

Spatial Patterns of Soil Surface C Flux in Experimental Canopy Gaps

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ABSTRACT

To explore within-gap spatial patterns of soil surface CO₂ flux, we measured instantaneous soil surface CO₂ flux, soil surface temperature, and soil moisture in north–south transects across canopy gaps and in adjacent contiguous forest from April to November 2010 in a second-growth northern hardwood forest in Wisconsin, USA. Throughout the growing season, soil surface CO₂ flux was higher in the northern 1/3 and northern edge of gaps compared to the central and southern portions. These patterns were driven primarily by within-gap variation in soil temperature, which was itself driven by within-gap patterns of insolation.

Most locations in the northern 1/3 and northern edge of gaps had significantly higher modeled total growing season C flux (mean 725 g C m⁻²) compared to the contiguous forest (mean 706 g C m⁻²), whereas C flux in the central and southern portions of gaps (mean 555 g C m⁻²) was significantly lower than both the contiguous forest and the northern portions of gaps.

Key words: Canopy gap; C flux; Gap microclimate; Respiration; Soil temperature; Soil flux; Northern hardwood forest.

INTRODUCTION

In northern hardwood forests, disturbance regimes tend to be dominated by relatively small scale disturbances leaving a patchwork of canopy gaps formed by the death of single trees or small groups of trees (Frelich and Lorimer 1991; Dahir and Lorimer 1996). At any given time, small gaps at various stages of succession cover a significant portion of the landscape, with typical estimates of 10 % or more in various eastern North American

forests (Runkle 1982; Kneeshaw and Bergeron 1998; Keller and Hicks 1999).

Soil surface CO₂ flux (R_s) constitutes the second largest carbon flux in forest ecosystems (Raich and Schlesinger 1992; Gower and others 1996) and is sensitive to many biotic and abiotic factors affected by canopy gaps, including soil temperature (T_s), soil moisture, and vegetation dynamics. Not surprisingly, gap formation has been found to affect R_s , although the magnitude and direction of that effect is not always consistent. Some studies have reported higher R_s within gaps compared to adjacent contiguous forest (for example, Scharenbroch and Bockheim 2008), some lower (for example, Brumme 1995), some found no significant differences (for example, Stoffel and others 2010), and others reported that relative R_s between canopy openings and contiguous forest changed with time since harvest (for example, Schilling and others 1999; Peng and Thomas 2006). Given the conspicuousness of small canopy gaps in northern

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hardwood and other forested landscapes, as well as the prominence of R_S in the global carbon cycle, it is clearly important to fully understand the influence of gaps on R_S .

T_S , soil moisture, and other drivers of soil surface R_S vary not only between gaps and non-gaps, but within gaps as well. Several studies have examined individual aspects of these within-gap spatial patterns, but we are not aware of any studies that specifically analyze within-gap spatial patterns of soil surface R_S and its drivers in a well-replicated experiment. For instance, Brumme (1995) found lower R_S in a gap center than at the southern gap edge and adjacent contiguous forest, which he attributed to root respiration, T_S , and soil moisture interactions. However, treatments were not replicated in the Brumme (1995) study. Other studies have reported within-gap spatial patterns of parameters related to R_S , including C mineralization (Bauhus 1996) and leaf litter decomposition rates (Bauhus and others 2004). These results suggest that R_S should vary predictably within gaps, but neither study measured R_S directly.

To directly explore R_S patterns within gaps, we measured R_S , T_S , and soil moisture in north-south transects across canopy gaps and in adjacent contiguous forest plots. We did not separate the autotrophic (R_A) and heterotrophic (R_H) components of R_S , so R_S includes all components of soil surface CO_2 flux. We hypothesized that: (1) There is significant variation in R_S within gaps, with higher R_S in the northern portions of gaps than the southern portions; (2) These patterns are driven primarily by within-gap patterns of T_S , which are in turn driven by within-gap patterns of cumulative insolation.

