4 a): Linear relationship between average soil respiration and soil moisture at the 60-year-old TPFS stand.

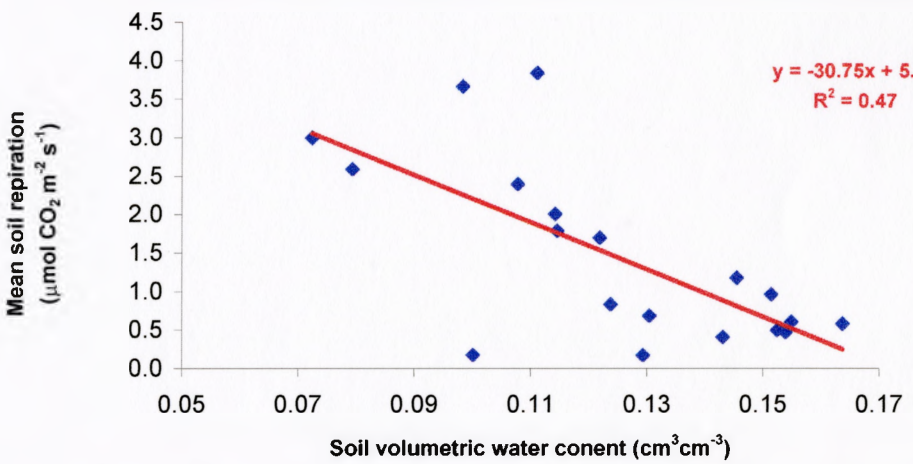


Figure 4.4 b): Linear relationship between average soil respiration and soil moisture at the 30-year-old TPFS stand.

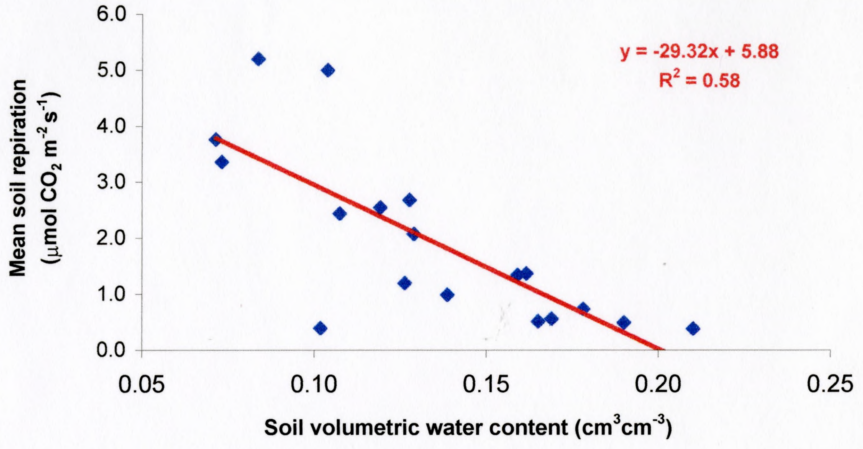


Figure 4.4 c) : Linear relationship between average soil respiration and soil moisture at the 15-year-old TPFS stand.

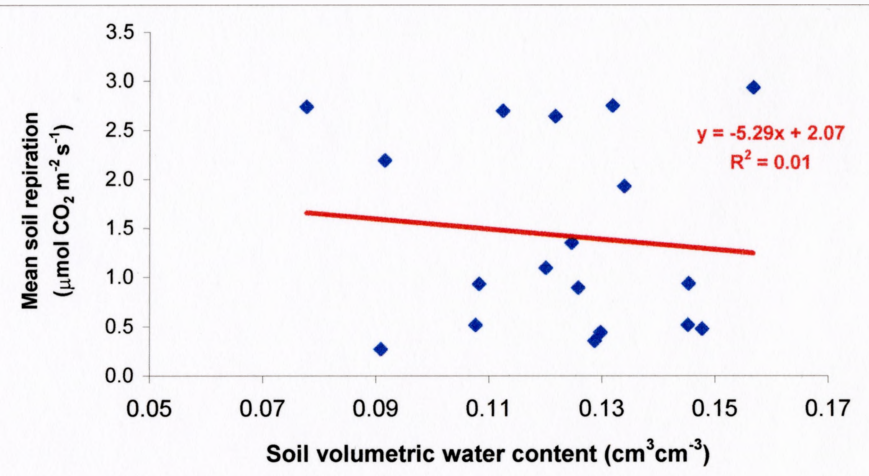


Figure 4.4 d) : Linear relationship between average soil respiration and soil moisture at the 1-year-old TPFS stand.

4.1.3 Spatial variability in soil respiration

4.1.3.1 Spatial variability across the chronosequence

For each site, figures 4.5 (a-d) show a colour-coded image of soil respiration (vertical), as it varied at each collar along the transect, plotted versus time (horizontal). Darker colours (towards red) represent higher soil respiration, while lighter ones (towards pale blue) represent low soil respiration. Spatial variability of soil respiration was observed at all sites. This variability was seasonal. The degree of spatial variability decreased with the onset of winter for all four sites. Spatial variability in soil respiration began to increase and differentiate again in spring towards June 2004. The largest variability in soil respiration was observed in August 2003 for all sites. This was also the time when highest average annual soil respiration values were observed. In terms of the chronosequence, the greatest degree of spatial variability was observed at the 60 and 15 year old forest stands (depending on the season, 7- 67% CV at the 60 year stand and 6 - 47% for the 15 yrs stand). At the 30 year stand the range of %CV was 1 to 27%, while at the 1 year stand it was in the 1 to 32 % range. For the 1 year site, the higher %CV values were observed during springs when weed growth peaked and later in autumn, probably due to increased decomposition of plant debris from senesced weeds.

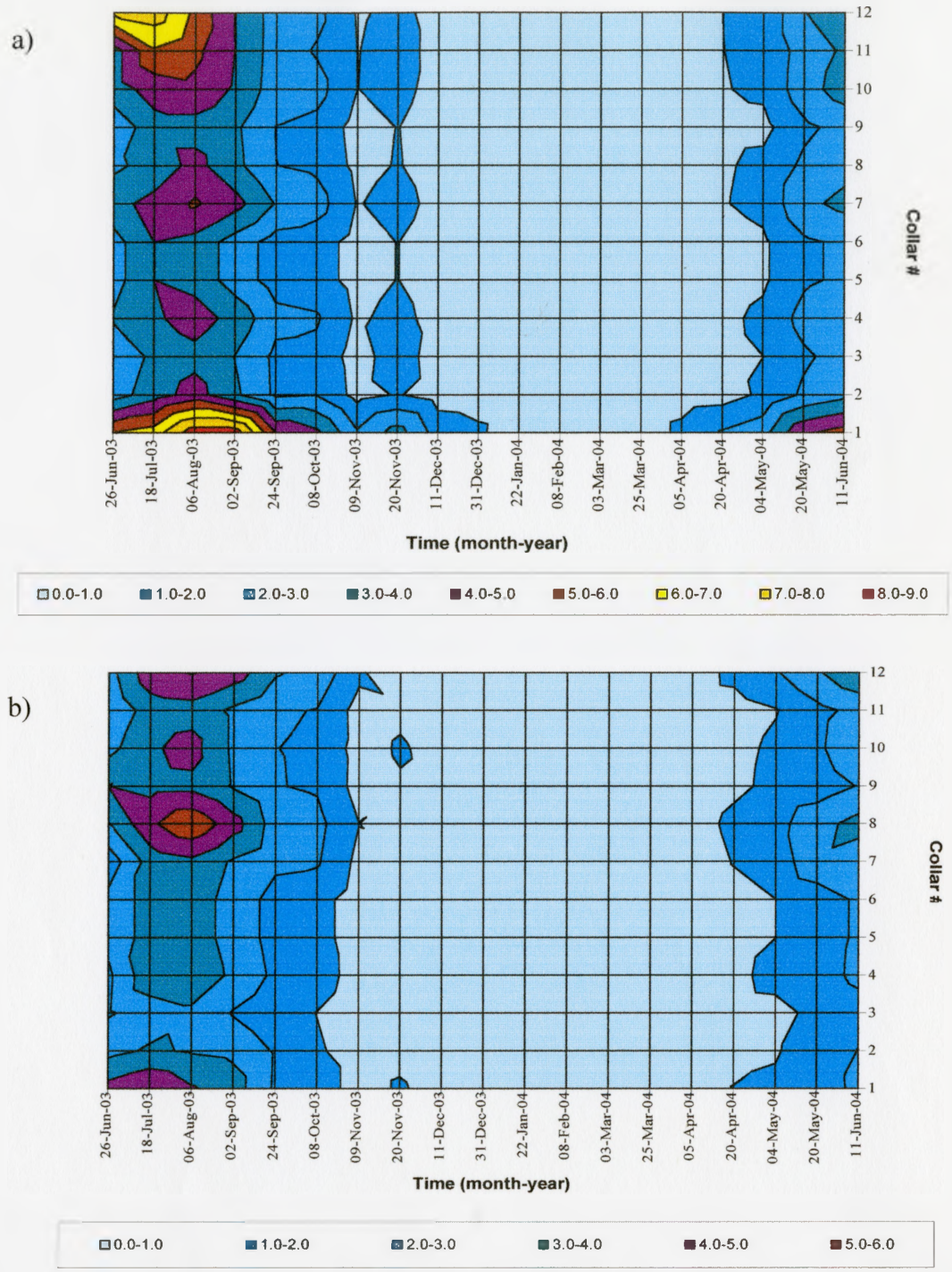
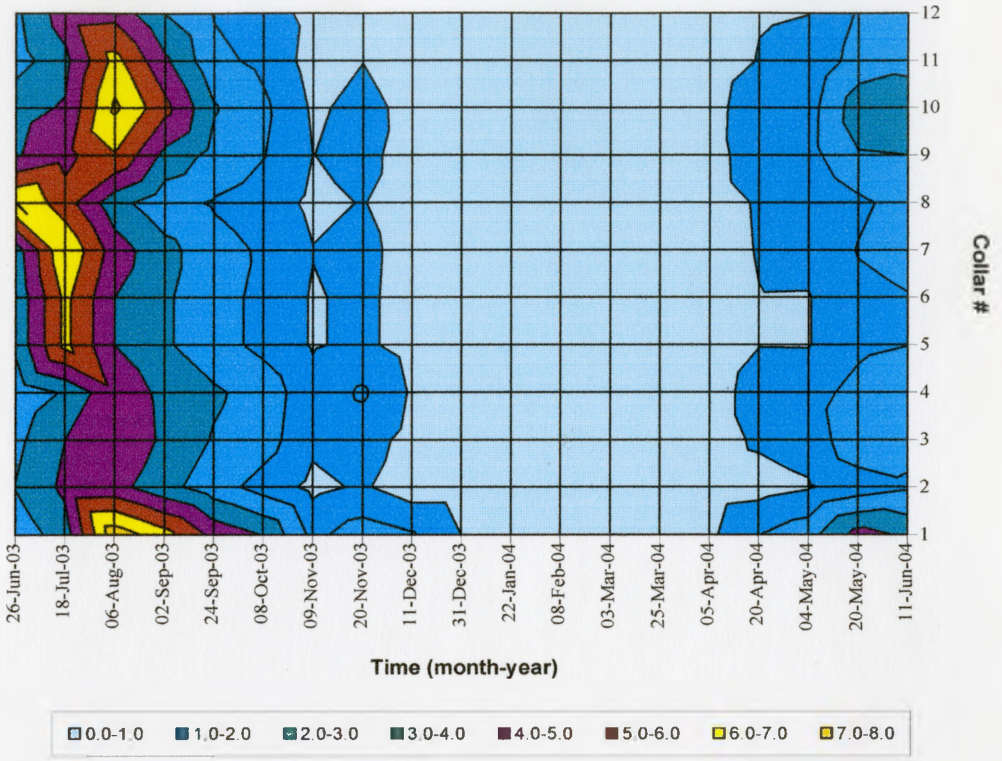


Figure 4.5 (a,b): Spatial variability of soil respiration along the measured transects at the 60-year-old (a) and the 30-year-old (b) TPFS stands, plotted versus time to show temporal variability. The degree of spatial variability in soil respiration varied over the course of the year, being minimum in winter and maximum in late summer/early fall. **The colour codes represent soil respiration in units of *μmol of* CO_2 m^{-2} s^{-1}.**

c)



d)

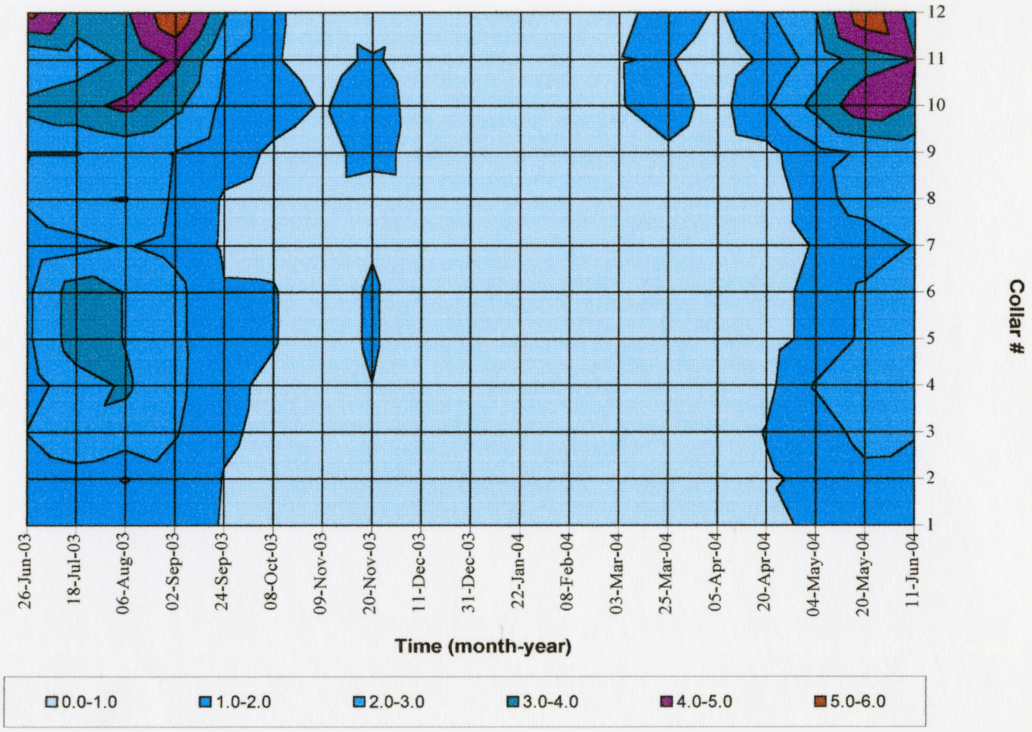


Figure 4.5 (c,d): Spatial variability of soil respiration along the measured transects at the 15-year-old (c) and the 1-year-old (d) TPFS stands, plotted versus time to show temporal variability. The degree of spatial variability in soil respiration varied over the course of the year, being minimum in winter and maximum in late summer/early fall. **The colour codes represent soil respiration in units of *μmol of* CO_2 m^{-2} s^{-1}.**

At the 60, 15 and 1 year old stands, there was always one or two collars that consistently gave higher respiration rates compared to the rest (from here on referred to as "outliers"). Those were located near tree trunks (within 50 cm) at the older two sites and in a dense area of weeds at the youngest site. When all collars along the transect were considered, the maximum standard deviation of mean respiration at the sites was 1.3, 0.9, 1.3, and 0.9 μmol CO_2 m^{-2} s^{-1} at the 60, 30, 15 and 1 year old stands, respectively, and occurred in July-August. The minimum standard deviation of mean respiration at the sites was 0.1 μmol CO_2 m^{-2} s^{-1} and occurred from December to March. When the "outliers" were excluded, standard deviations for summer months decreased for the 60 and 15 year old stands (0.6, 0.9, 0.9, and 1.1 μmol CO_2 m^{-2} s^{-1} at the 60, 30, 15 and 1 year old stands, respectively), but remained unchanged for the youngest stand.

Several factors were considered in this study as potential sources of soil respiration's spatial variability. These included: tree root density underneath respiration collars in relation to the proximity of the collar to a tree trunk, spatial variability of soil nutrients, and spatial variability in litter thickness.

4.1.3.2 Effects of tree root density bellow respiration collars

Figures 4.6 (a,b) show the course of soil respiration in relation to distance from tree trunk along established tree transects at the 30 year old forest stand. In the figure the tree would be situated at 0 m.

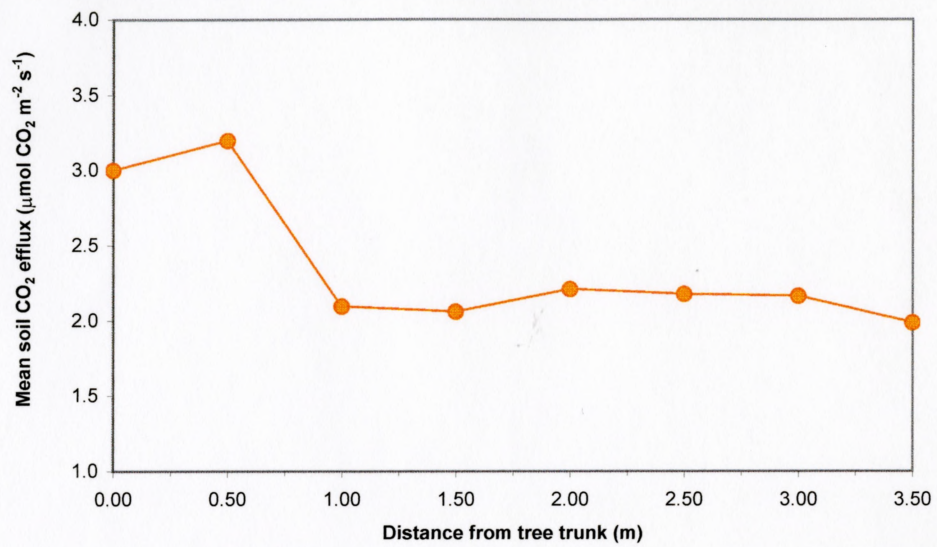


Figure 4.6 a): Pattern of soil respiration measured at the 30 year stand, along tree transect A, going from a tree trunk (0 m) to an open area. Measurements were taken in May 2004.

