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ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH PAPER

The autotrophic contribution to soil respiration in a northern temperate deciduous forest and its response to stand disturbance

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Abstract The goal of this study was to evaluate the contribution of oak trees (*Quercus* spp.) and their associated mycorrhizal fungi to total community soil respiration in a deciduous forest (Black Rock Forest) and to explore the partitioning of autotrophic and heterotrophic respiration. Trees on twelve 75 × 75-m plots were girdled according to four treatments: girdling all the oaks on the plot (OG), girdling half of the oak trees on a plot (O50), girdling all non-oaks on a plot (NO), and a control (C). In addition, one circular plot (diameter 50 m) was created where all trees were girdled (ALL). Soil respiration was measured before and after tree girdling. A conservative estimate of the total autotrophic contribution is approximately 50%, as indicated by results on the ALL and OG plots. Rapid declines in carbon dioxide (CO_2) flux from both the ALL and OG plots, 37 and 33%, respectively, were observed within 2 weeks following the treatment, demonstrating a fast turnover of recently fixed carbon. Responses from the NO and O50 treatments were statistically similar to the control. A non-proportional decline in respiration rates along the gradient of change in live aboveground biomass complicated partitioning of the overall rate of soil respiration and indicates that belowground carbon flux is not linearly related to aboveground disturbance. Our findings suggest that in this system there is a threshold disturbance level between 35 and 74% of live aboveground biomass loss, beyond which belowground dynamics change dramatically.

Keywords Soil respiration · Autotrophic respiration · Heterotrophic respiration · Tree girdling · Disturbance

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Introduction

Soils are a primary component of the terrestrial carbon sink (Intergovernmental Panel on Climate 2000) and are responsible for 60–70% of the carbon dioxide (CO_2) released from forest ecosystems (Malhi et al. 1999; Steinmann et al. 2004). Consequently, soils have a central role in the global carbon cycle. The efflux of CO_2 from the earth's surface is known as soil respiration and is typically divided into two source components—autotrophic and heterotrophic respiration. The autotrophic portion consists of living plant roots (as in other studies, we include their associated mycorrhizal fungi) whose energy source is derived from photosynthates, and the heterotrophic portion consists of organisms that derive their energy by breaking down living or dead organic matter. The biotic processes underlying soil respiration result in a dynamic soil carbon cycle that is sensitive to both biotic and abiotic perturbations. Therefore, scientists must have a detailed understanding of the processes governing soil respiration in order to make predictions about the rate and capacity of carbon sequestration in forests and to quantify feedback relationships with climate.

Until recently, most soil respiration studies focused on heterotrophic contributions, leaving gaps in our knowledge regarding the magnitude, mechanisms, and controls of the autotrophic component (Högberg and Read 2006).

Estimates of the autotrophic fraction range from 10 to 90% of total soil respiration (Hanson et al. 2000). Growing evidence for a large autotrophic contribution within forested landscapes (e.g., 46% in Hanson et al. 2000) has motivated ecologists to work towards a better understanding of respiratory partitioning and underlying environmental influences.

Plant community composition is likely to play an important role in regulating forest soil respiration. Not only do different types of plant communities vary in CO_2 efflux rates (Raich and Tufekciogul 2000; Carbone and Trumbore 2007), but differences in plant community composition (Johnson et al. 2008) and variations in plants at the species level also impact soil respiration rates (Fischer et al. 2007). These findings could result from indirect relationships between plant composition and soil respiration. For example, genotypic variation in *Populus* can influence both microbial biomass and microbial community composition (Schweitzer et al. 2008b). Similarly, variations in condensed tannins among *Populus* species and genotypes have been related to different rates of leaf litter decomposition (Schweitzer et al. 2008a). Finally, the rapid but variable relationship between the production of photosynthates and their release back to the atmosphere via autotrophic respiration (Craine et al. 1999; Högberg et al. 2001; Knohl et al. 2005; Kuzyakov and Gavrichkova 2010) results in another source of variability. Together, these examples demonstrate the myriad important influences of plant composition on belowground carbon dynamics.

In the eastern USA, recent concern has been raised on the decline of oak (genus *Quercus*) species. Pests, pathogens, and fungal diseases, including the European gypsy moth (Lovett et al. 2006), bacterial leaf scorch (Barnard 2007), and oak wilt (Wilson 2001), pose a direct threat to oak species and have already decimated a number of established oak populations. High deer populations (Rooney and Waller 2003), fire suppression (Shumway et al. 2001), and shade intolerance (Crow 1992) are all factors in the current, widespread failure of oak tree regeneration. The combined effect of threats to mature oaks and failure of regeneration creates a significant probability that this foundation taxon (sensu Dayton 1972) will decline, with the potential for large impacts on forest carbon cycling.