Our hypotheses are based on the observations that T_S and insolation tend to be higher in the northern portions of gaps compared to the southern portions in the northern hemisphere (Canham and others 1990; Wright and others 1998; Gray and others 2002; Milakovsky and others 2011), and R_S is positively related to T_S (Lloyd and Taylor 1994; Boone and others 1998). Furthermore, most studies in temperate forests have reported that T_S explains a large proportion of R_S variation (for example, Brumme 1995; Bond-Lamberty and others 2004; Scharenbroch and Bockheim 2008), including an earlier study at the same location as our present experiment (Stoffel and others 2010). Soil moisture also could have predictable within-gap patterns and we will consider its impact on R_S as well.

MATERIALS AND METHODS

Site Description

This study is part of a large-scale experiment established within the Flambeau River State Forest, an over-36,500 ha property located in north-central Wisconsin, USA. The 300 ha study site is located in the southernmost portion of the Flambeau (45°37.4'N, 90°47.8'W). Soils are predominantly well-drained silt loams (glossudalfs; Luvisols in FAO classification) of the Magnor and Freeon series overlaying dense glacial till. January and July air temperatures at the site (2005–2010) averaged -9.0 and 20.6 °C, respectively, with mean annual precipitation of 570 mm. The median length of the growing season is 105 days, generally occurring May–September (1971–2000; Midwest Regional Climate Center). The canopy is dominated by sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), and white ash (*Fraxinus americana*). The stand is largely an even-aged, second-growth, mature forest with most stems originating between the 1920s and 1940s. Before early 20th century logging, the site historically was dominated by eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), and sugar maple (Schulte and others 2002).

Study Design

The study described here was part of a larger experiment assessing how restoring structural features more abundant in old-growth forests, namely, canopy gap openings and greater volumes of coarse woody debris (CWD), influence productivity, diversity, and biogeochemistry in a second-growth northern hardwood forest (Stoffel and others 2010; Dyer and others 2010). Treatments in the larger experiment consist of five replicates of seven treatments (Control; Gap addition; CWD addition; Gap + CWD addition; Deer enclosure; Gap addition + Deer enclosure; Mechanized-control) that were randomly assigned to 34 80×80 m (0.64 ha) plots. Treatments were applied in late January 2007 with a PONSSE Ergo harvester and PONSSE Buffalo forwarder (both low-impact rubber-tired logging equipment) under frozen ground conditions and snow cover.

In all Gap addition treatments, three circular canopy openings (8, 16, and 22 m diameter; equivalent to removal of 1.5, 9, and 20 trees, respectively) were created per plot; sampling subplots of equal size also were established in all non-gap treatment plots. The sizes of gap openings were

selected to represent the range of gap sizes typical of old-growth northern hardwood forests in the region (Dahir and Lorimer 1996). In CWD addition treatments, the existing CWD in each plot was augmented up to the mean biomass expected in typical old-growth northern hardwood stands of the region (mean 28.7 Mg ha^{-1} ; Goodburn and Lorimer 1998). All added CWD was freshly cut to ensure uniform decay class.

Soil C Flux

R_s was measured in the large subplots (22 m diameter) of the Control ($n = 5$), Gap addition ($n = 5$), CWD addition ($n = 5$), and Gap + CWD addition ($n = 5$) treatment plots. Often during this analysis, we will refer to “gap plots,” which consist of all plots containing gaps (that is, Gap and Gap + CWD addition treatments) and to “non-gap” plots, which consist of plots in contiguous forest that do not contain experimental gaps (that is, Control and CWD addition treatments).

In mid-April 2010, six R_s collars (PVC pipe 20 cm diameter \times 10 cm height) per plot were inserted into the soil to a depth of approximately 7.5 cm. Collars were arranged in north–south transects with collars spaced 4 m apart and transects being 2.5 m east or west (random assignment) of the north–south axis of each subplot (Figure 1). Collar interiors were weeded periodically, although the forest floor and leaf litter were left undisturbed. R_s was measured with a LI-8100 infrared gas analyzer and 20 cm Survey Chamber (Li-Cor, Inc., Lincoln, NE) with a single 90 s measurement at each collar. R_s at all collars was measured over 1–2 consecutive days approximately every 4 weeks from April to