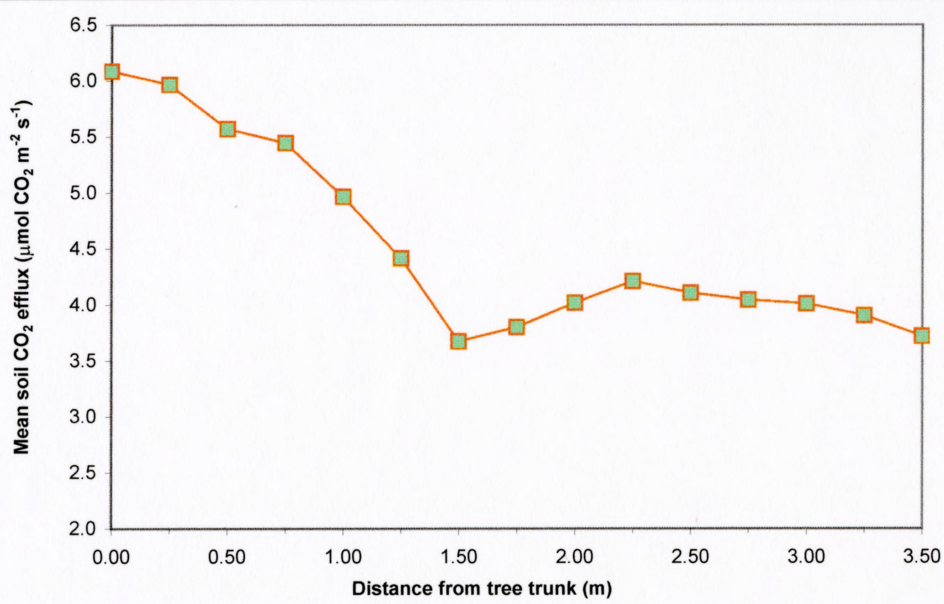


Figure 4.6 b) : Pattern of soil respiration measured along tree transect B, going-out from tree trunk (0 cm) at the 30 year stand. Measurements were taken in June 2004.

For transect A (Figure 4.6 (a)), soil respiration was high close to the tree trunk, but decreased by about one third of its highest value, within 1 metre of the trunk (3 μmol CO_2 m^{-2} s^{-1} to 2 μmol CO_2 m^{-2} s^{-1}). There was a slight increase in respiration between 2 and 3 metres. However, collar spacing along this transect was at a 50 cm spacing and did not allow for closer examination of this apparent increase.

A second transect was established with higher spatial resolution, near a different tree (Figure 4.6 (b)). This transect was measured later in the season (2004), which would explain why the overall respiration rates along transect B were higher compared to transect A. Soil respiration was also the highest near the tree trunk along transect B and decreased rapidly within the first 1.5 metre distance form the tree. Again, the decrease was on the order of about one third (from about 6 μmol CO_2 m^{-2} s^{-1} to about 4 μmol CO_2 m^{-2} s^{-1}). Interestingly enough, at about 2.25 m distance away from the tree, there was a slight rise (by about 0.5 μmol CO_2 m^{-2} s^{-1}) in soil respiration along this transect also.

4.1.3.3 Spatial variability in soil nutrients

Soil at all four sites was analyzed for spatial variability of several soil chemical properties that included soil pH, soil calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), total organic matter (TOM) and C:N ratios. Some of the chemical properties did not show significant spatial variability and thus could not be used to explain spatial variability in soil respiration. Others did vary spatially, but failed to explain spatial variability in soil respiration. Complete tables of detected soil nutrients and their coefficients of correlations (r-values) are given in APPENDIX C for all stands.

For the older three sites, soil chemical properties at two different mineral soil depths were considered from soil core samples collected in December 2003. In all cases, the degree of correlation between spatial variability of soil chemical properties and spatial variability in soil respiration appeared to be seasonal, as seen by the changing r-value between soil respiration measurement days. Similar observations were made by Xu and Qi (2001).

TPFS 60 year old forest stand

Spatial variability of soil magnesium (Mg) content in the top 20 cm of soil was able to explain up to 30 % of soil spatial variability at the 60 year old forest stand. The correlation between Mg and soil respiration was positive. When deeper soil was considered at the 60 year old stand (21-35cm depth), spatial variability in soil phosphorus (P) had a high positive correlation with soil respiration variability and could explain up 38% of the variability in respiration. Although no significant ($r \geq 0.5$) correlation between C:N ratio and respiration was found, it was noted that the relationship between the C:N ratio and soil respiration was consistently negative (a detailed discussion of this is given in Chapter 5).

TPFS 30 year old stand

At the 30 year old stand, a very high negative correlation was observed between spatial variability of soil phosphorus (P), in the top 20 cm of soil, and that of surface soil respiration. The high correlation was maintained for most measurement dates and could

explain up to 96% of spatial variability at the site. On the other hand, spatial variability in soil organic matter content (top 20 cm) had a strong positive correlation to spatial variability of soil respiration at the 30 year old stand. OM could explain up to 88% of this spatial variability, although this correlation seemed to vary with time.

TPFS 15 year old stand

At the 15 year old stand, a strong positive correlation was observed between spatial variability of soil phosphorus (P), in the top 20 cm of soil, and that of surface soil respiration, which could explain up to 68% of spatial variability of soil respiration at this site. In the deeper (21-35 cm) soil, soil potassium (K) was also highly and positively correlated to soil respiration and could account for up to 73% of spatial variability in soil respiration. Finally, spatial variability of soil pH was also found to be highly correlated to spatial variability of soil respiration, but the correlation was a negative one, accounting for up to 58% of the spatial variability in soil respiraiton.

TPFS 1 year old stand

Unlike in all of the older stands, the youngest one showed the most correlations to various soil nutrients, which could account for up to 92% of spatial variability observed at the site. Soil organic matter (OM) was positively correlated to spatial variability in soil respiration. Soil OM was able to account for up to 85% of respiration variability. Soil potassium (K) and aluminum (Al) also showed high positive correlations. The two variables were able to explain up to 78% and 92%, respectively, of spatial variability in

soil respiration at this forest stand. In contrast, soil calcium (Ca) had a strong negative correlation and was able to explain up to 78% of spatial variability in soil respiration at the youngest stand.

4.1.3.4 Spatial variability in litter thickness

No strong correlation between litter thickness and spatial variability in soil respiration was found at the three oldest TPFS stands, where litter was present. An exception to this was for the 15 and 30 year old stands in the fall. At the 15 year stand, litter thickness could explain up to 30% of spatial variability in soil respiration in October and November 2003. A similar result was observed at the 30 year stand, where litter thickness was able to explain up to 77% of spatial variability in soil respiration from September to October 2003. This may have been due to the effects of senescence that fed new supplies of fresh litter to decomposers, thus increasing heterotrophic respiration.

4.1.4 Simulations of annual soil respiration

Figures 4.7 (a-d) compare simulated daily mean soil respiration with observed daily means, for each forest stand at TPFS. Both model simulations followed the general seasonal pattern of observed soil respiration, but with more details, which were not captured by manual measurements. Mean annual soil respiration values calculated from models (1.3 – 2.1 μmol CO_2 m^{-2} s^{-1}) were comparable to the means derived from observations (1.3 – 1.7 μmol CO_2 m^{-2} s^{-1}).

The relative fit of each model varied among sites. The model that best fit observations data for the 60 year old stand was the soil moisture-C:N-ratio-sensitive model. In contrast, the simple exponential model failed to match observed soil respiration during the summer months, when most likely soil moisture played a role in regulating observed respiration rates. The simple model overestimated peak summertime fluxes. The relatively good fit of the moisture-C:N model also highlights the importance of including abiotic factors, other than soil temperature, in models that try to simulate ecosystem carbon fluxes.

One of the shortfalls of applying the moisture-C:N sensitive model to the 30 and 15 year old stands was the lack of C:N ratios for surface litter at those sites. To compensate somewhat, the C:N ratio from the litter of the 60 year old stand was used in the moisture-C:N-sensitive model in those stands. For the youngest stand, the C:N term was dropped from the equation, since there was no litter layer at the site. Consequently, the fit of the model was limited and the overall trend did not match observations as well as was seen for the oldest stand. This was especially true for the 15 year old stand where

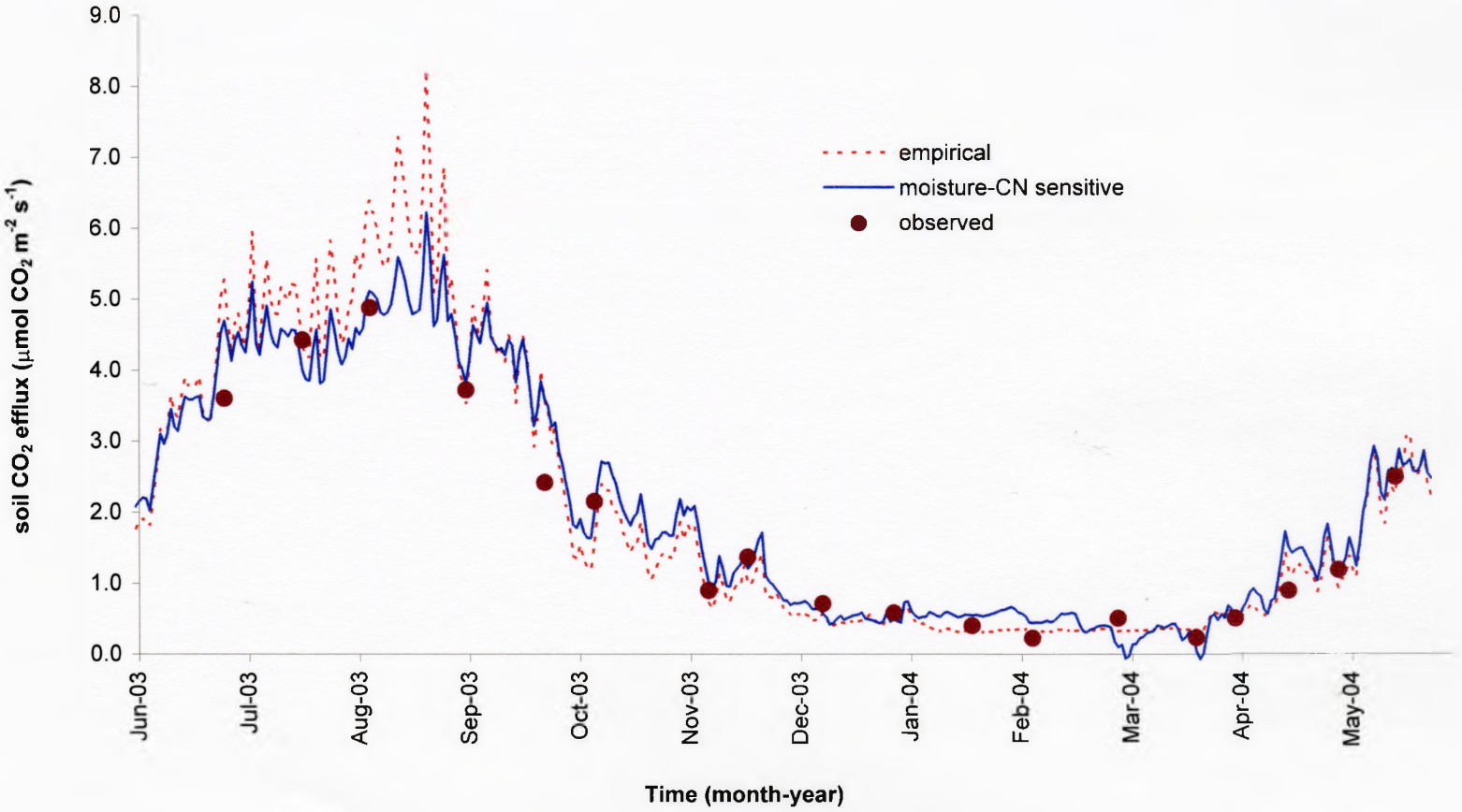


Figure 4.7 a) : Comparision of simulated annual trends in soil CO_2 emissions at TPFS 60 year old to observations done throughout the study year (June 2003 to May 2004).

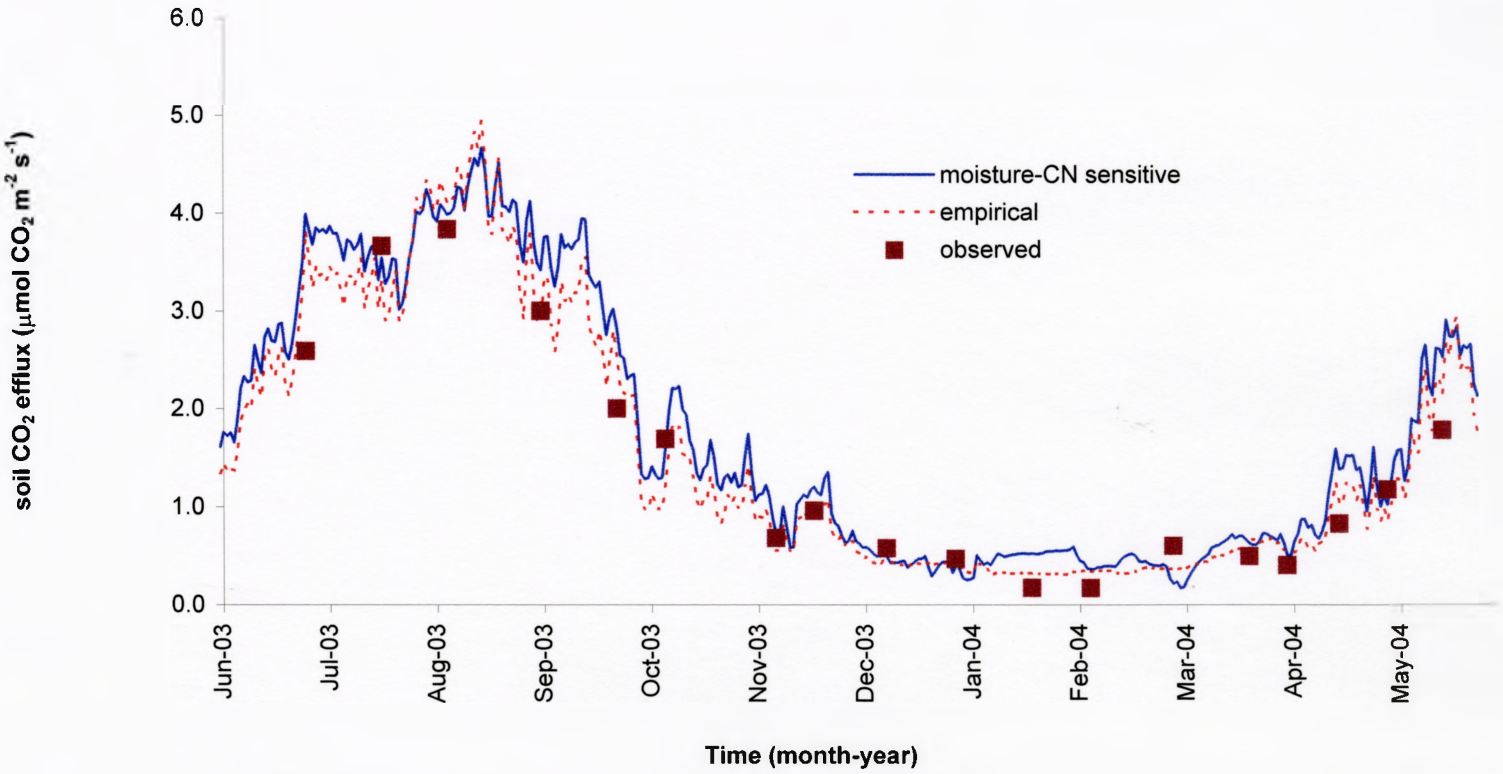


Figure 4.7 b) : Comparision of simulated annual trends in soil CO_2 emissions at TPFS 30 year old to observations done throughout the study year (June 2003 to May 2004).

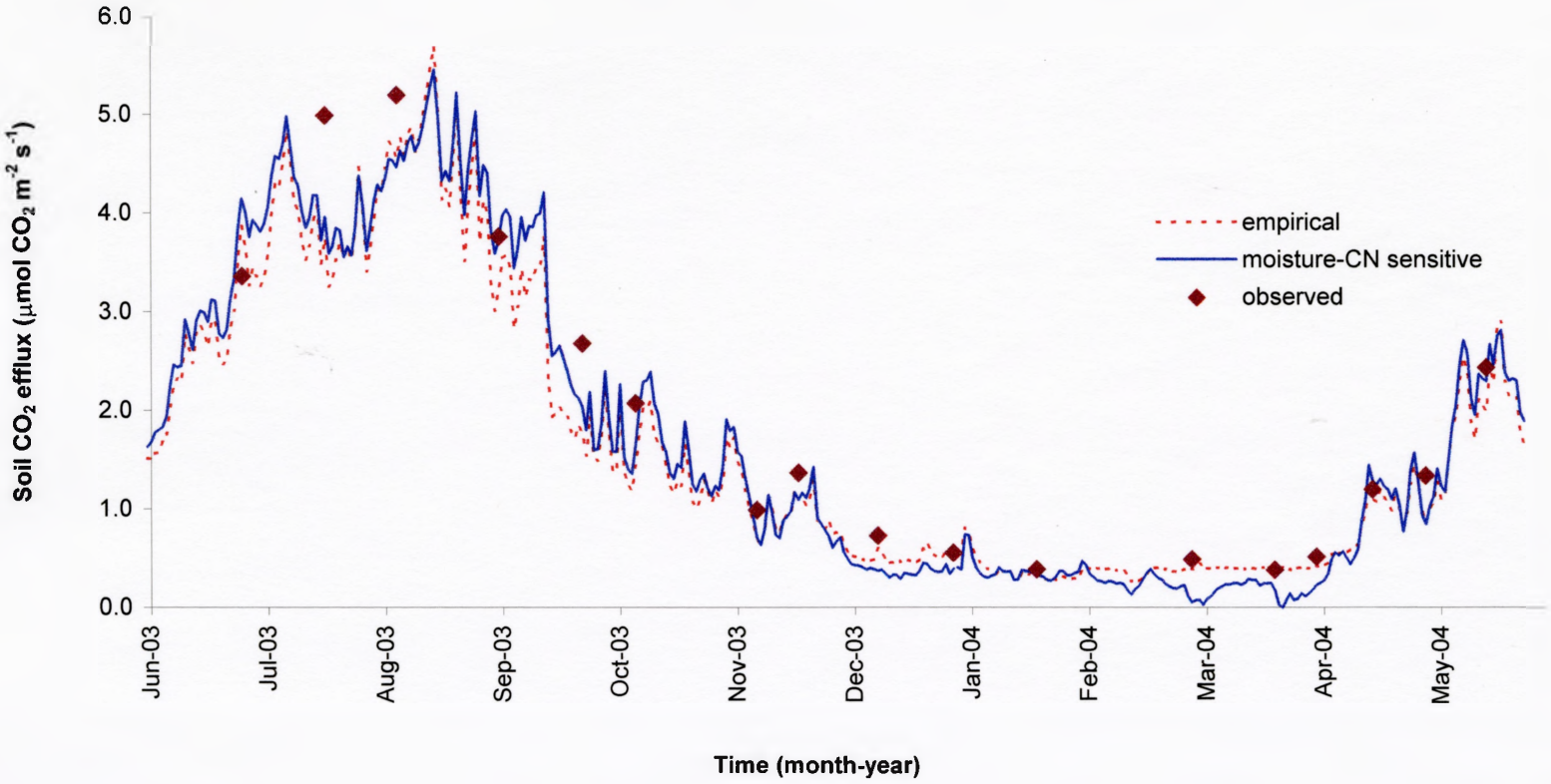


Figure 4.7 c) : Comparision of simulated annual trends in soil CO_2 emissions at TPFS 15 year old to observations done throughout the study year (June 2003 to May 2004).

