

Soil CO₂ efflux in uneven-aged managed forests: temporal patterns following harvest and effects of edaphic heterogeneity

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Abstract Forest management is expected to influence soil CO₂ efflux (FCO₂) as a result of changes in microclimatic conditions, soil properties, and root dynamics. We measured FCO₂ during the growing seasons of 2003 and 2004 in both gap and non-gap locations within stands ranging from 0 to 10 years after the most recent harvest in a selection-managed northern hardwood forest in central Ontario, Canada. Soil temperature, moisture, pH, depth to bedrock, and organic matter content were also measured to examine relationships between FCO₂ and soil properties. Timber harvesting resulted in large changes in FCO₂ that varied with time since harvest. Immediately following harvest (year 0) FCO₂ in gaps increased by ~55%, declined to 20–40% below pre-harvest levels during years 1–3, and recovered to pre-harvest levels 5–6 years post-harvest. A similar temporal pattern, but with smaller changes, was found in non-gap locations within harvested stands. We suggest that the initial increase in FCO₂ is due to a combination of root decay, soil disturbance, and increased soil temperature in gaps, while the subsequent

decrease and recovery are caused by the gradual regrowth of active roots. We also found strong effects of soil temperature, depth to bedrock, and soil water content on FCO₂; however, soil pH and soil organic matter concentration had no detectable effects. Our results suggest that selection harvests mainly influence FCO₂ through changes in tree root respiration, and that the net result is a decrease in FCO₂ through the entire felling cycle.

Keywords Forest carbon dynamics · Selection silviculture · Soil respiration · Soil temperature · Soil moisture · Soil depth · Soil pH · Soil organic matter

Introduction

The evolution of CO₂ from soils is the second largest term in the carbon budget of forest ecosystems (Gower et al. 1996) and is therefore one of the key components in the carbon cycle at regional and global scales (Raich and Schlesinger 1992; Schimel 1995). Many factors affect spatial and temporal patterns of soil CO₂ efflux (FCO₂) (Billings et al. 1998). At diurnal to annual temporal scales, variation in FCO₂ is mainly driven by soil temperature (T_{soil}) and soil moisture (W_{g}) (Singh and Gupta 1977; Billings et al. 1998). FCO₂ increases with temperature, and this relationship is usually

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described using an exponential (Arrhenius) equation (Lloyd and Taylor 1994). FCO₂ is usually low under dry conditions due to low root and microbial activities, and generally increases with soil water content (W_g), but can show decreases under waterlogged conditions (Londo et al. 1999). Soil organic matter concentration (SOM) is another critical factor controlling FCO₂ in some systems (e.g., Ewel et al. 1987). Other soil properties, such as depth, pH, parent material, chemical composition of litter fall, topography and forest age may also influence FCO₂ (De Jong 1981). Autotrophic respiration of tree roots commonly accounts for ~50–70% of FCO₂ in temperate forest ecosystems, so any factor that alters the amount or physiological activity of tree roots will also likely have a large impact on FCO₂ (Boone et al. 1998; Pregitzer et al. 1998; Hanson et al. 2000).

Forest harvesting is expected to cause changes in root density and production, insolation, litter-fall input, and soil microbial activity, and hence should result in predictable changes in CO₂ evolution from forest soils. However, studies examining forest harvest effects on FCO₂ have yielded quite inconsistent results (Laporte et al. 2003). Even within the same general ecological system both large increases and large decreases in FCO₂ have been reported after logging (e.g., Londo et al. 1999 and Edwards and Ross-Todd 1983 for mixed deciduous hardwoods). One important factor contributing to this variation is likely differences in the length of time following harvest among different studies. Harvesting will generally result in the death of root systems of harvested trees, which should greatly reduce or eliminate the contribution of root respiration to FCO₂ until root systems recover. However, carbon released by the decay of fine roots is also expected to result in a short-term increase in FCO₂. To date, only a few studies have examined the time-course of harvest effects on FCO₂ (Striegl and Wickland 1998, 2001; Pypker and Fredeen 2001; Wang et al. 2002; Wiseman and Seiler 2004). In the chronosequence study with the greatest temporal resolution published to date, Pypker and Fredeen (2001) reported that up to 10 years after clearcut harvesting, plant biomass,

rather than cut-block age, T_{soil} or W_g , had the greatest influence on the relative magnitude of FCO₂ in sub-boreal forests in British Columbia.