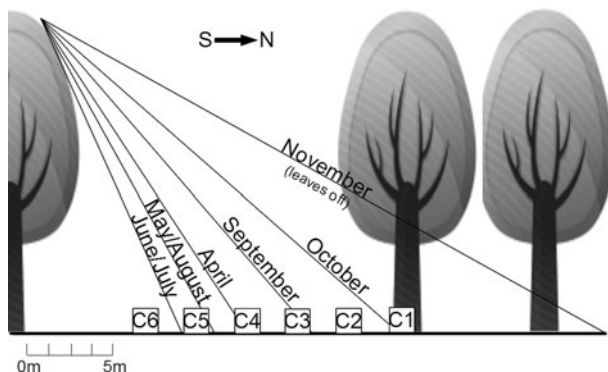


Figure 1. Layout of soil CO_2 flux collars (collar size not to scale) in experimental canopy gaps, as well as approximate maximum southern extent of direct beam insolation penetrating the canopy gap at peak solar angle on CO_2 flux sampling dates. Angles were calculated for a canopy height of 20 m.

Table 1. Soil CO_2 Flux Sampling Dates

Date(s)	
Apr	26–27
May	19–20
Jun	09–10
Jul	06–07
Aug	03–04
Sep	07
Sep ¹	27
Nov	01

¹ Referred to as “October” sampling throughout paper.

November 2010 (Table 1). Sampling was performed at least 24 h after rain events. Plot measurement order was randomized each month.

T_s and soil moisture were measured within 15 cm of R_s collars simultaneously with R_s . T_s was measured at two depths (2 and 10 cm) with digital long stem thermometers (model no. 15-078k, Fisher Scientific). Soil moisture was measured to a depth of 6 cm with a calibrated TDR probe attached to a HH2 Moisture Meter (Delta-T Devices, Cambridge, England). On April 27, iButton Temperature Loggers (Maxim Integrated Products, Inc., Sunnyvale, CA) were buried at two depths (2.5 and 7.5 cm) within 15 cm of each collar and recorded bihourly temperatures for the duration of the season.

Statistical Analyses

We used “proc mixed” in SAS v9.2 (SAS, 2008; System for Windows, SAS Institute, Inc., Cary, NC, USA) to fit two types of nested linear mixed models: (1) linear regression of the effects of T_s and soil moisture on R_s , and (2) ANOVAs of how gap treatment and collar position affected monthly R_s , T_s , soil moisture, and modeled total seasonal soil surface C flux. For our models, plot was the first level of nesting, within-plot collar position was nested within plot, repeated measures over time were nested within each collar, and a heterogeneous autoregressive covariance structure was used to account for autocorrelation of repeated measures.

The primary objective of our study was to explore within-gap spatial patterns of R_s . R_s in non-gap plots will a priori display no gap treatment-driven patterns, so in our final models, treatment consisted of the six within-gap locations ($n = 10$) and the full set of non-gap locations ($n = 60$) for a total of seven treatment levels.

The model was unbalanced due to the fact that each of the six within-gap locations was compared to the full set of non-gap collars to better discern general differences between contiguous forest and within-gap locations. CWD had no significant interaction with treatment in any of our models, but it was significant as a single factor and was retained as such in our final ANOVAs. Treatments were compared by least squares means at $\alpha = 0.05$ for the total C flux model and $\alpha = 0.10$ within each month for the monthly models. A lower significance level was chosen for monthly models to increase the power within each month due to the large number of month*treatment comparisons. For monthly models, the time of day at which measurements occurred was significantly related to R_s and T_s (but not soil moisture) and was included in those two models as a covariate.

In the linear regression, T_s at 10 cm depth explained slightly more variation in $\ln(R_s)$ than did T_s at 2 cm (R^2 of 0.512 and 0.506, respectively) and was used exclusively in all subsequent analyses involving T_s .

Linear regression models relating T_s and $\ln(R_s)$ were used to model total C flux from April 27 to November 1 using bihourly iButton soil temperature measurements. Soil moisture was not continuously monitored at the collars and was thus not used in the model. We fit six separate repeated measures models using “procglm” in SAS v9.2 for locations C1–C6 in the gap plots and another model for the full set of non-gap plot locations for a total of seven prediction models. All models were highly significant ($p < 0.001$) with adjusted R^2 ranging from 0.44 to 0.63 (Appendix A in Supplementary material). Modeled total C flux was averaged by week, which acted as the time unit for repeated measures.