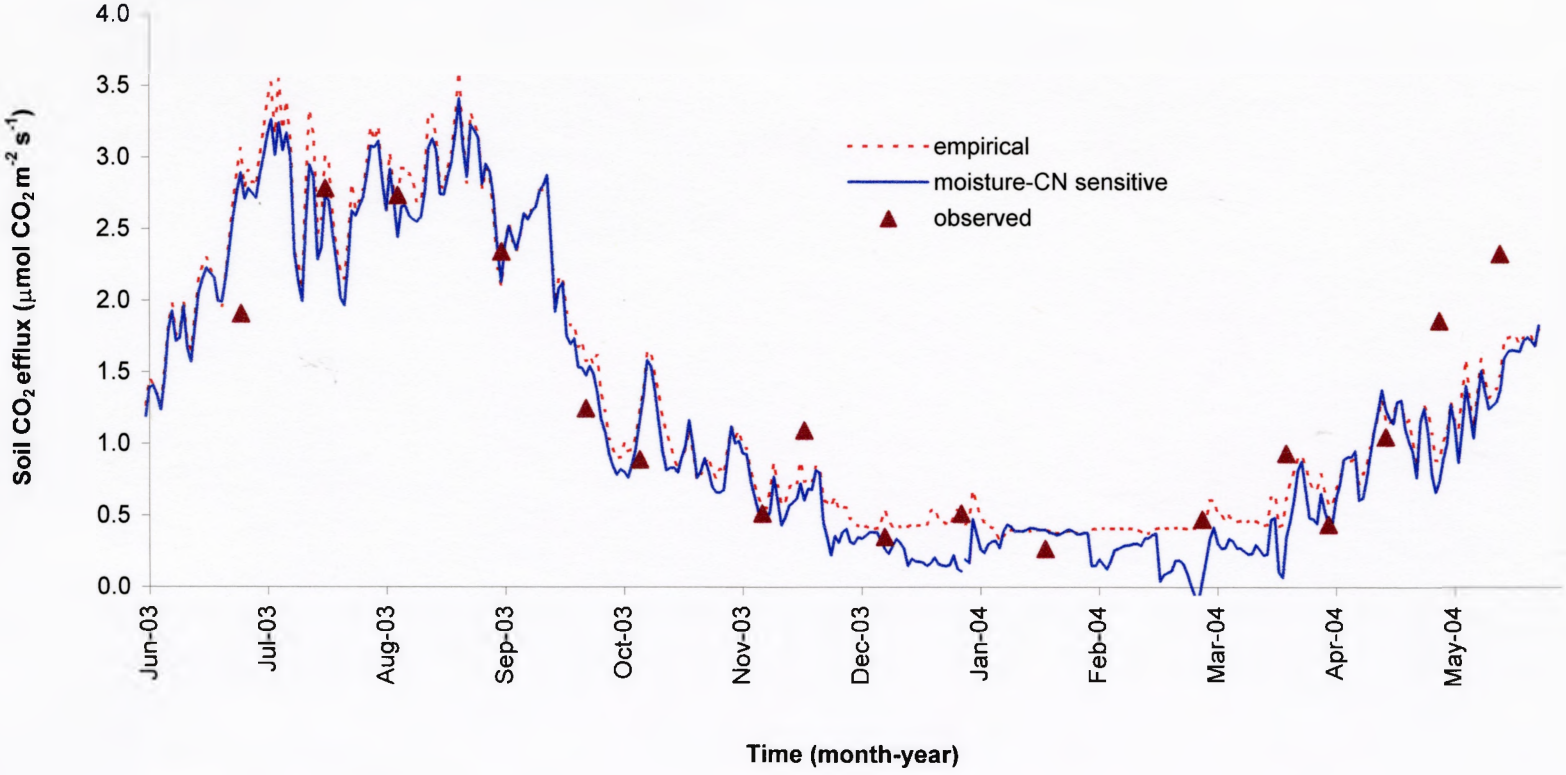


Figure 4.7 d) : Comparision of simulated annual trends in soil CO_2 emissions at TPFS 1year old to observations done throughout the study year (June 2003 to May 2004).

underestimation of summertime fluxes appears to have occurred. In contrast, for the 30 year old stand summer fluxes may have been slightly overestimated. This discrepancy was carried over into annual soil CO_2 -emission estimates, discussed later. For the one year old stand, underestimation in May 2004 and throughout winter were observed in the moisture-C:N model simulation, while in June/July 2003 overestimations were detected.

The simple, exponential model also did not fit observed results very well. For the 15-year-old stand, this model failed to simulate two peaks in summer soil respiration observed in August and early September. For the 1 year old stand, the model appeared to underestimate fluxes in the summer 2004 and overestimate them in July 2003.

Nonetheless, these models did provide a way to estimate annual soil CO_2 -emissions for TPFS stands.

4.1.5 Annual estimates of soil CO_2 -emissions

Calculated estimates of annual and seasonal carbon emissions from soils at TPFS forest stands for the year of the study are listed in Table 4.2 (in units of grams of C oer m^2 per year). Emissions calculated from both model simulations are shown, and, for comparison, % relative emissions (relative to total emissions per site) were also included for each season, for comparison.

Overall, during this study period (June 2003 to May 2004, inclusive), estimated *annual* CO_2 -emissions increased with forest stand age across the TPFS chronosequence, when the 15 year old forest stand is excluded. Emission estimated for the 15 and 30 year old stands were comparable. The differences in calculated emissions from both methods

differed at most by about 10%. The 60 year old stand was estimated to have emitted between 806 grams of C per m^2 for the study year, followed by the 15 year old stand with 644 g C m^{-2} yr^{-1}, then the 30 year old stand with 602 g C m^{-2} yr^{-1}, and finally the 1 year old stand with 508 g C m^{-2} yr^{-1}, based on calculations using the simple empirical exponential model; and 796, 672, 670 and 463 g of C per m^{-2} yr^{-1} for the 60, 30, 15 and 1 year stands, respectively, using the moisture-C:N-ratio sensitive model.

About 62% to 71% of annual emissions occur over the summer months across the chronosequence, the highest being at the 60 year old stand, followed by 15, 30 and 1 year stands. Emissions in the other three seasons vary between 8 and 15 %.

Table 4.2: Calculated annual CO_2 -emissions from forest floors at TPFS chronosequence sites in grams of C per m^2 per year. The year represented here is the study period (June 2003 to May 2004, inclusive). Terms in brackets show % CO_2 -emissions relative to annual totals for each stand. Results from both model simulations are shown ("E" stands for simple exponential model and "C:N" for the moisture-C:N sensitive model).
Winter = Dec to Mar; Spring = Apr & May; Summer = Jun to Sep; Fall = Oct & Nov

	Winter		**Spring**		**Summer**		**Fall**		**TOTAL**	
	E	**C:N**	**E**	**C:N**	**E**	**C:N**	**E**	**C:N**	**E**	**C:N**
60 year	52 (7)	62 (8)	92 (12)	101 (13)	576 (71)	528 (66)	106 (13)	86 (11)	806 (100)	796 (100)
30 year	53 (9)	62 (9)	84 (14)	97 (14)	400 (67)	433 (64)	65 (11)	80 (12)	602 (100)	672 (100)
15 year	56 (9)	41 (6)	81 (13)	84 (13)	429 (67)	460 (69)	79 (12)	85 (13)	644 (100)	670 (100)
1 year	59 (12)	38 (8)	75 (15)	70 (15)	318 (62)	306 (66)	56 (11)	50 (11)	508 (100)	463 (100)

4.2 DISCUSSION

4.2.1 Seasonal variability in soil respiration

The lowest mean soil respiration was observed at the youngest (1 year old) chronosequence stand. This was comparable to literature reports, where younger forest stands were shown to have lower soil respiration compared to their older counterparts (Wiseman et al, 2004; Litton et al, 2003; Anthoni et al, 2002; Irvine et al, 2002). However, the highest mean soil respiration observed during the course of this study occurred in August at the 15 year old stand, which was comparable to the mean rate observed at the oldest (60 year) stand and *higher* than the one observed at the 30 year old stand (Figure 4.2, page 66). One would expect older forests to have more litter and more extensive roots compared to younger ones, if grown under the same environmental conditions. Higher litter decomposition and higher root densities would imply higher respiration. Yet the results obtained in this study seem to disagree when the 15 year old stand is included in the TPFS chronosequence.

Annual litter fall has been related to soil respiration (Raich and Schlessinger, 1992). Sites that have greater litter fall tend to support greater micro-organism activities and thus may show higher soil respiration rates. Thus, annual litter fall per area was estimated for all of the stands in November 2003. Fresh litter was collected at all sites for comparison, with the exception of the youngest stand that effectively had to litter. It was found that the 15 year old site had the highest fresh litter accumulation of all stands (Figure 4.8), which in turn could support higher decomposition rates, increasing observed soil respiration rates (Law et al, 2001).

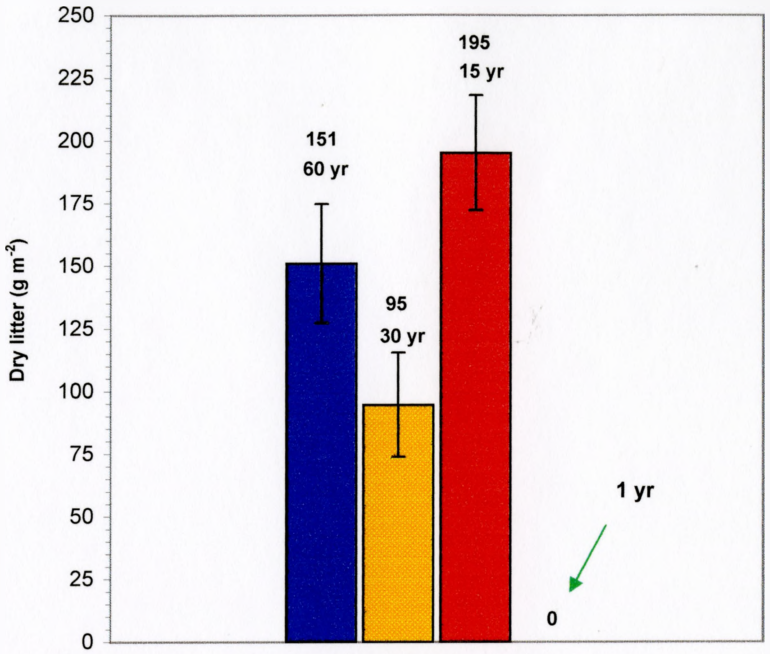


Figure 4.8: Estimated litter-fall density at each of the chronosequence sites. Litter collection and analysis was done in Novemeber, 2003 after all leaf-fall had ended. Error bars represent 1 std dev.

The relatively high annual estimated litter-fall at the 15 year old stand was in agreement with the high LAI observed there – the highest of all four stands (Table 2.1, *Section 2.1*). Greater fine root density would also be expected at this stand to support the greater amount of above ground needle production and also given its higher stem density compared to the 30 year old stand. The soil of the 15 year old stand was also found to contain almost twice as much organic carbon in the top 20 cm of its soil as was found in other sites (APPENDIX C). Higher organic carbon contents can translate into increased soil micro-organism activity. All this suggests that the 15-year-old stand may be at a very productive stage of its life.

For the other three chronosequence sites (60, 30 and 1 year old), older stands had higher respiration rates compared to their younger counterparts. The 30 year old stand had lower soil respiration than the 60-year-old one, and the 1-year-old stand had the lowest soil respiration of all.

The mean soil respiration range (0.2-5.2 μmol CO_2 $m^{-2}s^{-1}$) and the timing of respiration maxima and minima observed for TPFS sites were comparable to literature-reported studies. Irvine et al (2002) reported seasonal soil respiration between 0.4-4.0 μmol CO_2 m^{-2} s^{-1} for a ponderosa pine forest in Central Oregon, taken from year-round automated soil chamber flux measurements. Borken et al (2002) also reported a peak in August at their German site, a mixed-wood forest (131 year old beech, 90 year old spruce, 54 year old pine, growing on sandy soils). Their lowest respiration was observed in winter months, but was much higher than what was observed at TPFS (1.06 μmol CO_2 m^{-2} s^{-1}).

Using age as a predictor of relative soil respiration rates, where-by soil respiration is expected to increase with age, should be viewed with extreme caution. Not many studies have considered soil respiration as a factor of stand age. However, from those available, variable conclusions come out. For example in a recent study Wiseman and Seiler (2004) reported that soil respiration increased with stand age, for a loblolly pine chronosequence of 4-age clases (ages 1 to 25) in Virginia, USA. The lack of discrepancies at their sites were probably due to the history of the chronosequence. All stands were planted and maintained under the same management procedure, which would create more controlled experiment conditions in which to study the effects of age, but may not necessarily occur in nature. However, Litton et al (2003) also reported higher respiration rates for older sites compared to younger ones at a lodgepole pine forest in Yellowstone National Park, USA. Their youngest stand (13 yrs) ranged in respiration from 0.6 to 3.2 μmol CO_2 m^{-2} s^{-1}, while the older stand (111 yrs) had a respiration range of 1.3 to 3.6 μmol CO_2 m^{-2} s^{-1}. On the other hand, Irvine and Law (2002) reported that during their three year study of different-age ponderosa pine forests in Oregon, USA, only during one of those years did the older site (50-250 yrs) show higher respiration compared to the younger (14 yrs) site. The differences were due to lack of moisture experienced at the older stands during the study period. When soil moisture at 5 cm depths was compared among the TPFS stands (Figure 4.9), it was observed that the 15-year-old stand, for the most part of the study year, tended to have slightly higher soil moisture compared to the 30 and 60 year old stands. Thus, higher soil moisture

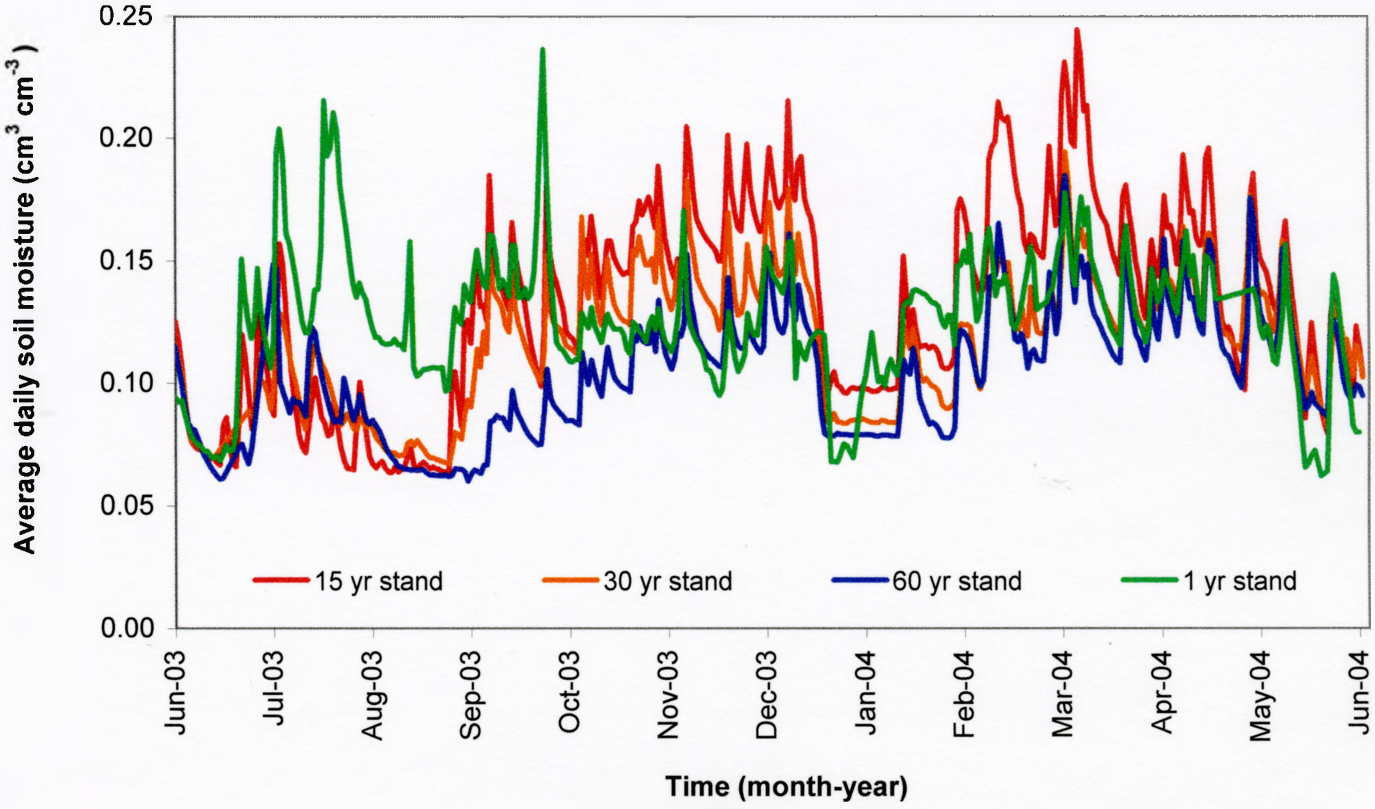


Figure 4.9: Time series of average soil mositure, at 5 cm depth, across the TPFS chronosequence stands. Average soil moisture was calculated as an average from 5 cm depth measuremets recorded in both soil pits at each site.

experienced at the 15 year old stand may explain some of the discrepancy observed in this study with respect to stand age and rate of soil respiration.

Soil Respiration and Environmental Variables

At the older forest stands, soil temperature was similar between sites. However, at the youngest stand, temperature was the highest during the 2003 growing season. It was also at the youngest forest stand that soils first thawed in spring 2004, causing an increase in soil respiration long before one was observed at the older stands. The soil at all four sites is mostly sand, which is a good conductor of heat. At the youngest site the small pine seedlings provide very little canopy cover for the soil and there is also no litter cover. Compared with the other sites, the soil at the 1 year old stand is effectively bare sand, exposed directly to the sun. It can heat up more quickly and efficiently under the sun, over the course of a day, and then cool-off at night under clear skies, in comparison to the other stands, where litter and canopy covers have greater control over the soil temperature regime. This would be supported by earlier results, from the comparison of morning and afternoon soil temperature measurements (Section 3.2).

