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Initial soil respiration response to biomass harvesting and green-tree retention in aspen-dominated forests of the Great Lakes region

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ABSTRACT

Contemporary forest management practices are increasingly designed to optimize novel objectives, such as maximizing biomass feedstocks and/or maintaining ecological legacies, but many uncertainties exist regarding how these practices influence forest carbon (C) cycling. We examined the responses of soil respiration (R_s) to biomass harvesting and green-tree retention in an effort to empirically assess their impacts on C cycling. We measured R_s and soil microclimatic variables over four growing seasons following implementation of these management practices using a fully replicated, operational-scale experiment in aspen-dominated forests in northern Minnesota. Treatments included three levels of biomass removal within harvested areas: whole-tree harvest (no slash deliberately retained), 20% slash retained, and stem-only harvest (all slash retained), and two levels of green-tree retention: 0.1 ha aggregate or none. The relative amount of biomass removed had a negligible effect on R_s in harvested areas, but treatment effects were probably obscured by heterogeneous slash configurations and rapid post-harvest regeneration of aspen in all of the treatments. Discrete measurements of R_s and soil temperature within green-tree aggregates were not discernible from surrounding harvested areas or unharvested control stands until the fourth year following harvest, when R_s was higher in unharvested controls than in aggregates and harvested stands. Growing season estimates of R_s showed that unharvested control stands had higher R_s than both harvested stands and aggregates in the first and third years following harvest. Our results suggest that retention of larger forest aggregates may be necessary to maintain ecosystem-level responses similar to those in unharvested stands. Moreover, they highlight the innate complexity of operational-scale research and suggest that the initial impacts of biomass harvest on R_s may be indiscernible from traditional harvest in systems where incidental breakage is high.

1. Introduction

Forests play a prominent role in global carbon (C) cycling because they store substantial quantities of C in their vegetation and soils (Dixon et al., 1994; Jobbágy and Jackson, 2000), and they are important terrestrial sinks for atmospheric CO_2 (Pan et al., 2011). In light of concerns about increasing atmospheric CO_2 concentrations, forest management strategies have become increasingly directed towards promoting C storage (Jandl et al., 2007; Lal, 2005; Liu et al., 2013; McKinley et al., 2011). The C sink capacity of forest ecosystems largely depends on the balance between photosynthesis and respiration of CO_2, the latter of which is dominated by the soil CO_2 efflux (soil respiration, R_s; Schlesinger and Andrews, 2000; Valentini et al., 2000). Forest management activities inherently influence this balance because decisions related to rotation age, species composition, and stand structural attributes have a large influence on C fixation, storage, and efflux over time (Gough et al., 2005; Hardiman et al., 2013; Liski et al., 2002). Managing for C benefits may include the utilization of woody biomass for energy (hereafter referred to as biomass harvesting) to displace fossil fuel-derived C in conjunction with strategies to increase C storage (Schlamadinger and Marland, 1996). However, since managing exclusively for C benefits may compromise the integrity of other ecosystem services, such as biodiversity, it is essential for management strategies to employ a broad

Abbreviations: AGR, aggregate; NONE, no green trees retained; R_s, soil respiration; SOH, stem-only harvest; WTH, whole-tree harvest; 20SR, 20% slash retained.

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framework to meet multiple objectives concurrently (D'Amato et al., 2011; Gustafsson et al., 2012; Ryan et al., 2010).

The intentional retention of pre-harvest structural elements in harvested stands (i.e., variable retention forestry; Franklin et al., 2007) is a component of ecologically-based forestry which can enhance the complexity and biodiversity of the regenerating forest while maintaining other benefits, such as C storage (Franklin et al., 1997; Gustafsson et al., 2012; Vanha-Majamaa and Jalonen, 2001). In particular, the retention of aggregate clumps of intact forest can serve as refugia for late-successional plant species (Halpern et al., 2012; Macdonald and Fenniak, 2007) and increase forest structural complexity (Kruys et al., 2013). Similarly, the retention of some fine and coarse woody debris during biomass harvesting is thought to ameliorate some of the effects on biodiversity associated with complete removal (Bouget et al., 2012; Brazee et al., 2012; Kebli et al., 2012; Riffell et al., 2011). Although there is a growing body of evidence documenting the benefits of aggregate and woody debris retention on forest biodiversity and stand development, there is little information regarding the effects of these practices on forest C dynamics, particularly in operational settings. Empirical quantification of forest C stocks and fluxes, notably R_s, in response to these practices is instrumental in evaluating the effects of variable retention forestry on terrestrial C cycling and improving the resolution of ecosystem process models. Moreover, this information is a critical to assessing our capacity to manage forests for multiple objectives, such as C benefits and biodiversity (Howard et al., 2004; McKinley et al., 2011).

Since R_s has both autotrophic (root) and heterotrophic (soil fauna and microbes) components, it is often expected that removal of overstory trees in a harvest operation will initially cause a decrease in autotrophic respiration, resulting in an overall reduction in R_s (Mattson and Swank, 1989; Nakane et al., 1986; Striegl and Wickland, 1998). However, recently clearcut areas generally have higher soil temperatures, moisture contents, and C substrate availability (from both slash residues and decomposing roots), all of which may enhance heterotrophic respiration and lead to higher overall R_s (Das Gupta and DeLuca, 2012; Gordon et al., 1987; Hendrickson et al., 1989; Londo et al., 1999; Lytle and Cronan, 1998). Retaining some slash residues during biomass harvesting increases shading and insulation of the soil surface, which can lower soil temperatures as well as buffer them from temperature extremes (Devine and Harrington, 2007; Slesak, 2013). Since R_s is largely dependent on soil temperature (Fang and Moncrieff, 2001), increasing slash retention could reduce harvest-related increases in R_s (Slesak et al., 2010). However, R_s responses to variable slash retention are unpredictable and include higher R_s associated with greater slash residues under moisture limiting conditions (Edwards and Ross-Todd, 1983), as well as no differences in R_s among different levels of slash retention (Hendrickson et al., 1989; Mattson and Swank, 1989). These inconsistencies may be the result of spatial variability in slash configurations (Eisenbies et al., 2005; Klockow et al., 2013), seasonal variability in microclimate conditions (Edwards and Ross-Todd, 1983), or site-to-site variability (Gough et al., 2005; Howard et al., 2004).

