Trees
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SHORT COMMUNICATION

# Decadal forest soil respiration following stem girdling

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## Abstract

***Key message*** **Large-scale stem-girdling experiment reduced soil respiration for five consecutive years. Timing and magnitude of soil respiration declines are better explained by changes in leaf area rather than in soil microclimate.**

**Abstract** Soil respiration (Rs) represents the largest flux of carbon (C) from forests to the atmosphere, but the long-term influence of phloem-disrupting disturbance on Rs is poorly understood, limiting robust forecasts of ecosystem C balance. Using a decade of observations from the Forest accelerated succession experiment (FASET), we examined relationships among Rs, soil temperature, soil moisture, and leaf area index (LAI) following the stem girdling-induced mortality of 40% of all canopy trees within a 39-ha area. Mean annual Rs declined by about 20% relative to the control two years after disturbance, but recovered to near pre-disturbance values within five years; this reduction correlated with LAI losses and lower Rs temperature sensitivity (i.e., $Q_{10}$), with the latter counteracting soil warming caused by partial canopy defoliation. These observations are consistent with progressive reductions in belowground labile C causing reductions in Rs. We conclude that the effects of stem girdling on Rs (1) were not immediate, occurring two years after the treatment, (2) were primarily influenced by biotic rather than soil microclimate changes, and (3) persisted for nearly a decade but were temporally dynamic, underscoring the value of long-term experiments.

**Keywords** Soil respiration · Moderate disturbance · Temperature sensitivity · Leaf area index

## Introduction

The soil-to-atmosphere flux of $CO_2$ generated by root and microbial respiration, commonly termed soil respiration (Rs), is a large component of ecosystem- to global-scale carbon (C) cycling and a primary determinant of ecosystem net C balance (Li et al. 2018). Interannual variation in Rs is driven by abiotic and biotic factors (Hursh et al. 2017; Xu and Shang 2016), including shifts in soil temperature (Davidson and Janssens 2006) and the supply of photosynthate supporting root respiration. Conditions that increase Rs may drive significant positive climate feedbacks as soil organic carbon is mineralized in a warming world (Bond-Lamberty et al. 2018), particularly in mid-latitude forests that are currently substantial carbon sinks (Pan et al. 2011).

Forest disturbances are increasing in many areas of the world, affecting these ecosystems' carbon, nutrient, and energy cycling (McDowell et al. 2020). Disturbances including fires (Pellegrini et al. 2021; Ribeiro-Kumara et al. 2020), storms (Vargas and Allen 2008; Lindauer et al. 2014; Fahey et al. 2020), and biotic pests (Moore

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et al. 2013; Borkhuu et al. 2015) may have lasting effects on Rs, and biotic disturbances are likely to increase with climate change (Weed et al. 2013; Seidl et al. 2017). Many insect pests operate by restricting or blocking the phloem, starving roots and eventually killing the tree. The effect of such insect disturbances on the C cycle may be large but temporally variable (Speckman et al. 2014; Kurz et al. 2008), resulting in an uncertain future for the land C sink.

Experimentally, phloem disturbance has been shown to restrict belowground carbon allocation, selectively kill trees, and mimic both biotic agents and successional change (Gough et al. 2021a). Stem girdling has been used for decades (Edwards and Ross-Todd 1979) to restrict belowground C accumulation, for the selective termination of trees and to mimic successional change, allowing for measurement of heterotrophic-dominated C fluxes (Högberg et al. 2001). For example, Högberg et al (2001) observed significant declines in Rs following girdling resulting from root rather than heterotrophic activity, although heterotrophic respiration may increase for a short time as well (Bhupinderpal-Singh et al. 2003). Such girdling experiments measuring Rs, however, have been quite short-term, typically only 1–2 years (e.g. Levy-Varon et al. 2012; Högberg et al. 2001; Bhupinderpal-Singh et al. 2003; Matteucci et al. 2015). While understandable—research funding cycles are short—this preponderance of short-term observations means that the longer-term Rs dynamics and drivers following phloem disturbance remain highly uncertain (Amiro et al. 2010; Gough et al. 2021a, b). Consequently, longer-term forecasts of disturbance response are poorly constrained (Goetz et al. 2012).