Soil respiration and soil temperature were positively correlated. Soil respiration appeared to be seasonally very sensitive to soil temperature at the three oldest sites. At the three oldest sites, average soil temperature could explain 90-96% of the seasonal variability of average soil respiration through an exponential relationship (based on the coefficient of determination, r^2). For the youngest site, average soil temperature was able

to explain only 80% of the seasonal soil respiration variability through a similar relationship.

Q_{10} values obtained from the relationships across the chronosequence (2.1 – 4.1) were somewhat on the high side of those usually reported in literature. Law et al (1999) reported Q_{10} value of 1.8 for their ponderosa pine forest in Oregon, USA. In contrast, Matteucci et al (2000), reported values of 2.5 to 4.11 for different forests across Europe. Drewitt et al (2002) also reported a range of Q_{10} values (2-5) for a Douglas fir forest in British Columbia, CA. They observed that when Q_{10} values are calculated for warmer parts of the year only, then the values are lower (2-3 range). However, when they are calculated using temperatures in the cooler part of the year, the Q_{10} values increase (4-5 range). The temperature sensitivity of Q_{10} values has been extensively discussed in literature (Lloyd and Taylor, 1994; Qi et al 2002).

The deviation at the youngest site may have been due to an increased influence of soil moisture. This appears to be most profound in June 2003 when soil temperatures (for measurement days) were at their peak for the study period, while soil respiration was not. Under dry conditions, soil respiration will tend to be controlled more by soil moisture (Davidson et al, 2000) . Soil organisms and plant roots need water to function properly. When this water is limited, biological activity may also be limited, despite favourable temperatures. The youngest site has small white pine seedlings, with less extensive roots, which may be more prone to drought conditions compared to the longer (deeper tapping) roots expected at oldest stands.

Irvine & Law (2002) found that soil temperature accounted for 73% of soil respiration variability (based on an exponential function), with minimal moisture control, at their 250 year old ponderosa pine forest in Oregon. At the same time, they reported that at their young site (14 years old) only 5% of seasonal variability in soil respiration was explained by soil temperature, and, instead, 80% of the variability was explained by soil moisture. Their explanation of the greater dependence on water moisture at the younger site was that the young site, compared to an older one, probably did not have deep enough roots to sustain trees during dry periods, so respiration was controlled by a moisture deficit (Irvine et al, 2002). However, the youngest stand at TPFS did not seem to be under great water stress for the most part of the study period, especially during late summer when respiration peaked. Soil moisture at the 1 year stand was the highest of all stands from July through September, as was seen in Figure 4.9, which compared soil moisture across the chronosequence at the 5 cm soil depth.

Winter Measurements

In winter, soil respiration hit a low of about 0.2-0.4 μmol CO_2 $m^{-2}s^{-1}$ across the chronosequence. The observed effluxes were near the detection limits of the LI-COR 6400 instrument (± 0.2 μmol CO_2 m^{-2} s^{-1}). Thus winter measurements should be viewed with caution. The first two winter measurements (January and February) were done over winter collars. During the January and February measurements, unrealistic (large, negative numbers) fluxes were detected at some collars. These were excluded from calculations of means and from plots.

There was snow inside the collars during January and February measurements, but the condition of this snow, in terms of its vertical structural characteristics, was unknown. In February, ice was also detected inside some winter collars. A thick ice cover was also present all around the site, formed during freeze-thaw conditions prior to the measurement day. Formation of ice lenses inside snow and ice-layers above snow may obstruct gas flow from below the lenses (where it is produced in soil) up towards the surface for detection (*pers. commun. Dr. Waddington*). The fluxes in February were very low to detect. At times, the instrument would sit idle for several minutes above a collar. Ice-layers inside the collars may have hindered gas flow. Furthermore, the soil was frozen in the top 15 cm, which may have greatly reduced biological activity in the upper, frozen soil (and consequently CO_2 production there). A frozen soil layer may also serve as a physical barrier to gas flow from any deep soil respiration. Low fluxes were especially a problem during February measurements at the younger two sites. The data collected in February for these two sites was dropped from analysis.

Nonetheless, winter soil respiration observed over snow measurements during this study was comparable to literature-reported winter soil respiration. Russell and Voroney (1998) measured soil respiration above frozen soils in a mature aspen forest in Saskatchewan, Canada, using an older version of LI-6400 (LI-6200). They reported rates of 0.45 to 0.91 μmol CO_2 m^{-2} s^{-1}. McDowell et al (2000) investigated CO_2 efflux from mixed-conifer and Mountain Douglas Fir forest soils in northern Idaho and Washington, USA. They measured CO_2 efflux from snow surfaces, using a LI-6400 system, and

reported rates as low as 0.11 μmol CO_2 m^{-2} s^{-1} to as high as 0.77 μmol CO_2 m^{-2} s^{-1} above soils that ranged in temperatures (10 cm depth) from -1.81°C to + 1.09°C.

4.2.2 Spatial variability in soil respiration

The degree of spatial variability in soil respiration was seasonal and may be subject to various physiological cycles of the forest stand over the course of the study year.

Spatial variability in relation to measurement location

The proximity of soil respiration measurement location to trees may influence the magnitude of the observed flux. In a recent study, Wiseman and Seiler (2004) studied spatial variability of soil respiration in a chronosequence of four plantation loblolly pine forests in Virginia, USA. They investigated the magnitude of soil respiration at different proximities to trees and found significantly higher rates of soil respiration closer to trees then further away. They explained the results with increased root density closer to trees, since roots are often responsible for the majority of CO_2 efflux from forest soils.

In this study, soil respiration rates were also shown to increase as one approached a tree. It was also found that respiration rates decreased rapidly by about 1/3 within the first 1 to 1.5 metres from the tree trunk. Furthermore, at a distance of about 2.5 metres from the tree trunk, root respiration may increase somewhat, probably due to increased density of finer roots at that distance from the tree. However this effect may be site

specific and was not confirmed by coring below measured locations in order to quantify fine root densities at those locations.

In their study, Wiseman and Seiler (2004) reported that the "position effect" appears to increase with stand age. In other words, spatial variability becomes more profound with stand age. This was also observed in this study, as older stands showed higher spatial variability compared to younger ones. Again the exception was the 15 year old stand. In that case, age was most likely not a strong factor in determining the degree of spatial variability – forest productivity and greater stem density may have been of greater importance.

Spatial variability in relation to soil chemical content

Spatial variability of some soil chemicals was able to explain anywhere from 30 to 92% of the spatial variability in soil respiration at TPFS stands. However, this relationship was not consistent throughout the chronosequence or throughout the year (keeping in mind the underlying assumption of this comparison, see *Section 2.3.6, page 40*). Even so, the high correlations that were observed were in line with arguments made in the Introduction (Chapter 1), which stated that spatial variability in soil chemical contents (nutrients) can cause spatial variability in the distribution of plant roots and microbial populations, in favor of hospitable conditions for those organisms.

For example, high positive correlations were found between spatial variability in soil phosphorus (P), potassium (K), magnesium (Mg) and organic matter (OM) contents and spatial variability of soil respiration. All of the above mentioned chemicals are

essential macronutrients required for plant growth and function, which plants obtain from soils. For example (Taiz and Seiger, 2002): P is important in energy storage and structural integrity of plant material; Mg is the central atom of the chlorophyll molecule and is required by many enzymes in their biochemical reactions; K is essential to maintaining osmotic potential of plant cells and is often involved in activation of enzymes involved in plant photosynthesis and respiration.

Spatial variability of soil P was positively correlated to soil respiration across the chronosequence, with the exception of the 30-year-old stand, where the correlation was highly negative. Keith et al (1997), who studied the effects of soil P fertilization on soil respiration in Eucalyptus forest stands, observed that soil respiration decreased with the addition of P to soils. This reduction they attributed to decreased root nutrient uptake demand, which in turn translated into reduced root activity. However, the P content of the 30 year old stand was the lowest of all four stands at TPFS. Thus, perhaps this negative correlation may be due to some other physiological processes, perhaps related heterotrophic activity.

In a study of spatial variability of soil respiration and some soil chemical properties in a 7-8 year old Ponderosa pine plantation, Xu and Qi (2001) found a strong positive correlation between spatial variability of soil respiration and spatial variability of soil Mg content and soil organic matter, but no significant correlation with Ca. They also found a strong negative correlation of soil respiration and soil pH. In this study, spatial variability in soil Mg was also found to have a strong positive correlation to soil respiration variability, but only at the 60 and 1 year old forest stands. Organic matter

content showed high correlations only at the 30 and 1 year stands. Similar to Xu and Qi's results, no significant correlation to soil Ca was found at TPFS stands, with the exception of the youngest stand, where a strong negative correlation was found. Soil pH at the youngest forest stand was the highest of all four stands, about 7.4, and was strongly negatively correlated to soil respiration. In basic soils, availability of soil Ca for plant uptake is reduced due to decreased mineral solubility at high pH levels (Taiz and Zeiger, 2002; Brady and Weill, 2002). Due to greater nutrient solubility and therefore availability, root growth tends to be favoured in slightly acidic conditions (Taiz and Zeiger, 2002). Spatial variability in soil *pH* at the 1-year-old stand was positively and highly correlated with spatial variability of *Ca* ($r = 0.71$) (i.e. as pH increases, Ca concentration decreases). Thus, the negative effect of Ca observed at the 1-year-old stand, may have been confounded by the effect of soil pH. The data obtained in this study was not analyzed for confounding effects of various combinations of nutrients on soil respiration, which may be interesting to investigate in the future. Negative correlations of soil respiration to soil pH were also found at the other three chronosequence stands, but were not significant.

In addition to information on possible effects of spatial variability in soil nutrients on spatial variability of soil respiration, soil chemical analysis provided other useful insights into the lives of TPFS chronosequence stands[3]. Despite the limited data set, when averages of soil chemical properties were compared across the chronosequence, they revealed some interesting observations to support what has been known from other

[3] Average content of various chemicals at each stand, used for comparison in this discussion are given in APPENDIX C.

observations and studies about the chronosequence - its history, current productivity and stand age. For example, soil organic carbon was higher (1.2-0.9 %) in the top 20 cm layer of older forest stands compared to the younger one (0.5%). As forests grow and mature, forest soils tend to accumulate organic carbon due to annual litter-fall, and decomposition activities of this litter and below ground fine root biomass. The highest carbon content was found at the 15 year stand (1.2%), which would at first appear to be out of line with the age argument. However, upon closer examination of all the sites, this forest stand had the highest stem density (and thus root density) and highest leaf area index (and thus greater litter-fall potential). Therefore, annual carbon accumulation at this stand would be expected to be higher compared to other stands, and that is what the soil chemical analysis reflected.

Even more interesting, if one considers pH values, which determine soil acidity or alkalinity, soil pH decreased with soil stand age (i.e. soils become more acidic). Coniferous forests are known to decrease soil pH due to the higher acid content of their litter, in comparison to broad-leaf species (Scholes and Nowicki, 2002). Thus, afforestation by coniferous species will tend to acidify underlying soils, as was observed across this chronosequence.

Furthermore, increased soil pH tends to alter soil nutrient availability that may potentially adversely affect forest growth in the future. Increased soil acidity facilitates liberation of aluminum (Al) from mineral soils and the two can severely limit plant available essential micronutrients, such as calcium (Ca) and magnesium (Mg), in soils (Scholes and Nowicki, 2002). In light of this, when one considers Al, Ca and Mg

concentrations across the chronosequence, the effects of low pH are evident. Ca and Mg concentrations in soils decreased with age, while Al concentrations increased. In relation to this, although no strong correlation was found for the majority of soil respiration measurements, spatial variability of soil Al (0-20 cm of soil) at the 60 year old stand was always *negatively* correlated with spatial variability of soil respiration. The 60 year old stand had the lowest pH and highest Al concentration. Thus, in the future, increased Al concentrations may be adversely affecting spatial distribution of tree roots at the 60- year-old stand and potentially soil respiration.

In terms of signatures of past-land use, soil chemical analysis of the youngest site tells an interesting story. Common ingredients of agricultural fertilizers are potassium (K) and phosphorus (P), which may accumulate in soils under agricultural use. Our youngest forest stand was a former farmland (still in use just three years prior to afforestation). Therefore, it was no surprise to find that the 1 year old stand had the largest soil K concentration and also larger P content compared to the oldest stands. Thus, this soil chemical composition is suggestive of the past-land-use of the youngest forest.

4.2.3 Annual estimates of soil C-emissions

The estimated annual soil carbon emissions at TPFS sites (Table 4.2, Section 4.1.5) were in good agreement to emissions reported in literature. McDowell et al (2000) reported annual soil CO_2 -emissions of 764 g of C per m^{-2} yr^{-1} (of which 132 g of C per m^{-2} yr^{-1} was calculated for winter emissions). They studied soil respiration in a 70 year old mixed-conifer temperate forest in Northern Idaho, for an entire year, including during

winter in the presence of snow cover. Law et al (2001) reported that their young (15 year) ponderosa pine stand, in Central Oregon, emitted 643 g of C per m^{-2} yr^{-1}, while their older stand (50-250 yr) emitted 781 g of C per m^{-2} yr^{-1}. In a separate study on the same stands, which lasted for a period of 3 years, Irvine et al (2002) reported a range of CO_2 emissions for the stands (483 to 597 g of C per m^{-2} yr^{-1} for the young one and 427 to 519 g of C per m^{-2} yr^{-1} for the mature one). Raich et al (1992) used the results of a number of literature-reported studies to estimate mean soil CO_2 -emissions for different terrestrial ecosystems around the world. Their estimate for temperate coniferous forests was 681 ± 95 g of C per m^{-2} yr^{-1}. Finally, Janssens et al (2001) reported a mean soil respiration of 760 ± 340 g of C per m^{-2} yr^{-1} based on results of the EUROFLUX study.

Furthermore, for the 60 year old TPFS forest stand, net ecosystem respiration rate was 1247 g of C per m^{-2} per year, based on Flux Tower measurements (*pers. commun.* Altaf Arain and Natalia Restrepo). Soil CO_2 -emissions calculated in this study for the site were 806 g of C per m^{-2} yr^{-1}, which would suggest that about 65% (from 806/1247*100%) of ecosystem respiration at the 60 year old forest stand came from soil respiration, which would be comparable to literature reports. For example, Law et al (1999) calculated that about 77% of ecosystem CO_2 efflux from their ponderosa pine forest in Oregon, USA was due to soil respiration.

Overall, during this study period (June 2003 to May 2004, inclusive), estimated *annual* soil CO_2 -emissions increased with forest stand age across the TPFS chronosequence, when the 15-year-old forest stand was excluded. Emissions estimated for the 15 and 30 year-old stands were comparable, but both models used to calculate

those emissions failed to simulate well the observed seasonal trend in soil respiration, especially for the 15-year-old stand. Thus, soil CO_2 -emissions may be underestimated for the 15-year-old stand and, if recalculated with a better fitting model, may in the end be higher than those of the 30-year-old stand. This then, would be in agreement with the actual mean respiration rates observed during this study (Figure 4.2), where the 15 year old stand was shown to have higher soil CO_2 efflux compared to the 30 year old one.

CHAPTER 5: BOREAL STUDY

5.1 RESULTS

5.1.1 Environmental conditions during study

Table 5.1 compares the minimum and maximum values of average daily air and soil temperatures and soil moisture at GRFS. The month(s), when the maxima or minima were observed, are also listed in the table, as are the yearly averages of all the variables.

Table 5.1: Comparison of environmental conditions at GRFS during the course of the study period (Sept'03 to Jul'04). Shown are air and soil temperatures and soil moisture, their average daily maximum and minimum values, the months during which those values where attained and the yearly average for the period.

	Max	Min	Ave
Air temperature	30.1	-38.5	0.9
month observed	*Jul-04*	*Jan-04*	
Soil temperature	14.7	0.6	5.09
month observed	*Aug-03*	*Jan-04*	
Soil moisture	0.53	0.33	0.44
month observed	*Apr-04*	*Sept -03, Jul-04*	

Figures 5.1 (a,b) show the course of average daily air and soil temperatures (average of 10 & 20 cm depths for soils) and volumetric water content (0-30 cm average) observed at GRFS from August 2003 to August 2004. Included in Figure 5.1 (a) are soil temperature measurements taken during soil respiration measurements with the LI-COR 6400-013 soil probe attachment that began at the end of July 2003 (shown as symbols in the figure). Figure 5.1 (b) also shows point-measurements of soil gravimetric moisture content measured throughout the study period in conjunction with soil respiration measurements.

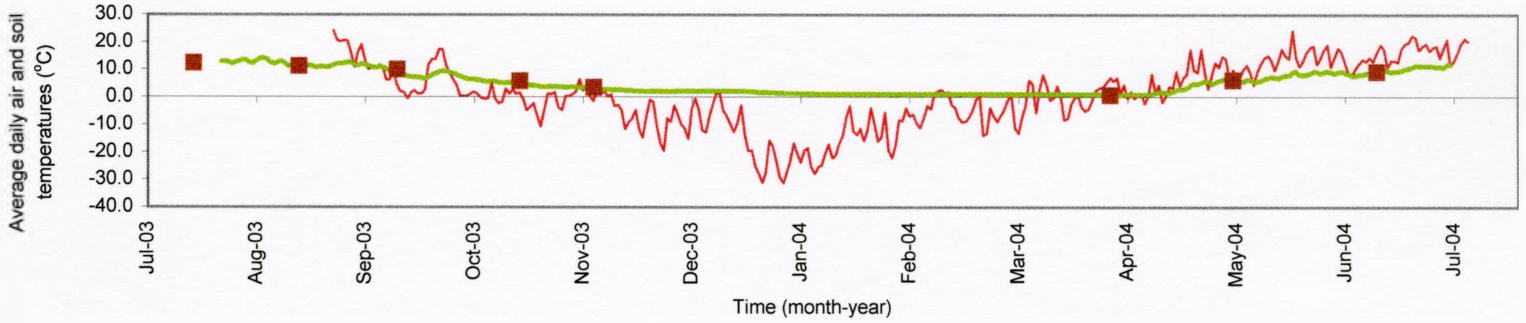


Figure 5.1 a): Trends in daily average air, Tair, and soil, Ts, (average of 10 & 20 cm depths from both soil pits) temperatures at GRFS over the course of the study period. Daily averages were calculated from half-hour measurements. LI-COR T-probe measurements are also included (symbols).

