Belowground carbon pools and fluxes in a northern temperate deciduous forest and their response to stand disturbance

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ABSTRACT

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Understanding the processes that govern terrestrial carbon fluxes and sequestration are fundamental to improving our understanding of climate feedbacks and ecosystem biogeochemistry. Biotic disturbances such as pest or pathogen attacks can have a large impact on forest carbon storage yet our knowledge of how these perturbations impact forest carbon cycling is limited. The goals of this dissertation were to gain insights into the processes governing soil respiration at Black Rock Forest (southeastern NY, USA) by quantifying the relative contributions of autotrophic and heterotrophic activity to soil respiration, to assess the short-term impact of mimicking a pathogen attack on soil carbon pools and fluxes, and to develop the first soil carbon budget for Black Rock Forest.

These goals were addressed by utilizing a large-scale manipulative experiment, which induced tree mortality through girdling. Trees on twelve plots (75m by 75m) were girdled according to four treatments: girdling all oaks, girdling half of the oaks, girdling all non-oaks, and a control. Additionally, one circular plot was created where all trees were girdled. Soil respiration was measured before the girdling and for three years afterwards. Forest floor litter and soil organic carbon at five depth intervals were measured on all plots two years after girdling.

The results from the first year of the experiment provided an initial estimate of 50% for the autotrophic component of soil respiration but continued declines in soil respiration rate into the second year provided a more accurate estimate of 58 %. Rapid declines in soil CO_2 flux from the fully girdled plot (37%) and from the oaks girdled treatment (33%) within two weeks following girdling demonstrate a fast turnover of recently fixed carbon.

The three-year time series of respiration measurements provided insights into the short-term impact of mimicking a pathogen attack on soil carbon fluxes. Respiratory rates on plots where all oaks, half of the oaks, and all trees were girdled declined for two years following treatment before attaining a full recovery of belowground activity in the third year. Soil respiration from the non-oak girdled treatment was similar to control for the duration of the study. The short-lived respiratory response on plots where all oaks, half of the oaks, and all trees were girdled suggests that belowground activity is highly resilient to disturbance. It also aligns with reported recovery patterns of net ecosystem production after a pest or pathogen attack. Overall, the reduction in soil respiration was not proportional to the degree of canopy loss, the magnitude of the respiratory response varied interannually, and was specific to the plant taxon impacted.

No changes across treatments in soil organic carbon storage were observed two years after the mimicked attack. These findings do not support a recent hypothesis that suggests disturbance should reduce soil carbon pools (Peltzer et al. 2010). Instead, it is proposed that shifts in the composition of carbon substrates within the belowground carbon pool occurred and that the changes may offset each other. This could result in a similar quantity of soil carbon storage between the disturbed and undisturbed forest stands. The first estimate for soil carbon storage at Black Rock Forest is 3.0 ± 0.5 kg C m^{-2}, which is 32% of the aboveground carbon storage. Together, the findings from this dissertation contribute to the limited knowledge of respiratory partitioning and of short-term impacts on soil carbon storage and fluxes following a partial stand disturbance in northeastern deciduous forests.

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Introduction

Carbon dioxide (CO_2) has been identified as the most important anthropogenic greenhouse gas causing global warming (IPCC 2007). Increases in atmospheric CO_2 concentrations from preindustrial levels of 280 parts per million (ppm) to 379 ppm in 2005 is primarily attributed to fossil fuel use and, to a lesser extent, land–use change (IPCC 2007). Rising concern for future changes in earth-system processes associated with a warming world and the resulting implications for society have driven scientists to seek a better understanding of the global carbon cycle. Globally, carbon is sequestered on land (terrestrial biosphere), in the atmosphere, and in the ocean. Exchanges of carbon in various chemical forms occur between all three carbon pools. Decreases in the rate of CO_2 uptake or increases in the rate of CO_2 release from either the biosphere or the ocean will contribute to rising atmospheric CO_2 levels, enhancing the rate of global warming. On interannual to decadal time scales, variability in atmospheric CO_2 concentrations is related to fluctuations in the land – atmosphere carbon flux (IPCC 2007). Understanding the processes that govern terrestrial carbon fluxes and sequestration are fundamental to improving our understanding of climate feedbacks and ecosystem biogeochemistry.

Terrestrial carbon cycle

On land, the carbon cycle consists of a series of pools and fluxes. Carbon is stored in the biomass of vegetation, in soils, and in detritus. In temperate forests, soils store almost 1.5 times the amount of carbon stored in vegetation (Watson and Intergovernmental Panel on Climate 2000). The largest fluxes within the terrestrial carbon cycle, photosynthesis and respiration, are biologically derived. Plants take up carbon from the atmosphere and transform CO_2 gas into a sugar through the process of photosynthesis. The sugar may be used directly or go through a series of transformations to produce an assortment of organic carbon substrates. The substrate can then be used by the plant for a variety of purposes that are generally categorized as growth (ex. making new leaves or growing taller) or maintenance (maintaining cellular processes). When plants use the substrate for growth, the carbon that was initially removed from the atmosphere is temporarily sequestered, becoming assimilated into the structural biomass of the plant. The residence time for that carbon may vary from years to centuries (Gaudinski et al. 2000), depending on type of plant structure the carbon is incorporated into. A portion of the carbon that is fixed during photosynthesis is transported belowground to the root system as well where again both growth and maintenance occur through the process of respiration. During respiration, these carbon substrates are broken down releasing carbon skeletons, CO_2 and importantly energy. Respiration also drives decomposition by biota that break down living or dead organic matter. The balance between carbon uptake by photosynthesis and carbon release by respiration can determine a forests standing as a carbon source or sink on an annual basis. Additional smaller fluxes within the terrestrial carbon cycle are the removal of organic and inorganic carbon from the ecosystem via ground water and inputs of detritus into the soil system by aboveground litter fall.

Soil respiration

The belowground component is one of the most poorly understood aspects of the terrestrial carbon cycle. However, soils are the primary component of the terrestrial carbon sink (Watson and Intergovernmental Panel on Climate 2000) and they are also one of the major sources of CO_2 efflux from a forest ecosystem (Malhi et al. 1999). The efflux of CO_2 from the soil surface is a measure of the rate of soil respiration. As described above, the CO_2 is derived from activity of the forest biota and the total flux is a measure of the combined activity of both the heterotrophs and autotrophs. Heterotrophic organisms derive their energy by breaking down living or dead organic matter. Autotrophs are organisms that derive their energy directly from photosynthates they create. Belowground, this consists of living plant roots and, as in other studies, we include their associated mycorrhizal fungi. The inclusion of mycorrhizal fungi in the autotrophic category is a matter currently under debate (Kuzyakov 2006a; Kuzyakov 2006b; Hobgerg, Buchmann & Read 2006). These organisms are taxonomically categorized as heterotrophic organisms (Hobgerg, Buchmann & Read 2006, Kuzyakov 2006a). However, they directly depend on recently fixed carbon from photosynthesis for their energy supply and there is no feasible way to separate mycorrhizal fungi activity from root activity without disrupting the transfer of carbon from the root to the fungus (Hobgerg, Buchmann & Read 2006). Therefore, in this thesis, mycorrhizal activity is included in the autotrophic assessment.

Separating the relative contributions of these two groups to total soil respiration is the first step towards gaining a mechanistic understanding of controls on soil respiration. Partitioning these components needs to be considered in order to evaluate individual responses of these groups to changing environmental factors and improve our understanding of soil carbon cycling in response to changes in climate. Until recently, the heterotrophic contribution was thought to dominate the soil respiratory flux and therefore has been studied more extensively than the autotrophic component (Högberg and Read 2006). Our understanding of the magnitude, mechanisms, and controls of the autotrophic component is limited (Högberg and Read 2006).

Estimates of the autotrophic fraction range from 10-90% of total soil respiration but within forested landscapes, there is evidence for a large autotrophic contribution of approximately 46% (Hanson et al. 2000).

Most methods used to separate autotrophic and heterotrophic soil respiration cause physical disturbance to the root-soil continuum or are very costly (Hanson et al 2000). Over the past nine years, tree girdling has gained popularity as a way to provide insight into the respiratory partitioning (Levy-Varon et al. 2011). Girdling blocks phloem transfer of photosynthates to roots with minimal disturbance to the root- mycorrhizal system (Högberg et al. 2001). The difference in respiratory rates between control and treated plots can then be used to make a conservative estimate of the autotrophic contribution. In chapters one and two of this thesis, soil respiration measurements from a large-scale tree girdling experiment were analyzed to partition the autotrophic and heterotrophic components of soil CO_2 efflux.

Partial stand disturbance and the carbon cycle

In addition to respiratory partitioning, partial stand girdling can provide insights into the impact of pest or pathogen attacks on forest carbon cycling and storage (Nuckolls et al. 2009; Nave et al. 2011). This method has been used previously to simulate a sudden oak death pathogen attack (Bergemann et al. 2005). Girdling treatments that target specific tree species within a mixed canopy, such as the study reported in this thesis, mirror the patterns and sometimes the mechanisms of tree mortality that are characteristic of these biotic disturbances (Nave et al. 2011).

Little is known about how both carbon cycling and storage are impacted by disturbance events (Kurz et al. 2008; Running 2008; Amiro et al. 2010). However, some studies that have assessed impacts of pest and pathogen attacks indicate that these disturbances can dramatically affect carbon cycling and subsequently alter a forest's carbon storage capacity (Kurz et al. 2008; Peltzer et al. 2010). In particular, the recovery pattern of soil respiration after a disturbance reflective of a pest or pathogen outbreak (i.e. actual biotic disturbance or partial stand tree girdling) has not been documented. In the second chapter of this thesis, soil respiratory fluxes from the first year are combined with two additional years of respiration and environmental measurements to examine the temporal response of soil respiration after a partial stand disturbance. Short-term impacts on soil carbon storage after this type of disturbance are also poorly understood. In a recent hypothesis, Peltzer et al. (2010) suggested that pest infestations could result in enhanced decomposition rates leading to short-term reductions in the soil carbon pool. Soil carbon storage two years after tree girdling is presented in chapter three of this thesis. This dataset provides an opportunity to test Peltzer's et al. (2010) hypothesis. In this chapter, it is proposed that shifts in the source components of carbon within the belowground carbon pool could offset carbon losses resulting from altered decomposition rates.

Northeastern forests, disturbance, and carbon storage

The northeastern United States is an ideal region to study the impact of a mimicked pest or pathogen attack on the belowground carbon cycle. Disturbances such as pest infestations, snowstorms, hurricanes, and fires have historically shaped forest ecology in this region. Some previous pest and pathogen infestations that have affected northeastern forests include the hemlock wooly adelgid, chestnut blight, Dutch elm disease, beech bark disease, and the gypsy moth (Ellison et al. 2005; Lovett et al. 2006). Further, this type of disturbance remains a serious threat to forest ecosystems into the foreseeable future (Lovett et al. 2006). Northeastern forests are also an important place to study the carbon cycle because they are a carbon sink (Turner et al. 1995). This means that they help mitigate the buildup of CO_2 in the atmosphere by removing more CO_2 from the atmosphere than they release into it via ecosystem respiration. Across the United States, northeastern forests have the largest amount of carbon storage of any region (Turner et al. 1995). Therefore, perturbations in the rate of terrestrial carbon uptake or release in this area could have greater impacts on atmospheric CO_2 levels than other regions of the country.

Overview

This thesis focuses on quantifying belowground carbon pools and fluxes in response to partial stand disturbance in a northeastern forest. All of the questions addressed in this thesis were designed to take advantage of a large-scale tree girdling experiment, located at Black Rock Forest (southeastern NY). Tree girdling experiments are relatively rare and offer an opportunity to study a variety of questions related to the belowground carbon cycle. The second chapter focuses on partitioning sources of soil respiration. The third chapter examines the temporal response of soil respiration for three years following tree girdling and the fourth chapter assesses short-term changes in soil carbon storage after this disturbance. The major conclusions are summarized in chapter five.

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

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2.1 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.

2.2 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. 2.1). Since 1989, Black Rock Forest has served as a nature preserve and research station for a consortium of academic institutions.

Experimental design

This study consisted of a large-scale girdling experiment established to assess the role of *Quercus* as a foundation taxon (Fig. 2.1). 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

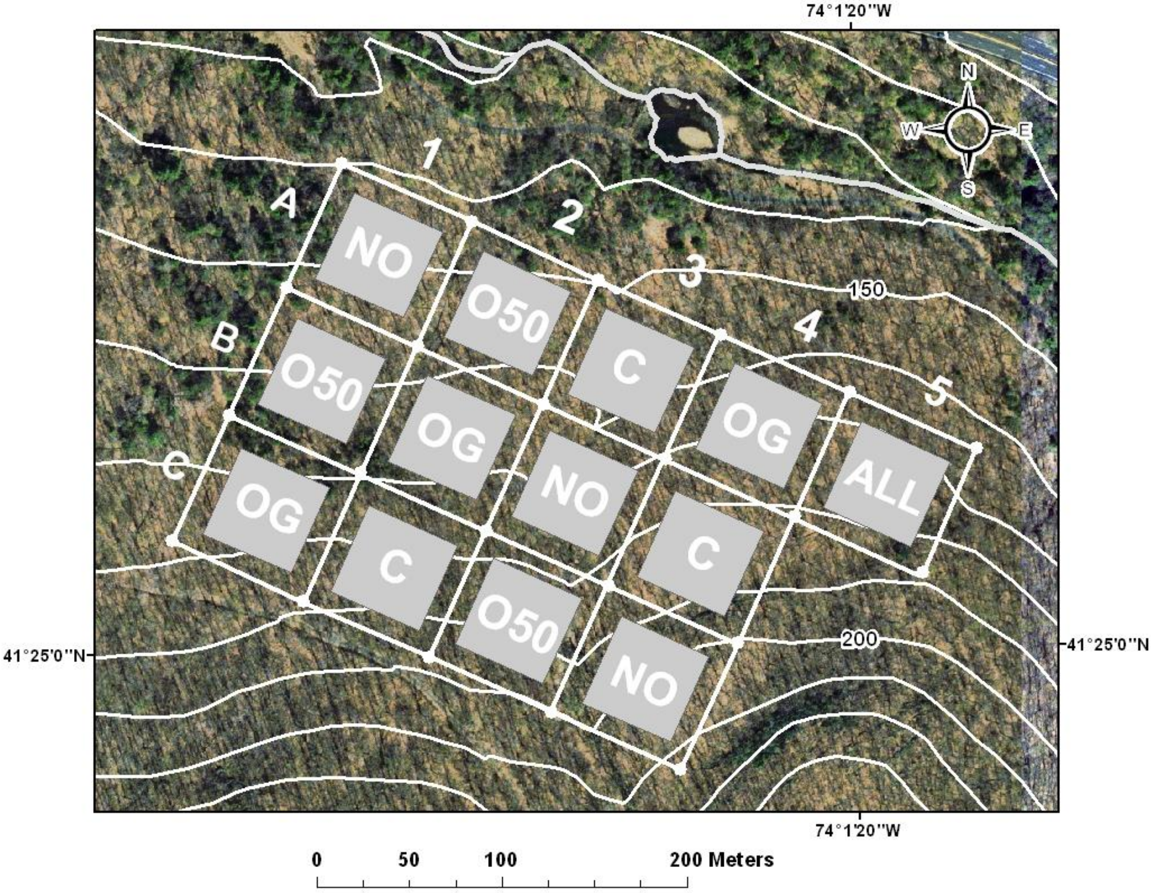

Figure 2.1 Map of the project area showing the location of plots and treatments on the north slope of Black Rock Mountain, Black Rock Forest, NY. *ALL* all trees girdled, *OG* all oaks girdled, *O50* 50% oaks girdled, *NO* all non-oaks girdled, *C* control

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. 1.2).

$$Flux = JulD + Tsr * DSG + Slope \qquad \left[Eqn. 1 \right]$$

$$\left(coded\ as : (gam(Flux) \sim s(JulD) + s(ALLsr*DSG) + s(O50sr*DSG) + s(OGsr*DSG) + s(NOsr*DST) + Slope) \right)$$

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 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).

$$\%\,change\ in\ Flux = \left(\frac{CFlux_{DSG} - TFlux_{DSG}}{CFlux_{DSG}} \right) * 100 \qquad \left[Eqn.\ 2 \right]$$

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. 2.2). 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.

