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Rapid rebound of soil respiration following partial stand disturbance by tree girdling in a temperate deciduous forest

Jennifer H. Levy-Varon · William S. F. Schuster · Kevin L. Griffin

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Abstract Forests serve an essential role in climate change mitigation by removing CO_2 from the atmosphere. Within a forest, disturbance events can greatly impact C cycling and subsequently influence the exchange of CO_2 between forests and the atmosphere. This connection makes understanding the forest C cycle response to disturbance imperative for climate change research. The goal of this study was to examine the temporal response of soil respiration after differing levels of stand disturbance for 3 years at the Black Rock Forest (southeastern NY, USA; oaks comprise 67 % of the stand). Tree girdling was used to mimic pathogen attack and create the following treatments: control, girdling all non-oaks (NOG), girdling half of the oak trees (O50), and girdling all the oaks (OG). Soil respiratory rates on OG plots declined for 2 years following girdling before attaining a full rebound of belowground activity in the third year. Soil respiration on NOG and O50 were statistically similar to the control for the duration of the study although a trend for a stronger decline in respiration on O50 relative to NOG occurred in the first 2 years. Respiratory responses among the various treatments were not proportional to the degree of disturbance and varied over time. The short-lived respiratory response on O50 and OG suggests that belowground activity is resilient to disturbance; however, sources of the recovered respiratory flux on these plots are likely different than they were pre-treatment. The differential taxon response between oaks and non-oaks suggests that after a defoliation or girdling event, the temporal response of the soil respiratory flux may be related to the C allocation pattern of the affected plant group.

Keywords Soil respiration · Autotrophic respiration · Forest disturbance · Tree girdling · Pathogen attack

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Introduction

Periodic disturbances such as extreme ice, snow, or rainstorms, hurricanes, insect outbreaks, droughts, and fires shape forest landscapes and ecology. These types of perturbations have been identified as the main drivers that can convert ecosystems from C sinks to C sources (Baldocchi 2008; Kurz et al. 2008). Disturbance can reduce net forest CO_2 uptake by reducing the amount of photosynthesizing leaf area and increasing the net forest CO_2 release by altering autotrophic and heterotrophic respiration in response to changes in C pools, resource allocation, and environmental conditions. The general trajectory of forest C dynamics after a disturbance is a loss of C from the system followed by a recovery period of up to 120 years (Law et al. 2003; Pregitzer and Euskirchen 2004; Amiro et al. 2010; Goulden et al. 2011), with the dynamic response depending on the type and severity of the disturbance. Furthermore, predicted changes in climate, mainly through alterations in

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temperature and atmosphere moisture loading, are expected to increase the frequency of extreme weather events and many disturbance regimes (Overpeck et al. 1990).

In the United States, disturbance from pest and pathogen outbreaks affects 20.4 million ha annually, an area approximately 8.5 times greater than the combined areas affected by fires, hurricanes, tornadoes, ice, and landslides (Dale et al. 2001). Climate change can directly affect the survival, dispersal, geographic range, and reproduction of pests and pathogens (Ayres and Lombardero 2000; DeLucia et al. 2012; Chakraborty 2013; Jamieson et al. 2012). It can also exert indirect effects on tree resistance to such attacks and population dynamics of natural enemies that regulate pest populations (Ayres and Lombardero 2000; Jactel et al. 2012; Pautasso et al. 2012; Jamieson et al. 2012). The general consensus is that this type of disturbance will increase as a consequence of climate change. However, the unique individual response of each biological agent complicates predictions about the spread and frequency of such outbreaks (Harrington et al. 2001; Harvell et al. 2002; Logan et al. 2003; Lovett et al. 2006; Liu et al. 2011; Pautasso et al. 2012; Jamieson et al. 2012).

Detailed information on how components of the forest C cycle are impacted by disturbance events is needed to inform model development and forecasts of the terrestrial C sink. In particular, we need data sets documenting the magnitude and temporal dynamic of C fluxes following disturbances in different types of ecosystems and for varying disturbance regimes and intensities (Liu et al. 2011). One critical gap in our understanding of defoliation events is how resilient forest stands are to varying levels of mortality (Goetz et al. 2012). Following a pest or pathogen outbreak, field observations and model projections of forest recovery show a wide range of responses and temporal dynamics (Clark et al. 2010; Peltzer et al. 2010; Pfeifer et al. 2011; Brown et al. 2010; Seidl et al. 2008). Given the variety of responses and the large number of ecological variables involved, it is likely that we are only just beginning to understand the mechanisms driving forest ecosystem response to disturbance, much less how global climate change will influence these responses.