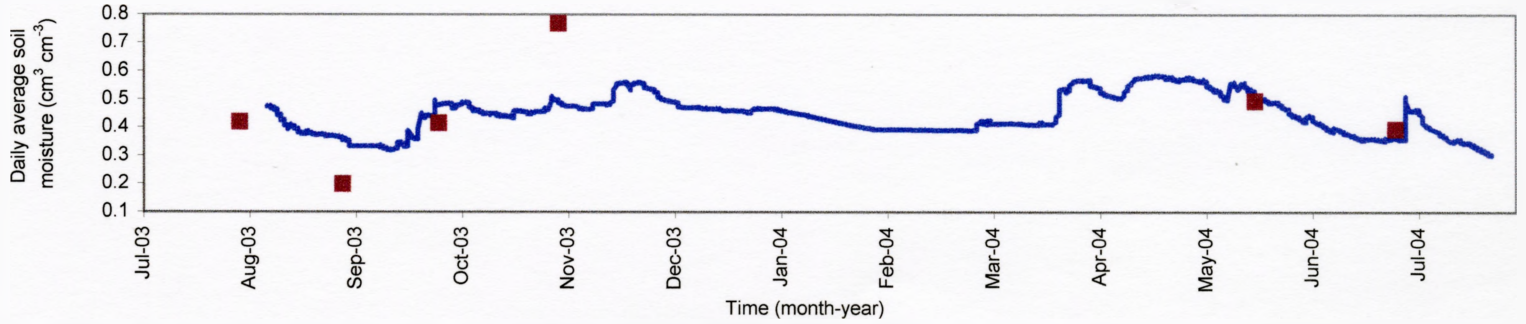


Figure 5.1 b): Trend in daily average soil mositure at GRFS over the course of this study period. Daily averages were calculated from soil pit measurements taken every 4 hours at 0-30 cm. Manual GWC content measurements (symbols) are also included for comparison.

Over the course of the study period, the mean yearly (Sep'03 to Jul'04, inclusive) air temperatures at GRFS was 0.9°C, which was comparable to the normal (1.5 ± 1.1 °C) reported for the area (Table 2.2, *Section 2.2*). During this study period, maximum average daily *air* temperature (30.1°C) was observed in mid July 2004, while the minimum average daily *air* temperature (-38.5°C) was observed at the end of January 2004.

The maximum average daily *soil* temperature for the site was observed at the end of August 2003 (14.7 °C), while the minimum was observed at the end of January 2004 (0.0 °C). There did not appear to be much lag between air and soil temperatures at the stand, but the response of soil temperature to air temperature diminished over winter months, when snow cover was present (Dec '03 to Apr '04). Overall, air temperature was more variable than soil temperature. However, both air and soil temperatures peaked over the summer months, fell during autumn, reached a minimum in winter months, and rose again in spring. Below freezing air temperatures first appeared at the end of September 2003, but in general constant below air freezing temperatures persisted from November 2003 to April 2004. Despite the freezing air temperatures, soil temperature at about 15 cm depth remained near zero, never completely frozen throughout that time. Soil temperatures began increasing at the end of April 2004. The manual soil temperature measurements (at 15 cm depth) correlated very well with soil pit temperatures (averages of 10 & 20 cm depth observations).

Soil moisture at GRFS was relatively high at all times between September 2003 and July 2004. The maximum recorded average soil moisture (0.53), along the top 30 cm

of soil, was observed in April 18, 2004, most likely corresponding to spring snow-melt, which began at the end of March (see Figure 5.1b – rapid rise in soil moisture at end of March, beginning of April). Soil moisture was relatively high from about October to December and then again in spring from April to May. The minimum daily average soil moisture (0.33) was observed in July 2004. Lower soil moisture was also observed in June 2004 and September 2003.

5.1.2 Seasonal variability in soil respiration

Seasonal Cycle of Respiration at Boreal Site

The seasonal cycle of observed mean soil respiration at GRFS, from end of July 2003 through July 2004, is shown in Figure 5.2. The highest mean soil respiration (6.8 μmol CO_2 m^{-2} s^{-1}) was observed at the end of July 2003, while the minimum (0.5 μmol CO_2 m^{-2} s^{-1} C) was observed in early March 2004. No soil respiration data was available for the period of December 2003 to February 2004 inclusive, but the trend is expected to follow the curve and soil respiration during those months was probably around 0.5 μmol CO_2 m^{-2} s^{-1} as well. Furthermore, when soil respiration measurements were resumed in March 2004, there was still a significant amount of snow accumulated on the ground (60-80 cm deep along the transect, from personal observations). Even in April, there was still some 20 cm deep snow cover in places along the transect. Thus measurements taken in March may be representative of winter measurements of soil respiration at GRFS. After the winter's low, soil respiration began increasing with time, towards early July 2004, such that the pattern observed in 2003 was beginning to re-emerge.

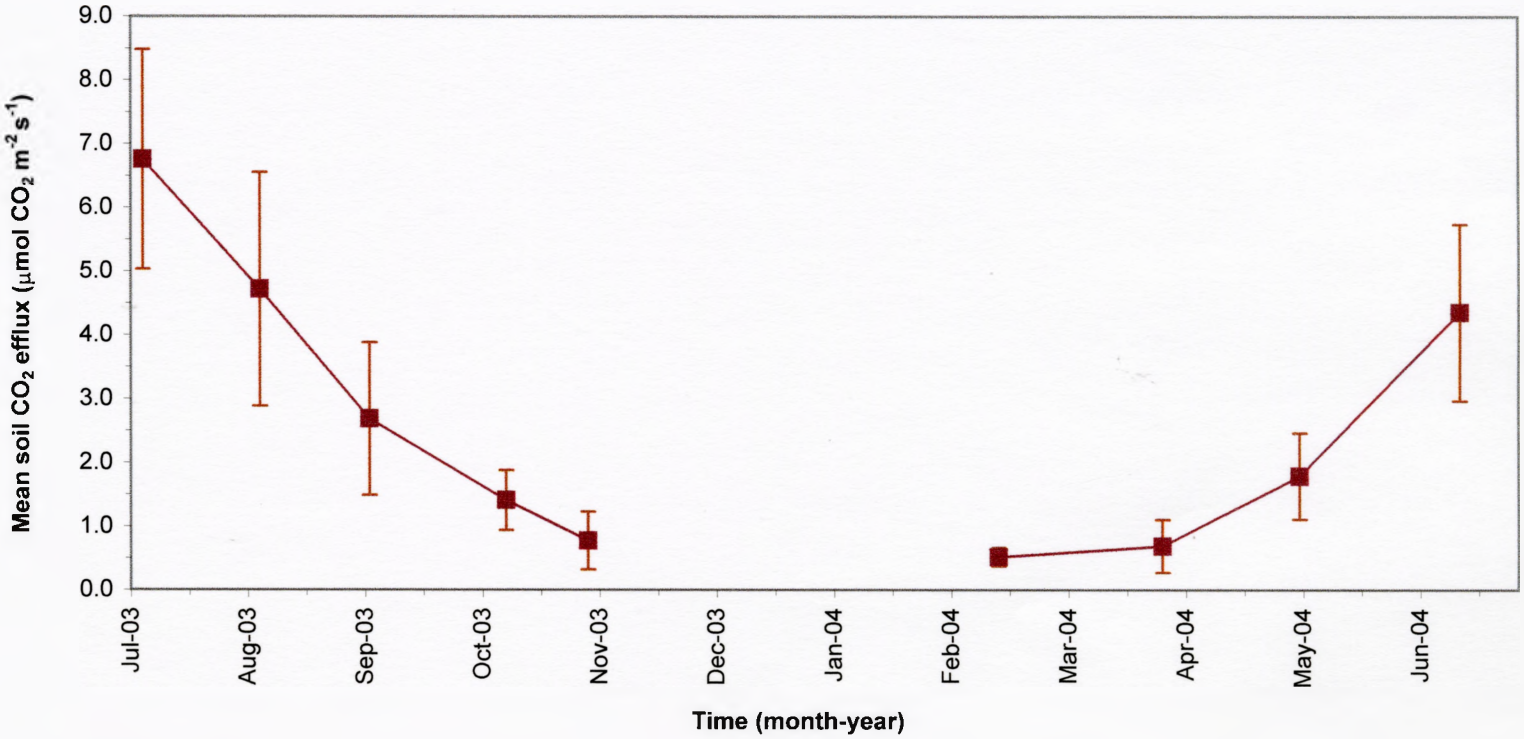


Figure 5.2: Seasonal trend of soil respiration at GRFS, from Aug '03 to Jul '04. Soil respiration was not measured from Dec'03 to Feb'04, inclusive. Error bars represent ± 1 standard deviation.

Soil respiration and environmental variables

In general, the seasonal variability of mean soil respiration followed seasonal variability of soil temperature. As temperatures began decreasing in the fall, and then increasing again in spring, so did soil respiration. Furthermore, a high positive correlation (r^2=0.95) was found between temporal variability in soil temperature and soil respiration at the site, as seen in Figure 5.3. This figure shows an exponential regression curve fit to the observed data and the equation of the curve. The Q_{10} value was also suggestive of high temperature sensitivity, especially during the growing season. The Q_{10} was 8.2 when full year's data was considered, 7.2 when data only for Jul'03-Sep'03 and May'04-Jul'04 was considered (r^2=0.96), but 5.4 when data for Sept'03 to Apr'04 was considered (r^2=0.79). When all soil respiration measurements at temperatures above 10°C (June, August, July) were removed, then the Q_{10} value went down to 5.0 (r^2=0.93, T range 0°C to 10°C).

Soil moisture may also have an influence on rates of soil respiration at GRFS. Although the number of data points is few, there appears to be a relatively strong, negative, linear correlation between soil moisture in the top 30 cm at GRFS and observed soil respiration measurements. Figure 5.4 (a) shows a linear regression plot of mean volumetric water content (0-30 cm average), calculated from soil pit data for the day when soil respiration was measured at the stand, and the corresponding rate of soil respiration. If March 2004 measurement is excluded (Figure 5.4 b), the data points appear to follow the linear regression pretty well. On several occasion during autumn, when soil cores for GWC analysis were taken, standing water was observed at some

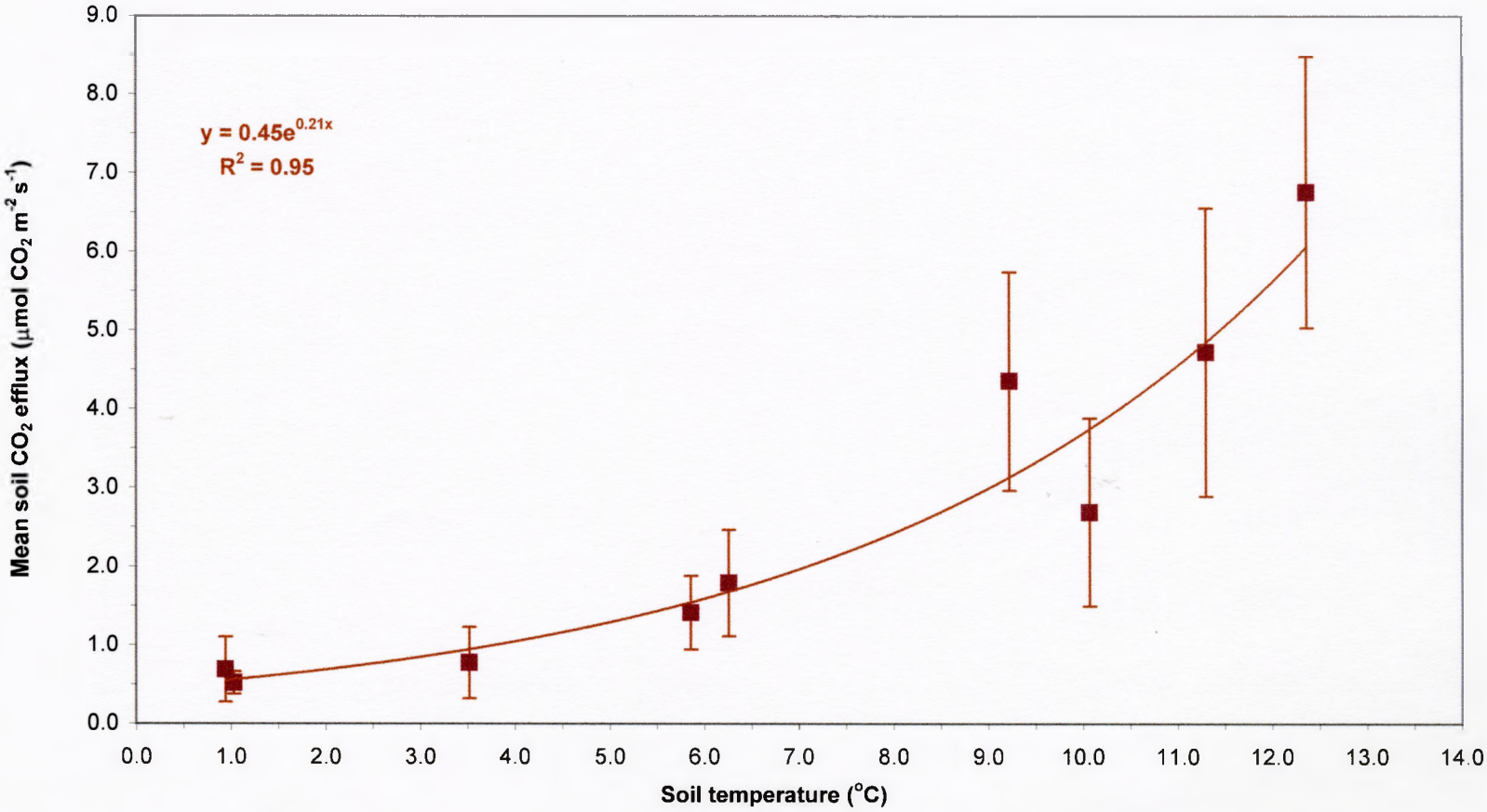


Figure 5.3: An empirically-derived, exponential relationship between mean daily soil respiration and mean daily soil temperature (15 cm depth) measured at GRFS. Each dot represents an average of 50 collars measured along the transect between August 2003 and July 2004, except during March (12 measurements) and April (20 measurements). No measurements were taken December 2003 to February 2004. Error bars represent ± 1 standard deviation.

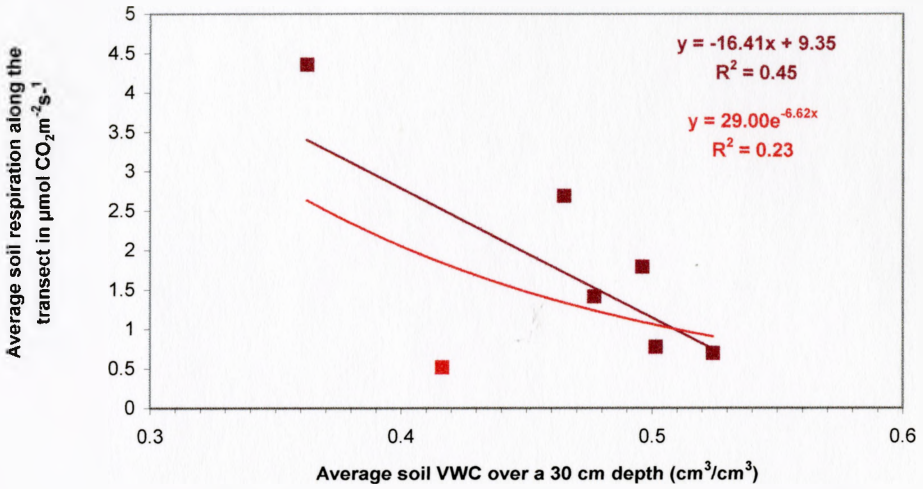


Figure 5.4 a): A look at empirically-fit relationships between soil moisture and respiration, measured at GRFS. When March measurement was excluded (b), a linear trend was observed.

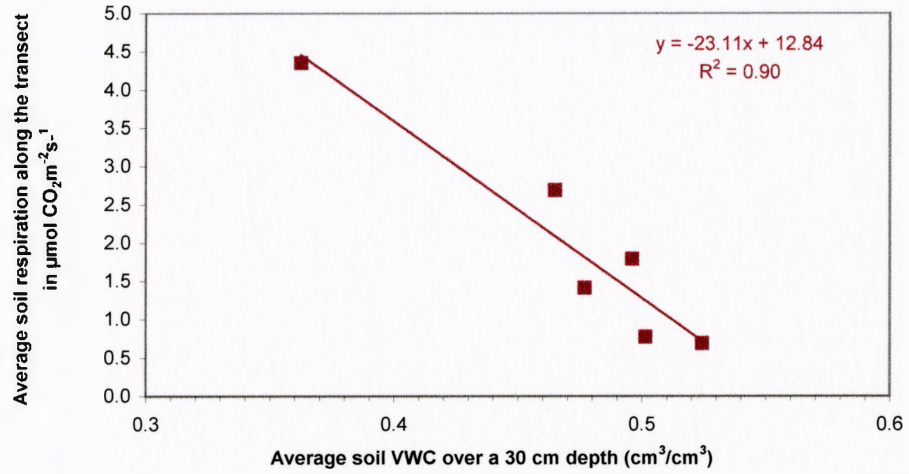


Figure 5.4 b): When March measurement was excluded from analysis in (a), a linear trend was observed between soil moisture and soil respiration.

locations along the transect at the bottom of the (24 cm) core. High soil moisture content at the stand may hinder soil respiration by clogging soil pore spaces with water and restricting gas movement. Water logging may create anaerobic conditions and significantly reduce respiration by reducing oxygen supplies to respiring microorganisms.

5.1.3 Spatial variability in soil respiration

Figure 5.5 shows a colour coded image of spatial variability of soil respiration along the transect (horizontal) plotted versus time (vertical) at GRFS, with darker colours (up to red) representing higher soil respiration rates and lighter colours (up to white) representing lower soil respiration rates. Data for late Nov'03 and Mar-Apr'04 were not included, because not all soil collars along the transect were measured on those days and gaps in the plot would make the representation confusing. As can be seen from the figure, spatial variability of soil respiration was relatively high along the transect during the summer and decreased with the onset of winter, after which it began increasing again in spring. The range of maximum and minimum soil respiration varied seasonally, being the highest in Aug'03 (8.4 μmol CO_2 m^{-2} s^{-1}) and lowest in Nov'03 (2.2 μmol CO_2 m^{-2} s^{-1}). The highest soil respiration shown in the plot, and recorded during the study period, was 10.76 μmol CO_2 m^{-2} s^{-1} at the end of July 2003. The minimum soil respiration shown was 0.61 μmol CO_2 m^{-2} s^{-1}, recorded in early November 2003.