Single-tree or small group selection management is the predominant silvicultural system throughout the eastern deciduous forest region of North America, and is increasingly practiced in Europe and parts of western North America as well (O'Hara 2002; Pommerening and Murphy 2004). Selection silviculture involves repeated partial stand harvests in which no more than 1/3 of canopy trees are removed, maintaining an uneven-aged or multi-cohort stand structure (OMNR 1998; O'Hara 2002). Although soil CO₂ fluxes are critical to understanding carbon processes under uneven-aged forest management, there have been very few studies examining FCO₂ responses to any type of partial stand harvest. We are aware of only one recent study specifically examining a selection-system harvest, which found reduced FCO₂ 1 year following harvest (Laporte et al. 2003). Several prior studies have examined FCO₂ responses to thinning in conifer stands (e.g., Ohashi et al. 1999; Son et al. 2004; Tang et al. 2005), but these studies also have not directly examined the time-course of the response. Comparisons of FCO₂ responses between gap and non-gap areas may provide insights into the relative role of root respiration (Brumme 1995; Hanson et al. 2000); however, there appear to have been no reports on the post-harvest patterns of FCO₂ in relation to gaps in managed forests.

The present study examines the impact of selection harvests in which ~1/3 of canopy trees are removed on soil surface CO₂ efflux. We sampled stands 0 to 10 years after harvest over two consecutive years, thus combining a “chronosequence” approach with a direct temporal sequence. The specific objectives of this study are (i) to examine the time-course of selection harvest effects on FCO₂; (ii) to compare selection harvest effects on FCO₂ between gap and non-gap locations; and (iii) to examine relationships between soil respiration and soil properties (T_{soil} , W_g , SOM, depth, and pH), and to test for harvest effects on FCO₂ independent of these relationships.

Methods

Study site

The study was conducted at Haliburton Forest and Wildlife Reserve, Ltd., a privately owned forest with a total area of ~25,000 ha located ~215 km northeast of Toronto, Ontario, Canada (45°13'N, 78°35'W). Mean annual temperature is 4.8°C; with mean January and July temperatures of -10 and 16°C, respectively. Mean annual precipitation is 1068 mm. Soil parent material consists of granite, syenite, and gneiss of the Precambrian Canadian shield. Topography is undulating, with an average elevation of 418 m. Soils vary in texture from clay loams to sandy loams, with an average pH of 5.3, and are classified as brunisols or young podsols on upland sites.

The study area is floristically representative of northern hardwood forests of the Great Lakes-St. Lawrence region of Ontario. Dominant tree species include sugar maple (*Acer saccharum* Marsh, representing >80% of basal area), American beech (*Fagus grandifolia* L.), Eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula alleghaniensis* Britt.). Selection harvesting silviculture system has been applied in these forest stands since the 1960s. Target basal areas at harvest are 18–20 m²/ha, following regional guidelines (OMNR 1998); average tree density in the areas studied was 640 trees/ha ≥8 cm diameter at 1.3 m height (Jones 2006). The understory is generally dominated by *Acer saccharum*, with common shrubs and herbaceous species including *Acer pensylvanicum*, *Viburnum alnifolium*, *Aralia nudicaulis*, *Dryopteris intermedia*, and *Rubus ideaus*.

Experimental design

The present study examines soil responses to partial stand harvests associated with selection system silviculture, in which no more than 1/3 of canopy trees are removed in a diffuse manner in a given harvested area (cut-block). Sampled cut-blocks were ~50–200 ha in size and included hundreds of canopy gaps created by harvesting of individual trees or small groups of trees. The

study was treated as a split-plot design where harvest year was the main plot effect, and gap versus non-gap location was the sub-plot effect. Cut-blocks harvested in 1995, 1997, 1999, 2000, and 2001 were investigated in both 2003 and 2004; additional cut-blocks harvested in 1994 and 2004 were investigated in 2004 only. The samples thus provided a range of 0–10 years since the most recent harvest. Each harvest year was represented by two replicate stands (“stand” designating a portion of a cut-block relatively homogeneous in species composition and forest structure). Thus a total of 14 stands were sampled, chosen on sites of similar soil and topography; replicate stands for a given harvest date were sampled in spatially non-contiguous cut-blocks where possible with locations chosen to maximize spatial interspersions among harvest dates. Chronosequence patterns for FCO₂ and other variables are represented by mean values for the entire growing season of 2003 for most harvest dates, with September 2004 measurements used for the 1994 and 2004 harvest dates (mean values for the entire growing season averages were closely approximated by September measurements for other harvest dates). Harvests were conducted from Jun.–Oct., with those for the 2004 cut-blocks completed in July, ~6 weeks prior to year 0 measurements. The minimum interval between harvests at the site is 10 years; patterns at 10 years post-harvest were therefore chosen to represent pre-harvest conditions.