In this paper, we present new results from a large-scale manipulative experiment that imposed partial stand disturbance, similar to a pest or pathogen attack. This experiment was first described in Levy-Varon et al. (2012) where we presented the initial soil CO_2 efflux (soil respiration) response to canopy disturbance. Here, we extend our record of soil C flux measurements to a full 3 years of respiratory and environmental measurements to capture the temporal dynamic of soil respiration after a partial stand disturbance. We examine the longer term response and the mechanisms of ecosystem adjustment that drive the respiratory pattern observed over several growing seasons.

Materials and methods

Site description

Black Rock Forest is located in the Hudson Highlands, Orange County, New York. Our study site is a 120-year-old *Quercus*-dominated forest on the north-facing slope of Black Rock Mountain (41.45°N, 74.01°W). The canopy comprises 67 % oak, predominately *Quercus rubra* L., *Quercus prinus* L., *Quercus velutina* Lam. and *Quercus alba* and 33 % non-oaks, *Acer rubrum* L., *Acer saccharum* March., *Betula lenta* L. and *Nyssa sylvatica* Marsh. The understory is sparse and primarily consists of *Hamamelis virginiana*, *Vaccinium angustifolium*, *Berberis thunbergii*, grasses, mosses and ferns. Site history was previously described in Levy-Varon et al. (2012). The soils are Swartswood and Mardin (National Resources Conservation Service). They are nutrient poor, slightly acidic, and extremely rocky. This region experiences a seasonal climate. The mean January air temperature in 2009 was −5.5 °C, the mean July air temperature was 23.1 °C, and the total annual precipitation was 1,218 mm. Growing season air temperature and precipitation for the study duration are shown in Fig. 1.

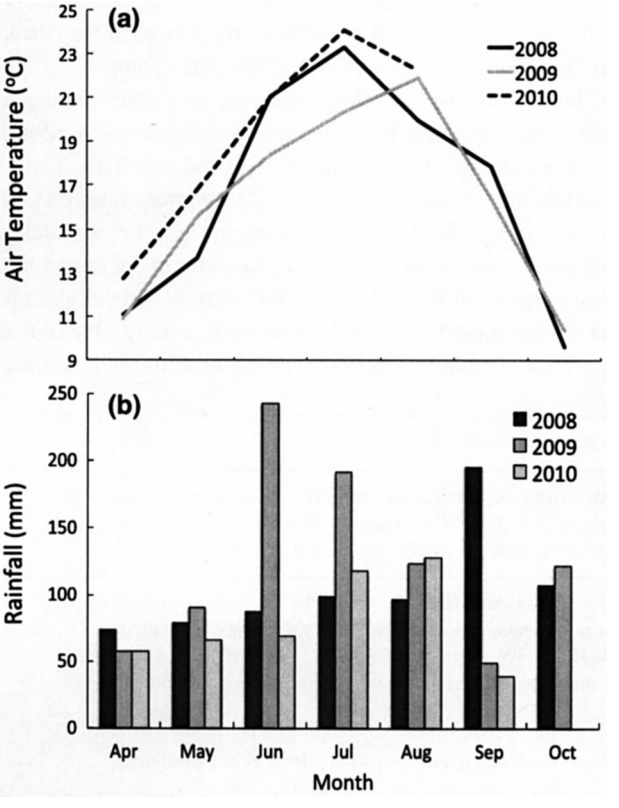


Fig. 1 **a** Average monthly air temperature (°C) and **b** total precipitation (mm) during the growing seasons of 2008–2010 at Black Rock Forest

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Experimental design and girdling treatment

We implemented a randomized block design for this study. Three blocks grouped by slope position (upper, middle, and lower) had trees girdled according to four treatments (Fig. S1). Within each block, depicted as row C (upper slope), row B (middle slope) and row A (lower slope), four plots were established. Each plot was 75 m × 75 m and a 25-m × 25-m center subplot was marked in the field. All measurements for this study were taken inside the center subplot. Each block contained one representative of the following treatments: control, girdling all non-oaks on a plot (NOG), girdling half of the oaks on a plot (O50), and girdling all the oaks on the plot (OG).

Notch girdling (Noel 1970) was applied during the summer 2008 by using a chainsaw to cut through the bark, phloem, cambium and outer xylem (approximately 5 cm deep) at breast height. The small fraction of trees (0–3 % on any plot) with a diameter at breast height (DBH) <2.54 cm were left ungirdled. Girdled trees that remained alive after the initial girdling in 2008 received an additional girdling in 2009 and, if necessary, again in 2010.