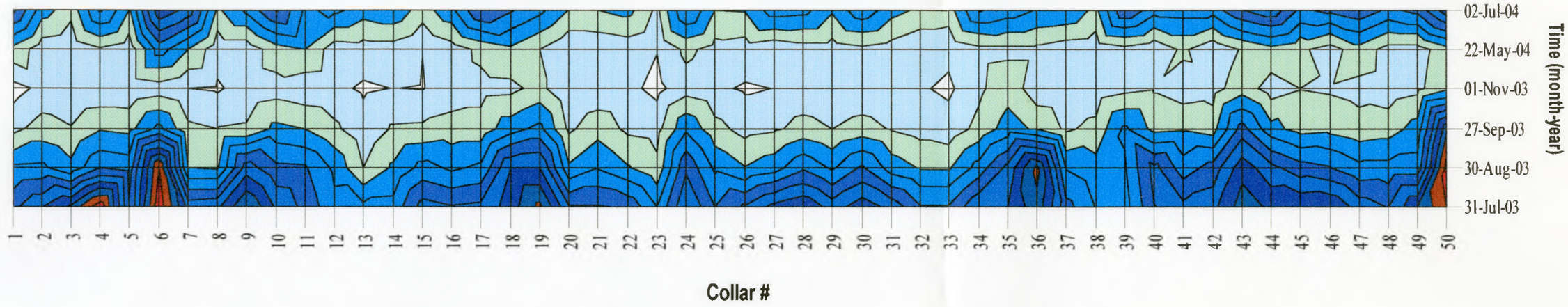


Figure 5.5: Spatial variability of soil respiration along the transect at GRFS plotted versus time to show temporal variability. The degree of spatial variability in soil respiration varied over the course of the year. Darker colours, up to red, represent higher respiration rates. Data from August to November 2003 and later May to July 2004 is shown. Respiration was also measured in March and April 2004, however not along the full length of the transect, therefore it was excluded from above plot.

Spatial variability in soil nutrients

Soil along the transect at GRFS was analyzed for spatial variability of several soil nutrients at three different mineral depths, in addition to the thick organic soil layer. Complete tables of detected soil nutrients and their coefficients of correlation (r) in relation to soil respiration along the transect are given in APPENDIX C. Poor correlation was found between spatial variability of soil chemical properties and spatial variability of soil respiration at GRFS. The C:N ratio in the top organic soil layer appeared to be negatively and highly correlated to spatial variability in soil respiration, without much seasonality. Spatial variability in organic soil's C:N ratio could explain about 33% of the spatial variability of soil respiration at GRFS. Among other nutrients, phosphorus (P), in the first mineral layer sampled (0-20 cm), was positively correlated to spatial variability in soil respiration and could explain up to 49 % of this variability. In the third layer (36-50 cm), spatial variability of soil sodium (Na) content showed consistently strong positive correlation and could account for up to 58% of the spatial variability in soil respiration.

Spatial variability in litter thickness

Figure 5.6 compares soil respiration measured over several adjacent collars, where one had the organic litter layer undisturbed and another had the litter removed to reveal the mineral layer. Removal of the litter layer caused a substantial (62-84%) decrease in observed soil respiration fluxes. This showed that the litter layer accounted for most of

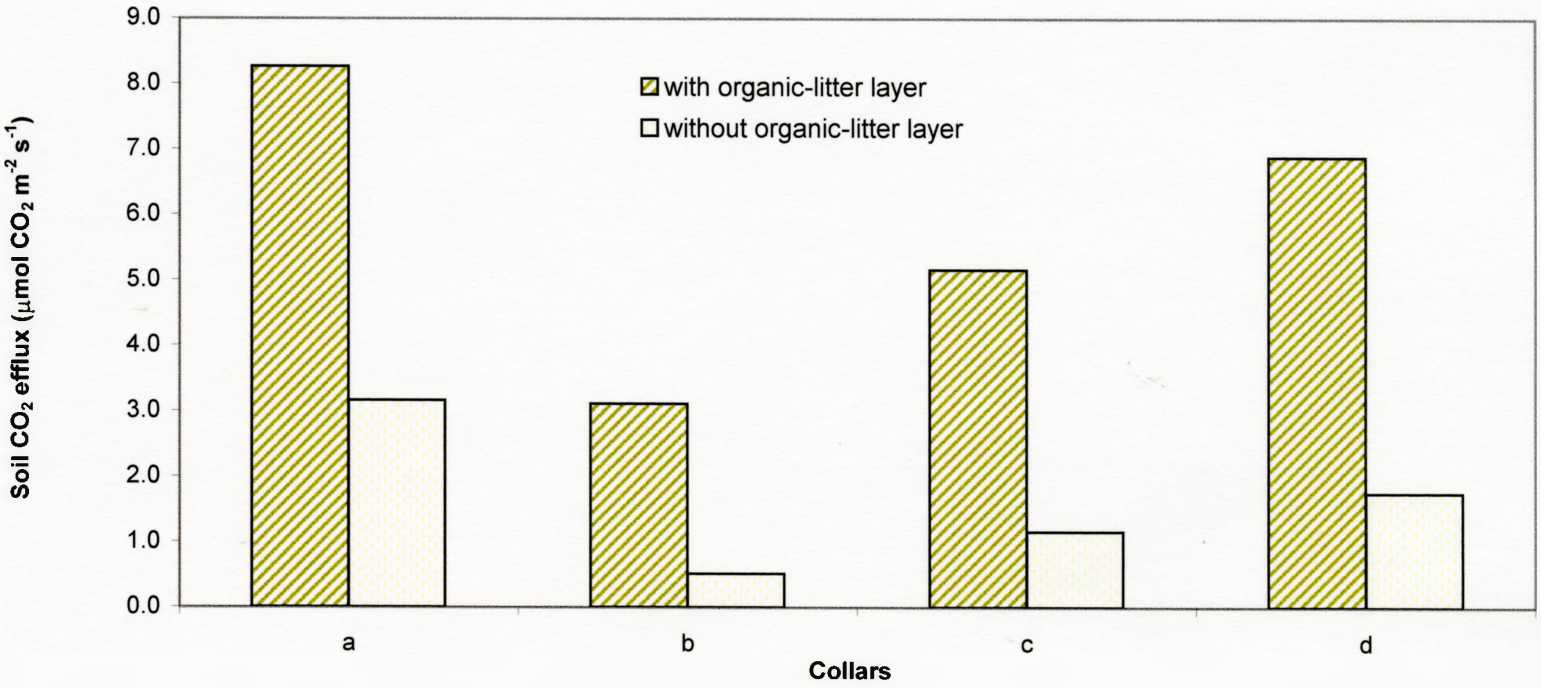


Figure 5.6 : Comparison of soil respiration from two adjacent collars at GRFS: one with the organic-litter layer removed and the second with the organic-litter layer intact.

the observed surface fluxes. Thus, one would have expected to see correlations between spatial variability in litter thickness and spatial variability in soil respiration. However, no strong correlation between the two variables was found at GRFS. One reason may be that increased *porosity* of the litter layer caused more rapid redistribution of CO_2 throughout the layer, than would otherwise be expected from mineral soils.

5.1.4 Modeled soil respiration

Figure 5.7 compares an annual trend in daily mean soil respiration simulated by an exponential model derived from observations and that simulated by the moisture-C:N ratio sensitive model (also used to simulate annual soil respiration at TPFS stands). Soil temperature and moisture data from August 9, 2003 to August 8, 2004 (at half-hour intervals) was used in modeling GRFS respiration. Also included in the figure are the monthly observed soil respiration values. Simulated soil respiration followed the general trend of observed values, with high rates observed during summer and low rates in winter. However, due to the limited number of observations, it is hard to say if the peaks observed in early August and September 2003 were real or an overestimate of soil respiration. An underestimation was also observed in July 2004. The annual mean soil respiration calculated from observations was 2.6 μmol CO_2 m^{-2} s^{-1} (9 months of measurements), the soil moisture-C:N model gave a mean of 2.0 μmol CO_2 m^{-2} s^{-1} and the exponential model a mean of 2.1 μmol CO_2 m^{-2} s^{-1}. Simulated soil respiration values were used to calculate annual soil CO_2 -emissions for GRFS from August 9, 2003 to August 8, 2004.

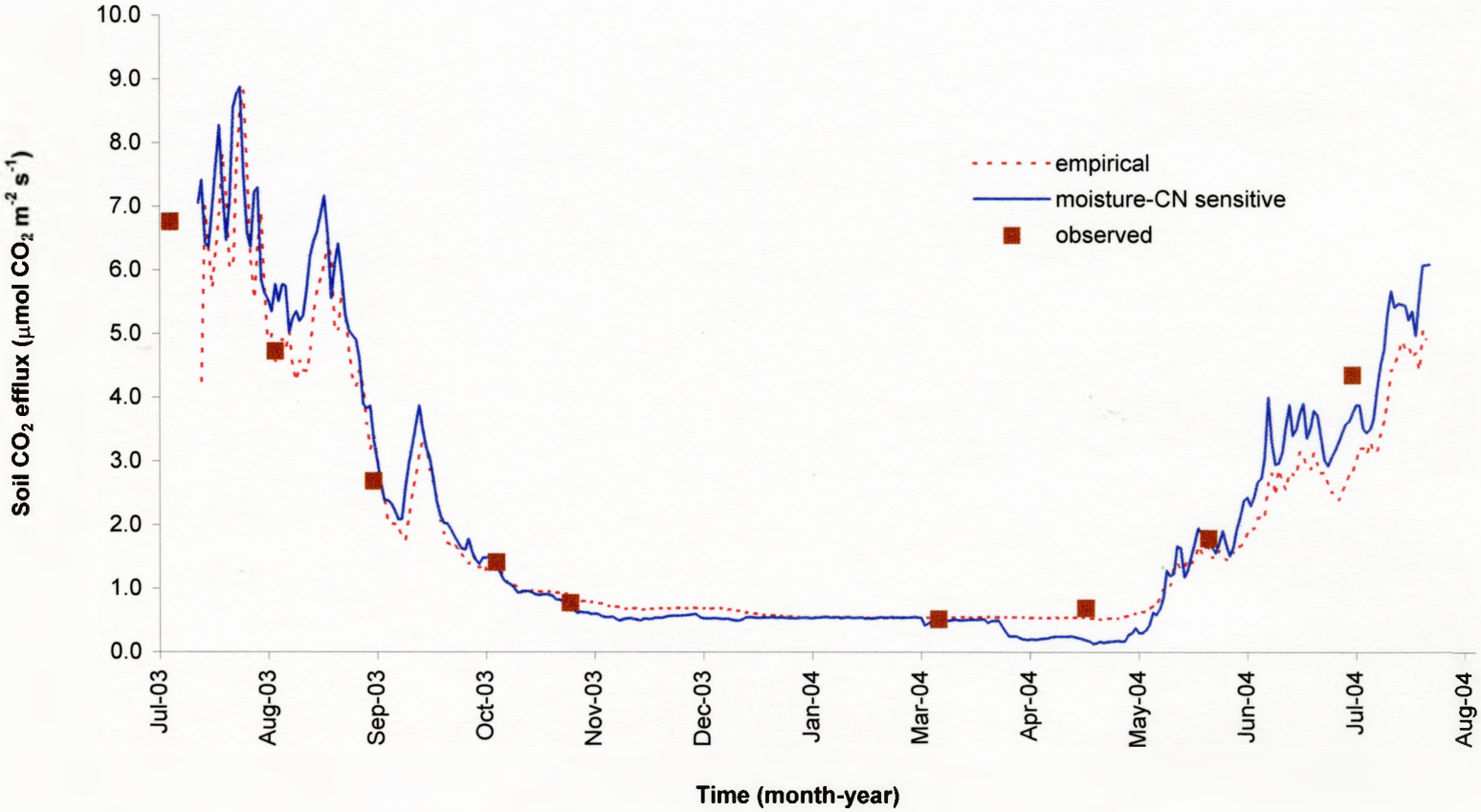


Figure 5.7: Comparison of simulated annual trends in soil CO_2 emissions at GRFS to monthly observations done throughout the study year (August 2003 to July 2004).

5.1.5 Annual estimates of soil C-emissions

Calculated estimates of annual and seasonal soil CO_2 - emissions for the GRFS are given in Table 5.2. The table also includes relative % C-emissions, for each season during the year. Total CO_2 -emissions due to soil respiration at GRFS for the study year were found to be 758 g of C per m^{-2} yr^{-1} based on the exponential model simulation and 816 g of C per m^{-2} yr^{-1} based on the soil moisture-C:N model simulation. When individual seasons were considered, summer had the highest emissions, accounting for 70 to 77 % of total annual emissions. Spring time at GRFS showed the lowest CO_2 - emissions (5 to 7%), while winter (8-10%) and fall (12-13%) had somewhat higher emissions.

Table 5.2: Calculated annual CO_2 -emissions from the forest floor at GRFS for the period of August 2003 to August 2004, using two different models to simulate annual soil respiration at the site. % relative CO_2- emissions (relative to total) for each model result are also given. Winter = Dec to Mar; Spring = Apr & May; Summer = Jun to Sep; Fall = Oct & Nov

	Winter	Spring	Summer	Fall	Total
From simple exponential model (g C m^{-2} yr^{-1})	80	55	528	95	758
% relative emissions	8	5	70	13	100
From moisture-C:N sensitive model (g C m^{-2} yr^{-1})	69	43	604	101	816
% relative emissions	8	5	74	12	100

5.2 DISCUSSION

5.2.1 Seasonal variability in soil respiration

The mean maximum and minimum soil respiration rates observed for the boreal forest stand during this study were within the ranges reported in literature. For example, Swanson and Flanagan (2001) reported rates in the range of about 0.1 to 7 μmol CO_2 m^{-2} s^{-1} over the 1996 growing season for a 120 year old boreal black spruce stand in central Saskatchewan, Canada. Scott-Denton et al (2003) studied a mixed-conifer sub-alpine forest stand in Boulder Colorado, USA for three summers between 1999 and 2001 and reported soil CO_2 fluxes in the range of 1-14 μmol CO_2 m^{-2} s^{-1}. Russell and Voroney (1998) studied soil respiration in a 70 year old boreal aspen forest near Prince Albert, Saskatchewan between April and September 1994 and reported a range of 0.6 to 9.3 μmol CO_2 m^{-2} s^{-1}. They reported April fluxes of 0.45 to 0.91 μmol CO_2 m^{-2} s^{-1}, which was comparable to April fluxes observed at GRFS at the same time (0.69 μmol CO_2 m^{-2} s^{-1}). In the above studies, either LI-COR 6400 or its earlier version, LI-COR 6200, was used to measure soil respiration. The relative peaks in summertime soil respiration (late July/early August) were also comparable to literature studies. Russel and Voroney (1998) showed increased soil respiration from July through August in their study, which was comparable to the periods of high flux observed by Schlentner and Van Cleve (1985) in Alaskan forests and in line with observations at GRFS.

A relatively high Q_{10} (8.2) value was observed at GRFS based on the exponential relationship derived from the empirical measurements for the entire year (temperature

range of 0.9 to 12.4°C). In contrast, upon the evaluation of several terrestrial and wetland ecosystem world-wide, Raich and Schlesinger (1992) reported a median value of 2.4. Several authors discussed the temperature sensitivity of Q_{10}, which can vary seasonally and can cause overestimations in Q_{10}, when calculated over large temperature ranges (Lloyd and Taylor, 1994; Qi et al, 2002). When summer (June to August) measurements were excluded, and measurements at a temperature range of only 0° -10°C were considered, then the Q_{10} value went down to 5.0 (r^2=0.93). However, even then the value was still on the high end of values often reported in literature.

Russell and Voroney (1998) reported a Q_{10} value of 3.9 to 5.1 for their study, which they also considered in the upper ranges normally reported in literature. More recently, Morgenstern et al (2004) reported Q_{10} values between 5.1 and 6.0 in their study of a Pacific Northwest Douglas-fir forest. Black et al (1996) reported Q_{10} values of 5.4 to 5.6, for their study of boreal forest stands in Saskatchewan, Canada. They suggested that the higher Q_{10} values may be due to increased microbial respiration at the stands (due to greater accumulation of more labile litter in boreal forests). Bunnell et al (1977) reported a Q_{10} value of 8.8 for microbial respiration of fresh plant litter. For GRFS, decomposers in the thick litter-organic soil layer appear to make an important contribution to the total soil respiration observed in the stand, and the high Q_{10} value is reflective of that contribution.

5.2.2 Spatial variability in soil respiration

Spatial variability in soil respiration at GRFS was high, with coefficients of variation ranging from 4 to 71% depending on the season. The greatest variability was observed in August, at the time when maximum soil CO_2 fluxes were also observed. This variability decreased with the onset of winter and was lowest in March 2004, when measurements above snow cover were taken.

In terms of spatial variability in soil chemical properties at GRFS, a high negative correlation was observed between the C:N ratio of the organic-humus litter layer and spatial variability of soil respiration, with relatively little seasonality in the relationship. Cotrufo et al (2000) reviewed some factors that affect litter decomposition in forest ecosystems. In boreal ecosystems fungi play an important role in decomposition activities. The organisms prefer substrates that are high in nitrogen (or low in C:N ratio). Metabolic activities of soil micro-organisms are one of the major sources of soil CO_2 efflux. Thus, in areas were C:N ratio of litter is high, one would expect lower soil respiration due to decreased decomposition activity.

Spatial variability in litter thickness was not correlated to spatial variability of soil respiration. Russell and Voroney (1998) also found little correlation between observed soil respiration and litter content in a boreal aspen forest, suggesting that most of the flux they observed was due to root respiration. However, when the organic layer was completely removed, soil respiration was reduced by 62-85% at GRFS. Thus, it would be useful to investigate further the sources of CO_2 fluxes at GRFS and the role of the litter-organic soil layer.

5.2.3 Annual estimates of soil C-emissions

Estimated annual soil CO_2 -emissions calculated for GRFS were much higher than those reported by Raich et al (1992) for boreal forests, , which they estimated from data collected from literature (322 ± 31 g of C per m^{-2} yr^{-1}). In contrast, soil CO_2 -emissions at GRFS were lower than those reported by Schelentner and Van Cleve (1985), who used direct measurements and models to estimate emissions for four mature forests in interior Alaska, including black spruce and aspen stands. Their estimates of soil CO_2 emissions for the period of May to September were 1315 to 1654 g of C per m^{-2} yr^{-1}. Russell and Voroney (1998) reported soil CO_2 -emissions of 809 to 905 g of C per m^{-2} yr^{-1} for their boreal forest, which were more in line with GRFS observations.

CHAPTER 6: COMAPRISON OF BOREAL vs TEMPERATE FOREST STANDS

As part of this study, a comparison was made between temporal and spatial variability of soil respiration observed at the 60-year-old temperate white pine forest stand from TPFS and the 74 year-old boreal mixed-wood stand from GRFS, in order to investigate any similarities and/or differences of soil respiration in two different climate zones in Ontario. What follows is a discussion of the comparison between those two sites.

6.1 Comparison of Environmental Conditions

As expected, given that the two forest stands are in two different climate zones, the observed environmental conditions at the two forest stands were quite different. To begin with, the range of mean annual *air* temperatures between the two sites varied greatly. At the 60-year-old temperate white pine forest stand, mean daily air temperature varied between +23.7°C and -18.1°C (about 42° range) over the course of this study, while at GRFS, mean daily air temperature varied between +30.1°C and -38.5°C (about 69° difference!). In contrast, the range of *soil* temperature values was greater at the temperate stand (about 22°C) compared to the boreal one (about 15°C). The soil in the temperate stand was warmer during the growing season, reaching an annual maximum of +21.9°C, compared to the boreal stand that only reached maximum of +14.7°C during the course of this study. Soil temperatures in the temperate forest stand were much more responsive to air temperature variability (at 15 cm depth) compared to boreal forest soil at the same depth. The sandy mineral soil at TPFS is better at conducting heat, compared to the porous organic soil at GRFS found at the same depth.