A large-scale tree girdling experiment, designed to quantify the role of *Quercus* in various components of ecosystem function, was implemented in Black Rock Forest during the summer of 2008, offering an opportunity to assess the role of *Quercus* in soil respiration. Girdling blocks the phloem transfer of photosynthates to the roots with minimal disturbance to the root–mycorrhizal system (Högberg et al. 2001). This approach allows for a conservative estimate of the autotrophic component of respiration to be made based on the difference between control and treated plots. Implications of the potential artifacts of this technique are discussed later in this paper.

Over the past 9 years, tree girdling has gained popularity as a way to provide insight into the respiratory partitioning in different types of ecosystems. However, the number of girdling experiments applied in this capacity remains extremely small (approximately 13 published studies) compared to the variety of climates and ecosystems that exist (Högberg et al. 2009). The goal of our research was to estimate both the overall partitioning of autotrophic and heterotrophic soil respiration in a northern temperate deciduous forest and the contribution of autotrophic respiration from the dominant taxon, *Quercus*, and its associated mycorrhizae. We hypothesized that soil respiration would decrease within a few weeks of girdling in direct proportion to the percentage of aboveground tree biomass girdled.

Materials and methods

Site description

Black Rock Forest is a 1,550-ha preserve located in the Hudson Highlands, Orange County, New York. The study site is 100 m a.s.l. on the north-facing slope of Black Rock Mountain (41.45°N, 74.01°W) (Ellison et al. 2007). The acidic and nutrient-poor soils are clay loams derived from glacial till overlying granitic bedrock (Lorimer 1981). The soils are classified as Chatfield and Rockaway series (Denny 1938). Detailed descriptions of these soil series can be found on the National Resources Conservation Service (United States Department of Agriculture—Official Soil Series Descriptions; available at http://www.soils.usda.gov/technical/classification/osd/index.html website). The north slope is dominated by mature (120-year-old) *Quercus rubra* L., *Q. prinus* L., *Q. velutina* Lam., and *Q. alba*., with *Acer rubrum* L., *A. saccharum* March., *Betula lenta* L., and *Nyssa sylvatica* Marsh also present in the canopy. Air temperatures vary seasonally, and in 2009 mean January air temperature −5.5°C and mean July air temperature was 23.1°C. Total annual precipitation was 1,218 mm.

The experimental area was subject to repeated clear cutting by European settlers prior to 1900 (Schuster et al. 2008). In 1933, a portion of the site was thinned for dead, dying, or diseased trees, and then in 1960 much of the site received a moderate thinning for cordwood as well as a 1-ha planting of Norway spruce trees (along the border between plots B1 and C1; Fig. 1). Since 1989, Black Rock Forest has served as a nature preserve and research station for a consortium of academic institutions.

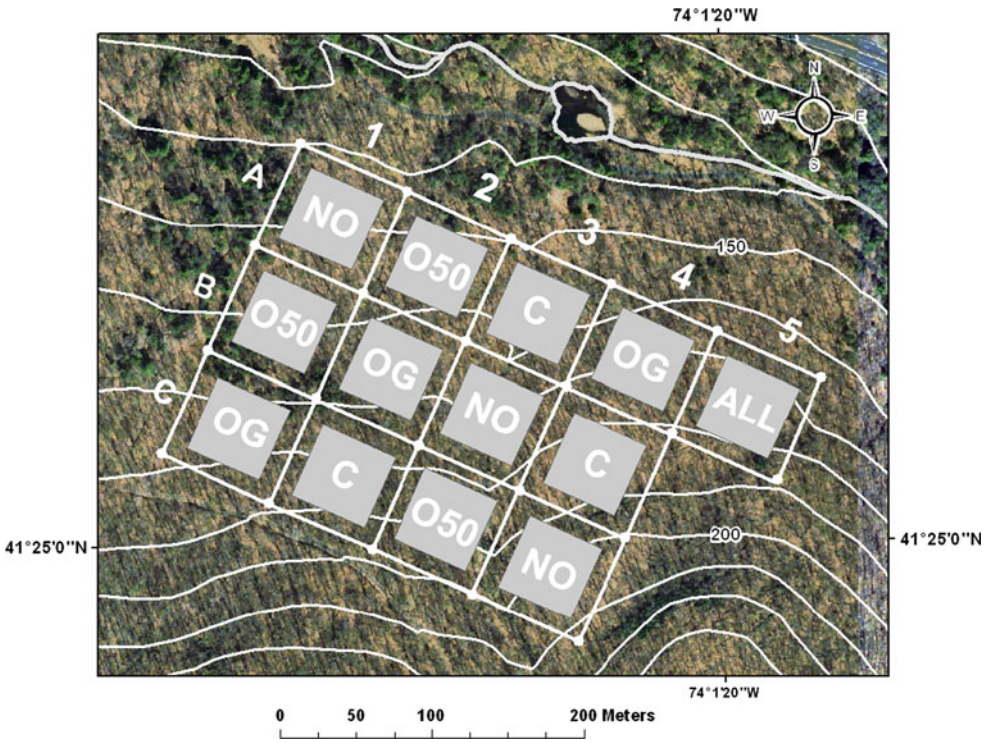


Fig. 1 Map of the project area showing the location of plots and treatments on the north slope of Black Rock Mountain, Black Rock Forest, NY. *ALL* all trees girdled, *OG* all oaks girdled, *O50* 50% oaks girdled, *NO* all non-oaks girdled, *C* control