Soil respiration measurements

In 2009 and in 2010, a LiCor 6400 portable photosynthesis system adapted with a soil respiration chamber (LI-900; LI-COR, Lincoln, NE) was used to measure the soil surface CO_2 efflux in each of the center subplots at ten locations. Plot sampling order was randomized as measurements and constrained to morning and early afternoon (8 a.m.–1 p.m.). As a result, only four to five plots could be measured on any day. The soil respiratory flux for individual plots was calculated as the average of the collar measurements and the treatment flux was calculated as the average of respiratory fluxes for the three replicated treatment plots. The measurement interval for a treatment captures some abiotic variability by averaging respiration rates measured on plots from 3 separate days. Therefore, in order to reduce errors associated with varying abiotic conditions, we chose to limit our estimate of the maximum decline in soil respiration to comparisons between plots measured on the same day. In 2009, soil respiration measurements were made bimonthly and in 2010 they were made monthly. To assess the taxon affect (oak/non-oak) we accounted for the differing amounts of biomass loss by dividing the reduction in soil respiration by the amount of live biomass on the plots. Soil respiration per unit of living biomass was calculated using the mean growing season soil respiration rate in each year divided by the mean living biomass per treatment (calculation described below) and adjusted for the study area.

Aboveground measurements

Change in live aboveground biomass for 2008 and percentages of trees leafing out and resprouting on the experimental plots in 2009 were presented in Levy-Varon et al. (2012). Measurements for this paper were made the same way as previously reported. Briefly, live aboveground biomass was measured on all plots in the summer 2007 (before girdling) and again on the control and treated plots NOG, O50, and OG at the end of the summer 2009 and 2010. Trees were considered to have live biomass if the crown leafed out for the season. Live aboveground biomass was calculated from DBH using previously derived species-specific allometric equations (Brenneman et al. 1978; Monteith 1979).

An inventory of girdled trees that leafed out or resprouted from the base or trunk was made during the summer 2009, 2010, and 2011. For both the change in live aboveground biomass and the inventory of leafing out/resprouting trees, numbers and percentages for oaks are based on a survey of the full plot area. For non-oaks, a survey of the 25-m × 25-m center subplot was extrapolated to the full 75-m × 75-m plot area for comparison.

Litter influx was measured using four litter baskets (0.36 m^2) in each center subplot. Litter collections occurred in the summer (late July/August) 2009, in the fall (November) 2008 and 2009 and once in December 2010. The litterfall collections in 2009 and 2010 were separated into leaf litter and non-leaf litter before being oven dried at 100 °C for 24 h and weighed. In fall 2008, the two components were not separated. The litter influx for individual plots was calculated as the average litter influx of the four litter baskets and the treatment flux was calculated as the average litter influx for the three replicated treatment plots.

Environmental parameters

Volumetric soil water content (SWC) using time-domain reflectometry (CS616 and CS615 Water Content Reflectometer; Campbell Scientific, Logan, UT) and soil temperature (107 Temperature Sensor; Campbell Scientific), were measured hourly on two plots from each treatment. All probes were set within the center subplot; two SWC probes were inserted at 45° and two soil temperature probes were located 15 cm below the soil surface. The daily mean of the two probes between 8 a.m. and 1 p.m. (time of respiration measurements) was used to calculate the plot averages, which were then used to calculate the daily treatment average. Air temperature and rainfall were recorded at the Black Rock Forest Consortium's Open Lowland monitoring station located 500 m northwest of the study site. Air temperature was measured with a Campbell Scientific HMP45C probe, rainfall with a Campbell Scientific TE525MM rain gage, and hourly averages and amounts were recorded on a

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Campbell Scientific CR10X datalogger. Unfortunately, air temperature and precipitation measurements for fall 2010 were unavailable.

Data analysis

A linear model (Eq. 1) was used to assess the effect of treatment, soil temperature, slope position, and the interaction between treatment and soil temperature on our measured respiration rates. Soil moisture was not included in the model because it did not improve model fit based on Akaike information criteria (Hilborn and Mangel 1997) or R^2 (coefficient of determination). This model allowed us to account for impacts of abiotic parameters on soil respiration rates. Information about interactions in each year was extracted from the following models by restricting the data set to the year of interest.

$$\text{Log(Flux)} = \text{Treatment} + T_{\text{soil}} + \text{Slope} + \text{Treatment} \times T_{\text{soil}} \quad (1)$$

where Flux is predicted soil CO_2 efflux (μmol m^{-2} s^{-1}), Treatment is control, NOG, O50 or OG, T_{soil} is mean treatment soil temperature (°C at 15 cm depth), slope is slope position (upper, middle, lower), and SWC is % saturation.

The impact of treatment on soil temperature was analyzed with a linear model and the impact of treatment on soil moisture was analyzed with a generalized least squares linear model. A generalized linear model was used because of the plausibility that soil moisture levels on nearby days could be correlated.

A one-way ANOVA was used to analyze treatment effects on soil respiration rate per kilogram of live aboveground biomass, total litter influx, leaf litter influx, and non-leaf litter influx for the fall collection in 2008, the composited collections from 2009, and the fall collection in 2010. The Tukey HSD post-hoc test was used for pair-wise comparisons. For additional site history as well as a detailed description of the methods and statistical analysis used in 2008 please see Levy-Varon et al. (2012). Statistical analysis was done using R version 2.15.1 (R Core Team 2012). An error probability of $p < 0.05$ was used to determine significant effects.

