

Soil surface CO₂ flux increases with successional time in a fire scar chronosequence of Canadian boreal jack pine forest

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Abstract. To fully understand the carbon (C) cycle impacts of forest fires, both C emissions during the fire and post-disturbance fluxes need to be considered. The latter are dominated by soil surface CO₂ flux (F_s), which is still subject to large uncertainties. Fire is generally regarded as the most important factor influencing succession in the boreal forest biome and fire dependant species such as jack pine are widespread. In May 2007, we took concurrent F_s and soil temperature (T_s) measurements in boreal jack pine fire scars aged between 0 and 59 years since fire. To allow comparisons between scars, we adjusted F_s for T_s (F_s^T) using a Q_{10} of 2. Mean F_s^T ranged from 0.56 (± 0.30 sd) to 1.94 (± 0.74 sd) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Our results indicate a difference in mean F_s^T between recently burned (4 to 8 days post fire) and non-burned mature (59 years since fire) forest ($P < 0.001$), though no difference was detected between recently burned (4 to 8 days post fire) and non-burned young (16 years since fire) forest ($P = 0.785$). There was a difference in mean F_s^T between previously young (16 years since fire) and intermediate aged (32 years since fire) scars that were both subject to fire in 2007 ($P < 0.001$). However, there was no difference in mean F_s^T between mature (59 years since fire) and intermediate aged (32 years since fire) scars that were both subjected to fire in 2007 ($P = 0.226$). Furthermore, there was no difference in mean F_s^T between mature (59 years since fire) and young scars (16 years since fire)

that were both subjected to fire in 2007 ($P = 0.186$). There was an increase in F_s^T with time since fire for the chronosequence 0, 16 and 59 years post fire ($P < 0.001$). Our results lead us to hypothesise that the autotrophic: heterotrophic soil respiration ratio increases over post-fire successional time in boreal jack pine systems, though this should be explored in future research. The results of this study contribute to a better quantitative understanding of F_s in boreal jack pine fire scars and will facilitate meta-analyses of F_s in fire scar chronosequences.

1 Introduction

Forest ecosystems sequester, store and release carbon (C) and have an integral role in the global C balance (Bonan, 2008). Boreal forests contain almost half of the C stored in forest ecosystems (Preston et al., 2006) and of the 3150 Pg C believed to be contained in the Earth's soils (Sabine et al., 2003), several hundred Pg are thought to reside in boreal systems (Goulden et al., 1998; Hobbie et al., 2000). The boreal forest biome is likely to be especially affected by climate change and average atmospheric temperatures may increase by 4 to 6 °C in the next 50 to 100 years (IPCC 2007). This has led to the suggestion that changes in boreal forest soil C storage, in particular through increased soil surface CO₂ flux (F_s), could significantly alter the global soil C balance (Cox et al., 2000).



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F_s is the second largest flux in the global terrestrial C cycle (Law et al., 1997; Janssens et al., 2001; Davidson et al., 2002; Milyukova et al., 2002; Yim et al., 2002; Hubbard et al., 2005). Soil CO₂ production occurs via respiring plant roots and associated mycorrhizal fungi (autotrophic component) and microorganisms and soil animals (heterotrophic component) (Ryan and Law, 2005). Principal factors controlling F_s include soil organic C (Franzluebbers et al., 2001), density of fine plant roots (Shibistova et al., 2002), soil temperature (T_s) (Lloyd and Taylor, 1994) and soil moisture (M_s) (Xu et al., 2004). F_s influences nutrient cycling (Zak et al., 1993), C balance at the ecosystem scale (Curtis et al., 2005) and can cause C cycle feedbacks to the climate system (Cox et al., 2000). Globally F_s produces 75 to 120 Pg CO₂-C yr⁻¹, 11 to 20 times that produced by the combustion of fossil fuels (Hibbard et al., 2005). There has been a substantial amount of F_s research over the last decade, though it remains one of the least understood processes in ecosystem ecology (Luo and Zhou, 2006).