2.3 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. 2.2). 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. 2.2). 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. 2.3a). This is reflected in Fig. 2.2 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. 2.2). 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. 2.4). 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. 2.3a).

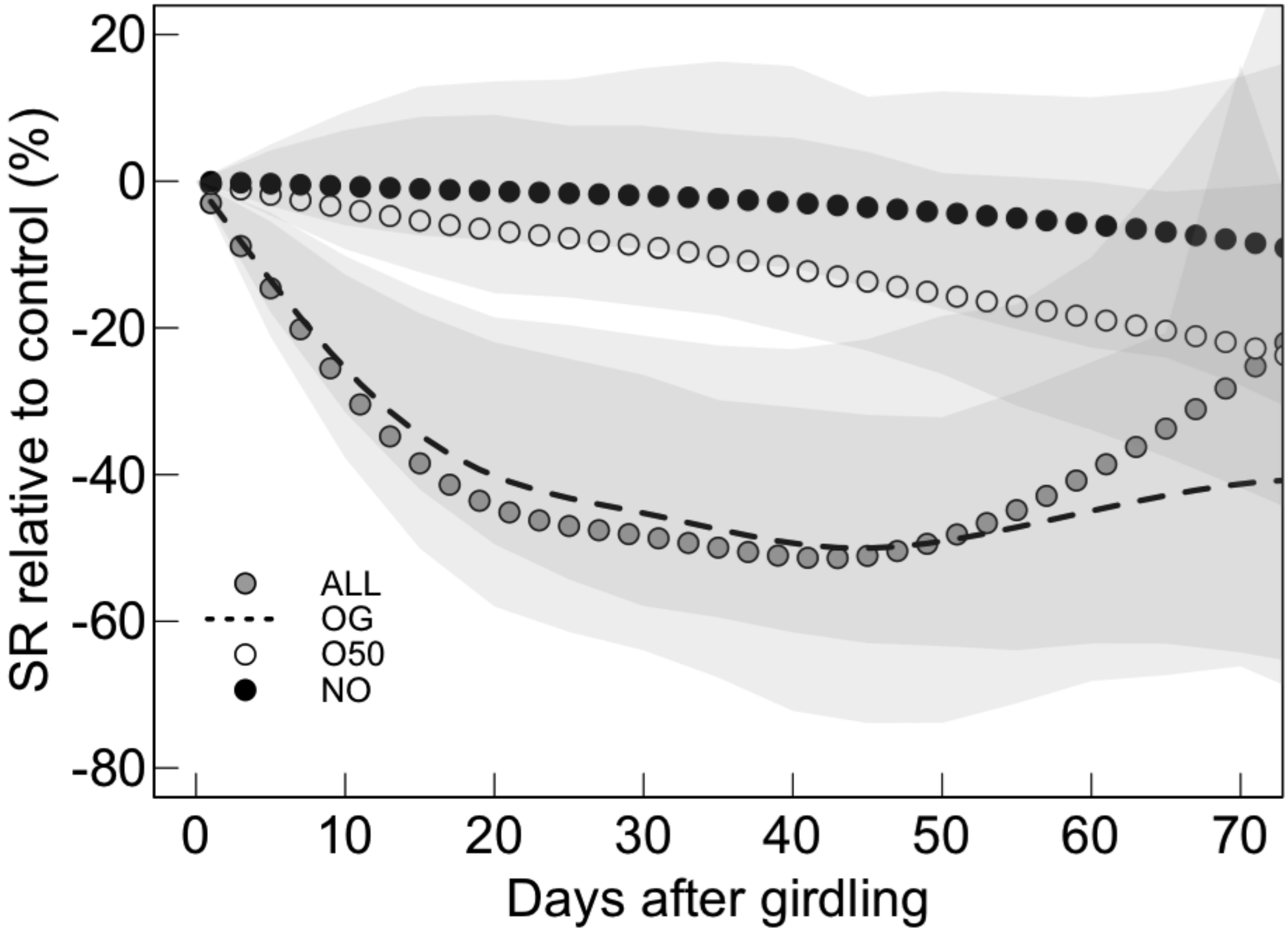

Figure 2.2 Model of percentage decrease in soil respiration (*SR*) through time for four treatments relative to the Control plots on the north slope of Black Rock Mountain. *Shaded gray areas* are 95% confidence intervals (CI). This model is based on three replicate plots for the control and each treatment except for ALL where *n* = 1. Measurements were made in the summer and continuing into the fall of 2008. Treatments are as defined in Figure 2.1

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. 2.3b). 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. 2.3b). 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. 2.3b).

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. 2.3c). 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. 2.3c). From September onwards, a constant gradient from NO < C < OG < ALL < O50 ensued.

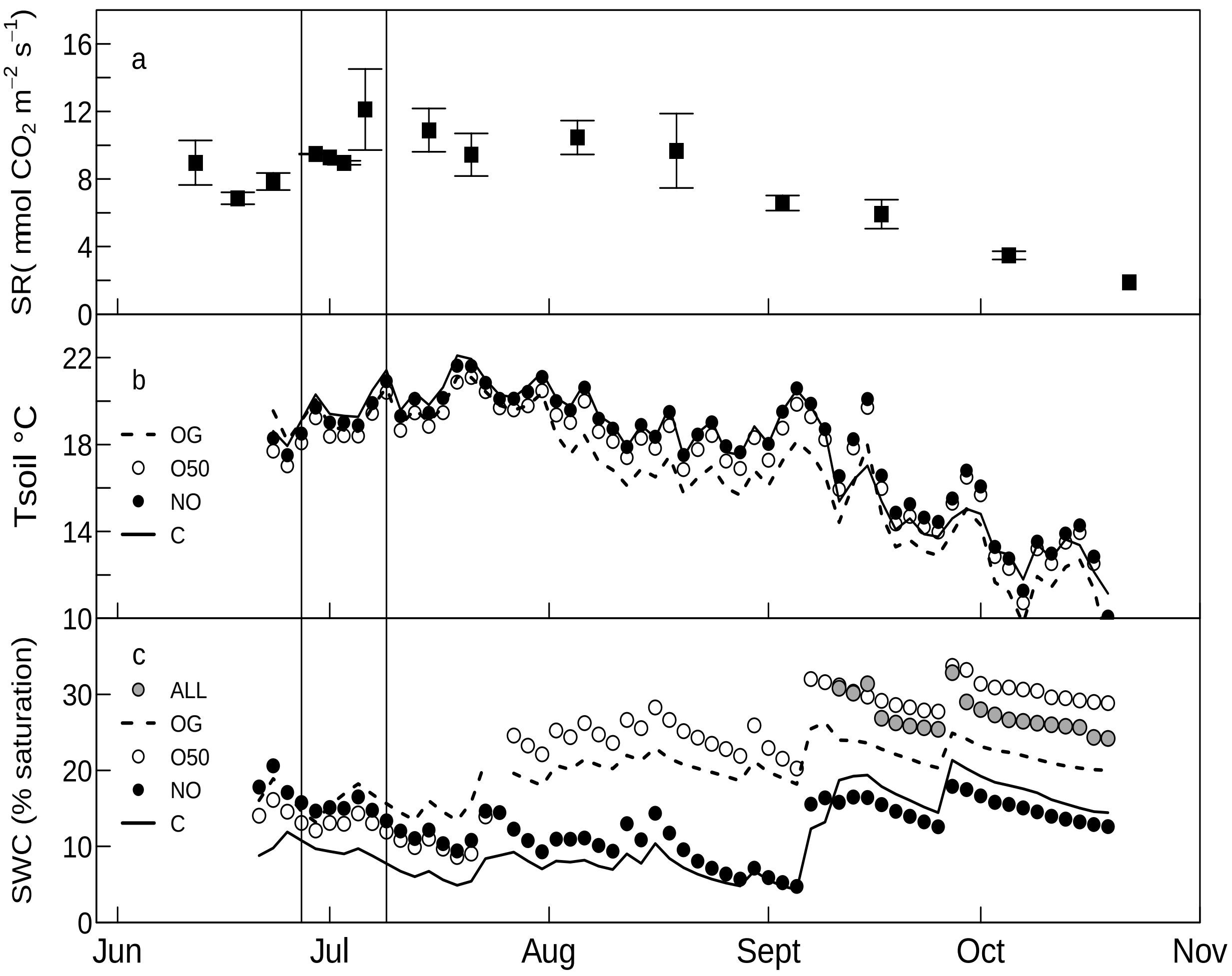

Figure 2.3 a Soil respiration (*SR*) on Control plots ± one standard error (SE) in 2008. Data are aligned to the middle date of the measurement interval. **b** Average daily soil temperature (*Tsoil*) at 15-cm depth. **c** Average daily soil water content (*SWC*; % saturation). All measurements were 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 Figure 2.1

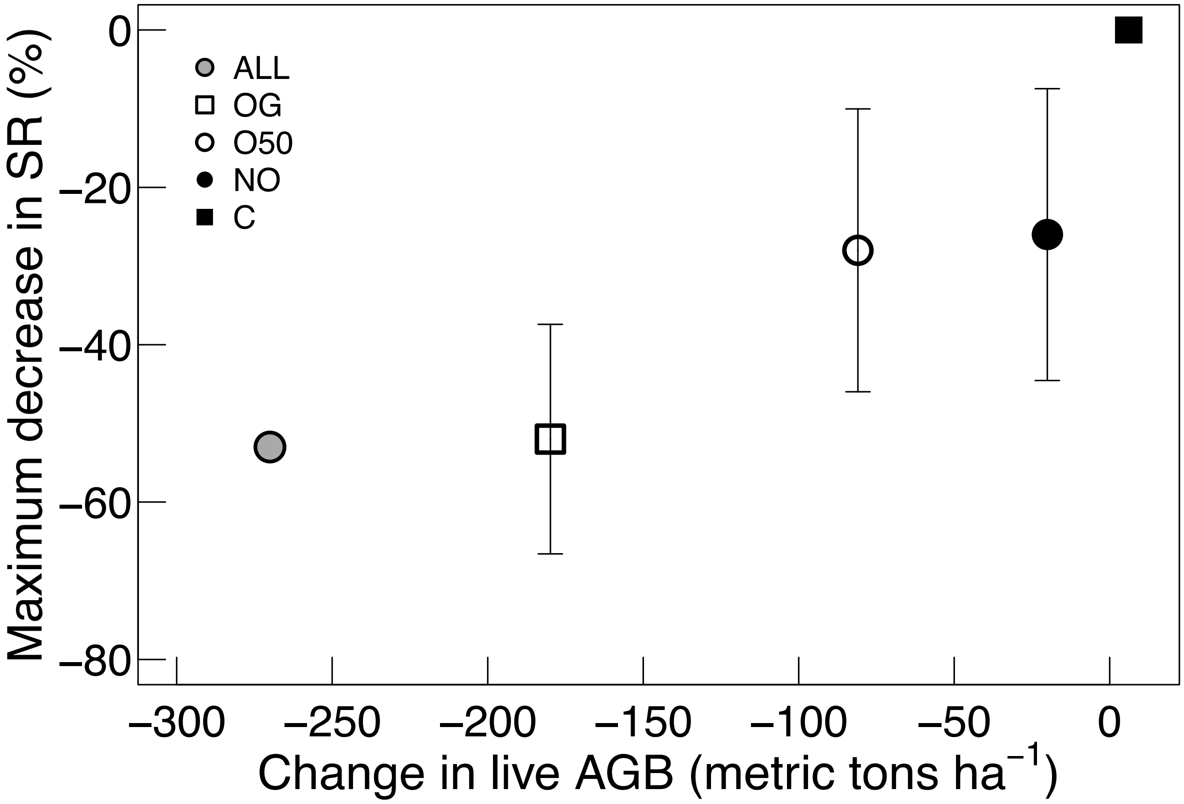

Figure 2.4 Maximum decline in soil respiration (SR) rate relative to a Control plot measurement on the same day along a change in the live aboveground biomass (AGB) gradient. All data are treatment means ± 1 SE. n = 3 for all treatments except for ALL where n = 1. Treatments are as defined in Figure 2.1

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 2.1).

2.4 Discussion

The goal of this study was to evaluate the contribution of *Quercus* and associated mycorrhizae to total soil respiration 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. 2.2). 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.

Table 2.1 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. Girdling took place late June/early July 2008, and leaf out and resprouting were recorded during the summer of 2009

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	1350	23	69

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. 2.2). 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 2.1).

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. 2.2).

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. 2.3) 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. 2.4), 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. 2.4); 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.

Temporal response of soil respiration following disturbance reveals strong resilience and complete recovery within a three-year period in a temperate forest

3.1 Introduction

Periodic disturbances such as snow or rainstorms, hurricanes, insect outbreaks, droughts, and fires shape forest landscapes and ecology. These types of perturbations have recently been identified as the main drivers that can convert ecosystems from carbon sinks to carbon sources (Baldocchi 2008; Kurz et al. 2008). They can reduce net forest carbon dioxide (CO_2) uptake by reducing the amount of photosynthesizing leaf area and they can increase the net forest CO_2 release by altering autotrophic and heterotrophic respiration in response to changes in carbon pools, resource allocation and environmental conditions. Additionally, biomass within carbon pools may be subject to removal via combustion by fire or logging. The trajectory of forest carbon dynamics after a disturbance is a loss of carbon from the system followed by a recovery period of up to 20 years (depending on the type of disturbance) (Amiro et al. 2010). Predicted changes in climate, mainly through alterations in temperature and atmosphere moisture loading, are expected to increase the frequency of many disturbance regimes (Overpeck et al. 1990).

In the United States, disturbance from pest and pathogen outbreaks affect 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 effect the survival, dispersal, geographic range, and reproduction of pests and pathogens (Ayres and Lombardero 2000). 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). The general consensus is that this type of disturbance will magnify 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; Liu et al. 2011).

Among the numerous ecological impacts of pest and pathogen attacks, alterations in forest biogeochemistry will be a particular concern for climate predictions. Pests and pathogens are more efficient in altering the species composition of a forest than a stand-replacing event because a pest or pathogen usually targets specific tree species (Lovett et al. 2006). Changes in overall forest biogeochemisty may follow this type of disturbance because tree species have different rates of photosynthesis, growth, and litter quality – all are linked to carbon cycling within a forest. The long-term effects of manipulating the forest biogeochemistry is thought to have a greater impact on carbon sequestration than the transient short-term carbon loss (Peltzer et al. 2010).