In all analyses, dependent variables were log-transformed as necessary to meet assumptions of ANOVA.

RESULTS

Regression Models

For $\ln(R_s)$, the effects of T_s were positive and highly significant ($p < 0.0001$), and there also was a significant T_s *soil moisture interaction ($p = 0.015$). However, removing soil moisture and fitting the model solely with T_s lowered the AIC from 719.5 to 702.7, whereas an additive model with soil moisture and T_s had an AIC of 710. This indicates that soil moisture, both as an interactive term and an additive term, did little to improve the model,

suggesting that, compared to T_s , soil moisture was not a strong explanatory factor of R_s .

Soil Moisture

There was a significant gap-collar position treatment effect ($p < 0.01$) on soil moisture, indicating that soil moisture differed between the seven gap-collar position treatments. Soil moisture was consistently higher in the southern than northern portions of gaps, following a relatively linear north–south gradient throughout the year (Figure 2). However, soil moisture was highly variable within individual plots and differences were not always significant. Nonetheless, all significant differences were of more northern locations being drier than more southern locations. Soil moisture in the southern portion of gaps was often significantly higher than in non-gaps, whereas soil moisture in the northern portion of gaps was consistently but non-significantly lower than in non-gaps (Figure 2).

Soil Temperature

There was a significant month*treatment interaction ($p < 0.05$) on T_s , indicating that T_s differences between the seven gap-collar position treatments changed during the growing season. At each R_s sampling date, peak T_s occurred in the northern 1/3 of gaps (C2 and C3) for most of the growing season, with steadily decreasing T_s to the north and south of those locations (Figure 3). C1 was located in the understory 3 m north of the gap (Figure 1) and became the warmest location in October and November (Figure 3) when solar angles were lowest and the direct sun penetrating the canopy gap was angled farthest to the north (Figure 1).

Monthly Instantaneous Soil Surface C Flux

There was a significant month*treatment interaction ($p < 0.05$) on R_s , indicating that R_s differences between the seven gap-collar position treatments changed during the growing season. In April–June, R_s at the northernmost collars (C1–C3) in gaps was consistently higher than at the southernmost collars (C4–C6), although these differences were generally only significant for C6, indicating that C6 consistently had the lowest R_s during the spring (Figure 4). In July–August, C1–C3 in gaps maintained higher average R_s than C4–C6, but these differences were more variable than in all other months and were only significant for C4. C6 had higher average R_s than C3 in July, although