One gap and one non-gap location within each of the 14 stands were sampled, and designated as the sub-plot effect in statistical analyses. Gap measurements were made within 4 m of stumps corresponding to trees harvested in the most recent cut. Measurements from prior studies at the site indicate that the average gap corresponds to 1.8 (±0.5 SD) canopy trees, and has an average projected area of 172 (±235 SD) m² (Jones and Thomas 2004). Non-gap sample locations within each stand were >50 m from the corresponding gap and at least 10 m from the nearest gap edge. Three measurement points spaced at distances of 3–5 m were established in each gap or non-gap location. There were thus a total of 84 measurement points in the study (7 harvest dates (main

plot treatments) \times 2 replicates \times 2 sub-plot treatments \times 3 measurement points).

Soil CO₂ efflux measurements

FCO₂ was measured on a monthly basis during the growing season in 2003 (from June 10, 2003 to November 17) and in September 9–12, 2004 (soil temperature and moisture at this time were near the mean value of entire growing season 2003) using a portable infra-red gas analyzer (LI-COR 6400) with soil CO₂ flux chamber (LI-6400-09, LI-COR inc, Lincoln, Nebraska, USA). In order to minimize soil disturbance effects from the utilization of the flux chamber, PVC collars were inserted into the soil at least 3 days prior to the first measurement of FCO₂, and kept in place through the entire study. The PVC collars used were 11.7 cm in diameter and 4.4 cm in height, and were installed to leave 2.5 cm protruding above the soil surface. Field measurements for each sampling location were taken twice between 9:00 AM and 6:00 PM on a given measurement date. The LI-6400 soil CO₂ flux system uses a closed system approach in which CO₂ is drawn down to a “target” point below the ambient concentration; during measurements soil CO₂ flux causes the CO₂ concentration in the chamber headspace to rise to a set-point a given “delta” above this point. In all cases, 390 and 10 ppm were used as the CO₂ “target” and “delta” values for measurements reported. Measurements generally required only a few minutes per sample point in summer, but up to ~30 minutes in fall and winter seasons. The FCO₂ value at each measurement point was the mean of three sequential flux estimates at each sampling interval; values are expressed as $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$. The monthly data collection was timed to span a few days with similar weather patterns since it was not possible to obtain all measurements in a single day (c.f., Laporte et al. 2003).

Soil property measurements

T_{soil} was determined using a LI-COR 6000-09TC soil probe thermocouple (LI-COR Inc., Lincoln, Nebraska, USA) at 5 cm below the soil surface during FCO₂ measurements. Five soil samples

were collected around each of PVC collars at a distance of <50 cm at the same time of each FCO₂ measurement, with samples for each measurement point physically pooled prior to analysis. Soil samples were taken from the uppermost mineral soil layer using a soil auger, with the top 0–10 cm collected for analysis. Soil samples were stored in airtight tubes and taken back to the laboratory for determination of W_g , SOM and soil pH. W_g was determined gravimetrically (Black 1965), and SOM content estimated according to Ball (1964). Soil pH was measured using a glass electrode in a saturated soil water paste. A soil core method (i.e., a soil auger is driven into the ground until bedrock is encountered) was used to estimate soil depth to bedrock (to the nearest cm).

Statistical analysis

Statistical tests for the effects of time since harvest, gap vs. non-gap location, temporal (month-to-month) variation, and their interactions on FCO₂, T_{soil} , and W_g were performed using analysis of variance (ANOVA). The original FCO₂ data were log-transformed to satisfy the normality and homoscedasticity assumptions of ANOVA; no transformation was necessary for T_{soil} and W_g . Multiple comparisons were conducted to identify among-harvest-year differences in FCO₂ and soil properties including T_{soil} , W_g , soil pH, soil depth and SOM. Pair-wise *t*-tests were used to examine differences between gap and non-gap within each harvesting year. Multiple regression analysis was employed to examine relationships between FCO₂ and soil properties, with the best-fit model chosen using Akaike's Information Criterion (AIC). In order to remove the majority of effects on FCO₂ resulting from changes in root systems change following harvests, only data from non-gap plots were used in the development of the model. Due to site access limitations, winter (November) measurements were made in only one cut-block (2001); this cut-block is therefore used to examine seasonal patterns. Statistical analyses were conducted using the SAS statistical package (SAS Institute Inc., Cary, NC 1999–2001), and the

statistical programming language R (R Core Development Team 2004).