There is a great necessity for information on how all types of disturbances impact forest carbon pools and fluxes. Understanding the temporal changes in net ecosystem exchange of carbon dioxide following pest and pathogen outbreaks will be useful for predictive models. Detailed information on how components of the forest carbon cycle (both above and belowground) are impacted by these events will help gain insights into the expected long term shifts in forest carbon storage and cycling. Forest type and degree of Gypsy moth defoliation had varying impacts on the net ecosystem exchange (NEE) in a New Jersey forest (Clark et al. 2010). A simulated outbreak of mountain pine beetle decreased aboveground carbon stocks 31-83% and aboveground carbon fluxes 28-73% immediately following the outbreak but carbon sequestration increased for subsequent years resulting in recovery of forest carbon storage to preoutbreak levels within 25 years (Pfeifer et al. 2011). In contrast, Brown et al. (2010) found that their study forest became a net carbon sink for the two years following a mountain pine beetle attack in lodgepole pine stands in British Columbia. Seidl et al. (2008) also found that a 100-year simulation of the bark beetle infestation resulted greater carbon storage of unmanaged lands due to higher tree density resulting from the attack.

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. (2011) where we presented soil CO_2 efflux (soil respiration) measurements from the first year of the experiment. It is also described in Levy-Varon et al. (in review) where we present an estimate of soil carbon storage two years after disturbance. In this paper, we extend our record of soil carbon flux measurements by combining the previously presented soil respiration results with two years of additional respiratory and environmental measurements to examine the temporal response of soil respiration after a partial stand disturbance. Additionally, we provide a more accurate estimate of the autotrophic and heterotrophic contributions to soil respiration at our study site, based on the second year of observations.

3.2 Materials and Methods

Site description

Black Rock Forest is located in the Hudson Highlands, Orange County, New York. Our study site is a120 year-old *Quercus* dominated forest on the north-facing slope of Black Rock Mountain (41.45° N, 74.01° W). The canopy trees are predominately *Q. 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. Site history was previously described in Levy-Varon et al. (2011). The soils are Chatfield and Rockaway series (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 total annual precipitation was 1218 mm.

Experimental design and girdling treatment

We implemented a randomized block design for this study. Three blocks grouped by slope position (upper, middle, and lower) were girdled according to four treatments. Within each block, depicted as row C (upper slope), row B (middle slope) and row A (lower slope) in Figure 3.1, four plots were created. Each plot was 75 m x75 m and had a 25 m x 25 m center subplot. All measurements for this study were taken inside the center subplot. Each block contained one representative of the following treatments: control (C), girdling all non-oaks on a plot (NO), girdling half of the oaks on a plot (O50), and girdling all the oaks on the plot (OG). Additionally, a circular plot 50 m in diameter was created at the lower slope position (row A) where all trees on the plot were girdled (ALL).

Notch girdling (Noel 1970) was applied during the summer of 2008 by using a chain saw 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 Inc., Lincoln NE) was used to measure the soil surface CO_2 efflux in each of the center subplots at 10 locations. Measurements were constrained to early morning and afternoon (8 am-1 pm). As a result, only four to five plots could be measured on any one day. On occasion, collars (10 cm diameter) would be knocked out of place so the measurement for that cycle would be skipped and the collar would be replaced for the next cycle of measurements. 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. For visual purposes, soil respiration measurements from the same cycle of measurements are aligned to the same Julian day, which represents the middle day of the measurement span (usually 3-7 days; Figure 3.2a). Maximum decline in respiration was calculated from the difference between control and treated plots measured on the same day. The measurement interval for a treatment captures abiotic variability by averaging respiration rates measured on plots from three separate days. Therefore, in order to reduce errors associated with varying abiotic conditions, we choose to limit our estimate of the autotrophic component of soil respiration (e.g. maximum decline in soil respiration) to comparisons between

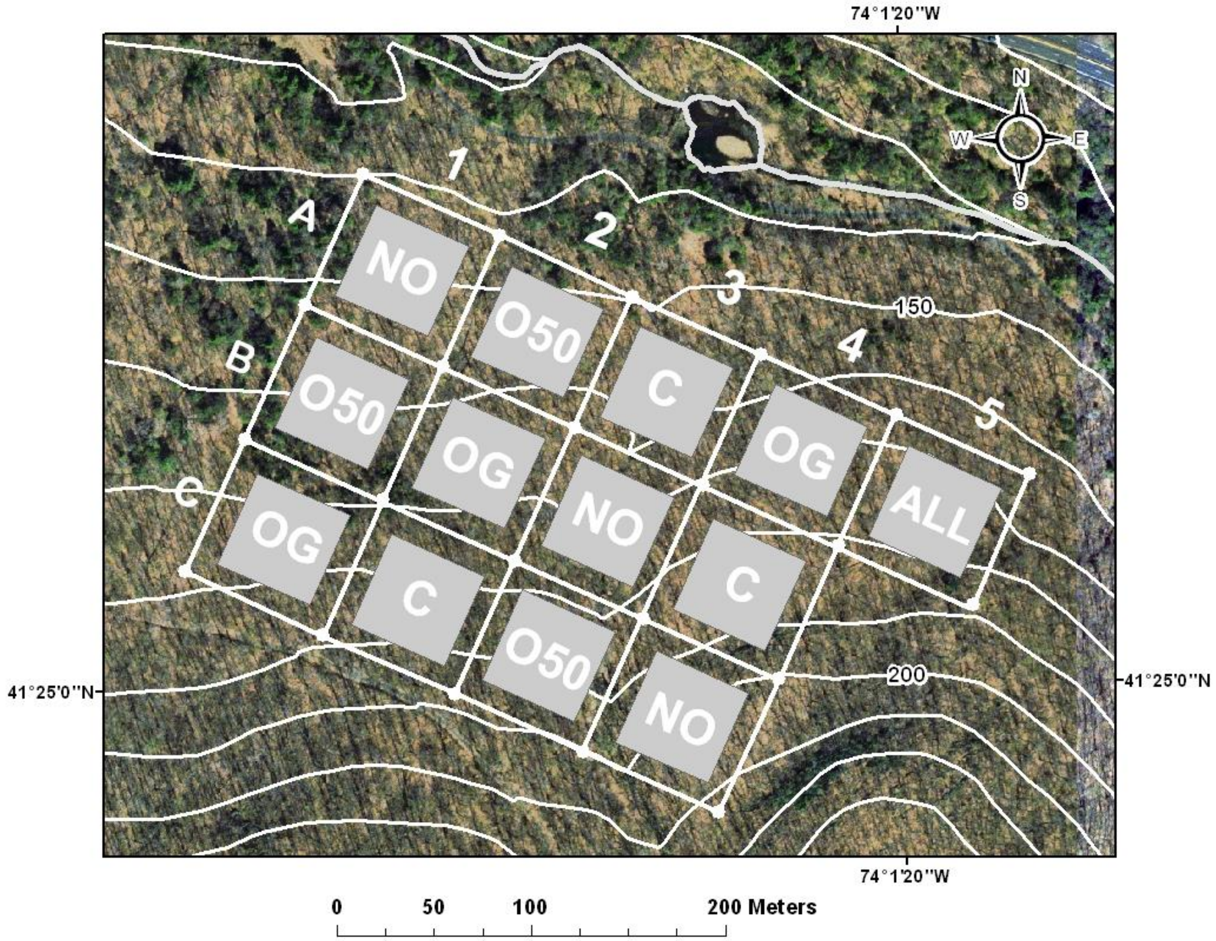

Figure 3.1 Map of the experimental area showing the location of plots and treatments. North slope of Black Rock Mountain, Black Rock Forest, NY. C-control, NO- all non-oaks girdled, O50- 50% oaks girdled, OG- all oaks girdled, ALL- all trees girdled (reprinted with permission from Levy-Varon et al. 2011)

plots measured on the same day. In 2009, soil respiration measurements were made bimonthly and in 2010 monthly.

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. (2011). Measurements for this paper were made the same way as previously reported. Briefly, live aboveground biomass was measured on all plots in the summer of 2007 (before girdling) and again on the treated plots OG, O50, and NO at the end of the summer in 2009 and 2010. The ALL plot was assumed to have 100% decline in aboveground biomass based on field observations. 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 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 summers of 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 x 25 m center subplot was extrapolated to the full 75 m x 75 m 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) of 2009, in the and Fall (November) of 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 ^{o}C for 24 hours and weighed. In the Fall of 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, Logan UT), were measured hourly on two plots from each treatment. All probes were set within the center subplot; two SWC probes were inserted at 45 degree angles and two soil temperature probes were located 15 cm below the soil surface. The daily mean of the two probes between hours 8 am and 1pm (time of respiration measurements) was used to calculate the plot average and plot averages were then used to calculate the daily treatment average. Unfortunately, soil temperature measurements were lost in 2008 on the ALL plot due to animal damage to the sensor cables.

Data analysis

After consulting with a statistician, a linear model (Eqn. 1) was developed to assess the effect of treatment, point in the growing season (Julian day), soil temperature, and slope position on our measured soil respiration rates. Soil moisture was not included in the model because it did not improve model fit based on Akaike Information Criteria (AIC; Hilborn&Mangel 1996) or R^2 (coefficient of determination). Using this model allowed us to include the single ALL plot in our comparison and 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 dataset to the year of interest.

$$Log(Flux) = T + JulD + JulD^2 + Temp_{soil} + Slope \qquad [Eqn.\ 1]$$

Where Flux = predicted soil CO_2 efflux (μmol m^{-2} s^{-1}), T = treatment (C, NO, O50, OG, ALL), JulD = Julian day of the soil respiration measurement, $Temp_{soil}$ = mean treatment soil temperature (^{o}C at 15 cm depth), and Slope=slope position (upper, middle, lower).

The impact of treatment on soil temperature and soil moisture was analyzed with a linear model (Eqn. 2) and a generalized least squares linear model (Eqn. 3) respectively.

$$Temp_{soil} = T + JulD + JulD^2 \qquad [Eqn.\ 2]$$

$$SWC = T \qquad [Eqn.\ 3]$$

Where $Temp_{soil}$ = soil temperature (^{o}C at 15 cm depth), T = treatment (C, NO, O50, OG, ALL), JulD = Julian day of the soil respiration measurement, and SWC = soil water content (% saturation).

The amount of variability in soil respiration rate associated with soil temperature and soil moisture was determined by taking the differences in the adjusted R^2 between the model in Eqn. 4 and either Eqn. 5 or Eqn. 6 for the respective parameters.

$$Log(Flux) = T \qquad [Eqn.\ 4]$$

$$Log(Flux) = T + Temp_{soil} \qquad [Eqn.\ 5]$$

$$Log(Flux) = T + SWC \qquad [Eqn.\ 6]$$

Where Flux = predicted soil CO_2 efflux (μmol m^{-2} s^{-1}), T = treatment (C, NO, O50, OG, ALL), $Temp_{soil}$ = mean treatment soil temperature (^{o}C at 15 cm depth), and SWC = soil water content (% saturation).

A one-way analysis of variance (ANOVA) was used to analyze treatment effects on 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. Tukey HSD Post-hoc test was used for pair-wise comparisons. For litter influx analysis, the ALL plot was not included due to the lack of true replication. 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. (2011). R statistical software (http://www.r-project.org) was used for all of the analyses with an error probability of $p<0.05$ used to determine significant effects.

3.3 Results

Soil Respiration

In 2008, soil CO_2 efflux decreased on the ALL and OG plots, -37 % and -33 % respectively, within two weeks of girdling. Respiration rates continued to decline reaching a maximum difference in soil CO_2 efflux at six weeks in the ALL (-51 %) and OG (-50 %) treatments. The NO and O50 treatments remained statistically similar to the control plots but a trend in the modeled mean percent decrease of soil respiration suggests that the O50 treatment had larger effect on respiration than the NO treatment (Levy-Varon et al. 2011). In 2009, soil respiration in the O50, OG, and ALL plots had significantly lower soil respiration rates over the course of the growing season compared to the control and NO plots (Fig. 3.2a). Within treatments, ALL had lower soil respiration rates over the course of the growing season than all other treatments. The maximum decline in soil respiration was NO (31 %), O50 (38 %), OG (51 %), and ALL (58 %) (Fig. 3.3). In 2010, no differences in soil respiration rate over the course of the growing season were observed between the control and each of the treatments. Additionally, no differences were found within the treatment comparisons (Fig. 3.2a). The maximum decline in soil respiration was NO (10 %), O50 (23 %), OG (22 %), and ALL (15 %) (Fig. 3.3). Note, the day with the largest difference was not the same for each treatment in either year.

The mean control soil respiration rate in 2008 averaged 8.29 μmol CO_2 m^{-2} s^{-1} in June, peaked at 12.11 μmol CO_2 m^{-2} s^{-1} in early July and declined to 1.88 μmol CO_2 m^{-2} s^{-1} by the end of October. In 2009, May rates averaged 2.18 μmol CO_2 m^{-2} s^{-1}, peaked at 8.78 μmol CO_2 m^{-2} s^{-1} in late July and declined to 4.36 μmol CO_2 m^{-2} s^{-1} by September. In 2010, early growing season respiration rates were 1.63 μmol CO_2 m^{-2} s^{-1} at the end of April, they increased to 7.79 μmol CO_2 m^{-2} s^{-1} in mid-July and then declined to 3.15 μmol CO_2 m^{-2} s^{-1} in September (Fig. 3.2a). Overall, the model in Eqn. 1 accounted for 69% 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 the lower slope position had significantly higher soil respiration rates by 0.36 μmol CO_2 m^{-2} s^{-1} ($p < 0.01$) compared to the upper slope position.