Fire is regarded as the most significant natural factor controlling succession in the boreal forest biome (Zackrisson, 1977; Stocks, 1991; Kasischke and Stocks, 2000; Amiro et al., 2001; Wang et al., 2001; Stocks et al., 2002; Bond-Lamberty et al., 2004) and fire adapted species such as jack pine (*Pinus banksiana* Lamb.), which relies on the heat of fire to open their serotinous cones, are widespread. High population densities and combustible foliage render jack pine systems prone to fire (Yermakov and Rothstein, 2006). There have been few studies into the effect of fire on F_s in boreal jack pine systems. Comparisons between burned and non-burned jack pine forest have found a reduction in F_s due to fire (Burke et al., 1997) or no significant differences (Euskirchen et al., 2003). In recent studies of jack pine fire scar chronosequences, F_s has shown no clear pattern with stand age (Yermakov and Rothstein, 2006; Singh et al., 2008). However, to date, there has been no study into the immediate effect of fire on F_s in jack pine systems. The present study tests the null hypothesis (H_0) that there is no change in F_s over post-fire successional time in boreal jack pine ecosystems.

2 Materials and methods

2.1 Field site

Between 17 and 21 May 2007 (early growing season), an intensive field campaign was carried out at Sharpsand Creek (latitude 46°47' N, longitude 83°20' W) located approximately 60 km North of Thessalon, Ontario, Canada. Since the mid- 1970's, numerous prescribed burns have been carried out on forest plots (0.4 to >3 ha) at Sharpsand Creek. Further data from prescribed burns, e.g. fire weather index system components and fuel consumption are provided in Stocks (1987). Sharpsand Creek is dominated by jack pine,

and the availability of replicate, different aged fire scars at similar geographic location minimizes the effect of confounding variables that may influence F_s measurements.

The Sharpsand Creek area experiences short, warm summers and long, cold winters, with mean daily atmospheric temperatures of 16°C and -17°C in July and January respectively (Stocks, 1987). Mean annual precipitation is 760 mm, of which approximately one third falls as snow (Stocks, 1987). The growing season has a mean annual length of 162 days, beginning early May and ending mid-October (Stocks, 1987). The site is located on level ground (Stocks, 1987) above a granite substratum. Soils in the area are nutrient-poor petawawa outwash sands (humo-ferric podzols) that have high water-washed boulder contents due to their glacio-fluvial origin.

On 13 May 2007, a prescribed burn was carried out at Sharpsand Creek. An unprecedented number of spot fires and fire whirl behaviour caused the fire to escape from the plot and burn through large areas of the field site. This event allowed us to take measurements of F_s on recently burned fire scars of different ages, as well as from areas the fire did not affect. We selected five fire scar age categories named on the basis of: (1) time since last fire (excluding 2007 burn); and (2) whether they were burnt (B) or not burnt (NB) in 2007. Our categories are therefore: 16B, 16NB, 32B, 59B and 59NB. For example, "16B" represents fire scars that were burnt in 1991 and 2007; 59NB represents a fire scar that was last burnt in 1948 and not subjected to the 2007 fire. For the B categories, we were able to use three replicate fire scars, but for each of the NB categories, there was only one scar available due to the extent of the 2007 burn. Excluding the 2007 fire, scars from the 16 and 32 age categories were last subject to prescribed burns in 1991 and 1975 respectively; and the 59 category subject to wildfire in 1948 (Stocks and Walker, 1973). It is believed that previous wildfires occurred in the Sharpsand Creek area in 1850, 1880, 1901 and 1919 (Stocks, 1987). The fire scar age categories 32B, 16NB and 59NB were chosen to represent the chronosequence 0, 16 and 59 years since fire respectively. 32B was chosen to represent 0 years, since the burn history more closely matched those of the other scar age categories (32B, 0 years since most recent fire, burnt 32 years previously; 16NB, 16 years since fire, burnt 43 years previously; 59NB, 59 years since fire, burnt 29 years previously).