Experimental design

This study consisted of a large-scale girdling experiment established to assess the role of *Quercus* as a foundation taxon (Fig. 1). In the main project area, trees on 12 plots (75 × 75 m) in a randomized block design grouped by slope position (lower, middle, and upper) were girdled according to four treatments. Each block (rows A, B, and C) contained four plots with one representative of the following treatments: girdling all the oaks on the plot (OG), girdling half of the oaks on a plot (O50), girdling all non-oaks on a plot (NO), and a control (C). Thus, all treatments were replicated three times. Mean values for tree density, basal area, aboveground biomass, and species composition did not differ between plots selected for different treatments before those treatments were initiated. In addition to the 12 established plots, an adjacent circular plot (diameter 50 m) was created specifically for this experiment where all trees on the plot were girdled (ALL). Within the 12 main experimental plots, all measurements were made within a 25 × 25-m center subplot. All manipulations and measurements reported here were made between June and October 2008.

Girdling and soil respiration measurements

Trees were girdled by making a 5-cm-deep incision at breast height around the circumference of the tree with a chain saw that penetrated bark, phloem, cambium, and outer xylem. Girdling through the outer xylem may have had a greater effect on the water flux than if only the phloem had been stripped off. On all plots, the few trees with a diameter at breast height (dbh) <2.54 cm were left ungirdled. Due to a history of heavy deer herbivory in this forest, only 135 of the more than 7,100 trees in the study area fell into this size class; this small fraction represented 0–3% of trees on any given plot. If girdling left trees unstable and near collapse, typically trees that were >2.5 cm dbh but <7.5 cm dbh, the trees were completely felled for the safety of the researchers working on the plots. Girdling took place between June 27 and July 9.

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. Ten collars (diameter 10 cm) made from PVC pipe were inserted approximately 2 cm into the soil to facilitate soil respiration measurements. Collars had been installed in six of these plots (A1, A2, B1, B2, C1, C2) during the summer of 2007 for a previous experiment, and they were used again in this study. In the remaining plots, new collars were installed 2 weeks prior to measurements. On June 6 and August 16 an additional five collars were added to one of the control plots (A3) and the fully girdled plot (ALL), respectively. If, as happened occasionally, a collar was knocked out of place, the measurement for that spot would be skipped and a new collar would be inserted at another location for the next cycle of measurements.

Three consecutive respiration measurements were made each day at each collar, and the efflux rate of each collar was considered to be the mean value of the last two measurements in order to reduce the effect of any initial disturbance incurred during the placement of the chamber on the collar. The mean value of all 10–15 collars per plot was used in data analyses. The maximum decline in respiration rate as well as the standard error (SE) were calculated using the mean value of control plot measurements taken on the same day as the treatment plot measurement. To reduce errors associated with litter layer heterogeneity, we gently removed surface litter from each collar before the measurement and then replaced it after. In a separate study, consecutive measurements were made first with leaf litter and then with the litter removed. Comparison between the two methods revealed no statistical difference in measured efflux rate (data not shown). Additionally, the measuring time was constrained to early morning and afternoon (0800–1300 hours) to minimize natural variability associated with a diel cycle. Consequently, four to five plots were measured on any given day. Weekly measurements began 2 weeks prior to the first girdling treatment, and sampling efforts increased for 2 weeks following treatments (almost all plots had 3–4 measurement dates within the first 2 weeks of girdling). From the beginning of August through to the beginning of October, measurements were made once every other week on all plots.

Change in live aboveground biomass was measured on all plots in the summer of 2007 (before girdling) and again on the OG and O50 plots at the end of the summer in 2008 (after girdling). The change in live aboveground biomass on NO plots was measured at the end of 2009. This increment on the NO plots captures the amount of biomass converted from live to dead by the treatment as well as growth of the remaining live trees during the 1.5-year time interval. Live aboveground biomass was calculated from the diameter at breast height using previously derived allometric equations (Brenneman et al. 1978; Monteith 1979). Trees were considered to have live biomass if the crown leafed out for the season. Additionally, an inventory of girdled trees that leafed out or resprouted from the base or trunk the following spring was made during the summer of 2009. 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 (75 × 75-m) plot area. For non-oaks, girdled tree measurements from the 25 × 25-m center subplot were extrapolated to the full 75 × 75-m area for comparison.