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 C (6.1 ± 0.1 Mg ha^{-1}), -9 % for NO (-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}), and -100 % for ALL (-270.0 Mg ha^{-1}). These values did not vary substantially for the second and third year of the study

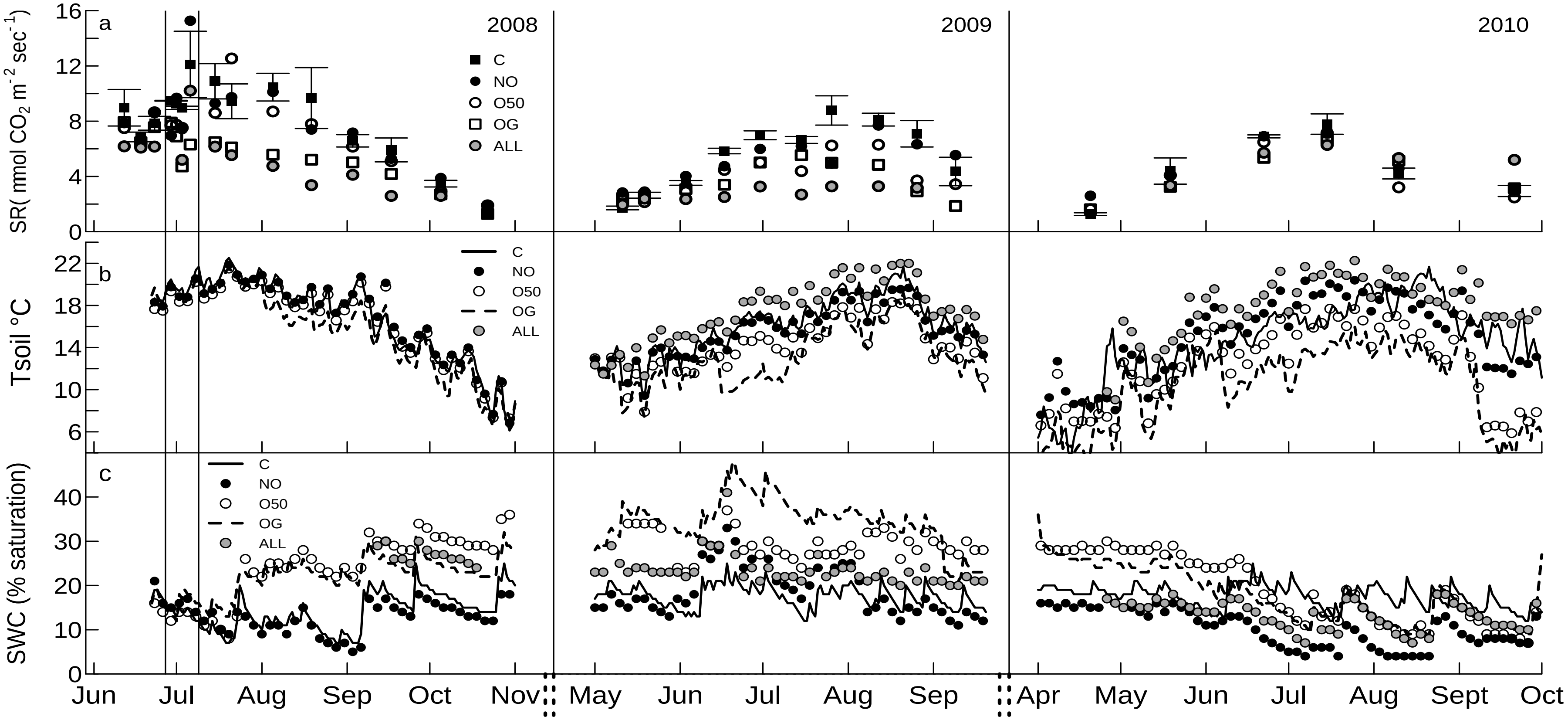

Figure 3.2 a) Soil respiration (SR) following girdling ± one standard error (SE) on Control plots. Data are aligned to the middle date of the measurement interval. b) Average daily soil temperature (T_{soil}) at 15 cm depth. c) Average daily soil water content (*SWC*; % saturation). All measurements 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 a 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 except for ALL where n=1. For T_{soil} and *SWC*, n=2 for OG, O50, NO, n=3 for C, and n=1 for ALL. Treatments are defined in figure 3.1.

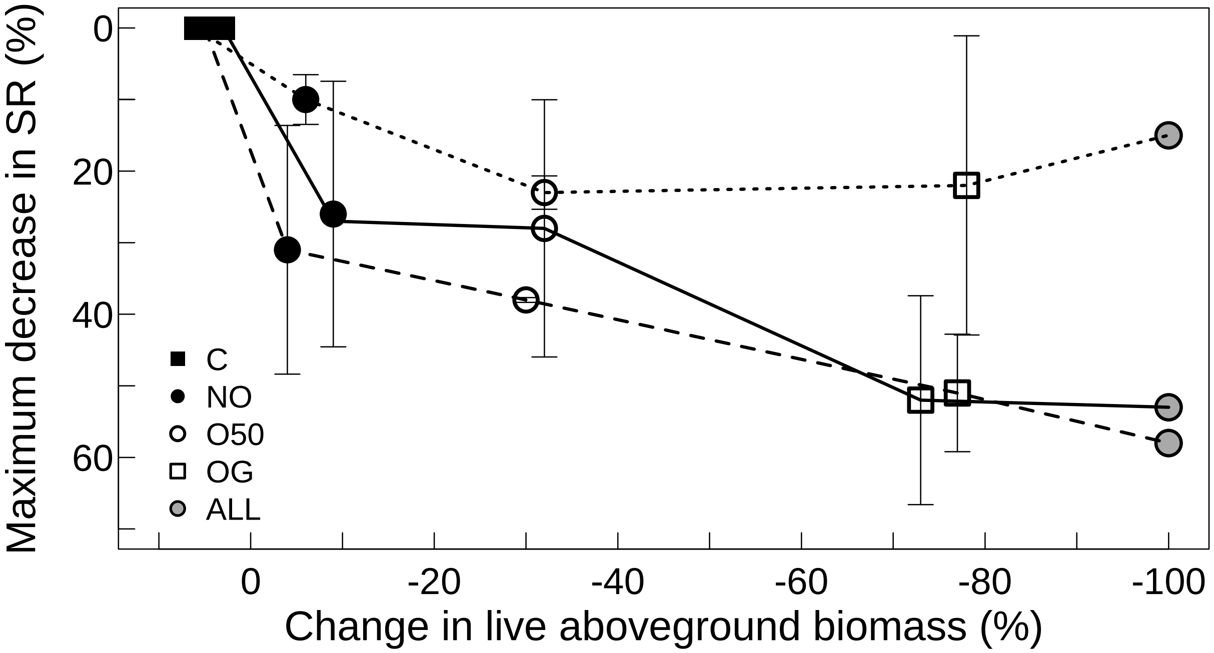

Figure 3.3 Maximum decline in soil respiration *(SR)* rate from 2008 – 2010 relative to Control plot measurement along a change in the live aboveground biomass *(AGB)* gradient. All data are treatment means ± 1 SE. n= 3 for all treatments except for ALL where n=1. Lines represent treatment year: 2008 (solid), 2009 (dashed), 2010(dotted). Treatments are defined in Fig. 3.1.

In the second year, the mean change in live aboveground biomass from 2007 to 2009 was +5 % for C (10.9 ± 0.5 Mg ha^{-1}), -4 % for NO (-11.0 ± 6.1 Mg ha^{-1}), -30 % for O50 (-76.9 ± 5.7 Mg ha^{-1}), -77 % for OG (-188.2 ± 6.07 Mg ha^{-1}), and -100 % for ALL (-270.0 Mg ha^{-1}). In the third year, the mean change in live aboveground biomass from 2007 to 2010 was +6 % for C (14.3 ± 1.3 Mg ha^{-1}), -6 % for NO (-17.3 ± 15.4 Mg ha^{-1}), -32 % for O50 (-82.7 ± 3.2 Mg ha^{-1}), -78 % for OG (-191.6 ± 5.4 Mg ha^{-1}), and -100 % for ALL (-270.0 Mg ha^{-1}). Along this gradient, we observed non-linear trends for the maximum decline in soil respiration from 2008 to 2010 relative to the control (Fig. 3.3).

Soil Temperature

In 2009, soil temperature on the control plots increased from 5.42 °C in beginning of April to 21.7 °C in late August before declining through the rest of the growing season. In 2010, soil temperature on the control plots increased from 8.46 to 21.23 °C in late April to early July (Fig. 3.2b). Soil temperature had a significant influence on soil respiration rates over the course of the growing season in both 2009 and in 2010. In 2009 and 2010 respectively, 68 % and 52 % of the variability in soil CO_2 efflux was accounted for by including information on soil temperature. In 2009, NO was the only treatment that experienced a similar soil temperature regime to the control but in 2010 both ALL and NO experienced similar soil temperature regimes to the control. All other treatments differed from each other. In 2009, soil temperature followed the general pattern from warmest to coolest ALL > C = NO > O50 > OG. This pattern remained similar in 2010 (C = NO = ALL > O50 > OG) (Fig. 3.2b).

Soil Water Content

Treatment did impact the soil moisture regimes but soil moisture did not influence soil respiration rates. Soil moisture accounted for 0 % and 3 % of the variability in soil CO_2 efflux in 2009 and 2010 respectively. In 2009, NO 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. In 2010, both ALL and NO had statistically similar soil moisture regimes to the control. All other treatment interactions differed from each other with the exception of the OG-O50, OG-ALL, and NO-ALL. In 2009, soil moisture followed the general pattern from wettest to driest OG > O50 >ALL > C = NO. In 2010, O50 had the highest soil moisture content followed by OG. C had statistically similar moisture contents to NO and ALL over the course of the growing season and ALL was had wetter soils than NO (Fig. 3.2c).

Girdling Efficacy

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 3.1) (Levy-Varon et al. 2011). In 2010 and 2011, the phenomenon of higher survival and resprouting on the O50 plots compared to the OG plots was less distinguished. On both the O50 and OG plots, 0-2 % of the girdled oaks leafed out in either year. On the O50 plots, 59 % and 50% of the trees resprouted in 2010 and 2011 respectively. On the OG plots, 52 % and 43 % resprouted in 2010 and in 2011. Comparison of oak and non-oak leafing out and resprouting rates are shown in Table 3.1.

Table 3.1. Percentage of trees that leafed out or resprouted from the base or trunk for the first three years after the girdling treatment on the north slope of Black Rock Mountain. Girdling took place late June/early July 2008 and leaf out and resprouting were recorded during the summer of 2009, 2010, and 2011.

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	1350	23	6	4	69	78	67

Litter influx

Following girdling in 2008, there was a non-significant trend for O50 to have higher total litter influx than the C ($p = 0.11$), OG ($p = 0.12$), and ALL plots. 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 C and NO treatments. 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 C and NO treatments. In the third year of the experiment, 2010, differences in total litter influx were not significant but C and O50 treatments tended to have higher litter influx than the OG, ALL, and NO treatments. As in 2009, the OG treatment had lower leaf litter input than the control and comparable leaf litter influx to ALL (Fig. 3.4).

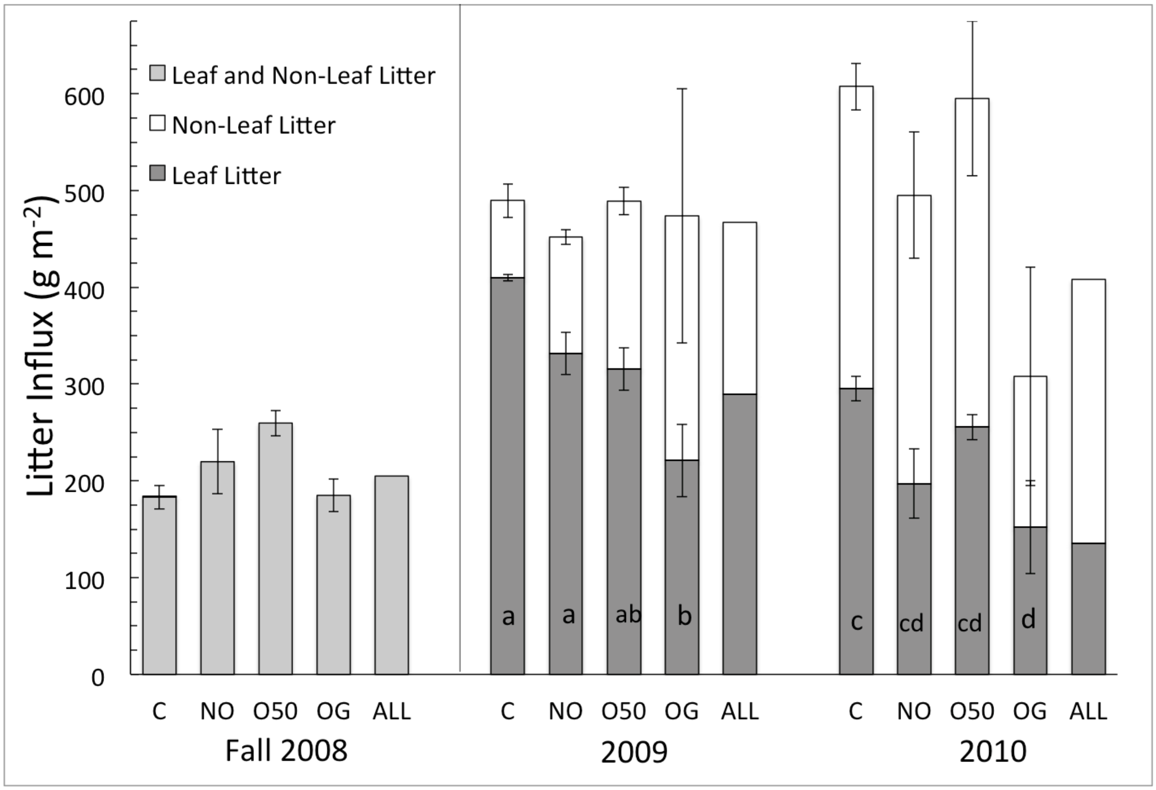

Figure 3.4 Total litter influx, leaf litter influx, and non-non leaf litter influx (g m^{-2}) for experimental treatments from 2008 to 2010 on the north slope of Black Rock Mountain. Year 2008 shows the Fall litter collection only whereas 2009 and 2010 show annual litter influx. Error bars are ± 1 SE. 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 except for ALL where n=1. Treatments are defined in Figure 3.1

3.4 Discussion

Our observations from three consecutive years of field measurements suggest that the response of soil CO_2 efflux to a non-stand replacing disturbance is a relatively very short-lived reduction in belowground carbon 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 mychorrhizal fungi) of soil respiration, and varies non-linearly in magnitude as a function of the severity of canopy disturbance and specific plant taxon impacted. The nearly complete recovery of the soil CO_2 flux after three years suggests that northeastern temperate deciduous forest ecosystems may be highly resilient to canopy disturbance.

Girdling studies that affect only part of a forest canopy or target specific tree species within a mixed canopy mirror the patterns (Nave et al. 2011) and sometimes the mechanisms of tree mortality that are characteristic of pest or pathogen attacks. Although not a perfect mimic, partial stand girdling can provide insight into ecosystem dynamics following these biotic disturbances (Nuckolls et al. 2009; Nave et al. 2011). Nuckolls et al. (2009) found similar patterns of decline in magnitude and timing of soil respiration from girdled stands and hemlock wooly adelgid infested stands, providing additional support for the use of girdling to understand patterns in soil CO_2 efflux after a pest disturbance. To our knowledge, this is the first study to present three 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 or partial stand tree girdling) and document the recovery pattern returning to undisturbed levels.

The rapid recovery of soil respiration was surprising since aboveground signs of disturbance are strikingly evident on treatment plots. Studies reporting soil respiration rates after a pest or pathogen outbreak are limited (Hicke et al. 2011) and thus it is difficult to draw general conclusions about the temporal trends or recovery patterns of soil CO_2 efflux following partial stand disturbance. The small number of investigations reporting soil CO_2 efflux differ in the measurement interval after disturbance and the means of reporting tree mortality, further complicating the comparison of our results with those of previous studies. A 20-40% depression in soil respiration shortly after a pest or partial stand girdling disturbance has been reported (Binkley et al. 2006; Hancock et al. 2008, Nuckolls et al. 2009; Nave et al. 2011, *n.b.* Morehouse et al. 2008), and is similar to the results from NO and O50 treatments in our experiment (Fig. 3.3). Interestingly, the rapid recovery of belowground fluxes in our study aligns with the trajectory of forest net ecosystem production (NEP) after a pest or pathogen attack, which generally declines in the year of disturbance and then is followed by a rapid recovery within 1-5 years (Amiro et al. 2010).

