Controls on Carbon Uptake and Storage in Southeastern Forests

by

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University Program in Ecology
Duke University

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University Program in Ecology in the Graduate School of Duke University

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ABSTRACT

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Abstract

Uptake and storage of carbon by forest ecosystems continues to be a major research topic needed for the quantification of global budgets in an increasing atmospheric carbon dioxide environment. However, there are considerable challenges in quantifying carbon budgets of forest across a wide range of spatial and temporal scales. Although general trends in the components of carbon budgets emerge when analyzed over large spatial or temporal scales, these relationships tend to weaken, or even reverse, at smaller spatial (e.g. stand level) and temporal scales. On the other hand, continuous measuring and monitoring is not a feasible or sensible approach for the range of global forests. There is growing need to identify the key variables that drive variability in these localized budgets at multiple time scales. These results will assist in upscaling stand-level observations into large-scale modeling approaches.

Forest carbon dynamics are closely-coupled with the hydrologic cycle, so an approach that attempts to bridge these dynamics must incorporate water availability and use. Water is necessary for trees to transport nutrients, maintain cellular function, and regulate stomatal conductance; however, water is also related to other biological processes, including microbial decomposition of soil carbon, and physiologically-important abiotic factors, such as atmospheric vapor pressure deficit. Thus, much of the key to understanding the variability in forest carbon cycles is identifying the sensitivity of the processes of the carbon cycle to water availability.

Therefore, my research takes the following approach: I begin by using sap flux sensors to measure tree-level transpiration over a four-year period and combine these values with other estimates of stand-level evaporation to generate an accurate estimate of total evapotranspiration, partitioned by component and tree species (Chapter 2). To
assess the sensitivity of the water fluxes in the forest, I next establish a complete hydrologic budget for the forest stand over four years, including one severe and one mild drought (Chapter 3). I then focus on the flux of carbon from the soil and its variability over space and time. Using automated, high-frequency measurements of soil CO$_2$ flux over a 10-year period and including 3 forest stands, I assess inter- and intra-stand variability as well as inter- and intra-annual variability in soil flux in relation to climatic factors and stand characteristics representing productivity (Chapter 4). In order to assess how soil CO$_2$ flux may change over longer periods of time within the context of global change, I analyze how enrichment of [CO$_2$] independent of and combined with soil nitrogen availability alter the balance of carbon in a stand (Chapter 5). Finally, building off these previous chapters, I examine the relationship between carbon uptake, allocation, and turnover in a mixed-species forest experiencing interannual variability in water availability (Chapter 6).

I conclude that (Chapter 2) sap flux sensors can successfully be used to estimate tree- to stand-level transpiration if one accounts for both nocturnal water movement through the tree stem and spatial variability of species composition and demography within a stand. (Chapter 3) Despite reductions in transpiration by some species during water-limited (i.e. drought) periods, the magnitude and duration of these reductions results in annual water use that is similar to a non-drought year. The consequence of this invariability in transpiration and evapotranspiration for the hydrologic cycle is that changes in annual precipitation translate directly to changes in water supplied to rivers and streams. (Chapter 4) Diurnal to seasonal variability in soil CO$_2$ flux is driven by temperature, whereas interannual variability is most-strongly influenced by soil moisture. Furthermore, spatial variability of soil CO$_2$ flux is directly related to forest

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productivity, and by proxy, leaf production, across biomes and, to a lesser extent, across stands within a region. However, within-stand variability may be inversely related to leaf production as a result of differential allocation of carbon between aboveground and belowground uses based on local resource availability. (Chapter 5) Although elevated atmospheric [CO$_2$] enhances productivity, it may only result in a small increase in the flux of CO$_2$ from soils. Instead, nitrogen availability explains much of the variability within a forest stand, regardless of [CO$_2$], with increasing nitrogen availability resulting in lower allocation of carbon belowground and greater aboveground productivity. (Chapter 6) Interannual variability in water availability can affect gross primary productivity in mature forests but these effects may primarily affect the following growing season. The proportionate changes in gross primary productivity appears to show greater reductions with previous year's soil moisture than net primary productivity, leading to increased carbon use efficiency following drought. Variability in leaf biomass in this relatively stable, mature stand appears to drive the interannual variability in photosynthesis as well as the demand for carbon used for biomass production and metabolic activity.
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1. Introduction

The amount of carbon fixed by photosynthesis and partitioned to biomass is a critical aspect of estimating uptake and storage of carbon in forest ecosystems. Predicting carbon accumulation in the form of plant biomass, also known as net primary productivity (NPP), has long been of great importance to foresters managing timber yield for forest products and more recently in the context of storage and potential sequestration of atmospheric CO$_2$. Through extensive research, much is known about the processes influencing NPP; however, gaps in knowledge remain, particularly with regard to accurately accounting for the variability of NPP over a wide range of stands given local variability in species composition and resources and within the context of global change.

Improving understanding in this area is necessary for resolving discrepancies in large-scale terrestrial carbon estimates (Houghton 2003), particularly for dynamic global vegetation models (DGVMs) which use plant physiological parameters and stand biomass estimates in conjunction with climatological data from general circulation models (GCMs) to estimate long-term carbon uptake (Cramer et al. 2001). DGVMs depend upon simple models for estimating NPP across a range of vegetation types, but assume that all vegetation cover can be categorized as one of relatively few plant functional types (PFTs). While DGVMs provide powerful tools in forecasting potential responses to climate change, they are all dependent upon reliable estimates of NPP. Thus, there is great importance in establishing a model for estimating NPP that is applicable across a range of vegetation types, but employs a small number of parameters and the appropriate environmental drivers.

Estimating NPP based primarily on environmental variables may pose additional challenges. NPP is the difference between carbon gains (gross primary
productivity, GPP) and losses (autotrophic respiration $R_A$) and these inputs and outputs respond differently to environmental conditions. Although some respiration is closely coupled with GPP at short time scales (Johnsen et al., 2007; Högberg et al., 2007; Mencuccini and Hölttä, 2010), other respiratory fluxes associated with biomass construction may be highly seasonal and out of phase with GPP (Arneth et al., 1998). The result is that although a wide variety of forest stands have a similar proportion of NPP:GPP (Waring et al., 1998), there is considerable variability among stands (DeLucia et al., 2007) and across fertility gradients (Vicca et al., 2012). Additionally, growth in a given year may be dependent on the previous year’s conditions (Arneth et al., 1998; Zweifel et al., 2006), so environmental drivers may be temporally decoupled from observed NPP. Given these challenges, as well as the uncertainties involved with measuring NPP directly, an alternative approach is to estimate NPP as the difference between independent estimates of GPP and NPP. Although neither of these fluxes can be measured directly, they are based on well-established principals that allow for increasingly-reliable estimates to be made.

Therefore, my research combines NPP estimates from biometric data with estimated GPP and respiration at the plant and ecosystem ($R_{eco}$) level to attempt to identify the underlying processes that affect these fluxes. In chapters 2 and 3, I focus on one of the major environmental drivers that influences both GPP and $R_A$, precipitation and subsequently, water availability. During seasonal drought, water limitations have been shown to cause stomatal closure (Oren et al. 1998; Schafer et al., 2002), which should result in reductions in GPP. However, I focus on a mature hardwood stand that shows both tree-level reductions in water use (Pataki and Oren, 2003) but generally conservative total evapotranspiration (Stoy et al., 2006). Thus, the sensitivity of GPP to drought in this type of system is uncertain. In order to accomplish this analysis, I begin
by examining the hydrologic budget of the ecosystem in order to estimate the transpiration by individual trees and species and test their sensitivities to drought. As a component of this approach, I also examine the implications for forest water use, in the form of evapotranspiration, and its consequence to water supply to downstream users.

I then focus on the major source of respired CO$_2$ at the ecosystem level, soil CO$_2$ flux ($F_{soil}$). $F_{soil}$ shows strong sensitivity to temperature and soil moisture (Fang and Moncrieff, 2001; Davidson and Janssens, 2006) so I begin by examining how these environmental variables affect temporal variability. However, $F_{soil}$ includes not only $R_A$ from roots, but also heterotrophic respiration ($R_{hi}$) and has been shown to be related to recently assimilated carbon at time scales ranging from 1-5 days (Johnsen et al., 2007; Högberg et al., 2007; Mencuccini and Hölttä, 2010) and leaf production (as leaf litterfall; Davidson et al., 2002; Palmroth et al., 2005). Since respiration represents a cost that detracts from potential NPP, my research aims to identify what factors lead to potential tradeoffs between $F_{soil}$ and NPP, particularly with respect to aboveground NPP (Palmroth et al., 2006). In chapter 4, I utilize high-frequency $F_{soil}$ measurements taken across several forest stands over a 10-year period to analyze the sources of spatial and temporal variability. Next, in chapter 5, I focus within one stand on the effects of elevated atmospheric [CO$_2$] and nitrogen availability, both native and with fertilization, to examine how $F_{soil}$ varies with resource availability.

Finally, in chapter 6, I synthesize stand characteristic data and species-specific transpiration estimates from the first two chapters to drive a photosynthesis model used to estimate GPP over four years, including a severe and a moderate drought. These results are combined with $F_{soil}$ data from chapter 4 and estimates of other $R_A$ components to examine the interannual variability of carbon use efficiency and water use efficiency this forest.
2. Estimating components of forest evapotranspiration: A footprint approach for scaling sap flux measurements

2.1 Introduction

Stand-level water vapor fluxes are now monitored across many ecosystems with eddy covariance systems, providing continuous, long-term measurements of latent heat flux (LE); however, this approach does not quantify the individual components of evapotranspiration: interception of precipitation during rain events ($I_C$), evaporation from the soil and forest floor ($E_S$), and transpiration ($E_T$). (See Table 2.1 for a full list of abbreviations.) Quantifying these components is an essential step in assessing and modeling the processes controlling these physiological and ecosystem fluxes. A common approach for estimating $E_T$ is the scaling of sap flux density ($J_s$) measured with the popular thermal dissipation probes (Granier, 1987; Oren et al., 1998b). Correct applications of these probes can provide reliable estimates of species-specific transpiration at the stand level (Clearwater et al., 1998; Ford et al., 2007; Lu et al., 2004; Oren et al., 1998b; Phillips et al., 1996; Williams et al., 2004).

Although some studies have found good agreement between component-based estimates of evapotranspiration ($ET_s$), including sap flux-based $E_T$, and LE (Arneth et al., 1996; Granier, 1987; Granier et al., 2000; Köstner et al., 1992), others have found that thermal dissipation probes may underestimate high flux rates, generally leading to $ET_s$ that is lower than LE (Bovard et al., 2005; Hogg et al., 1997; Schäfer et al., 2002; Wilson et al., 2001). This discrepancy may be the result of three methodological challenges: (1) improper processing of the sap flux sensor output, including failure to account for non-zero nocturnal water uptake, (2) failing to scale sap flux measurements to a similar
footprint as the LE measurements, and (3) failing to accurately quantify all components of evapotranspiration when comparing ET$_S$ to LE.

Some recent research has focused on (1), demonstrating that accurate stand-level hydrologic budgets must account for nocturnal sap flux, used either to recharge storage (Daley and Phillips, 2006; Köstner et al., 1992; Meinzer et al., 2001; Phillips et al., 1996) or to provide for water loss from leaves maintaining finite stomatal conductance at night (Daley and Phillips, 2006; Dawson et al., 2007; Oren et al., 1999). There is some evidence that nocturnal sap flow observed in data from heat pulse velocity sensors may have been missed in data from thermal dissipation sensors (Hogg et al., 1997), possibly because of incorrect signal processing (Lu et al., 2004). In order to process data from thermal dissipation sensors, Lu et al. (2004) pointed out that the baseline connecting points where zero flux occurs ($\Delta T_{\text{max}}$, see Eq. (3) in Section 2) must be dynamic, reflecting changes in sapwood moisture content, and might not be reached every night. Mischaracterizing this baseline not only results in missed nocturnal water uptake, but also translates to a large underestimate of daytime transpiration.

The second methodological challenge, scaling to the appropriate footprint, requires that probes are installed properly in sapwood (Clearwater et al., 1998), whole-tree transpiration estimates account for radial variability in flow for a sufficient number of sample trees (Ford et al., 2004; Phillips et al., 1996), and species-specific sapwood area within the reference footprint is characterized accurately (Wullschleger et al., 2001). Finally, because other evaporative fluxes may contribute to nearly half of evapotranspiration (Table 2.2), any comparison of ET$_S$ and LE requires reliable estimates of $E_S$ and $I_C$, yet $E_S$ is not often measured directly and is difficult to model (Wilson et al., 2000).
Here, we investigate the relative contributions of the first two methodological challenges to the discrepancy between component-based and eddy covariance-based ET estimates, after carefully quantifying the evaporation components of ET$_S$. We developed estimates of evapotranspiration in a mature oak-hickory forest in the southeastern U.S. over a 4-year period (2002–2005), which included both a severe drought year and a very wet year. Tree-level sap flux was monitored with thermal dissipation probes, corrected for nighttime fluxes, and scaled to the stand level, accounting for radial patterns, tree size, and species distribution within the eddy covariance footprint and subplots therein, allowing us to separate the effects of signal processing from scaling. Sap flux-scaled transpiration was combined with measured and modeled evaporative losses ($I_c$ and $E_s$, respectively), thus accounting for all components of evapotranspiration (ET$_S$), to permit a proper comparison with LE measurements.

2.2 Materials and Methods

2.2.1 Setting

The study was conducted at the Duke Forest Ameriflux Hardwood site, Orange County, North Carolina (36°58’41.430”N, 79°05’39.087”W). The forest stand is comprised of mixed hardwood species with a maximum age of ca. 80–100 years. Mean canopy height is 25 m with emergent crown tops extending above 35 m. The stand is dominated by hickories (Carya tomentosa (Poir.) Nutt., C. glabra (P. Mill.) Sweet.), yellow poplar (Liriodendron tulipifera L.), sweetgum (Liquidambar styraciflua L.), and oaks (Quercus alba L., Q. michauxii Nutt., Q. phellos L.). Other species that contribute to the mid- and understory include Carpinus caroliniana Walt., Ostrya virginiana (P. Mill.) K. Koch., Ulmus sp., Cornus florida L., and Cercis canadensis L. Coniferous species including Pinus taeda L. and Juniperus virginiana L. make up a minor component of the over-and understory, respectively.
Long-term (115-year) mean annual precipitation for the area is 1146 (±166) mm, with 630 (±133) mm occurring between April and September (www.ncdc.noaa.gov/). The soil is an Iredell gravely loam and topography is relatively flat with <4% slope. The upper 35 cm is a clay loam with a porosity of 0.54 m$^3$ m$^{-3}$. A clay pan with low hydraulic conductivity limits the majority of the rooting zone to approximately 35 cm (Oren et al., 1998a). Soil depth can be as deep as 2 m (Richter, personal communication), which overlays bedrock. The site has been the subject of a previous investigation on the transpiration of several canopy and sub-canopy species (Pataki and Oren, 2003).

1.1.2 Monitoring design and biometric measurements

An area of approximately 6.25 ha around the AmeriFlux tower (represented by LAI shading in Fig. 2.1) was identified for this study because it included most of the dynamic flux footprint (Stoy et al., 2006), estimated using the semi-empirical model of Hsieh et al. (2000). Within this area, two 25 m-radius plots were established for the sap flux study. These two circular plots, henceforth the ‘sap flux plots’, were chosen to represent a wet (to the west) and a dry micro-site. Species and diameter at breast height (1.45 m aboveground; DBH), down to a minimum diameter of 40 mm, were recorded in the two sap flux plots, and in an entire hectare surrounding the tower (henceforth the ‘hectare plot’). Bark thickness ($T_B$) was measured on several trees and estimated for each individual using the best fit (linear or exponential) with DBH for each species or genus (Table 2.3). Cross-sectional sapwood area for individual trees ($A_{sj}$) was estimated from tree cores of sapwood depth ($T_{sw}$) taken at the site, using the equation:

$$A_{sj} = \pi \left( \frac{DBH}{2} - T_B \right)^2 - \pi \left( \frac{DBH}{2} - T_B - T_{sw} \right)^2$$

Eq. 1

where DBH, $T_B$ and SW are in cm. A generalized estimation of $A_{sj}$ for each species was developed using:
\[ A_{sj} = a \times \text{DBH}^b \]  \hspace{1cm} \text{Eq. 2}

where \( a \) and \( b \) are empirical parameters (Table 2.3).

Leaf litter was collected in 48 baskets, each with an area of 0.5 m\(^2\). Eight baskets were positioned in a circular arrangement, 15 m from the tower in primary and secondary compass directions. Beyond this 15 m circle, in the S, SW, and W directions, seven baskets were placed at 30 m intervals along transects (Fig. 2.1), sampling the area most commonly within the tower’s footprint (Geron et al., 1997; Stoy et al., 2006). Each sap flux plot also contained 10 baskets, with the second basket along the westward transect doubling as 1 of the 10 in the western plot. Leaves were collected as often as every 2 weeks when litterfall was heaviest, and sorted by species. One-sided surface area of 20-leaf sub-samples of each species was measured using a Digital Image Analysis System (DIAS, Decagon Devices, Inc., Pullman, WA, USA), and the weight of each leaf was obtained after drying (70°C for 48 h). A specific leaf area (SLA) of each species was estimated using a linear regression of leaf surface area versus mass with a zero-intercept (p < 0.001, Table 4). Leaf area index (LAI) was estimated by multiplying SLA for each species by the total mass of leaves for that species after similar drying (Table 2.4).

2.2.2 Environmental Measurements

Air temperature (\( T_a \)) and relative humidity (RH) were measured at two-thirds canopy height using HMP35C \( T_a / \text{RH} \) probes (Campbell Scientific, Logan, UT, USA) and were used to calculate vapor pressure deficit (\( D \)). Photosynthetically active radiation (PAR) and net radiation were measured above the canopy at 42 m (see Stoy et al., 2006). Precipitation (\( P \)) was measured daily with a rain gauge and partitioned over half-hourly values using data from tipping buckets (TR-525USW, Texas Electronics, Dallas, TX, USA) positioned at the Duke FACE site, <1 km away. Throughfall (\( P_T \)) was measured with 6 rain gauges on the forest floor, manually collected once or twice per week.
Soil moisture ($\theta$, m$^3$ m$^{-3}$) was measured with 12 ThetaProbe sensors (Delta-T Devices, Cambridge, UK), four in each of the wet and dry sap flux plots and four next to the eddy covariance tower; at each location two were installed at 5–10 cm depth and two at 20–25 cm. Data were filtered for unrealistic spikes after rain events. Missing data, due to power outages in one of the plots or sensor failure, were gap-filled using the best linear regressions with other working sensors. The regressions were comprised of data on both sides of the gap, equal to the length of the gap in each direction. Periods where $\theta$ reached saturation (0.54 m$^3$ m$^{-3}$) or the hygroscopic minimum (0.125 m$^3$ m$^{-3}$) were identified and the recorded u values for each sensor were rescaled to match these values (Schäfer et al., 2002).