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 continuously on two plots from each treatment (except ALL) starting 26 June 2008. Two SWC and temperature probes were set within each center sub-plot, and the daily mean was used for analysis. Soil moisture probes were inserted into the soil at 45° angles, and soil temperature probes were located 15 cm below the soil surface. Unfortunately, environmental measurements from the ALL plot were lost due to animal damage to the sensor cables.

Data analysis

Working within a natural forest over a large spatial area posed challenges for the data analysis. Simple direct comparisons between control and treated plots were complicated by influences of slope position on respiration rate, differences in measurement dates (only four of the 13 plots could be measured in 1 day) and, importantly, differences in the girdling date (span of 2 weeks, for operational reasons). Therefore, after consulting with a statistician, we chose to combine the use of a generalized additive model (GAM) (Eq. 1) and a standard percentage change formula (Eq. 2) to estimate the minimum autotrophic contribution to total soil respiration through the growing season for each of treatments relative to a synchronous start date (Fig. 2).

$$\begin{aligned}\mathrm{Flux} &= \mathrm{JulD} + \mathrm{Tsr} \times \mathrm{DSG} + \mathrm{Slope} \\ &(\text{coded as}: \ (\mathrm{gam(Flux)} \sim \mathrm{s(JulD)} + \mathrm{s(ALLsr} \times \mathrm{DSG}) \\ &+ \mathrm{s(O50sr} \times \mathrm{DSG}) + \mathrm{s(OGsr} \times \mathrm{DSG}) + \mathrm{s(NOsr} \times \mathrm{DST}) \\ &+ \mathrm{Slope})) \end{aligned} \quad (1)$$

where Flux = predicted soil CO_2 efflux (μmol m^{-2} s^{-1}), JulD = Julian day of the soil respiration measurement, Slope = slope position (lower, middle, upper), DSG = days

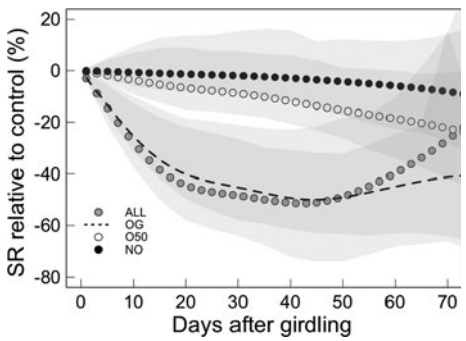


Fig. 2 Model of percentage decrease in soil respiration (*SR*) through time for four treatments relative to the Control plots on the north slope of Black Rock Mountain. *Shaded gray areas* are 95% confidence intervals (CI). This model is based on three replicate plots for the control and each treatment except for ALL where $n = 1$. Measurements were made in the summer and continuing into the fall of 2008. Treatments are as defined in Fig. 1

since girdling, and Tsr = mean measured soil CO_2 efflux (μmol m^{-2} s^{-1}) on each plot for all treatments (ALL, OG, O50, NO, C).

This model accounts for the natural variability in soil respiration rate associated with both slope position and seasonal cycle, thereby rectifying differences among blocks as well as measurement dates. Since soil moisture and soil temperature measurements were not recorded on the ALL plot throughout the duration of the experiment, these parameters could not be included in the model. For modeling purposes, July 3 was chosen as the treatment start date (middle date of the treatment span).

A bootstrapping algorithm randomly modeled the lower slope position data set 1,000 times, and the resulting variation was used to estimate the 95% confidence intervals (CI). This method was chosen because the complexity of working with a percentage change complicated standard error calculations. The lower slope position was selected for the analysis because measurements for all treatment plots (including the single fully girdled plot) were made at this position and, qualitatively, the error was assumed to be similar for all slope positions.

A minimum estimate of the autotrophic contribution to total soil respiration was extracted by calculating the percentage change in soil respiration rate derived by the model between the control and each treatment (Eq. 2).

$$\%\ \text{change in flux} = \left(\frac{\text{CFlux}_{\text{DSG}} - \text{TFlux}_{\text{DSG}}}{\text{CFlux}_{\text{DSG}}}\right) \times 100 \quad (2)$$

where CFlux = predicted control soil CO_2 efflux (μmol m^{-2} s^{-1}), DSG = days since girdling, and TFlux = predicted treatment [(ALL, OG, O50, or NO) soil CO_2 efflux (μmol m^{-2} s^{-1})]. This percentage change was calculated for 80 days following the girdling treatment (Fig. 2). R statistical software (R Development Core Team 2009) was used for all of the analyses with an error probability of $p < 0.05$ used to determine significant effects.