Results

Impact of selection harvesting on soil respiration and soil properties

Selection harvesting significantly affected FCO_2 , which showed large differences among harvest years ($P < 0.0001$, Table 1). There was likewise a significant difference in FCO_2 between gap and non-gap sites ($P = 0.0005$, Table 1). Figure 1 shows the dynamic pattern of forest FCO_2 after selection harvesting. Immediately following harvest (year 0) FCO_2 in gaps was $7.7 \pm 1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($\pm\text{SE}$). By comparison with year 10, this suggests an increase of ~55% above pre-harvest levels. During the next 3 years FCO_2 declined gradually to ~20–40% below the level of year 10, with values of 4.1 ± 0.6 , 3.3 ± 0.6 , and $3.0 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 1, 2 and 3 years post-harvest, respectively (Fig. 1). Thereafter, FCO_2 increased at ~4 years and arrived at a stable state at ~5–6 years post-harvest. A similar temporal pattern, but with smaller overall changes, was found in non-gap locations within harvested stands (Fig. 1). FCO_2 was highest in

both gap and non-gap plots at immediately after harvesting (year 0), but was lower ($P < 0.05$) in gap than in non-gap plots during years 1–3 post-harvest. FCO_2 was similar in gap and non-gap plots at 4, 5 and 10 years post-harvest, though higher (but not significantly so) in non-gap plots than in gap plots at 6 and 8 years post-harvest (Fig. 1).

Temporal trends in T_{soil} and W_{g} versus harvest year in gap and non-gap locations were also compiled by pooling data recorded through the entire growing season in 2003 and for September 2004 (Fig. 2). Mean T_{soil} in gap plots was higher than non-gap plots for all harvest years except year 8 and 10 (Fig. 2a), with differences of 0.71, 0.71, 0.77, and 0.49°C at 0, 1, 2 and 4 years after harvesting, respectively. T_{soil} was similar in gap and non-gap plots at 6, 8 and 10 years post-harvest (Fig. 2a). The mean values of W_{g} were consistently higher in gap plots than non-gap plots (Fig. 2b). Although the pooled ANOVA indicated both significant harvest date and gap effects on W_{g} , pairwise tests for differences were not significant ($P > 0.05$). The peak value of W_{g} is at year 0 after harvesting; thereafter, W_{g} decreased from year 2–3, and showed similar values from years 4 to 10 post-harvest. Gap and non-gap plots had nearly identical mean values for soil pH (4.5),

Table 1 Analysis of variance (ANOVA) results for soil CO_2 efflux (FCO_2), soil temperature (T_{soil}) and soil moisture (W_{g})

Source	DF	FCO_2			T_{soil}			W_{g}		
		MS	<i>F</i>	Pr > <i>F</i>	MS	<i>F</i>	Pr > <i>F</i>	MS	<i>F</i>	Pr > <i>F</i>
Year post-harvest	4	1.60	16.55	<0.0001	10.37	24.08	<0.0001	529.96	18.40	<0.0001
Whole-plot Error	5	0.09			0.43			28.80		
Gap	1	1.63	16.86	0.0005	5.91	13.72	0.0014	644.37	22.37	0.0001
Year*Gap	4	1.31	6.80	<0.0001	1.44	3.34	0.0299	56.71	1.97	0.1383
Whole-plot*Gap	5	0.09			0.43			26.41		
Time	2	4.09	45.20	<0.0001	16.62	53.45	<0.0001	6688.19	253.19	<0.0001
Year*Time	8	0.17	1.84	0.0983	14.08	45.30	<0.0001	148.43	5.62	<0.0001
Gap *Time	2	0.20	2.25	0.1188	4.62	14.87	<0.0001	84.95	3.22	0.0507
Y*G*T	8	0.09			0.31			26.41		
Exp. Error	40									
Samp. Error	100									
Corr. Total	179									