2.2 Instruments

F_s point measurements were made at Sharpsand Creek with the PP Systems (Hitchin, Hertfordshire, UK) portable soil respiration system which consists of a cylindrical chamber (SRC-1: height = 15 cm; diameter = 10 cm; ground surface area = 78 cm²) connected to an infra-red gas analyser (IRGA), the CIRAS-1 (PP Systems 2003). CIRAS-1 has an absolute precision for CO₂ measurements of 0.2 μmol mol⁻¹ at 0 ppm and 0.7 μmol mol⁻¹ at 2000 ppm as well as

a linearity >1% throughout the measurement range 0 to 9999 $\mu\text{mol mol}^{-1}$ (PP Systems 2003). In CIRAS-1, the measured change in CO₂ concentration (DC; units ppm) and elapsed time (DT; units s) are used in the calculation of F_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). T_s was measured with a Cole Parmer temperature probe (at 2 cm depth) and M_s with a Delta T Theta probe (0 to 6 cm depth).

2.3 Experimental design

All field measurements were made during the growing season at Sharpsand Creek, from areas considered representative of each fire scar (in terms of dominant vegetation cover). At each fire scar, three parallel 10 m line transects were set up (spaced 5 m apart) and PVC soil collars (diameter = 10.1 cm; height = 5 cm) placed at 0, 5 and 10 m along each transect. An additional soil collar was placed randomly within the 10 × 10 m area, making a total of ten soil collars per fire scar. A similar transect type method has been used previously (Striegl and Wickland, 2001). Soil collars were inserted into the soil (2 to 3 cm depth) at least 12 h prior to measuring F_s (Wang et al., 2005) in order to minimize soil disturbance at the time of measurement (Luo and Zhou, 2006). Soil collars represented the sampling points for F_s measurements within each fire scar. Since we wanted to compare F_s from non-burnt and recently burnt scars (where the soil surface was bare), in non-burnt scars live and dead soil surface vegetation was removed at the time of collar insertion (e.g. litter removed; moss layer peeled back; grasses clipped) in order to minimise above ground F_s .

F_s measurements were taken in the daytime between 09:00 and 18:00 hours using a single CIRAS-1. The F_s chamber was placed onto each soil collar immediately prior to taking F_s measurements and removed thereafter. CIRAS-1 records CO₂ build-up in the chamber until either: (1) DC = 50 ppm; or (2) DT = 120 s. Consequently, the chamber remained on the ground at most two minutes. Single T_s (at 2 cm depth) and M_s (0 to 6 cm depth) measurements were made concurrently with F_s . Voltage (V) output from the Theta probe was converted to volumetric M_s ($\text{m}^3 \text{ m}^{-3}$) as described in Delta-T (1999):

$$M_s = \frac{1.1 + (4.44 \cdot V) - a_0}{a_1} \quad (1)$$

where $a_0 = 1.3$ and $a_1 = 7.7$ (both dimensionless parameters).

2.4 Soil surface CO₂ flux adjustments for soil temperature

F_s is commonly assumed to be exponentially dependant on T_s (Luo and Zhou, 2006), and this temperature dependence is frequently modelled using:

$$f(T_s) = Q_{10}^{\wedge} \left(\frac{T_s - T_0}{10} \right) \quad (2)$$

Table 1. Descriptive statistics of soil surface CO₂ flux data obtained from five fire scar age categories at Sharpsand Creek.

Scar age category	N	Mean F_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Mean F_s^T ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
59B	26	0.79 (0.39)	0.79 (0.40)
59NB	9	1.62 (0.63)	1.94 (0.74)
32B	26	0.72 (0.57)	0.56 (0.30)
16B	27	2.07 (0.77)	1.01 (0.35)
16NB	10	0.91 (0.38)	0.85 (0.43)

F_s – soil surface CO₂ flux; F_s^T – soil surface CO₂ flux adjusted for soil temperature assuming $Q_{10} = 2$ (dimensionless) and reference soil temperature = 10 °C; N – sample size; values in parenthesis represent one standard deviation of the mean.

where T_s is soil temperature (°C); Q_{10} (dimensionless) is the factorial increase in F_s for every 10° C rise in T_s and T_0 is a reference soil temperature (°C) (Campbell and Law, 2005).