R_s responses in retained forest aggregates are likely to differ from both intact mature forest and other variable retention harvests. For example, although microclimate conditions inside aggregates are more similar to the interior of a mature forest than other silvicultural systems (such as shelterwood systems; Franklin et al., 1997), soil and air temperatures can still vary widely within an aggregate, especially near the edges (Heithecker and Halpern, 2007), which may increase variability in R_s. Also, tree mortality rates within aggregates are generally lower than those of retained dispersed trees (Urgenson et al., 2013), which would result in higher inputs from root respiration inside retained aggregates compared to dispersed tree systems. Ecosystem responses are likely to be variable and largely depend on the size and shape of the retained aggregate; nonetheless, the increasingly common use of intentional aggregate retention during harvesting operations (Franklin et al., 1997; Gustafsson et al., 2012; Klockow et al., 2013) underscores a need to quantify the potential impacts of these aggregates on stand-level R_s.

To better understand the initial effects of woody biomass removal and forest aggregate retention (green-tree retention) on C fluxes, we measured R_s at a site-replicated harvest manipulation in mature aspen-dominated forest of northern Minnesota during the first four growing seasons following harvest treatments. Trembling aspen (*Populus tremuloides* Michx.) is a vigorous early-successional species that reproduces clonally from root suckers. It is the most widely distributed tree species in North America, and it is commercially important, particularly in the northern Great Lakes region (Perala, 1990, 1977). We investigated biomass removal and green-tree retention effects on R_s using a factorial design fully replicated at four study sites. Our treatments included green-tree retention (forest aggregates) factorially combined with three levels of biomass removal. In addition to the more common stem-only harvest (merchantable boles of trees harvested with all slash residues retained on site) and whole-tree harvest (merchantable boles of trees harvested along with slash residues) biomass removal treatments, we also assessed harvest with retention of 20% slash on site, which follows the site-level guidelines for biomass harvesting in several regions, including Minnesota (MFRC, 2007). Collectively, this design allowed us to evaluate the effects of a multiple objective approach (i.e., increased biomass utilization with some retention for biodiversity and structural complexity). We expected that (1) retained biomass residues would moderate soil temperatures via shading and cause R_s to decrease with decreasing biomass removal. Additionally, we expected (2) R_s in harvested stands with no green-tree retention to be greater than that in aggregates and the controls because the harvested stands would have a flush of labile C inputs from decomposing roots and slash material, as well as warmer soil temperatures. We also expected R_s in aggregates to respond similarly to unharvested controls.

2. Materials and methods

2.1. Study site description and experimental design

Four study sites (blocks) were established in 2009 in northern Minnesota, USA, near the towns of Independence (47°0′N, −92°24′W), Melrude (47°15′N, −92°19′W), and Orr (48°9′N, −92°59′W and 48°1′N, −92°59′W) in St. Louis County. The sites were similar in elevation (395–428 m) and slope (0–8%). The climate is northern continental, with mean annual precipitation of 660–710 mm, most of which occurs during the growing season of May to October. Mean annual temperatures range from −16 °C in January to 26 °C in July. All of the sites were established in mature aspen-dominated stands that had regenerated after clearcut harvest (stand age: 55–68 years). The dominant hardwood species was *P. tremuloides* (aspen); other common species included *Betula papyrifera* Marshall, *Acer rubrum* L., *Fraxinus nigra* Marshall (hardwoods), *Abies balsamea* (L.) Mill., *Picea mariana* (Mill.) Britton, and *Picea glauca* (Moench) Voss. (softwoods) and occasional *Thuja occidentalis* L. and *Pinus strobus* L. The soils at all of the sites are till-derived loams; one of the sites has stony to very stony loams and sandy loams while the remaining three sites have silt loams and loams. Prior to the harvest disturbance in the current study, the mean mineral soil C and N contents were 66.41 ± 4.03 Mg ha^{-1} and 4.03 ± 0.07 Mg ha^{-1}, respectively (0–20 cm depth). The mean preharvest forest floor depth was 2.29 ± 0.05 cm. Additional detailed information about site characteristics can be found in Klockow et al. (2013) and Slesak (2013).

This study is part of a larger experiment that included multiple levels of green-tree retention nested within biomass removal treatment stands (see Klockow et al., 2013). We focused on the effects of variable (1) biomass removal levels in harvested areas (stem-only harvest, SOH; 20% slash retained, 20SR; and whole-tree harvest, WTH), and (2) green-tree retention (intact forest aggregate, AGR and no green-trees retained, NONE). Both biomass removal and green-tree retention treatments were compared to unharvested control stands. The treatments were applied in a completely randomized design that was blocked by site. Each replicate stand within a block was approximately 4.1 ha in size. Stands were harvested in February 2010 with the exception of two roughly rectangular aggregates (~0.1 ha each) of trees retained in each. Aspen in harvested areas regenerated rapidly; post-harvest seedling densities were 45,955–65,450 stems ha^{-1} one year following harvest. Four circular (0.04 ha) plots were established within each treated stand: two in the aggregate condition and two in the open, harvested condition. Plots in the aggregate condition were established in the middle of each aggregate such that the entire plot fell within it. The two plots in the open condition were randomly selected from an original set of six plots in each stand that were established prior to harvest. Thus, we used three treated stands within each of the four blocks, which allowed us to efficiently examine the effects of biomass removal and green-tree retention. The two plots in the open, harvested condition of each stand represented one level of biomass removal (SOH, 20SR, and WTH; n = 8 plots in each biomass removal treatment; Online resource 1). The two plots placed in the aggregates nested within each of the biomass removal treatments represented the AGR condition, and the two plots in the open, harvested condition represented the NONE condition, amounting to a total of n = 24 plots in the green-tree retention treatments (Online resource 1). One unharvested stand at each block contained three randomly established control plots (n = 12).

2.2. Soil respiration and microclimate measurements

Respiration collars (polyvinyl chloride, 20 cm diameter, 12.5 cm height) were installed following harvest in May of 2010. Collars were beveled to minimize soil disturbance during insertion and inserted into the soil to a depth of 5–7 cm. Collars were left in place during the course of the study, but re-fitted in May 2011, 2012, and 2013 and allowed to equilibrate for at least three days prior to the first respiration measurement. Four collars were placed in each plot (one at plot center; three at 11 m from plot center at 30°, 150° and 270° azimuths; Online resource 2). Measurements were taken between 0900 and 1400 h to reduce diel variation, and times (e.g., morning or afternoon) were randomly varied among plots within a site throughout the growing season to compensate for daytime variability (Davidson et al., 2002). All live vegetation inside the collars was clipped prior to measurement.

R_s was measured as soil CO_2 efflux with a portable gas analyzer (Li-8100 Soil CO_2 Flux System; Li-COR Biosciences, Lincoln, NE, USA) attached to an Li-8100–103 chamber. Measurements were made every 3–4 weeks throughout the growing season (five measurements in 2010; six measurements in 2011 and 2012; three measurements in 2013), and sites were measured in the same order throughout the growing season. Simultaneous measurements of soil temperature (10 cm) and moisture (6 cm) were recorded next to the collar by the Li-8100 temperature and moisture probes. Additionally, continuous measurements of soil temperature (approx. 7.5 cm) were logged at 2-h intervals at each collar using Thermochron iButton temperature loggers (Model DS1921G; Maxim Integrated Products Inc., San Jose, CA).

