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Patterns and processes of soil carbon dynamics in a northeastern United States forest

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PATTERNS AND PROCESSES OF SOIL CARBON DYNAMICS IN A NORTHEASTERN UNITED STATES FOREST

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ABSTRACT

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Forest soils represent a substantial component of the terrestrial carbon cycle and are an important research area for a number of carbon cycle science initiatives. Whereas patterns of aboveground productivity have been relatively well measured and are increasingly included in regional-scale model analyses, belowground estimates are still highly uncertain and progress has been hampered by methodological difficulties. The lack of data poses a problem because belowground measurements are needed to create complete carbon budgets for terrestrial ecosystems at local, regional and global scales. Ecosystem carbon balances will help identify how and where carbon is being stored, as well as how carbon storage may change as forests recover from past disturbance or transition into different forest types as a result of climate changes.

In this study, I examined patterns of soil respiration and belowground carbon allocation at the Bartlett Experimental Forest, a north temperate forest landscape located in New Hampshire, USA. Soil respiration was measured at a total of 24 plots spanning a range of site and vegetation conditions. Total belowground carbon allocation (TBCA)

was estimated using a mass balance approach as the difference between soil respiration and aboveground litterfall. Soil respiration and TBCA were compared with measurements of nitrogen mineralization, leaf chemistry and various site characteristics in order to explain spatial and temporal variation and to extend discrete daily measurements to annual fluxes.

Across sites, instantaneous measurements of soil respiration were significantly correlated with soil temperature, N mineralization, foliar nitrogen and the foliar lignin:nitrogen ratio, although the majority of the observed variation was explained by soil temperature alone. Across all sites, the soil temperature response was best fit with a Lloyd and Taylor function, which was used to extrapolate measurements to annual soil respiration fluxes. Annual soil respiration was inversely related to N mineralization and positively correlated to LAI across sites. Estimated total belowground carbon allocation ranged from 505 g C m^{-2} yr^{-1} to 711 g C m^{-2} yr^{-1} and was inversely related to aboveground litter inputs. Belowground carbon allocation was also related to foliar lignin, cellulose, and lignin:nitrogen ratios. These results have increased our understanding of soil carbon dynamics at Bartlett, and some relationships may prove useful in extending plot relationships over the landscape through remote sensing techniques.

CHAPTER I

INTRODUCTION

Background

Carbon dioxide concentrations in the Earth's atmosphere have increased substantially since the onset of the industrial revolution, from 280ppm before the industrial revolution to 367ppm in 1999 (IPCC 2001). It is also well documented that current CO_2 levels are well outside the realm of natural variability as seen in ice core records of the past 420,000 years and most likely the past 20 million years (Figure 1; IPCC 2001). Increases of CO_2 in the atmosphere is a direct result of increased emissions from fossil fuel burning and land use change, primarily deforestation (CCSP 2004-2005).

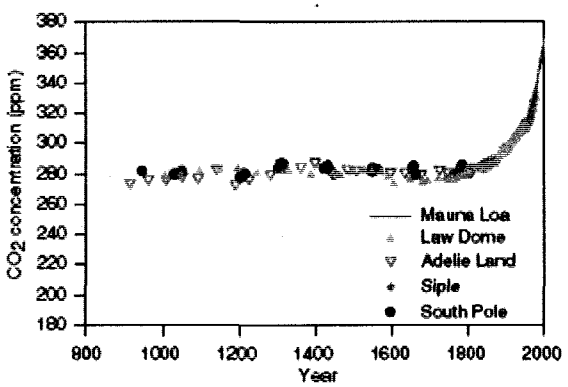

Figure 1. Changing CO2 concentrations in the atmosphere over the last 1,200 years as estimated from ice core data and the Mauna Loa Curve (red line) (IPCC 2001).

Recent estimates indicate that CO_2 emissions equal 6300 Pg C yr^{-1} (CCSP 2004-2005), with only 760 Pg C being stored in the atmosphere, the remainder of which is sequestered by either Earth's oceans or terrestrial ecosystems (Kump et al. 2004). The

flux of C from the atmosphere to the biosphere is estimated at -1.4±0.7 Pg C y^{-1} (IPCC 2001). This estimate, however, does include fluxes from the biosphere back to the atmosphere due to changes in land use, thus reducing overall carbon sink strength (IPCC 2001).

Since the release of the 2001 IPCC report, there has been growing recognition that reductions of CO_2 and other greenhouse gases in the atmosphere are essential to mitigating future climate changes. These reductions could come from either (1) reduction of carbon emissions at their source and/or (2) increasing the rate of carbon sequestration through biological or engineering solutions. The latter is the focus of current U.S. policy (CCSP 2004-2005). Ultimately:

> *"Successful carbon management strategies will require solid scientific information about the processes of the carbon cycle and an understanding of its longer-term interactions with other components of the Earth system, such as climate and the water and nitrogen cycles" (CCSP 2004-2005).*

The necessity for further scientific knowledge and a better understanding of the carbon cycle has led to numerous plans, programs and committees dedicated to this task. The North American Carbon Program was designed specifically under these goals.

North American Carbon Program (NACP)

The North American Carbon Program (NACP) outlines the implementation of a principal recommendation made by the U.S. Carbon Cycle Science Plan (Sarmiento and Wofsy, 1999). The focus of the NACP is on carbon-containing gases and carbon stocks in North America and adjacent ocean basins in order to address societal concerns and provide a complete and accurate scientific assessment to inform policy and management decisions (Wofsy and Harriss 2002). The NACP has three major research goals:

- *Develop quantitative scientific knowledge, robust observations, and models to determine the emissions and uptake of CO_2, CH_4, and CO, the changes in carbon stocks, and the factors regulating these processes for North America and adjacent ocean basins.*
- *Develop the scientific basis to implement full carbon accounting on regional and continental scales. This is the knowledge base needed to design monitoring programs for natural and managed CO_2 sinks and emission of CH_4.*
- *Support long-term quantitative measurements of sources and sinks of atmospheric CO_2 and CH_4, and develop forecasts for future trends.*

The NACP has three components geared toward reaching these goals: atmospheric monitoring, observations to delineate land and ocean based sinks and sources, and data synthesis and integration into newly developed models. The land measurement scheme, of which the present study is a part, aims to use high frequency, small-scale measurements such as those from eddy covariance flux towers (Tier 1) in conjunction with lower intensity plot-level observations and remote sensing across landscapes (Tier 2 & 3, 4) (Table 1; Denning 2005; Wofsy and Harriss 2002).

Table 1. Multi-tiered approach of the NACP terrestrial measurements focused on full carbon accounting (Denning 2005; Wofsy and Harriss 2002).

	4th Tier Mapping and Remote Sensing	**3rd Tier** Extensive Inventory (FIA and NRI)	**2nd Tier** Medium-Intensity Sample	**1st Tier** Intensive sites (e.g., Ameriflux)
# of sites	$>10^7$	10^5	10^3	10^2
Frequency	10days-annual	5-10 years	Annual	Continuous
Example Data Elements				
Land cover class	X	X	X	X
Leaf area index	X	X	X	X
Live biomass	X	X	X	X
Land cover change	X	X	X	
Wildfire disturbance	X	X	X	
Climate variability			X	X
Soil CO_2 flux			X	X
Methane flux			X	X
Dissolved organic C				X
Ecosystem CO_2 flux				X

In addition to the NACP, parallel programs exist in Europe, Australia and Japan. All programs are designed to gain the best scientific understanding of the carbon cycle and ultimately climate change.

Soils and the Carbon Cycle

Terrestrial soils represent a critical component of the global carbon cycle and are the largest flux of carbon in terrestrial ecosystems, after gross primary production (GPP) (Janssens et al. 2001). On a global scale soils store 1500-1600 Pg C, nearly three-quarters of total terrestrial carbon (C) stock, and are second only to the deep ocean as long-term C reservoirs (Bowden et al. 2004; Johnston et al. 2004). Given their importance, understanding soil carbon fluxes and how they change spatially and temporally along ecosystem gradients is essential to assessing interactions between terrestrial systems and the atmosphere.

Although uncertainties remain, aboveground components of the terrestrial carbon cycle have been relatively well studied and patterns of aboveground net primary productivity (ANPP) are predicted with increasing accuracy by models. ANPP for forests globally, ranges from 500 g m^{-2} y^{-1} to 2000 g m^{-2} y^{-1} and estimates continue to improve as a combination of methods including field campaigns, modeling and remote sensing are employed (Jang et al. 1996; Raich 1998; Fehse et al. 2002; Ollinger et al. 2002a; Ollinger & Smith 2005). By contrast, our understanding of belowground carbon cycling has lagged far behind. Although the number of studies measuring total CO_2 flux from the soil has recently increased, individual components of the belowground carbon cycle remain poorly understood.

Total soil respiration is most often defined as the sum of heterotrophic and autotrophic respiration, derived from three sources: respiration by living roots and their associated mycorrhizal fungi, microbial respiration produced by decomposing

aboveground litter, and microbial respiration of belowground litter (Sulzman et al. 2005). Two of these sources—respiration of live tissues and decay of belowground litter—result from belowground carbon allocation by plants. As a result, total belowground carbon allocation (TBCA) can often be estimated as the difference between total soil respiration and carbon inputs from aboveground litter (Raich & Nadelhoffer 1989; Ryan 1991; Davidson et al. 2002a; Giardina & Ryan 2002). TBCA estimation uses a carbon balance approach based on the conservation of mass, which requires soil C pools to be at or near steady state. The allocation of C belowground for use by plant structures is an extremely important component of the total carbon cycle in terrestrial ecosystems (McDowell et al. 2001), and together with soil respiration represents a major portion of ecosystem carbon budgets.

It has long been understood that the quantity of C released through soil respiration is influenced by a number of factors including soil temperature and moisture, soil substrate, inputs to the soil through litterfall, and activities within the soil including root and microbial biomass, production and respiration (Singh & Gupta 1977). However, models of soil respiration have traditionally only included soil temperature-dependent relationships, although many studies have suggested the importance of soil moisture (Davidson et al. 1998; Sato & Seto 1999; Savage & Davidson 2001; Subke et al. 2003; Tang & Baldocchi 2005). A variety of temperature response functions have been developed, including exponential Q10 and Arrehnius-like models such as Lloyd and Taylor (1994), but none have been able to capture all of the variation within and between sites on interannual time scales (Buchmann 2000; Hibbard et al. 2005; Davidson et al. 2006). Recently, several studies have tried to evaluate relationships between soil respiration and a variety of ecosystem parameters in order to better understand belowground carbon allocation and to allow construction of models that will come closer to accurately predicting total ecosystem carbon budgets (Giardina et al. 2003; Campbell

et al. 2004; Litton et al. 2004a; Davidson et al. 2006). However, a number of these studies have reached contradictory conclusions, prompting the need for additional research.

In one study, soil respiration was found to be, on average, 10% lower in coniferous forests than broad-leaved deciduous forests (Raich and Tufekcioglu 2000). Vegetation type also explained 35% of the variation in soil respiration at an experimental site in Poland (Laskowski et al. 2003). However, these results were in contrast to an earlier study where no significant differences were found between forest types (Raich & Potter 1995). Similarly, many studies have found a strong association between soil respiration and litterfall across mature forest ecosystems globally (Raich & Nadelhoffer 1989; Nadelhoffer & Raich 1992; Raich & Tufekcioglu 2000; Davidson et al. 2002a), although this trend is not always observed at local scales where the range of variation is narrower (Davidson et al. 2002a; Giardina & Ryan 2002). Although Giardina and Ryan (2002) found that the globally derived equations for estimating TBCA by Raich and Nadelhoffer (1989) yielded generally poor predictions for a tropical forest plantation, the authors noted that predictions improved as the stands matured. Aboveground biomass has been correlated to annual soil respiration in at least one study (Campbell et al. 2004), but is generally considered to be a poor predictor of flux and partitioning in forests because most of the carbon stored in biomass pools (e.g. tree boles) is biologically inert (Litton et al. *In Review*). LAI has also been correlated with total belowground carbon allocation and has been suggested as a possible surrogate for other forest variables (Litton et al. 2004; Martin & Bolstad 2005; Reichstein et al. 2003).