Results

Soil respiration

In 2008 and 2009, the NOG and O50 treatments remained statistically similar to the control plots but a trend suggests that the O50 treatment had a larger effect on respiration than the NOG treatment in both years. The OG treatment was significantly lower over the course of the growing season compared to the control (Fig. 2a). The maximum decline in soil respiration declined non-linearly with degree of disturbance for the duration of the experiment and rebounded in the third year for all treatments (Fig. 3). Note, the day with the largest difference was not the same for each treatment in either year. For the duration of the experiment, OG had a significantly higher growing season respiration rate per unit of living biomass than all other treatments (Fig. 4). Soil temperature had a highly significant influence over soil respiration rates in both years ($p < 0.0003$) and the interaction between treatment and soil temperature was only significant in 2009 for the OG plot ($p < 0.01$). This interaction indicates that for the same incremental increase in temperature, the change in respiration rate in OG was lower by 0.05 μmol CO_2 m^{-2} s^{-1} compared to the control. The model assessing treatment impacts on soil respiration (Eq. 1) was highly significant ($F = 32.83$, $df = 170$, $p < 0.0001$) and accounted for 59 % of the variability observed in our soil respiration measurements. There was no indication that slope position influenced soil respiration rates in 2009, but in 2010 there was a trend for the lower slope position to have higher soil respiration rates by 0.21 μmol CO_2 m^{-2} s^{-1} ($p = 0.06$) compared to the upper slope position.

Tree biomass and girdling efficacy

The initial live biomass in 2007 varied between plots from 209 to 300 Mg ha^{-1}. In 2008, the mean change in live aboveground biomass from 2007 to 2008 was +3 % for the control (6.1 ± 0.1 Mg ha^{-1}), −9 % for NOG (−20.1 ± 6.7 Mg ha^{-1}), −32 % for O50 (−80.9 ± 3.9 Mg ha^{-1}), −73 % for OG (−179.9 ± 7.2 Mg ha^{-1}) (mean ± 1 SE). These values did not vary substantially for the second and third year of the study.

In 2009, within plots where only oaks were girdled (OG and O50) nearly twice as many oaks leafed out and/or resprouted the following spring on the O50 plots compared to the OG plots. On the O50 plots, 15 % of trees leafed out and 46 % resprouted, whereas on the OG plots, 8 % leafed out and 27 % resprouted. More than twice as many non-oaks leafed out after girdling (23 %) as oaks (10 %), especially larger trees, and more than twice as many non-oaks resprouted (69 %) as oaks (33 %) (Table 1) (Levy-Varon et al. 2012). In 2010 and 2011, the phenomenon of higher survival and resprouting on the O50 plots compared to the OG plots was less notable. On both the O50 and OG plots, 0–2 % of the girdled oaks leafed out in either year. Comparison of oak and non-oak leafing out and resprouting rates are shown in Table 1.

Soil temperature

In 2009 and 2010, NOG was the only treatment that experienced a similar soil temperature regime to the control. All other treatments differed from each other. In 2009,

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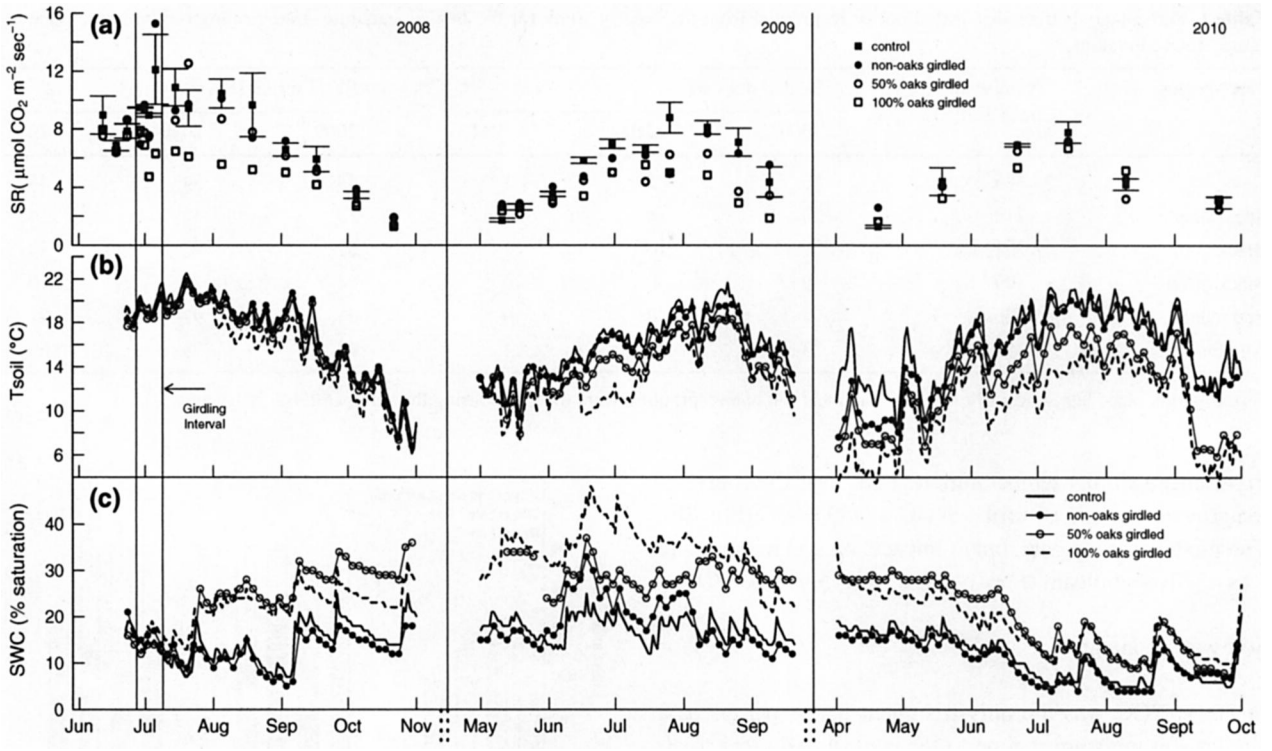