The findings from this experiment at Black Rock Forest are consistent with Nave et al. 's (2011) disturbance recovery hypothesis that suggests that partial canopy disturbance results in a short-term perturbation of forest carbon and nitrogen cycling followed by a relatively rapid recovery (within a few years) and stabilization of the two cycles. Compensating nitrogen uptake and growth from healthy trees facilitates the rapid rate of recovery (Nave et al. 2011). At our site, we observed a perturbation in the forest carbon cycle *via* declines in soil respiration, and a disruption in the nitrogen cycle as increased levels of nitrate and ammonium availability in the girdled plots (Melillo and Schuster, unpublished data). Compensating nitrogen uptake by healthy trees resulted in foliar %N enrichment in understory birch trees (15.5% in the O50 and 30.6% in the OG plots relative to the control) in the third year of the experiment (Flaxa-Raymond et al. in review). The elevated foliar %N suggests there was compensatory uptake of soil nitrogen that was facilitated by reduced competition and nitrogen uptake by the girdled trees (Nave et al. 2011). Compensating growth from healthy trees was evident in our study as a 625% and 121% increased growth rate of birch on OG and O50 plots respectively (Flaxa-Raymond et al. in review). Similarly Nave et al. (2011) documented increased foliar %N and inferred compensating growth. Together, our observations are congruent with the disturbance and rapid recovery of the biogeochemical cycles as suggested in Nave et al.'s (2011) hypothesis.

The rapid recovery of belowground activity observed in the third year of this experiment suggests the belowground carbon cycle is resilient to partial stand disturbance. Importantly, the similar respiratory patterns from ALL and OG treatments in the first year followed by higher rates from OG, but not ALL, in the second year suggest that belowground carbon dynamics rebound faster following a partial stand disturbance than a full stand disturbance. In contrast to the early successional species girdled by Nave et al. (2011), our study affected dominant late successional canopy oaks. The findings of Flaxa-Raymond et al. (in review) show that the compensatory activity of healthy plants occurs independent of successional position. In addition to compensatory activity, healthy trees may contribute to resilience in biogeochemical cycling by aiding stressed trees through resource sharing belowground via mychorrhizal networks and/ or root grafting (see also Levy-Varon et al. 2011).

The reduction in soil respiration was non-proportionally related to the severity of canopy disturbance. In the first year of disturbance, the modeled response of respiration to treatment revealed a non-proportional decline in soil respiration rate, through the growing season, along a gradient of change in live biomass (C < NO < O50 < OG < ALL). The large drop in respiration rate (approximately 50 %), from ALL and OG coupled with statistically similar respiration rates from C, NO, and O50 indicated a threshold type response of belowground dynamics occurring somewhere between 35-75 % AGB loss (Levy-Varon et al. 2011). In the second year, the threshold response was no longer present (Fig. 3.2a). However, non-proportional declines in soil respiration along the AGB loss gradient were still observed. Patterns of soil CO_2 efflux from O50 and OG were similar (despite 30 and 77 % AGB loss, respectively) as were the responses from C and NO (0 and 4% ABG loss). The seasonal patterns of soil CO_2 efflux from both the first and second year of this study highlight the non-linear response of the soil respiration to severity of stand disturbance.

The maximum decline in soil respiration rate in each treatment also varied disproportionately with the degree of AGB loss (Fig. 3.3). Although the maximum difference can provide insight into the potential impact of the disturbance on autotrophic soil respiration, it does not necessarily predict the seasonal response of respiration because environmental variables are generally in a state of flux and date of the maximum difference represents only a specific set of conditions and differs among the treatments. Interestingly, in both the first and second years of the experiment, the change in maximum decline in soil respiration rate for an incremental change in AGB (slope of lines in Fig. 3.3) 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 both the seasonal and maximum difference trends, the observations suggest that disturbance to the belowground carbon cycle is not linearly related to aboveground degree of canopy loss and that there are interannual differences in this dynamic response following disturbance. It also suggests that the initial stages of disturbance could have a greater impact on belowground carbon dynamics than later stages of infestation.

The specific plant taxon targeted also influenced the magnitude of the respiratory response. Throughout the duration of the experiment, soil respiration rates, moisture levels, and temperature regimes from the NO treatment were statistically similar to those measured on C. In contrast, depressions in soil respiration rate were observed within the first two years of this experiment on all treatments where at least some oak trees were girdled. The lack of respiratory response from 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 three years. It could also indicate that changes in the belowground system over the three 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 3.1 and Fig. 3.2c) support the idea that reserve respiratory substrates in the root systems of the non-oaks were able to sustain root respiratory activity throughout this experiment. Utilization of root carbohydrate reserves following girdling has been observed in other forests (Högberg et al. 2001; Frey et al. 2006; Nave et al. 2011). Ecologically, this indicates that the short-term response for impacts on belowground dynamics after this type of disturbance partially depends on the type of tree targeted and the root carbohydrate stores accessible.

One uncertainty in the analysis of data from the first year of this experiment was the influence of soil moisture and soil temperature on respiration rates (Levy-Varon et al. 2011). Based on the extended records, soil respiration rates were strongly correlated to soil temperature at our field site. In contrast, the amount of variability in soil respiration associated with soil moisture was only 0-3% in either 2009 or 2010 respectively. Taking into account the influence of soil temperature on soil respiration, treatment impacts were still observed. As proposed in Levy-Varon et al. (2011), we believe that the increased soil moisture on O50 and OG accompanied by decreased soil temperature for most of the study period was a result of reduced water uptake in girdled oaks and possibly a greater loss of latent heat from evaporation in the wetter soils. Additionally, elevated soil moisture levels would also occur if oaks contributed more to stand transpiration than other tree species (Levy-Varon et al. 2011). The increased soil temperature on ALL is likely a result of the open canopy following 100 % AGB loss. The open canopy would allow more solar radiation to reach the forest floor. ALL soil moisture regimes could be associated with understory activity that is described later in this discussion. Overall, it is unlikely that alterations in soil moisture had a large impact on the respiratory response in the first year of this study. Based on the analysis from the second and third year of the study, both soil temperature and treatment impacts were likely dominant components of the respiratory signal in the first year.

Based on the second year of this experiment, we revise our estimate of the autotrophic component of soil respiration upward to a maximum of 58 %. In the first year, we estimated the autotrophic component to be approximately 50 % (Levy-Varon et al. 2011), however continued declines in respiration rate on NO, O50, and ALL relative to controls were observed into the second year (Fig. 3.3). This revised estimate is based on the maximum difference between ALL and C (Fig. 3.3). Bhupinderpal-Singh et al. (2003) suggested that the second year of girdling could provide a more accurate estimate for partitioning the source components of soil respiration.

In their study, sugar and starch reserves sustaining root activity were exhausted and there was evidence for the turnover of decomposing ectomycorrhizal fungi in the second growing season (Bhupinderpal-Singh et al. 2003). Our revised estimate remains within the range of other studies that report a large autotrophic contribution to soil respiration, 50-65%, based on fully girdled plots (Bhupinderpal-Singh et al. 2003; Subke et al. 2004; Anderson et al. 2005; Olsson et al. 2005; Högberg et al. 2009). Additionally, the maximum decline of 38 % observed on the O50 plot was similar to the of 39 % reduction in soil respiration following girdling of a similar basal area (36 % vs. 39 %) in another northern temperate forest (Nave et al. 2011).

Short-term artifacts of girdling may extend into the second growing season of this experiment. As noted in Levy et al. (2011), some of the residual sources of error could include: delayed stimulation of heterotrophic respiration resulting from additional substrate inputs that require a year or a winter to be released (Denton et al. 2006), elevated microbial decomposition of organic matter (Ekberg et al. 2007), depressed microbial decomposition due to limited substrate supply (Binkley et al. 2006), decomposing substrate sources such as dead roots and their symbionts (Högberg et al. 2001), changes in litter input and soil temperature regimes (Bhupinderpal-Singh et al. 2003), continued use of starch reserves by 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 mostly work toward an underestimation of the autotrophic component. Therefore, our updated estimate of 58 % may still be conservative.

Observed alterations in the belowground system during our study do not confound our revised estimate. In this study, substrate input into the belowground system via litterfall in 2008 (year 1) was not dramatically altered, as expected in a deciduous ecosystem where all of the trees shed their leaves annually. By 2009 there was a shift in the distribution of leaf vs non-leaf litter in OG compared to all other treatments (Fig. 3.4). Visual observations suggest that this shift also occurred on the ALL plot. The modification in substrate quality associated with increased non-leaf litter could slow decomposition rates on the OG and ALL treatments and, as a result, overestimate the autotrophic contribution. Additionally, we observed a dense colonization of American burnweed (*Erechtites hieracifolia*) in the understory of the ALL plot in 2009 and 2010 along with elevated soil temperatures. The root respiration and litter inputs from American burnweed as well as higher soil temperatures (Fig. 3.2b) would enhance soil respiration, skewing the autotrophic estimate from the ALL plot towards an underestimation. Furthermore, transpiration associated with this colonization could be responsible for maintaining a soil moisture regime closer to C and NO than the elevated soil moisture regime observed on the OG treatment. Despite these uncertainties, we continued to observe a decline in soil respiration beyond the first year of the treatment. Therefore, we consider the second year to provide a more accurate assessment of the autotrophic contribution to total soil respiration.

Overall, we observed a short-lived depression in soil respiration on treated plots, lasting just two years post disturbance and followed by a full recovery of belowground activity in the third year. The rapid recovery is similar to documented patterns of NEP after a pest or pathogen attack (Amiro et al. 2010). The reduction in soil respiration was not proportional to the degree of canopy loss, the magnitude of the response varied interannually, and was specific to the plant taxon impacted. Our findings alongside of those in Flaxa-Raymond et al. (in review) support a recent hypothesis proposed by Nave et al. (2011), which attributes the resiliency of a coupled C-N biogeochemical cycle, in response to partial stand disturbance, to compensating activity of the healthy trees within the affected forest stand. Finally, we revise our estimate of the autotrophic component of soil respiration to 58 % at Black Rock Forest. Documenting the recovery patterns of forest carbon fluxes after a disturbance is fundamental to improving our understanding of climate feedbacks and predictions as well as ecosystem biogeochemistry.

Impact of a simulated pathogen attack on soil carbon storage in a northern temperate deciduous forest

4.1 Introduction

Recently attention has been called to a gap in knowledge about the impact of disturbance on terrestrial carbon cycling and storage (Amiro et al. 2010; Kurz et al. 2008; Running 2008). This interest stems from the important role that terrestrial systems have as a carbon pool within the context of climate change concerns. On land, the majority of carbon is stored in the soil (IPCC 2000) . The ability of soil biota to utilize organic carbon as an energy source means that some organic carbon stored in soils can be transferred to the atmosphere in the form of carbon dioxide (CO_2), a byproduct of decomposition. In the atmosphere, this CO_2 functions as a greenhouse gas. One potential consequence of a disturbance event is altered decomposition rates. If decomposition rates are enhanced, the rate of global warming could be accelerated by the increased production of CO_2. Much research has focused on developing baseline measures of terrestrial carbon storage (Adams et al. 1990; Dixon et al. 1994; Schimel et al. 2000; Turner et al. 1995) but disturbances such as extreme snow or rainstorms, hurricanes, insect outbreaks, diseases, droughts, and fires have the potential to dramatically impact the carbon cycle and subsequently alter the forest's carbon storage capacity (Dale et al. 2001; Harden et al. 2000; Peltzer et al. 2010). Canada's managed forests provide a recent documented example. Following an outbreak of the mountain pine beetle, a rapid transition of the forests from a carbon sink into a carbon source was observed (Kurz et al. 2008).

Of the many disturbances affecting forests in the United States, pest and pathogen outbreaks are the most widespread (20.4 million ha/yr) (Dale et al. 2001). Examples of such occurrences include Dutch elm disease, bark beetle outbreaks, beech bark disease, oak wilt disease, chestnut blight, gypsy moth outbreaks, sudden oak death, and hemlock woolly adelgid outbreaks (Ellison et al. 2005; Lovett et al. 2006). The scarcity of information about how both the soil carbon pool and belowground carbon fluxes respond to this type of disturbance has been acknowledged (Amirio et al. 2010; Clark et al. 2010; Lovett et al. 2010; Peltzer et al. 2010). In a synthesis of the responses of carbon fluxes to various types of disturbances, the typical trajectory of forest carbon dynamics after a pest or pathogen attack is an initial decrease in Net Ecosystem Production (NEP) in the year of disturbance, followed by a recovery period of 1-5 years before NEP returns to normal (Amiro et al. 2010). In contrast to Amirio et al.’s (2010) study, no such review has occurred for soil carbon pools in response to pest or pathogen attacks. The general impact of such pestilence on belowground carbon storage for either short or long time scales is poorly understood (Peltzer et al. 2010).

Peltzer et al. (2010) hypothesize that terrestrial carbon pools should decline shortly after the introduction of pests due to reduced productivity and increased decomposition. This hypothesis groups the entire terrestrial carbon pool into a single category but presumes the same directional response for both the aboveground and belowground components. Few studies have measured belowground carbon storage after this type of disturbance to test the belowground aspect of this hypothesis (Peltzer et al. 2010). One study found the forest floor and mineral soil carbon pools were not affected shortly after a hemlock wooly adelgid invasion (Jenkins et al. 1999).

A recent manipulative experiment designed to mimic a pathogen attack in Black Rock Forest, southeastern NY (Levy-Varon et al. 2011), provides another opportunity to test Peltzer et al.'s (2010) hypothesis. This study was prompted by concerns over the decline of oak (genus *Quercus*) species in the eastern United States. The widespread failure of oak tree regeneration (Crow et al. 1992; Rooney and Waller 2003; Shumway et al. 2001) coupled with a array of pests, pathogens, and fungal diseases (Barnard 2007; Lovett et al. 2006; Wilson 2001) that directly threaten established oak populations creates a significant probability that this foundation taxon (*sensu* Daton 1972) will decline. To better understand the role of oaks as a foundation tree species in Black Rock Forest, we simulated sudden oak death (SOD).

Sudden Oak Death is a disease caused by infection of trees with the non-native, pathogenic water mold *Phytophthora ramorum* (Garbelotto et al. 2001; Rizzo et al. 2002). The disease affects over 100 plant species (USDA 2007) and in California and Oregon has killed hundreds of thousands of oak (genus *Quercus*) and tanoak (genus *Lithocarpus*) trees (Meentemeyer et al. 2008; USDA 2005). Entire forest stands can be colonized by *P. ramorum* within one season and longer distance dispersal can occur rapidly through human transport, stream dispersal, or via heavy rains and strong winds (Meentemeyer et al. 2004; Prospero et al. 2007). Spread of this disease remains a concern because contaminated hosts of *P. ramorum* were transported around the country for years through the nursery industry (Frankel 2008). Modeling and greenhouse trial results indicate that much of the eastern deciduous forest may be susceptible to SOD spread (Kelly et al. 2007; Magarey et al. 2006; Tooley and Kyde 2003; Tooley and Kyde 2007; USDA 2005).

The pathogen enters hosts through the bark and kills trees by creating lesions that girdle the tree's cambium and occlude phloem and xylem cells (Garbelotto and Schmidt 2009). Death can occur within a few months or over a few years, with most trees eventually exhibiting a complete browning of the crown (Rizzo and Garbelotto 2003). Aboveground parts may fail structurally at the lesion, but trees may re-sprout from trunk and roots below the lesion. Mortality of oaks and tan-oaks in infected stands can vary from less than 50% up to as much as 100% (Davidson et al. 2005; Maloney et al. 2005, Palmieri and Frankel 2005).