Several studies have also examined a variety of belowground factors that can influence soil respiration such as soil texture and aeration, substrate quantity and quality (organic C availability), root and mycorrhizal biomass, production and respiration, and nutrient availability. Davidson et al. (2006) recently suggested that substrate availability

to microbes involved in soil respiration might be the largest overlooked factor in accurately estimating soil respiration on greater spatial and temporal scales. Nutrient availability has also been shown to be important in the few studies where it has been considered. Allocation theory was described by Giardina et al. (2003) and suggests that the alleviation of nutrient limitations to plant growth allows a shift of carbon allocation away from roots and mycorrhizae to leaves and stems. Fertilization experiments have shown an overall decrease in TBCA on plots with greater nitrogen (N) availability, likely due to greater aboveground allocation, resulting in greater litter inputs (Haynes & Gower 1995; Giardina et al. 2003), but soil respiration responses differed between the two sites. A post fire lodge-pole pine site showed that C allocation patterns were independent of gradients in N availability (Litton et al. 2004), while allocation to belowground production increased with N across nine temperate forests (Nadelhoffer et al. 1985). A review study also found that greater nutrient availability increased partitioning to aboveground components while decreasing partitioning to belowground ecosystem components (Litton et al. *In Review*).

Although the studies mentioned above include a wide variety of factors, there is considerable variability in factors of importance at both local and regional levels. Further investigation into ecosystem variables mentioned here, and their influence on belowground carbon cycling, is necessary to complete carbon budgets and improve models.

The purpose of the present study was to examine the patterns and processes of soil carbon dynamics across a diverse temperate forest landscape. The NACP land based objective guiding this research is: "[To] provide the information on plant and soil components of ecosystem carbon fluxes necessary to understand and interpret larger scale regional and continental fluxes" (Wofsy and Harriss 2002). This study was conducted at the Bartlett Experimental Forest in north-central New Hampshire, a mixed-

temperate forest landscape that spans a variety of forest types and site conditions. The primary objectives were 1) to quantify and understand soil carbon fluxes, including soil respiration and belowground C allocation, across a range of site types, and 2) to examine how these soil carbon components are linked to other ecosystem parameters such as soil nitrogen transformations, foliar chemistry and climatic variables.

CHAPTER II

METHODS

Study Area

The Bartlett Experimental Forest (BEF) was established in 1931 as a long-term research site managed by the USDA Forest Service. It is located (N 44.05, W –71.29) within the White Mountain National Forest in north central New Hampshire, USA (Figure 2a & 2b). BEF is 1052 ha of secondary successional deciduous and coniferous forest including forest types representative of the larger White Mountain National Forest and northeast region: northern hardwood [sugar maple (*Acer saccharum* Marsh), beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton)], red spruce-balsam fir (*Picea rubens* Sarg. – *Abies balsamea* (L.) Carr.), and red oak-white pine (*Quercus rubra* L. – *Pinus strobus* L.) (Smith & Martin 2001). Topography is varied, ranging in elevation from 210 m-915 m with a northeasterly aspect. Soils are coarse-textured inceptisols and spodosols, being typically moist and well drained. They are derived from granitic drift, and range from shallow bedrock and sandy sediments to washed ablational tills and basal tills (Leak 1982). Climate in this region is characterized by warm summers, a short growing season, and cold winters; temperatures can range from -34°C to 32°C in January and July, respectively. Precipitation is evenly distributed throughout the year, averaging 120 – 140 cm per year, with about one-third of it in the form of snow (Smith & Martin 2001). Snowpack can reach up to 180 cm before spring melt occurs.

At its establishment in 1932 a regular grid of 500 permanent forest inventory plots 0.1 ha in size were set up on east-west transects 200 m apart with a plot every 100 m (Figure 2c). Four full measurements of the inventory plots have been completed to date, 1931-1932, 1939-1940, 1991-1992 and 2001-2003 as well as numerous other partial grid measurements. These inventories included the measurement of all trees > 2 in DBH. The entire area has a history of logging, but approximately 45% of the plots have remained uncut since 1890. The remaining plots have been subjected to various harvest treatments that are typical to those performed throughout the region.

Natural disturbances also play a large role in the current forest structure. On record, there was a late 19th century fire, severe wind damage from hurricanes in 1938 and 1954, ice storm damage in 1998 and beech scale-Nectria complex that has caused significant mortality in beech beginning as early as the 1940s. Other pests and invasive species such as hemlock wooly adelgid, emerald ash borer and Asian long horned beetle have the potential to threaten forest integrity in the future.

In addition to full grid measurements, intensive plot measurements on a fifty-plot subset were initiated in 1995 in conjunction with the start of hyperspectral remote sensing studies geared toward the detection of biogeochemical cycling and ecosystem productivity (Ollinger et al. 2002b; Smith et al. 2002). Measurements on this subset included foliage height, canopy structure and foliar chemistry. A smaller subset of 18 plots contained more detailed measures: foliar production, leaf area index, and soil nitrogen cycling (nitrification, mineralization, and C:N ratios) (Smith et al. 2003). In November 2003 an eddy covariance flux tower to record continuous CO_2, water vapor, and energy flux was erected as part of the Ameriflux network. Ongoing studies are focused on adherence to both the Ameriflux and NACP protocols.

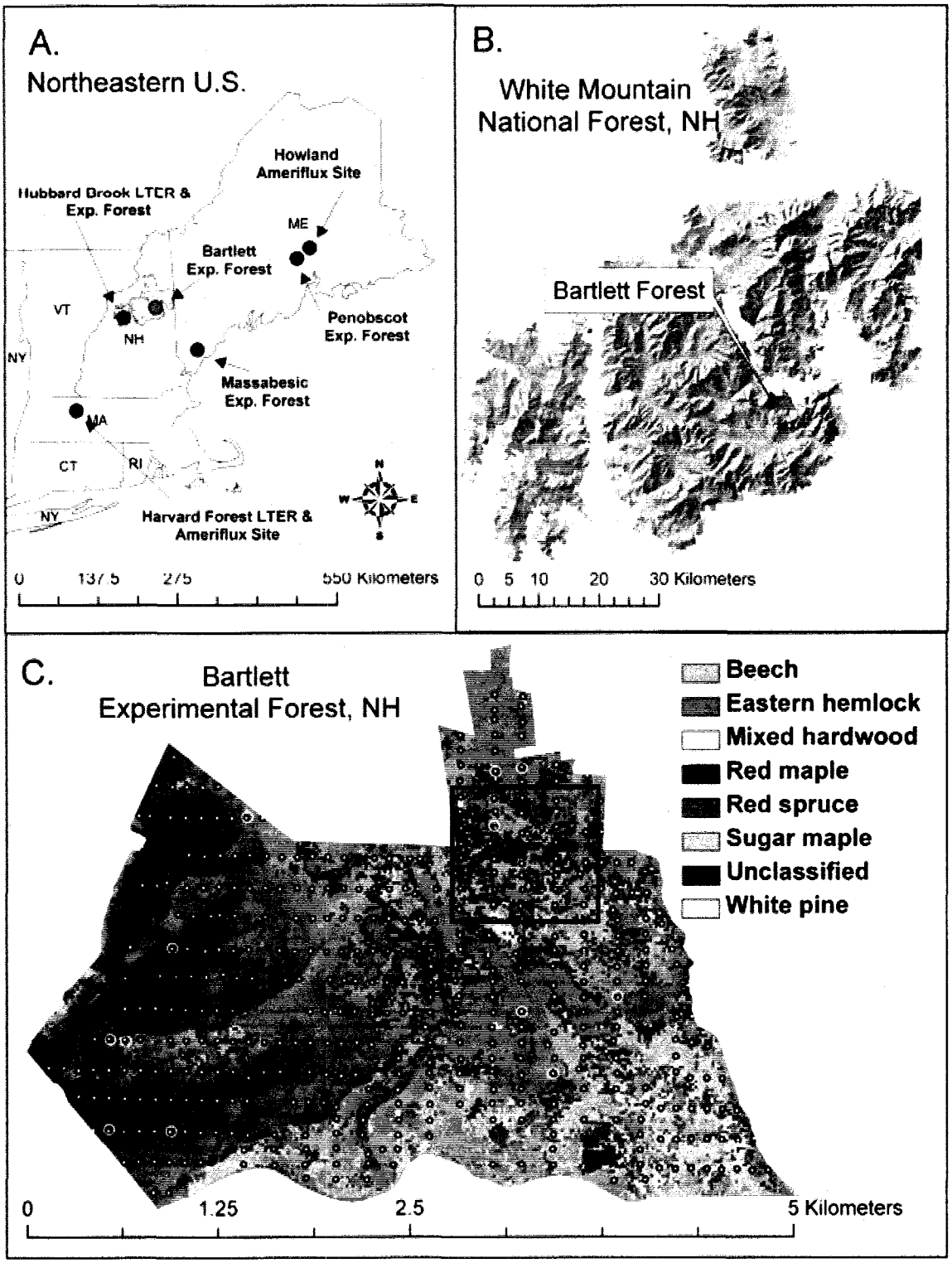

Figure 2. Location of the Bartlett Experimental Forest A) in relation to other northeast experimental monitoring sites and B) nested in the White Mountain National Forest of New Hampshire. C) Bartlett includes a set of permanent Forest Inventory Plots as well as new plots designed under the NACP framework (12 in 1km^2 area around an eddy flux tower –star). Plots span across a range of vegetative species and topographic variation, which is representative of the greater White Mountains (12 circled plots).

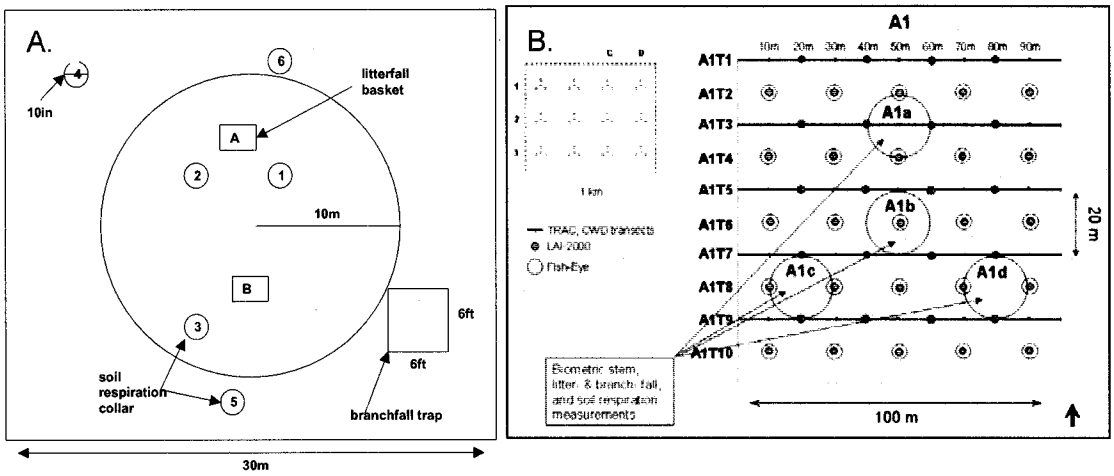

Figure 3. A) Dispersed plots are the one-tenth hectare permanent inventory plots with a 10 m radius subplot. Subplots contain two fine litterfall traps, one coarse litter trap and three soil respiration collars. Three additional collars lie outside the subplot to capture plot variability. B) NACP tower plots are 1 ha in area with four 10 m radius subplots. Subplots within the NACP plots are identical to those found on dispersed plots.