Note: Year (or Y) = categorical variable for years post-harvest, Gap (or G) = gap versus non-gap sites, Time (or T) = measurement times

Exp. Error. = Experimental error, Samp. Error = Sampling error, Corr. Total = Corrected Total

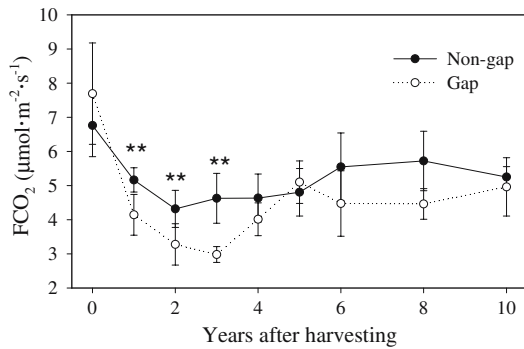


Fig. 1 Variation in soil CO₂ efflux (FCO₂) with time since harvest in gap and non-gap sites. FCO₂ values shown combine the mean value of FCO₂ for the entire growing season 2003 with data from September 2004; mean values of soil temperature and moisture in growing season 2003 were similar to those for September 2004. ** Indicates significant ($P < 0.05$) differences between gap and non-gap at the corresponding year. Error bar indicates ± 1 SE

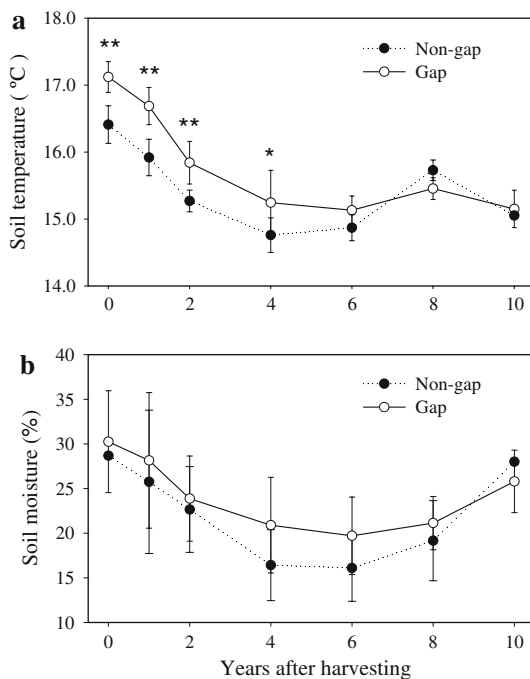


Fig. 2 Variation in soil temperature (°C) and soil moisture (%) with time since harvest in (a) gap and (b) non-gap sites. Data shown combine the mean values of soil temperature and moisture for the entire growing season 2003 with data from September 2004; ** indicates significant ($P < 0.05$) and * marginally significant ($0.05 < P < 0.10$) differences between gap and non-gap in the corresponding year. Error bar indicates ± 1 SE

and did not differ significantly in SOM content (12.3% vs. 9.6%; $P > 0.05$).

Seasonal patterns of FCO₂ and soil temperature

A typical time-course of FCO₂ and soil temperature during the study period in 2003 for gap and non-gap locations is shown in Fig. 3 (at 2 years post-harvest). FCO₂ peaked in July for gap and non-gap with the lowest values corresponding to measurements taken in November. The measured CO₂ fluxes ranged from 0.3–0.5 $\mu\text{mol m}^{-2}\text{s}^{-1}$ in November to highs of 3.9–4.2 $\mu\text{mol m}^{-2}\text{s}^{-1}$ in July for gap and non-gap sites (Fig. 3). FCO₂ was higher in non-gap than in gap sites during the studied period except in September. There is a similar seasonal pattern in soil temperature in both gap and non-gap except in July (Fig. 3). The maximum soil temperature occurred in July with values of 17 and 15°C in gap and non-gap sites, respectively.