2.3. Data analysis

All analyses were conducted in SAS (Version 9.3, SAS Institute, Inc., 2010) using PROC MIXED, which is robust to unbalanced designs, and plot means were considered the experimental unit (each the mean of four collars). Separate models were developed to test for effects of biomass removal or green-tree retention, but both models included the unharvested control. To account for non-simultaneous measurements and site-to-site variability, biomass removal models included plots nested within sites as random effects. Similarly, green-tree retention models included plots nested within stands and sites as random effects; this nesting approach accounted for variable slash loadings in the NONE treatment. R_s data were log transformed to stabilize the variance, and residuals were visually inspected to confirm the assumptions of ANOVA were met (normality and homoscedasticity).

A two-parameter exponential function (Eq. (1)) was used to analyze the relationship between empirical measurements of R_s and soil temperature (Fahey et al., 2005; Lloyd and Taylor, 1994; Pang et al., 2013; Tang et al., 2009; Tang et al., 2008) for each growing season and treatment (biomass and green tree retention separately):

$$R_S = R_0 e^{\beta T} \quad (1)$$

where R_s is measured soil CO_2 efflux, T is the soil temperature at 10 cm, and R_0 and β are regression coefficients. Note that the temperature sensitivity (Q_{10}) can be estimated from Eq. (1) from β by $Q_{10} = e^{10\beta}$. Regression parameters (R_0 and β) were compared to detect treatment differences among three alternative models: (1) different slopes, (2) different slopes and intercepts, or (3) no differences among treatments. Bayesian information criteria (BIC) were used to determine the best-fitting model. Soil moisture was also initially explored as an additional potential parameter in log-transformed Eq. (1), but plot-level models showed that it was not a significant predictor of R_s on its own ($r^2 < 0.05$ in 80% of models), and when it was used in combination with soil temperature, it was rarely a significant term in the model ($P > 0.1$ in more than 70% of models). This is consistent with similar studies in the Great Lakes region (Bolstad et al., 2004; Euskirchen et al., 2003; Stoffel et al., 2010; Tang et al., 2009).

Treatment effects on discrete measurements of R_s, temperature, and moisture, for each growing season were assessed using repeated measures two-way analysis of variance (ANOVA). Both models (biomass removal and green-tree retention) tested for the main effects of treatment, month, and treatment by month interactions with month as the repeated factor and a Satterwaite approximation for the denominator degrees of freedom. Tukey–Kramer tests were used to separate treatment means of significant main effects. The SLICE command was used to separate means within a month when significant treatment by month interactions were encountered. Given the existing variability in soil respiration over the course of the growing season and our research objectives, we focused on treatment, not seasonal, effects, in this analysis. Moisture probe failure at the beginning of the 2010 growing season led to missing soil moisture data at two sites during the first month, so we excluded May measurements from the 2010 soil moisture analysis. Temperature probe failure in 2013 led to an inadequate number of discrete soil temperature measurements for that year. Thus, for 2013, we only analyzed the discrete measurements of R_s and soil moisture (not soil temperature), and we did not conduct any analyses that relied on R_s-soil temperature relationships (e.g., temperature sensitivity function and estimates of growing season respiration). Treatment variability was assessed using the coefficients of variation (CV) computed for each plot; CVs were analyzed in the same way as the other discrete measurements.

Cumulative growing season respiration was modeled by fitting Eq. (1) to each treatment, site, and year to develop stand-specific respiration models (Laganière et al., 2012; Savage and Davidson, 2001). These models were applied to continuous temperature data for each collar, extrapolated to 2-h intervals, and summed to get daily totals (g C m^{-2}). Daily sums were averaged for each plot, and plot-level, growing season R_s was computed as the sum of all the days between mid-May and mid-October (157 days). However, due to a 3-week gap in the continuous temperature data in late fall of 2010, the growing season R_s extends to late September in 2010 (127 days). Treatment differences were examined for each year using ANOVA and Tukey–Kramer tests to separate means.

3. Results

3.1. Relationships between soil temperature and R_s

Soil temperature explained much of the variation in R_s in the biomass removal and green tree retention treatment models throughout 2010, 2011, and 2012 (r^2 = 0.30–0.80; Table 1; Fig. 1). R_s exhibited a bell shaped-curve throughout the growing season that was positively related to soil temperature (Fig. 1–3). The best-fitting model determined by BIC was that where the slopes and intercepts did not differ among biomass removal or green-tree retention treatments in any of the years (alternative model 3). However, model slopes were generally higher in the controls than in the treatments in 2010 and 2011, and overall values were generally higher in 2012 than 2010 and 2011 (Table 1).

3.2. Biomass removal effects on R_s and soil microclimate

None of the monthly discrete variables measured (R_s, soil temperature, soil moisture) differed among the three levels of biomass removal (SOH, 20SR, or WTH; Fig. 2; Table 2), but some differences existed between biomass removal and the unharvested control, which typically had the highest R_s throughout the study period (Fig. 2a–d). Differences in R_s between biomass removal level and the unharvested control varied interannually and seasonally; for example, R_s in the control was higher than 20SR and SOH late in the growing seasons of 2010 (Fig. 2a), but lower than 20SR early in 2011 (Fig. 2b). No differences in R_s were observed between any of the biomass removal levels and the unharvested control in 2012 (Fig. 2c). The biomass removal effect was significant for R_s in 2013 (P = 0.040), but Tukey–Kramer tests did not reveal any differences among the treatments at $\alpha = 0.05$ (Fig. 2d). Soil temperature and moisture responses were inconsistent, but both tended to be lower in the unharvested controls compared to the biomass removal treatments (Fig. 2e–l). Growing season R_s was higher in the unharvested control than all three harvested biomass removal treatments in 2010 and 2012, but no differences were observed in 2011 (Fig. 4a).

3.3. Green-tree retention effects on R_s and soil microclimate

R_s in the harvested NONE stands (all biomass removal levels) were lower than those of the unharvested control stands in the latter part of 2010 and throughout 2012 and 2013 (Fig. 3a–d; Table 2). R_s in the AGR treatments was generally intermediate in magnitude, and it did not differ from the NONE or the unharvested control stands in the first three years following harvest (2010–2012). In 2013, R_s in the AGR treatment was less than the unharvested control stands, but it did not differ from the NONE stands. R_s in the NONE stands tended to peak earlier in the summer (June) than the unharvested control and AGR treatments (July/August for both) during the first three measurement years (Fig. 3a–d). This contrasted with soil temperature, which peaked in July for all treatments during the first three years and was higher in NONE stands than the unharvested control stands in 2011 and 2012

Table 1
Model parameters (SE) estimated from temperature sensitivity function, $R = R_0 + \beta T$, where R is the natural logarithm of the soil respiration flux and T is the soil temperature at 10 cm. Measurements were made at four replicated sites in the first 3 years following harvest in aspen-dominated forests of northern Minnesota with manipulated levels of biomass removal and green-tree retention. Correlation coefficients (r^2) were estimated using the relationship between observed and predicted values; P-values are given for the slope term. The slopes and intercepts did not differ among the biomass removal or green-tree retention treatments during any of the measurement years.