2.2.3 Sap flux measurement

Granier-type, heat dissipation sensors were used to monitor $J_s$ (Granier, 1987). Each pair of sensors was 20mm in length and the heated element received a constant power of 0.2 W. Five *L. tulipifera* and *L. styraciflua* were equipped in each plot. In addition, five *C. tomentosa* and *Q. alba* were equipped in the dry sap flux plot, and five *Q. michauxii* and *Q. phellos* in the wet plot. These species were selected because they comprised the majority of sapwood area at the site, and because fluxes monitored on several other species in this and a nearby site were similar for a given xylem type (i.e. within ring- or diffuse-porous groups; Oren and Pataki, 2001; Pataki and Oren, 2003; Wullschleger et al., 2001). To quantify the radial profile of sap flux density, sensors were installed at 20-mm depth intervals based on the expected sapwood depth. Tree DBH and sensor depths are listed in Table 2.5.

Sap flux sensors measure the temperature differential ($\Delta T$) between the paired heated and unheated probes. $\Delta T$ (recorded in mV) for each sensor pair was measured at 30 s intervals and 30 min averages were stored on a CR23X datalogger (Campbell
Scientific, Logan, UT, USA). To convert these data into water flux, the following equation is used:

\[ J_S = 119 \times \left( \frac{\Delta T_{\text{max}}}{\Delta T} - 1 \right)^{1.23} \quad \text{Eq. 3} \]

Where \( \Delta T_{\text{max}} \) is the maximum temperature differential at which sap flux is zero (Granier, 1987). In generating sap flux estimates, we accounted for sensor contact with poorly conductive xylem; sap flux is underestimated if a portion of the sensor is in contact with heartwood (Lu et al., 2004). Although corrections were made to account for flux underestimation by sensors so positioned (Clearwater et al., 1998), the exact proportion of a particular sensor’s length that extends into non-conductive sapwood cannot be determined without a destructive harvest; with other ongoing studies at the site, determination through such harvest could not be made. Inaccurate estimates of inactive sapwood in contact with sensors can lead to large under- or over-estimates of sap flux after corrections are implemented. Thus, data were discarded if corrected fluxes were outside two standard deviations from the mean of similar sensors (species and depth) and replacement sensors were installed in new positions on the same tree. In all, 8 of the 83 sensors were partially in contact with heartwood; data from two sensors were considered unreasonable resulting in sensor replacement. Table 2.5 details the sensors that underwent corrections based on Clearwater et al. (1998) and were considered acceptable.

To account for potential nocturnal fluxes due to both transpiration and recharge, we selected the highest daily \( \Delta T \) to represent \( \Delta T_{\text{max}} \) if two conditions are satisfied simultaneously: (a) the average, minimum 2-h \( D \) is \(<0.05 \) kPa, thus assuring that water loss to the atmosphere is negligible, and (b) the standard deviation of the four highest \( \Delta T \) values is \(<0.5\% \) of the mean of these values; such stable measurement of maximum
ΔT ensures that recharge of water above the sensor height is completed or negligible. In our sap flux time series, zero-flux nighttime conditions were often not met for several consecutive days.

We developed a modified method for scaling tree-level transpiration that accommodates changes in $J_S$ with depth. Sap flux density in the outer 20 mm did not vary with tree diameter for any of the species (minimum $p > 0.60$), which allowed us to combine these data into a time series of mean $J_{Si}$ (where subscript $i$ represents an individual species) in the outer xylem. Measured daily $J_{Si}$ values from deeper sensors in each tree were normalized by the mean $J_{Si}$ of all outer sensors. These normalized values were fit to a Gaussian function, $y = \exp(-0.5(x-a/b)^2)$, where $y$ is the normalized flux and $x$ is the relative depth of the sensor’s center point in the sapwood, normalized between 0 at the cambium and 1 at the sapwood–heartwood interface (SigmaPlot 2002, version 8.02, SPSS Inc.). For species in which the peak of the curve did not occur at the edge of the sapwood–cambium interface, a maximum rate of normalized sap flux (i.e. 1) was assumed between the position of the peak and the cambium. Integrated whole-tree $J_S$ was estimated using Pappus’s second theorem for calculating the volume of a rotated geometric solid:

$$V_j = 2\pi c_j A_{Fj} \quad \text{Eq. 4}$$

where $A_{Fj}$ is the area beneath the fitted curve for an individual tree, $c_j$ is the distance from the center of that tree to the centroid of the curve, and $V_j$ is a volume that represents the effective amount of highly conductive sapwood. We can consider this volume with respect to time (cm$^3$ s$^{-1}$) in terms of a velocity (cm s$^{-1}$) multiplied by an area (cm$^2$) where the velocity is $J_S$ (cm$^3$ H$_2$O per cm$^2$ s$^{-1}$, or cm s$^{-1}$) and the area is $A_{sj}$. Thus, multiplying $V_j$ by the mean, outer-xylem $J_{Si}$ for that species yields whole-tree transpiration.
Occasional sensor failure and power outage in a particular plot produced missing data. Data before and after each gap was fitted to a power function with all functioning sensors and gap-filled using the best fit against a functioning sensor. The best fitting sensor was identified based on $r^2$, closeness to linearity (i.e. exponential parameter closest to 1), and the distribution of residuals. In all, 40% of growing season data was gap-filled.

2.2.4 Stand-level transpiration

Using allometric relationships, $A_s$ was estimated for the area covered by the two sap flux plots and the hectare plot (Table 2.3). Large differences were observed among the three estimates of $A_s$, either for a particular species or in total (Table 4), with likely effect on stand-level transpiration estimates. To allow comparison of stand-level component-based estimate of evapotranspiration with LE from the larger area representing the eddy covariance footprint, it was necessary to expand the spatial scale of our sap flux study plots.

We first established a linear relationship between species-specific LAI data from the 10 litter baskets in the hectare plot and the total $A_s$ within an optimized distance (based on $r^2$) from each basket. Combining all species from the *Carya* and *Quercus* genera produced the best fits, $A_s = 3.287 \times $LAI + 0.166 ($r^2 = 0.914; p < 0.0001$) and $A_s = 1.428 \times $LAI + 0.363 ($r^2 = 0.902; p < 0.0001$), respectively, where LAI is in m$^2$ m$^{-2}$ and $A_s$ is in cm$^2$ m$^2$ of ground area. The relationship for *L. tulipifera* was $A_s = 5.028 \times $LAI + 0.157 ($r^2 = 0.758; p = 0.0011$). No suitable relationship was found for *L. styraciflua* and for the less abundant and sub-canopy species, so the mean $A_s$ (3.43 and 2.89 cm$^2$ m$^2$, respectively) was applied over the entire site. Species-specific LAI at each of the 29 transect trap locations was converted to a spatial map for the entire stand using simple kriging (ArcGIS 9, ESRI, Redlands, CA; Fig. 2.1). Using the relationships or averages, we used
LAI to estimate $A_s$ across the entire kriged area. Inter-annual mean maximum LAI at the site was 6.3 (±0.4) m$^2$ m$^{-2}$. The two sap flux plots and the hectare plot were positioned in an area with LAI similar to the EC footprint (6.8 ±0.3 m$^2$ m$^{-2}$), yet the contribution of each species or genera varied among some of these areas. The LE footprint included areas ranging in LAI by as much as ±1.7 m$^2$ m$^{-2}$ from the mean (Fig. 2.1).

For the two sap flux plots and the hectare plot we summed whole-tree transpiration to estimate $E_C$. Across the larger domain, representing the eddy covariance flux footprint, $E_C$ was based on scaling with LAI-based $A_s$ estimate:

$$E_C = \sum_i \left( E_{Ch_i} \times \frac{A_{Si}}{A_{Sih}} \right)$$

Eq 5

where $E_{Ch_i}$ is $E_C$ for the hectare plot, $A_{Sih}$ is sapwood area for species i in the hectare plot, and $A_{Si}$ is sapwood area for the entire stand. The hectare plot was used as a basis for scaling because trees in this plot were a more complete representation of the species and range of size classes found in the larger eddy covariance footprint than the trees in the smaller sap-flux plots.

In scaling, the mean sap flux of the three monitored Quercus species was employed for unmonitored Quercus species (Q. coccinea and Q. prinus, together comprising 3% of $A_s$). Sap flux of C. tomentosa was used for unmonitored Carya species (C. glabra and C. ovata; 15% of AS). Unmonitored diffuse-porous and ring-porous genera were estimated to contribute 20% of stand $A_s$ in the eddy covariance footprint. This sapwood was partitioned between the two xylem types based on their proportions in the hectare plot (Table 4). The average sap flux of Quercus and Carya was employed to estimate transpiration of the other ring-porous genera, and that of L. styraciflua and L. tulipifera of the other diffuse-porous genera. Using the sap flux of either of the latter species alone affected stand transpiration ($E_C$) during the growing season by an average
of 2.3 (±0.08) mm, or less than 1% of total growing season transpiration, demonstrating that the EC estimate is reasonably robust to the choice of representative species.

2.2.5 Evaporation losses

Latent heat flux (LE) measured with eddy covariance (expressed in mm H$_2$O) should balance against the components of evapotranspiration such that:

\[
LE = I_C + E_S + E_C \quad \text{Eq. 6}
\]

where $I_C$ is canopy interception and $E_S$ is evaporation from the forest floor and soil surface.

LE was measured using the eddy covariance method comprising of a triaxial sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA) and an open-path infrared gas analyzer (IRGA, LI-7500, Li-Cor, Lincoln, NE, USA) positioned 39.8 m above the forest floor. Vertical wind velocity, temperature, and scalar concentrations of H$_2$O were sampled at 10 Hz and averaged for half-hour periods. For processing, density corrections, and analyses of the seasonal and dynamics of components of the energy balance including its closure, see Stoy et al. (2006). The path between transducers in the sonic anemometer or optical length in the open path IRGA may be blocked during and immediately following rain events, and correctly identifying these data ‘gaps’ is required to ensure that long-term sums are correct (Falge et al., 2001).

$I_C$ was estimated by subtracting $P_T$ from $P$ measured between collection periods. An exploratory investigation on the proportion of $P$ reaching the forest floor as stemflow was conducted over a 2-month period with varying LAI. The exploratory study was conducted on six trees representing the most abundant species and a range of sizes. The rate of stemflow, normalized by tree circumference, was unrelated to tree size ($p > 0.3$), consistent with Granier et al. (2000). When scaled to the stand, stemflow was estimated to contribute <1% of annual precipitation and was excluded from further consideration.
To convert weekly and bi-weekly $I_C$ measurement to continuous, half-hourly values, $P_T$ accumulated between measurements was distributed based on a normalized time series of $P$. For dates of missing $P_T$ measurements, estimates for each throughfall gauge were made using a linear regression with $P$ (Table 2.6). To avoid mischaracterizing interception associated with multiple, small rain events as a single, large rain event, data for these regressions were filtered to include collection periods in which only one precipitation event occurred.

$E_S$ was not measured directly. The decoupling coefficient (Jarvis and McNaughton, 1986) approaches zero in winter (Stoy et al., 2006), indicating a strong coupling between surface conductance and evaporative demand. Thus, $E_S$ was estimated using the wintertime (DOY 300–75) relationship between $D$ and LE from the eddy covariance system. We excluded data from the first 3 days after precipitation events to avoid double-counting $I_C$ and discounted the small amounts of water loss through the bark surface (available from scaled sap flux measurements) to avoid double-counting $E_C$.

We found significant ($p < 0.001$) differences between the power function in 2002 and the subsequent years (Table 2.6). This difference was possibly due to inter-annual variation in surface water availability, generated by consecutive growing season droughts in 2001 and 2002. Peak values in $E_S$ showed maximum cross-correlation with peak $D$ values at a 3-h time lag, which was incorporated into the regression to eliminate a pattern in the residuals. We tested these estimates of $E_S$ by comparing them with nighttime LE during the growing season, using non-gap-filled data and again avoiding periods after precipitation. We found no significant difference between estimated $E_S$ and measured nighttime LE ($p > 0.6$).
2.3 Results and Discussion

We focus first on methodological aspects of sap flux measurements, then analyze our procedure for scaling sap flux measurements to the canopy level and conclude by evaluating the contribution of individual components to the closure of stand-level evaporation balance. We note that high variability in intra- and inter-annual weather (Fig. 2.2) presents an opportunity to use our sap flux processing and scaling methodology over a wide range of environmental conditions.

2.3.1 Revised methodology for sap flux signal processing

The revised approach for converting sap flux data by selecting $\Delta T_{\text{max}}$ only during nights with stable $\Delta T$ and $D = 0$ kPa accounts for both the seasonal shifts of $\Delta T_{\text{max}}$ due to the hydration state of the sapwood, and the combined effects of nocturnal water loss from leaves and recharge of water above sensor height. With the revised processing in place, sap flux was frequently observed throughout nighttime hours. A representative set of diurnal courses (Fig. 2.3) illustrates a five-fold increase in nocturnal $J_s$ for all species except L. styraciflua, which increased by ~50%. Revised daytime maximum $J_s$ estimates were also higher during this sample period, showing increases of nearly 20% in L. tulipifera and Quercus spp. and nearly 35% in C. tomentosa. The smaller increase in nocturnal $J_s$ of L. styraciflua during this period did not lead to a noticeable change in daytime $J_s$. Later we discuss the effect of the increase in $J_s$ of some of the most prevalent species on stand $E_C$.

Daley and Phillips (2006) used sap flux sensors at two heights on the stem along with leaf-level gas exchange measurements to detect and partition nocturnal fluxes into recharge and conductance in three deciduous species. In their study, shade-intolerant, early-successional paper birch (Betula paprifa) exhibited the highest nocturnal fluxes, which were almost exclusively due to transpiration. Nocturnal fluxes of red oak
(Quercus rubra) and red maple (Acer rubrum), more shade-tolerant species, were used almost entirely to re-supply water to the trunk. In our study, early-successional species showed lower nighttime $J_s$ than late-successional species (early-successional L. tulipifera and L. styraciflua $J_s$ of 13.1 ±0.2 and 10.1 ±4.4 g H$_2$O m$^{-2}$ sapwood area per night, respectively, and late-successional C. tomentosa and Quercus spp. 21.6 ±5.8 and 21.7 ±4.7 g H$_2$O m$^{-2}$ sapwood area per night, respectively). Our design did not permit species-specific partitioning of these nocturnal fluxes into recharge versus transpiration; however, Dawson et al. (2007) observed nocturnal transpiration across a wide range of woody species. We did find that the large absolute differences in nocturnal $J_s$ translated to similar proportional changes in estimated total growing season $E_{Ci}$, amounting to ~11% in early-successional species and ~14% in late-successional species.

Species using nocturnal water uptake to supply transpiration more than recharge show a rapid rise in sap flux with increasing $D$ (Oren and Pataki, 2001). We found such a trend based on mean nighttime $J_s$ and $D$ after days without rainfall (data not shown). Following rain events, nocturnal sap flux exhibited much more erratic responses to $D$. And although the majority of afternoons following rains were characterized by low $D$ and low $J_{sr}$, the majority of these nights had high $J_s$ when compared to the expected flux based on the sensitivity to $D$ as observed on dry days. These large nocturnal fluxes following drought-breaking rains represent recharge of stored water progressively depleted over entire drying cycles.

During a particular drying cycle, the amount of water recharging trees at night has been shown to increase with soil moisture depletion (Phillips et al., 1996), causing recharge to account for an increasing proportion of daily transpiration (Oren et al., 1998b). In this study, average nocturnal flux was significantly higher ($p < 0.001$) when $u < 0.20$ m$^3$ m$^{-3}$, a value shown to limit stomatal conductance and transpiration in this
stand (Pataki and Oren, 2003). Thus, as soil drying intensifies during a cycle, more water is taken up each night. Our study does not permit a species-specific evaluation of whether the increased nocturnal flux with soil drying represents increasing amount of water drawn from storage each day and recharged each night, or increasing nocturnal water loss from leaves driven by increasing $D$ with the progression of drying cycles. However, we show later that, on average for the stand and over the 4-year study, nightly water uptake was used to both supply water lost from leaves and recharge the storage. Considering that the forest is composed nearly equally of shade-tolerant and shade-intolerant species, this finding is consistent with that of Daley and Phillips (2006).

### 2.3.2 Scaling sap flux measurements to the eddy covariance footprint

Sap flux density can be highly variable among individuals of a given species, necessitating a large number of replicates to attain an accurate estimate of the mean flux (Oren et al., 1998b). This is difficult to achieve in species-rich forests, where increasing replicate numbers can be achieved only by setting more plots spaced further apart, each requiring power and a full complement of environmental sensors to capture the spatial variability in conditions. Kumagai et al. (2005) recommended monitoring a minimum of six trees to account for random variation. We were able to position our dataloggers such that five individuals of each species in each plot were monitored. Furthermore we found that neither *L. tulipifera* nor *L. styraciflua*, the two species sampled in both the wet and dry plots, showed plot-level differences in daily $J_{si} (p > 0.1)$, allowing to pool the individuals of each species (thus producing $n = 10$). Similarly, the three monitored *Quercus* species showed similar daily $J_{si} (p > 0.1)$ allowing us to pool the individuals of this genus ($n = 15$). This left only *C. tomentosa* ($n = 5$) with less than the minimum recommended sample size.
Radial patterns in flux were assessed based on sensors installed at different depths. Radial sap flux trends for ring-porous and diffuse-porous species were consistent with some but not all studies (Phillips et al., 1996; Wullschleger and Norby, 2001). The $J_{Si}$ pattern in the sapwood of diffuse-porous species, *L. tulipifera* and *L. styraciflua*, as well as ring-porous *C. tomentosa*, was best described as Gaussian (Fig. 2.4). Nevertheless, based on a synthesis of studies on radial patterns in flux (Phillips et al., 1996), sapwood between the cambium and the peak of the Gaussian curve was assumed to transpire at the maximum rate (represented by the dashed line in Fig. 2.4).