FCO₂ as a function of soil temperature (T_{soil}) and moisture (W_{g})

FCO₂ was strongly correlated with T_{soil} ($P < 0.0001$) and W_{g} ($P = 0.0119$, Table 2). The relationship between FCO₂ and T_{soil} was described using an exponential function (Fig. 4a). Instantaneous FCO₂ data in non-gap plots was exponentially related to T_{soil} , and can be described using the model:

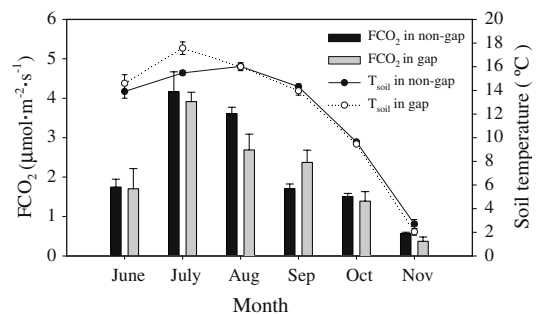


Fig. 3 Seasonal patterns of FCO₂ and soil temperature in gap and non-gap sites at year 2 post-harvest. Error bar indicates ± 1 SE

Table 2 Correlations between FCO₂ and soil parameters under different selection harvesting year stands (Pearson Correlation Coefficients, Prob > |r| under H₀: Rho = 0, d.f. = 204)

	<i>T</i> _{soil} (°C)	<i>W</i> _g (%)	Depth (cm)	pH	SOM (%)
FCO ₂ (μmol m ⁻² s ⁻¹)	0.46 <0.0001	0.18 0.0119	0.41 <0.0001	0.11 0.1226	-0.13 0.0642
<i>T</i> _{soil} (°C)	1	0.18 0.0126	0.18 0.0071	-0.06 0.3618	0.10 0.1387
<i>W</i> _g (%)		1	-0.14 0.0550	-0.04 0.6030	0.01 0.8847
Depth (cm)			1	0.06 0.3768	0.35 <0.0001
pH				1	-0.11 0.1024

Note: FCO₂ = soil respiration rate, *T*_{soil} = soil temperature, *W*_g = soil moisture, SOM = soil organic matter content

The top number in each cell presents the *R* value, the number below presents the probability. Correlations significant at *P* < 0.05 listed in bold

Fig. 4 FCO₂ as a function of microenvironmental and edaphic variables. (a) soil temperature at 5 cm depth; (b) soil moisture (%) at 10 cm depth; (c) soil organic matter (SOM); (d) soil pH; (e) soil depth (cm). Data are pooled across all sites, with the exception of soil temperature, which is shown for the 2001 harvest block only. The solid line in (a) represents the non-linear regression of FCO₂ as a function of soil temperature (5 cm depth) (Eq. 1). The solid line in (b) represents the non-linear regression of FCO₂ as a function of soil moisture (%) (Eq. 2). The solid line in (c) represents the non-linear regression line relating soil depth (cm) to FCO₂ (FCO₂ = -3.325 + 0.162*depth *r*²_{adj} = 0.38)



$$\text{FCO}_2 = 0.535e^{0.1108T_{\text{soil}}} \quad r_{\text{adj}}^2 = 0.62, \text{ AIC} = 154.1 \quad (1)$$

The corresponding Q_{10} for FCO_2 was calculated from Eq. 1 to be 3.03 ± 0.49 (SE)

The relationship between FCO_2 and W_g was significantly upwardly convex (2nd order polynomial term significant at $P < 0.001$, Fig. 4b). The relationship was therefore also described using an exponential function:

$$\text{FCO}_2 = 0.756e^{0.0437W_g} \quad r_{\text{adj}}^2 = 0.30, \text{ AIC} = 191.0 \quad (2)$$

A variety of functional forms for explaining the simultaneous effects of T_{soil} and W_g on FCO_2 were investigated using multiple non-linear regression models. The following simple compound exponential equation provided the lowest AIC value of models examined:

$$\text{FCO}_2 = 0.427e^{0.0903T_{\text{soil}}} e^{0.0207W_g} \quad r_{\text{adj}}^2 = 0.73, \text{ AIC} = 134.5 \quad (3)$$

Including a second-order interaction term in this equation (i.e., $\text{FCO}_2 = ae^{bT_{\text{soil}}} e^{cW_g} e^{dT_{\text{soil}}W_g}$ where a , b , c and d are constants) did not further reduce AIC.

FCO_2 versus soil depth, soil pH and SOM

Samples with greater soil depth had higher FCO_2 values ($P < 0.0001$, Fig. 4e, Table 2). However, correlations of FCO_2 with soil pH and SOM concentration on FCO_2 were not significant ($P > 0.05$, Table 2, Fig. 4c, d).