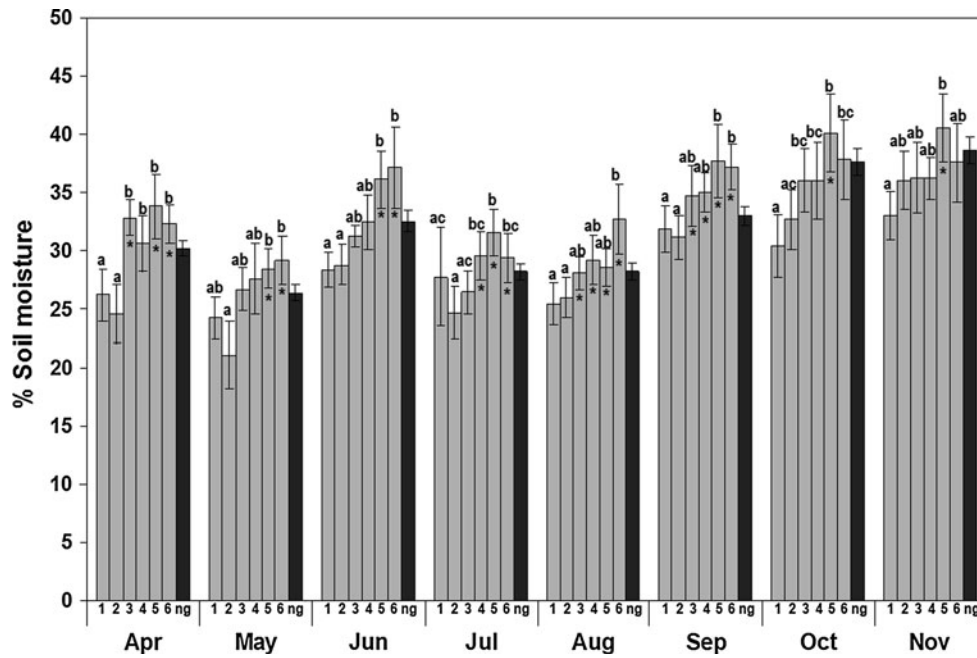


Figure 2. Average soil moisture measured simultaneously with monthly soil CO₂ flux measurements. In each month, *light gray bars* represent average soil moisture ($n = 10$) at locations C1–C6 (from left to right sequentially) in gaps; *dark gray bars* represent the average of non-gap (ng) treatment plots ($n = 60$). Error bars are SEM. Different letters indicate significant within-month differences detected via least squares means comparisons from nested repeated measures mixed model ANOVAs ($\alpha = 0.10$). Asterisks (*) indicate that a within-gap location was significantly different from the non-gap treatment ($\alpha = 0.10$).

the difference was not significant; notably, this was the only instance of a location in the southern 2/3 of the gap having higher average R_s than a location in the northern 1/3. In September–November, gaps displayed a clear north–south threshold where R_s at the northernmost collars (C1–C3) was consistently higher than R_s at the central and southern collars (C4–C6). Within each of those two groups of collars, R_s was very similar. In summary, although differences between the northern collars (C1–C3) and southern collars (C4–C6) were not always significant, R_s was consistently higher in the northern portions of gaps.

Seasonal C Flux

The effect of gap-collar position treatment on modeled seasonal soil surface C flux was highly significant ($p < 0.0001$). C flux from April 27 to November 1 at C1–C3 in gaps was comparable to or significantly higher than flux in non-gaps (Table 2). C4–C6 in gaps had significantly lower total flux than both non-gaps and C1–C3 in gaps. Differences within the C1–C3 and C4–C6 groups were sometimes significant but were relatively small in absolute terms.

DISCUSSION

We observed a clear pattern of higher R_s in the northern 1/3 and northern edge of gaps compared to the central and southern portions at our northern hemisphere site. Because R_s was sufficiently variable, this did not occur in every replicate subplot, but the overall pattern was clear. This pattern appeared to be driven primarily by T_s , which accounted for 51 % of the variation in R_s , and was itself driven primarily by within-gap patterns of insolation. Most studies of within-gap light dynamics have found higher insolation and corresponding higher T_s in the northern portions of gaps, with light levels rapidly diminishing to the south (Wright and others 1998; Gray and others 2002; Milakovsky and others 2011). In studies of northern hemisphere gaps with similar height:diameter ratios as ours (1:1), peak insolation occurred at positions corresponding to C2 and C3 in our study (Canham and others 1990; Gray and others 2002; Gendreau-Berthiaume and Kneeshaw 2009), placing the highest insolation in the northern 1/3 of our gaps where we consistently observed the highest T_s . Notably, this pattern of insolation is not static throughout the year (Figure 1). At our