Experimental Design

The eddy covariance flux tower was constructed on a relatively flat, vegetatively homogenous area in the northeast corner of BEF. This location allowed the establishment of 12 NACP Tier 2 plots in a 1 km^2 area centered on the tower in June 2004. Plots are 1 ha each and contain four 10 m radius subplots (Figure 3b). Each subplot contains three soil respiration chambers (507 cm^2), two fine litter collectors (0.23 m^2), and one coarse litter collector (3.35 m^2). To capture greater variability within the experimental forest 12 additional subplots, identical to those described above were set up at the center of existing BEF permanent inventory plots (Figure 3a). Three additional respiration collars were also placed within the 0.1 FIA plot, but outside the new subplot to capture spatial heterogeneity (Davidson et al. 2002b). These dispersed plots include both higher and lower elevations and capture a wider breadth of vegetative composition (Figure 2c) (Table 3). Additional variables either measured specifically for this study (nitrogen mineralization, foliar chemistry, and aboveground biomass) or measured in previous years at BEF (aboveground net primary productivity and leaf area index), as

described below, were not available across all plots. Although comparable data across all plots over the same years would be ideal, their potential to increase the understanding of soil carbon dynamics at BEF directed their use in this analysis.

Soil Moisture

Four soil moisture probes set around the eddy flux tower collect data at half-hour increments and have been averaged to achieve daily soil moisture totals. Precipitation data are recorded by an automated tipping bucket and can be used as a proxy for soil moisture. These data have been recorded since January 2004 and were summed to get total precipitation for the two days prior to each soil respiration measurement, since respiration responds rapidly to large rain events (Lee et al. 2004). Prior to use in regression analyses, mean soil moisture and two day precipitation were natural log transformed for normality.

Soil Temperature

Temperature was taken at 5 cm depth next to each respiration chamber at the time of flux measurements, creating a discrete set of soil temperature throughout the year. Daily soil temperatures at each plot were also required for conversion of individual soil respiration measurements to annual totals. Because daily soil temperatures for individual sites were not available, soil temperatures continuously recorded at the flux tower were adjusted to plots using their relationship to tower soil temperature and plot elevation through a multiple linear regression.

Soil Respiration

Within each of the established NACP tower subplots, there were three soil respiration collars, totaling 144 for the 1 km^2 area. Each dispersed plot had six collars;

three clustered inside the subplot and the remaining three within the 0.1 ha area to account for total plot variation. The collars were 506.7 cm^2 in area and were made from 10" diameter PVC pipe inserted into the ground. Four depths from soil surface to collar top were used to calculate actual chamber volume. Carbon fluxes were determined by placing a top over the collar and measuring the concentration of CO_2 build up in the chamber headspace with a Li-cor 820 Infrared Gas Analyzer (IRGA). One minute after the chamber top was placed over the collar, the CO_2 flux rate was determined using linear regression and adjusted for air temperature and atmospheric pressure.

Flux measurements were taken every three weeks and were typically measured between 7.00 h-17.00 h, to avoid portions of the day when the highest and lowest respiration rates have been recorded (Savage and Davidson 2003). The order in which fluxes were measured was randomized so that diel variation would not be confounded with differences between study sites (Davidson et al. 2002). It should be noted that exclusion of nighttime measurements from the sampling rotation could result in a bias when instantaneous fluxes are extended to annual estimates, but at the same time, responses of soil to increased moisture can obscure typical daily respiration patterns.

Two models based on the empirical relationship between soil temperature and soil respiration were compared for their ability to estimate CO_2 flux. The exponential Q_{10} function is commonly used (Raich & Schlesinger 1992; Davidson et al. 1998; Fahey et al. 2005), but thought to underestimate respiration at low temperatures and overestimate at high temperatures (Lloyd & Taylor 1994). The Q_{10} function is described by:

Equation 1. $R(Tsoil) = R^{*}e^{q10^{*}[(Tsoil-To)/10]}$

Equation 2. $Q_{10} = e^{q10}$

where R(Tsoil) (μmol $m^{-2}s^{-1}$) is the measured CO_2 flux, Tsoil (°C) is the temperature in the upper 5 cm of soil, R (μmol $m^{-2}s^{-1}$) is the flux at To (°C) and To is the initial soil temperature, in this case set to equal zero.

An Arrhenius type function developed by Lloyd and Taylor (1994) has been found to reduce these errors (Savage & Davidson 2001); (Hibbard et al. 2005):

Equation 3. $R(T_{soil}) = R(T_{ref})*e^{Ea[(1/Tref - To)-(1/Tsoil-To)]}$

where T_{soil} (°C) is the soil temperature in the upper 5 cm of soil, $R(T_{ref})$ (μmol $m^{-2}s^{-1}$) is expected respiration at the reference temperature (T_{ref}, °C), T_o (°C) is the soil temperature where respiration is equal to zero, and Ea ($°C^{-1}$) is the parameter that determines temperature sensitivity to changes in CO_2 flux. Values for T_{ref} and T_o were 15 and –46.02°C (absolute zero) respectively, as given by Lloyd and Taylor (1994).

Backward stepwise regression was used to determine whether additional climatic or site-specific data, from respiration chambers, plots, the eddy flux tower and associated tower instruments, might play a significant role in predicting soil respiration fluxes. Factors considered in the regression model are shown in Table 2. Before regressions were performed, variables were tested for normality and multicollinearity. Air temperature was removed as a variable because of its strong relationship to soil temperature.

Table 2. Factors included in stepwise regression analysis to predict annual soil respiration flux.

Collar	Plot	Tower
Flux	Elevation	Air temp
Soil temp	Aboveground biomass	Precipitation
	Aboveground NPP	Soil moisture
	Litterfall carbon	
	Leaf area index	
	Foliar nitrogen	
	Foliar lignin	
	Foliar cellulose	
	Nitrogen mineralization	
	Nitrification	

Litterfall and Aboveground Production

Litterfall

Leaf litter was collected using two 0.23 m^2 traps at each subplot for both tower and dispersed plots. Litter traps on the tower plots were set out in June 2004 and litter collections were made every three weeks from early September until leaf drop was complete. Litter traps on dispersed plots were set out in June 2005 and collections were made in November. Collections from each subplot were composited into one sample, air-dried, and sorted into leaf and non-leaf fine litter (seeds, fruits, twigs and flowers). Leaf litter was then sorted by species, oven dried at 70°C for 24 h and weighed. Although the summer and fall fine litter collections represent the dominant portion of annual litterfall, a small amount if litter is also typically produced in the winter and spring. Although we did not have data from winter or spring collections, previous annual litterfall collections from 1998 and 1999 from plots at BEF and the larger White Mountain area (Ollinger & Smith 2005; Smith, unpublished data) allowed us to determine the relative proportion of annual litterfall that occurs during these seasons. Mean winter and spring litterfall across plots was only 10% of total annual litterfall. We used these values to scale our summer-fall collections up to estimated annual totals.

Branch fall can contribute a substantial fraction of total soil carbon inputs on an annual basis. To capture this carbon component, one 3.35 m^2 tarp was set out at each subplot and was allowed to accumulate fallen branches for one year before collection. Branchfall litter was collected on NACP plots from 2004-2005, whereas litter accumulation on dispersed plot tarps began in June 2005. Samples were collected from the tarps, excluding the portions of branches extending beyond the edge, air-dried for several months (after which moisture was assumed to be negligible), measured for diameter and then weighed. Branches greater than 1 cm and less than or equal to 5 cm were weighed to find annual coarse litter values by plot. Branches >5 cm were

considered part of the coarse woody debris pool and not included in this study. For plots where branch fall accumulation has not reached one year, the current mean from the NACP tower 2004-2005 collection was used.

Branchfall and leaf litter mass were converted to litterfall carbon assuming a tissue carbon content of 50%.

Biomass

Aboveground biomass (AGB) was estimated using allometric equations developed for specific species, based on field measurements of diameter at breast height (DBH) for all trees greater than 5 cm. DBH was measured on tower plots in September 2004 and October 2005, while dispersed plots were measured in July 2005. Separate equations were used to calculate each component: foliage, branch, or bole, and summed to achieve total biomass. The equations used in this study were those directly derived from studies in the Northeast region (Ribe 1973; Whittaker et al. 1974; Young et al. 1980; Hocker and Early 1983).

Aboveground Net Primary Production

Aboveground net primary productivity (ANPP) can be calculated as the difference between biomass in year 2 and year 1, and divided by the length of time for growth between the two measurements. For the tower plots this was one year. ANPP for the dispersed plots was taken from previous studies, which calculated change in biomass over several years.

Leaf Area Index

Estimates of leaf area index (LAI) for dispersed plots were calculated by Smith (2000). Values for each plot were calculated as the ratio of total leaf area within a fine litter trap and litter trap ground area. To calculate LAI for tower plots this method was employed using leaf area from Smith and Martin (2001) and 2004-collected litter.

Total Belowground Carbon Allocation

Estimates of belowground carbon allocation were derived using the conservation of mass approach, where all carbon inputs to the system must either leave the system or increase soil C stocks (Raich & Nadelhoffer 1989; Nadelhoffer et al. 1998). Because changes in soil carbon stocks are difficult to measure, this approach is often used under the assumption that soil carbon pools are at or near a state of equilibrium, where annual changes in carbon storage are minimal in comparison to annual fluxes (Raich & Nadelhoffer 1989; Davidson et al. 2002a). Hence, this method cannot be used reliably in stands undergoing rapid gains or losses of soil C, through changes in the forest floor, prevalent soil erosion or leaching of dissolved organic carbon from soil organic matter, such as those that have recently undergone a major disturbance. Plots for this project were selected, in part, because no logging or other anthropogenic disturbances have recently occurred, increasing the likelihood that the system meets the requirements for a steady state assumption.

Methods for estimating total belowground carbon allocation were initially described by Raich and Nadelhoffer (1989) and later validated by Davidson et al. (2002a) using more advanced and likely more accurate measurement techniques of individual components (e.g. use of IRGAs for soil respiration instead of the soda lime method). The steady state assumption means the inputs from litter production, root biomass stocks, and mineral soil layers of organic carbon, are equal to decomposition:

Equation 4. $Rh \approx Pa + Pb$

Where Rh = heterotrophic respiration, Pa = aboveground detritus production, and Pb = belowground detritus production. By including autotrophic respiration the result is total soil respiration:

Equation 5. $Rs = Rh + Rr$

Where Rs = soil respiration and Rr = root respiration:

Equation 6. $Rs - Pa \approx Pb + Rr$

This final equation indicates that total allocation to roots (Pb + Rr) can be estimated by soil respiration (Rs) measurements and aboveground detritus production (Pa). Here Pa is estimated using litterfall and excluding coarse woody debris (CWD), branches with diameter greater than 5 cm. Coarse woody debris, although it can have higher detritus production than fine litterfall, releases most of its CO_2 directly to the atmosphere and only becomes part of soil organic matter at advanced stages of decay. Because CWD is an important part of aboveground detritus production and it is not included as an input, it must be expected that estimates of TBCA will be greater than true values by an undefined amount. The final equation for belowground allocation was altered slightly by Davidson et al. (2002a) to yield:

Equation 7. $TBCA = Rs - litterfallC$

Using these equations, Raich and Nadelhoffer (1989) and Davidson et al. (2002b) showed that annual soil respiration was approximately three times litterfallC and comes close to predicting TBCA on the averaged global scale.