Fig. 2 **a** Soil respiration (*SR*) dropped on all plots where at least some oaks were girdled and rebounded to control rates within two growing seasons following girdling. *Error bars* are ±1 SE for the control treatment. For presentation purposes, data are aligned to the middle date of the measurement interval (usually 3–7 days). **b** Average daily soil temperature (T_{soil}) at 15-cm depth. **c** Average daily soil water content (*SWC*; % saturation). All measurements were made on the north slope of Black Rock Mountain between 2008 and 2010. The measurement interval varied each year; therefore, the *x*-axis is not continuous. *Vertical black lines* in 2008 show when tree girdling occurred. All data shown are treatment averages. $n = 3$ for soil respiration measurements on all plots. For T_{soil} and SWC, $n = 2$ for 100 % oaks girdled (OG), 50 % oaks girdled (O50), all non-oaks girdled (NOG), and $n = 3$ for the control

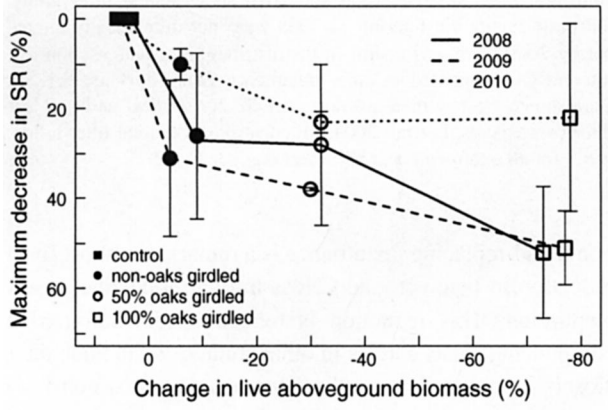


Fig. 3 Maximum decline in SR rate from 2008 to 2010 relative to control plot measurement varies disproportionately in all years along a gradient of change in live aboveground biomass. All data are treatment means ±1 SE. $n = 3$ for all treatments

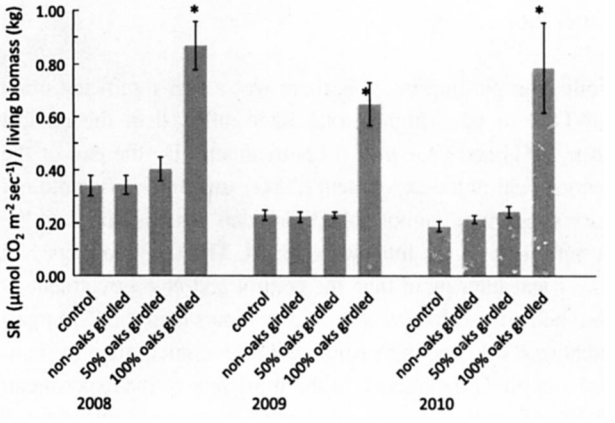


Fig. 4 Mean growing season SR rate from 2008 to 2010 per unit of living aboveground biomass (kg). The OG treatment had higher respiration rates for the same amount of living aboveground biomass than all other treatments for the duration of the study, precluding the ability to distinguish variations in respiratory response resulting from the loss of oaks compared to non-oaks. *Asterisks* indicate significant difference between OG and each of the treatments within each year. All data are treatment means ±1 SE. $n = 3$ for all treatments. For abbreviations, see Fig. 2

soil temperature followed the general pattern from warmest to coolest: control = NOG > O50 > OG. This pattern remained similar in 2010 but the O50 and OG treatments