Results

Soil respiration

Pretreatment soil respiration was similar on all plots. The model showed that within 2 weeks of girdling, the ALL plot and OG treatment experienced an average decrease in soil CO_2 efflux of 37 and 33%, respectively (Fig. 2). Respiration rates continued to decline, reaching a maximum difference in soil CO_2 efflux at 6 weeks in the ALL (51%) and OG (50%) treatments (Fig. 2). Subsequently, relative differences between the control and treated plots were moderated by an overall decline in respiratory activity in all plots that was associated with the end of the growing season. By mid-October, all of the plots exhibited a similar basal respiration rate of approximately 2 μmol CO_2 m^{-2} s^{-1} (Fig. 3a). This is reflected in Fig. 2 as an increasing slope. A trend in the modeled mean percentage decrease of soil respiration suggests that the O50 treatment had a slightly larger effect on respiration than the NO treatment, although this was not significant at the 5% level (Fig. 2). Overall, the model accounted for 71.8% of the variability observed in soil respiration. The CO_2 efflux rate decreased with slope position ($p < 0.001$) by −1.34 μmol CO_2 m^{-2} s^{-1} (middle) and −2.16 μmol CO_2 m^{-2} s^{-1} (lower) compared to the upper position.

The initial live biomass in 2007 varied between plots from 209 to 300 metric tons per hectare. The change in live aboveground biomass for individual plots was ALL (−270.0 metric tons ha^{-1}), OG (−190.0, −165.9, −183.7 metric tons ha^{-1}), O50 (−77.7, −76.5, −88.7 metric tons ha^{-1}), NO (−21.8, −30.6, −7.7 metric tons ha^{-1}), and C (6.3, 5.9, 6.3 metric tons ha^{-1}). Along this gradient, we observed a non-linear trend for the maximum decline in soil respiration, relative to the control, when the day with the largest difference was isolated [ALL (53%), OG (55, 37, 65%), O50 (7, 40, 36%), NO (8, 26%, 45)]. This snapshot did not occur on the same day for each plot. Treatment means of biomass change and maximum measured decline in soil respiration illustrate this non-linear trend (Fig. 4). Pretreatment respiration rates (without model adjustments) were 8.48 ± 1.1 (ALL), 7.97 ± 0.54 (OG), 8.36 ± 0.5 (O50), 9.01 ± 0.81 (NO), and 9.31 ± 0.34 (C) μmol CO_2 m^{-2} s^{-1} ± 1 SE. Control plot respiration rates increased from June to the middle of July and ranged from 6.31 to 15.75 μmol CO_2 m^{-2} s^{-1} before slowly declining through October (Fig. 3a).

Soil temperature

Average daily soil temperature on treated and control plots followed a similar increasing trend from June through July. During this period, soil temperatures increased from 17 to 22°C, then steadily declined through October (Fig. 3b). Until the middle of September, the O50 plots mimicked control plot temperatures but at a slightly lower value (1°C), at which point the relationship reversed and the O50 plots had a slightly warmer soil temperature for the rest of the growing season (Fig. 3b). For most of September, mean temperatures on NO and O50 plots were approximately 1°C above that of the control plots, but the differences were not significant. In August, the OG treatment average fell below those of the rest of the plots by approximately 2°C, and this difference was maintained for the remainder of the growing season (Fig. 3b).

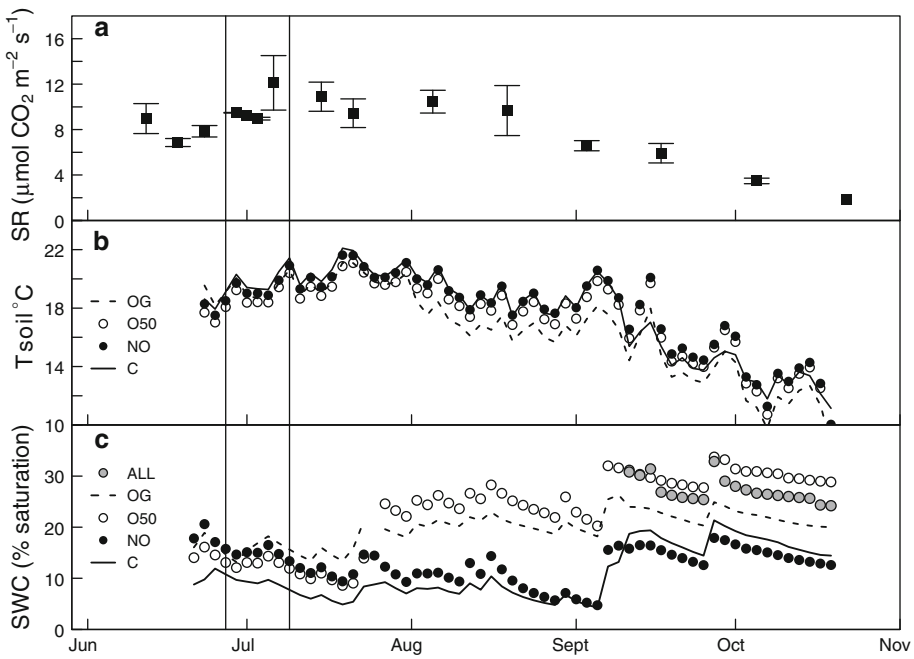


Fig. 3 **a** Soil respiration (*SR*) on Control plots ± one standard error (SE) in 2008. Data are aligned to the middle date of the measurement interval. **b** Average daily soil temperature (*Tsoil*) at 15-cm depth. **c** Average daily soil water content (*SWC*; % saturation). All measurements were made on the north slope of Black Rock Mountain in 2008. *Vertical black lines* show the interval when tree girdling occurred. All data shown are treatment averages. $n = 2$ plots for OG, O50, NO; $n = 3$ plots for C. Treatments are as defined in Fig. 1