Snow accumulation in the boreal forest was much higher compared to the temperate forest stand. In March 2004, there was still about 60-80 cm of snow on the ground there. Snow cover at GRFS persisted for the entire winter season, acting as an insulator, protecting the soil from the extreme cold air temperatures and preventing the soil from freezing at the 15 cm depth. In contrast, at the temperate stand, snow-cover was periodic over the study period and the overall accumulation was relatively low (20-30 cm) and sporadic, when compared to the boreal stand. Thus, despite the air temperatures being relatively "warmer" at the temperate stand, the overall lack of snow insulation caused soil to freeze (15 cm depth) at TPFS site between January and March 2004, although occasional thaws did take place there.

When soil moisture is considered, once again, obvious differences between the two forest stands were observed. Soil moisture at the boreal stand was always higher compared to the temperate one, even when the boreal site was at its minimum moisture content (Figure 6.1). However, one interesting observation was that the timing of minimum soil moisture content was about the same for both stands. Soil moisture was low from August to September 2003 and then again from December 2003 to March 2004, for both stands.

At the root of the difference in the soil moisture regime between the two stands was, in part, the difference in soils. In the boreal forest, a thick layer of litter (12 – 24 cm thick), which contained an intricate network of roots, overlay a poorly drained silt-sand mineral soil. In contrast at TPFS, the litter layer was only about 5 cm thick, with little tree root content, which overlay mostly sandy, easily drained mineral soil. The thick

porous organic layer at GRFS was good at retaining water, while the underlying layer was slow to drain it. Thus, water accumulates more readily there.

6.2 Comparison of Temporal Variability in Soil Respiration

Figure 6.2 compares the seasonal trend in soil respiration at the boreal and temperate forest stands. Mean soil respiration for both forest stands followed the same general seasonal pattern, following the seasonal trends in soil temperatures: falling from summer to winter, when it converged, and then increasing again in spring. During the summer months, soil respiration for the boreal forest stand was consistently higher compared to the respiration rates observed in the temperate forest stand by 1 to 2 μmol CO_2 m^{-2} s^{-1}. The difference was greatest at the end of July to early August 2003, when observed soil respiration was at its highest for both stands (4.9 and 6.8 μmol of CO_2 m^{-2} s^{-1} for the temperate and boreal stands, respectively). The higher rate of soil respiration at GRFS may have been due to increased soil decomposition activities in its extensive humus layer. GRFS also has higher stem density and higher density of understory species compared to TPFS. Increased stem density and dense undestory may translate into increased tree root density, which may cause increased soil respiration. The peak in soil respiration appeared at around the same time for both stands (late July, early August 2003).

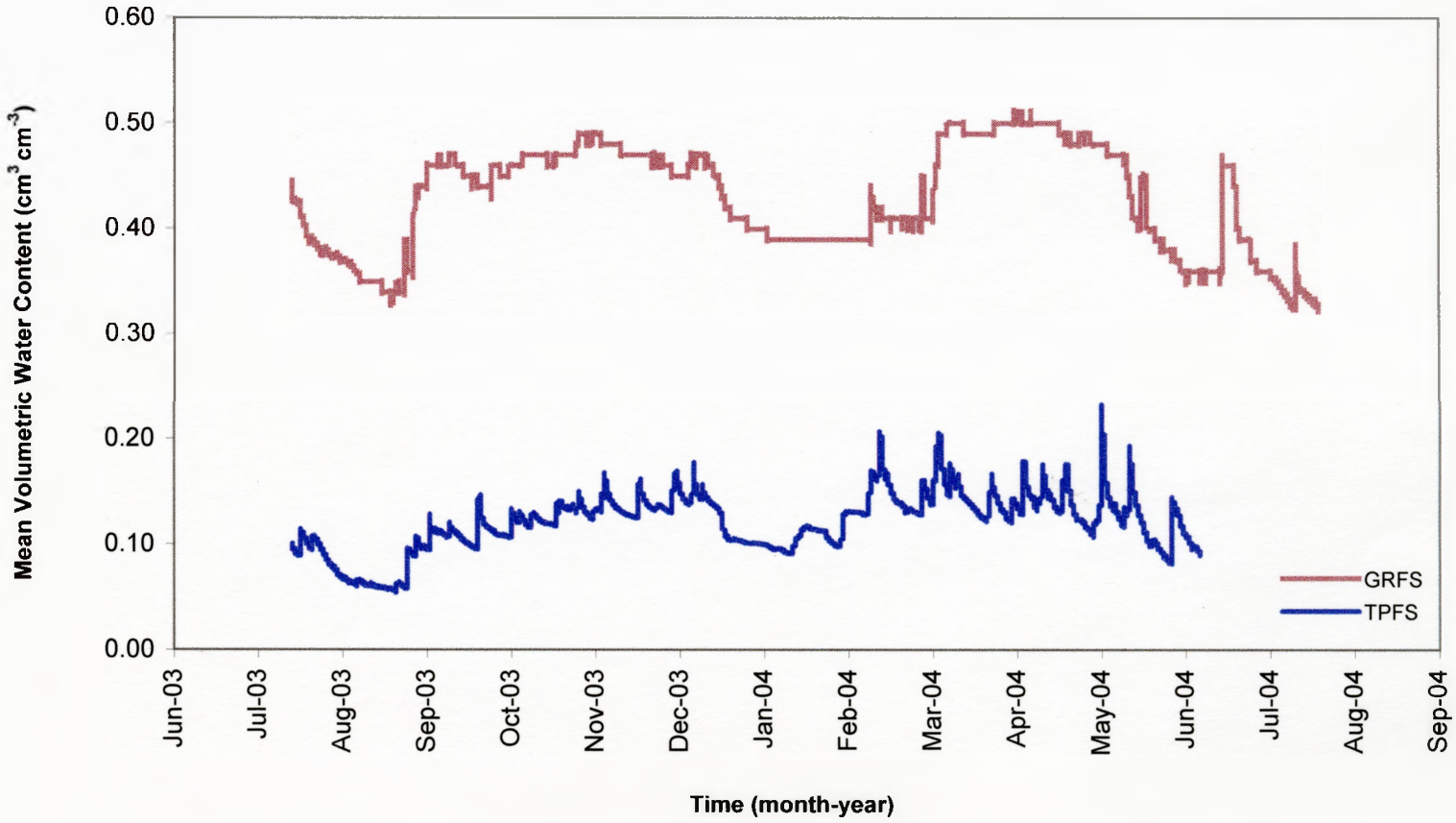


Figure 6.1: Comparison of soil moisture between GRFS and TPFS over the course of the study. Volumetric water content is shown as an average of 0-30 cm soil moisture measurements for GRFS and 0-20 cm for TPFS. Half-hourly series are shown.

Soil respiration at the boreal forest stand appeared to decrease more rapidly with the onset of winter, compared to the temperate stand. Similarly, with the onset of summer in the region, soil respiration appeared to increase more rapidly than at TPFS. This would be in line with the higher temperature sensitivity observed at GRFS (Q_{10} = 8.2) compared to TPFS (Q_{10} = 4.1). Soil respiration in the colder boreal forest was more sensitive to increases in soil temperature compared to the temperate forest. For example, when soil maxima was observed in August 2003, the boreal forest was respiring at a higher rate (6.8 ± 1.7 μmol CO_2 m^{-2} s^{-1}) at a cooler soil temperature (12.4 ± 0.1 °C) compared to the temperate forest that respired at a rate of only 4.9 ± 1.3 μmol CO_2 m^{-2} s^{-1} in soil temperatures of 18.9 ± 0.1 °C. Lindroth et al (1998) also observed high temperature sensitivity of soil respiration in a boreal forest in Sweeden, based on two-year-long observations. Results from EUROFLUX studies, showed that annual ecosystem respiration tends to increase with latitude, despite decreases in mean annual temperatures (Janssens et al, 2001; Matteucci et al, 2000), which was explained with a higher temperature sensitivity for organic matter decomposition in colder regions (Mateucci et al, 2000). Thus, although boreal forests may be actively respiring for a shorter period of time during a year (the growing season), during that time their respiration rates may be higher compared to cool temperate forest stands. This may also explain why similar modeled annual soil CO_2 -emissions were observed for the two forests, despite climatic differences between them.

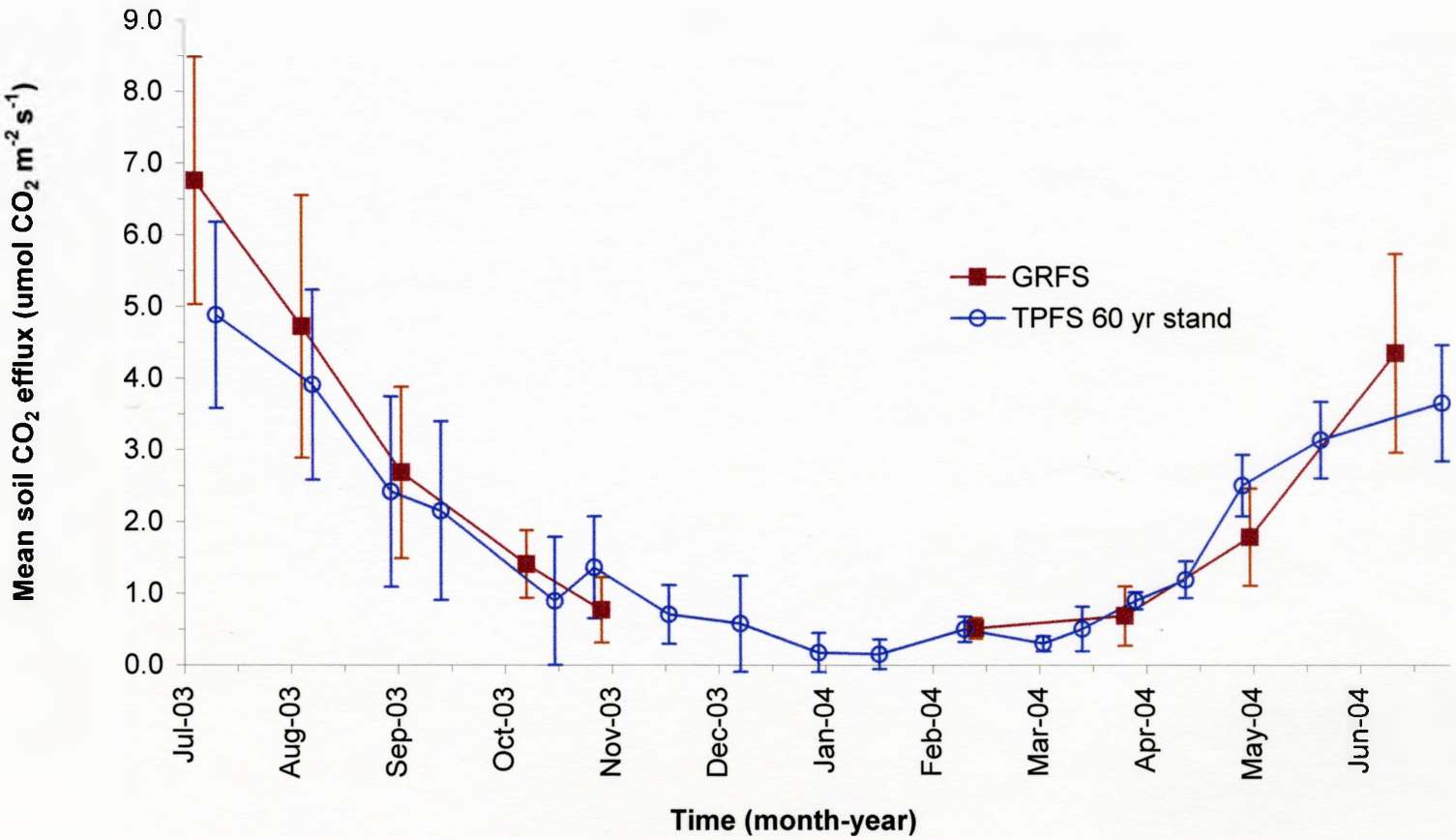


Figure 6.2: Compatison of seasonal trends in soil respiration between boreal GRFS forest and temperate TPFS forest for the period of August 2003 to July 2004. Error bars represent ± 1 standard deviation.

6.3 Comparison of Spatial Variability in Soil Respiration

Spatial variability in soil respiration at both stands was high, and followed the seasonal pattern of mean soil respiration, decreasing in winter and increasing in summer. At the boreal stand, litter C:N ratio had a much stronger correlation to spatial variability in soil respiration than at the temperate stand. However, in both cases the correlation was negative.

The litter-organic soil layer was much thicker at the boreal stand and accounted for most of the soil respiration observed there. Despite this, no correlation was found between the spatial variability of litter-layer depth and soil respiration at either stand. As a result of a cooler overall climate, litter accumulation in the boreal stand occurs at a greater rate compared to temperate forest. The shorter growing seasons prevent soil organisms from decomposing the majority of the litter within a year, causing a greater accumulation of more labile litter that can support higher decomposition activity the following growing season. Thus, the quality of the remaining litter may have greater control on soil decomposers at the boreal stand compared to the temperate one, where the litter layer was relatively small and what was left from the previous year was probably less labile in comparison.

6.4 Comparison of Annual Estimates of Soil CO_2 -emissions

Table 6.1 compares the seasonal CO_2-emissions, from the soils of boreal and temperate forests, over a period of a year (June 2003 to May 2004 for the temperate stand, and August 9, 2003 to August 8, 2004 for the boreal stand).

Table 6.1 Comparison of soil CO_2 - emissions in g of C per m^{-2} yr^{-1} for the year of the study period in temperate and boreal forest stands. The values in brackets indicate % CO_2-emissions relative to total.
Winter = Dec to Mar; Spring = Apr & May; Summer = Jun to Sep; Fall = Oct & Nov

	Boreal (GRFS)		**Temperate (TPFS-60yr)**	
	Exponential model	Moisture-C:N sensitive model	Exponential model	Moisture-C:N sensitive model
Winter	80 (10)	69 (8)	62 (8)	52 (7)
Spring	55 (7)	43 (5)	101 (13)	92 (12)
Summer	528 (70)	604 (74)	528 (66)	576 (71)
Fall	95 (13)	101 (12)	106 (13)	86 (11)
Total	758 (100)	816 (100)	796 (100)	806 (100)

Estimated annual soil CO_2 -emissions between the two forests, in two different climate zones, were surprisingly similar. Maximum emissions occurred during the summer season in both stands. For both stands, their site specific, empirically derived exponential relationships gave the same estimates of summer CO_2 emissions. In contrast, the moisture-C:N ratio sensitive model produced slightly higher soil CO_2-emissions in the boreal forest.

Some differences in emissions do appear, if seasonal fluxes are considered. %-Relative springtime emissions from temperate forest soils were estimated to be almost twice those of the boreal forest stand. However, the boreal stand seemed to make up for

the difference during the summer. Harsher, colder climates in boreal forests reduce the growing seasons and accumulate large amounts of carbon in the litter there. At the same time, the increased temperature sensitivity of decomposition in such regions seems to translate into higher soil respiration during the growing season, which over the course of year will level-off the overall soil CO_2 emissions, making these forests comparable in CO_2 -emissions of cooler temperate forests. However, this conclusion is based on the assumption that modeled estimates were relatively accurate for both stands.

CHAPTER 7: CONCULSIONS AND SUGGESTIONS FOR FUTURE WORK

7.1 Summary and Conclusions

TPFS chronosequence study

The seasonal trend in soil respiration at all four chronosequence sites followed closely the seasonal pattern of soil temperature. Seasonal variability in soil temperature was able to explain 81-96% of seasonal variability in soil respiration through an exponential relationship. The Q_{10} values for the relationship that covered the whole study year were 4.4, 3.6, 4.1 and 2.2 for the 60, 30, 15 and 1 year old stands, respectively. The range of mean soil respirations measured during the study period (June 2003 to May 2004, inclusive) for the four sites was as follows: 4.7, 3.7, 4.8 and 2.6 μmol CO_2 m^{-2} s^{-1} for the 60, 30, 15 and 1 yr stands, respectively.

Spatial variability in soil respiration was observed at all forest stands and followed the seasonal trend of mean soil respiration for each stand. The degree of this spatial variability varied across the chronosequence and with season (3-63 %CV range observed). Some soil nutrients were found to be highly correlated with spatial variability in soil respiration, while litter thickness was not. Spatial variability in soil respiration was also correlated to root density underneath the measurement location. Areas with estimated higher root densities showed higher soil respiration rates.

Soil CO_2 -emissions across the chronosequence were estimated to be from 796 to 806 g of C per m^{-2} yr^{-1} for the 60 year old stand, 608 to 672 g of C per m^{-2} yr^{-1} for the 30 year old stand, 644 to 670 g of C per m^{-2} yr^{-1}, and 508-463 g of C per m^{-2} yr^{-1} at the 1 year old stand.

GRFS study

Seasonal variability in soil respiration at all GRFS also followed closely the seasonal pattern of soil temperature. Seasonal variability in soil temperature was able to explain 95% of seasonal variability in soil respiration through an exponential relationship, with a Q_{10} value of 8.2 when full year's data was considered and a Q_{10} value of 5.0 when data corresponding only temperatures of 0-10°C wasconsidered. The range of mean soil respiration measured during the study period (August 2003 to July 2004) was 6.2 μmol CO_2 m^{-2} s^{-1}.

Spatial variability in soil respiration was observed throughout the year and the degree of this variability was seasonal (4-53% range). Spatial variability of most soil chemical properties failed to correlate well to the spatial variability of soil respiration. Litter-thickness was also unable to explain spatial variability in soil respiration. However, when the litter-organic layer was completely removed, respiration was reduced by 62-84%.

Mean annual soil CO_2 emissions were estimated to be about 758-816 g of C per m^{-2} yr^{-1} for GRFS.

Comparison between Temperate and Boreal Stands

The two stands followed the same general trend in soil respiration over the course of a year with a maximum observed around July/August. The mean rate of soil respiration at the boreal stand was higher by about 2 μmol CO_2 m^{-2} s^{-1} compared to the

temperate stand, during the peak rates in summer. Respiration was observed to increase faster with the onset of warmer temperatures and also decrease faster with the onset of colder winter temperatures at the boreal stand, compared to the temperate one. Total annual soil CO_2 -emissions for the two stands were comparable at around 800 g of C per m^{-2} yr^{-1} for both.