The goal of this study was to understand decadal Rs change following phloem disruption and subsequent mortality in a mixed temperate forest. Our specific objectives were to (1) characterize the 10-yr response of Rs to a phloem-disrupting disturbance (O1); (2) probe how such disturbances can modify Rs temperature sensitivity (O2); and (3) test whether disturbance-driven changes in Rs are caused primarily by biotic or abiotic (i.e., microclimatic) factors (O3). We hypothesized that (1) the effects of disturbance would be relatively short-lived, resolving by the end of the decade, (2) the temperature sensitivity of Rs would decrease as labile root carbohydrate diminished, and (3) that large biotic (i.e., LAI) effects would overwhelm more modest abiotic changes following disturbance. We leverage long-term observations from the Forest accelerated succession experiment (FASET) in which 40% of mature canopy trees within a 39-ha area were stem girdled. Our Short Communication provides a focused interpretation of Rs responses to the FASET treatment as a complement to analyses emphasizing meteorological tower-based C fluxes (Gough et al. 2021b).

## Materials and methods

### Site description

The study was conducted at the University of Michigan Biological Station (UMBS) in Pellston, Michigan, USA (45° 35′N, 84°43′W), about 213 m above sea level. The 30-year average precipitation and air temperatures are 1113 mm per year and 4.6 °C, respectively, and most soils are frigid Entic Haplorthods. The UMBS landscape is primarily a secondary forest, established following clearcutting and wildfires that occurred in the late nineteenth century through the early twentieth century. The UMBS hosts long-term control (US-UMB) and FASET (hereafter, “disturbed”, US-UMB) Ameriflux sites (Gough et al. 2021b), which have collected C cycling data using meteorological flux towers and ground observations since 1998 and 2007, respectively.

The goal of the FASET study is to examine how a moderate severity disturbance, which kills early- but not mid-late successional tree species, affects C cycling processes. Canopy dominant species, prior to the FASET disturbance, included bigtooth aspen (*Populus grandidentata*), eastern white pine (*Pinus strobus*), red oak (*Quercus rubra*), red maple (*Acer rubrum*), and white birch (*Betula papyrifera*). In 2008, the FASET treatment was implemented by stem girdling 6,700 aspen and white birch trees within a 39-ha area (Nave et al. 2011), constituting 39% of the total basal area. One 1-ha and seven 0.1-ha plots in each of the control and disturbed sites were paired (for 16 total) based on pre-disturbance similarities in leaf area index (LAI) and aspen and birch abundance. Within paired plots, measurements of LAI from litter traps, and concurrent Rs, soil temperature (Ts), and soil moisture (Ms) were conducted for 10 years, beginning in 2008. Data collection methods are detailed elsewhere (Gough et al. 2021b) and briefly described below. Prior C cycling-focused studies emphasized meteorological tower-based observations of production and ecosystem respiration, but not Rs (Nave et al. 2011; Gough et al. 2013, 2021b).

### Field measurements

We repeatedly measured Rs, Ts, and Ms from five locations within each of the 16 plots monthly during April through September each year. Rs was measured using a LI-COR 6400 (LI-COR Biosciences, Lincoln, NE, USA) from randomly distributed PVC collars. At the same location, Ts was measured at a soil depth of 7 cm and volumetric water content (Ms) was measured using a HydroSense II Handheld Soil Moisture Sensor (Campbell Scientific, Logan, UT, USA) at 20 cm soil depth. Due to equipment malfunction, Ms was not measured in 2009. A total of 4359 Rs measurements were co-located with Ts, and Ms observations during a 10-yr period for an average of 217 measurements per treatment (control and disturbed site) each year. Data are available via the COSORE database (Bond-Lamberty et al. 2020).

We estimated LAI from repeated collections of leaf litterfall. Leaf litter was removed from three litter traps (0.264 $m^2$) per 0.1-ha plot and 20 litter traps per 1.1-ha plot weekly during autumn and monthly during other seasons, pooled by plot, separated by species, dried, and weighed. The LAI was calculated from species- and site-specific litterfall mass and specific leaf area values (Gough et al. 2021b).