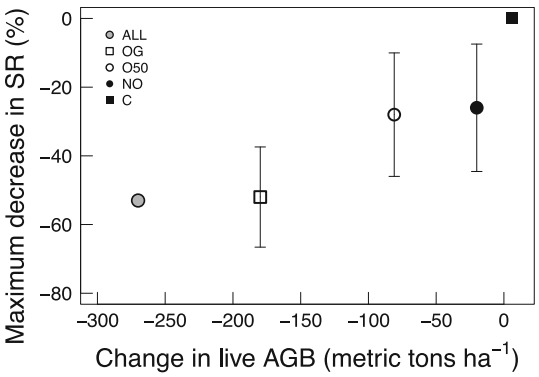


Fig. 4 Maximum decline in soil respiration (*SR*) rate relative to a Control plot measurement on the same day along a change in the live aboveground biomass (*AGB*) gradient. All data are treatment means ± 1 SE. $n = 3$ for all treatments except for ALL where $n = 1$. Treatments are as defined in Fig. 1

Soil water content

Soil water content was more variable than soil temperature throughout the growing season. Pre-treatment measurements indicate that control plots had a lower average soil water content than OG, O50, and NO plots from the initiation of the experiment (Fig. 3c). The three treatments had similar soil water contents until June 25 when NO plots became relatively drier and O50 plots became relatively wetter than OG plots. This separation created a moisture gradient increasing from C < NO < OG < O50 until September when the control plots exceeded the soil water content of the NO plots (Fig. 3c). From September onwards, a constant gradient from NO < C < OG < ALL < O50 ensued.

Girdling efficacy

Within the OG and O50 plots, i.e. those where only oaks were girdled, nearly twice as many oaks leafed out and/or resprouted the following spring on the O50 plots than on the OG plots. On the O50 plots, 15% of trees leafed out and 46% resprouted, whereas 8% leafed out and 27% resprouted on the OG plots. 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).

Discussion

The goal of this study was to evaluate the contribution of *Quercus* and associated mycorrhizae to total soil respiration

Table 1 Percentage of trees that leafed out or resprouted from the base or trunk 1 year after the girdling treatment on the north slope of Black Rock Mountain

Tree species	Number of trees girdled	Leafed out (%)	Basal sprout (%)
Oaks	385	10	33
Sugar maple	216	50	33
Black gum	261	31	62
Black birch	99	9	64
Red maple	576	9	84
All non-oaks	1,350	23	69

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

and to gain a better understanding of the partitioning of autotrophic and heterotrophic soil respiration at Black Rock Forest. A non-proportional response of soil respiration to girdling, through the season, was observed along the following gradient of change in live aboveground tree biomass: ALL > OG > O50 > NO > C (Fig. 2). In agreement with our initial hypothesis, both the ALL and OG treatments exhibited a rapid decrease in respiration rate within the first few weeks of girdling but, unexpectedly, the magnitude was not proportional to the change in living biomass. Instead, the respiration rate in the single ALL plot decreased by 51% and that in the OG plots by 50%. Therefore, based on these two treatments, a conservative estimate for the autotrophic contribution to the total soil respiration in this system is 50%. These observations are comparable to reported values for fully girdled plots in other studies. For example, the autotrophic component was estimated to be 65% in a Scots pine forest in Sweden (Bhupinderpal-Singh et al. 2003), 50% for a European beech stand in Central Europe (Andersen et al. 2005), and 60, 53, and 50% in three Norway spruce stands located in Sweden (Olsson et al. 2005; Högberg et al. 2009) and Germany (Subke et al. 2004), respectively.