Soil respiration is inherently influenced by both long-term (decades) and short-term (days) factors, such as litter quality and quantity, and soil temperature and moisture respectively. Thus interannual variability of soil respiration can be extremely high based solely on differences in soil temperature from one year to the next. As a result soil temperature is also the strongest driver of TBCA estimates between years, given that litterfall amounts stay relatively constant over time in steady state forests. Although an average of litter collection and flux measurements across many years would be best for

calculating TBCA and measurements of litter and flux over the same time period would be ideal, complete long-term datasets are rare and were not available for this study. Because long-term averages are unavailable and measurements were made across different years, we set temporal variability aside to better focus on spatial variability. TBCA across all plots is best calculated using 2005 annual respiration rates based on 2005 soil temperatures and available litter collections, regardless of year.

N Mineralization and Nitrification

Measurements of N mineralization (nmin) and nitrification (nit) were conducted using the polyethylene bag technique described by Pastor et al. (1984) with 28 day lab incubations. Although *in situ* incubations are preferable, several studies have found a high degree of correlation between field and lab incubations giving us confidence that lab incubations would be adequate for characterizing variability among plots (Zak et al. 1989; Carlyle et al. 1998; Ollinger et al. 2002b). Soil cores for N analysis were collected in September 2005. Two pairs of cores were taken next to each soil respiration collar across the 12 dispersed plots. Cores were 6 cm in diameter and were taken from the top of the organic soil down to 10 cm in the mineral soil unless bedrock or other impenetrable materials were encountered. Samples were separated into organic and mineral components. All samples were stored at 3°C until processed, not exceeding three days.

One core from each pair was put aside to incubate in the dark at 22°C for 28 days. The other two cores were homogenized and passed through either a 5.6 mm sieve (organic) or a 2 mm sieve (mineral). A subsample of 10 g was extracted in 100 mL of 1 N KCl for 24 hours. A second subsample was oven-dried at 105°C for 48 hours to determine soil moisture content. Extracted samples were then filtered and analyzed for

ammonium and nitrate using an Astoria2 autoanalyzer (Astoria-Pacific International, Clackamas, Oregon, USA). The same procedure was repeated for incubated cores. Net N mineralization is calculated as the difference between the sum of NH_4^+-N and NO3$^-$-N for the incubated samples versus that for the initial samples. Similarly net nitrification is the difference between NO_3^-N for the incubated versus initial samples. Mass per area values over the 28-day incubation period were expanded to annual values using the field to lab relationships developed in the White Mountains region and described by Ollinger et al. (2002b).

Equation 8. N mineralization (annual) = 2.44 * N mineralization (lab) – 5.94

Equation 9. Nitrification (annual) = 2.52 * Nitrification (lab) + 0.60

Final nitrification values were log transformed to achieve normality.

Foliar Chemistry

Determination of growing season foliar chemistry on each plot required collection of leaves from dominant and co-dominant trees at several heights in the canopy. Shotguns were used to take down small branches for green leaf collection in mid-July, which were then oven-dried at 70°C for 24 h. Leaves were ground using a Wiley mill and passed through a 1 mm mesh screen. Samples were re-dried overnight and foliar nitrogen, lignin and cellulose were measured using a NIRSystems model 6500 near-infrared spectrophotometer (Foss NIRS Systems, Silver Spring Maryland, USA) (Mclellan et al. 1991a; Mclellan et al. 1991b; Bolster et al. 1996).

Individual species means of foliar chemistry concentrations were weighted by the fraction of canopy foliar mass per species to calculate plot-level whole canopy concentrations (g per 100 g foliar biomass). Species fractions by plot were gained using the camera-point quadrant method, which gives an accurate vertical profile distribution of

leaf area by height and by species and allows estimation of total canopy chemistry (MacArthur & Horn 1969; Aber 1979b, Aber 1979a, Parker et al. 1989, Smith & Martin 2001).

CHAPTER III

RESULTS

Variability in Instantaneous CO_2 Efflux

Soil respiration data for all plots and measurement periods are shown in figure 4a. Respiration rates generally followed the seasonal temperature cycle with the exception of several anomalously high measurements in October and November of 2005. October and November 2005 showed unusually variable fluxes (e.g. 8 μmol m^{-2} s^{-1} to 27 μmol m^{-2} s^{-1}) both at the chamber and tower level (Figure 4b), many of which were elevated beyond the typical range for temperate forests. Such high fluxes were not recorded at BEF in 2004, nor were measured soil respiration rates at Harvard Forest, a Long Term Ecological Research Site in Petersham, Massachusetts, found to deviate from the expected seasonal pattern during the October-November time period (J.Mohan, personal communication, January 12, 2006).

We eliminated instrument malfunction as a potential source of error because eddy flux tower measurements collected during the same time period showed a similar pattern (Figure 4b). Additionally, the difference between actual flux in 2005 and mean flux (2004 and 2005 not including October and November) by day of year showed no pattern by subplot. All subplots varied around the mean with a difference of less than 4 μmol m^{-2} s^{-1} until October and November, where respiration differences ranged from 0-26 μmol m^{-2} s^{-1}. Temperature, which is typically the strongest driver of respiration, explained only 48% ($P < 0.001$) of the variation in seasonal flux patterns, suggesting that soil temperature alone did not explain high October and November fluxes (Figure 5).

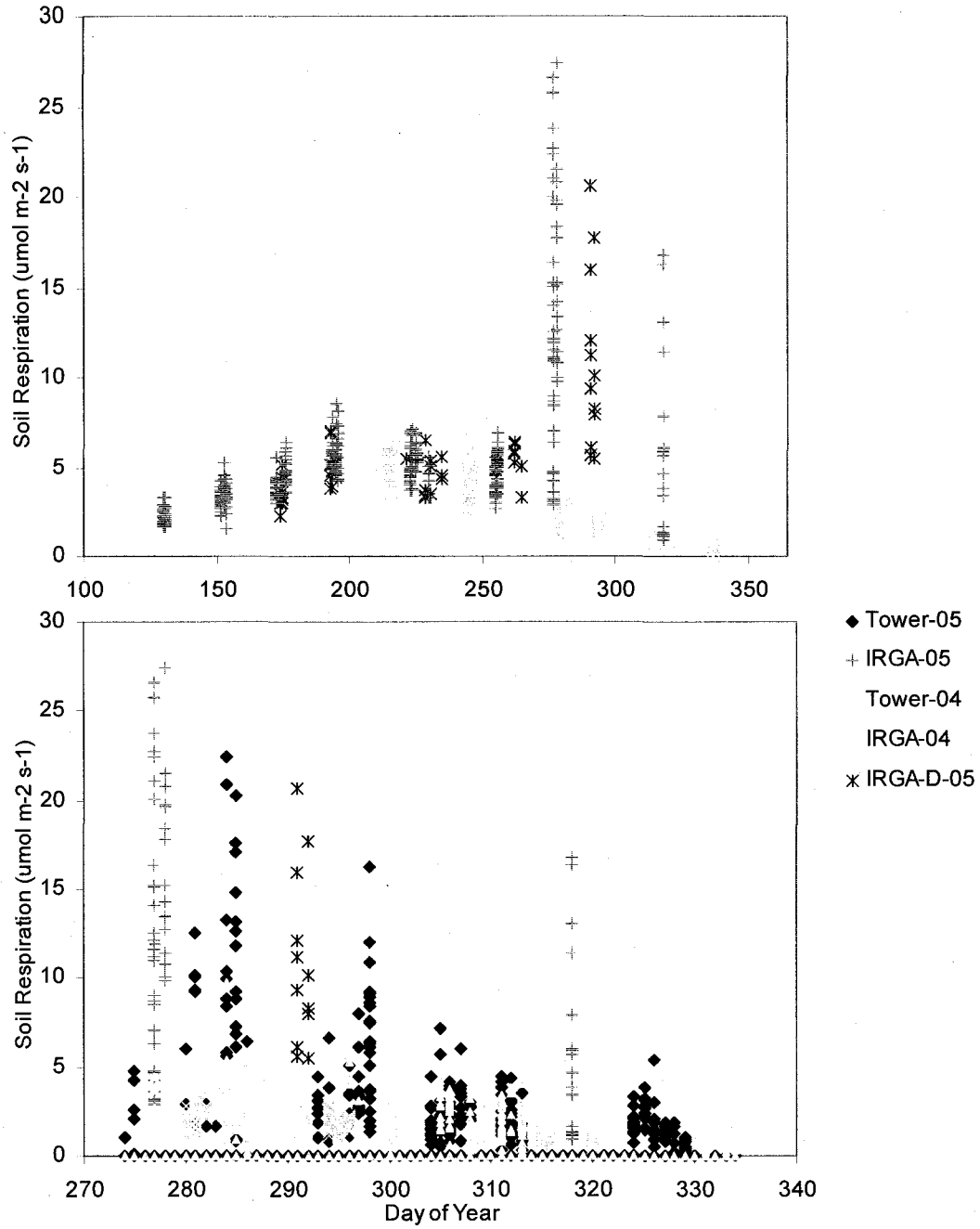

Figure 4. A) Soil CO_2 flux in 2004 and 2005 by day of year as measured at the chamber level using the soil respiration unit (IRGA) and B) both chamber values and estimated values from the eddy flux tower (Tower), over the period of concern (October-November). IRGA refers to individual chamber measurements in NACP tower plots, while IRGA-D values were those collected at dispersed plots. *Day 274 is October 1st.

We examined the degree to which other factors might help explain these anomalous fluxes using a variety of linear and nonlinear regression methods where respiration fluxes were regressed against various combinations of the measured variables shown in Table 2. From this analysis, only precipitation and soil moisture improved the predictability of high soil fluxes, increasing the correlation from r^2=0.48 with soil temperature only to r^2= 0.59, $P < 0.001$. Because the anomalous respiration values clearly departed from both literature values and from the remainder of observations at Bartlett, we decided to exclude these measurements from subsequent analyses aimed at deriving response functions to temperature and other environmental variables. Although we recognize that excluding these data will likely result in an underestimation of soil respiration when extended to annual fluxes, we felt that including them would cause an unacceptable bias in the degree to which we could explain variability in the remaining data. Hence, we chose to exclude the anomalous values from subsequent analyses in the hope that a more satisfying explanation of their origin can be found in the future.

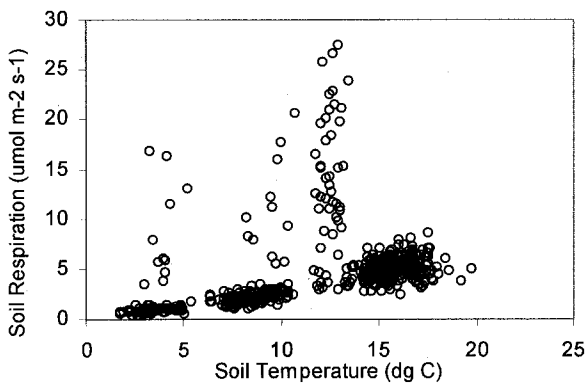

Figure 5. Soil CO_2 is typically highly correlated to soil temperature. Here high flux values in October and November 2005 distort this relationship.