Year	Treatment		R_0	β	N	r^2	P-value
2010	Control		0.0605 (0.27)	0.111 (0.02)	58	0.72	0.001
	Biomass removal[a]	WTH	0.663 (0.19)	0.052 (0.01)	38	0.30	<0.0001
		20SR	0.328 (0.28)	0.079 (0.02)	38	0.34	0.141
		SOH	−0.234 (0.30)	0.106 (0.02)	34	0.54	0.007
		All	0.253 (0.13)	0.083 (0.01)	168	0.59	<0.0001
	Green-tree[b]	AGR	0.150 (0.34)	0.090 (0.01)	119	0.50	0.123
		NONE	0.390 (0.34)	0.075 (0.01)	110	0.35	0.010
		All	0.244 (0.10)	0.087 (0.01)	287	0.64	<0.0001
2011	Control		−0.226 (0.17)	0.118 (0.01)	59	0.80	<0.001
	Biomass removal	WTH	0.219 (0.13)	0.073 (0.01)	44	0.70	<0.0001
		20SR	0.330 (0.21)	0.069 (0.01)	42	0.44	0.750
		SOH	0.109 (0.21)	0.079 (0.01)	39	0.38	0.661
		All	0.076 (0.08)	0.086 (0.01)	184	0.75	<0.0001
	Green-tree	AGR	0.004 (0.15)	0.093 (0.01)	127	0.63	0.016
		NONE	0.218 (0.15)	0.074 (0.01)	125	0.51	<0.0001
		All	0.061 (0.07)	0.090 (0.01)	311	0.77	<0.0001
2012	Control		−0.239 (0.32)	0.143 (0.02)	72	0.67	0.762
	Biomass removal	WTH	−0.471 (0.23)	0.139 (0.01)	48	0.74	<0.0001
		20SR	−0.174 (0.33)	0.122 (0.02)	48	0.74	0.287
		SOH	−0.602 (0.35)	0.146 (0.02)	47	0.69	0.648
		All	−0.364 (0.11)	0.137 (0.01)	215	0.80	<0.0001
	Green-tree	AGR	−0.224 (0.21)	0.130 (0.01)	143	0.64	0.364
		NONE	−0.400 (0.21)	0.135 (0.01)	143	0.72	0.570
		All	−0.259 (0.11)	0.134 (0.01)	358	0.80	<0.0001

[a] Biomass removal treatments: WTH, whole-tree harvest; 20SR, 20% slash retained; SOH, stem-only harvest.
[b] Green-tree retention treatments: AGR, green-tree clump; NONE, clearcut harvest (all biomass removal levels combined).

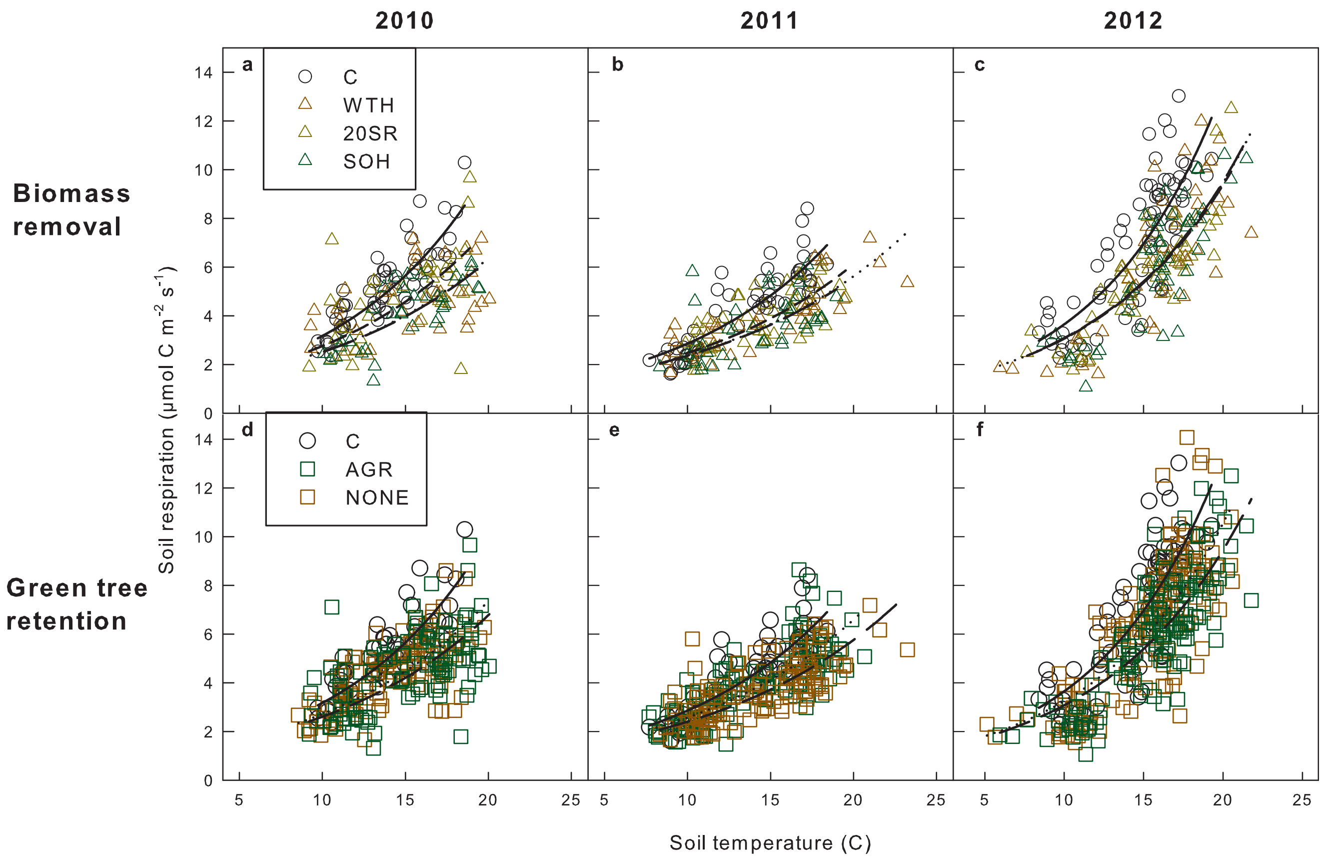

Fig. 1. The relationships between soil respiration and soil temperature (10 cm) for biomass removal (a–c) and green-tree retention (d–f) treatments. Measurements were taken in the first three growing seasons following harvest in an aspen-dominated forest in northern Minnesota. Points are the plot mean of four collar measurements. An exponential function of the form $R_S = R_0 e^{\beta T}$ was created for each year and treatment, and regression curves were fitted for each treatment level using the natural logarithm of R_S. See Table 2 for model parameters. Biomass removal treatment are abbreviated as: WTH = whole-tree harvest (dotted line), 20SR = 20% slash retained (short dash line), SOH = stem-only harvest (long dash line); green-tree retention treatments are abbreviated as: AGR = aggregate (dotted line), NONE = no green trees retained (long dash line), and C = unharvested control for both treatments (solid line).