## Statistical analysis

Supporting O1, analysis of variance (ANOVA) was performed using the PROC GLM procedure in SAS V9.4 (SAS Institute) to compare the Rs, Ts, and Ms means of control and disturbed sites (Tables S1, S2). Pairwise comparisons were conducted using the PROC MEANS procedure from SAS via Duncan's test (alpha = 0.05). For O2, we calculated the temperature sensitivity of soil respiration ($Q_{10}$) separately for periods during which control and disturbed sites exhibited statistically similar and different soil respiration using a 2-parameter exponential function (Sigmaplot V14.01). Control and disturbed Q10 values were considered statistically different when the 95% confidence intervals were non-overlapping. For O3, we conducted path analysis using PROC CALIS in SAS V9.4, testing whether differences in control and disturbed Rs (e.g., as mean control Rs–disturbed Rs) were explained directly by treatment differences in LAI, Ts, and/or Ms or whether LAI's influence on Rs was indirect, through its influence on Ts and/or Ms.

## Results and discussion

Our decade-long observations of soil respiration, microclimate, and LAI following the stem girdling of 40% of canopy trees provide insight into the long-term patterns and mechanisms controlling soil C efflux following a partial (i.e., non-stand replacing) disturbance. Long-term observations of soil respiration following disturbance are rare, but critical to assessing ecosystem disturbance-response dynamics, from initial response through recovery (Mathes et al. 2021).

We found that, (1) Rs in the disturbed site was 10 to 24% lower than that of the control for five of 10 years, with treatment differences emerging two years after stem girdling (Fig. 1a, O1), suggesting root non-structural carbohydrates may have sustained root metabolism (Gough et al. 2009), (2) Rs was lower in the disturbed forest even when soil

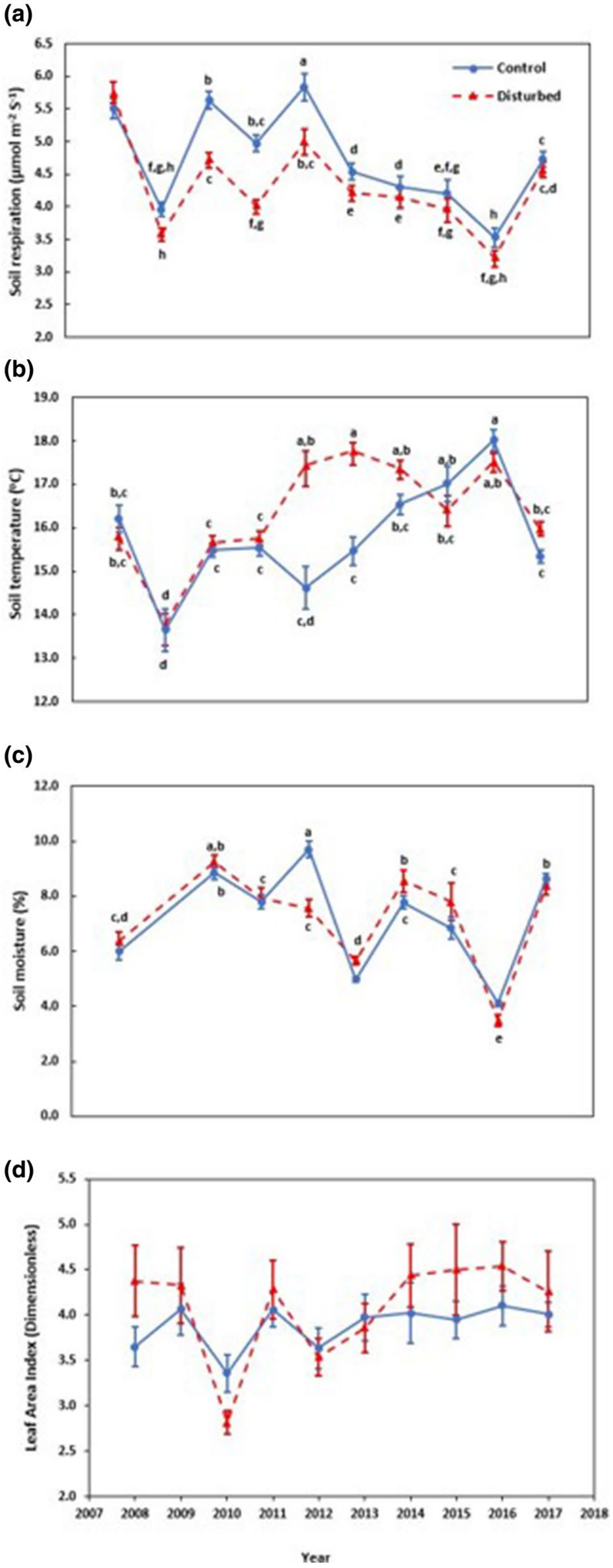

**Fig.1** Mean soil respiration (**a**), soil temperature (**b**), soil moisture (**c**), and leaf area index (**d**) for the control and disturbed sites, 2008–2017. Non-overlapping letters denote significant pairwise differences among mean ($P < 0.05$). Means ± 1 S.E