Regressions using sensors’ relative depth in sapwood, rather than absolute depth in sapwood, had higher $r^2$ values and showed similar patterns in trees of different diameters. None of the three *Quercus* species showed a radial pattern in sap flux and were assumed to have uniform flow throughout the sapwood, similar to results from *Q. alba* (Phillips et al., 1996). Ring-porous species with thin sapwood are especially prone to errors in $J_s$ estimates if the sensors extend into heartwood (Clearwater et al., 1998; Wullschleger and Hanson, 2006), can show a sharp decrease over small intervals within the sapwood (see Phillips et al., 1996), and may support flow even beyond the visually determined sapwood (Poyatos et al., 2007). These factors conspire to produce a large degree of variation among individuals of ring-porous species, necessitating a higher number of replicates to attain a similar degree of accuracy than is required for diffuse-porous and non-porous species (Oren et al., 1998b).

Further complication in scaling may occur when the proportion of sap flux measured in inner sensors varies with environmental conditions and seasons, requiring sufficient data to quantify the changing patterns. In *Pinus taeda* this ratio decreased with soil water availability (Phillips et al., 1996), and was near unity in winter, reaching a minimum in mid-growing season (Schäfer et al., 2002). Here, despite large inter-annual
variability in growing season soil moisture, the relationships between radial depth and flux were similar under drought and non-drought conditions within a year, and did not change among years ($p > 0.1$). Thus, transpiration for each tree within our sap flux plots and the hectare plot was estimated based on Eq. (4), using the mean species- or genus-specific flux in the outer xylem, the radial sap flux patterns (Fig. 2.4), and sapwood area estimated based on allometric equations (Table 2.3).

Species-specific values of transpiration ($E_{Ci}$, where $I$ represents an individual species; Fig. 2.5a and b) for the hectare plot, obtained by summing individual tree transpiration, were normalized by $A_{Si}$ in that plot then multiplied by the EC footprint $A_{Si}$ (Table 2.4). Values of $E_{Ci}$ were combined to produce $E_C$ (Fig. 2.5c). Growing season (April–October) $E_C$ was very consistent among years, comprising approximately 65% of growing season ETS (Table 2.2), despite large differences in the amount and timing of precipitation (Fig. 2.2c). Over the growing season, *Quercus* spp. accounted for 38% ($\pm 2\%$ among the 4 years) of total $E_C$. The rest of $E_C$ was contributed by *Carya* spp., *L. styraciflua*, and *L. tulipifera* at 19 ($\pm 2\%$), 16 ($\pm 1\%$), and 11 ($\pm 1\%$), respectively. Other species, which included most understory and some overstory trees, accounted for the remaining 16 ($\pm <1\%$) of $E_C$. The order of contribution was poorly related to the order of the species or genus $A_{Si}$ (Table 2.4), reflecting the differences observed in $J_{sv}$ as observed in another study in a similar forest (Wullschleger et al., 2001).

Pataki and Oren (2003) measured sap flux in a different plot in the same stand in 1997, and found lower growing season $E_C$ (264 mm), similar to an estimate at a nearby, upland broadleaf stand (278 mm, Oren and Pataki, 2001). Basing their scaling on the findings of Phillips et al. (1996), these previous studies did not account for differential radial flow patterns, which would tend to overestimate $E_C$ (Ford et al., 2004). However, their plots were positioned in areas with lower sapwood area density than this study,
which should somewhat compensate. Indeed, estimates from the previous studies are very similar to our estimates before we accounted for nighttime fluxes (279 ±11 mm). Thus, we conclude that the previous studies underestimated $E_C$ because they failed to account for the effects of nocturnal fluxes in data processing. Other estimates for similar sites show similar annual $E_C$ as well as the proportion of $P$ used as EC (Table 2.2).

Sap flux measurements continued through the winter after $E_C$ loss of leaves and showed low, but detectable, fluxes that may be attributed to water loss from the bark surfaces (Kozlowski, 1943; Oren and Pataki, 2001; Weaver and Mogensen, 1919). The half-hourly fluctuations in $\Delta T$ were often $\Delta T_{\text{max}}$ a similar magnitude to the diel fluctuations, making it difficult to identify a reliable $\Delta T_{\text{max}}$ for many winter days. Therefore, $E_C$ was modeled for winter months by combining reliable data from all trees using a power function with day-length-normalized vapor pressure deficit ($D_Z$; Table 2.6). This function was used to estimate $E_C$ during winter months (December–March, classified by LAI < 1) for the entire stand, which averaged 20 (±0.8) mm year$^{-1}$, about 6% of annual $E_C$. Mean winter $E_C$ was 0.17 (±0.01) mm d$^{-1}$, higher than that previously reported in this area for *Acer rubrum* and *Q. alba* (0.07 mm d$^{-1}$, Pataki and Oren, 2003), most likely due to accounting for nocturnal sap flux. Wintertime $E_C$ was allocated among species based on their proportion of growing season $E_C$.

The large footprint of LE measurements above tall forests can present challenges for scaling sap flux as a component of ET$_S$ at a comparable scale. As a reminder, we scaled sap flux to three areas of the stand based on $A_s$ obtained from the inventory in (1) the two sap flux plots, (2) the hectare plot around the tower, and (3) from LAI in the approximately 250m × 250m area representing most of the eddy covariance footprint (Fig. 2.1). Estimated annual $E_C$ for the eddy covariance footprint was 338 (±7) mm (Table 2.2), 8% lower than for the two sap flux plots due to an overrepresentation of *Quercus* in
the wet sap flux plot (Table 2.4), and 17% higher than the hectare plot due to an under-representation of this genus in the area immediately surrounding the tower. Thus, despite the similarity of average LAI among these sample areas, non-uniform species distribution in the forest (affecting the scaling $A_{si}$) combined with species differences in sap flux produced substantially different estimates of $E_C$. A proper comparison of ET$_s$ with LE requires scaling sap flux to $E_C$ that accounts for species or functional groups, rather than only the bulk canopy properties in the sap flux and eddy covariance footprints.

### 2.3.3 Evaporative losses

As expected, sap flux-scaled daily EC and LE followed similar trends (Fig. 2.5d). However, because annual $E_C$ comprised only 54 (±3) % of LE, other components of total evapotranspiration required accurate quantification to make the conclusions regarding correction for nocturnal flux and scaling meaningful.

Annual estimates of $I_C$ are presented in Table 2.2. Our mean growing season estimate of 96 (±49) mm was approximately 14% of growing season $P$, similar to the 14% reported in previous studies in this area (Pataki and Oren, 2003). While these mean values for the site agree well with previous results (Table 2.2), the standard deviation of annual $I_C$ (based on variation in throughfall among gauges) was nearly 60 mm, or about 9% of ET$_s$. This variability represents the spatial heterogeneity of interception, translating to uncertainty in estimated ET$_s$.

The estimates of $E_S$ (Table 2.2) were constructed based on a subset of the wintertime eddy covariance-measured LE. These half-hourly estimates based on the wintertime relationships were close to nighttime LE values during the growing season, suggesting that the relationship was useful for $D$ values outside the range used in its derivation. We note that the estimate of $E_S$ is thus not entirely independent of LE with
which we ultimately compare the component-sum evapotranspiration ($\text{ET}_s = \text{EC} + \text{ES} + \text{IC}$). Mean annual $\text{ES}$ estimate was 103 ($\pm 14$) mm. For a different estimate of $\text{ES}$ in this stand (Stoy et al., 2006), combined modeled growing season $\text{ES}$ based on radiation penetration through the canopy with wintertime measured LE, arriving at an annual value of 176 $\pm 7$ mm. Our estimates of $\text{ES}$ are more similar to LE measured with an eddy covariance system at 2 m above the forest floor in another southeastern deciduous forest (88 mm) where LE above the forest was similar to ours (Table 2.2; Wilson et al., 2001). Few other studies of broadleaf forests in this region have incorporated estimates of forest floor evaporation and this component of $\text{ET}_s$ remains the source of some uncertainty.

We assessed the agreement between estimates of various components of ET in time scales ranging from daily to interannually. Two methods for estimating forest evaporation (i.e. excluding transpiration), LE - $\text{EC}$ and $\text{ES} + \text{IC}$, are compared in Fig. 2.5d. At the daily time scale, $\text{ES} + \text{IC}$ was typically higher than LE - $\text{EC}$ during and immediately after rain events, but was frequently lower during periods of high radiation loads. On a monthly basis, ET$_s$ showed good agreement with LE but, consistent with the daily comparisons above, monthly ET$_s$ was somewhat higher during periods of low to intermediate radiation loads and lower during periods of very high radiation loads (Fig. 2.6). Routines used to gapfill eddy covariance-measured LE (Falge et al., 2001; Stoy et al., 2006) may not completely account for potentially high evaporation rates from wet canopy and forest floor following rain events, because relationships derived from data obtained when surfaces are dry would underestimate evaporation following rain events when surface conductance is high. This effect is magnified during periods with low radiation loads, because sensors remain wet for longer periods producing higher proportion of unacceptable eddy covariance data. This is reflected in a significant linear
increase in the number of gapfilled data points with decreasing monthly net radiation (linear regression: \( p = 0.0015 \)). Although underestimate of \( E_s \) following rains will similarly bias evaporation estimates based on both methods, only LE-based evaporation estimate includes underestimated \( I_c \) as well. The component-based \( I_c \) estimate uses throughfall measurements that, although are spatially very variable, are largely immune to technical problems that cause a bias under particular conditions.

Periods of high radiation loads are restricted to the months in which solar zenith angle is low. During these periods, but excluding times in which the canopy is wet, \( E_T \) is often lower than LE (Bovard et al., 2005; Oren et al., 1998b; Schäfer et al., 2002; Wilson et al., 2001). This may be the result of underestimating stand-level \( E_C \). \( E_C \) may be underestimated for two reasons: (1) the signal may be saturating under high flux rates, as has been commonly observed (Bovard et al., 2005; Hogg et al., 1997; Wilson et al., 2001) and (2) the contribution of the sub-canopy to \( E_C \) may be higher during periods in which radiation penetrates deeper in the canopy. The contribution of small understory individuals (<40 mm in diameter) and herbaceous vegetation was not estimated in this study, but can be large (Gholz and Clark, 2002; Vincke et al., 2005). In support of (2), Granier et al. (2000) found a linear relationship between \( E_C \) and LE (i.e., no sign of saturation) in a study in which equal attention was given to monitoring large and small individuals. The importance of the sub-canopy to stand transpiration has been shown in many studies. Transpiration rates of canopy and sub-canopy trees compensate as stands develop, leading to a conservative forest transpiration (Phillips and Oren, 2001) as has been shown spatially among stands of different degrees of canopy closure (Roberts, 1983). Thus, we conclude that underestimation of stand-level \( E_C \) is often the result of inadequate representation of the sub-canopy components in scaling, rather than instrument deficiencies.
Nocturnal sap flux scaled to nocturnal $E_C$ (occurring as recharge or water loss from leaves when PAR = 0) averaged 0.19 (±0.11) mm d$^{-1}$ over the growing season. The ratio of night/day $E_C$, 0.17 ±0.19, is within the range of 0–0.25 for deciduous trees (Dawson et al., 2007). Assuming for simplicity that nocturnal $E_C$ is used entirely for recharge, the average nocturnal recharge rate, or even the highest rate of ~0.6 mm d$^{-1}$, fall well within the ~1.0 mm d$^{-1}$ estimated based on a relationship between recharge and sapwood area (Goldstein et al., 1998). Nocturnal LE, which includes evaporation in addition to transpiration, was less than half of nocturnal water uptake (0.08 ±0.11 mm d$^{-1}$). Thus, the results suggest that at least half of this nighttime flux is used to resupply the trunk with water used earlier in the day, while some portion of the remainder may be lost as nocturnal transpiration.

At annual time scale, estimates of $E_T$ and LE showed good agreement (see Table 2.2, Fig. 2.7). $E_T$ was lower than LE in each year before accounting for nighttime sap flux in estimates of $E_C$, averaging -6 (±3) %, reversing to +5 (±3) % after sap flux data were processed based on the new approach. Accounting for nocturnal flux had a more striking effect during the growing season—with the difference decreasing from -16 (±2) % to -4 (±3)%. Thus, although accounting for the effect of nocturnal fluxes did not resolve the discrepancy between $E_T$ and LE in each day and each month – possibly due to underestimation of $E_C$ from small trees and other understory species during high radiation periods – the approach resulted in a substantial 18 (±2) % increase in the estimate of annual $E_C$ (61 ±9mm year$^{-1}$), leading to both annual and seasonal similarity of $E_T$ and LE. The increase in estimated growing season $E_C$ of 22 (±4) % based on the new method for accounting for nocturnal fluxes was intermediate compared to increases produced by other methods: a 12% increase in a *Populus trichocarpa* x *P. deltoides*
plantation (Kim et al., 2008) and 30% increase in boreal *Picea abies* (L.) Karst. stands (Ward et al., 2008).

### 2.3.4 Implications

The analysis showed that mischaracterization of the footprint area is not the likely source of the reported consistent lower estimates of $ET_s$ than LE. Scaling to $E_C$ based on the hectare plot, $ET_s$ would have been only 3 (±3) % lower than LE, while scaling based on the two sap flux plots, would have resulted in $ET_s$ that was 10 (±3) % higher than LE. Thus, when scaled properly, and after accounting for the major contributing fluxes, seasonal and annual estimates of evapotranspiration that include sap flux-scaled $E_C$ were in good agreement with those based on eddy covariance.

Accounting for nocturnal sap flux in trees caused by the recharge of water to upper trunks and branches, as well as nocturnal water loss, is a vital step for accurately estimating $E_C$. Failure to account for nocturnal fluxes is the most likely explanation for the previously observed bias towards lower estimates of component-based evapotranspiration. Nevertheless, comparisons of daily and monthly estimates of evapotranspiration indicate that the eddy covariance approach tends to underestimate during low radiation-high surface wetness periods, while the component sum tends to underestimate during periods of high radiation. Thus, the agreement between the methods at coarser temporal resolution is somewhat achieved by compensating errors, making it case specific.
Table 2.1: List of abbreviations with definitions and units.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_B$</td>
<td>Basal area of trees per unit ground area</td>
<td>cm² m⁻²</td>
</tr>
<tr>
<td>$A_{fi}$</td>
<td>Integrated area beneath fitted curve of radial sap flux profile (see Eq 4)</td>
<td>cm²</td>
</tr>
<tr>
<td>$A_S$</td>
<td>Sapwood area of trees per unit ground area</td>
<td>cm² m⁻²</td>
</tr>
<tr>
<td>$A_{Si}$</td>
<td>$A_S$ for species $i$</td>
<td>cm² m⁻²</td>
</tr>
<tr>
<td>$A_{sh}$</td>
<td>$A_S$ for one-hectare plot</td>
<td>cm² m⁻²</td>
</tr>
<tr>
<td>$A_{Si}$</td>
<td>Sapwood area for individual tree</td>
<td>cm² m⁻²</td>
</tr>
<tr>
<td>$c_j$</td>
<td>Distance from center of tree to centroid of fitted curve of radial sap flux profile (see Eq 4)</td>
<td>cm</td>
</tr>
<tr>
<td>$D$</td>
<td>Vapor pressure deficit</td>
<td>kPa</td>
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<tr>
<td>$D_Z$</td>
<td>Day-length-normalized vapor pressure deficit</td>
<td>kPa</td>
</tr>
<tr>
<td>DBH</td>
<td>Tree diameter at breast height</td>
<td>cm</td>
</tr>
<tr>
<td>$E_C$</td>
<td>Canopy transpiration</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$E_{Ci}$</td>
<td>$E_C$ for species $i$</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$E_{Gh}$</td>
<td>$E_{Ci}$ for one-hectare plot</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$E_S$</td>
<td>Soil surface evaporation</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>ET</td>
<td>Evapotranspiration</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$ET_S$</td>
<td>Evapotranspiration, estimated from sap flux-scaled budget</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$I_C$</td>
<td>Canopy interception</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$I_S$</td>
<td>Sap flux density</td>
<td>g H₂O m⁻² s⁻¹</td>
</tr>
<tr>
<td>$I_{Si}$</td>
<td>Sap flux density for species $i$</td>
<td>g H₂O m⁻² s⁻¹</td>
</tr>
<tr>
<td>LAI</td>
<td>Leaf area index</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>LE</td>
<td>Latent heat flux</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$P$</td>
<td>Precipitation</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$P_T$</td>
<td>Throughfall ($P-I_C$)</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>PAR</td>
<td>Photosynthetically active radiation</td>
<td>µmol m⁻² s⁻¹</td>
</tr>
<tr>
<td>RH</td>
<td>Relative humidity</td>
<td>%</td>
</tr>
<tr>
<td>SLA</td>
<td>Specific leaf area</td>
<td>cm² g⁻¹</td>
</tr>
<tr>
<td>$T_A$</td>
<td>Air temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$T_B$</td>
<td>Bark thickness</td>
<td>mm time⁻¹</td>
</tr>
<tr>
<td>$T_{SW}$</td>
<td>Sapwood thickness</td>
<td>cm</td>
</tr>
<tr>
<td>$V_j$</td>
<td>Volume of a rotated geometric solid (see Eq 4)</td>
<td>cm³</td>
</tr>
<tr>
<td>$\Delta T$</td>
<td>Temperature difference between heated and unheated sap flux probes</td>
<td>mV</td>
</tr>
<tr>
<td>$\Delta T_{max}$</td>
<td>Maximum daily $\Delta T$</td>
<td>mV</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Volumetric soil moisture</td>
<td>m³ m⁻³</td>
</tr>
</tbody>
</table>
Table 2.2: Components of forest evapotranspiration from published studies using thermal dissipation probes in comparable regional deciduous forests and from this study. Annual and growing season values of precipitation (P), canopy interception (IC), soil evaporation (ES), canopy transpiration (EC), sap-flux based canopy evapotranspiration (ETS), ET estimated through other means (eddy covariance as LE unless noted), lack of closure between ETs and LE, and the proportion of EC to ET. All values are mm yr⁻¹, except EC/ET which is unitless.