(Fig. 3e–h). Soil moisture was consistently higher in the NONE than the unharvested control and the AGR treatments in 2010, 2012, and 2013, but this pattern was more variable in 2011 (Fig. 2i–l). Growing season R_s was higher in the unharvested control stands than the NONE and the AGR treatments in 2010 and 2012, but no differences were observed in 2011 (Fig. 4b).

3.4. Treatment and among-site variability

The variability in R_s (CV) among biomass removal and green-tree retention treatments was similar in all years (24, 22, 23, and 24%, $P = 0.502$, 0.908, 0.148, and 0.369 for biomass removal, $P = 0.870$, 0.919, 0.654, and 0.703 for green-tree retention, all values for 2010, 2011, 2012, and 2013, respectively). Overall, among-site variability in R_s was generally low in 2010 and 2012 (all growing season site R_s means of unharvested controls were within 0.5 µmol C m^{-2} s^{-1} of each other). Higher among-site variability was observed in 2011, when respiration at one of the sites was lower than the other three by about 1.5 µmol C m^{-2} s^{-1}.

4. Discussion

Our study adds to the growing body of research that examines R_s responses to harvest in forest ecosystems, and, to our knowledge, it is the first to integrate two contemporary management practices, biomass harvest and variable retention forestry. Empirical estimates of R_s responses to different forest management approaches are increasingly important as practitioners strive to meet multiple objectives simultaneously. The discrete R_s measurements we observed are within the range reported by other studies in the Great Lakes region (Curtis et al., 2005; Forrester et al., 2013; Martin and Bolstad, 2005), but our modeled growing season estimates are on the low end of annual values in the literature in this region (Bolstad et al., 2004; Forrester et al., 2013; Stoffel et al., 2010), probably because we did not include non-growing season measurements. The variability we report (CVs) for R_s (12–36% across all treatments and years) is also within the commonly reported range for these measurements for other disturbed and intact forests (Davidson et al., 2002; Edwards and Ross-Todd, 1983; Kobziar and Stephens, 2006). Hence, our research is widely relevant for estimating and projecting biomass and variable retention effects on temperate forest C cycling.

4.1. General effects of harvest on R_s in aspen-dominated forests

We expected R_s in the harvested stands to exceed that in unharvested control stands because warmer soil temperatures and inputs of C substrate from slash and decaying fine roots would facilitate microbial activity and increase heterotrophic respiration. In contrast, our data suggest that R_s is reduced in harvested stands compared to unharvested control stands, and this pattern persists for at least four growing seasons following harvest. The direction of the post-harvest R_s response largely depends on the balance between harvest-induced increases in heterotrophic respiration and changes in autotrophic respiration relative to unharvested