In order to compare F_s across sites we therefore needed to account for the different soil temperatures because we measured at different locations, different times throughout the day and different days.

All F_s measurements were adjusted for T_s (F_s^T) using:

$$F_s^T = \frac{F_s}{Q_{10}^{\wedge} \left(\frac{T_s - T_0}{10} \right)} \quad (3)$$

where $Q_{10} = 2$ and $T_0 = 10^\circ\text{C}$. We report both F_s and F_s^T in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

2.5 Statistical analyses

Statistical analyses were performed in Microsoft Excel, Genstat and SPSS. We analyzed the square root of F_s^T ($\sqrt{F_s^T}$) since raw data did not conform to the assumptions of General Linear Models (non-homogenous variances and/or non-normality of residuals). Potential influences on $\sqrt{F_s^T}$ were evaluated in a General Linear Model (backwards stepwise analysis of covariance (ANCOVA)) (Quinn and Keough 2002), initially containing fire scar age category, M_s , and their interaction as explanatory variables. In order to arrive at the most parsimonious model, explanatory variables were removed by deletion tests where $P > 0.05$; those at $P \leq 0.05$ were retained in the model. Model checking plots in Genstat supported the assumptions of normally distributed residuals and homogeneity of variances, the latter also checked by Levene's test: ($F_{4,93} = 1.489$; $P = 0.212$). We used the Tukey Honestly Significant Difference (HSD) test to compare mean $\sqrt{F_s^T}$ between fire scar age categories. We set $\alpha = 0.05$, i.e. $P \leq 0.05$ was considered significant. We report degrees of freedom values from our statistical analyses in subscript after each test statistic.

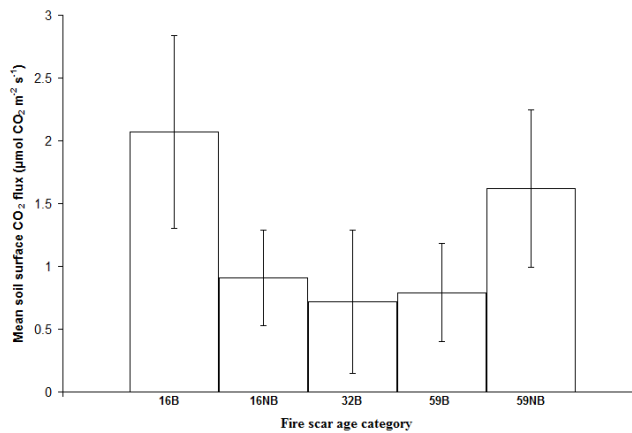


Fig. 1. Mean soil surface CO₂ flux for the five fire scar age categories at Sharpsand Creek. Error bars represent ± 1 standard deviation of the mean.