Annual Soil Respiration

Although discrete daily respiration measurements from throughout the growing season are important, annual soil respiration is required for estimating TBCA. This means that individual measurements must be extended throughout the year through a statistical model that can be applied using daily environmental data available for the entire year. As an initial step towards accomplishing this, stepwise regression was used to examine which ecosystem parameters explained variance in instantaneous CO_2 fluxes after excluding the anomalous values discussed in the preceding section. Results indicated that the only significant predictors at the $P < 0.05$ significance level were soil temperature, foliar nitrogen, foliar lignin, and the lignin to nitrogen ratio, yielding an $r^2 = 0.74$. This method, however, did not satisfactorily account for the non-linear relationship between soil temperature and respiration.

To better capture the effect of temperature, two well-known, non-linear temperature-dependent statistical models were tested; the Q_{10} and Lloyd and Taylor (1994) functions. Both methods produced higher r^2 values than the regression results mentioned above, although results showed little difference in the degree to which either equation could account for temperature-induced variation. Predictions yielded r^2 values

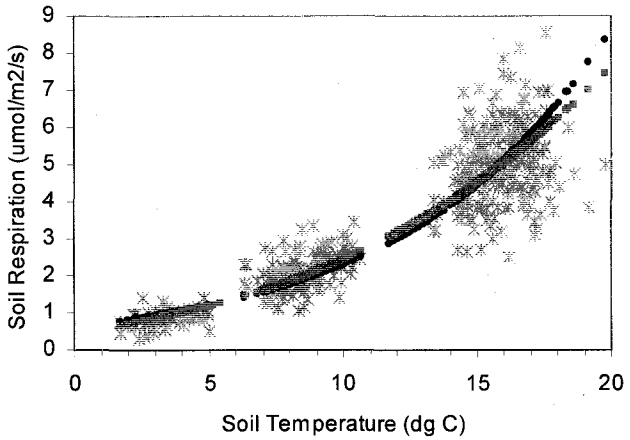

Figure 6. Comparison of Q_{10} (dark blue) and Lloyd and Taylor (1994) (pink) temperature-dependent models for estimating annual soil respiration.

of 0.87 and 0.89 for Q_{10} and Lloyd and Taylor, respectively (Figure 6). Across all plots the average Q_{10} value was 3.76. Although the Q_{10} model is more simplistic, the potential for overestimation of high fluxes, as cited by Lloyd and Taylor (1994), prompted us to use annual respiration values produced by the Lloyd and Taylor model for the rest of our data analysis.

Using the Lloyd and Taylor function along with daily mean temperatures estimated for each plot, calculated annual soil flux values, which ranged from 647 g C $m^{-2} y^{-1}$ to 846 g C $m^{-2} y^{-1}$ with a mean of 791 ± 62 g C $m^{-2} y^{-1}$ (Table 3). When tower and dispersed plots were considered separately, variance was greater among dispersed plots. Additional regression analysis using residuals from the Lloyd and Taylor temperature relationship showed that nitrogen mineralization and leaf area index explained 29% of the remaining variance. However, because the absolute amount of variation these variables explained was small, and because N mineralization was not available across the 12 tower plots, we felt that the Lloyd and Taylor model represented the best choice for calculating annual soil respiration across the Bartlett landscape.

Leaf and Branch Litterfall

Whereas the range of soil fluxes within BEF was small in comparison to the range observed globally, this was not true of fine litterfall carbon estimates (35 g C $m^{-2}y^{-1}$ to 177 g C $m^{-2}y^{-1}$), which covered just under half the range of estimates found in several global datasets (Raich & Nadelhoffer 1989; Davidson et al. 2002a) (Table 3). Coarse litterfall (1 – 5 cm diameter) for the tower plots averaged 24 g C $m^{-2}y^{-1}$ (Table 3), but was extremely variable between plots, sometimes contributing more than half of total litterfall. Temporal variability in coarse litterfall is also likely to be high, given the potential for infrequent, but large, pulse inputs from disturbances such as windthrow or ice storm damage. However, because we have just a single year of measurements that do not include any such events, we cannot evaluate their long-term importance to soil carbon inputs. Given these caveats, total carbon inputs to the soil, as used in the TBCA equation (Equation 7), are equal to the sum of fine litter and available coarse litter input values and range from 60 g C $m^{-2}y^{-1}$ to 217 g C $m^{-2}y^{-1}$ (Table 3).

Total Belowground Carbon Allocation

Annual respiration values and total litterfall carbon were used in Equation 7 to estimate total belowground carbon allocation (Table 3). Across all plots TBCA ranged from 505 g C $m^{-2}y^{-1}$ to 711 g C $m^{-2}y^{-1}$, a 29% difference between plots with the least carbon allocation and those with the greatest.

Table 3. Site description and characteristics, C cycling, N cycling, and foliar chemistry for plots across the Bartlett Experimental Forest.

Study sites				C cycling (g C m-2 yr-1)				(g C m-2)				N cycling (g N m-2 yr-1)		Foliar chemistry (%)			
Plot	Plot Set*	Species[$]	Elevation	CO_2 Flux	Leaf Litter	Branch Litter	Total Litter	TBCA	ANPP	AGB	LAI	Nmin	Nit	Nitrogen	Lignin	Cellulose	Lignin:N
10T	D	Red spruce	547	701	35	24	60	641	280	4310	1.80	3.38	0.09	1.10	21.50	36.01	19.52
14Z	D	S.maple-beech	327	797	102	24	126	671		9685		2.25	0.68	2.14	23.62	41.84	11.04
30AF	D	Paper birch	226	844	120	24	144	700		8953		-0.38	0.09	1.45	23.03	36.21	15.85
30Y	D	Beech	260	828	107	24	132	697	603	11041	3.35	0.74	0.16	1.91	23.76	40.89	12.46
32AF	D	Hemlock	221	846	140	24	165	682	542	7402	3.46	0.67	0.13	1.22	20.48	35.87	16.85
32P	D	Hemlock	292	813	89	24	113	699	402	12965	3.09	4.01	0.06	1.43	17.74	34.41	12.44
34K	D	Hemlock	306	806	93	24	117	688	397	14234	2.78	2.60	0.10	1.34	16.13	33.01	12.06
38Q	D	Beech	332	792	87	24	111	681	531	11801	3.04	0.76	0.24	1.68	19.32	34.35	11.48
5D	D	S.maple-beech	593	679	99	24	123	556		14036		8.37	1.97	2.25	20.75	40.33	9.22
6N	D	Red spruce	676	647	46	24	70	577	224	7146	1.82	6.92	0.26	1.01	25.53	38.36	25.35
7N	D	Red spruce	651	657	128	24	152	505	287	10958	1.90	7.97	0.06	1.19	24.80	40.08	20.78
9D	D	S.maple-beech	546	703	155	24	179	524	565	8049	3.52	2.75	0.06	2.43	25.72	45.93	10.60
A1	T	Beech	252	832	84	57	126	706	230	10536	4.2			1.65	20.76	37.06	12.60
A2	T	Beech	269	823	100	15	113	711	83	7786	4			1.68	21.01	36.88	12.54
A3	T	Beech	281	818	152	21	165	652	211	10147	4.9			1.81	20.61	37.40	11.38
B1	T	Beech	257	829	108	19	134	695	185	8612	4			1.83	22.14	39.61	12.07
B2	T	Red maple	267	824	100	33	127	698	143	12626	5.1			1.72	19.26	35.95	11.20
B3	T	Beech	283	817	124	27	150	667	223	10500	3.7			1.91	21.49	38.34	11.23
C1	T	Beech	249	833	177	20	217	616	132	11715	4.8			1.68	17.77	36.55	10.56
C2	T	Beech	271	822	89	15	115	707	182	10433	4.8			1.74	20.11	36.46	11.53
C3	T	Hemlock	288	814	98	39	121	693	183	9878	4.2			1.33	16.59	32.17	12.45
D1	T	Red maple	243	835	138	20	182	653	27	8446	4.7			1.63	18.58	35.09	11.41
D2	T	Beech	263	826	118	19	147	679	179	7045	4.8			1.94	21.49	39.59	11.10
D3	T	Beech	297	805	94	7	127	678	238	10025	4.8			1.88	20.97	38.73	11.13

*D stands for dispersed plots, while T stands for plots centered around the eddy flux tower.
[$] S.maple-beech are stands where Sugar maple and American beech are co-dominant species.

Annual Soil Respiration in Relation to Ecosystem Variables

Annual soil respiration is largely derived from its consistent relationship to soil temperature, thus correlations of respiration to other ecosystem variables are largely a result of their own relationship to temperature. Elevation is the clearest example of this pattern. Where elevation was high (> 500 m) estimated mean CO_2 fluxes were low and plots with low elevation typically showed high fluxes. Yet, it remains important to understand how these variables change across the landscape as they relate to soil properties if we are ever to map them at larger than local scales. The following results indicate how ecosystem variables changed across all plots, and how they differ between dispersed plots, which capture larger site variability, and tower plots, which focus on micro-site variability and homogeneity needed for understanding eddy flux tower measurements (Table 4).

When all plots were treated together, neither litterfall nor ANPP showed significant relationships to annual soil respiration, despite results from previous studies. However, when dispersed and tower plots were separated, litterfall remained insignificant (Figure 7), but ANPP became significant for both plot sets, albeit following different patterns (Figure 8). For dispersed plots, soil respiration was positively related to ANPP, whereas tower plots showed only a weak and inverse relationship with ANPP. It should be pointed out, however, that ANPP values from the NACP plots were based on a single year of measurements, which may be inadequate for accurate ANPP estimation. Aboveground biomass (AGB) was not significantly related to soil respiration across plots or when plots were grouped by set. However, a negative trend did surface when high elevation plots were excluded from analysis ($r^2 = 0.17$, $P > 0.05$). Soil respiration was positively related to LAI across dispersed plots. Across all plots the lignin, cellulose, and lignin:nitrogen ratio components of live foliage were found to

significantly correlate with annual values of soil respiration. The relationship between foliar N and soil respiration was non-linear, with respiration increasing from low to mid foliar N values and declining towards the high end of the foliar N range (Figure 9). Among all variables tested, annual nitrogen mineralization showed the most significant and strongest relationship to mean soil respiration on an annual basis (Figure 10), although mineralization was only measured on dispersed plots for this study.

Table 4. Correlation of ecosystem parameters to annual soil respiration and estimated total belowground carbon allocation across all plots and separated into plot set. Non-significant relationships are noted as ns; r^2 of significant relationships are given with coefficients listed in parentheses. Coefficients shown are the change in flux for every one unit change in the listed ecosystem variable.