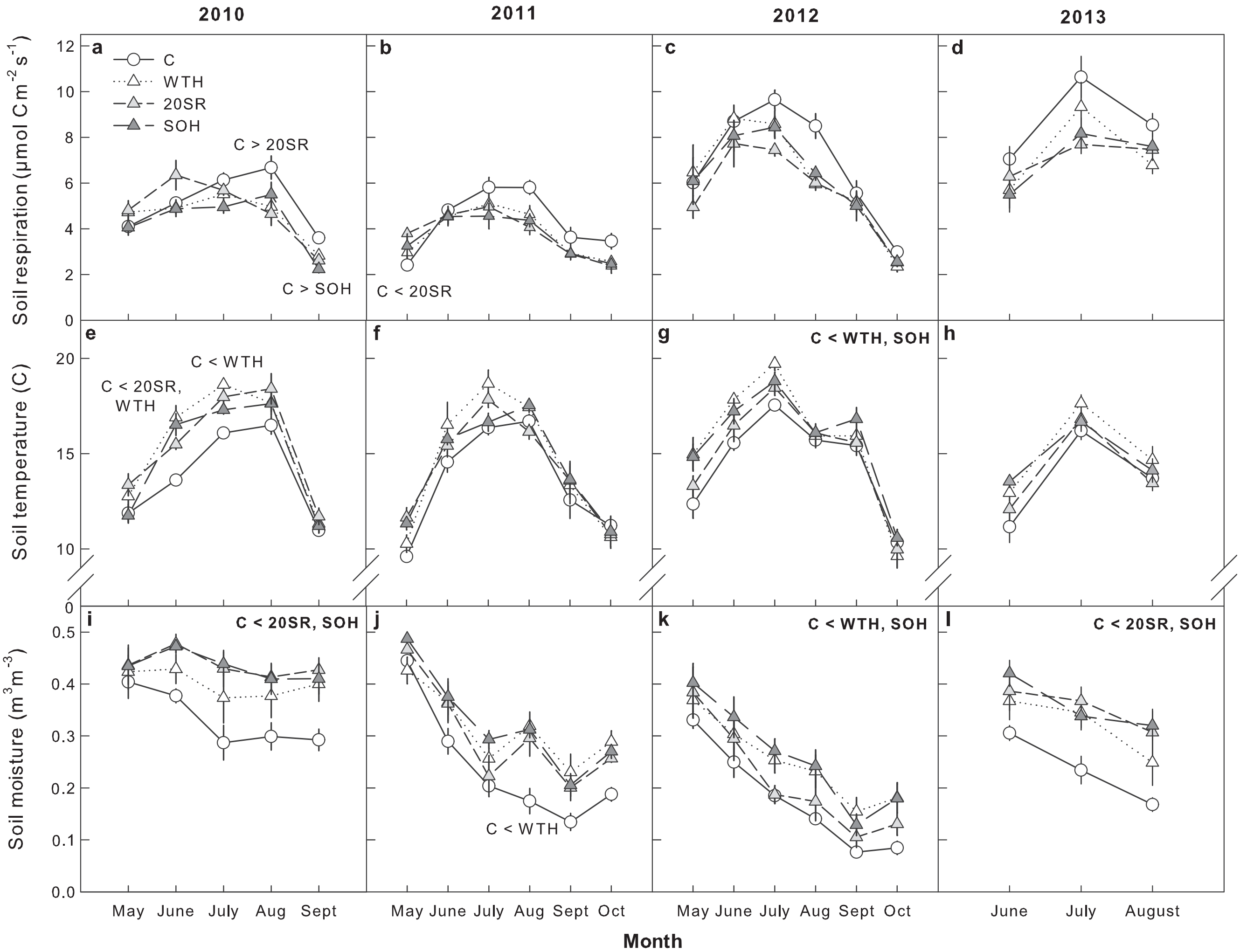

Fig. 2. Biomass removal effects on discrete measures of soil temperature (10 cm; a–d), soil moisture (6 cm; e–h), and soil respiration (i–k) in the first four years following harvest in an aspen-dominated forest in northern Minnesota. Significant treatment differences ($P < 0.05$) from repeated measures ANOVA are shown in top right corner (**bold**) for each variable and year. When slash retention effects changed over time (significant treatment by time interaction), treatment differences are shown by month. The analysis for 2010 soil moisture does not include May because of missing data. The temperature data from 2013 was not analyzed due to equipment failure; points were estimated based on continuously logged temperature data for comparison purposes. Each point represents the mean of 8 treated plots ($n = 8$) or 12 unharvested control plots ($n = 12$) ± 1 SE. See Fig. 1 for treatment abbreviations.

forests, and it can also be site- and species-dependent (Lavoie et al., 2013). For example, the lag time between harvest and root mortality can range from months to years (Noormets et al., 2012) and rates of vegetation regeneration vary among ecosystems (Howard et al., 2004). Responses may also depend on site fertility (Smolander et al., 2010) and the temperature sensitivity of the dominant tree species (Laganière et al., 2012). Although many studies have quantified post-harvest R_s responses, few have explicitly tracked R_s following harvest in aspen-dominated forests. A study by Weber (1990) in aspen forests of eastern Ontario also documented a decrease in R_s after harvest that lasted for the subsequent two growing seasons before recovering in the third. Our results, which suggest a longer post-harvest recovery in R_s, indicate that C cycling processes in aspen-dominated forests may not recover as quickly from harvest disturbance as concluded by Weber (1990).

R_s was generally lower in harvested stands in spite of generally warmer soil temperatures and relatively rapid post-harvest aspen regeneration, both of which would be expected to contribute to higher R_s during stand development. Harvesting most likely led to a reduction in belowground allocation to fine root growth and metabolism (Nave et al., 2011) because regenerating aspen suckers expend more resources to aboveground structures (FitzGerald and Hoddinott, 1983), and this probably reduced R_s in harvested areas compared to unharvested forest. In addition, although not statistically significant, unharvested control stands generally had greater regression coefficients for soil temperature and temperature explained a larger proportion of the variation in R_s, in comparison to harvested stands. This suggests that the temperature sensitivity of R_s was lower in harvested stands, presumably due to lower root growth and metabolism (Boone et al., 1998), and is consistent with earlier findings from a harvested northern hardwood forests (Toland and Zak, 1994).

4.2. Effects of biomass removal

We expected that R_s would vary among the biomass removal levels such that treatments with less biomass retained would be less shaded and, thus, associated with warmer soil temperatures and greater R_s (WTH > 20SR > SOH > control). Instead, none of the variables we measured (R_s, soil temperature, or soil moisture), nor the modeled growing season estimates, varied among the different levels of biomass removal, and the only differences we observed were relative to the unharvested control stands. The lack