3 Results

We analyzed a total of 98 F_s values (59B: N= 26; 59NB: N = 9; 32B: N = 26; 16B: N = 27; 16NB: N = 10) from which we calculated means and standard deviations (sd) (Table 1). Mean F_s values varied between 0.72 ± 0.57 sd $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (32B) and 2.07 ± 0.77 sd $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (16B) (Table 1; Fig. 1). These raw F_s data, that have not been corrected for the effects of T_s , are provided to enable comparisons with published data. Rather, it is F_s data that have been corrected for T_s (F_s^T) that was used to make comparisons between fire scars in our study. ANCOVA suggested there was no effect of either an M_s * scar age category interaction ($F_{4,88} = 0.80$; $P = 0.527$) or M_s ($F_{1,88} = 0.73$; $P = 0.396$) on $\sqrt{(F_s^T)}$. Therefore, we did not adjust our F_s measurements for M_s . F_s^T varied between 0.56 ± 0.30 sd $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (32B) and 1.94 ± 0.74 sd $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (59NB) (Table 1; Fig. 2). ANCOVA did however suggest there was an effect of scar age category on $\sqrt{(F_s^T)}$: ($F_{4,88} = 10.27$; $P < 0.001$). Post-hoc Tukey Honestly Significant Difference tests revealed there was a difference in mean $\sqrt{(F_s^T)}$ for: 59NB vs. 59B: ($P < 0.001$); 59NB vs. 32B: ($P < 0.001$); 59NB vs. 16NB: ($P < 0.001$); 59NB vs. 16B: ($P < 0.001$) and 32B vs. 16B: ($P < 0.001$), but not 59B vs. 32B: ($P = 0.226$); 59B vs. 16NB: ($P = 0.988$); 59B vs. 16B: ($P = 0.186$); 32B vs. 16NB: ($P = 0.244$) and 16NB vs. 16B: ($P = 0.785$) (see also Fig. 2).

Our results indicate a difference in mean $\sqrt{(F_s^T)}$ between recently burned (4 to 8 days post fire) and non-burned mature (59 years since fire) forest ($P < 0.001$), though no difference was detected between recently burned and non-burned young (16 years since fire) forest ($P = 0.785$). There was a difference in mean $\sqrt{(F_s^T)}$ between previously young (16 years since fire) and intermediate aged (32 years since fire) scars that were both subject to fire in 2007 ($P < 0.001$).

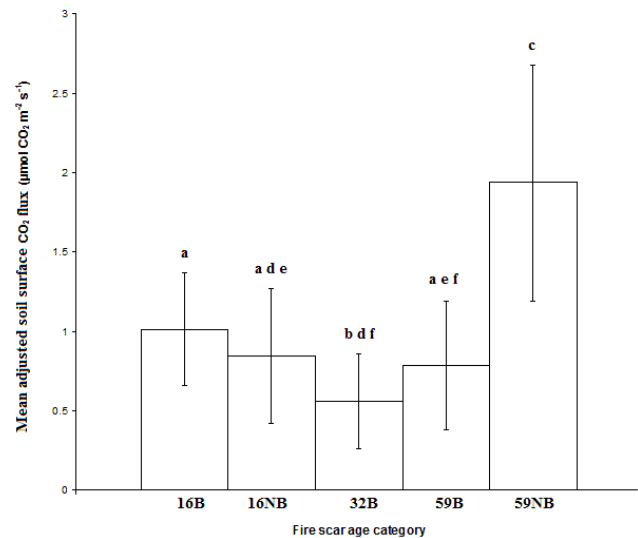


Fig. 2. Mean soil surface CO₂ flux adjusted for soil temperature for the five fire scar age categories at Sharpsand Creek. Soil temperature adjustment assumes $Q_{10} = 2$ (dimensionless) and reference soil temperature = 10°C. Error bars represent ± 1 standard deviation of the mean. Different letters indicate differences at $P \leq 0.05$.

However, there was no difference in mean $\sqrt{(F_s^T)}$ between mature (59 years since fire) and intermediate aged (32 years since fire) scars that were both subjected to fire in 2007 ($P = 0.226$). Furthermore, there was no difference in mean $\sqrt{(F_s^T)}$ between mature (59 years since fire) and young scars (16 years since fire) that were both subjected to fire in 2007 ($P = 0.186$).

Based on all 44 measurements from the fire scars 32B, 16NB and 59NB there was a linear increase in $\sqrt{(F_s^T)}$ over the chronosequence 0, 16 and 59 years since fire (linear regression: $F_{1,43} = 52.18$; $P < 0.001$) (see also Fig. 3).