<table>
<thead>
<tr>
<th>Site description</th>
<th>Year</th>
<th>P</th>
<th>IC</th>
<th>ES</th>
<th>EC</th>
<th>ET</th>
<th>LOC</th>
<th>EC/ET</th>
<th>Notes</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td><strong>Annual Sums</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eddy covariance-generated study area</td>
<td>2002</td>
<td>1092</td>
<td>440</td>
<td>610</td>
<td>0.72</td>
<td></td>
<td></td>
<td></td>
<td>+ EC modeled as component of LE (Stoy et al., 2006)</td>
<td></td>
</tr>
<tr>
<td>Upland oak-dominated broadleaf forest, Oak Ridge, TN</td>
<td>2003</td>
<td>1346</td>
<td>410</td>
<td>580</td>
<td>0.71</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>2004</td>
<td>992</td>
<td>460</td>
<td>640</td>
<td>0.72</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>934</td>
<td>460+</td>
<td>640</td>
<td>0.72</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Upland oak-dominated broadleaf forest, Oak Ridge, TN</td>
<td>1998</td>
<td>1225</td>
<td>104</td>
<td>86</td>
<td>230</td>
<td>420</td>
<td>547 &amp; 502§</td>
<td>-127</td>
<td>0.42</td>
<td>§ ET estimated through catchment water balance (Wilson et al., 2001)</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>1152</td>
<td>105</td>
<td>91</td>
<td>269</td>
<td>465</td>
<td>605 &amp; 642§</td>
<td>-140</td>
<td>0.44</td>
<td></td>
</tr>
<tr>
<td>Upland oak-dominated broadleaf forest, Oak Ridge, TN</td>
<td>2000</td>
<td>766</td>
<td>325</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Wullschleger and Hanson, 2006)</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>539</td>
<td>309</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>2002</td>
<td>730</td>
<td>255</td>
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</tr>
<tr>
<td></td>
<td>2003</td>
<td>968</td>
<td>315</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>This study</td>
<td>2002</td>
<td>1092</td>
<td>189</td>
<td>84</td>
<td>336</td>
<td>610</td>
<td>577</td>
<td>33</td>
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<tr>
<td></td>
<td>2003</td>
<td>1346</td>
<td>236</td>
<td>102</td>
<td>329</td>
<td>668</td>
<td>618</td>
<td>50</td>
<td>0.53</td>
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<td>2004</td>
<td>992</td>
<td>181</td>
<td>108</td>
<td>346</td>
<td>635</td>
<td>618</td>
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<tr>
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<td>157</td>
<td>119</td>
<td>343</td>
<td>619</td>
<td>605</td>
<td>15</td>
<td>0.57</td>
<td></td>
</tr>
<tr>
<td><strong>Growing season</strong></td>
<td>1997</td>
<td>626</td>
<td>88</td>
<td>264</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Different plots within same study area</td>
<td>1993</td>
<td>642</td>
<td>90</td>
<td>278</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Pataki and Oren, 2003)</td>
</tr>
<tr>
<td>Upland hardwood stand, Duke Forest, NC</td>
<td>1996</td>
<td></td>
<td>267</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upland oak-dominated broadleaf forest, Oak Ridge, TN</td>
<td>2002</td>
<td>610</td>
<td>80</td>
<td>68</td>
<td>306</td>
<td>453</td>
<td>505</td>
<td>-52</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>859</td>
<td>123</td>
<td>69</td>
<td>299</td>
<td>491</td>
<td>531</td>
<td>-40</td>
<td>0.61</td>
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</tr>
<tr>
<td></td>
<td>2004</td>
<td>720</td>
<td>145</td>
<td>72</td>
<td>311</td>
<td>529</td>
<td>525</td>
<td>4</td>
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</tr>
<tr>
<td></td>
<td>2005</td>
<td>426</td>
<td>34</td>
<td>88</td>
<td>311</td>
<td>433</td>
<td>517</td>
<td>-84</td>
<td>0.72</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.3: Allometric relationships from data collected to estimate bark thickness (mm) based on diameter at breast height (DBH, cm) using either an exponential function \((a \times \exp(b \times DBH))\) or linear function \((a \times DBH + b)\)

<table>
<thead>
<tr>
<th>Diffuse Porous</th>
<th>Bark Thickness</th>
<th>Sapwood Area Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n)</td>
<td>Function</td>
</tr>
<tr>
<td>(L.\ tulipifera)</td>
<td>19</td>
<td>Exp</td>
</tr>
<tr>
<td>(L.\ styraciflua)</td>
<td>19</td>
<td>Exp</td>
</tr>
<tr>
<td>Ring Porous</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Carya)</td>
<td>11</td>
<td>Linear</td>
</tr>
<tr>
<td>(Q.\ alba &amp; Q.\ michauxii)</td>
<td>11</td>
<td>Linear</td>
</tr>
<tr>
<td>(Q.\ phellos)</td>
<td>9</td>
<td>Linear</td>
</tr>
<tr>
<td>Combined (Quercus)</td>
<td>22</td>
<td>Linear</td>
</tr>
</tbody>
</table>
Table 2.4: Basal area ($A_b$) and sapwood area ($A_s$) in cm$^2$ m$^{-2}$ ground area for the dry and wet sap flux plots, the hectare plot surrounding the eddy covariance tower, and for the kriged area representing the footprint for measured latent heat flux (LE). Leaf area index (LAI, m$^2$ m$^{-2}$) derived from specific leaf area (SLA, cm$^2$ g$^{-1}$) was used to scale $A_s$ across the LE footprint (see Fig. 1).

<table>
<thead>
<tr>
<th></th>
<th>Dry Plot</th>
<th>Wet Plot</th>
<th>Hectare Plot</th>
<th>LE Footprint</th>
<th>SLA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$A_b$</td>
<td>$A_s$</td>
<td>$A_b$</td>
<td>$A_s$</td>
<td></td>
</tr>
<tr>
<td><strong>Diffuse Porous</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. tulipifera</em></td>
<td>9.80</td>
<td>4.97</td>
<td>3.22</td>
<td>1.63</td>
<td>6.29</td>
</tr>
<tr>
<td><em>L. styraciflua</em></td>
<td>5.38</td>
<td>3.52</td>
<td>6.89</td>
<td>4.79</td>
<td>4.53</td>
</tr>
<tr>
<td>Mixed species</td>
<td>4.33</td>
<td>2.52</td>
<td>3.25</td>
<td>1.87</td>
<td>4.17</td>
</tr>
<tr>
<td><strong>Ring Porous</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All <em>Carya</em></td>
<td>8.03</td>
<td>4.44</td>
<td>4.76</td>
<td>2.78</td>
<td>6.20</td>
</tr>
<tr>
<td>All <em>Quercus</em></td>
<td>4.59</td>
<td>1.34</td>
<td>14.61</td>
<td>4.30</td>
<td>4.67</td>
</tr>
<tr>
<td><em>Q. alba</em></td>
<td>4.59</td>
<td>1.34</td>
<td>1.08</td>
<td>0.34</td>
<td>1.73</td>
</tr>
<tr>
<td><em>Q. michauxii</em></td>
<td>0</td>
<td>0</td>
<td>6.75</td>
<td>2.08</td>
<td>1.95</td>
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<tr>
<td><em>Q. phellos</em></td>
<td>0</td>
<td>0</td>
<td>6.77</td>
<td>1.88</td>
<td>0.99</td>
</tr>
<tr>
<td>Mixed species</td>
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<td>0.07</td>
<td>3.48</td>
<td>1.14</td>
<td>1.28</td>
</tr>
<tr>
<td><strong>Plot Total</strong></td>
<td>32.35</td>
<td>16.86</td>
<td>36.21</td>
<td>16.51</td>
<td>27.13</td>
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</tbody>
</table>

Leaf area index (LAI, m$^2$ m$^{-2}$) derived from specific leaf area (SLA, cm$^2$ g$^{-1}$) was used to scale $A_s$ across the LE footprint (see Fig. 1).
Table 2.5: Diameter at breast height (DBH, cm) and maximum sap flux sensor depth (mm) for trees sampled at the wet and dry sites

<table>
<thead>
<tr>
<th>Dry Site</th>
<th>DBH</th>
<th>Depth</th>
<th>Wet Site</th>
<th>DBH</th>
<th>Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. tulipifera</em></td>
<td>65.4</td>
<td>40-60</td>
<td><em>L. tulipifera</em></td>
<td>59.8</td>
<td>40-60</td>
</tr>
<tr>
<td></td>
<td>44.4</td>
<td>40-60</td>
<td></td>
<td>38.7</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>42.0</td>
<td>40-60</td>
<td></td>
<td>37.7</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>26.4</td>
<td>20-40</td>
<td></td>
<td>36.0</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>16.1</td>
<td>20-40+</td>
<td></td>
<td>26.6</td>
<td>20-40</td>
</tr>
<tr>
<td><em>L. styraciflua</em></td>
<td>48.0</td>
<td>40-60</td>
<td><em>L. styraciflua</em></td>
<td>55.6</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>47.4</td>
<td>40-60</td>
<td></td>
<td>42.8</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>35.0</td>
<td>40-60</td>
<td></td>
<td>37.5</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>24.3</td>
<td>20-40</td>
<td></td>
<td>34.4</td>
<td>20-40</td>
</tr>
<tr>
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<td>19.7</td>
<td>20-40</td>
<td></td>
<td>21.1</td>
<td>20-40</td>
</tr>
<tr>
<td><em>C. tomentosa</em></td>
<td>58.4</td>
<td>40-60</td>
<td><em>Q. michauxii</em></td>
<td>54.4</td>
<td>20-40+</td>
</tr>
<tr>
<td></td>
<td>54.4</td>
<td>40-60</td>
<td></td>
<td>47.6</td>
<td>20-40+</td>
</tr>
<tr>
<td></td>
<td>25.1</td>
<td>20-40</td>
<td></td>
<td>30.2</td>
<td>20-40+</td>
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<tr>
<td></td>
<td>20.0</td>
<td>20-40</td>
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<td>20.1</td>
<td>0-20</td>
</tr>
<tr>
<td></td>
<td>12.7</td>
<td>0-20</td>
<td></td>
<td>16.1</td>
<td>0-20</td>
</tr>
<tr>
<td><em>Q. alba</em></td>
<td>57.7</td>
<td>20-40+</td>
<td><em>Q. phellos</em></td>
<td>63.6</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>43.1</td>
<td>20-40+</td>
<td></td>
<td>53.5</td>
<td>20-40</td>
</tr>
<tr>
<td></td>
<td>30.8</td>
<td>0-20</td>
<td></td>
<td>44.0</td>
<td>20-40+</td>
</tr>
<tr>
<td></td>
<td>16.4</td>
<td>0-20</td>
<td></td>
<td>43.2</td>
<td>20-40+</td>
</tr>
<tr>
<td></td>
<td>13.7</td>
<td>0-20</td>
<td></td>
<td>43.1</td>
<td>20-40+</td>
</tr>
</tbody>
</table>

† Deepest sensor required correction due to contact with non-conductive tissue (Clearwater et al., 1998).
Table 2.6: Parameters for equations used to estimates components of evaporation. Canopy interception ($I_c$) was estimated as precipitation ($P$) minus measured throughfall ($P_T$). Missing $P_T$ data were estimated for each throughfall gauge using the linear function $P_T = aP + y_0$. Soil evaporation ($E_S$) used a power function: $E_S = aD^b$ where $D$ is vapor pressure deficit. Winter canopy transpiration ($E_C$) was estimated using a power function: $E_C = aD_Z^b$ where $D_Z$ is day-length-normalized vapor pressure deficit. All regressions are significant at $p < 0.0001$.

<table>
<thead>
<tr>
<th>Canopy Throughfall</th>
<th>$a$</th>
<th>$y_0$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gauge 1</td>
<td>0.8675</td>
<td>-0.5272</td>
<td>0.90</td>
</tr>
<tr>
<td>Gauge 2</td>
<td>0.7886</td>
<td>-0.4780</td>
<td>0.94</td>
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<tr>
<td>Gauge 3</td>
<td>0.9000</td>
<td>-0.6791</td>
<td>0.94</td>
</tr>
<tr>
<td>Gauge 4</td>
<td>0.9040</td>
<td>-0.4229</td>
<td>0.92</td>
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<tr>
<td>Gauge 5</td>
<td>0.8469</td>
<td>-0.4582</td>
<td>0.86</td>
</tr>
<tr>
<td>Gauge 6</td>
<td>0.9366</td>
<td>-0.4670</td>
<td>0.94</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Soil Evaporation</th>
<th>$a$</th>
<th>$b$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>0.0066</td>
<td>1.4320</td>
<td>0.09</td>
</tr>
<tr>
<td>2003-2005</td>
<td>0.0123</td>
<td>1.3003</td>
<td>0.14</td>
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</table>

<table>
<thead>
<tr>
<th>Canopy Transpiration</th>
<th>$a$</th>
<th>$b$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter (LAI&lt;1)</td>
<td>0.3114</td>
<td>0.3305</td>
<td>0.24</td>
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</tbody>
</table>
Figure 2.1: Estimated leaf area index (LAI, m² m⁻²) for the ca. 6.25 ha overlapping most of the eddy covariance-based flux footprint at the Duke Ameriflux Hardwood Forest near Durham, NC. Black circles represent the boundaries of the wetter (to the west) and drier sap flux plots. The blue diamond delineates the area of the one-hectare plot. Gray squares represent the location of litter traps. Isometric lines represent the probability distribution of the peak of the source-weight function of acceptable eddy covariance flux measurements estimated using the semi-empirical footprint model of Hsieh et al. (2000). The peak of the source weight function lies within the white line 50% of the 2002–2005 measurement period, and within the green line 95% of the period. In November 2002, a clearcut was created to the south of the tower, outside of the study area. Fluxes originating from this area were excluded from flux estimates as described by Stoy et al. (2006).
Figure 2.2: Environmental variables measured at hardwood stand at Duke Forest, 2002–2005. (a) Above-canopy photosynthetically active radiation (PAR), (b) daily mean mid-canopy vapor pressure deficit (D) and air temperature (Tₐ), (c) weekly totals of precipitation (P), and (d) volumetric soil moisture (θ) for the wet and dry sap flux plots.
Figure 2.3: Sap flux density by species or genus ($J_{si}$) for 3 days during the 2005 growing season with nighttime $D > 0.05$ kPa. Black circles show data converted using a method that establishes a baseline value under the assumption that fluxes drop to zero every night. Open circles show data converted with the revised method in which the $\Delta T_{max}$ baseline allows for nighttime flux. Error bars represent 1 S.E.
Figure 2.4: Radial profiles of sap flux ($J_{SI}$) based on relative sapwood depth (beginning in the cambium interface) and normalized mean sap flux. Data were fitted to a Gaussian equation. The equation for normalized daily sap flux for *L. tulipifera* was $\exp(-0.5(x - 0.055/0.568)^2)$ (adjusted $r^2 = 0.37; p = 0.003$), *L. styraciflua* was $\exp(-0.5(x - 0.222/0.343)^2)$ (adjusted $r^2 = 0.21; p = 0.047$), and *C. tomentosa* was $\exp(-0.5(x - 0.078/0.396)^2)$ (adjusted $r^2 = 0.48; p = 0.029$), where $x$ is the relative sapwood depth. Dashed lines in the top two panels indicate sections where the peak of the curve did not occur at the sapwood–cambium interface and where a maximum rate of normalized sap flux (i.e. 1.0) was assumed. The horizontal dashed line in the *Quercus* spp. panel indicates that no radial pattern was observed in any species and a uniform sap flux was assumed throughout the sapwood.
Figure 2.5: Stand-level fluxes over the four study years. (a) and (b) show sap flux-scaled canopy transpiration by species ($E_{Ci}$), (c) shows total sap flux-scaled canopy transpiration ($E_{C}$) and eddy covariance-measured latent heat flux (LE), (d) estimates for the remaining components of stand evapotranspiration (soil evaporation, $E_{s}$) plus canopy interception ($I_{C}$, plotted as a 3-day moving average) compared to the difference LE - $E_{C}$, (e) leaf area index (LAI, m$^2$ m$^{-2}$).
Figure 2.6: Comparison of monthly ecosystem evapotranspiration from eddy covariance-measured latent heat flux (LE) and from sap flux-scaled hydrologic budget (ET_s). ET_s includes E_c estimates that ignore nighttime sap flux (a) and those that account for nighttime sap flux (b).
Figure 2.7: Annual ET budgets for 2002–2005 including sap flux-based $E_c$ and the remaining evaporation components, and eddy covariance based estimates (LE). Lack of closure represents the relative difference between the two methods (using LE as the base).
3. Interannual Invariability of Forest Evapotranspiration and Its Consequence to Water Flow Downstream

3.1 Introduction

Evapotranspiration is a large component of the hydrological budget of forests, exerting great influence on the flow of water to downstream users, including aquatic ecosystems and human populations. Forest transpiration in temperate regions has shown remarkable consistency as stands develop, regardless of the accompanying increases in canopy leaf area and changes in species composition (Roberts, 1983; Phillips and Oren, 2001). This “conservative” behavior (Roberts, 1983), is achieved in some forests through relatively low transpiration rates (compared to precipitation or potential evapotranspiration) and compensatory behavior among canopy strata or species. However, some forests decrease canopy transpiration during periods of limited water availability through large reduction of average canopy stomatal conductance (Oren et al., 1998; Bréda et al., 2006; Koecher et al., 2009). In these forests, large interannual variation of precipitation is reflected in variation of annual transpiration (e.g., a pine plantation in Stoy et al., 2006). More difficult to reconcile are observations in stands where transpiration of a number of dominant species decreases with water availability, yet stand-level annual transpiration remains relatively unaffected (Wullschleger and Hanson, 2003; Bovard et al., 2005; Sinclair et al., 2005; Wullschleger and Hanson, 2006).

Total evapotranspiration is also affected by precipitation ($P$), which indirectly affects transpiration by influencing soil moisture ($\theta$), and directly affects evaporation by influencing surface wetness (Wilson et al., 2000). Like transpiration, the amount of interannual variation of evapotranspiration differs among forests. For example, the variation of annual evapotranspiration data from the pine plantation mentioned above
was higher and more sensitive to changes in $P$ than that of an adjacent hardwood stand (Stoy et al., 2006).

The objective of this study was to resolve the apparent contradictions between the observed drought response of the individual components of evapotranspiration (reduced transpiration of drought-sensitive species and evaporation) and the lack of response of total canopy transpiration ($E_C$) and evapotranspiration. To accomplish this, we focused on a mature, southeastern bottomland hardwood stand, which contains drought-sensitive species (Pataki and Oren, 2003) but exhibits little variation in annual evapotranspiration (Stoy et al., 2006). The soil is frequently saturated in the dormant season, but the relatively thin, well-drained rooting zone regularly dries to the hygroscopic point in the growing season (Oosting, 1942). This type of mesic site, which makes up 16% of forested land in the southern U.S. (Wear and Greis, 2002), represents an ideal setting to examine drought response of components of the hydrologic budget because the trees, species, and stands are not specifically adapted to xeric or hydric extremes (e.g., Addington et al., 2006). Using data collected over four years (2002-2005), including years with mild and severe droughts as well as an uncharacteristically wet year, we produced component-based evapotranspiration ($ET_{comp}$), combining $E_C$ from scaled sap flux measurements, measured canopy-intercepted precipitation ($I_C$), and modeled soil evaporation ($E_S$). Previous work described in Oishi et al. (2008) demonstrated an excellent agreement between eddy covariance estimates of latent heat flux of evapotranspiration ($LE$) and $ET_{comp}$. (For clarity of terminology, $ET_{comp}$ and LE shall refer to estimates of evapotranspiration based on component sums and eddy covariance, respectively.)