Discussion

Harvesting effects on soil CO_2 efflux

FCO_2 showed an immediate increase after harvest, declined in the following 3 years, and then gradually increased and arrived at a stable state approximately 5–6 years post-harvest (Fig. 1). We suggest that the short-term increase

in FCO_2 is likely a result of soil disturbance and carbon released by the decay of fine roots. Following this initial decay, the death of root systems of harvested trees should greatly reduce the root component of FCO_2 until root systems recover, and thus provides an explanation for the reduction and gradual recovery in FCO_2 in subsequent years. Changes in the soil microenvironment must also contribute to these patterns to some extent; however our results indicate that neither the initial short-term increase in FCO_2 nor the later suppression can be explained as a result of the relatively small observed changes in soil temperature and moisture. Equation 3, which describes the observed temperate and soil moisture response at the site, predicts a ~38% increase in FCO_2 in year 0; however, a ~55% increase was actually observed. The increase in FCO_2 above that predicted from microenvironmental effects presumably reflects increased microbial respiration. The reduction in FCO_2 in years 1, 2 and 3 years post-harvest cannot be explained even in part by observed changes in soil temperate and moisture, since in this case Eq. 3 predicts an increase in FCO_2 .

Comparisons between gap and non-gap sites are also consistent with the hypothesis that root death, decay, and regrowth are largely responsible for the temporal pattern described. There is a small but significant increase in T_{soil} following harvest in both gap and non-gap sites (Fig. 2a) attributable to increased light penetration in gaps (c.f. Striegl and Wickland 1998, 2001), and a similar increase in W_g (Fig. 2b). The latter effect can be attributed to a reduction of plant utilization of soil water through transpiration (Puhe and Ulrich 1985), and the increase in W_g in both gap and non-gap location suggests considerable overlap of tree rooting zones. For this reason, comparisons between gap and non-gap location do not allow for a straightforward partitioning of root vs. microbial respiration (cf. Brumme 1995; Hanson et al. 2000). As the establishment of new vegetation progresses, the initial harvest impact on soil temperature and moisture should decline gradually, and patterns in gap and non-gap sites should converge, as was observed. Under a common biophysical model,

increased T_{soil} and W_g in gaps are expected to increase microbial and root respiration, resulting in higher FCO_2 in gaps than non-gap sites. However, we found a substantial reduction in FCO_2 1–3 years after harvesting in gaps compared to non-gap sites, during a time period of pronounced increases in T_{soil} in gaps. Thus one critical implication of our findings is that using soil temperature and moisture alone to model harvest effects on FCO_2 would result in serious biases in estimates of long-term fluxes.

In comparison with most prior chronosequence studies of FCO_2 in stands after clear-cut harvesting, our study of selection-system harvests found a much clearer temporal pattern. The peak value of FCO_2 at year 0 after harvesting in our study contrasts with the results of Pypker and Fredeen (2002), who found that the 0-year's cut block had the lowest FCO_2 and who describe an early peak of FCO_2 at 2 years post-harvest in sub-boreal forests of central British Columbia. Interestingly, there was actually less aboveground biomass 10 years post-harvest than at 2 years in their study, and the early peak in FCO_2 was attributed to herbaceous vegetation proliferation in the clear-cut: i.e., to a root respiration response. In contrast, Toland and Zak (1994) found no effect of clear-cutting on FCO_2 during the growing season following harvest in northern hardwoods in MI, USA. Our finding of decreased FCO_2 over the first 3 years post-harvest is similar to that of Striegl and Wickland (1998, 2001), who studied the influence of a clear-cut harvest on FCO_2 in a jack pine–lichen woodland. They found that FCO_2 decreased during the first and second growing season and returned to the pre-harvest level in the third growing season. Weber (1990) obtained similar results in a study of aspen stands in eastern Ontario. Prior chronosequence studies have generally not made measurements in the first weeks to months following harvest, and so may have missed an initial transient peak in FCO_2 noted in the present study.

Selection harvesting did not have a significant impact on soil pH or SOM. This is consistent with other findings in temperate forest. Selection harvesting has not been found to result in detectable changes in carbon storage in the

mineral soil or in the top organic layer within the first few years after harvesting (Puhe and Ulrich 2001), though impacts of selection harvesting on SOM may become evident in the longer term (e.g. Huntington and Ryan 1990).