4 Discussion

F_s and F_s^T values reported herein are within the range reported in the literature for jack pine systems (0.35 to $7.20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Burke et al., 1997; Savage et al., 1997; Euskirchen et al., 2003). The results of this study also agree with the literature in that the majority of studies have demonstrated a reduction or no change in F_s following fire (Weber, 1985; Burke et al., 1997; Singh et al., 2008).

Burning had an immediate effect of decreasing F_s^T in mature (59 years old) jack pine stands. However, burning did not seem to reduce F_s^T from young (16 years old) jack pine stands. The absence of a 32NB category prevents firmer conclusions into the effect of fire on F_s in 32 year old jack pine systems. The difference in mean F_s^T between 32B and 16B, however, provides evidence that differences can be maintained between different aged fire scars beyond being subjected to the same fire. This means that jack pine stands may

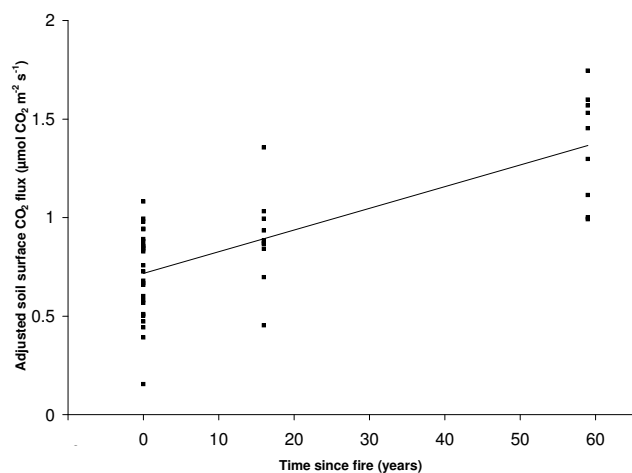


Fig. 3. Adjusted soil surface CO₂ flux versus time since fire at Sharsand Creek. Individual data points represent $\sqrt{(F_s^T)}$ (Sect. 2.4–2.5) assuming $Q_{10} = 2$ (dimensionless) and reference soil temperature = 10°C. Regression equation: $y = 0.011x + 0.7168$; $r^2 = 0.55$.

retain legacies of pre-fire conditions after fires. We think that further work exploring the impacts of fires with different severity on belowground C dynamics would be very important. The decrease of F_s after fire in the 59 year old stands could be the result of fire related damage to roots and mycorrhizae and thus strongly suppressed autotrophic soil respiration (Wang et al., 2002; Yermakov and Rothstein, 2006). Though fire may suppress autotrophic soil respiration in the younger scars as well, an increase in heterotrophic soil respiration as a result of fire (Pregitzer and Euskirchen, 2004; Yermakov and Rothstein, 2006) could mask this effect and account for no overall change in F_s in young scars. The autotrophic: heterotrophic soil respiration ratio may thus be smaller in younger jack pine systems. Although heterotrophic soil respiration may also increase as a result of fire in older jack pine systems, a larger autotrophic: heterotrophic soil respiration ratio could mean any fire stimulated increase in heterotrophic soil respiration is insufficient to mask the reduction in autotrophic soil respiration caused by damage to roots. Indeed, absence of a difference in mean F_s^T between 59B and 16B, but presence of a difference between 59NB and 16NB is further evidence that fire suppresses F_s in older, but not younger jack pine systems. Fire induced reduction in F_s in the older scars could explain the absence of differences in mean F_s^T after fire.