Conclusions

Reflecting back on the results, it was shown that age alone may not be a good predictor of expected soil CO_2-emissions in forest ecosystems. As was observed, due to environmental and physiological differences among forest stands, sometimes a younger stand showed consistently higher and more spatially variable respiration compared to older ones.

Despite having a harsher climate and shorter growing season, soil CO_2-emissions from the boreal forest stand were comparable to soil CO_2-emissions from the temperate stand. The boreal site experienced higher rates of soil respiration at lower soil temperatures, when compared to the temperate forest stand, and the degree of this difference may be seasonal.

7.2 Suggestions for Future work

During this study it was seen that the seasonal trend in soil respiration has many finer details that are difficult, if not impossible, to capture with periodic manual soil respiration measurements. For example, it was observed that rain events or warm-spells

in air temperature can cause short-term spikes in soil CO_2 emissions. Soil respiration during springtime thawing and freezing events are also hard to capture with manual measurements. Yet such details may be very important on yearly scales, in refining estimates of soil CO_2 -emissions and C-budgets of forest ecosystems. One solution to capturing these details is to use automatic soil chambers to continuously monitor soil respiration at the sites in the future. Automatic soil chambers would also allow for direct measurements of annual soil CO_2 emissions, which can then be used to create better soil respiration simulation models for the stands. Nonetheless, manual soil respiration measurements should still be retained in order to capture spatial variability in soil respiration across forest stands.

It would also be interesting to further investigate the sources of soil CO_2 fluxes at the stands, by separating heterotrophic and autotrophic respiration. This may help to better understand the spatial variability of soil respiration and its variation with seasons. A further investigation on the effects of nutrients may also be interesting to pursue, especially to determine any confounding effects of groups of soil chemical properties on soil respiration.

Finally, it would be of interest to continue soil respiration measurements at the stands in order to get an inter-annual comparison. For example, the summer of 2004 looks wetter and cooler compared to 2003, so how will respiration vary during 2004? It would also be interesting to get a dry year (or capture a dry spell) to get a better understanding of moisture's control on soil respiration, especially for the TPFS stands.

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APPENDIX A

LIST OF ABBREVIATIONS USED IN TEXT

(in alphabetical order)

Al - aluminum
ave – average
C - carbon
C:N – carbon to nitrogen ratio
Ca – calcium

CL (%) – confidence level (in %)
CO_2 – carbon dioxide
CV (%) – coefficient of variation (in %)
DBH – diameter at breast height (1.33m)
GRFS – Groundhog River Flux Station
GWC (θ_{GWC}) – gravimetric water content (g/g)
IRGA – Infra red gas analyzer
K – potassium
LI-6400 – Li-COR 6400 portable photosynthesis system with the LI-COR 6400-09 soil chamber attachment, used for soil respiration measurements in this study.
Mg – magnesium
N - nitrogen
Na – sodium
OM – organic matter
P – phosphorus
Rs – soil respiration = soil CO_2 efflux
Tair – air temperature
TOC – total organic carbon
TPFS – Turkey Point Flux Station
Ts, # – soil temperature (at # depth)
VWC (θ_{VWC}) – volumetric water content (cm^3/cm^3)

LIST OF UNITS USED IN TEXT

°C – degree Celsius
cm – centimeter
g – gram
kg - kilograms
m – metre
µmol (umol) – micro moles = 10^{-6} moles
ppm – part per million
Pt – peptogram = 10^{15} grams
s – second

APPENIDIX B

Table 1B: List of parameters used in the moisture-C:N model to simulate C-emissions at TPFS and GRFS site.

Site	*a*	*b*	*c*
60 yr TPFS	18.3	-7.0	0.086
30 yr TPFS	18.3	-6.7	0.077
15 yr TPFS	18.3	-7.0	0.095
1 yr TPFS	-	-7.0	0.05
GRFS	38.5	-3.0	0.16

For all stands C:N ratio of the litter-organic soil layer was used in the model. For the 30 and 15 year old TPFS stands, those ratio's were not available, so the ratio from the 60 year old stand was used. For the 1 year old TPFS stand, the C:N component of the equation was dropped (i.e. C:N=0) since there was no such soil layer at that stand.

APPENDIX C

TABLES 1C to 5C, which follow, list statistics of soil chemical properties and correlation coefficients between those properties and soil respiration measured at different times of the year at each forest stand.

Absolute values of the correlation coefficient (r) above 0.5 were considered to represent a significant correlation. Only soil properties that showed significant correlations more than three times during the year were considered in explaining spatial variability of soil respiration in a stand. The sign of r told what sort of a correlation existed. A positive r value meant that the correlation was positive and that as the nutrient content increased, so did the rate of soil respiration. A negative r-value indicated a negative correlation, whereby if the nutrient concentration increased, then soil respiration decreased. % correlations where calculated by squaring r, to get the coefficient of determination, and multiplying r^2 by 100. Data was analyzed using Microsoft® Excel Spreadsheets Data Analysis Tool Pack.

TABLE C1: List of correlation coefficients between spatial variability in soil respration at the **60 year old TPFS** forest stand and spatial variability of soil chemical properties. The table also includes average values of the chemicals and their standard deviation.

	Litter		Mineral soil (0-20 cm)							Mineral soil (21-35 cm)						
	C:N	TOM (%)	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm
Mean value along the transect	18.3	9.2	1.3	139	12	10	109	5.5	1716	0.8	127	7	8	86	5.6	1749
St Dev	4.8	7.4	0.3	18	5	3	28	0.4	69	0.3	35	4	4	27	0.3	82
Measurement Date	**Correlation Coefficients**															
26-Jun-03	-0.28	0.00	-0.14	0.18	-0.25	0.34	0.61	-0.10	-0.61	0.33	0.48	0.07	-0.06	0.19	-0.08	-0.19
18-Jul-03	-0.19	0.30	-0.28	0.29	-0.17	0.31	0.55	-0.20	-0.66	0.24	0.62	0.15	-0.02	0.15	0.03	-0.25
6-Aug-03	-0.22	0.08	-0.02	0.23	-0.10	0.53	0.44	-0.15	-0.39	0.29	0.49	0.07	0.20	0.23	-0.09	-0.02
2-Sep-03	-0.34	-0.03	0.10	0.19	0.00	0.51	0.38	-0.17	-0.23	0.30	0.43	0.09	0.25	0.14	-0.16	0.10
24-Sep-03	-0.34	-0.02	0.09	0.19	-0.03	0.49	0.45	-0.19	-0.29	0.34	0.44	0.08	0.26	0.20	-0.12	0.06
8-Oct-03	-0.39	-0.12	0.13	0.17	-0.11	0.46	0.35	-0.12	-0.27	0.33	0.42	0.04	0.24	0.20	-0.20	0.08
9-Nov-03	-0.38	0.00	0.02	0.20	-0.05	0.52	0.37	-0.18	-0.31	0.27	0.49	0.09	0.20	0.08	-0.14	0.04
20-Nov-03	-0.34	-0.08	0.11	0.05	-0.02	0.38	0.20	-0.07	-0.04	0.14	0.30	0.00	0.16	-0.08	-0.26	0.23
11-Dec-03	-0.37	-0.05	0.05	0.19	-0.02	0.52	0.36	-0.13	-0.23	0.25	0.45	0.10	0.22	0.08	-0.15	0.07
31-Dec-03	-0.36	0.04	-0.02	0.23	-0.03	0.50	0.34	-0.12	-0.26	0.24	0.51	0.15	0.28	0.08	-0.07	0.07
25-Mar-04	-0.35	-0.19	0.28	0.09	0.04	0.47	0.00	-0.12	0.01	0.15	0.23	-0.05	0.01	-0.20	-0.46	0.35
5-Apr-04	-0.41	-0.21	0.16	0.18	-0.01	0.55	0.26	-0.04	-0.12	0.27	0.34	0.11	0.22	0.03	-0.22	0.21
20-Apr-04	-0.40	-0.01	0.11	0.22	0.02	0.55	0.40	-0.23	-0.33	0.37	0.47	0.13	0.15	0.03	-0.22	0.17
4-May-04	-0.33	-0.11	0.01	0.11	-0.12	0.52	0.31	0.00	-0.25	0.27	0.37	0.11	0.24	0.08	-0.12	0.14
20-May-04	-0.33	-0.04	0.03	0.20	-0.13	0.53	0.44	-0.12	-0.37	0.32	0.46	0.06	0.19	0.19	-0.14	0.02
11-Jun-04	-0.15	0.09	0.16	0.23	-0.06	0.49	0.33	-0.31	-0.34	0.26	0.42	-0.09	0.09	0.26	-0.27	-0.02

TABLE C2: List of correlation coefficients between spatial variability in soil respration at the **30 year old TPFS** forest stand and spatial variability of soil chemical properties. The table also includes average values of the chemicals and their standard deviation.

	Mineral soil (0-20 cm)							Mineral soil (21-35 cm)						
	OM	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm	OM	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm
Mean value along the transect	1.1	117	10	13	153	5.5	1633	0.4	106	6	6	78	5.5	1507
St Dev	0.3	21	3	6	107	0.3	299	0.3	23	2	2	15	0.3	356
Measurement Date	**Correlation Coefficients**													
26-Jun-03	0.94	-0.86	0.35	0.32	0.45	-0.01	0.29	0.22	0.57	-0.31	-0.16	0.51	0.34	0.40
18-Jul-03	0.76	-0.96	0.18	0.00	-0.07	-0.18	0.20	0.25	0.24	-0.40	-0.09	0.40	0.34	0.35
6-Aug-03	0.66	-0.85	0.11	0.05	0.02	0.09	0.13	0.27	0.35	-0.12	-0.09	0.41	0.19	0.37
2-Sep-03	0.70	-0.89	0.07	-0.03	-0.04	-0.05	0.22	0.32	0.32	-0.27	-0.15	0.39	0.20	0.43
24-Sep-03	0.30	-0.35	-0.29	-0.14	0.09	0.33	0.19	0.50	0.41	0.17	-0.28	0.30	-0.28	0.53
8-Oct-03	0.16	-0.17	-0.39	-0.16	0.13	0.37	0.23	0.48	0.45	0.23	-0.35	0.19	-0.43	0.54
9-Nov-03	0.26	-0.40	-0.15	-0.03	0.03	0.32	0.08	0.26	0.37	0.20	-0.16	0.20	-0.17	0.36
20-Nov-03	0.74	-0.91	0.15	0.07	0.05	0.05	0.15	0.28	0.36	-0.18	-0.09	0.45	0.25	0.39
11-Dec-03	0.83	-0.70	0.09	0.29	0.60	0.27	0.40	0.37	0.86	-0.06	-0.37	0.45	-0.04	0.62
31-Dec-03	0.93	-0.75	0.28	0.42	0.68	0.34	0.25	0.32	0.78	0.01	-0.20	0.62	0.17	0.50
25-Mar-04	0.91	-0.85	0.26	0.30	0.45	0.35	0.11	0.38	0.58	0.04	-0.07	0.71	0.26	0.46
5-Apr-04	0.21	-0.21	-0.54	-0.62	-0.27	-0.07	0.30	0.87	-0.07	-0.21	-0.33	0.38	-0.29	0.64
20-Apr-04	0.12	-0.46	-0.11	-0.08	-0.26	-0.32	0.35	-0.18	0.33	-0.35	-0.33	-0.39	-0.14	0.19
4-May-04	0.22	-0.34	0.01	0.25	0.24	0.40	0.06	-0.05	0.58	0.31	-0.15	0.02	-0.16	0.21
20-May-04	-0.51	0.35	-0.45	-0.24	-0.23	0.20	0.03	-0.01	0.06	0.31	-0.19	-0.40	-0.53	0.07
11-Jun-04	0.29	-0.57	-0.02	-0.13	-0.27	0.10	-0.07	0.20	0.01	0.02	0.05	0.26	0.12	0.18

TABLE C3: List of correlation coefficients between spatial variability in soil respration at the **15 year old TPFS** forest stand and spatial variability of soil chemical properties. The table also includes average values of the chemicals and their standard deviation.

	Mineral soil (0-20 cm)							Mineral soil (21-35 cm)						
	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm
Mean value along the transect	2.0	188	32	33	827	6.1	1422	1.3	117	14	18	557	6.2	1430
St Dev	0.3	56	18	34	994	1.0	335	0.5	60	4	19	711	1.0	411
Measurement Date	**Correlation Coefficients**													
6-Aug-03	0.49	-0.07	0.37	0.30	0.31	0.12	-0.45	-0.19	-0.52	0.42	0.33	0.25	0.24	-0.48
2-Sep-03	0.10	0.24	0.12	-0.12	-0.11	-0.30	-0.06	-0.32	-0.36	0.52	-0.08	-0.16	-0.18	-0.12
24-Sep-03	-0.18	0.56	0.14	-0.37	-0.39	-0.56	0.26	-0.36	-0.08	0.69	-0.36	-0.31	-0.41	0.23
8-Oct-03	-0.20	0.59	0.09	-0.39	-0.41	-0.57	0.28	-0.27	-0.03	0.70	-0.38	-0.34	-0.43	0.22
9-Nov-03	-0.48	0.82	0.07	-0.59	-0.65	-0.76	0.56	-0.28	0.30	0.82	-0.62	-0.46	-0.61	0.50
20-Nov-03	-0.29	0.63	0.10	-0.46	-0.50	-0.65	0.36	-0.40	0.01	0.73	-0.46	-0.39	-0.50	0.32
11-Dec-03	-0.22	0.49	0.07	-0.41	-0.43	-0.59	0.25	-0.48	-0.13	0.65	-0.39	-0.38	-0.46	0.20
31-Dec-03	-0.33	0.64	0.09	-0.48	-0.52	-0.67	0.37	-0.41	0.04	0.74	-0.49	-0.41	-0.52	0.33
25-Mar-04	-0.63	0.10	-0.37	-0.57	-0.59	-0.50	0.44	-0.63	0.15	-0.10	-0.58	-0.57	-0.58	0.46
5-Apr-04	-0.20	0.71	0.41	-0.29	-0.39	-0.52	0.33	-0.29	0.20	0.85	-0.34	-0.13	-0.31	0.35
20-Apr-04	0.15	0.37	0.58	0.04	-0.06	-0.21	-0.06	-0.39	-0.12	0.77	0.00	0.15	0.00	-0.02
4-May-04	0.02	0.43	0.38	-0.11	-0.18	-0.34	0.03	-0.34	-0.10	0.78	-0.13	-0.04	-0.16	0.00
20-May-04	0.13	0.38	0.35	-0.04	-0.07	-0.25	-0.03	-0.20	-0.17	0.69	-0.04	0.01	-0.08	-0.07
11-Jun-04	0.36	0.11	0.47	0.20	0.16	-0.02	-0.30	-0.28	-0.38	0.58	0.20	0.21	0.15	-0.30

TABLE C4: List of correlation coefficients between spatial variability in soil respration at the **1 year old TPFS** forest stand and spatial variability of soil chemical properties. The table also includes average values of the chemicals and their standard deviation.

	Mineral soil (0-20 cm)						
	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm
Mean value along the transect	0.8	169	48	44	1669	7.4	0.5
St Dev	0.2	82	18	5	753	0.4	0.1
Measurement Date	**Correlation Coefficients**						
26-Jun-03	0.57	0.58	0.73	0.02	-0.72	-0.65	0.67
18-Jul-03	0.57	0.39	0.66	0.09	-0.49	-0.77	0.49
6-Aug-03	0.80	0.68	0.85	0.03	-0.73	-0.92	0.75
2-Sep-03	0.78	0.60	0.67	0.47	-0.43	-0.93	0.61
24-Sep-03	0.22	0.37	0.32	0.50	-0.31	-0.14	0.33
8-Oct-03	-0.15	-0.27	-0.09	0.35	0.27	-0.05	-0.25
9-Nov-03	0.50	0.35	0.58	0.49	-0.32	-0.63	0.39
20-Nov-03	0.16	0.18	0.10	0.65	0.03	-0.06	0.08
11-Dec-03	-0.05	-0.12	-0.38	0.31	0.48	0.16	-0.25
31-Dec-03	0.14	0.43	0.38	-0.45	-0.72	-0.11	0.51
25-Mar-04	0.54	0.44	0.79	0.12	-0.62	-0.58	0.51
5-Apr-04	-0.22	-0.34	-0.38	0.74	0.66	0.33	-0.48
20-Apr-04	0.70	0.48	0.70	0.82	-0.26	-0.58	0.41
4-May-04	0.92	0.95	0.88	0.15	-0.88	-0.91	0.96
20-May-04	0.47	0.49	0.56	0.05	-0.57	-0.62	0.58
11-Jun-04	0.66	0.64	0.77	-0.19	-0.81	-0.82	0.75

TABLE C5: List of correlation coefficients between spatial variability in soil respration at the **GRFS** forest stand and spatial variability of soil chemical properties. The table also includes average values of the chemicals and their standard deviation.

	Litter		Mineral soil (0-20 cm)							Mineral soil (21-35 cm)							Mineral soil (21-35 cm)							
	C:N	TOM (%)	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm	OM (%)	P ppm	K ppm	Mg ppm	Ca ppm	pH	Al ppm	Na ppm
Mean value along the transect	38.5	72	1.3	7	23	126	534	6.2	664	0.6	7	20	143	611	7.2	674	0.4	5	24	297	1170	7.7	574	8
St Dev	15.7	14	0.5	3	5	5	230	1.4	163	0.2	2	3	51	229	0.6	57	0.2	1	3	149	604	0.5	66	1
Measurement Date	**Correlation Coefficients**																							
31-Jul-03	-0.50	-0.42	-0.14	0.52	0.36	-0.28	0.02	0.14	0.22	-0.13	-0.31	-0.62	-0.53	-0.14	-0.16	0.01	0.37	0.14	0.39	0.19	0.23	0.22	-0.14	0.75
30-Aug-03	-0.48	-0.74	-0.15	0.48	0.24	-0.16	-0.01	0.19	0.17	-0.37	-0.10	-0.46	-0.64	-0.49	-0.11	-0.21	-0.09	-0.24	-0.05	0.14	-0.14	-0.02	-0.11	0.61
27-Sep-03	-0.50	-0.38	-0.25	0.13	0.18	0.15	0.24	0.30	-0.20	-0.15	-0.09	0.02	-0.23	-0.06	0.16	-0.33	0.22	0.04	0.15	0.44	0.16	0.23	-0.53	0.60
1-Nov-03	-0.57	-0.56	-0.31	0.26	0.44	0.13	0.09	0.31	-0.10	-0.20	-0.19	-0.04	-0.20	-0.03	0.25	-0.30	0.33	0.13	0.24	0.46	0.18	0.38	-0.48	0.76
22-Nov-03	-0.52	-0.82	-0.04	0.50	0.51	-0.10	-0.10	0.10	0.25	-0.26	0.13	-0.24	-0.51	-0.36	0.02	-0.24	0.00	0.02	-0.04	0.12	-0.18	0.04	-0.08	0.68