	Soil Respiration			**TBCA**		
	All plots[x]	Dispersed	Tower	All plots[x]	Dispersed	Tower
Foliar (mass-based, %)						
Nitrogen	ns	ns	ns	ns	ns	ns
Lignin	0.24** *(-12.40)*	ns	ns	0.21* *(-11.28)*	0.26* *(-13.73)*	ns
Cellulose	0.12* *(-8.18)*	ns	ns	0.26** *(-10.56)*	0.34* *(-12.22)*	ns
Lignin:Nitrogen	0.28** *(-9.04)*	ns	ns	ns	ns	0.48** *(31.17)*
Overstory						
Litterfall C (g C m^{-2} yr^{-1})	ns	ns	ns	ns	ns	0.92*** *(-0.87)*
ANPP[#] (g C m^{-2} yr^{-1})	ns	0.41* *(0.38)*	0.26* *(-0.08)*	ns	ns	ns
AGB (g C m^{-2})	ns	ns	ns	ns	ns	ns
LAI (m^2 m^{-2})	ns	0.50* *(80.95)*	ns	ns	ns	0.81*** *(-39.89)*
Soil (g N m^{-2} yr^{-1})						
N mineralization[$]	NA	0.70*** *(-21.80)*	NA	NA	0.54** *(-18.92)*	NA
Nitrification[$]	NA	0.00	NA	NA	ns	NA

[x]All plots, n=24; Each plot set, dispersed and tower, n=12
[$]nitrogen mineralization and nitrification were only measured on dispersed plots, n=12
[#]aboveground net primary productivity and LAI not available for all plots, n=21
*$P < 0.05$; **$P < 0.01$;***$P < 0.001$

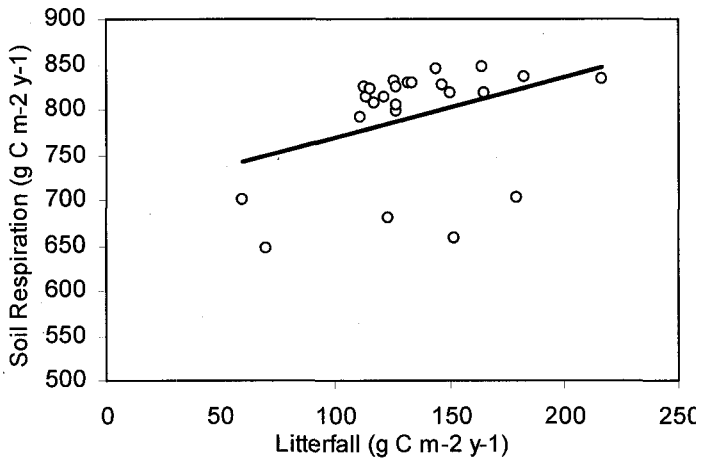

Figure 7. Non-significant relationship between annual soil respiration (g C m^{-2} yr^{-1}) and total litterfall carbon inputs (g C m^{-2} yr^{-1}) across all plots, n=24. y = 0.6569x + 703.31, R^2 = 0.13.

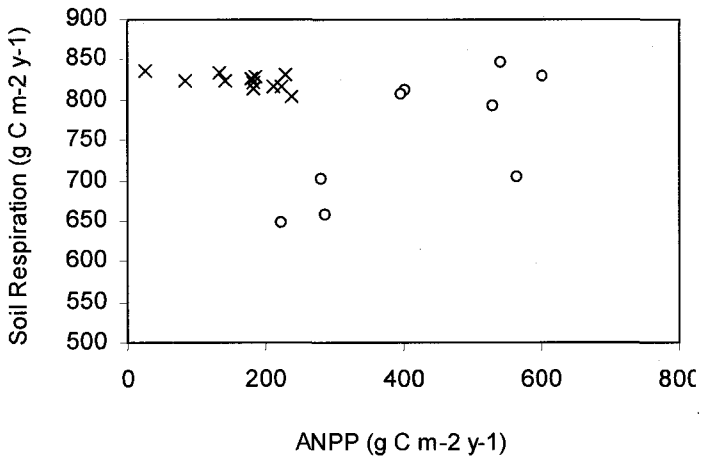

Figure 8. Relationship of soil respiration (g C m^{-2} yr^{-1}) and ANPP (g C m^{-2} yr^{-1}) as it differs by plot set. Soil respiration on dispersed plots (◊) has a positive relationship with ANPP. ANPP values for tower plots (x) were much lower than values on dispersed plots and showed a weak inverse relationship to soil respiration. Low values and lack of clear trends may indicate that a single of year of ANPP measurement was inadequate assessing this relationship.

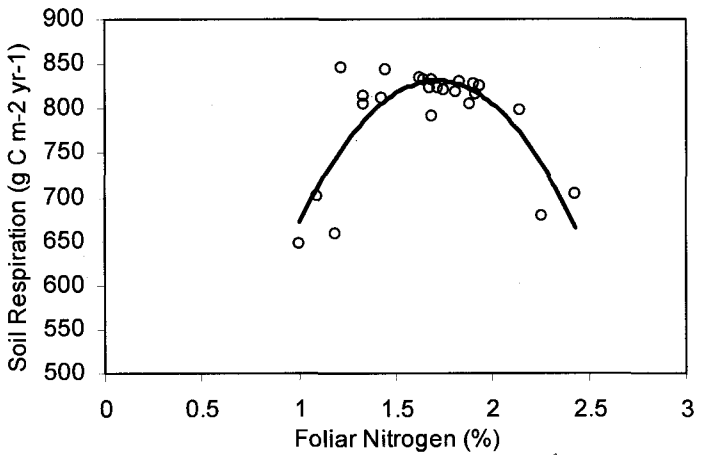

Figure 9. Non-linear relationship between soil respiration (g C m^{-2} yr^{-1}) and foliar nitrogen concentration (%). y = -324.18x2 + 1109.3x - 117.08, R^2 = 0.69.

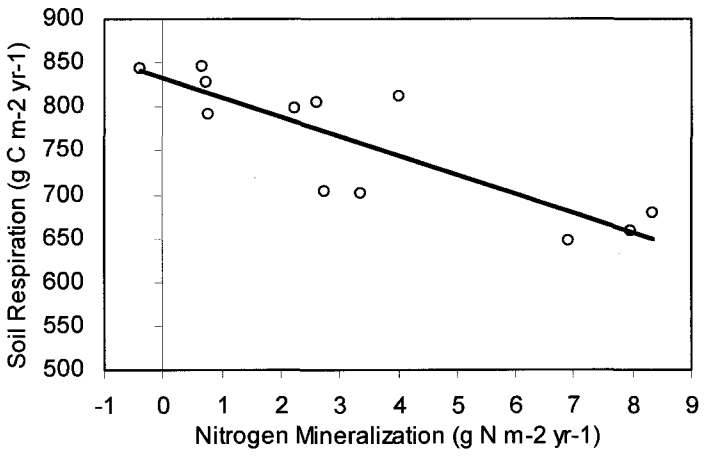

Figure 10. Comparison of annual soil respiration (g C m^{-2} yr^{-1}) and annual net nitrogen mineralization (g N m^{-2} yr^{-1}), for dispersed plots, n=12. y = -21.797x + 832.16, R^2 = 0.72.

Relationships and influences on TBCA

Two high elevation plots, 9D and 7N have much lower estimated TBCA than the rest of the dispersed plots, as a result of greater litterfall inputs and low CO_2 fluxes. Their disproportionately low carbon allocation weakens relationships between TBCA and most of the measured variables. A regression of belowground allocation against litterfall carbon showed a significant negative relationship, with allocation decreasing as litterfall production increased across all plots (Table 4). At the plot level, there was an interesting pattern of two parallel relationships in TBCA vs. litterfall, where the lower line includes plots at higher elevations and the upper line includes all lower elevation plots (Figure 11). Also interesting was the ratio of TBCA to litterfall carbon along a gradient of increasing litterfall (Figure 12). The only other ecosystem parameter that explained significant variance in total belowground carbon allocation was foliar cellulose concentrations (Table 4).

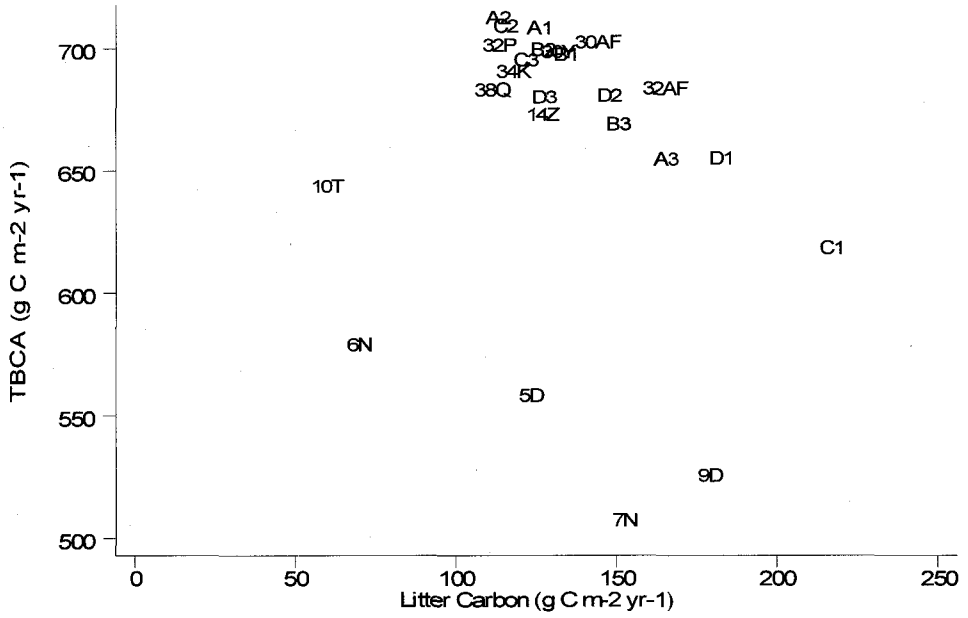

Figure 11. Correlation between total belowground carbon allocation and total litterfall carbon inputs by plot.

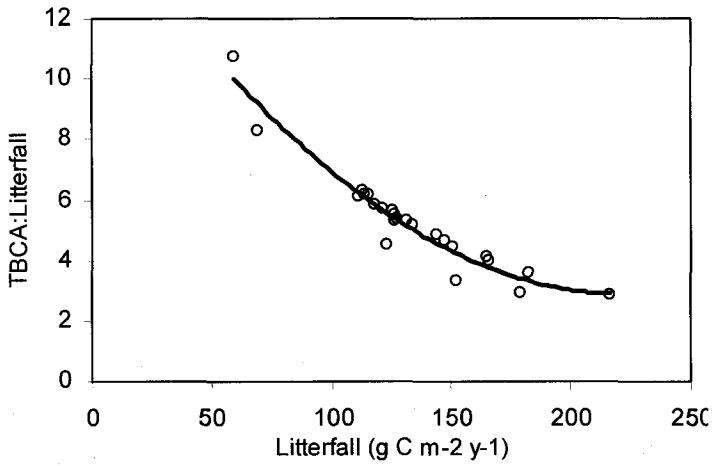

Figure 12. Ratio of predicted total belowground carbon allocation to total litterfall carbon along the litterfall carbon gradient found in BEF.

Multiple Variable Analyses

In addition to single variable comparisons analysis of multiple variables showed that soil respiration and TBCA were often best explained using a combination of ecosystem parameters, and the combination that best captured variance among plots changed based on plot grouping (Table 5). Across all plots live foliar components explained the greatest variance in soil carbon fluxes, which was also true for soil respiration on tower plots. In contrast, LAI, on its own, was the strongest predictor of TBCA on tower plots. Given that dispersed plots had the most ecosystem parameters available for understanding patterns in soil carbon components, it is not surprising that for both CO_2 flux and TBCA, more than one combination of variables explained patterns across the landscape. Prediction of TBCA on dispersed plots requires N mineralization but can be used with either foliar lignin or cellulose concentrations depending on which variable is available. Soil respiration on dispersed plots can be estimated by a number of ecosystem variables, or by just two, LAI and foliar cellulose.

Table 5. Multiple linear regressions across all plots, dispersed plots and tower plots for both soil respiration and TBCA showed that a combination of ecosystem variables in most cases better predict spatial patterns of these soil carbon fluxes than individual variables. All variables included in final equation, $P<0.05$.