Using $ET_{comp}$, we first investigated whether drought led to decreases in species-level transpiration at reference atmospheric conditions. Provided that drought affects
transpiration of enough trees within a forest, and given that drought persists through a sizable portion of the growing season, we would expect to observe reductions in annual transpiration. However, drought periods are characterized by sunny (i.e. high radiation loads) and dry (i.e. high atmospheric demand for water) weather, leading to favorable conditions for both evaporation and transpiration (Juang et al., 2007). Indeed, atmospheric demand for water vapor is much greater during drought periods than in the frequently cloudy and rainy weather characteristic of wet growing seasons. We therefore hypothesized that conservative annual transpiration can be achieved if drought-induced reductions in transpiration are similar to the reductions caused by weakened atmospheric demand during non-drought years. (See Appendix 3.6 for a theoretical basis for this hypothesis.) Furthermore, to achieve conservative evapotranspiration at the site, we hypothesized that during dry years lower $I_c$ is compensated for by higher $E_s$.

The mechanisms leading to the observed invariance in evapotranspiration in some forests not only regulate ecosystem productivity, dynamics, and resilience, but also have consequences for ecosystem services that rely on water draining from forests such as maintaining stream flow for downstream aquatic ecosystems and recharging groundwater and reservoirs for human consumption. Therefore, we completed our analysis by producing modeled estimates of the remaining components of the hydrologic budget, drainage ($Q$) and surface runoff ($F_o$). We assessed how variability in precipitation affects these components and how forest outflow ($O=Q+F_o$) compares to water supply to downstream users.
3.2 Materials and Methods

3.2.1 Study Site

The study was conducted at the Duke Forest Ameriflux Hardwood site, Orange County, North Carolina (36°58'41.430"N, 79°05'39.087"W). This bottomland forest stand is described in other studies (Pataki and Oren, 2003; Stoy et al., 2006; Oishi et al., 2008). Briefly, it is an 80-100 year-old mixed broadleaved deciduous forest dominated by hickories (*Carya tomentosa*, *C. glabra*), yellow poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), and oaks (*Quercus alba*, *Q. michauxii*, *Q. phellos*). Mean canopy height is 25 m with emergent crown tops extending above 35 m. Peak leaf area index (LAI) is approximately 7.0 m$^2$ m$^{-2}$, occurring from mid-May until early-September (Fig. 3.1d). Stand characteristics, including stand basal area and sapwood area per unit ground area ($A_s$), were taken in a one-hectare area surrounding the Ameriflux tower and two subplots of approximately 25 m radius (hereinafter the “wet and dry sap flux plots”). These data were scaled up to the 6.25 ha area surrounding an eddy covariance tower (hereinafter the “eddy covariance footprint”) (Table 3.1; for methodological details, see Oishi et al., 2008). The growing season was defined as April through October (DOY 91-304), a period characterized by LAI >2.0 m$^2$ m$^{-2}$.

With 3° slope, the site is nearly flat. The soil is an Iredell gravelly loam, with the upper 0.35 m a clay loam overlying a clay pan with low hydraulic conductivity that inhibits the rooting zone (Oren et al., 1998). Soil depth can be 2 m which overlays bedrock (D. Richter, unpublished data).

3.2.2 Environmental measurements

Air temperature ($T_a$) and relative humidity (RH) were measured at two-thirds canopy height using HMP35C $T_a$/RH probes (Campbell Scientific, Logan, UT, USA) and were used to calculate the vapor pressure deficit ($D$). Photosynthetically active radiation
(PAR) and net radiation \((R_n)\) were measured above the canopy at 38.9 m (see Stoy et al., 2006). Precipitation \((P)\) was measured daily with a rain gauge and partitioned over half-hourly values using data from tipping bucket gauges (TR-525USW, Texas Electronics, Dallas, TX, USA) positioned at the Duke FACE site, <1 km away. Long-term (115-year) mean annual \(P\) for the area is 1146 (standard deviation (SD) = 166) mm, with 654 (SD = 183) mm occurring during the growing season (www.ncdc.noaa.gov).

Soil moisture \((\theta, \text{m}^3\text{m}^{-3})\) was measured with 12 sensors (ThetaProbe, Delta-T Devices, Cambridge, UK), four in each of the wet and dry sap flux sites and four next to the eddy covariance tower, half installed from 0.05-0.10 m and half installed at 0.20-0.25 m. Values were rescaled based on periods when \(\theta\) reached saturation (set to 0.54 m\(^3\) m\(^{-3}\)) or the hygroscopic minima (set to 0.125 m\(^3\) m\(^{-3}\)), based on procedure and soil characteristics described in Oishi et al. (2008). With these estimates of saturated and hygroscopic soil moisture states, the maximum amount of plant extractable water in a 0.30 m root-zone is \(~125\) mm.

### 3.2.3 Hydrologic balance

The forest hydrologic budget can be framed using a simple equation balancing outputs with precipitation:

\[
P = I_C + E_s + E_c + Q + F_o + \Delta S
\]

(1)

where \(\Delta S\) is change in soil water storage. Stemflow was estimated to contribute <1\% of annual precipitation and excluded from further consideration (Oishi et al., 2008).

Precipitation passing through the canopy and reaching the forest floor as throughfall \((P_T)\) was measured manually once or twice weekly with six rain gauges positioned on the forest floor. \(I_C\) was estimated as \(P-P_T\) between measurement periods, partitioned proportionately with the time-series of \(P\). Occasional periods in which no \(P_T\)
was recorded were gapfilled using linear relationships between $P$ and $P_r$ (Oishi et al., 2008).

Methods for generating half-hourly estimates of $E_C$ are described in Oishi et al. (2008). Briefly, sap flux ($J_s$) measurements were made using 20 mm length, thermal dissipation probes (Granier, 1987) on forty trees. Five trees each of $C$. tomentosa and $Q$. alba were measured in the dry sap flux plot and five each of $Q$. michauxii and $Q$. phellos were measured in the wet sap flux plot. Additionally, five trees each of $L$. tulipifera and $L$. styraciflua were measured in both the wet and dry plots. Probes were installed at 20 mm depth intervals to the maximum depth of active sapwood (up to 60 mm) to account for radial variability in flow rates (Phillips et al., 1996). In total, 84 sensors were deployed at breast height in the forty sample trees. Flow of water through the trunk during the night, either resulting from nighttime conductance or recharge of stored water to the trunk and branches, have been shown to occur across a variety of species and climates (Oren et al., 1999, Oren et al., 2001, Daley and Phillips, 2006, Dawson et al., 2007) and, if not adequately identified, can lead to substantial underestimations in $E_C$ (Kim et al., 2008; Oishi et al., 2008; Ward et al., 2008). We assumed that nighttime flux did not occur in times in which simultaneously (1) the average two-hour $D$ was $<0.05$ kPa and (2) the coefficient of variation (CV = standard deviation / mean) of the four temperature differential values ($\Delta T$) from the heat dissipation sensor were $<0.5\%$ (Oishi et al., 2008). These conditions were used to set the baseline for converting the output signal to water flux (Granier, 1987).

No differences in $J_s$ were observed between the populations of the same species from the wet and dry sap flux plots (i.e. $L$. tulipifera and $L$. styraciflua), or among species of the genus Quercus (minimum $p$–value $>0.1$) so the mean $J_s$ from all monitored trees of a given genera ($J_{si}$, where subscript $i$ represents an individual genera) was applied to all
trees of that genera in the stand. All Carya species were assumed to behave like C. tomentosa. Tree-level $J_s$ estimates were scaled to canopy transpiration of each genera ($E_c$) based on estimates of sapwood area in the eddy covariance footprint (Table 3.1). Estimates of $A_s$ were generated for each genera based on linear relationships between leaf area (collected in litter baskets) and $A_s$ from the one-hectare and two sap flux plots. These relationships were then applied to 29 litter baskets distributed throughout a 300 m $\times$ 300 m area representing approximately 95% of the daytime footprint of the eddy covariance instruments (for details, see Oishi et al., 2008).

Half-hourly estimates of $E_s$ previously described in Oishi et al. (2008) based on the relationship between $D$ and wintertime LE measured using eddy covariance were used after filtering out days following recent rain events and subtracting water vapor losses through bark. Oishi et al. (2008) investigated the causes of the often-observed lack of agreement between $ET_{\text{comp}}$ and LE, but did not assess how the components of evapotranspiration respond to interannual variation in weather nor the effect on forest water outflow.

Total evapotranspiration measured by the eddy covariance system as LE is described in Stoy et al. (2006). The 35% lack of closure in the energy balance at the site was due largely to convective conditions influencing sensible heat flux more than LE. The error in the annual LE component ranged 7-14%.

A Richards’ equation was used to estimate vertical water movement in the soil using standard retention and hydraulic conductivity functions (Clapp and Hornberger, 1978). Water redistribution between 7.5 mm soil layers up to 0.50 m depth was calculated at 4 second intervals, with soil physical properties taken from Oren et al. (1998). At each time step, $P_r$ (if any precipitated) was added to the soil surface and estimated $E_s$ was subtracted from the top soil 5 layers (37.5 mm). In addition, $E_c$ was
subtracted from the soil profile based on root distribution data and the relative amount of available water (see Katul et al., 1997). Diagnostic soil pits (0.40 m × 0.40 m, n=3) showed that root biomass in the upper 0.40 m of soil was 426 g m⁻²; 0.015 (SD = 0.007), 0.017 (0.009), 0.008 (0.011), and 0.002 (0.002) g m⁻² at 0.00-0.05, 0.05-0.10, 0.10-0.20, and 0.20-0.30 m, respectively (K. Johnsen, unpublished). Over 75% of the root mass in the upper 0.12 m while root biomass between 0.30 and 0.40 m was <5% of the total for these pits, indicating that the clay pan severely restricted rooting below 0.30 m. Although evidence of roots up to 2 m have been found near this site (D. Richter, unpublished), the sparseness of deep roots, along with the low hydraulic conductivity of this soil makes water availability in the upper 0.30 m the most important for trees. Therefore, Q was equated to water draining below 0.30 m.

To determine $F_O$, the maximum ponding height ($h_{max}$) was calculated based on Paul et al. (2003) as

$$h_{max} = 0.5v\left(\frac{\sin^2(\zeta - s)}{\sin(\zeta)}\right) \times \left(\frac{\cot(\zeta + s) + \cot(\zeta - s)}{2\cos(\zeta)\cos(s)}\right)$$

where $v$ is litter depth (25 mm), $\zeta$ is clod angle (30°), and $s$ is the average site slope (3°). Based on this $h_{max}$ at the site was estimated at 10 mm. When $P_T$ exceeded the infiltration rate estimated from the drainage model, water accumulated up to 10 mm, with the excess designated as $F_O$.

### 3.3 Results

#### 3.3.1 Site and environmental variables

The severe 2002 growing season drought, preceded by the milder 2001 growing season drought, ended with heavy, late-summer rainfall (Fig. 3.1b). Thus, despite a severe summer drought, annual $P$ in 2002 was only slightly lower than the long-term mean (Table 3.2). In contrast, 2003 presented the second wettest growing season in the
115-year local record. Both 2004 and 2005 were relatively dry, close to one standard deviation below the mean annual precipitation; however, 2004 was characterized by a relatively wet growing season and dry dormant season, while 2005 experienced a dryer than normal growing season and typical dormant season.

The primary force driving daily evapotranspiration at the site, day-length normalized vapor pressure deficit ($D_z$), was higher during the dry 2002 growing season than in other years of the study (Fig. 3.1a). Potential evapotranspiration (PET) was estimated based on the Priestley-Taylor method, recommended for the southeastern US (Lu et al., 2005). Annual PET was typically close to annual $P$ (Table 3.2), although $P$ was greater than PET in the wet year of 2003. Cumulative daily values of $P$-PET showed a deficit ($P$-PET < 0) for the majority of the growing season in 2002 (DOY 120 until the end of the year) and 2005 (DOY 129 through 345).

Soil water storage, represented by $\theta$, was high during the dormant season and declined substantially during the growing season (Fig. 3.1c). Differences in $\theta$ between the wet and dry sap flux plots were most evident in winter months when either within-stand $F_o$ or horizontal soil moisture redistribution drained the dry plot and accumulated in the wet plot, keeping it near saturation for a longer period. During the growing season of any year, differences in $\theta$ between the two plots were small owing to high evapotranspiration.

The presence of a clay pan restricts >95% of fine root mass to the upper 0.30 m; however, roots up to 10 mm diameter can occasionally penetrate as deep as 2 m (D. Richter, unpublished data). For the purposes of this analysis, we define drought as periods in which soil moisture in the upper 0.30 m drops below 0.20 m$^3$ m$^{-3}$, a value shown to limit stomatal conductance in pine and hardwood forests in the study area and in a nearby grass/hay field (Oren et al., 1998; Pataki and Oren, 2003; Novick et al., 2004;
Based on this definition, drought days represent 15% of growing season days over the entire study period. During the wet years of 2003 and 2004, \( \theta \) dropped below 0.20 m\(^3\) m\(^{-3}\) for only 14 and 18 growing season days, respectively. However, the forest experienced some degree of soil water limitation during nearly half of the growing season in 2002 (90 days or 42% of the growing season) and 2005 (98 days or 47% of the growing season). Thus, the duration of drought in 2002 and 2005 should provide an adequate contrast to the wetter growing seasons of 2003 and 2004. The reliability of this definition of drought is considered in the Discussion section.

### 3.3.2 Transpiration

At a daily time-scale, marked differences in transpiration were observed among species. To illustrate these differences, we focus on three sample days from the 2002 growing season (Fig. 3.2): an early growing season day that received 14.8 mm of precipitation distributed throughout the day (May 4), an early growing season day with no precipitation but relatively high \( \theta \) (May 12), and a mid-summer day with similar PAR to May 12, but at the peak of the drought (August 13). Precipitation on May 4 resulted in low PAR and \( D \), as well as low \( J_{Si} \) for all species. On May 12, ample soil moisture and favorable atmospheric conditions resulted in high and similar \( J_{Si} \) in all species. The reduction of \( J_{Si} \) at the peak of the drought was greatest in *L. tulipifera*, followed by *Quercus*, and *C. tomentosa*; the average flux of *L. styraciflua* was unaffected by the drought although the variance increased.

Examined at a daily time-scale for the entirety of the study period, drought sensitivity was consistent with the diurnal pattern (Fig. 3.3 & Table 3.3). Daily \( J_{Si} \) followed the commonly-observed relationship with \( D_Z \), increasing rapidly at low \( D_Z \) and tending to saturate with increasing \( D_Z \) (Pataki and Oren, 2003; Bovard et al., 2005; Ewers et al., 2007; Köecher et al., 2009). At a given \( D_Z \), *L. tulipifera*, *C. tomentosa*, and *Quercus*...
spp. exhibited lower $J_{si}$ when $\theta <0.20$ m$^3$ m$^{-3}$ (see Table 3 for information on regression statistics). However, while maximum $J_{si}$ in *L. tulipifera* and *Quercus* spp. decreased during drought by 59 and 31 g H$_2$O m$^{-2}$ d$^{-1}$ (34% and 15%), respectively, *C. tomentosa* exhibited a decrease of only 15 g H$_2$O m$^{-2}$ d$^{-1}$ (8%). Drought response of $J_{si}$ to $D_Z$ in *L. styraciflua* was significant ($p$-value <0.001) leading, nevertheless to only a slight decrease in $J_{si}$ at intermediate $D_Z$ (0.2-0.6 kPa), with negligible differences in the maximum transpiration at high $D_Z$. The relationship between $D_Z$ and species-level $J_{si}$ kept its features upon scaling to stand-level EC (Fig. 3.4 & Table 3.3).

### 3.3.3 Seasonal Patterns of Transpiration

When examining daily trends in transpiration throughout the four growing seasons, it was found that, at a given $D_Z$, maximum $J_{si}$ and EC (the asymptotic values in Figures 3 & 4) decreased when $\theta$ was low; however, under dry soil conditions we also observed the expected absence of very low $D_Z$ conditions, conditions that are common in the wetter periods (Figure 5). Thus, comparing daily means of growing season transpiration rates over the entire study period show that average $J_{si}$ (and thus $E_{ci}$) did not differ greatly between drought and non-drought periods (see box plots in Figures 2.3 & 2.4). Aggregating transpiration rates during drought and non-drought periods across all four years demonstrate that mean transpiration of *L. tulipifera* decreased appreciably during drought periods (19%; $p$-value <0.001), but less than the 34% decrease reflected in the asymptotic maximum values. Despite a decrease in maximum $J_{sr}$ no significant decrease in mean transpiration was observed in *Quercus* spp ($p$-value >0.5). In contrast, transpiration of *C. tomentosa* increased slightly under drought (5%; $p$-value <0.04), while average $J_{si}$ of *L. styraciflua* increased by 14% ($p <0.001$). It is important to note that this apparent increase in the average $J_{si}$ of *C. tomentosa* and *L. styraciflua* during the drought was not due to an increase in the sensitivity of transpiration to $D_Z$, but rather from a
similar sensitivity to $D_Z$ coupled with continuously high $D_Z$ days. This trend is even more apparent when comparing the sensitivity of stand-level $E_C$ to $D_Z$ during the drought because drought-insensitive species buffered the response of drought-sensitive species (Fig. 3.4). The overall effect is that $J_{si}$ and $E_C$ on any given drought day can be similar to that of a non-drought day.

Growing season (April-October) $E_C$ was very consistent among years (Table 2), despite large differences in the amount and timing of precipitation. Over the growing season, *Quercus* spp. comprised 38% (SD = 2% among the four years) of total $E_C$. Groups making the next largest contributions were *Carya* spp., *L. styraciflua*, and *L. tulipifera* at 19 (SD = 2), 16 (SD = 1), and 11 (SD = 1) %, respectively. Other species, which included most understory and some overstory trees, accounted for the remaining 17 (SD < 1) % of $E_C$.