Our results do differ from those of two studies similar in either design (girdling proportions of trees) (Binkley et al. 2006) or forest type (deciduous forest in northeastern USA) (Edwards and Ross-Todd 1979). Neither of these studies observed a large decrease in respiration following girdling. Binkley et al. (2006) proposed that in both systems, large carbohydrate reserves in the root systems were utilized to sustain root activity. This has also been suggested in other deciduous forest systems (Frey et al. 2006; Chen et al. 2010). We do not believe this is a major source of error in the *Quercus* population. *Quercus* is known to resprout vigorously after damage to young trees, but the probability of resprouting decreases with increasing age and size (Johnson 1975; Burns and Honkala 1990). This pattern suggests that allocation of root carbohydrates may change with maturity. Furthermore, the 120-year-old stand at Black Rock Forest showed a decline in soil respiration that was large and comparable to several other studies (50%). An additional explanation for the lack of response in the Edwards and Ross-Todd (1979) mixed-deciduous forest study was their small plot sizes (10 × 20 m), which were subject to incursion of roots from outside plot edges (Högberg et al. 2001). We suspect that the combined differences in plot size (200 vs. 5,625 m^2), forest stand age (36 vs. 120 years), and species composition (tulip poplar vs. oak-dominated forest) can account for the differences in our observed results. The efficacy of girdling treatments in hardwood temperate deciduous ecosystems is strongly dependent on various forest stand characteristics, such as age, species composition, and resprouting ability, as well as on issues of experimental design.

Our most unexpected finding was the non-proportional decline in soil respiration along a gradient of live biomass impacted by the girdling treatments. The similar responses observed from the ALL and OG treatments as well as the non-proportional response of the O50 and OG plots preclude the ability to directly quantify the contribution of *Quercus*, compared to other taxa, on the overall contribution to soil respiration. We propose that utilization of stored carbohydrates below the girdle of many non-oak trees and a general redistribution of belowground energy worked in conjunction to produce these observations.

The basic assumption that girdling trees, especially non-oaks, severed the energy supply to their root system may have been inaccurate. If many girdled trees were able to access carbohydrate reserves that were stored below the girdle, the reserves would have been used as an energy source to sustain autotrophic respiration, perhaps at a reduced rate. If this were happening on the non-oak plots, we would expect the observed respiration to be similar to, or only slightly lower than, that of the control. Furthermore, both the ALL and the OG plots would exhibit comparable respiration rates because similar amounts of biomass would be affected by the girdling treatment. These two predictions were observed, providing support to this theory (Fig. 2). Additionally, leaves on many non-oak trees remained green throughout the growing season, whereas evidence of girdling was indicated by brown leaves on most oak trees within a few weeks of the treatment. Carbohydrate reserves in the non-oaks could have kept the root system active enough to allow continued transport of xylem water and nutrients from the roots to the leaves. This would provide a mechanism to maintain leaf vitality. Conversely, if oak trees could not get access to the recent photosynthate and did not have enough reserves to maintain root function, the roots would die, water transport would cease, and the leaf mortality would ensue. Perhaps the most convincing evidence for the utilization of carbohydrate reserves in the non-oak population is that 23% of girdled non-oaks leafed out the following spring (especially larger trees) and 69% grew new sprouts, whereas only 10% of girdled oak trees leafed out and only 33% resprouted (Table 1).

Tree response to girdling is known to vary substantially among species (Noel 1970; Chen et al. 2010). The large discrepancy in resprouting and leafing out rates between girdled oaks and girdled non-oaks suggests that trees differ in their storage capacity and/or their ability to use recent versus stored carbon for foliage production or basal sprouts. The varying proportions for leafing out compared to basal sprouting among species indicate that the strategy for regeneration after girdling differs among species. In our study, we believe that the oaks and non-oaks differed in the use of stored carbohydrates below the girdle and that either

non-oaks had larger carbohydrate reserves or they were better able to utilize the existing reserves. Since most oaks responded to the girdling treatment, we would expect the O50 plots to show approximately half the response (25% decline) that the OG plots exhibited. This was not observed (Fig. 2).

The second phenomenon under discussion is a redistribution of remaining energy in the belowground system, prompted by the girdling disturbance (potential mechanisms are discussed below). For example, when only half of the oak trees were girdled in a plot, the healthy trees that continued to photosynthesize may still have transferred carbon substrates belowground. We propose that some girdled trees are gaining access to that energy source. As a result, the observed decline in respiratory activity would be buffered on the O50 plots but not on the OG plots, which is the pattern that was observed. Our findings of differential oak leaf-out rates on the O50 and OG plots further support this hypothesis. If the energy supply were to be redistributed to aid girdled trees, it would be expected that girdled trees on the O50 plots would show increased survival. In fact, in the year after girdling, we observed twice as many oaks leafing out on the O5O plots than on the OG plots. Alternatively, if the great majority of girdled oak trees respond to the treatment, the photosynthate supply that would normally be transferred from aboveground to belowground would be halted, and the entire system that depended on that autotrophic source of energy would collapse. In fact, a large reduction in respiratory activity was observed in both the ALL and OG plots, providing a conservative estimate of the autotrophic component (or more likely the *Quercus* component) of soil respiration.