This research is the first to report an increase in F_s^T over post-fire successional time in jack pine systems over the chronosequence 0, 16 and 59 years since fire. Our measurements are unique in that we include conditions right after the fire. Also, we are able to control somewhat for the conditions before the fire in that we chose stands that were recovering for similar periods of time from the previous fire (see Sect. 2.1). Although Yermakov and Rothstein (2006)

found no clear pattern for growing season F_s with stand age of a 72 year old jack pine wildfire chronosequence, our results are in agreement with Weber (1985) who found greater F_s^T in older compared to younger scars in his study of jack pine ecosystems (63 years since fire > 21 years since fire; 63 years since fire > 6 years since fire; 20 years since fire > 6 years since fire, Weber, 1985). Singh et al. (2008) also found that their youngest site generally had lower F_s in a jack pine fire scar chronosequence (6 to 7 years since fire; 15 to 16 years since fire; 27 to 28 years since fire), but although F_s was greater in 16 year old vs. 7 year old scars, F_s in 16 year old scars was greater than that in 28 year old scars (Singh et al., 2008). The increase of F_s with time since fire can be explained again with increasing contribution from autotrophic soil respiration as the root and mycorrhizal system recovers from disturbance. This is consistent with the above discussion of the decrease in F_s after fire in stands of different ages.

We suggest here that it is largely the differences and changes in autotrophic soil respiration that explain our observations. Indeed, in particular when comparing before and after fire F_s^T it is difficult to understand why a difference based on heterotrophic soil respiration between stands should not persist beyond the fire (note that we measure F_s proper and have excluded litter respiration). Since F_s measurements were made at different times of the day, and over a number of days, we needed to adjust for T_s to make our measurements comparable. We chose to adjust the measurements using a Q_{10} approach where $Q_{10} = 2$. The concept of the Q_{10} for comparing field measurements of F_s across ecosystems and time periods has recently been criticized (Davidson and Jansens 2006, Davidson et al., 2006). The criticism includes that there may be confounding effects of plant phenology on soil respiration, the calculated Q_{10} may differ with the depth where the T_s has been measured, and the calculated Q_{10} frequently depends on the composition of the decomposing material. None of these issues applies to our study, however. All our measurements have been made during a short period of time in the same ecosystem suggesting that there is no significant influence from phenological differences or different compositions of the respiring pools. Also, all our soil temperature measurements have been made at the same depth. Overall we think that using a Q_{10} approach is a valid way to model the effects of soil temperature differences on our F_s measurements because of the specific experimental design.

Future work in separating the source components of soil respiration in jack pine post fire chronosequences will provide more insight into ecosystem physiological response to fire and post fire successional changes. Although over our range of F_s measurements, M_s did not appear to be a significant driver of F_s , the F_s vs. M_s response should be investigated further in individual scar age categories. It is thought that M_s may suppress F_s at low and high M_s levels (Xu et al., 2004) though the M_s response of F_s is still subject to uncertainty (Luo and Zhou, 2006) and is itself an area for further work. In addition, F_s can vary temporally at diurnal scales

due to barometric pressure changes (Kimball, 1983) and this may account for some of the variability in our F_s measurements.

Our study was able to detect a fire scar age specific response of F_s in jack pine systems. Our selection of field site enabled us to perform an intensive field campaign over a short time period. However, we recognize that temporal variability of F_s can occur at seasonal (Borken et al., 2002) and inter-annual (Irvine and Law, 2002) scales. Although we were unable to perform long term assessment of post fire F_s , we hope our study will provide a catalyst for similar research over longer time periods.

5 Conclusions

There is strong evidence against our H_0 that there is no change in F_s over post fire successional time at Sharp-sand Creek, a boreal jack pine ecosystem. Our results lead us to formulate a new hypothesis; that the autotrophic: heterotrophic soil respiration ratio increases over post fire successional time in boreal jack pine systems. This should be explored in future research. The results of our study contribute to a better quantitative understanding of F_s in boreal jack pine systems and will facilitate meta-analyses of F_s in fire scar chronosequences.

Appendix A

Abbreviations

B – burnt in 2007; DC – change in carbon; DT – change in time; F_s – soil surface CO₂ flux; F_s^T – soil surface CO₂ flux adjusted for soil temperature; M_s – soil moisture; NB – not burnt in 2007; Q_{10} – rate of soil surface CO₂ flux increase for every 10°C rise in soil temperature; T_0 – reference soil temperature; T_s – soil temperature.

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