**Table 1** Q10 values for the control and disturbed sites calculated from soil respiration temperature-response curves

| Period | Rs treatment differences? | Treatment | $Q_{10}$ | 95% C.I |
|---|---|---|---|---|
| 2008–2009 | No | Control | 2.39 | 0.18 |
| | | Disturbance[1] | 2.35 | 0.21 |
| 2010–2014 | Yes[2] | Control | 2.28 | 0.12 |
| | | Disturbance | 1.86 | 0.11 |
| 2015–2017 | No | Control | 1.52 | 0.25 |
| | | Disturbance | 1.33 | 0.34 |

[1] The stem-girdling treatment was implemented in 2008

[2] Italics denote significance between treatments, $P < 0.05$

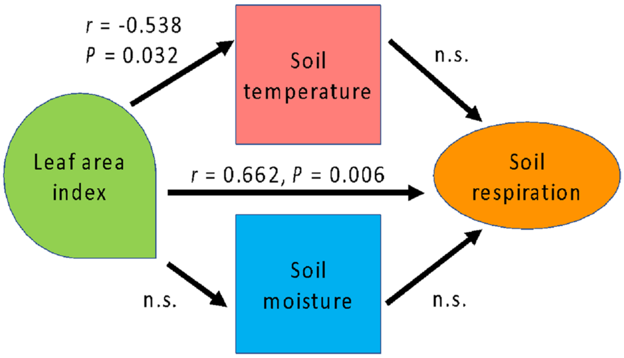

**Fig. 2** Maximum likelihood estimates derived from path analysis, relating differences in mean soil respiration between the control and disturbed forests to differences in mean annual leaf area index, mean soil temperature, and mean soil moisture, 2008–2017

temperatures were elevated over the control because the temperature sensitivity of Rs (i.e., $Q_{10}$) temporarily declined (Table 1, O2), and (3) control and disturbed site Rs differences were driven by relatively small treatment departures in LAI rather than microclimatic differences (Fig. 2, O3). These findings suggest a mechanistic basis for the timing and magnitude of Rs decline and recovery, in which the exhaustion of the root labile carbohydrate pool lagged behind an immediate reduction in photosynthate supply. Our findings also demonstrate the value of decadal observations when characterizing disturbance responses (Harmon et al. 2011), illustrating a long-term pattern of decline and recovery over several years.

Specific to our first objective, we found Rs and microclimatic responses lagged stem girdling and this lag declined as the decade progressed (Fig. 1). Soil respiration was significantly lower—by up to 20%—for five consecutive years in the disturbed forest when compared to the control, but treatment differences did not emerge until two years after stem girdling, which is a contrast to some experiments observing immediate declines in Rs (Högberg et al. 2001; Levy-Varon et al. 2012). Interestingly, the period of lower Rs in the disturbed forest relative to the control coincided with higher soil temperatures and lower soil moistures during the two years, with soils up to about 3 °C warmer and 20% drier in the stem-girdled forest. LAI did not differ significantly between treatments after stem girdling. Soil respiration and microclimate values in disturbed forests returned to control levels within seven years of stem girdling, underscoring the relatively long-term interval between response and recovery, a duration that matches theoretical expectations (Harmon et al. 2011) and eddy-covariance tower C fluxes following partial disturbance (Amiro et al. 2010).

The observed timing and duration of Rs decline following stem girdling is also similar to that predicted by model simulations of the FASET disturbance (Bond-Lamberty et al. 2015) and congruent with some, but not all, shorter-term (1 to 5-yr) forest disturbance studies (Vargas and Allen 2008; Moore et al. 2013; Borkhuu et al. 2015). Paralleling our observations, ecosystem respiration, of which Rs is the largest component (Curtis et al. 2005), was predicted by two of three models to reach a low point two years after stem girdling and then gradually return to control levels (Bond-Lamberty et al. 2015). Elsewhere, observations indicate that the timing, extent, duration, and sign of Rs response to stem girdling varies depending on the plant taxa affected (Levy-Varon et al. 2012), the source of phloem-disrupting disturbance (Concilio et al. 2006), and the degree of tree mortality (Borkhuu et al. 2015).