### 3.3.4 Evapotranspiration

Atmospheric and soil conditions interact to affect components of evapotranspiration. Conditions that lead to drought, and thus high resistance to water flux from the biosphere to the atmosphere, are also associated with high atmospheric demand for biospheric moisture (Fig. 3.5).

The components of evapotranspiration along the range of soil moisture are shown in Fig. 3.6 not to imply causality, but to provide a frame of reference for atmosphere-soil conditions. Regression lines in Fig. 3.6 were selected based on $r^2$ and distribution of residuals. In cases where no regression was significant, the mean value is depicted as a horizontal dashed line (Table 4).

Despite reductions in daily $J_{si}$ at low $\theta$, when sap flux was scaled to the canopy-level, weekly $E_C$ during the growing season was weakly related to $\theta$, declining slightly at
very high or low θ values (Fig. 3.6a). Weekly $E_C$ typically ranged from 5 to 15 mm, although high $E_C$ (>12 mm week$^{-1}$) was not observed at the lowest θ.

$I_C$ was closely related to $P$ from daily to annual time scales. Thus, increasing $P$ led to a positive correlation between $I_C$ and θ at a weekly time scale (Fig. 3.6b). This linear relationship did not vary seasonally, despite large changes in LAI (Oishi et al., 2008). Annually, $I_C$ was 17.5 (SD = 0.6)% of $P$ (Table 2) and was the most variable component of ET$_{comp}$.

Daily $E_s$ varied with atmospheric conditions ($P$, $D$, and $R_{net}$), reaching highest daily maximum values during the summer months (Oishi et al., 2008). The majority of annual $E_s$ occurred during the growing season and was invariable among years (Table 3.2). Winter $E_s$ was more variable, but was a small portion of the hydrologic budget. Examining growing season trends, weekly $E_s$ was fairly invariable along the range of θ, with a slight increase at low θ (Figure 6c) reflecting the corresponding increase of $D_Z$ (Fig. 3.5). Our method for estimating $E_s$ as a function of $D$ is rather simplistic, yet the daily values were similar to those obtained based on the difference between LE and $E_C + I_C$ (Oishi et al., 2008). $D$ at the floor of deciduous forests has been shown to be similar to that above the canopy, and understory evaporation is better related to $D$ than to net radiation (Baldocchi and Meyers, 1991; Wilson et al., 2000), making $D$ the driver of choice for estimating $E_s$. Confidence in our estimates of $E_s$ is further enhanced noting that they were within the range observed by a sub-canopy eddy covariance system in a similar southeastern deciduous forest (Wilson et al., 2000).

Daily ET$_{comp}$, the sum of $E_s$, $E_C$, and $I_C$, varied widely mostly depending on the occurrence of rain events. Variability in growing season ET$_{comp}$ was still apparent when integrated weekly, ranging from about 5 to 30 mm week$^{-1}$ (Fig. 3.6d). However, similar
to the weekly variations in \( E_C \) and \( E_S \) (Figure 6a and c), the variation in growing season \( ET_{\text{comp}} \) was unrelated to \( \theta \).

Annual \( ET_{\text{comp}} \) averaged 633 mm yr\(^{-1}, 4.8\% \) (SD = 2.6\%) higher than LE but well within the uncertainty of LE estimates (Stoy et al., 2006; Oishi et al., 2008). Growing season \( ET_{\text{comp}} \) was fairly consistent amongst years. If we consider the moderately-wet year of 2004 as ‘normal’, growing season \( ET_{\text{comp}} \) in the dry years of 2002 and 2005 was approximately 16\% lower than normal, and was about 7\% lower than normal in the very wet growing season of 2003 (Table 3.2). Annual \( ET_{\text{comp}} \) was not as consistent as weekly growing season data (Fig. 3.6d) due to the incorporation of winter \( I_C \) and the distribution of environmental variables (e.g., \( P \) and \( D \)). \( E_C \) was consistently ~60\% of \( ET_{\text{comp}} \) throughout the growing season and this ratio showed little variability across the range of \( \theta \) (Fig. 3.6e). The sum of \( E_C \) and \( E_S \) ranged only 42 mm (from 420 to 462 mm yr\(^{-1} \)) or 7\% of mean annual \( ET_{\text{comp}} \). \( I_C \) varied 79 mm among years, or 12\% of annual mean \( ET_{\text{comp}} \).

### 3.3.5 Drainage and Runoff

\( Q \) was estimated as water draining below 0.30 m, the depth delineating the active rooting zone. \( Q \) occurred only when soil was sufficiently wet, greater than ~0.40 m\(^3\) m\(^{-3}\), conditions more frequently observed in winter months. Consequently, during the winters (2002, 2003, and 2005), \( Q \) comprised a large portion of the seasonal hydrologic budget (Table 2). \( P \) in winters of these years was similar, producing fairly similar \( Q \). The dry winter of 2004 had approximately half the \( Q \) of other years. Regardless of the total winter precipitation, low evaporative demand during this period allowed rainfall to fully recharge soil water to the point of saturation prior to each growing season.

Similar to winter months, growing season \( Q \) followed trends of \( P \). Seasonal \( F_O \) generally increased with \( P \); however, because overland flow requires rain falling on saturated soil surface, these events depended primarily on the timing of precipitation
events, as opposed to the seasonal total. $F_o$ exceeding 5 mm occurred on only 5 days in the wettest year (2003) and only once in 2002. Although this site is fairly flat and $F_o$ is not expected to be high, the combination of frequently saturated soil in the winter and micro-topographic features can result in redistribution of water either out of the stand or into low-lying areas within the stand where it is inaccessible to most trees, thus continuing to feed drainage.

### 3.3.6 Site water balance

Fig. 3.7 illustrates environmental drivers and the soil water budget over the beginning of the 2002 growing season, a time period characterized by high evapotranspiration and low $P$. Early growing season $E_C$ quickly increases during leaf expansion, and then follows a similar pattern to $E_S$ (Fig. 3.7b). These fluxes and their sum (Fig. 3.7c) show daily variation consistent largely with variations in the atmospheric drivers associated with $D_z$ and $P$ (Fig. 3.7a), but ultimately decline as the soil dries towards the end of the growing season. Daily $Q$ quickly declines to near-zero 20 days after the onset of the growing season, briefly punctuated by higher flows after rain events. However, because $P$ must first partially recharge soil water storage ($S$) before drainage can occur and available soil water is quickly used for evapotranspiration, very little $P$ is converted to $Q$ during the growing season. In Fig. 3.7d, modeled soil water storage in the upper 0.30 m was defined as $S_{mod} = P - (I_c + E_c + E_s + Q)$ (no $F_o$ occurred during this period). While $S_{mod}$ follows $S$ estimated from soil moisture probes ($S_{so}$ scaled for the upper 0.30 m) during the beginning of this period, $S_{mod}$ exceeds the amount of plant available water in that layer by DOY 155. This illustration demonstrates that without adequate precipitation, soil water storage in the upper 0.30 m was not sufficient to meet growing season water demands and water extraction from deeper soil must be invoked.
The full hydrologic balance, based on measured $P$, estimated $E_C$ and $E_S$, and modeled $Q$ and $F_O$ is displayed as cumulative totals in Fig. 3.8. As previously mentioned, annual $E_S$ was generally insensitive to $P$ ($p$-value >0.50). Annual $E_C$ showed a relationship with $P$ ($p$-value=0.064), but the low-significance of the slope (-0.038) shows only a small decrease in transpiration with increasing $P$. Annual $I_C$ does exhibit a linear increase with $P$ ($I_C = 0.175 \times P$; $p$-value <0.001, intercept not significant). Averaging the four years, our hydrologic budget overestimated total $P$ by <5% (SD = 3%). Hence, with the modeled estimates of $Q$ and $F_O$, we demonstrate a nearly balanced annual hydrologic budget (lack of closure not significantly different than zero, $p$-value=0.85; Table 2). While $I_C$ increased with $P$, after accounting for $E_S$ and $E_C$, changes in $P$ did not appear to lead to changes in $ET_{\text{comp}}$. Consequently, the variability in annual $P$ matched well the variability in outflow ($O = Q + F_O$).

3.4 Discussion

We found that the transpiration rate of certain species was greatly reduced by drought when compared under similar atmospheric conditions at diurnal and daily time scales. However, no drought effects were noticeable when transpiration was integrated seasonally or annually. At these longer periods, large interannual variation in precipitation was accompanied by much smaller variation in transpiration as well as in total evapotranspiration. We first discuss the processes responsible for producing conservative interannual transpiration and evapotranspiration, followed by an analysis of the implication to downstream water users.
3.4.1 Species differences of drought sensitivity and conservative stand transpiration

Among the species investigated in this study, L. tulipifera showed the strongest JS sensitivity to drought, similar to previous findings for this species which experiences premature leaf loss during prolonged droughts (Pataki and Oren, 2003). In contrast, L. styraciflua in our study did not show the level of sensitivity observed in that study. We confirmed that Carya is one of the most drought-tolerant genera in southeastern hardwood stands (Oren and Pataki, 2001; Wullschleger and Hanson, 2003). However, although Quercus species typically exhibit low degrees of drought-sensitivity in this region (Oren and Pataki, 2001; Wullschleger and Hanson, 2003), often attributed to deeper rooting than co-occurring species (Bovard et al., 2005), our study showed that once $\theta$ in the upper rooting zone of our stand dropped below 0.20 m$^3$ m$^{-3}$, species of this genus exhibited a pronounced sensitivity to drought (Fig. 3.3d).

Had the distribution of tree species been such that drought-insensitive species were concentrated in the dry plot and drought-sensitive species in the wet plot, an apparent stand-level drought-insensitivity of transpiration could have been attributed to within-site differences in species composition. However, the most drought-sensitive species (L. tulipifera) represented a greater proportion of sapwood area in the dryer site (Oishi et al., 2008). Similarly, the drought-sensitive understory species Cornus florida and Acer rubrum (Wullschleger and Hanson, 2006) were present in both plots. These results suggest that conservative annual $E_C$ can be achieved though a mechanism other than shifts in species composition.

One third of the total sapwood area in the stand belonged to drought-sensitive species. During our example drought day, their $J_s$ decreased, leading to a lower $E_C$ than on the reference non-drought day (1.51 mm d$^{-1}$ versus 2.12 mm d$^{-1}$; compare Fig. 3.2e,f), even though $D$ was 2.5 times greater (Fig. 3.2b & c), providing a greater force to drive
evapotranspiration. However, the very low \(D\) on the rainy day led to much greater reductions in \(E_C\) than the drought, declining to 0.21 mm d\(^{-1}\) (Fig. 3.2a,d). The effect of rainy days goes beyond drastically reducing \(D\) in the same day; rain events keep soil moist and \(D\) low for several days. Indeed, over the four growing seasons, weekly \(D_z\) remained low as long as precipitation kept \(\theta\) above 0.20 m\(^3\) m\(^{-3}\); however, as \(\theta\) dropped below this threshold, \(D_z\) increased rapidly (Fig. 3.5). Based on these results, rainy conditions with moist soil can lead to depressed \(E_C\) on time scales ranging from diurnal to seasonal (Table 3.2) and even annual. Indeed, \(E_C\) was lowest in 2003, the wettest year in our study period, causing a slightly declining trend in transpiration with \(P\) (reflected in the narrowing of the white band in Fig. 3.8 with increasing \(P\); Table 3.2).

Although \(E_C\) across all times scales was sensitive to precipitation, the sensitivity decreased with integration time. The decrease in sensitivity of \(E_C\) despite changing soil moisture is driven by the interactions between \(\theta\) and \(D_z\) (Fig. 3.5) and modulated by the stomatal response to \(D\) (Oren et al., 1999, see Appendix). For example, the long-term, daytime, growing season mean \(D\) at the site is 0.75 kPa; however, mean growing season daytime \(D\) during the drought year of 2002 was 1.37 kPa, theoretically maintaining annual \(E_C\) at 95% of the average rate (see Appendix 3.6). Based on the analysis shown in Appendix 3.6, average \(D\) over the growing season would have to be \(\approx 1.54\) kPa for the atmospheric demand to fully compensate for drought-induced reductions in conductance.

Because low \(D_z\) days are not present during drought periods, the average stand-level transpiration rates may remain similar to the rates during wet periods regardless of species composition. To examine the maximum possible influence species composition could have over \(E_C\) under drought conditions, we ran simulations assuming all trees in our stand were a single species, either the most drought sensitive \(L.\) tulipifera, or the least...
sensitive *L. styraciflua* using $D_Z$ and $P_T$ from the drought year 2002 as inputs. Trees within the one-hectare plot surrounding the tower were assigned sapwood area depending on the characteristics of either species. $E_s$ as a function of $D$, and $I_C$ as a function of $P$ remained the same. $E_C$ was estimated using functions from Table 3.3 (after scaling $J_S$), thus allowing for different responses to $D_Z$ depending on our dynamic `0 calculations. Our hypothetical forest comprised exclusively of *L. tulipifera* resulted in a decrease of only 7% (21 mm) of the annual $E_C$ in 2002 relative to the actual forest. When the characteristics of *L. styraciflua* were assigned to all trees, annual $E_C$ in 2002 was practically unaffected (+4 mm). Thus, regardless of species composition, the high $D$ conditions during drought period are sufficient to maintain average $E_C$ similar to that of wet periods.

Clearly, this conclusion cannot be generalized to a long series of drought years. For example, a similar hardwood forest in this region (Wilson et al., 2001), also exhibited small interannual variability in $E_C$ (C.V. $= 10\%$) with no apparent response to annual $P$; however, in a long-term experiment where throughfall was manually reduced by a third growing season $E_C$ was reduced an average of 23% (SD $= 8\%$) compared to ambient plots (Wullschleger and Hanson, 2006). These results suggest that droughts of increasing severity and frequency could ultimately result in mortality of certain species and a change in the forest’s species composition.

Because we estimated the components of the hydrologic budget over the majority of the eddy covariance footprint (Oishi et al., 2008) and positioned sensors in one of the wettest micro-sites, it is not likely that spatial variation in the hydrological budget is responsible for the apparent water deficit in the upper 0.30 m soil (Fig. 3.7). Instead, the results suggest that trees were accessing water beneath the depth of the lower soil moisture probes even though the majority of fine roots were concentrated in
the upper 0.30 m. Uptake from deeper soil can sustain transpiration in hardwood species during drought, albeit at a reduced rate (Wullschleger and Hanson, 2006). Based on the modeled drainage, this water extraction was estimated to range from 23 mm (3% of ET$_{\text{comp}}$) during the wet year of 2003 to 53 mm (9%) during the dry year of 2002.

### 3.4.2 Evaporation and drought

Although we have shown how species’ sensitivities to soil moisture and atmospheric conditions, combined with the frequency distributions of these conditions, can help stabilize annual $E_C$, we must also consider other evaporative losses to explain the observed invariability in evapotranspiration.

Again, let us consider the example drought and non-drought days (Fig. 3.2). Rain did not occur for several days prior to either of these days, so $I_C$ can be assumed zero. $E_C$ decreased with drought but eddy covariance-based LE increased from 3.05 mm to 3.28 mm, suggesting that ES compensated for the reduction in $E_C$. Approximating $E_S$ using LE- $E_C$, evaporation increased by 0.81 mm from the non-drought to the drought day (from 0.95 to 1.76 mm), similar to the difference between these days in the D-based estimates of $E_S$ (0.85 mm; 0.27 and 1.12 mm, respectively).

Roots that extended below 0.30 m are able to tap into deeper pools of water when the upper layers are exhausted, supplying not only $E_C$, but also potentially $E_S$ through hydraulic redistribution (Emerman and Dawson, 1996; Caldwell et al., 1998). According to a modeling study for this soil type and shallow rooting depth, hydraulic redistribution is at its maximum when $\theta$ is between 0.15 and 0.20 m$^3$ m$^{-3}$ (Siqueira et al., 2008). Under peak drought conditions in our study ($\theta < 0.20$ m$^3$ m$^{-3}$), several $\theta$ sensors positioned at 0.05-0.10 m depth exhibited nightly increases of 0.0075 m$^3$ m$^{-3}$. When these increases are scaled to the upper 0.15 m soil, they translate to 1.125 mm d$^{-1}$, approaching the 2 mm d$^{-1}$ of $E_S$ estimated during these periods. Because water is simultaneously
added to the top soil layer through hydraulic redistribution and subtracted through evaporation, the pattern observed by the soil moisture sensors represents only a portion of the hydraulic lift.

Daily, drought conditions which reduced $E_C$ corresponded with increased $E_S$. Weekly, as $\theta$ decreased, no changes were observed in weekly $ET_{comp}$ or the ratio of $E_C$ to $ET_{comp}$ (Fig. 3.6 & Table 3.4), suggesting that evaporative losses were fairly consistent through the growing season. Integrated over the growing season or annually, the relatively high rates of $E_S$ during droughts did not completely compensate for the reduction in the other component of evaporation, $I_C$, though they weakened the relationship between $ET_{comp}$ and $P$ (Fig. 3.8). These processes, driven by the inverse, non-linear relationship between $D$ and $\theta$, produce annual stand evapotranspiration that is a fairly conservative quantity ($CV = 4\%$) in comparison to average annual $P$ ($17\%$) or PET ($10\%$). The annual precipitation in the driest year of this study exceeded $ET_{comp}$ and extrapolation of the observed patterns (Fig. 3.8) suggests that the evapotranspiration demands of the forest would likely be met even in the driest year on record.

3.4.3 Downstream implications

At an annual time-scale, each component of the hydrologic budget showed a different sensitivity to changes in $P$ (Fig. 3.8). Assessing the annual hydrologic budget (Eq. 1) in terms of changes in precipitation can be done based on

$$\delta P = \delta I_C + \delta E_S + \delta E_C + \delta Q + \delta F_O$$

(Changes in annual storage ($\Delta S$) are $<15 \text{ mm yr}^{-1}$ due to ample winter precipitation and can be neglected.) The combination of these terms based on the information in Figure 6 results in $\delta I_C + \delta E_S + \delta E_C = 0$ with respect to $\delta P$ ($p$-value $>0.20$), allowing Eq. (3) to be expressed as $\delta P = \delta Q + \delta F_O$. Thus, once precipitation (reasonably well-distributed throughout the growing season) exceeds the annual minimum used by the forest for
evapotranspiration (~577 mm, indicated by the dotted line in Fig. 3.8), each millimeter increase of P should lead to a millimeter increase of outflow \( (O = Q + F_o) \) from this forest stand, augmenting the supply to groundwater and downstream water bodies.