	Soil Respiration				TBCA			
	All plots[x]	Dispersed	Dispersed	Tower	All plots[x]	Dispersed	Dispersed	Tower
Foliar (mass-based, %)								
Nitrogen	x	x		x				
Lignin				x	x		x	
Cellulose			x		x	x		
Lignin:Nitrogen	x			x	x			
Overstory								
Litterfall C (g C m^{-2} yr^{-1})								
ANPP[#] (g C m^{-2} yr^{-1})								
AGB (g C m^{-2})		x						
LAI (m^2 m^{-2})		x	x					x
Soil (g N m^{-2} yr^{-1})								
N mineralization[$]		x				x	x	
Nitrification[$]								
Adjusted R^2	0.68	0.92	0.86	0.29	0.57	0.74	0.71	0.81

[x]All plots, n=24; Each plot set, dispersed and tower, n=12
[$]nitrogen mineralization and nitrification were only measured on dispersed plots, n=12
[#]aboveground net primary productivity and LAI not available for all plots, n=21

CHAPTER IV

DISCUSSION

Results of this study provided new estimates of soil respiration and belowground carbon allocation for a northern temperate forest ecosystem. Annual soil respiration showed a positive relationship with LAI and negative relationship with N mineralization. TBCA at Bartlett ranged from 505 g C m^{-2} yr^{-1} to 711 g C m^{-2} yr^{-1} and varied inversely with foliar lignin and cellulose. Although these results are interesting, they are not without uncertainties. Annual soil respiration, for example, was derived using a statistical model based solely on temperature and excluding anomalous measurements from two months in 2005. TBCA, although comparable to estimates from similar ecosystems, is dependent on litterfall values, which are highly variable due to their branchfall component.

Instantaneous CO_2 Efflux

Instantaneous soil fluxes could be largely accounted for by soil temperature alone, with the exception of high fluxes in October and November of 2005. Here an additional 12% of variance in soil respiration was explained by soil moisture, and precipitation summed over the two days prior to chamber measurements. These factors, however, only capture temporal variation in soil CO_2 flux and cannot explain the difference in the strength of response to wetting between plots because moisture measurements were only taken at the tower. It is also possible that the combination of high soil moisture content following several unusual rainfall events and increased availability of nutrients and labile C from recently fallen leaf litter hyper stimulated

microbial activity for a brief period of time that coincided with field respiration measurements. Measurement of soil moisture and soil C:N ratios in the organic layer throughout the year near individual collars, as well as partitioning between autotrophic and heterotrophic fluxes would improve our understanding of values that depart from the mean.

Although exclusion of the October and November fluxes undoubtedly led to an underestimation of soil respiration when extended to annual estimates, these fluxes clearly departed from both literature values and from the remainder of observations at Bartlett. Including them would, therefore, have caused an unacceptable bias in the degree to which we were able to explain variability in the remaining data.

Estimating Annual Soil Respiration

The annual estimate of total soil respiration at Bartlett (791 ± 62 g C $m^{-2} y^{-1}$) is comparable to, but higher than, fluxes at both the Hubbard Brook Experimental Forest also located in northern New Hampshire (660 ± 54 g C $m^{-2} y^{-1}$; Fahey et al. 2005) and fluxes for Harvard Forest, Massachusetts (530 g C $m^{-2} y^{-1}$ to 870 g C $m^{-2} y^{-1}$; Davidson et al. 1998). However, discrete soil CO_2 flux values measured at Bartlett, from throughout the growing season, are within the range of values found across deciduous, mixed, and evergreen forests reported by Hibbard et al. (2005).

Although estimation of annual soil respiration flux was achieved using the Lloyd and Taylor (1994) function, the Q_{10} values we obtained are worthy of some discussion. Recent work by Davidson et al. (2006) examined how Q_{10} values for soil respiration varies between seasons, plots, and sites. The authors state that a Q_{10} greater than 3 indicates temperature is not the only factor contributing to variation in soil respiration.

Across all plots at Bartlett Q_{10} was 3.76, suggesting possible influence by soil moisture, substrate availability and/or some other factor.

Soil temperature and soil moisture have often been identified as the strongest drivers of variation in soil CO_2 flux (Singh & Gupta 1977; Sato & Seto 1999; Savage & Davidson 2001; Subke et al. 2003; Martin & Bolstad 2005). However, Davidson et al. (1998), in a study at a temperate mixed hardwood forest in Massachusetts, state most seasonal and diel variation in soil respiration can be attributed to soil temperature, which is consistent with results we obtained at BEF. In this study, two factors likely account for the lack of influence caused by soil moisture on CO_2 flux. First, water limitations at BEF are thought to be rare on an annual basis. Therefore, fluctuations in precipitation and soil moisture over the growing season may play only a small role in affecting annual soil respiration values. However, it should be noted that both precipitation and soil moisture were measured at a single location, the eddy flux tower. This measurement scheme did not allow us to examine micro-site variation in soil moisture, which can play a large role in individual chamber fluxes (Lee et al. 2004). Soil moisture measurements at individual respiration chambers are planned for the 2006 field season and may shed additional light on the role of variability in soil moisture on long-term CO_2 fluxes.

Stepwise regression analysis indicated that, in a linear model, the addition of foliar nitrogen, lignin and lignin:nitrogen ratios explained more of the variance in soil respiration than temperature alone, with lignin:nitrogen ratio having the greatest influence. Although lignin:nitrogen ratios are not a direct measure of soil substrate, they do provide a commonly used index of litter quality and are related to decomposition rates, soil C:N ratios and soil N dynamics through a well-documented series of feedbacks (Scott and Binkley 1997; Ollinger et al. 2002b; Satti et al. 2003). Senescent foliage with greater lignin:N ratios limits N availability in soils, decreasing microbial activity and total soil respiration. In an additional stepwise regression using residuals

from the Lloyd and Taylor function, which accounts for the non-linearity of soil temperature change with soil CO_2 efflux, N mineralization, and LAI became significant predictors of soil respiration. Together these factors show an inverse relationship between instantaneous soil flux and site quality. Results do support findings from other studies that conclude substrate quality is important in deriving accurate annual soil fluxes (Davidson et al. 2006), but cannot not be used quantitatively until the sample size of N mineralization is increased and similar trends are found across all plots.

Litterfall

Although the mean fine litterfall value of 108 g C m^{-2} y^{-1} ± 32 was somewhat lower than production reported for similar sites in Maine, New Hampshire and Massachusetts, which ranged from 158 g C m^{-2} y^{-1} to 219 g C m^{-2} y^{-1} (Davidson et al. 2002a; Fahey et al. 2005), the range was complimentary to foliar production measured at BEF by Ollinger and Smith (2005). Because Bartlett has a wide variation in species composition across its landscape, and dispersed plots were designed to specifically capture that variability, lower values are likely a result of the greater number of upper-elevation evergreens in the BEF estimates. Although it is estimated that only 10% of litter comes down in winter and spring months, obtaining a full year of litter collections would increase our confidence in estimating TBCA.

Because coarse litter is often collected either with leaf litter or as part of coarse woody debris, few estimates that are comparable to the measurements made for this study are available in the literature. Fahey et al. (2005) provided an estimate of 15 g C m^{-2} y^{-1}, but indicated that precision of this estimate is low, based on the twofold difference found in values over a six-year collection period. The coarse litter production range for tower plots showed equally high variability (7 g C m^{-2} y^{-1} to 57 g C m^{-2} y^{-1})

between plots over a one-year collection. Although high spatial and temporal variability is an expected characteristic of this carbon flux, it is still a component of total carbon input that needs to be considered in TBCA, regardless of its annual uncertainty.

Annual Soil Respiration in Relation to Ecosystem Variables

Elevation

A correlation between annual soil respiration and elevation as reported here was also seen by Fahey et al. (2005) at the Hubbard Brook Experimental Forest. However, the authors note that this relationship may not be indicative of a simple pattern. Many factors change with increasing elevation including: decreased air and soil temperatures, increased precipitation, possible changes in soil type, prevalence of rock fragments and ledges, changes in vegetation composition and thus litter quality and nutrient cycling. From our results we cannot conclude which variables play the most important role in the observed elevational trends.

Nitrogen Mineralization

N mineralization is the conversion of N from organic to inorganic forms, making it available for plant uptake, and annual net N mineralization is the largest component of belowground nitrogen cycling. N mineralization is of particular interest to this study because the coupling of belowground carbon and nitrogen cycling has not previously been investigated. Results showed a strong negative correlation of N mineralization to annual soil respiration across the dispersed plots at Bartlett, the opposite of what might be expected based on other ecosystem factors (Figure 9). Previous studies have shown that, N mineralization can decline with increasing elevation, decreasing temperatures, and on N-poor sites (determined mainly by specific species litter quality) (Knoepp & Swank 1998; Knoepp & Swank 2002). However, Knoepp and Swank (1998) and Bonito et al. (2003) found that in the Southern Appalachian Mountains the greatest N

mineralization rates were at high elevation sites. In both studies, northern hardwoods dominated the high elevation plots, and high N cycling rates could be explained by large total nitrogen pools. At BEF, N mineralization rates were also high at high elevations (Figure 13), but vegetative composition between plots is very different. Differences in species composition typically mean differences in nitrogen pool size and thus, N cycling rates. Two plots are dominated by sugar maple-beech, which should have large N pools based on their high foliar N concentrations and low lignin:N ratios and the three additional high elevation plots are comprised mainly of red spruce. Red spruce, have low foliar nutrient concentrations which should cause high nutrient use efficiency not allowing for much N to accumulate in soils to be cycled (Binkley & Giardina 1998). This dichotomy between species type and N pool size prevents a clear understanding of why N mineralization increased with elevation at the Bartlett site. In this study, a direct effect of temperature could not have contributed to N mineralization patterns because annual values were based on laboratory incubations where temperature was held constant.

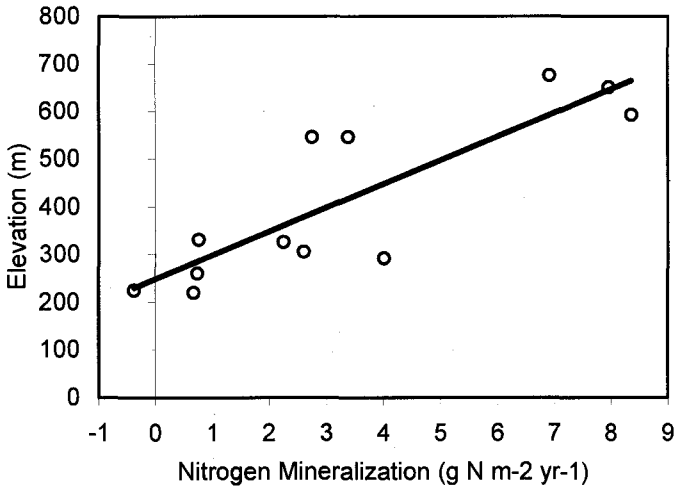

Figure 13. Relationship between plot elevation and nitrogen mineralization (g N m-2 yr-1).

Comparison of N mineralization and lignin:nitrogen ratios typically show a non-linear negative relationship across a range of species (Scott & Binkley 1997; Ollinger et al. 2002b). Results in this study show no trend between mineralization and the ratio (Figure 14). Lignin:N ratios ranged from 9 to 25 with a mean of 13 ± 4 almost identical to those found across the White Mountains (Ollinger et al. 2002b). Lignin:nitrogen ratio patterns were also typical of what might be expected; high on plots where red spruce is the dominant species, and low on plots comprised largely of northern hardwoods. Plots where hemlock is dominant or high amounts of white pine are present have intermediate lignin:nitrogen values. However, when net N mineralization rates from this study (-4 to 84 kg N $ha^{-1}yr^{-1}$) are compared to those previously measured for the greater White Mountains region, values reported here only capture the lower half of the range (32 to 162 kg N ha^{-1} yr^{-1}) reported by Ollinger et al. (2002b). Overall, N mineralization results thus cannot be explained by temperature, elevation, species composition or litter quality independently.