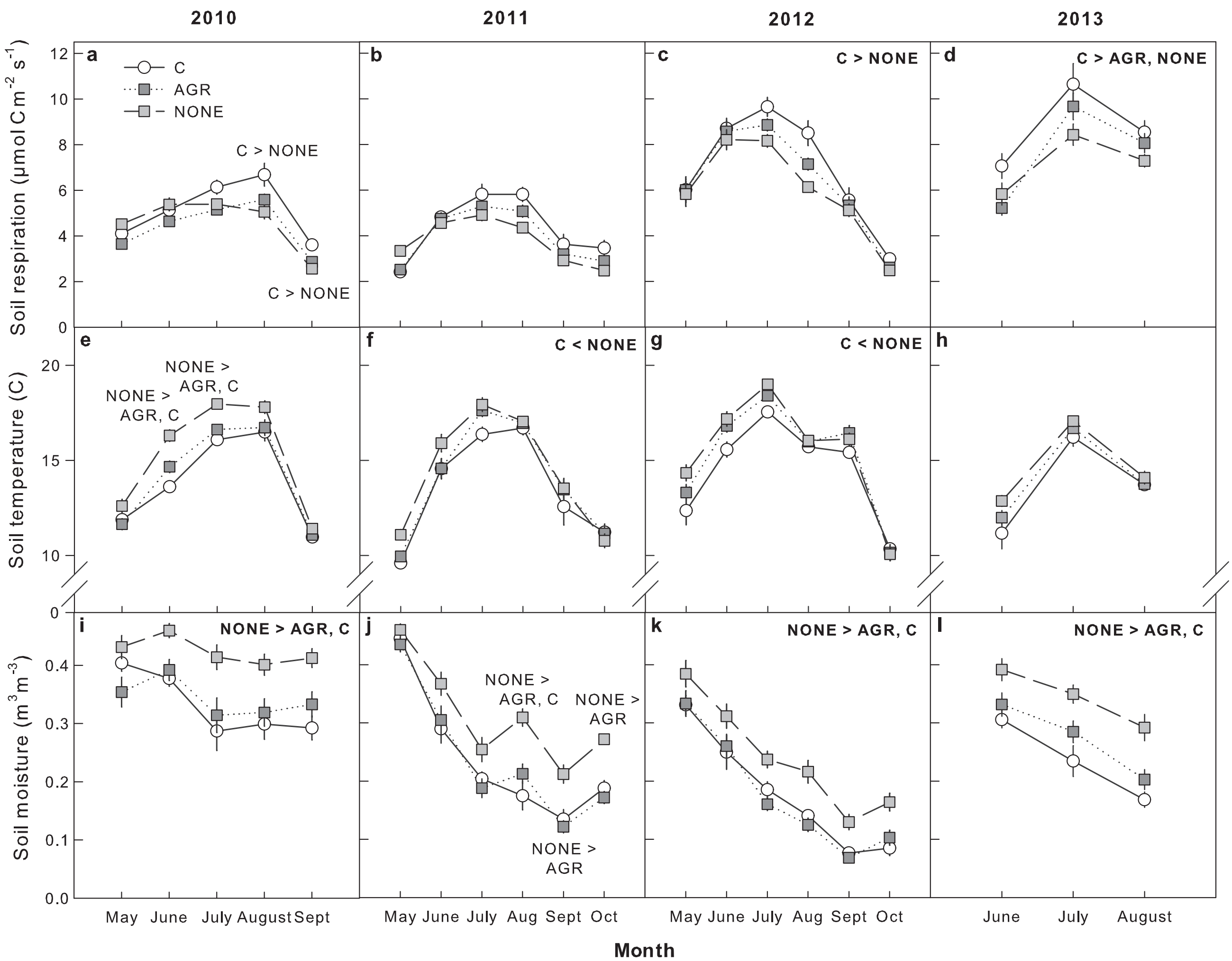

Fig. 3. Green-tree retention effects on discrete measures of soil temperature (10 cm; a–d), soil moisture (6 cm; e–h), and soil respiration (i–k) in the first 4 years following harvest in an aspen-dominated forest in northern Minnesota. Significant treatment differences ($P < 0.05$) from repeated measures ANOVA are shown in top right corner (**bold**) for each variable and year. When green-tree retention effects changed over time (significant treatment by time interaction), treatment differences are shown by month. The analysis for 2010 soil moisture does not include May because of missing data. The temperature data from 2013 was not analyzed due to equipment failure; points were estimated based on continuously logged temperature data for comparison purposes. Each data point represents the mean of 24 treated plots ($n = 24$) and 12 control plots ($n = 12$) ± 1 SE. See Fig. 1 for treatment abbreviations.

Table 2
F-statistic *P*-values from repeated measures ANOVA for soil temperature (10 cm), soil moisture (6 cm), and soil respiration for each year by biomass removal (BR), month (M), and green-tree retention (GTR). Measurements were made in the first four years following harvest at four replicate sites in aspen-dominated forest of northern Minnesota.

	Soil temperature				Soil moisture				Soil respiration			
	2010	2011	2012	2013[a]	2010	2011	2012	2013	2010	2011	2012	2013
BR	**<0.0001**	0.103	**0.005**	–	**<0.001**	**0.010**	**0.003**	**0.002**	**0.027**	0.257	0.149	**0.040**
M	**<0.0001**	**<0.0001**	**<0.0001**	–	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
BR x M	**0.003**	0.525	0.194	–	0.583	**0.010**	0.263	0.275	**<0.001**	**0.004**	0.787	0.660
GTR	**<0.0001**	**0.036**	**0.015**	–	**<0.001**	**<0.0001**	**<0.001**	**<0.001**	**0.006**	0.094	**0.049**	**0.008**
M	**<0.0001**	**<0.0001**	**<0.0001**	–	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
GTR x M	**0.031**	0.667	0.167	–	0.596	**0.016**	0.055	0.495	**<0.0001**	**<0.001**	0.142	0.210

Bold values indicate significance at $P < 0.05$.
[a] Soil temperature data from 2013 was not available.

of differences among biomass removal levels may be partially explained by the unpredictable relationship between prescribed and actual levels of biomass retention at these sites. Klockow et al. (2013), working at these study sites, observed that actual biomass retention levels in WTH and 20SR stands were more than half that of the available biomass following harvest, which they attributed to a high rate of incidental breakage. Higher levels of breakage are associated with winter harvests because cold conditions make trees, particularly aspen, brittle (Rittenhouse et al., 2012). Although it is likely that heterogeneity in biomass quantities and spatial configurations masked treatment effects among the biomass removal treatments (Eisenbies et al., 2005; Slesak et al., 2011), they are inextricably linked to the operational scale of our study, and, thus, our results captured the innate and realistic variability of harvesting operations.

In addition to variability in actual amounts of biomass retention, treatment differences may have also been too subtle to detect within the context of the broader harvest disturbance and

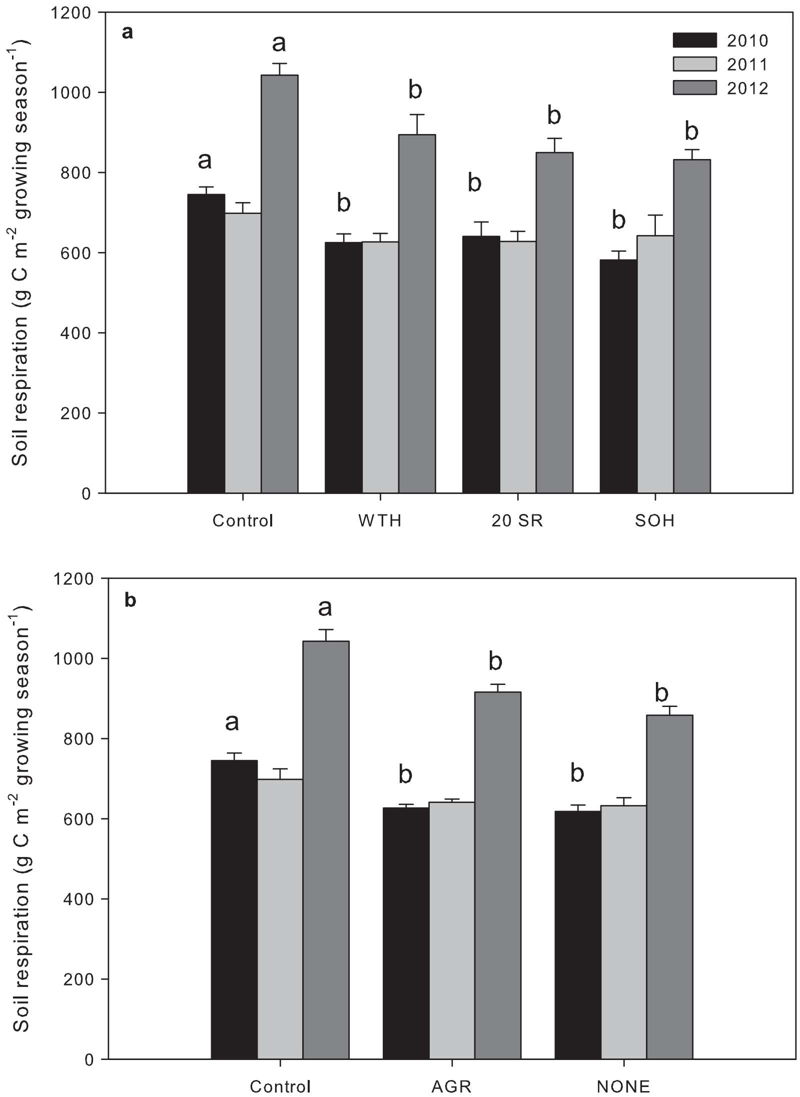

Fig. 4. Modeled growing season (mid-May to mid-October) soil respiration by biomass removal (a) and green-tree retention (b) treatments. Measurements of soil respiration and temperature were taken following harvest in an aspen-dominated forest of northern Minnesota. Growing season soil respiration was modeled using discrete measurements and continuous soil temperature measurements. Bars represent plot means ($n = 8$ for biomass removal; $n = 24$ for green tree retention; $n = 12$ for all unharvest controls) ± 1 SE. Unique letters denote differences ($P < 0.05$) among treatments for each year. The growing season estimate for 2010 was calculated to late-September because of a gap at the end of the continuous temperature record during that year. See Fig. 1 for treatment abbreviations.