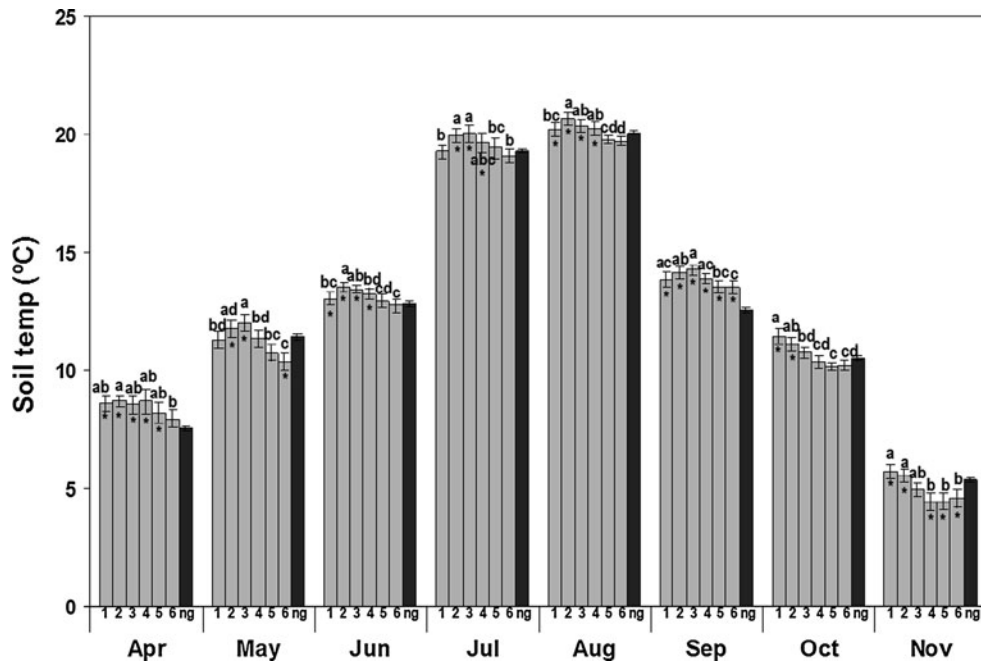


Figure 3. Average soil temperature ($^{\circ}\text{C}$) at 10 cm depth measured simultaneously with monthly soil C flux measurements. In each month, *light gray bars* represent average temperature ($n = 10$) at locations C1–C6 (from left to right sequentially) in gaps; *dark gray bars* represent the average of non-gap (ng) treatment plots ($n = 60$). Error bars are SEM. Different letters indicate significant within-month differences detected via least squares means comparisons from nested repeated measures mixed model ANOVAs ($\alpha = 0.10$). Asterisks (*) indicate that a within-gap location was significantly different from the non-gap treatment ($\alpha = 0.10$).

site, peak T_s (and presumably peak insolation) shifted to the northern-gap-edge location in October and November, when solar angles were lowest and leaf-off was occurring. In any case, although T_s was the proximate driver of the major R_s patterns within gaps, insolation was likely the ultimate driver. The greater R_s variability in the warmer summer months may relate to R_s being less responsive to T_s at higher temperatures (Qi and others 2002) or to higher R_A by surrounding canopy trees during the peak growing season.

Soil moisture in gaps varied along a north–south gradient with lower soil moisture in the north than the south (Figure 2). The year of this study, 2010, had the wettest April–October on record for north-central Wisconsin, with 88.1 cm of rainfall compared to the 1895–2010 average of 62.8 cm (NOAA National Climatic Data Center 2011). This created very saturated conditions at our site that would be consistent with higher R_s in the relatively dry northern portions of our gaps. Soil moisture did little to improve our regression model of R_s , however, so it is unlikely to be the driver of the R_s patterns we observed. Although many studies report significant effects of soil moisture on R_s (Londo

and others 1999; Scharenbroch and Bockheim 2008), others have observed little or no relationship, particularly when moisture is not limiting (Edwards and Ross-Todd 1983; Buchmann 2000; Stoffel and others 2010).

One surprising result was that R_s did not track within-gap T_s patterns as closely as may be expected given the strong relationship between T_s and R_s . Instead, a north–south threshold persisted throughout the year, with the northern 1/3 and northern edge of gaps maintaining higher R_s than the southern 2/3. In other words, R_s was not perfectly coupled to T_s . This was particularly true for the northern-gap-edge, which was not the warmest location until late in the year yet consistently maintained among the highest average R_s . This indicates that other important factors influenced differences in R_s between gaps and gap edges. Relative to interior locations, collars nearer to the understory may have had higher litterfall rates, more optimal soil moisture, and greater R_A and C inputs from the roots of surrounding canopy trees, all of which are well known to influence R_s (Buchmann 2000; Raich and Tufekcioglu 2000; Bond-Lamberty and others 2004). Additional