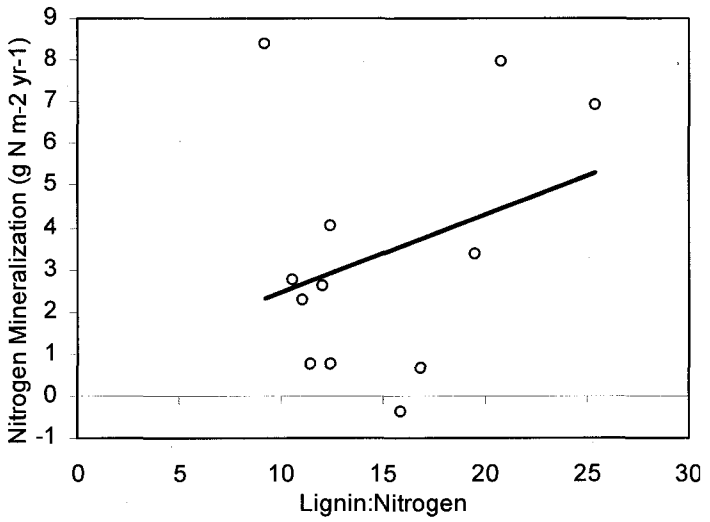

Figure 14. Nitrogen mineralization (g N m-2 yr-1) on a gradient of lignin:nitrogen ratios.

The absence of clear trends in N mineralization at Bartlett further confounds the fact that soil respiration decreases with increases in N mineralization. However, there are two major factors that may explain this trend, but only when considered simultaneously. First is the dichotomy of respiration and N mineralization rates on high litter quality versus low litter quality sites. On high quality sites, organic matter pools are small and litter is quickly decomposed leading to high rates of CO_2 efflux. Low quality sites on the other hand can have a much greater mass of organic matter. As a result, although decomposition and N cycling per unit organic matter can be slow, total C and N transformation rates per unit area can still be high. The second factor relates to allocation theory. When nitrogen mineralization rates are high, a lower investment in roots may be required to obtain those nutrients, shifting a greater amount of carbon toward aboveground tissues and away from belowground tissues. The significant relationship between soil respiration and annual net N mineralization across dispersed plots suggests a coupling of belowground C and N cycling at spatial scales greater than the individual plot level. Although it is not surprising that belowground nutrient cycles appear to be correlated, these relationships have not been previously explored. Further validation of these results both at Bartlett and at other sites is required before strong conclusions can be reached regarding how soil carbon dynamics change as a function of nutrient availability and site quality.

Vegetation Type

Previous analyses of the effect of vegetation type on soil respiration yielded inconsistent results. A review by Raich and Tufekcioglu (2000) found significant differences in soil respiration between coniferous and broad-leaved forests, while Martin and Bolstad (2005) found the influence of vegetation type on soil respiration to be less than other site or stand characteristics across a relatively homogeneous set of site

conditions. An earlier study by Raich and Potter (1995) showed no difference in soil CO_2 fluxes across a variety of vegetation types.

In the present study, no distinct difference in mean soil respiration rates were observed between plots that are dominantly deciduous versus those that are coniferous. The hemlock and pine plots of lower elevations have respiration rates similar to beech plots at low elevations. Similarly, sugar maple-beech plots at upper elevation sites showed patterns similar to the upper elevation red spruce plots. Given that annual soil respiration by plot is based on its relationship to soil temperature, within which elevation is imbedded, the influence of vegetation on CO_2 flux may be obscured.

Foliar Chemistry

Although there appears to be a negative relationship between soil respiration and lignin, cellulose and lig:N ratios across all plots, the trend is artificially created due to the grouping of high elevation plots at low respiration rates and low elevation plots at high respiration rates. Low elevation plots regardless of plot set (e.g. tower or dispersed) showed no trend between soil respiration and foliar concentrations of lignin, cellulose or lig:N. High elevation plots, which consistently had lower respiration also showed no trend in these foliar components. Foliar N also showed no clear trend, but as suggested in the results a non-linear relationship with soil respiration seems to be present. Foliar chemistry varies expectedly by vegetation type and environmental conditions, so it is our lack of understanding about soil respiration by elevation that prevents further understanding of the overall pattern at Bartlett. As mentioned earlier additional plots at mid-latitudes would allow us to assess if any relationship does between foliar chemical components and soil respiration.

Aboveground production

Annual litterfall has been found to be strongly correlated to soil respiration at global scales (Nadelhoffer & Raich 1989; Davidson et al. 2002a; Hibbard et al. 2005),

but the relationship breaks down at local scales where micro-site variability plays a larger role in determining respiration rates across the same gradient in annual litterfall (Giardina & Ryan 2002; Davidson et al. 2002a). Not surprisingly, the latter was also true at Bartlett; across all plots litterfall showed no relationship to soil respiration. Despite a lack of trend in litterfall production alone, ANPP had a positive trend with CO_2 flux across dispersed plots. However, when tower plots were included the relationship was obscured because alone, tower plots showed a weak but significant negative trend with soil respiration. It is possible that this relationship with ANPP may change as ANPP can be averaged across years, as was the case for dispersed plots because growth in one year may not be representative of typical growth for a particular plot.

Aboveground biomass

AGB explained some variation in soil respiration, resembling patterns found by Campbell et al. (2004), even though biomass is typically a poor predictor of both carbon flux and partitioning (Reichstein et al. 2003; Litton et al. *In Review*). Significant relationships between AGB and soil respiration were only seen in plots at low elevations. Exclusion of plots at high elevations to achieve such a relationship limits the use of that relationship to predict soil respiration over the greater landscape.

Leaf Area Index

LAI, which has been related to patterns of soil respiration across a variety of sites in Europe and North America (Reichstein et al. 2003), was strongly correlated with soil respiration across dispersed plots at BEF (Table 4). LAI is a common parameter in remote sensing, used to predict both net and gross primary productivity. Its relationship here to soil respiration suggests the possibility of remote estimation of CO_2 efflux across the broader landscape. However, in at least one other study, LAI was not correlated to respiration (Campbell et al. 2004), and, in general, the relationship is not as direct or stable as with primary production (Reichstein et al. 2003).

Multiple Variables

Although it is important to understand how individual ecosystem variables vary along a gradient in soil respiration, soil fluxes are undoubtedly influenced by any number of variables at the same time. Across all plots foliar N and the lignin:N ratio explain more than half of the variance in total soil respiration. Dispersed plots showed that in combination, AGB, LAI, N mineralization and foliar N accounted for nearly all of the variance in annual soil respiration. As we evaluate how soil respiration really changes at the landscape scale knowing which combination of variables explains CO_2 flux becomes indispensable. Some of these variables have been used in hyperspectral remote sensing studies (Zagolski et al. 1996; Ollinger et al. 2002b; Ollinger & Smith 2005) and others are often included in ecosystem models.

Relationships and influences on TBCA

Our results for TBCA are within the range of values found globally for mature forests by Davidson et al. (2002a), but cover a narrower range. Mean TBCA for our site was 657 g C m^{-2} yr^{-1}, higher than the mean estimate for Hubbard Brook by Fahey et al. (2005). Raich and Nadelhoffer (1989) and Davidson et al. (2002a) generally found that TBCA is roughly twice that of C inputs from litterfall, but potentially more if litterfall values were low. They also state that, because only fine litter is used for aboveground detritus inputs, TBCA is likely to be overestimated by Equation 7. At BEF, belowground allocation ranged from 3 to 10 times greater than litterfall even though litterfall included both fine and coarse fractions. This indicates the strong role of soil respiration at BEF, where estimated CO_2 fluxes are proportionately larger for all plots than measured litterfall (similar to findings by Litton et al. 2004a) (Table 4).

The decrease of TBCA with an increase in litterfall is contrary to results found at the global scale as cited by (Raich and Nadelhoffer 1989). However, studies that

address allocation theory as it applies to nutrient dynamics (Haynes & Gower 1995; Giardina et al. 2003) may offer an explanation for this trend. Regardless of the contrary results, as long as the trend in litterfall with TBCA can be explained we have confidence that the use of soil respiration and litterfall inputs does lead to a relatively accurate estimation of TBCA at regional and local scales.

Raich and Nadelhoffer (1989) found the ratio of TBCA to aboveground litterfall along a litterfall gradient declined steeply at low litterfall values, but leveled off as litterfall production increased. They also suggested, that because few data were available, values at the low end of the litterfall gradient are highly uncertain. BEF showed a similar pattern of steep declines in the TBCA:litterfall ratio, and uncertainty is likely at the lowest of litterfall values, but TBCA:litterfall ratios did not become constant across the range of high litter production even though values were similar to those found globally.

Several factors could contribute to the difference between total belowground carbon allocation at Bartlett and that reported in a global study by Raich and Nadelhoffer (1989). Raich and Nadelhoffer (1989) state that their equation can only be used in forests where steady state assumptions have been met. Although the plots used in this study are all over 65 years old and lack significant recent disturbance, it is possible that our results differ because the soils are not in steady state, i.e. the forest floor is accumulating, soil erosion is prevalent, or leaching of dissolved organic carbon (DOC) from soil organic matter (SOM) are significant.

Another possible cause for discrepancy is the use of only 1 year of litterfall collections on each set of plots and only 2 seasons of soil respiration measurements. Davidson et al. (2002a) state that interannual variation in both soil carbon inputs and exports could highly affect estimates of total belowground carbon allocation even if ecosystems are at steady state on decadal scales. Year to year differences in foliar production due to climate or herbivory and variations in soil respiration based on

changes to global or local weather patterns (altering soil temperature and moisture) will cause root allocation to vary simultaneously. The best way to overcome this is to continue data collection so averages can be made over several years, reducing the bias of an abnormal year. A third possible reason for differences in TBCA at Bartlett may simply be the lack of trend between soil respiration and litterfall as the scale is reduced from global to local levels (as discussed by Davidson et al. 2002a). If micro-site variability becomes a greater factor in determining soil respiration at finer scales, but litterfall production rates remain the same across plots, TBCA values are ultimately driven by these micro-site factors.

CHAPTER V

CONCLUSION

Many variables were considered in this analysis, but only a few were found to improve our ability to predict belowground carbon cycling at the Bartlett Experimental Forest. The relationship between soil respiration and nitrogen mineralization suggests that C and N cycle together in a pattern that extends across plots. It may also be possible to predict soil respiration not only across plots, but also across the landscape by combining the positive soil respiration-LAI relationship with remote sensing. Another important finding was that although the carbon balance approach gave relatively good estimates of total belowground carbon allocation, relationships between TBCA and litterfall might not follow patterns found at the global scale.

Several more years of litterfall collection will decrease variability in branchfall while continued soil respiration measurements will increase certainty about 2005 October and November anomalies. By accounting for interannual variability in major carbon fluxes, estimation of belowground carbon allocation will be substantially improved (Davidson et al. 2002a). Linking these components to current knowledge of aboveground biomass and productivity (Ollinger & Smith 2005), eddy flux tower measurements, and future belowground work on roots and soil carbon stocks will provide a comprehensive ecosystem carbon budget as described by the NACP.

While our estimates of individual carbon pools and fluxes were similar to previous studies, relationships to other ecosystem characteristics such as ANPP, AGB, litter quality, and N cycling, were variable. Additional plots covering gaps in elevation, species composition and foliar chemical content will allow greater assessment of trends

from this study that were either weak or non-existent. Soil respiration and TBCA relationships to other ecosystem parameters largely confirm that patterns in flux and partitioning at individual sites do not always coincide with those found across sites (Litton et al. *In Review*). However, changes in resources (e.g. LAI, N mineralization, foliar chemistry) at the local level may possibly be used in remote sensing studies to map soil carbon fluxes over the landscape.

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