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Table 1 Percentage of trees that leafed out or resprouted from the base or trunk for the first 3 years after tree girdling on the north slope of Black Rock Mountain

Tree species	Number of trees girdled	Leafed out (%)			Basal sprout (%)		
		2009	2010	2011	2009	2010	2011
Oaks	385	10	2	1	33	54	45
Sugar maple	216	50	8	0	33	42	4
Black gum	261	31	10	1	62	97	83
Black birch	99	9	0	0	64	29	0
Red maple	576	9	0	0	84	92	91
All non-oaks	1,350	23	6	4	69	78	67

Girdling took place late June/early July 2008 and leaf out and resprouting were recorded during the summer 2009, 2010, and 2011

experienced similar temperature regimes over the course of the growing season: control = NOG > O50 = OG (Fig. 2b). The model assessing treatment impacts on soil temperature was highly significant ($F = 14.79$, $df = 175$, $p < 0.0001$).

Soil water content

In 2009, NOG was the only treatment that experienced a similar soil moisture regime to the control. All other treatments differed from each other over the course of the growing season following the general pattern from wettest to driest: OG > O50 > NOG = C. In 2010, all treatments were statistically similar to the control and to each other over the course of the growing season although there was a trend for higher soil moisture content in OG and O50 relative to the control and NOG (Fig. 2c).

Litter influx

Following girdling in 2008, there was a non-significant trend for O50 to have higher total litter influx than the control ($p = 0.11$) and OG ($p = 0.12$) treatment. By the end of the second year of the experiment (2009), total litter influx did not vary substantially among the treatments but alterations in the composition of the litter were found. The OG treatment had lower leaf litter input than the control and NOG treatment. It also had a trend for lower leaf litter inputs than the O50 treatment ($p < 0.1$) and higher non-leaf litter content than the control and NOG treatments. In the third year of the experiment, 2010, differences in total litter influx were not significant but the control and O50 treatment tended to have higher litter influx than the NOG and OG treatments. As in 2009, the OG treatment had lower leaf litter input than the control (Fig. 5).

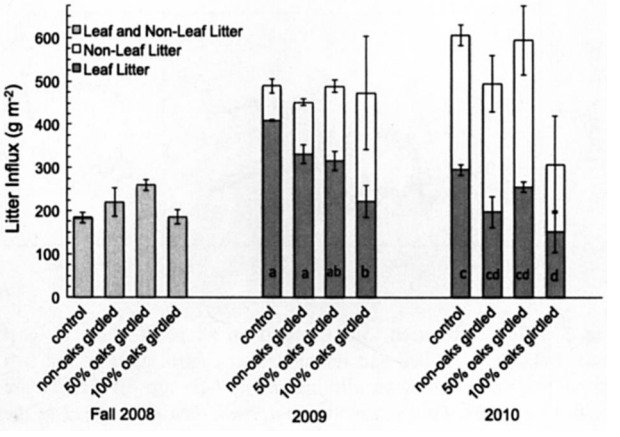


Fig. 5 Total litter influx, leaf litter influx, and non–non leaf litter influx (g m^{-2}) for experimental treatments from 2008 to 2010 on the north slope of Black Rock Mountain. Year 2008 shows the fall litter collection only, whereas 2009 and 2010 show annual litter influx. Substrate inputs via litterfall in 2008 were not dramatically altered but by 2009 there was a shift in the distribution of leaf vs. non-leaf litter in OG compared to other treatments. *Error bars* are ±1 SE. Data shown are treatment averages ±1 SE for the leaf and non-leaf litter components. For fall 2008, SE corresponds to total litter influx. $n = 3$ for all treatments. For abbreviations, see Fig. 2

Discussion

Our observations from 3 consecutive years of field measurements suggest that the response of soil CO_2 efflux to non-stand-replacing disturbance is a remarkably short-lived reduction in belowground C loss through a decline in soil respiration. This reduction is related to the autotrophic component (plants and, as in other studies, we include their closely associated mycorrhizal fungi) and varies non-linearly in magnitude as a function of canopy disturbance and specific plant taxon impacted. The rebound of the soil CO_2 flux after 2 years indicates that disturbed northeastern temperate deciduous forest soils can be very resilient (sensu Nave et al. 2011) to canopy disturbance.

Girdling studies that affect only part of a forest canopy or target specific tree species mirror the patterns—and sometimes the mechanisms—of tree mortality that are characteristic of pest or pathogen attacks. For this reason, girdling can provide insight into ecosystem dynamics

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following biotic disturbances (Nuckolls et al. 2009; Nave et al. 2011; Moore et al. 2013; Orwig et al. 2013). Nuckolls et al. (2009) and Moore et al. (2013) found similar patterns of decline in magnitude and timing of soil respiration from girdled and insect-infested stands, providing additional support for the use of girdling to understand patterns in soil CO_2 efflux after a pest disturbance.