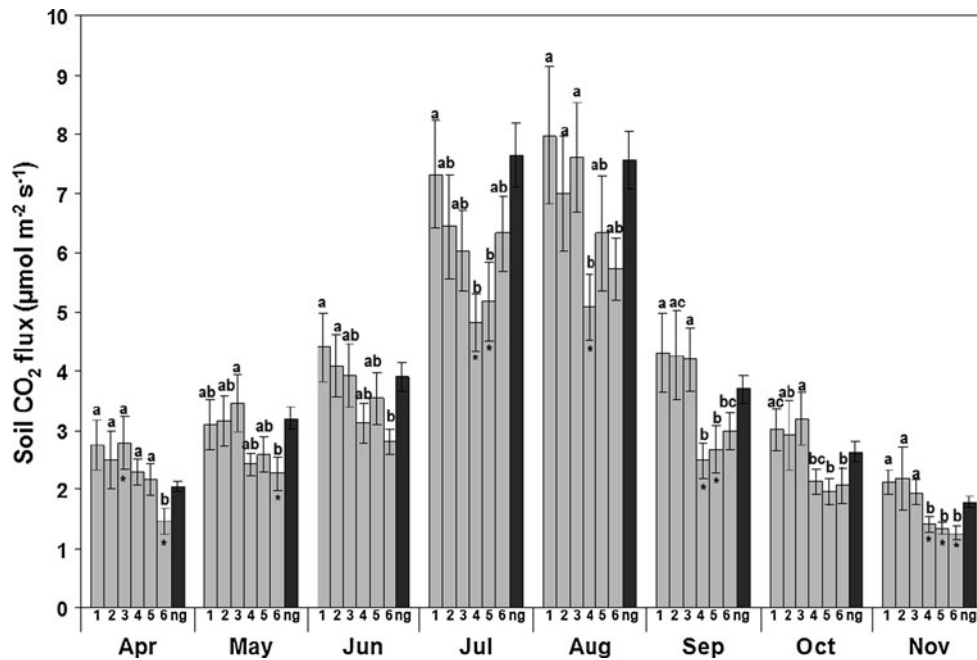


Figure 4. Average instantaneous soil CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) measured approximately once monthly from April to November. In each month, *light gray bars* represent average flux ($n = 10$) at locations C1–C6 (from left to right sequentially) in gaps; *dark gray bars* represent the average of non-gap (ng) treatment plots ($n = 60$). Error bars are SEM. Different letters indicate significant within-month differences detected via least squares means comparisons from nested repeated measures mixed model ANOVAs ($\alpha = 0.10$). Asterisks (*) indicate that a within-gap location was significantly different from the non-gap treatment ($\alpha = 0.10$).

Table 2. Total Soil C Flux by Treatment and Within-gap Position

Treatment	Total flux (g C m^{-2}) Apr 27–Nov 1
Non-gap (all collars)	$706 \pm 1.8\text{a}$ (SE)
Gap-C1	$727 \pm 5.8\text{b}$
Gap-C2	$693 \pm 7.3\text{a}$
Gap-C3	$754 \pm 7.1\text{b}$
Gap-C4	$533 \pm 2.8\text{c}$
Gap-C5	$568 \pm 6.5\text{d}$
Gap-C6	$563 \pm 3.7\text{d}$

N = 10 for each within-gap collar location; N = 60 for Non-gap treatment. Flux calculated using bihourly soil temperature measurements in location-specific models of concurrent soil temperature and soil flux measurements. Unique letters indicate significant differences detected via least squares means comparisons from repeated measures ANOVA ($\alpha = 0.05$).

measurements of above and belowground productivity, litter inputs, and the relative contribution of R_H and R_A would be required to fully account for these patterns.

In an earlier study in the same experimental plots (Stoffel and others 2010), we measured R_S in each subplot in two north–south transects that approximately spanned the C3–C6 locations in the present study. Stoffel and others (2010) did not distinguish by within-gap position and concluded

that C flux did not differ significantly between gaps and non-gaps in the first two post-harvest years (2007 and 2008). Distinguishing finer scale within-gap patterns of C flux was one of the goals of this follow-up study, and although the present study in no way invalidates our earlier study, it does suggest that significant gap effects may have been present at finer scales.

CONCLUSIONS

We hypothesized that: (1) There is significant variation in R_S within gaps, with higher R_S in the northern portions of gaps than the southern portions; (2) These patterns are driven primarily by within-gap patterns of T_S , which is itself driven by within-gap patterns of cumulative insolation. Although factors other than T_S appeared to influence patterns of R_S , our data were nonetheless consistent with these hypotheses, illustrating the importance of accounting for within-gap variation when comparing both instantaneous and modeled total soil surface C flux of gaps and non-gaps.

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