Edaphic factors influencing FCO_2

The relationship between FCO_2 and T_{soil} is usually modeled by an exponential equation (Kucera and Kirkham 1971; Fernandez et al. 1993; Toland and Zak 1994; Striegl and Wickland 1998; Maier and Kress 2000; Chen et al. 2002; Irvine and Law 2002; Rey et al. 2002). Our Q_{10} for soil respiration was 3.03, which is slightly higher than many values in the literature (1.99–2.9) (Maier and Kress 2000; Striegl and Wickland 2001; Chen et al. 2002; Rey et al. 2002). However, comparably high Q_{10} values have been reported in temperate forests: e.g., 3.12–3.26 calculated by Kang et al. (2003), 3.4–5.6 reported by Davidson et al. (1998), and 3.30–6.29 reported by Pumpanen et al. (2003).

We suggest that the high value for Q_{10} reported here may result from seasonal variation in microbial or root activity. When the Q_{10} is calculated from a sequence of measurements taken over a period of time during which the temperature is changing, the resulting value may be the product of the response of the respiratory process itself to temperature and the response of the population of respiring organisms, such as roots or microorganisms, to temperature (Raich and Schlesinger 1992). During the growing season, when the temperature increases, both the specific rate of respiration *per se* and the size of population of the respiring organisms also increase. Thus, if both the Q_{10} and the response of the microbial and root population were 2, the total Q_{10} would be 4 (Simmons et al. 1996).

The effect of W_g on the soil respiration is generally considered to be unimodal or “parabolic” (Londo et al. 1999). As soil approaches saturation or drought conditions, FCO_2 rate generally decreases, because the conditions are not favorable for microbial decomposition (Kucera and Kirkham 1971; Londo et al. 1999). In very high W_g conditions, soil CO_2 efflux is reduced due to the limitation of oxygen diffusion

and effects of hypoxia on respiration rates. This relationship can be approximated by a quadratic equation (Mielnik and Dugas 2000), though a variety of functional forms have been used (Schlentner and Van Cleve 1985; Carlyle and Than 1988; Norman et al. 1992). T_{soil} and W_{g} often interact with each other to influence the rate of soil respiration (Carlyle and Than 1988); however, we failed to detect such statistical interaction in the present study. Combining the effects of T_{soil} and W_{g} in this study, a multiple regression was developed with an R^2 of 0.73 (Eq. 3).

Deeper soils are likely to have higher roots root mass, more microbial biomass, and more SOM than shallow soils, but surprisingly few studies have previously examined the correlation of soil depth and FCO_2 . We found a strong positive correlation between FCO_2 and soil depth (Table 2, Fig. 4e). We are not aware of directly comparable data from prior studies; however, a strong relationship was previously found between the predicted total annual carbon efflux and the thickness of the light brown mat of dead peat moss between the living moss and the darker in a boreal black spruce stand by Rayment and Jarvis (2000). As a general rule, sites with higher SOM should have higher evolution of CO_2 (Schimel et al. 1994; Mallik and Hu 1997; Chen et al. 2002). However, SOM had no significant effect on FCO_2 in this study (Table 2, Fig. 4c). The lack of a SOM effect suggests a predominant contribution of root respiration to FCO_2 , since microbial respiration should show a positive response. Likewise, soil pH has very strong effects on microbial activity (e.g., Paul and Clark 1996), but we detected no effect of pH on FCO_2 . These observations are thus also consistent with our inference that the root respiration dynamics largely determine post-harvest trends in FCO_2 .

Conclusions

Knowledge of the mechanisms controlling C loss from the soil surface is essential for understanding the impact of forest management practices on CO_2 release from the forest soil. Overall, selection harvesting had significant effects on FCO_2

and this impact lasted several years following harvesting. The observed temporal pattern, relative differences between gap and non-gap sites, and lack of strong effects of SOM and pH on FCO_2 all suggest that root respiration of large trees is predominant in this system, and that post-harvest dynamics is largely controlled by tree root dynamics as well. Our results indicate a short initial increase in FCO_2 followed by several years of decrease and a gradual return to stable FCO_2 levels. Thus, the integrated FCO_2 flux would appear to be lower in harvested stands than in non-harvested stands (though more intensive sampling in the weeks to months following harvest would be necessary to provide an accurate estimate of net C loss immediately post-harvest). This result, combined with the maintenance of high levels of living biomass in selection managed forests (and the production of long-lived forest products), suggests that uneven-aged management systems may maintain sustained, strong C sinks.

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