The rapid rebound of soil respiration was surprising since aboveground signs of disturbance are strikingly evident on treatment plots. Several factors that vary over the study time frame could drive this response. Following girdling, heterotrophic respiration could be sustained or elevated if root exudates and/or detrital input are increased from healthy or dead trees (Scott-Denton et al. 2006; Ekberg et al. 2007). In disturbed evergreen ecosystems, the timing of litterfall input was associated with increased heterotrophic respiration (Berryman et al. 2013; Moore et al. 2013), highlighting one source of variability in the temporal response of C fluxes to disturbance. Heterotrophic activity could also be reduced as substrate supply declines in association with increased tree mortality and could be affected by changes in soil moisture or temperature (Bhupinderpal-Singh et al. 2003; Scott-Denton et al. 2006). At the same time, autotrophic respiration could continue to decline beyond the first year as root carbohydrate reserves are depleted from girdled trees, but it could also increase if healthy trees increase C allocation belowground to support new root growth and enhanced activity.

What mechanisms could contribute to the unexpected rebound of soil CO_2 efflux at our site? This response is not due to recovery of disturbed trees since very few girdled oaks leafed out in the second and third year of the experiment (10 and 1 % respectively, Table 1). Instead, our findings are consistent with Nave et al.'s (2011) disturbance recovery hypothesis. Their hypothesis suggests that partial canopy disturbance causes a short-term perturbation of forest C and N cycling followed by a rapid recovery (within a few years) and stabilization of the two cycles along a new trajectory. Compensating N uptake and growth from healthy trees creates a functional resilience for the C and N cycles (Nave et al. 2011; Gough et al. 2013). At our site, we observed a perturbation in the forest C cycle via declines in soil respiration, and a disruption in the N cycle as increased NO_3^- and NH_4^+ in the girdled plots (Melillo and Schuster, unpublished data). Compensating N uptake by healthy understory birch trees (the only species examined) resulted in foliar %N enrichment of 15.5 and 30.6 % in the O50 and OG treatments (Falxa-Raymond et al. 2012), respectively. Similarly, Rhoades et al. (2013) observed compensating N uptake following a mountain pine beetle outbreak. Compensating growth from healthy trees was evident as a 625 and 121 % increased growth rate of birch on OG and O50 plots, respectively (Falxa-Raymond et al. 2012). The higher respiration rate per unit of living biomass on the 100 % oak girdled treatment than on the 50 % oak-girdled treatment (Fig. 4) reflects this pattern of increased plant activity on OG relative to O50. The dramatic difference in plant growth and soil respiration illustrates the importance of plant competition on C flux dynamics following disturbance.

Changes in heterotrophic activity could also contribute to the interesting findings in Fig. 4. Substrate inputs via litterfall in 2008 (year 1) were not separated into leaf and non-leaf components (e.g. acorns, woody detritus) but by 2009 OG had a higher fraction of non-leaf litter input relative to all other treatments (Fig. 5). The modification in substrate quality associated with this composition change could slow heterotrophic decomposition rates on the OG treatment. Additionally, observed cooler soil temperatures (Fig. 2b) would also reduce heterotrophic respiration rates. Although changes in soil moisture did occur, it is unlikely that the soil moisture status greatly impacted the respiratory response at our field site. Including this information into Eq. 1 did not improve the model fit. It is possible that this is simply because saturation did not drop below the range where it became limiting to the biological activity in this soil system. In addition to compensatory activity, continued activity of girdled trees that resprouted or resource sharing between healthy and stressed trees via mycorrhizal networks and/or root grafting could also contribute to the resilience in biogeochemical cycling (see also Levy-Varon et al. 2012). Together, our observations of C and N dynamics are congruent with the disturbance and rapid recovery of biogeochemical cycles resulting from many process-level changes, as suggested by Nave et al. (2011).

Interestingly, the reduction in soil respiration was not linearly related to the severity of canopy disturbance. In the first year of this study (Levy-Varon et al. 2012), a threshold-type response of belowground dynamics occurred somewhere between 35 and 75 % aboveground biomass (AGB) loss. In the second year, the threshold response was less distinct, although statistically significant, along the AGB loss gradient (control < NOG < O50 < OG) (Fig. 2a). This growing-season response could be driven by increased understory plant activity (Falxa-Raymond et al. 2012) or from alterations in litterfall quality along the disturbance gradient (Fig. 5). The non-linear respiratory response aligns with observations of Binkley et al. (2006) and supports their conclusion that tree girdling has limited use with regards to the identification of the contribution of a cohort of trees within a forest stand. One implication of these observations is that modeling the impact of pest or pathogen attacks will improve with the representation of a heterogeneous forest where individual plant growth responds to spatially distributed resource availability (light, water, nutrients). Another corollary is that the belowground activity of oak vs.