To estimate long-term mean outflow from our site, we linearly regressed annual outflow versus P and employed the long-term average P at the site (1146 mm). Based on the regression for our site \( (O = 0.881 \times P - 478, r^2=0.99, n=4 \text{ years}) \), long-term mean outflow was 535 mm, close to (only 8% lower) the outflow from a similar Tennessean forest \( (O = 0.720 \times P - 317, r^2=0.85, n=8 \text{ years}; \text{after } (Hanson \text{ et al., 2003; } Hanson \text{ et al., 2004}) \). Although species composition can alter outflow if it leads to differences in \( E_C \) (Hornbeck et al., 1997), and certain species are indeed so sensitive to drought that a strong reduction is observed in evapotranspiration in years of low P (Stoy et al., 2006), the simulated annual water budgets based on the most drought-sensitive broadleaved species in this study resulted in only small changes \( E_C \) and thus \( Q \). Our results support the notion that forest transpiration can be interannually conservative, largely independent of precipitation or exact species richness, making downstream outflow the most sensitive hydrologic flux to variations in \( P \).

Drainage and runoff from forests depend not only on precipitation, but also evapotranspiration and soil moisture. We compared streamflow from seven watersheds to precipitation and our estimate of outflow. Although this type of broadleaf stand represents on average 44% of the watershed area, outflow from such forests is similar to that estimated from pine covered areas (Schäfer et al., 2002; Kim, 2009), so our estimate of outflow represents approximately two thirds of the area, with the remainder covered mostly by agriculture and pasture fields. Assuming that our forest outflow rates represents the rates from the entire watersheds, we find that the variation in monthly streamflow was explained appreciably better by outflow than precipitation (Fig. 3.9a, b).
Annually, the estimated outflow set an upper limit for water flow in nearby streams, and by extension to inflow of a reservoir fed by these streams (Fig. 3.9c). The upper limit represents the maximum potential drainage to downstream water supply, excluding other water losses from the system such as subsurface flow, deep infiltration, groundwater withdrawal, and additional evaporation from locally impounded water, together producing an average offset of 143.8 (SD = 69.5) mm yr\(^{-1}\). Fig. 3.9c illustrates that water supply downstream is not proportionate to precipitation, but is offset by a relatively consistent evapotranspiration demands (nearly 700 mm yr\(^{-1}\) in this area) and then receives nearly all subsequent precipitation. Clearly, different dominant mechanisms and evapotranspiration responses can be expected in different biomes, further complicated by land cover conversions. However, our analysis shows that in areas dominated by forests, tree physiology and forest hydrology extract a tax on precipitation before allowing water to move on to downstream water users.

### 3.5 Summary

Species-level reductions in transpiration during drought often result in lower-than-maximum canopy-level transpiration observed under comparable atmospheric conditions. However, on the annual time scale, even severe growing season droughts may not lead to reductions in annual transpiration because the magnitude and duration of drought-induced reductions of canopy transpiration are similar to the magnitude and frequency of reductions in transpiration associated with rain events in wet years. Furthermore, evapotranspiration can remain consistent among years because atmospheric conditions associated with drought (i.e. high radiation and atmospheric vapor deficit) provide a strong driving force for both canopy transpiration and soil evaporation, compensating for reduced canopy interception losses. The resulting conservative behavior of evapotranspiration means that changes in annual precipitation
lead to similar changes in the amount of water that flows from forests to streams and reservoirs.
Table 3.1: Stand characteristics. Coefficients of the relationship between sapwood area ($A_S$) and basal area ($A_B$) for the equation in the form $A_S = \alpha \times A_B^b$ where both variables are in cm$^2$ per m$^2$ ground area. The stand-level mean of $A_S$ and leaf area index (LAI) is in m$^2$ m$^{-2}$ represents an average over the four study years (after Oishi et al., 2008).

<table>
<thead>
<tr>
<th>Species</th>
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<th>$b$</th>
<th>$A_S$</th>
<th>LAI</th>
</tr>
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<td>2.010</td>
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<td>L. styraciflua</td>
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<td>2.202</td>
<td>2.96</td>
<td>0.69</td>
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<td>Carya spp.</td>
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<td>1.669</td>
<td>3.41</td>
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<td>Q. alba</td>
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<td>1.737</td>
<td>0.52</td>
<td>0.57</td>
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<td>1.737</td>
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<td>Q. phellos</td>
<td>0.284</td>
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<td>0.11</td>
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<tr>
<td>Other species</td>
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<td>2.202</td>
<td>2.78</td>
<td>2.11</td>
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<tr>
<td><strong>TOTAL</strong></td>
<td></td>
<td></td>
<td>13.71</td>
<td>6.17</td>
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Table 3.2: Flux components of the annual hydrologic budget for each year and partitioned to growing season (April through October), and dormant season (January through March and November through December): Precipitation ($P$), potential evapotranspiration (PET), canopy interception ($I_C$), transpiration ($E_T$), soil evaporation ($E_s$), evapotranspiration ($ET_{comp}$), latent heat flux (LE), overland flow ($F_O$), drainage ($Q$), outflow ($O = F_O + Q$), residual ($R + P - ET + O$) (all values in mm).

<table>
<thead>
<tr>
<th>Year</th>
<th>$P$</th>
<th>PET</th>
<th>$I_C$</th>
<th>$E_T$</th>
<th>$E_S$</th>
<th>$ET_{comp}$</th>
<th>LE</th>
<th>$F_O$</th>
<th>$Q$</th>
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<td>84</td>
<td>610</td>
<td>577</td>
<td>62</td>
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<td>618</td>
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<td>346</td>
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<td>635</td>
<td>618</td>
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<tr>
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<td>339</td>
<td>103</td>
<td>633</td>
<td>605</td>
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<tr>
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<td>26</td>
<td>19</td>
<td>50</td>
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<td>59</td>
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<td>873</td>
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<td>69</td>
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<td>520</td>
<td>49</td>
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<tr>
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<td><strong>Dormant Season</strong></td>
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<td>9</td>
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<td>75</td>
<td>85</td>
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Table 3.3: Regression information for Figures 3.3 and 3.4. Equations relating day-length normalized vapor pressure deficit ($D_Z$, kPa) to water flux based on either limiting ($\theta < 0.20 \text{ m}^3 \text{ m}^{-3}$) or non-limiting ($\theta \geq 0.20 \text{ m}^3 \text{ m}^{-3}$) soil moisture conditions. Data were fit with an exponential rise to maximum function; $y = a(1-\exp(-b \cdot D_Z))$ where $y$ is $J_{sl}$ (g H$_2$O m$^{-2}$ sapwood area d$^{-1}$) for individual genera or $E_C$ (mm H$_2$O d$^{-1}$). All regressions and the effect of $\theta$ (extra sum of squares F-test) are significant ($p$-value <0.001).

<table>
<thead>
<tr>
<th>Species</th>
<th>$\theta$</th>
<th>$a$</th>
<th>$b$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. tulipifera</em></td>
<td>Non-limiting</td>
<td>173.0803</td>
<td>6.7442</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Limiting</td>
<td>113.5015</td>
<td>3.0316</td>
<td>0.15</td>
</tr>
<tr>
<td><em>L. styraciflua</em></td>
<td>Non-limiting</td>
<td>150.2446</td>
<td>4.9187</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>Limiting</td>
<td>151.7859</td>
<td>3.5586</td>
<td>0.49</td>
</tr>
<tr>
<td><em>Carya</em> spp.</td>
<td>Non-limiting</td>
<td>186.5391</td>
<td>8.4670</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>Limiting</td>
<td>171.7235</td>
<td>8.8670</td>
<td>0.36</td>
</tr>
<tr>
<td><em>Quercus</em> spp.</td>
<td>Non-limiting</td>
<td>212.6332</td>
<td>7.5055</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>Limiting</td>
<td>181.4982</td>
<td>9.4501</td>
<td>0.27</td>
</tr>
<tr>
<td>$E_C$</td>
<td>Non-limiting</td>
<td>2.0791</td>
<td>6.9150</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Limiting</td>
<td>1.7708</td>
<td>7.5950</td>
<td>0.42</td>
</tr>
</tbody>
</table>
Table 3.4: Regression information for Figures 3.5 and 3.6. Equations relating mean weekly soil moisture ($\theta$; m$^3$ m$^{-3}$) for 2002-2005 growing seasons and day-length normalized vapor pressure deficit ($D_Z$; kPa), canopy transpiration ($E_C$; mm), canopy interception ($I_C$; mm H$_2$O), soil evaporation ($E_S$; mm H$_2$O), component-based evapotranspiration ($ET_{comp}$; mm H$_2$O), and the ratio of $E_C$ to $ET_{comp}$. Regressions were selected based on $r^2$ and distribution of residuals. In cases where regressions were not significant ($p$-value >0.01), the mean value is given.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Equation</th>
<th>$r^2$</th>
<th>$p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$D_Z$</td>
<td>0.30+$8.47\exp(-20.02\theta)$</td>
<td>0.54</td>
<td>$&lt;0.0001$</td>
</tr>
<tr>
<td>$E_C$</td>
<td>$8.06+26.75\theta-54.64\theta^2$</td>
<td>0.09</td>
<td>0.0070</td>
</tr>
<tr>
<td>$I_C$</td>
<td>18.76\theta-0.52</td>
<td>0.18</td>
<td>$&lt;0.0001$</td>
</tr>
<tr>
<td>$E_S$</td>
<td>5.92-22.78\theta+31.94\theta^2</td>
<td>0.16</td>
<td>0.0001</td>
</tr>
<tr>
<td>$ET_{comp}$</td>
<td>19.21</td>
<td>--</td>
<td>0.30</td>
</tr>
<tr>
<td>$E_C/ET_{comp}$</td>
<td>0.593</td>
<td>--</td>
<td>0.73</td>
</tr>
</tbody>
</table>
Figure 3.1: Environmental variables measured at the studied broadleaf deciduous forest. (a) daylength normalized vapor pressure deficit ($D_z$), (b) weekly totals of precipitation ($P$), (c) soil moisture ($\theta$) measurements from dry and wet sap flux plots, with the value at which stomatal closure begins (0.20 m\(^3\) m\(^{-3}\)) indicated as horizontal dashed line, (d) canopy leaf area index (LAI), (e) canopy transpiration from scaled sap flux measurements ($E_C$), estimated canopy interception ($I_C$), and total component-based evapotranspiration ($ET_{comp}$).

Duke Forest, NC 2002-2005
Figure 3.2: Time series from three example days representing an early growing season day receiving 14.8 mm in a rain event lasting most of the day (a, d), an early growing-season dry day with ample soil moisture (b, e), and a late growing season day under drought conditions (c, f). Half-hourly values of vapor pressure deficit (D) and above-canopy photosynthetically active radiation (PAR) (a, b, and c); sap flux density ($J_{si}$) for the outer 20 mm of xylem for the observed species (error bars represent 1 S.E.).
Figure 3.3: Response of daily species-specific sap flux \(J_{si}\) to day-length normalized vapor pressure deficit \(D_z\) under non-limiting soil moisture conditions \(\theta \geq 0.20 \text{ m}^3 \text{ m}^{-3}\), open circles) and limiting conditions \(\theta < 0.20 \text{ m}^3 \text{ m}^{-3}\), closed triangles) during growing seasons 2001–2005. Corresponding box plots of \(J_{si}\) for normal (white box) and drier (grey box) conditions show median, 25th/75th percentile, 10th/90th percentile, and 5th/95th percentile with the center line, box, whiskers and +, respectively. See Table 3.3 for information on regression statistics.
Figure 3.4: Response of daily stand-level transpiration ($E_C$) to day-length normalized vapor pressure deficit ($D_2$) under non-limiting soil moisture conditions ($\theta \geq 0.20 \text{ m}^3 \text{ m}^{-3}$, open circles) and limiting conditions ($\theta < 0.20 \text{ m}^3 \text{ m}^{-3}$, closed triangles) during growing seasons 2001–2005. Corresponding box plots of $E_C$ for normal (white box) and drier (grey box) conditions show median, 25th/75th percentile, 10th/90th percentile, and 5th/95th percentile with the center line, box, whiskers and +, respectively. PDF of $D_2$ during limiting and non-limiting soil moisture conditions; triangles are positioned at mean values. See Table 3.3 for information on regression statistics.
Figure 3.5: Relationship between mean weekly soil moisture (\( \theta \)) during the four growing seasons and day-length normalized vapor pressure deficit (\( D_z \)). See Table 2.4 for information on regression.
Figure 3.6: Relationship between mean weekly soil moisture ($\theta$) during four growing seasons and (a) canopy transpiration ($E_c$), (b) canopy interception ($I_c$), (c) soil evaporation ($E_s$), (d) component-based evapotranspiration ($ET_{comp}$), and (e) ratio of EC to $ET_{comp}$. See Table 4 for information on regressions.
Figure 3.7: Time series from the driest growing season of (a) day-length normalized vapor pressure deficit ($D_z$) and precipitation ($P$), (b) evaporative fluxes of canopy transpiration ($E_c$) and soil evaporation ($E_s$), (c) soil water fluxes from the top 0.30 m of soil from $E_s + E_c$ and drainage ($Q$), (d) soil water storage in the top 0.30 m of soil based on scaled soil moisture probe values ($S_i$) and estimated based on throughfall precipitation ($P_f$) minus $E_s + E_c + Q$ ($S_{mod}$).
Figure 3.8: A comparison of annual precipitation with additive components of hydrologic budget. Closed symbols represent components of evapotranspiration whereas open symbols represent components of water outflow. The dashed vertical lines represent the lowest (714 mm) and highest (1591 mm) annual precipitation in the past 115 years. Dashed diagonal lines represent linear regressions approximating the sensitivity of components of the hydrologic budget to precipitation. Dotted line and arrow indicate the level of annual precipitation where drainage is theoretically equal to zero (577 mm).
Figure 3.9: Comparisons of monthly stream flow from seven local gauging stations with (a) precipitation and (b) water outflow (drainage + runoff) from the study site (volume per unit time per unit watershed area) from 2002–2005. The relationship with precipitation has a significant negative intercept ($p$-value $<0.05$) whereas that with outflow is not significant (0.44). (c) Comparisons of annual precipitation from seven meteorological stations in the watershed with estimated watershed outflow (based on combined broadleaf and pine forest outflow; dashed line) and with stream-flow (closed circles) and inflow to a nearby reservoir (open circles). Annual downstream water flow varied linearly with precipitation ($r^2 = 0.77$, $p$-value $<0.0001$). Error bars represent 1 standard deviation. Stream flow was highly correlated with inflow rate to local reservoirs ($r^2 = 0.91$, $p$-value $<0.0001$, data not shown).
3.6 Appendix: Theoretical basis for invariability in transpiration

When the canopy is well coupled to the atmosphere, canopy-level transpiration \( (E_c) \) can be expressed as a function of vapor pressure deficit \( (D) \) and canopy-level conductance \( (G_s) \),

\[
E_c = G_s \cdot D \quad \text{(A1)}.
\]

Thus, changes in \( E_c \) with respect to changes in precipitation \( (P) \) at an annual or growing season time scale, can be expressed as

\[
\frac{\partial E_c}{\partial P} = \frac{\partial}{\partial P} (G_s D) \quad \text{(A2)}.
\]

If transpiration is invariable with annual \( P \), then \( \frac{\partial E_c}{\partial P} = 0 \). Rearranging Eq. (A2) gives us

\[
0 = D \frac{\partial G_s}{\partial P} + G_s \frac{\partial D}{\partial P} = D \frac{\partial G_s}{\partial P} + G_s \frac{\partial D}{\partial P} \quad \text{(A3)}
\]

or,

\[
D \frac{\partial G_s}{\partial \theta} \frac{\partial \theta}{\partial P} = -G_s \frac{\partial D}{\partial P} \quad \text{(A4)}.
\]

Under wet conditions, we expect that changes in \( P \) and subsequent changes in \( \theta \) will not result in changes in \( G_s \) (conductance is no longer water limited) or \( D \) (relative humidity is not varying appreciably and much of the variations in \( D \) are induced by variations in air temperature through the saturation vapor pressure). Hence, in a first order analysis, wet conditions result in \( \frac{\partial G_s}{\partial \theta} = 0 \) and \( -G_s \frac{\partial D}{\partial P} = 0 \). However, under dry conditions, reductions in \( P \) lead to reductions in \( \theta \) and rearranging Eq. (A4) results in

\[
\frac{\partial G_s}{G_s} \approx -\frac{\partial D}{D} \quad \text{(A5)}.
\]
The invariance in $E_C$ can occur if changes in $D$ due to precipitation are balanced by change in $G_S$. That is, low $P$ at seasonal or annual time scales leads to high $D$, the driving force for $E_C$, but increasing $D$ is countered by reduced $G_S$, leading to invariant $E_C$. The negative relationship between $G_S$ and $D$ (Eq. A4) is well-established, given for example by

$$G_S = G_{S\text{ref}} (1 - m \cdot \ln(D))$$  \hspace{1cm} (A6)

where $G_{S\text{ref}}$ is the a reference value of $G_S$ at $D=1$ kPa (Oren et al., 1999). Using this formulation, the sensitivity of $G_S$ with respect to $D$ respect to is

$$\frac{\partial G_S}{\partial D} = \frac{-G_{S\text{ref}} m}{D}$$  \hspace{1cm} (A7).

Combining Eqs. (A6) and (A7) results in

$$\frac{\partial G_S}{G_S} = -\frac{m}{1-m \cdot \ln(D)} \frac{\partial D}{D}$$  \hspace{1cm} (A8).

If $\frac{m}{1-m \cdot \ln(D)} = 1$, Eq. (A8) will be identical to Eq. (A5). Note that $\frac{m}{1-m \cdot \ln(D)}$ is primarily driven by long-term $D$ values at the site and by the species’ sensitivity to $D$ through $m$. In this bottomland hardwood forest $m$ across species was estimated at ~0.7 (Pataki and Oren, 2003) and because the variation of $D$ originates from coarse-scale climatic factors, this formulation should hold for the entire stand. Estimating

$$\frac{m}{1-m \cdot \ln(D)}$$

using average daytime growing season $D$ (on a half-hourly basis, to account for the non-linearity of this function, and for fully-expanded leaf area index >5 \text{m}^2 \text{m}^{-2}), a value of 0.95 was obtained. In other words, the \(\theta-D\) interaction and stomatal response to $D$ during the dry 2002 growing season explained 95\% of the invariability in $E_C$. 