Mechanical girdling (trunk incision to completely sever phloem and cambium) has been used previously to simulate SOD (Bergemann et al. 2005). This treatment mimics the impact of SOD on cambium and conducting tissue function, disrupting carbohydrate translocation and leading to death of aboveground parts within a season or two, though the tree may survive through the production of basal sprouts (Noel 1970). Girdling stands of trees can thus produce similar stand-level mortality pattern to a severe outbreak of SOD. It can also simulate the impact of other pathogens such as chestnut blight (*Cryphonectria parasitica*) an ascomycete fungus which grows in the inner tree bark and cambium, producing mycelial fans which girdle and kill branches and stems (Anagnostakis 1987).

This experiment was first described by Levy-Varon et al. (2011) where we presented soil CO_2 efflux (soil respiration) measurements from the first year of the experiment. The goal of the current study was to assess short-term changes in the soil carbon pool two years after the simulated attack. In this paper, we treat the soil carbon pool as the unit of study and assess the belowground aspect of Peltzer et al.'s (2010) hypothesis considering the collective results of relevant studies. In accordance with Peltzer et al.'s (2010) hypothesis, we predicted a reduction in the overall soil carbon pool in direct proportion to the change in live aboveground biomass (AGB).

4.2 Materials and Methods

Site description

The site is located on the north-facing slope of Black Rock Mountain (41.45° N, 74.01° W) in the Hudson Highlands, Orange County, New York (Fig.1). The 120 year old forest is dominated by *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. The National Resources Conservation Service (NRCS) classified the soils at Black Rock Forest as Chatfield and Rockaway series (Denny 1938). They are shallow, extremely rocky, nutrient poor, and slightly acidic. The clay loams are derived from glacial till that overlays granitic bedrock (Lorimer 1981). This region experiences a seasonal climate. In 2009, mean air temperature in January was − 5.5 °C, in July was 23.1°C, and total annual precipitation was 1218 mm. For additional site information please see Levy-Varon et al. (2011).

Experimental design and girdling treatment

As first described in Levy-Varon et al. (2011), we used a randomized block design for this manipulative experiment. Three blocks were assigned by slope position with row C representing the upper slope, row B the middle slope, and row A the lower slope (Fig. 4.1). Each block contained four plots (75m x75m) with one representative from each of the following treatments: control (C), girdling all non-oaks on a plot (NO), girdling half of the oaks on a plot

(O50), and girdling all the oaks on the plot (OG). Within each plot, a 25m by 25m center subplot was delineated where measurements were made to minimize edge effects. Additionally, a circular plot 50m in diameter was created at the lower slope position (row A) on which all trees on the plot were girdled (ALL). 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.

Notch girdling (Noel 1970) was done during the summer of 2008 by using a chain saw to cut through the bark, phloem, cambium and outer xylem (approximately 5cm deep) at breast height. Trees with a diameter at breast height (dbh) < 2.54cm were left ungirdled (0-3% of trees on any given plot). If girdling left trees unstable and near collapse, most often those between 2.5cm and 7.5cm dbh, they were completely felled for the safety of the researchers. In 2009 and again in 2010, girdled trees that remained alive received an additional girdling in close proximity to the initial incision.

Forest floor litter

In late April 2010 forest floor litter samples (undecomposed Oi and partially decomposed Oe layers) were collected at three locations within each center subplot. The sampling locations were haphazardly selected and a rectangle of 0.036m^2 was dropped to delineate the sample area. All litter covered by the rectangle was collected and oven dried at 70^{o}C. The dried sample was weighed as branch and non-branch components before being analyzed for total carbon via CHN analysis (Elementar Vario Macro NCS, Elementar Analysensysteme GmbH, Hanau Germany).

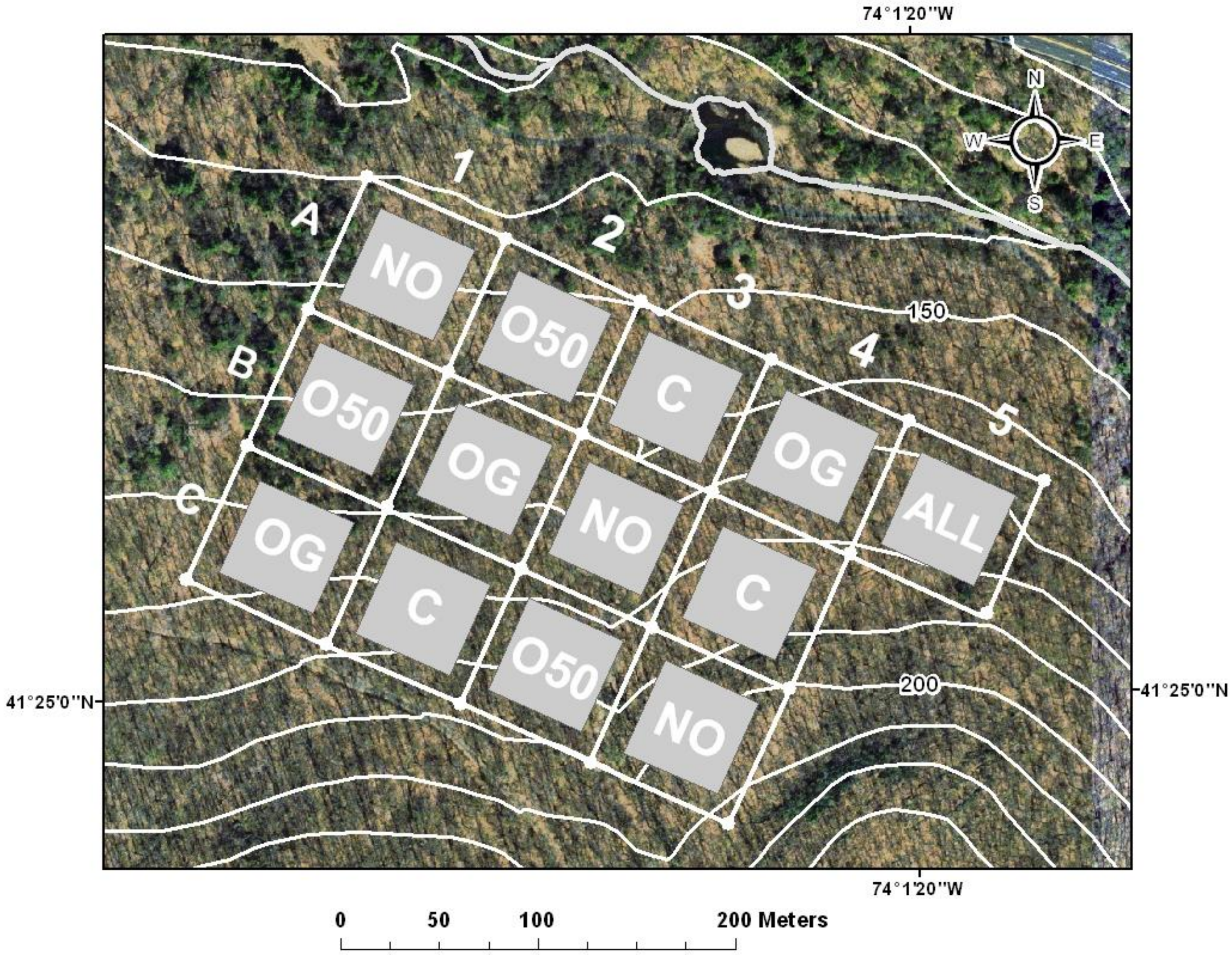

Figure 4.1 Map of the experimental area showing the location of plots and treatments. North slope of Black Rock Mountain, Black Rock Forest, NY. C-control, NO- all non-oaks girdled, O50- 50% oaks girdled, OG- all oaks girdled, ALL- all trees girdled (reprinted with permission from Levy-Varon et al. 2011)

Forest floor litter (FFL) carbon was calculated as %C x dried sample mass and scaled to the collection area (0.036m^2).Treatment values were calculated as the mean of the three replicate plot averages.

Soil Carbon

Three soil cores were collected immediately outside of each center subplot using a slide hammer style sampler lined with a plastic tube (1.9cm diameter). The sampler was driven approximately 32cm into the soil. Each core was cut into segments at depth intervals of 0-3cm, 3-6cm, 6-9cm, 9-15cm, and >15cm after scaling the length of these intervals to the amount of observed compaction for the individual core (mean compaction was 44%). Samples from plot B1 were lost and therefore not included in the analysis. All soil cores were immediately frozen at -20^{o}C and subsequently freeze dried (within a month). The fine fraction soil was isolated with a 2mm sieve and weighed before being measured for total carbon content by CHN analysis (Elementar Vario Macro NCS, Elementar Analysensysteme GmbH, Hanau Germany). Inorganic carbonate carbon was assumed to be absent in these soils based previous field tests with HCL (Scholz 1931). Soil organic carbon (SOC) was calculated for each sample increment as:

$$SOC = \frac{Sample\ Weight * OC * (1 - RC)}{Area} \qquad [Eqn. 1]$$

Where Sample Weight is the freeze dried (<2mm) sampled soil (g), OC is the organic carbon concentration (g g^{-1}), RC is the rock concentration (m^3 rock volume m^{-3} soil pit volume) determined to be 24% (see rock content estimation), Area is the cross-sectional area sampled

($0.0003 m^2$). Total soil organic carbon ($g\ m^{-2}$) for each soil core was calculated as the sum of the SOC at each depth interval plus the FFL carbon. Since the core length was 32cm, the >15segment was scaled to 30cm by using the carbon density ($m^{-2}\ cm^{-1}$) for that interval. Treatment values were calculated as the mean of the three replicate plot averages.

Rock Content

A first order approximation of the rock volume at our field site was made by extracting all soil and rock from a soil pit ($0.14 m^3$) dug adjacent to the control A3 center subplot (Fig. 1). Rocks were isolated by sieving the dirt and rock mixture on a 6mm by 6mm grid and then rinsed with water to remove excess dirt. Total rock volume was measured by water displacement and was determined to be 24% of the soil volume for the top 50cm of soil. Rocks of all sizes were observed at all depth intervals. For our carbon pool calculations, we assume rock volume was 24% of the total soil volume at each depth interval.

Aboveground Biomass

Live aboveground biomass was measured on the 12 main plots in the summer of 2007 (before girdling) and again in early summer 2010 (year two post girdling). In each plot, the dbh of all oaks was measured on the full 75m x75m plot area. The dbh of all non-oaks was measured on the 25m x 25m center subplot and then extrapolated to the full 75m X 75m area. If the crown leafed out for the season, a tree was considered alive. Live aboveground biomass was calculated from dbh using previously derived allometric equations (Brenneman et al. 1978; Monteith 1979) and the percent change in live aboveground biomass was calculated for the interval from 2007 to 2010. The values reported for 2010 were within 5% of those observed in 2008 and 2009 for the same treatment. We present our belowground carbon results alongside of the change in live aboveground biomass in order to scale our observations to treatment efficacy and degree of canopy disturbance.

Statistical Analysis

A one way analysis of variance (ANOVA) was used to analyze treatment effects on total SOC, FFL carbon, branch concentration in FFL, %C at each depth increment, and SOC at each depth increment. Tukey HSD Post-hoc test was used for pair-wise comparisons. In all cases, the ALL plot was left out of the analysis due to the lack of true replication and O50 had a sample size of n=2. Linear regression analysis was used to examine the effect of degree of canopy disturbance on forest floor litter composition. The design of this experiment was intended to accommodate several research objectives while spanning an appropriate land area that could be manipulated and studied. Our study took advantage of this experiment but the high spatial heterogeneity of soils and low number of plot replicates ultimately resulted in limited statistical power. Using a Cohen's d measurement of effect size, only changes greater than 40-50% would have been detected with the ANOVA analysis at a power of 0.8. Therefore, we focus on the trends in our dataset. R statistical software (http://www.r-project.org) was used for the analyses (R Development Team 2009).

4.3 Results

In 2007, the initial live aboveground biomass varied between plots from 209 to 300 Mg ha^{-1}. The mean change in live aboveground biomass from 2007 to 2010 was +6% for C (14.3 ± 1.3 Mg ha^{-1}), -6% for NO (-17.3 ± 15.4 Mg ha^{-1}), -32% for O50 (-82.7 ± 3.2 Mg ha^{-1}), -78% for

OG (-191.6 ± 5.4 Mg ha^{-1}), and -100% for ALL (-270.0 Mg ha^{-1}). There were no significant differences between treatments (ALL excluded from the analysis) in total SOC, FFL carbon, branch concentration in FFL, SOC at each depth interval, or %C at each depth interval, at the $P<0.05$ level.

Total SOC to 30cm depth was 3.0 ± 0.5 kg C m^{-2} (C), 3.3 ± 0.5 kg C m^{-2} (NO), 3.2 ± 0.2 kg C m^{-2} (O50), 2.6 ± 0.5 kg C m^{-2} (OG) (mean ± one standard error), and 2.8 kg C m^{-2} (ALL) (Fig. 4.2). We found that 53-60 % of the total SOC was located in the top 9 cm of the profile. A trend for higher FFL carbon (Fig. 4.3), branch proportion within FFL ($p=0.09$), and lower 0-3 cm SOC ($p= 0.09$) (Table 1) in O50, OG, and ALL plots compared to the C or NO plots was observed. Along the gradient of biomass change, regression analysis revealed that the branch concentration in the forest floor litter increased with increasing tree mortality ($p<0.001$) (Fig. 4.4).

In the top 0-3 cm of the soil profile, the C-O50 ($p=0.28$) comparison reflected a stronger treatment effect than the C-OG ($p=0.53$) and C-NO ($p= 0.83$) comparisons. Additionally, the carbon concentration from soil in the ALL plot at depths of 0-3 and 3-6 cm was much lower, approximately 50%, than the carbon concentration found in soils at similar depths from all other treatments (Table 4.1). The pattern of SOC distribution within the soil profile was similar for all treatments except ALL. In ALL, equal proportions of the total SOC was found in the litter and 0-3cm depths followed by an increase in the 3-6cm depth. Most other treatments show lower proportions of SOC in the litter followed by an increase in the 0-3cm and a decrease in the 3-6cm intervals (Fig. 4.5).