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non-oak trees is difficult to assess because interpretation of the respiratory response is complicated by differences in biomass loss and the altered activity of undisturbed trees.

The maximum decline in soil respiration rate also varied non-linearly with the degree of AGB loss (Fig. 3). The maximum difference can provide insight into the potential impact of disturbance on autotrophic soil respiration but it does not necessarily predict the seasonal response. This is because environmental variables are highly dynamic and the date of the maximum difference represents a specific set of conditions, which differ among the treatments. Interestingly, in both the first and second years of the experiment, the change in the maximum decline in the soil respiration rate for an incremental change in AGB (slope of lines in Fig. 3) was disproportionately greater when only a small fraction of the canopy was impacted (<10 % AGB loss) than when a larger fraction was impacted (>10 % AGB loss). Based on trends in both the seasonal and maximum difference, the observations suggest that disturbance to the belowground C cycle is not linearly related to the degree of aboveground canopy loss and that there are interannual differences in this dynamic response. It also suggests that the initial stages of disturbance could have a greater impact on belowground C dynamics than later stages of infestation.

Differences in the soil respiratory response associated with varying treatment efficacy between oaks and non-oaks suggest that C allocation patterns could influence the timing and magnitude of soil C dynamics following disturbance. Species leaf out rates from 2009 to 2011 show a wide variation in the timing of mortality following girdling (Table 1). Throughout the experiment, soil respiration rates, moisture levels, and temperature regimes from the non-oak girdled treatment were statistically similar to the control. In contrast, depressions in soil respiration rate were observed in the first 2 years of this experiment on all treatments where at least some oaks were girdled. Sustained activity on the non-oak girdled treatment could indicate that carbohydrate reserves in the root systems of the non-oaks were able to sustain root activity for at least 3 years. It could also indicate that changes in the belowground system over the 3-year period resulted in elevated heterotrophic respiration rates that masked the autotrophic and disturbance signal. The high resprouting rate in all years and unaffected soil moisture regimes (Table 1; Fig. 2c) support the idea that reserve respiratory substrates were able to sustain root respiratory activity throughout this experiment. Differential species responses to girdling (Andersen et al. 2005; Chen et al. 2010) as well as utilization of root carbohydrate reserves following girdling has been observed in other forests (Högberg et al. 2001; Bhupinderpal-Singh et al. 2003; Frey et al. 2006; Nave et al. 2011). Ecologically, this suggests that after a defoliation or girdling event, the temporal response of the soil CO_2 flux may be related to the C allocation pattern of the affected plant group.

Studies reporting soil respiration rates after a pest or pathogen outbreak are limited (Hicke et al. 2011). To our knowledge, this is the third study to present 3 consecutive years of soil CO_2 efflux observations following a partial stand disturbance reflective of a pest or pathogen attack (i.e., actual biotic disturbance that has <100 % mortality or partial stand tree girdling). Orwig et al. (2013) observed changes in respiration rate over 6 years but did not find treatment differences, while Detto et al. (2013) observed depressed respiration rates on their girdled plot relative to their control plot for the 3 years. Studies of shorter durations report a 20–40 % depression in soil respiration shortly after a pest or partial stand girdling disturbance (Binkley et al. 2006; Hancock et al. 2008; Nuckolls et al. 2009; Nave et al. 2011; Orwig et al. 2013, n.b. Morehouse et al. 2008), and are similar to the results from NOG and O50 treatments in our experiment (Fig. 3). Interestingly, the rapid recovery of belowground fluxes aligns with the trajectory of forest net ecosystem production (NEP) after a partial stand disturbance from a pest or pathogen attack (Amiro et al. 2010), recovery of NEP following creation of a small gap by logging (Forrester et al. 2013), and recovery of leaf (Uhl and Jordan 1984; Bormann and Likens 1994; Goulden et al. 2011) and fine root biomass (Claus and George 2005; Yuan and Chen 2010) following a stand-replacing disturbance.

Overall, we observed a short-lived depression in soil respiration on treated plots, lasting just 2 years post-disturbance followed by a full rebound of belowground activity in the third year. The reduction in soil respiration was not proportional to the degree of canopy loss and the magnitude of the response varied interannually. Our findings, alongside those of Falxa-Raymond et al. (2012), support a hypothesis proposed by Nave et al. (2011), which attributes the functional resilience of a coupled C–N cycle to compensatory activity of the healthy trees within the affected forest stand. The altered aboveground plant composition, litter quality, and soil moisture and temperature regimes indicate that the processes governing the respiratory flux in the disturbed oak girdled plots differ from those governing the respiratory flux in the undisturbed forest. Documenting patterns of forest C fluxes after a disturbance is fundamental to improving our understanding and predictions of climate feedbacks and ecosystem biogeochemistry.

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