While the stem girdling of all trees within an experimental unit rapidly dampens Rs by immediately eliminating photosynthate allocation to roots (Högberg et al. 2001), we may have observed a more moderate and lagged Rs response because (1) the FASET treatment targeted only 40% of canopy trees, and (2) root systems at our site and elsewhere (Binkley et al. 2006) contain a large pool of labile carbohydrates with which to temporarily sustain root metabolism (Gough et al. 2009). Focusing on our second objective, mean Rs was lower in the disturbed forest because diminished temperature sensitivity offset the positive influence of temporary increases in soil temperature, a primary abiotic driver of Rs in forest ecosystems (Bond-Lamberty et al. 2018). From 2010–2014, when Rs was significantly lower in the disturbed forest relative to the control (Fig. 1a), Ts was intermittently higher (Fig. 1B) while the $Q_{10}$ values of disturbed and control forest Rs were 1.86 and 2.28, respectively. Lower $Q_{10}$ was associated with short-term reductions in Rs following the stem girdling of planted forest trees, and may reflect a reduction in photosynthate supply to the roots (Chen et al. 2009; Maier et al. 2010). Even so, the extent to which Rs temperature sensitivity shifts in response to disturbance is variable across disturbance types, severities, and forest compositions and thus remains a source of uncertainty when projecting ecosystem C balance following perturbation (Hu et al. 2017).

Finally, our path analysis suggested that disturbance-driven changes in LAI, rather than soil temperature or moisture, was the primary determinant of Rs responses to stem girdling, possibly because LAI losses caused a reduction in the supply of metabolically-critical photosynthate to the roots. This should be considered a tentative finding, given that the LAI differences were themselves not statistically significant, but is nonetheless intriguing. It implies that small differences in LAI between the control and disturbed forests had disproportionate effects on soil respiration, with a temporary loss of leaf area in the stem-girdled forest directly reducing Rs even while increasing Ts (Fig. 2). This stronger influence of LAI over microclimate has been reported for some undisturbed forests (Reichstein et al. 2003; Lindroth et al. 2008) and is consistent with progressive limitations in belowground C allocation constraining Rs following stem girdling.

In summary, our findings suggest the primary mechanism regulating the response of Rs through a full disturbance-recovery cycle is biotic rather than abiotic, and likely associated with a lagged reduction in belowground labile C pools following disturbance (Gough et al. 2009). The divergence of control and disturbed forest Rs two years after stem girdling is coincident with peak tree mortality in the FASET manipulation (Gough et al. 2013). Somewhat unexpectedly, large but transient increases in soil temperature were not substantial enough to overcome a reduction in Rs temperature sensitivity.

## Conclusion

In a world of rising biotic disturbances driven by land-use and climate changes (Weed et al. 2013; Seidl et al. 2017), understanding the resulting ecosystem carbon-cycle changes—and possible climate feedbacks—is increasingly critical. This study elucidates the complex and unexpected interplay that can occur between biotic (e.g. LAI) and abiotic (Ts and Ms) drivers. It emphasizes the value of longer-term experiments and observational campaigns in characterizing ecosystem response to disturbance—particularly when responses may be transient or unsustainable (Norby et al. 2010)—and the necessity of robust theoretical frameworks for synthesizing understanding (Mathes et al. 2021). For these reasons we concur that decadal observations are necessary to understand ecosystem response to disturbance (Harmon et al. 2011). Our study also underlines the value of early and long-term observations of disturbance events in a world of increasing climate variability in which pre-disturbance conditions can never be re-created, and subtle responses require synthesis to fully understand (Wolkovich et al. 2012; Yang et al. 2021).

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00468-022-02340-x.

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**Availability of data and materials** All data have been previously published (see Bond-Lamberty et al. 2020; Gough et al. 2021a, b). All codes used are publicly available on Figshare (https://doi.org/10.6084/m9.figshare.16958794.v1).

## Declarations

**Competing interest** The authors declare that there are no personal, professional or financial relationships that could potentially be construed as a conflict of interest.

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