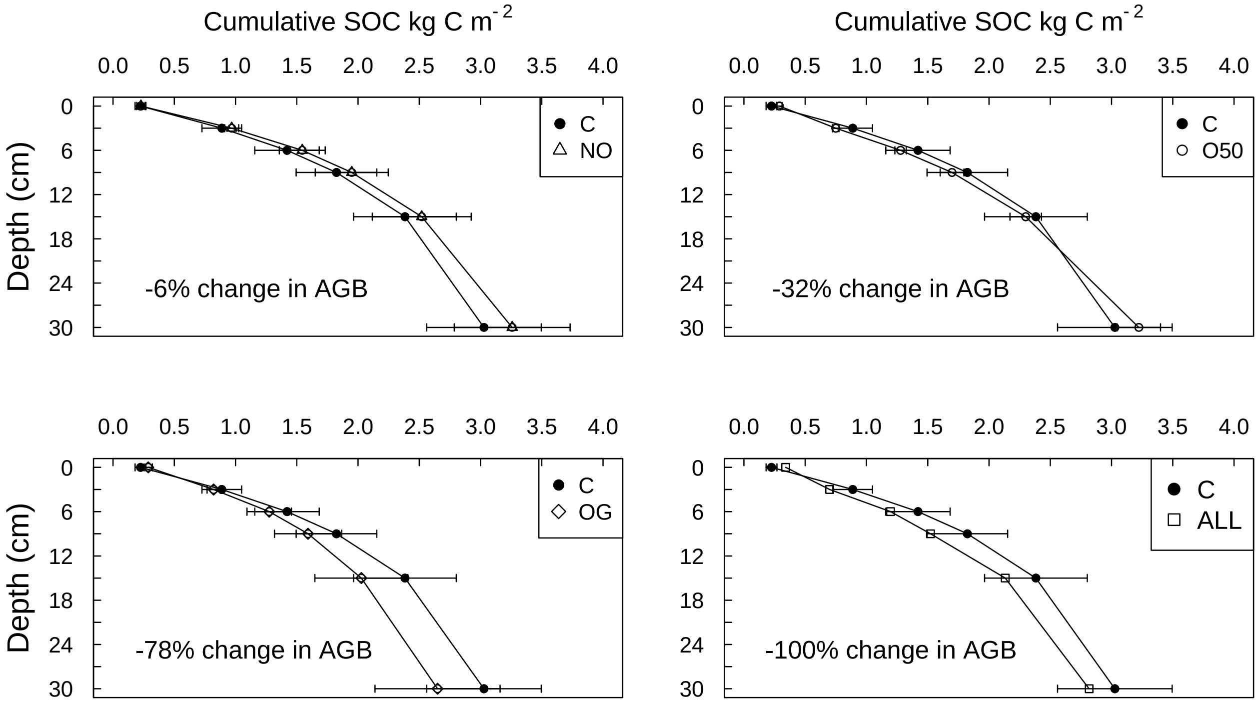

Figure 4.2 Cumulative soil organic carbon (SOC) kg C m^{-2} to a depth of 30cm for C (closed circle), NO (open triangle), O50 (open circle), OG (open diamond), and ALL (open square). Depth 0 represents forest floor litter and data shown are treatment averages ± one standard error. n=3 for C, NO, and OG, n=2 for O50 and n=1 for ALL. Measurements were made two years after tree girdling on the north slope of Black Rock Mountain. Changes in live aboveground biomass (AGB) are based on the difference in biomass from 2007 (pre-girdling) to 2010 (year 2 post girdling). C had +6% change in AGB. C-control, NO- all non-oaks girdled, O50- 50% oaks girdled, OG- all oaks girdled, ALL- all trees girdled

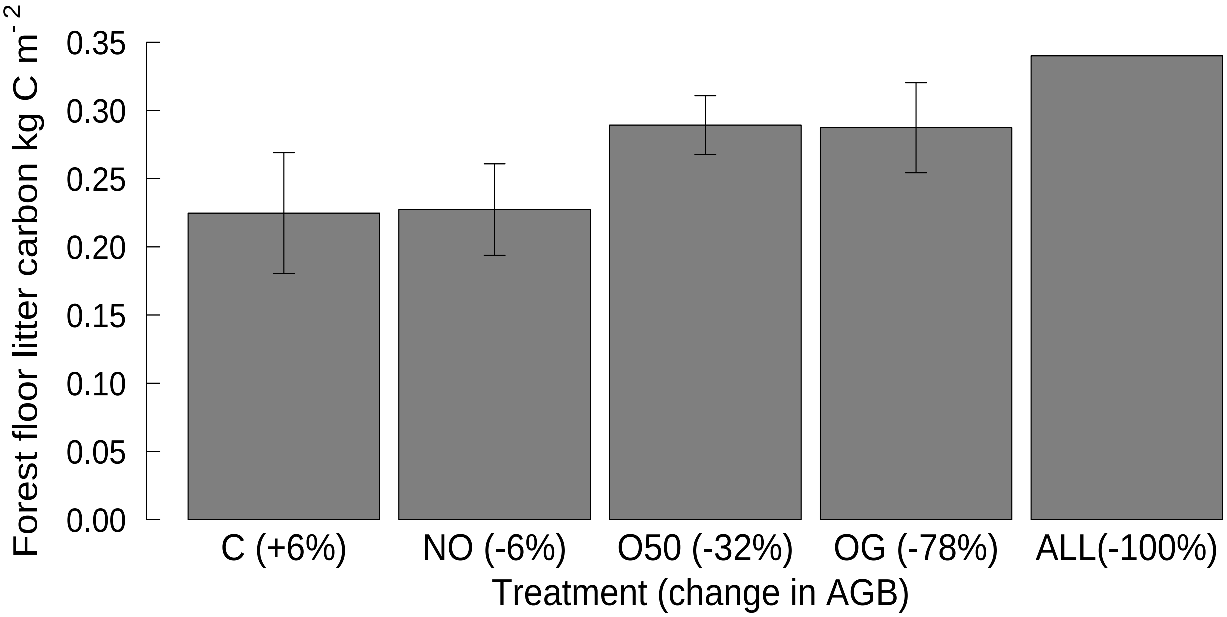

Figure 4.3 Mean forest floor litter carbon (kg C m^{-2}) for treatments on the north slope of Black Rock Mountain. Error bars are ± one standard error. n=3 for all treatments except for ALL where n=1. Measurements were made two years after tree girdling (2010). Change in live aboveground biomass (AGB) is based on the difference in biomass from 2007 (pre-girdling) to 2010. C- control, NO- all non-oaks girdled, O50- 50% oaks girdled, OG- all oaks girdled, ALL- all trees girdled

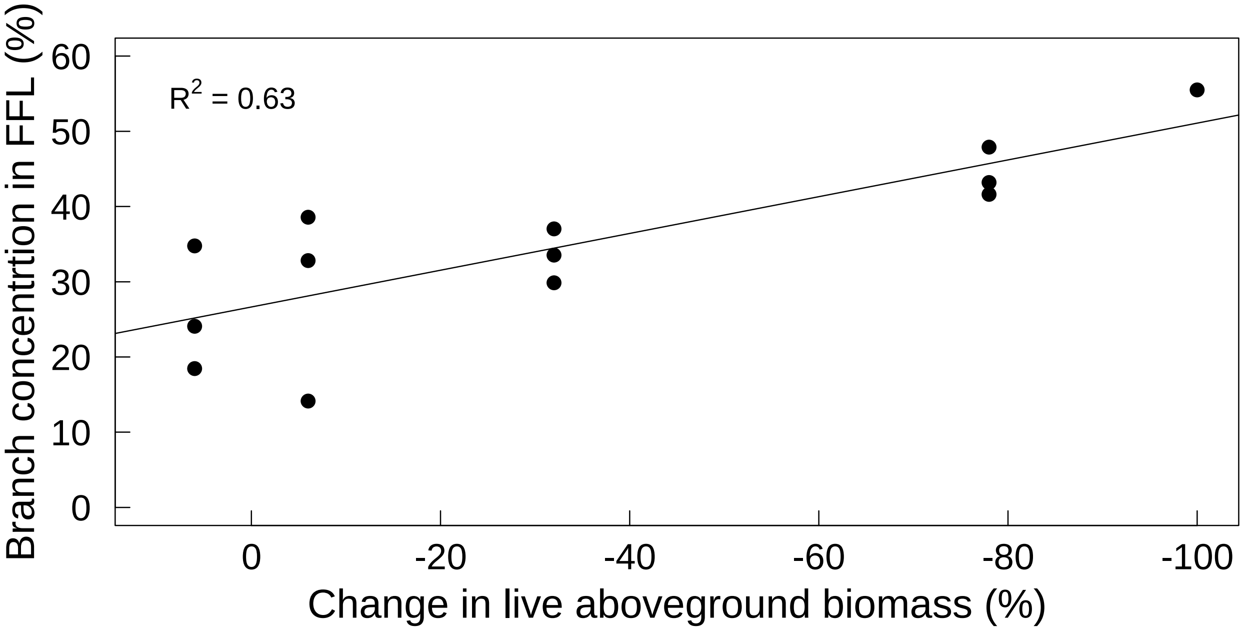

Figure 4.4 Linear regression analysis of mean branch concentration in forest floor litter (FFL) (%) for all treatment plots as a function of change in live aboveground biomass ($p<0.001$). Measurements were made two years after tree girdling (2010) on the north slope of Black Rock Mountain. Change in live aboveground biomass (AGB) is based on the difference in biomass from 2007 (pre-girdling) to 2010. C-control, NO- all non-oaks girdled, O50- 50% oaks girdled, OG- all oaks girdled, ALL- all trees girdled

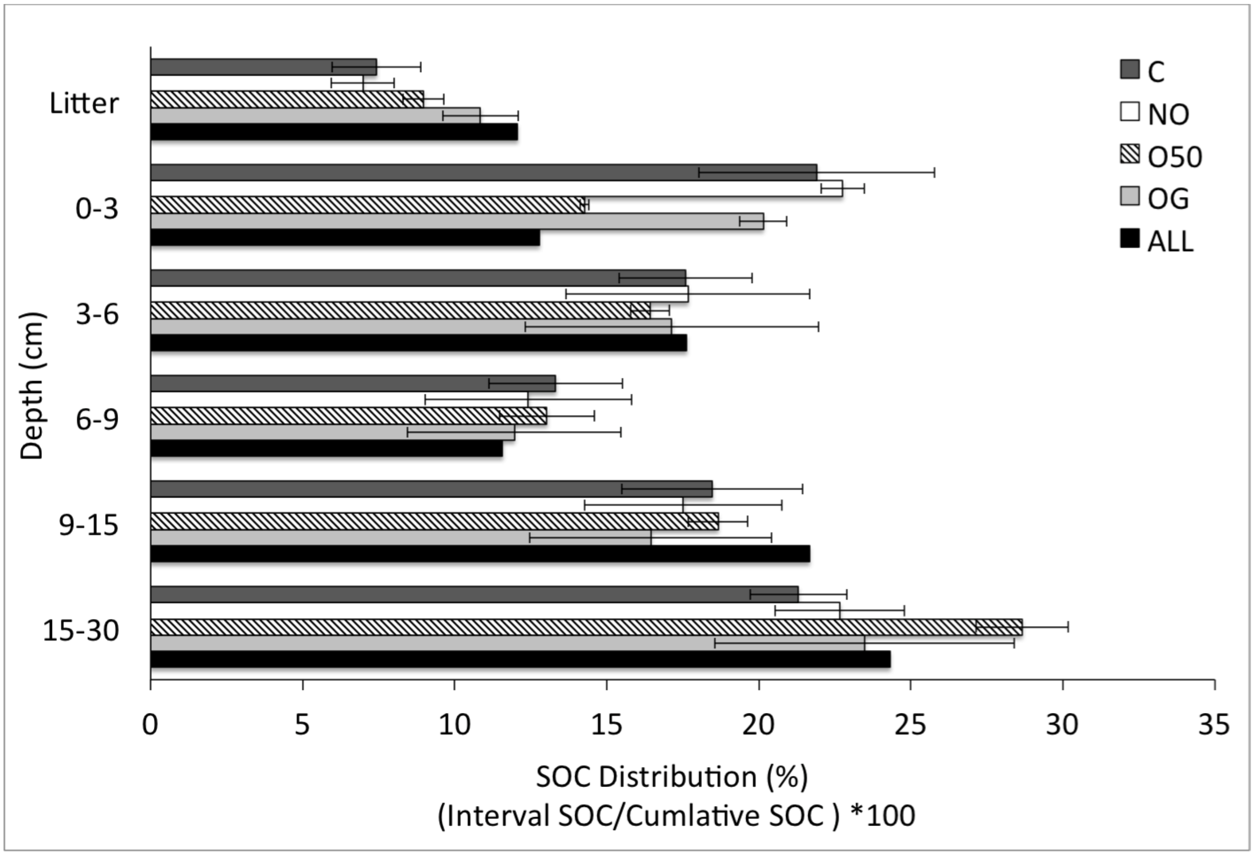

Figure 4.5 Proportion of SOC for each depth interval in total carbon storage to 30cm depth. C (dark gray), NO (white), O50 (diagonal lines), OG (light gray), and ALL (black). The bars for each treatment add up to one. Note that the two lowest depth increments are 6cm and 15cm compared to the upper sections that display carbon stored in 3cm increments. Data shown are treatment averages ± one standard error. n=3 for C,NO,OG, and Litter, n=2 for O50 and n=1 for ALL. Measurements were made two years after tree girdling on the north slope of Black Rock Mountain. C-control, NO- all non-oaks girdled, O50- 50% oaks girdled, OG- all oaks girdled, ALL- all trees girdled

Table 4.1. Litter carbon (kg C m^{-2}), soil organic carbon density (kg C cm^{-1} m^{-2}), and organic carbon concentration (%) for each depth interval (cm). Data shown are mean values of treatment averages and ± one standard error is shown in parenthesis. For litter, n=3 for all treatments except ALL where n=1. For soil, n=3 for OG, NO, and C, n=2 for O50 and n=1 for ALL. Measurements were made two years after tree girdling on the north slope of Black Rock Mountain. Change in live aboveground biomass (AGB) is based on the difference in biomass from 2007 to 2010

Mean change in live AGB (%)	+6	-6	-32	-78	-100
Treatment	Control	Non-oaks girdled	50% oaks girdled	All oaks girdled	All trees girdled
Mean Litter Carbon (kg C m^{-2}) or Mean Soil Organic Carbon density (kg C cm^{-1} m^{-2})					
Litter	0.2 (0.04)	0.2 (0.03)	0.3 (0.02)	0.3 (0.03)	0.3
0-3	0.2 (0.04)	0.2 (0.008)	0.2 (0.002)	0.2 (0.007)	0.1
3-6	0.2 (0.03)	0.2 (0.04)	0.2 (0.007)	0.2 (0.04)	0.2
6-9	0.1 (0.02)	0.1 (0.04)	0.1 (0.02)	0.1 (0.03)	0.1
9-15	0.09 (0.01)	0.1 (0.02)	0.1 (0.005)	0.07 (0.02)	0.1
15-30	0.04 (0.003)	0.05 (0.005)	0.06 (0.003)	0.04 (0.009)	0.05
Mean % Organic Carbon by depth (cm)					
Litter	45.61 (0.68)	45.32 (0.66)	45.47 (0.12)	43.86 (0.87)	44.59
0-3	36.69 (3.70)	23.89 (10.84)	39.07 (2.83)	24.27 (7.52)	11.85
3-6	19.96 (6.16)	13.48 (7.77)	23.67 (0.13)	11.76 (6.46)	7.46
6-9	8.46 (2.83)	5.65 (2.96)	8.05 (1.05)	4.72 (1.99)	3.57
9-15	3.35 (0.62)	2.61 (0.53)	3.86 (0.15)	3.00 (1.08)	3.42
15-30	1.53 (0.06)	1.24 (0.15)	2.36 (0.12)	1.45 (0.45)	1.42

4.4 Discussion

The goal of this study was to evaluate the short-term impact of a mimicked pathogen attack on soil carbon stocks in a northeastern forest and to test the Peltzer et al. (2010) hypothesis that the soil carbon pool would decrease shortly after this type of event. We found no discernable change in the total carbon content in the upper 30cm of the soil profile for any treatment in the second year after girdling. To our knowledge, only one other study has measured soil carbon pools shortly after an insect or pathogen infestation. Jenkins et al. (1999) also found no significant changes in forest floor or mineral soil carbon (to 10cm depth) approximately 5 years after an eastern hemlock decline due to hemlock wooly adelgid infestation in southern New England. Kizlinski et al. (2002) measured soil carbon pools (to 15cm depth) in forests that experienced defoliation by the hemlock wooly adelgid and likewise found no changes in the forest floor or mineral soil carbon pools, but the time of infestation in this study was not reported. A recent study on the impacts of beach bark disease in the Catskills, New York assessed carbon pools along a gradient of beech decline. Unlike sudden oak death, gypsy moth, or the hemlock wooly adelgid, beech bark disease results in a much slower death that is hypothesized to curtail the short-term impacts of this disturbance (Lovett et al. 2010). The authors suggest that the stage where beech trees are mostly present as standing dead can be used as an analogue for the short-term impacts expected from attacks with more abrupt symptoms. At this stage, the authors also found no change in forest floor or mineral soil carbon (to 12cm) (Lovett et al. 2010). Empirical studies documenting both the short and long-term impacts of pest or pathogen attacks on soil carbon stocks are limited.