Two potential mechanisms for belowground energy redistribution could be a network of ectomycorrhizal fungi connecting oak trees and/or root grafting. Networks of mycorrhizae connecting individual trees and those of resource sharing via a source/sink relationship have been observed in a natural forest setting (Simard et al. 1997). In the Black Rock Forest, *Quercus* associates with ectomycorrhizal fungi (Turner et al. 2009), whereas the most common non-oak populations that dominate our field site (*Acer rubrum L.*, *A. saccharum* Marsh., *Nyssa sylvatica* Marsh.) are commonly associated with endomycorrhizal species (Keeley 1980; Phillips and Fahey 2006). These association patterns create a spatial separation of potential resource sharing belowground and thus reduce the likelihood of resource sharing between oak and non-oak populations. Root grafting is also likely to provide a spatial separation among oak and non-oak populations since most forest tree species are known only to have intraspecific root grafts (Graham and Bormann 1966). Healthy trees sustaining the root systems of girdled trees through intraspecific root grafts has been observed in other forests (Bormann 1966; Stone 1974).

The ecological implication of our findings suggests that in our system, there may be a threshold somewhere between 35 and 74% loss of aboveground biomass at which the forest is capable of maintaining processes both above- and belowground. If energy is redistributed in the system to aid in the survival of damaged trees, as illustrated by higher rates of resprouting and leafing out on the moderately disturbed O50 plots, this redistribution may contribute to the resilience and recovery of the ecosystem following a major disturbance. However, beyond a certain disturbance threshold, the change in belowground processes may ultimately lead to large-scale changes in ecosystem function, as suggested by the observed decline in respiratory activity in the ALL and OG treatments.

Respiration rates may have also been influenced by the specific environmental conditions of the plots and the effect of the girdling treatment on these abiotic parameters. Notably, soil temperature was similar in all measured plots for the first 4 weeks of the experiment (Fig. 3) and therefore is unlikely to have influenced respiration during this time. Soil water content was more variable, ranging from 5 to 35% saturation among plots (Fig. 4), similar to values found in other studies (Andersen et al. 2005; Olsson et al. 2005). Pre-treatment measurements indicate that the C plots had a lower soil water content than all other plots right from the initiation of the experiment. Approximately 3 weeks into the study, water content rose approximately 10–15% in the O50 and OG plots compared to the C plots (Fig. 4); this increased soil moisture in these plots likely resulted from decreased water uptake in the girdled oaks. The temperature drop in the OG plots around the same time might be linked to a greater loss of latent heat from evaporation in the wetter soils. This phenomenon of increased soil moisture was also observed in a boreal forest (Olsson et al. 2005) and could stimulate respiratory activity on these plots, resulting in an underestimation of the autotrophic portion of soil respiration. Interestingly, the increased saturation happened only on plots where at least some oaks had been girdled. The NO treatment maintained water content levels closer to those of the control than any other treatment, supporting the concept that the non-oaks were less responsive to the treatment than oaks. This phenomenon could also result from oaks contributing more to stand transpiration than other tree species. Although technical problems precluded the direct inclusion of soil temperature and moisture in our analysis, it is clear that these variables deserve further attention and would likely strengthen our predictive model.

The interpretation of girdling experiments such as ours must consider potential unintended effects of the experimental manipulations. Short-term artifacts of the treatment may include increases in heterotrophic respiration due to new substrate sources, such as dead roots and their

symbionts (Högberg et al. 2001), utilization of starch reserves in fine roots (Högberg et al. 2001), alterations in normal root processes (Li et al. 2003), and altered respiration of understory plants (Högberg et al. 2001). These changes in the belowground carbon cycle bias the results toward an underestimation of the autotrophic component. Therefore, it is important to recognize that the proximate response of soil respiration to the treatment is conservative.

In summation, a conservative estimate of the total autotrophic contribution to soil respiration in this forest is approximately 50%, as revealed from the ALL and OG treatments. As described above, this finding is consistent with several previous studies that reported a large autotrophic component to forest soil respiration (Bhupinderpal-Singh et al. 2003; Subke et al. 2004; Andersen et al. 2005; Olsson et al. 2005). The contribution of *Quercus* to total soil respiration could not be directly decoupled from overall soil respiration due to non-proportional declines in respiration rate along a gradient of change in live aboveground biomass. The buffered respiratory response on O50 and NO plots align with the fact that the girdling treatment was more effective on oaks compared to non-oaks at our study site. The lack of a proportional response on the O50 plots suggests that carbon is being redistributed belowground from ungirdled to girdled trees in response to the treatment. There appears to be a threshold, somewhere between a 35 and 74% loss of aboveground biomass, at which girdling becomes more effective and belowground autotrophic activity collapses. Rapid declines observed within the first month of the treatment demonstrate a fast turnover of recently fixed photosynthates and their release back to the atmosphere via autotrophic respiration. These findings indicate that biotic and abiotic controls on photosynthesis can have large implications for forest carbon budgets. Factors that affect the rates of photosynthate production and soil biotic activity, such as herbivory, defoliation (Frey et al. 2006), nutrient availability (Olsson et al. 2005), and forest stand decline, have the potential to profoundly alter forest carbon balance.

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