regeneration dynamics. The removal of overstory trees is a considerable disturbance compared to the slash manipulations; as a result, the harvest itself may have overwhelmed any differences among the levels of biomass removal (Mattson and Swank, 1989). Additionally, rapid post-harvest aspen regeneration may have dampened the biomass removal responses by increasing the amount of shading on the soil surface, which would reduce the influence of slash on microclimate (Gough et al., 2005; Slesak, 2013). Thus, while our findings demonstrate that the relative amount of biomass removed has a negligible impact on post-harvest R_s, these results are applicable to operational settings in forests that experience rapid post-harvest regeneration and growth.

4.3. Retention of aggregate clumps in biomass harvest

One of the goals of retaining forest aggregates is to ameliorate changes in microclimatic conditions in the surrounding harvested areas and, thus, provide refugia for late successional species (Franklin et al., 1997; Halpern et al., 2012). Smaller aggregates, such as those in our study (0.1 ha), are more susceptible to edge effects (Aubry et al., 2009; Heithecker and Halpern, 2007), which may dampen aggregate buffering ability and could disproportionately increase the variability of R_s inside aggregates. In particular, soil temperature, which influences a range of critical biological activities, including R_s (Kirschbaum, 1995; Lloyd and Taylor, 1994), tends to be more spatially variable within an aggregate than soil moisture (Heithecker and Halpern, 2007). Additionally, greater light penetration on the edges of aggregates could enhance understory growth and regeneration compared to unharvested forest (Nelson and Halpern, 2005), which could, in turn, increase autotrophic respiration.

Edge effects probably promoted high variability within aggregates, which may have precluded our ability to distinguish R_s and soil temperature in the aggregates from the harvested treatments and the unharvested control stands during the first three growing seasons. Although our study design did not allow us to explicitly test spatial variability or edge effects inside aggregates, the green-tree retention treatment responses of R_s more closely resembled those of soil temperature than soil moisture in that both R_s and soil temperature were somewhat intermediate between the harvested treatments and the unharvested control stands. Thus, although it appears that the aggregates mitigated some of the environmental changes from the surrounding harvested areas, particularly soil moisture, their prominent edge effects probably inhibited the amelioration of soil temperature and R_s responses inside aggregates during the first three growing seasons. Over time, aspen regeneration in the harvested areas may diminish edge effects in aggregates, which could explain why R_s inside aggregates responded similarly to harvested areas during the 2013 growing season.

4.4. Variability and limitations

Interannual climate variability often has a greater impact on R_s responses than forest silvicultural treatments, such as thinning, which can make it difficult to distinguish treatment effects (Pang et al., 2013; Tang et al., 2005), especially over relatively short-term time scales (Sierra et al., 2009). Climate variability may explain why the treatment differences we observed varied among years. Growing season soil temperatures were generally higher for a longer duration in 2012 than in the preceding two years, which likely promoted greater R_s rates in that year (Euskirchen et al., 2003; Goulden et al., 1996). Consistent with this, air temperatures were generally warmer in 2012 than the other study years (Online supplement 3). Similarly, soil moisture was not a significant predictor of R_s, but variable precipitation patterns (Online supplement 3) may have constrained discrete R_s responses in some instances, particularly during 2012, when precipitation was uneven during the course of the growing season (Fahey et al., 2005; Savage and Davidson, 2001; Zhou et al., 2007).

In addition to climate variability, other sources of variability, including spatial and measurement, likely contributed to the inconsistencies in treatment responses. Our study was conducted across four replicated sites harvested at the operational scale, and, while this undoubtedly increased the overall spatial and treatment variability, it greatly increases the applicability of our results to realistic forest management scenarios. However, even slight differences in micro-topography can increase spatial variability in forests by creating micro-depressions that can saturate soils (Rayment and Jarvis, 2000). In addition, disturbances, such as forest harvesting, are known to increase the spatial variability of R_s measurements (Laporte et al., 2003). Our study was not specifically designed to assess post-harvest spatial variability, so we cannot test for treatment variability within-sites (Online supplement 4). However, we accounted for potential variability among sites, stands, and plots by nesting them within our statistical models. Even so, the combined effects of non-uniform biomass configurations in the harvested areas (Klockow et al., 2013) and edge effects in the aggregates, most likely added to the variability we observed among the management treatments. Finally, logistic constraints made it impossible to measure all four sites in the same day, so we compensated by measuring sites in the same order throughout the growing season and limiting our measurements to midday (0900–1400 h; Davidson et al., 2002). Still, stochastic weather events, such as rainfall, probably influenced R_s measurements to some extent.

5. Conclusions

The broad impacts of woody biomass utilization on forest C dynamics need to be carefully assessed to guide effective policy-making for climate change mitigation (McKechnie et al., 2011). Moreover, green-tree retention is increasingly being integrated into forest harvesting prescriptions to maintain mature forest conditions and processes in clear-cut areas (Franklin et al., 2007), but the effectiveness at maintaining pre-harvest C cycling patterns has been little studied. Our research fills an important knowledge gap in both of these areas area by offering an operational-scale, empirical analysis of the impacts of biomass harvest and green-tree retention on R_s. Although the relative amount of biomass removed did not affect R_s, the collective effect of harvesting (all three biomass removal levels combined, NONE) generally reduced R_s compared to unharvested control stands. Given this, we infer that the harvest disturbance has a much greater impact on R_s than the relative amount of biomass removed. However, we caution that these results may be forest type-dependent given the high amount of incidental breakage that occurred (Klockow et al., 2013) and the rapid post-harvest regeneration in aspen forests. Retention of green-tree aggregates appeared to mitigate changes in soil moisture, which is a central goal in utilizing them during forest management, but the variable responses of soil temperature and R_s inside aggregates suggests that edge effects were still quite pronounced in these relatively small aggregates. As green-tree retention strategies are more broadly applied, our results indicate that an increase in the recommended aggregate size may help to maintain ecosystem-level processes. Additional research is necessary on both biomass harvest and green-tree retention practices to better refine management guidelines, but our results provide important baseline information on the combined impacts of these practices on forest C dynamics.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.05.052.

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