Peltzer et al. (2010) hypothesized that pests and pathogens would decrease ecosystem carbon pools in the short-term (years to decades) as a result of reduced plant productivity and increased decomposition stimulated by more solar radiation reaching the forest floor. Others have also postulated that modifications to the soil microclimate would change the rate of soil carbon cycling (Jenkins et al. 1999; Lovett et al. 2006). At our study site, decreased soil temperature and increased soil moisture accompanied a depression in soil respiration rate on the O50 (although not statistically significant) and OG treatments relative to the control in both the first (Levy-Varon et al. 2011) and second year (unpublished) of the experiment. Although alterations in carbon cycling have been observed both above and belowground in response to disturbance (Clark et al. 2010; Kizlinski et al. 2002; Kurtz et al. 2008; Lovett et al. 2010; Pfeifer et al. 2011) our findings along with those of Jenkins et al. (1999) and Lovett et al. (2010) have not found short-term changes (2-5 years) in soil carbon storage. We recognize that the probability of detecting changes in the soil carbon pool at our study site is limited by the high amount of heterogeneity inherent in soil carbon pools and the low statistical power attained with our methodology, however, the trends in our dataset are consistent with the few available studies that report SOC after this type of event. No strong trends for total SOC down to 30cm were observed (Fig. 4.2), indicating no large differences (>40-50%) in the total SOC among treatments.

We propose that the short-term alterations in carbon cycling may not result in an overall reduction of the soil carbon pool, at least within the first 5 years of a pest or pathogen attack. This time frame is based on the collective literature described above. An underlying assumption of Peltzer et al.'s (2010) hypothesis is that the carbon distribution and form within the soil system remains constant, except for changes in decomposition rates. We hypothesize that rapid shifts in the distribution of carbon within the soil carbon pool, following such attacks, could compensate for soil carbon losses resulting from increased decomposition rates. For example, the absolute amount of carbon stored in forest floor litter is comparable for most treatments in this experiment (except ALL) but there are clear trends in the composition of the litter. This trend suggests that with increasing tree mortality, more carbon is found in the form of branches rather than the more easily degradable tissue material (Fig. 4.4), as might be expected. After the first year of girdling and subsequent tree mortality, litterfall additions to the soil system should be greatly reduced. The litter on the forest floor may be subject to increased decomposition rates diminishing the amount of SOC stored in the leaf litter but the tree mortality also prompted additional inputs of carbon into the soil system in the form of branches. This shift from leaf to branch composition in the forest floor litter appears to offset the absolute amount of carbon lost through possible increased decomposition rates. We also observed a trend for greater amounts of FFL in ALL, which could have negated the effects of the lower carbon storage at the 0-3cm depth (Table 4.1). In the rooting zone of the soil, carbon inputs via root exudates were likely reduced on the girdled plots but that may have been offset by increases in soil carbon inputs via root mortality. Additionally, carbon stored in the biomass of ectomycorrhizal fungi, which commonly associates with *Quercus* (Turner et al. 2009), may be shifted to increased biomass of saprotrophic fungi or endomycorrhizal fungi on the girdled plots. These types of changes could be reflected in the changes in C:N quality of the forest floor (Klinski et al. 2002; Lovett et al. 2010) and mineral soils (Lovett et al. 2010) observed in other studies. We believe that both alterations in decomposition rates resulting from changes in microclimate as well as a reorganization of carbon components within the soil system could impact the soil carbon pool. The short-term shifts in carbon sources along with changes in aboveground species composition will ultimately modify the long-term soil carbon storage due to differences in turnover times of the various components and alterations in biogeochemistry.

Our hypothesis that there would be a reduction in the total soil carbon pool that was directly proportional to the aboveground tree biomass killed was not supported. The gradient of change in live aboveground biomass created in this study: +6% (C), to -6% (NO), to -32% (O50), to -78% (OG), to -100% (ALL) may be indicative of a progression of sudden oak death on the oak girdled plots. Following the initial girdling during the summer of 2008, we found a rapid decline in respiration rate (approximately 50%) on the OG and ALL plots (Levy-Varon et al. 2011). This finding was comparable to reported values for fully girdled plots in other studies (Hogberg et al. 2001; Högberg et al. 2009; Olsson et al. 2005; Subke et al. 2004). A buffered soil respiration response along with almost double the *Quercus* survival rate on the O50 plots compared to OG plots suggested a possible threshold effect for this type of disturbance (Levy-Varon et al. 2011). This threshold effect is not evident in differences of soil carbon storage in the second year after the mimicked attack. The most notable shifts in the proportion of SOC found at each depth interval was observed in the ALL plot (Fig. 4.5) but neither the degree of canopy loss nor the specific genus targeted (*Quercus* vs other) show strong trends for a reduction in the overall soil carbon pool in the treatment plots.

This study provides the first estimate for a soil carbon budget at Black Rock Forest. Based on the three control plots, an average of 3.0 ± 0.5 kg C m^{-2} was found in the upper 30cm of the soil profile (including litter). This is lower than the national average of 5.6 kg C m^{-2} for southern New York (Kern 1994). The lower SOC is likely a result of our field site being situated on a slope that has shallow, nutrient poor, and very rocky soils. The slope increases erosion and the thin nutrient poor soils make this site less than optimal for tree growth. Unlike nearby regions such as the Catskills NY, the hard basement bedrock of granite and gneiss also reduces the probability of carbon being brought into this system via groundwater. Reductions in forest growth rates since 1998 (Schuster et al. 2008) have been observed and could contribute to slower belowground carbon accumulation at our site. Further, the calculations for the national average were based on classifying the region as having a different soil suborder (Ochrepts) than the suborders of the two identified soil series in our forest (Udults and Udepts). Black Rock Forest lies in a unique region referred to as the Highlands Physiographic Province. To our knowledge, no studies have published a soil carbon budget for sites in the Highlands Physiographic Province to use for comparison. Nearby studies located outside of the Highlands have found higher soil organic carbon contents. In northeastern Connecticut Kulmatiski et al. (2003) found that the upper 15cm alone contained 5.79 kg C m^{-2} and Pouyat et al. (2002) found 5 kg C m^{-2} in the forest floor and upper 10cm of mineral soil at sites near Westchester, New York and Litchfield County Connecticut. Both of these measures would exceed the national average if the 15-30cm depth were included in the analysis. Davis et al. (2004) measured soil organic carbon in four soil series in southern New England and found that the Windsor soil series was approximately double the national values while the Carlisle series was 30-60% lower than the national values reported by Kern (1994). Finally, based on a live aboveground carbon estimate of 9.5 kg C m^{-2} for Black Rock Forest in 2000 (Shuster et al. 2008), the carbon storage of the soils is 32% of the aboveground carbon storage. If we had used the national estimates, we would have assumed it to be 59% of the aboveground carbon storage.

Conclusion

The long-term results of this experiment are yet to be determined. Within the first two years of this mimicked pathogen attack, we did not find evidence for large shifts in the soil carbon pools along a gradient of change in live aboveground biomass. Our findings align with other studies that report soil carbon measurements shortly after a pest or pathogen infestation.

The scarcity of studies measuring soil organic carbon after such an event highlights the need to better understand the impact of this type of disturbance on forest carbon storage and cycling, both at short and long timescales. Viewed as a case study, we cannot reject the hypothesis of Peltzer et al. (2010) but we propose that relatively rapid shifts in source components of soil carbon pools could offset soil carbon losses during a pest or pathogen attack. The long-term impacts will undoubtedly be linked to the characteristics of the next generation of replacement trees.

Concluding Remarks

The overarching goal of this dissertation was to advance our knowledge of natural processes that govern terrestrial carbon fluxes and carbon sequestration. Climate change concerns have generated a necessity for improved understanding of the global carbon cycle. Although there have been great advances in carbon cycling research over the past few decades, there is still much to learn. The belowground system is arguably the most poorly understood aspect of the terrestrial carbon cycle. It is incredibly important because it contains the majority of carbon stored on land (Watson and Intergovernmental Panel on Climate 2000) but it is challenging to study due to limits with available methodology. The work in this dissertation was designed to address fundamental uncertainties in belowground carbon cycling research by utilizing a large-scale tree girdling experiment, located in southeastern NY (USA).

The specific goals of this dissertation were to gain insights into the processes governing soil respiration by quantifying the relative contributions of autotrophic and heterotrophic activity to soil respiration, to assess the short-term impact of mimicking a pathogen attack on soil carbon pools and fluxes, and to develop the first soil carbon budget for Black Rock Forest. In addition, the unexpected findings from this dissertation have unveiled a layer of the ecological complexity of northeastern forest ecosystems. They have enhanced our understanding of the link between aboveground and belowground carbon cycling as well as demonstrated how healthy trees contribute to the biogeochemical resilience of disturbed forest ecosystems.

The relative contribution of autotrophic activity to total soil respiration was determined to be approximately 58%, based on the second year of the girdling experiment. Separating the relative contributions of these two groups to total soil respiration is the first step towards gaining a mechanistic understanding of controls on soil respiration. Given the large contribution of the autotrophic activity found in a variety of forests worldwide (Hansen et al. 2000; Högberg et al. 2009), predictive models that capture both variations in canopy photosynthesis (correlated to autotrophic activity) as well as the soil environment (correlated to heterotrophic activity) will likely yield more accurate predictions of seasonal soil CO_2 efflux.

At Black Rock Forest, this could be achieved by combining the canopy photosynthesis model described by Whitehead et al. (2004) with the soil temperature and soil respiratory measurements presented in this dissertation. Although soil moisture information is available, it was not a strong predictor of soil respiration (chapter 2) and therefore is unlikely to improve model fit. Additional studies elucidating the diurnal partitioning of the autotrophic/heterotrophic activity as well better constraining the time lag between carbon fixation at the canopy and the release of carbon to the atmosphere via soil respiration would further improve predictive modeling efforts.

One major uncertainty in soil carbon cycling research is how both carbon pools and fluxes respond to biotic disturbances. By doing a manipulative experiment, the impact of a partial stand disturbance could be studied in a relatively controlled manner— constraining the time of disturbance, the temporal response of changes in the carbon cycle, and the degree of canopy mortality. In chapter 2 the recovery pattern of soil respiration after a disturbance was documented and in chapter 3, the short-term impact of the disturbance on soil carbon storage was presented.

The main finding from chapter 2 was that belowground activity only declined for two years following disturbance followed by a full recovered in the third year. Additionally, the reduction in soil respiration was not proportional to the degree of canopy loss, the magnitude of the response varied interannually, and was specific to the plant taxon impacted. To my knowledge, this is the first study to present three consecutive years of soil CO_2 efflux observations following a partial stand disturbance and document the recovery pattern returning to undisturbed levels. Thus, it is difficult to draw general conclusions about the temporal trends or recovery patterns of soil CO_2 efflux following partial stand disturbance. The rapid recovery suggests that biogeochemical cycling in northeastern forests may be highly resilient to partial stand disturbance. The non linear decline in soil respiration along a gradient of canopy loss as well as the varied taxon respiratory response will complicate efforts aimed at projecting alterations in carbon cycling associated with biotic disturbances. Documenting the recovery patterns of forest carbon fluxes after all types of disturbances will be important for both carbon cycling research and policy development.

In chapter 3, the first estimate for a soil carbon budget (3.0 ± 0.5 kg C m^{-2} in the upper 30cm of the soil profile) at Black Rock Forest was created. This value appears to be the first soil carbon budget for the Highlands Physiographic Province (NY). The soil carbon storage on the north slope of Back Rock Mountain is lower than the national average of 5.6 kg C m^{-2} for southern New York (Kern 1994). However, the national average was based on a different soil suborder than the identified soil series in Black Rock Forest. Site conditions were also likely factors in ascribing the low carbon storage for the field site. Based on a live aboveground carbon estimate of 9.5 kg C m^{-2} for Black Rock Forest in 2000 (Shuster et al. 2008), the carbon storage of the soils was determined to be 32% of the aboveground carbon storage. Typically, temperate forests soils store almost 1.5 times the amount of carbon stored in vegetation (Watson and Intergovernmental Panel on Climate 2000). The lower than average soil carbon storage on Black Rock Mountain highlights the large spatial variability in the ratio of carbon stored above and belowground under varying site conditions.

Additionally, a new hypothesis that describes many compositional changes in belowground carbon storage following a pest or pathogen attack was introduced in chapter 3. We had expected to observe a decline in the soil carbon pool following the experimental disturbance as a result of increased decomposition, a hypothesis proposed by Peltzer et al. (2010). Our finding of no change in total soil carbon storage aligned with other studies that reported soil carbon measurements shortly after a pest or pathogen infestation. Viewed as a case study, the hypothesis of Peltzer et al. (2010) cannot be rejected but the newly proposed hypothesis suggests that additional changes beyond decomposition could occur in the belowground system. It is proposed that shifts in the composition of carbon substrates throughout the soil profile occur and that the changes may offset each other regarding the overall impact on total belowground carbon storage. Additional studies on soil carbon storage following partial stand disturbances are necessary to test this hypothesis.

Unexpected results highlighting the link between aboveground and belowground carbon cycling and evidence for biogeochemical resilience of forest ecosystems were described in first and second chapters of this dissertation. In the first chapter, the link between aboveground and belowground carbon cycling was demonstrated by rapid decline in CO_2 flux from both the ALL and OG treatments immediately following girdling. Biogeochemical resilience to partial stand disturbance was demonstrated through observations of respiratory and tree survival rates on oak girdled plots. In the second chapter, biogeochemical resilience was demonstrated through the rapid recovery of belowground activity observed in the third year of the experiment. The results from this dissertation alongside of Flaxa-Raymond et al. (2012) support Nave et al.’s (2011) disturbance recovery hypothesis. In addition to compensatory activity, healthy trees may contribute to resilience in biogeochemical cycling by aiding stressed trees through resource sharing belowground via mychorrhizal networks and/ or root grafting (see also Levy-Varon et al. 2011). The activity of healthy trees within a disturbed forest stand set biotic disturbances apart from stand replacing disturbances. The ability of forest organisms to respond rapidly to a disturbance is an important mechanism for maintaining ecological and biogeochemical intergrity within a disturbed forest stand.

Together, the findings from this dissertation advance our knowledge of terrestrial carbon cycling in northeastern forests. Specifically, the relative contributions of autotrophic and heterotrophic activity to total soil respiration have been partitioned and the short-term response of soil respiration and soil carbon storage to partial stand disturbance has been documented. The results have revealed an important link between aboveground and belowground carbon cycling as well as demonstrated how healthy trees within a disturbed forest stand contribute to the biogeochemical resilience of forest ecosystems. Additionally, the first soil carbon budget for Black Rock Forest and the Hudson Highlands has been developed. Research on the recovery patterns of forest carbon storage and fluxes after a disturbance is greatly needed to improve our understanding of the impact of disturbance on terrestrial carbon cycling.

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