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4. Spatial and temporal variability of soil CO$_2$ efflux in three proximate temperate forest ecosystems

The magnitude of CO$_2$ flux from soil ($F_{\text{soil}}$) varies with primary productivity and environmental drivers of respiration, soil temperature ($T_{\text{soil}}$) and moisture, all of which vary temporally and spatially. To quantify the sources of $F_{\text{soil}}$ variability, we compared $F_{\text{soil}}$ of three proximate forests ranging in age, composition, soil, and environment and, thus, productivity. We collected data during a 10-year period with automated soil respiration chambers in a mid-rotation (PP) and mature (OP) *Pinus taeda* stands and a mature, mixed-species hardwood (HW) stand; PP and HW were on clay-loam soil and OP on a sandy soil. Among stands, sensitivity to $T_{\text{soil}}$ was lowest in OP and highest in PP, reflected in mean annual $F_{\text{soil}}$ of 1033 (OP), 1206 (HW), and 1383 (PP) g C m$^{-2}$, increasing with leaf litterfall. Among four plots within PP, sensitivity of $F_{\text{soil}}$ to $T_{\text{soil}}$ was similar, yet higher leaf area lowered soil temperature, belowground carbon flux, and $F_{\text{soil}}$. Temporally, diurnal to seasonal variation of $F_{\text{soil}}$ followed $T_{\text{soil}}$ whereas inter-annual variability was driven by soil moisture. Spatially, among stands in a similar region, $F_{\text{soil}}$ increased with leaf production, whereas within a stand (PP) $F_{\text{soil}}$ decreased with increasing leaf production.

4.1 Introduction

Terrestrial ecosystem respiration is the second largest flux of CO$_2$ globally, just shy of terrestrial photosynthesis (Raich and Schlesinger, 1992; Schimel *et al.*, 2001). Because the balance between carbon (C) loss and gain greatly influences terrestrial C storage, quantifying the sources of variation of ecosystem respiration is critical for assessing the influence of terrestrial ecosystems on atmospheric CO$_2$ concentrations.

The largest loss of C from terrestrial ecosystems occurs as CO$_2$ flux from the soil surface (hereinafter $F_{\text{soil}}$; Ryan and Law, 2005). $F_{\text{soil}}$ is comprised of both autotrophic and
heterotrophic respiration and is affected by a set of interacting environmental and physiological variables, leading to large variability spatially and temporally (Curiel Yuste et al., 2005; Litton et al., 2007; Martin and Bolstad, 2009). Empirical models of $F_{soil}$ typically employ soil temperature ($T_{soil}$) and moisture that implicitly capture the primary biophysical processes driving $F_{soil}$ (Fang and Moncrieff, 2001; Davidson and Janssens, 2006). $T_{soil}$ directly affects enzyme kinetics, but it also co-varies with solar radiation and physiological seasonality, and thus belowground photosynthetic inputs (Irvine et al., 2008; Savage et al., 2009). In addition, the seasonal and spatial pattern of $T_{soil}$ likely affects fine root and microorganisms population size (Fenn et al., 2010; Taneva and Gonzalez-Meler, 2011; but see Moyano et al., 2008). Thus, high temporal resolution $T_{soil}$ often explains much of the temporal variability of $F_{soil}$ at a given site (Palmroth et al., 2005; Martin and Bolstad, 2009; Phillips et al., 2010). In contrast, the low-resolution mean annual $T_{soil}$ typically fails to explain much of the spatial, among-forest variation of annual $F_{soil}$ (Janssens et al., 2001; Reichstein et al., 2003; Bahn et al., 2010). Soil moisture has a direct effect on $F_{soil}$, limiting microbial activity at low values (Gaumont-Guay et al., 2006; J.E. Drake, unpublished), and indirectly by reducing air-filled porosity and limiting CO$_2$ diffusion to the surface at high values (Risk et al., 2002; Suwa et al., 2004; Riveros-Iregui et al., 2007; Maier et al., 2011). Drought stress can also limit photosynthesis through stomatal regulation (Oren and Pataki, 2001; Schäfer et al., 2002) and result in decreased fine root production (Pritchard et al., 2008). Indeed, the number and complexity of processes ultimately producing the measured $F_{soil}$ facilitates parameterization of physical-physiological models of $F_{soil}$ in only few intensively studied stands (e.g., Suwa et al., 2004; Phillips et al., 2011).

Considering the complexities of process-based soil respiration models (Manzoni and Porporato, 2009) it is unlikely there will ever be enough information available to
parameterize such models for the wide range of conditions needed for broad application. Therefore, to provide information for constraining global vegetation-modeled estimates of terrestrial respiration, efforts have been made to empirically summarize the results of the few available studies – each essentially based on point measurements as indicator variables – to facilitate scaling $F_{\text{soil}}$ to regions and beyond with simple indices. Such empirical relationships rely on the aforementioned physical variables, or their ecological reflection: gross primary production (GPP) or the more easily obtained leaf area index (LAI) and associated litterfall (Davidson et al., 2002; Palmroth et al., 2005; Bahn et al., 2010; Bond-Lamberty and Thompson 2010; Chen et al., 2010).

Primary production supplies carbon for $F_{\text{soil}}$. Although certain fractions of soil organic matter shows very slow turnover time, ranging to centuries (Trumbore, 2000), much of $F_{\text{soil}}$ is comprised of recently-assimilated C (Johnsen et al., 2007; Högberg et al., 2007; Mencuccini and Hölttä, 2010). However, estimates of primary productivity (GPP and net primary production, NPP) and partitioning of GPP to belowground (total belowground C flux, TBCF, Giardina & Ryan, 2002) are often difficult to obtain with precision, making LAI (or its correlate – litterfall) an attractive proxy often used to explain the variation of $F_{\text{soil}}$ (Davidson et al., 2002; Reichstein et al., 2003; Palmroth et al., 2005). And yet LAI may relate to $F_{\text{soil}}$ positively or negatively, depending on resource availability and associated partitioning of GPP between above-and belowground parts (McCarthy et al., 2006; Palmroth et al., 2006; Novick et al., 2012). Palmroth et al. (2006) showed that across young forests of different species and stages of development, $F_{\text{soil}}$ seemed to increase with LAI at very low LAI, essentially reflecting increasing soil volume occupation by roots. At moderate to high LAI the relationship reversed as TBCF decreased with increasing LAI, because over this part of the range in LAI its increase
was driven by increasing soil fertility (McCarthy et al., 2007), reducing the need for and amount of fine roots (Jackson et al., 2009).

Total belowground carbon flux provides for respiration, production of root biomass, and exudation of carbohydrates. Because much of this material turns over quickly (Pritchard et al., 2008), TBCF and $F_{\text{soil}}$ are closely related (Palmroth et al., 2006). On the other hand, because much of aboveground NPP consists of foliage production, increases in aboveground C partitioning leads to increased litterfall and forest floor decomposition (Davidson et al., 2002; Schäfer et al., 2003). Thus, a negative relationship between LAI and TBCF and a positive relationship between LAI and litterfall have opposite effects on annual $F_{\text{soil}}$. Furthermore, seasonal dynamics of LAI and its activity, which vary among forest types, may play an important role in determining TBCF and litterfall (Curriel Yuste et al., 2004), as well as modulating $T_{\text{soil}}$ (Palmroth et al., 2005; Phillips et al., 2010) and soil moisture. Thus, neither LAI not leaf litterfall are likely to provide a general index of $F_{\text{soil}}$ among and within forest types (Litton et al., 2007).

In our previous studies we found that a mid-rotation loblolly pine plantation (PP) and a mature mixed-species deciduous hardwood stand (HW), both on clay-loam soil and similar maximum LAI, showed similar sensitivities of $F_{\text{soil}}$ to $T_{\text{soil}}$ and soil moisture. However, different LAI dynamics and forest floor thickness affected both these variables, resulting in different annual $F_{\text{soil}}$; roughly, ~1 °C higher mean annual temperature caused ~10% higher $F_{\text{soil}}$ (Palmroth et al., 2005). However, within a single PP plot, ~1 °C higher $T_{\text{soil}}$ in years with low LAI showed ~60% higher $F_{\text{soil}}$, indicating that decreasing TBCF with increasing LAI can have a greater effect on interannual variability of $F_{\text{soil}}$ than environmental variables (Butnor et al., 2003; Palmroth et al., 2006). Therefore, certain ecological indices seem to better explain the variation of $F_{\text{soil}}$ among forest types.
of largely different characteristics, while others may be more useful for explaining the variation within a forest type.

Here we use \( F_{\text{soil}} \) collected with an automated respiration chambers over multiple years ranging in temperature and precipitation, in three forest stands experiencing similar climatic conditions, but varying in LAI due to differences in resource availability (as affected by soil type), age, and species composition. In addition to PP and HW, we include a mature loblolly pine stand on sandy soil (OP). We begin the analyses accounting for the sources of variation of individual chamber \( F_{\text{soil}} \) over a range of intra-annual scales and, use the information to generate plot scale and stand scale estimates of annual \( F_{\text{soil}} \). We then test whether leaf litterfall is best at explaining the variation of annual \( F_{\text{soil}} \) among forest types (Davidson et al., 2002; Palmroth et al., 2005), while LAI is best at explaining the variation within a forest type (PP, Palmroth et al., 2006). We also assess the sensitivity of annual \( F_{\text{soil}} \) to indices of water availability.

### 4.2 Materials and methods

#### 4.2.1 Study sites

The study was conducted in three stands within Duke Forest in central North Carolina, USA (Table 4.1). An 18 year-old (in 2001) loblolly pine plantation (PP) and 80-100 year-old mixed-species deciduous hardwood stand (HW) are adjacent stands in the Blackwood Division, within 1 km of one another. Soil at both of these sites have moderate water-holding capacity in the upper layer, but low permeability in the lower level, so it does not readily release water to plants (Soil Survey of Orange County, 1977). The PP plots are part of the Duke Free Air CO\(_2\) Enrichment (FACE) site, but measurements for this study were taken in four ambient CO\(_2\) in sectors without nitrogen amendments. Sampling at HW was at the base of the Duke Hardwood Ameriflux tower.
The third stand was a 35 year-old (in 2003), mature loblolly pine stand (old pine; OP), located in the Dailey Division of Duke forest, approximately 30 km northwest of the other two stands. This site was thinned in 1993 and 1998, leaving a partially-open canopy with a small hardwood understory. Despite similar porosity at all sites (Table 4.1), OP had deeper soil that drained rapidly, as opposed to PP and HW, which had a low-permeability clay layer at 0.35 m (Oren et al., 1998).

### 4.2.2 Instrumentation

Air temperature ($T_{air}$) was measured with sensors installed at 2/3 canopy height (HMP35C, Campbell Scientific, Logan, UT), and incoming precipitation was measured at each site with above-canopy tipping bucket installed at the top of a walkup tower (TE525M, Texas Electronics, Dallas, TX).

Soil temperature was measured at each plot with a permanently-installed thermistor buried at 10 cm ($T_{10}$). Soil moisture ($\theta$) was measured as volumetric water content with two Campbell Scientific CS-615 at installed at 0-30 cm depth at each PP plot. At HW and OP $\theta$ was measured with, respectively, six and four Delta-T ML2x Theta Probes installed half at 0-5 cm and half at 20-25 cm and a stand-level average $\theta$ was generated averaging data from all sensors at both depths. Data were filtered for unrealistic spikes after rain events. (See Appendix, Section 4.5.1.)

To normalize soil moisture amongst stands, soil moisture is expressed in this study as relative extractable water (REW), a percentage of water from the hygroscopic point to field capacity. Thus, REW at both PP and HW ranged from 0 at the hygroscopic point ($\theta=0.125 \, m^3 \, m^{-3}$) and 1.0 at field capacity, ($\theta=0.35 \, m^3 \, m^{-3}$). REW at OP was determined empirically from soil moisture probe data. The hygroscopic point was set to the recorded value where soil moisture hit the stable, minimum point in the drought of
2005 ($\theta=0.05$ m$^3$ m$^{-3}$) and field capacity was set to the average value reached during non-growing season months at least two days after large precipitation events ($\theta=0.20$ m$^3$ m$^{-3}$).

### 4.2.3 Leaf litterfall and leaf area index

Leaf litter was collected periodically throughout the study with an array of baskets at each site and used to estimate litter mass and LAI. Data from PP and HW have been presented in McCarthy et al. (2007) and Oishi et al. (2008), respectively.

At OP, litter was collected in ten 0.5 m$^2$ baskets, oven dried, sorted into pine and hardwood components, and weighed for total mass. Leaf area index (LAI) was estimated from total litter mass and specific leaf area, measured using a light table or digital scanner. Time trends of LAI were measured with a Li-Cor LAI-2000 plant canopy analyzer (Li-Cor, Lincoln, NE). Since LAI at OP was lower than the point of optical saturation (McCarthy et al., 2007), data from the LAI-2000 at OP was not rescaled to match litter-based LAI estimates.

### 4.2.4 Soil CO$_2$ efflux

$F_{\text{soil}}$ was measured using the Automated Carbon-dioxide Efflux System (ACES, USDA Forest Service, US Patent 6692970). The system has been described in previous studies (Butnor et al., 2003; Palmroth et al., 2005); briefly, it is an IRGA-based open system that sequentially samples 15 chambers plus one null chamber (491 cm$^2$ footprint, 10 cm height). Each chamber is sampled for a 10-minute cycle and the final record is accepted if air flow rates and CO$_2$ concentrations are stable and within a specified range; thus a maximum of 9 measurements for each chamber throughout each day is possible.

Terms relating to the spatial aggregation of samples are described as follows: location refers to a measurement taken at a specific soil efflux chamber in a specific position, plot refers to an array of chambers connected to a single ACES (~25 m diameter range), and stand refers to a forested area with a similar age, species composition, and
soil characteristics (~1 km diameter). The HW and OP stands each consisted of one plot that ran 2001-2004 and 2003-2004, respectively (Table 1). Of the four PP plots, PP8 (the number referring the FACE plot number) includes data from 2001-2010. Additional ACES were added to PP1 and PP6, in early 2005 and PP5 starting in 2006 (this setup included redeployed ACES from HW and OP). For each of the ACES, four of the chambers were connected to tree stems and data collected are not used in this study. In PP plots, five of the remaining chambers were located in the N-fertilized sectors of the FACE plots. Therefore, PP consists of data from six chambers while HW and OP consist of data from 11 chambers.

Each chamber was alternated between one of two fixed locations in the plot and ran in a given position for 3-4 day periods. Chamber movement is intended to minimize chamber effects on the amount of litter and moisture arriving at the monitored surface, and to increase the spatial sampling. Chamber locations were changed several times during the study period, initially to minimize disturbance to a sampling area and later to examine variability with proximity to trees. The chamber bases have a sharp, metal edge that cut into the soil approximately 1 cm, but do not use a permanently-installed collar. Each chamber is equipped with a 5 cm $T_{soil}$ probe that is manually inserted into the ground beneath the chamber when the sampling location is moved. Litter excluded during measurement cycles was replenished (See Appendix, Section 4.5.2).

ACES are designed to run continuously; however, several factors reduced the amount of usable data. First, individual measurements are filtered to exclude sampling periods where either air flow or CO$_2$ concentrations were out of range. Second, systems were offline periodically for general maintenance and recalibration. Third, over the long duration of the study, systems began to breakdown more frequently. Therefore, the measurements were not continuous throughout the study period. In the case of PP6 and
PP8, few short segments between repairs beginning in 2009 and 2008, respectively, forced us to exclude these data (Table 4.2). Nevertheless, measurements did encompass much of the environmental variability that occurred over the past decade, including several droughts and wet growing seasons.

To fill gaps in data coverage, we utilized the model for $F_{soil}$ as a function of $T_{soil}$ and REW previously described in Palmroth et al. (2005):  

$$F_{soil} = F_{soil}' \times f(REW)$$  \hspace{1cm} \text{Eq. 1}

where $F_{soil}$ is mean daily soil CO$_2$ flux for a specific location where >4 daily measurements were available ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$), and $F_{soil}'$ is $F_{soil}$ for a given $T_{10}$ under non-limiting REW. Our approach to fit parameters differed as follows. We first estimated $F_{soil}'$ by fitting measured $F_{soil}$ from each chamber location as a function of $T_{10}$ under non-limiting soil moisture conditions. These conditions were defined as REW>0.33 in PP and HW (equivalent to $\theta$>0.20 m$^3$ m$^{-3}$ in Palmroth et al. 2005) and as REW>0.45 at OP, the point below which $F_{soil}$ was on average 90% of the values in wetter conditions. The form used is

$$F_{soil}' = R_{b10}e^{b(T_{10} - 10)}$$  \hspace{1cm} \text{Eq. 2.}

where $T_{10}$ is daily mean $T_{soil}$ ($^\circ$C) at 10 cm for the corresponding plot, $R_{b10}$ is estimated “basal” respiration at 10 $^\circ$C ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$), and $b$ is the temperature sensitivity parameter ($e^{b(10)} = Q_{10}$). The values of $F_{soil}$ were Log$_e$ transformed so the data could be fit as a linear function using the ACOTOOL function in Matlab (Version 6.0.1.450, Release 12.1, MathWorks Inc.), with year as a categorical variable. Linear regressions were not possible for all locations in all years due to limitations in data for reasons described previously as well as uneven representation of $T_{10}$ ranges. For example, during the drought year of 2005, there were very few days with temperature above the annual mean and non-limiting soil moisture. Least squares fitting of these data led to some
unreasonable $Q_{10}$ values (e.g. $<0$). Therefore, we constrained each location’s regressions by assuming a constant $Q_{10}$ parameter across years, but allowing for varying $R_{b10}$.

Limitations to $F_{\text{soil}}$ imposed by REW, $f(\text{REW})$, were accounted by fitting the proportionate reduction from $F'_{\text{soil}}$ under non-limiting REW using Matlab’s least-squares, nonlinear NLINFIT function for each chamber location:

$$f(\text{REW}) = 1 - e^{-c \times \text{REW} + d}$$  \hspace{1cm} \text{Eq. 3}

where $c$ and $d$ are coefficients describing the sensitivity of $F_{\text{soil}}$ to low REW. Because some years experienced few low-REW days, data were pooled across years.

In both analyses, parameters from each chamber location and from each of the years with enough data were within the 95% confidence interval of parameters generated from the fit of the pooled data of all years 78% of the time. Matlab was also used to process raw data and for linear regressions and statistical tests. SigmaPlot (v8.0.2, SPSS Inc.) was used for additional curve fitting.

4.3 Results

We analyzed 283,572 data points across 6 plots over the between 2001 and 2010, accounting for 31 plot-years (See Appendix, Section 4.5.3, Table 4.3), allowing us to analyze variability in $F_{\text{soil}}$ across a temporal and spatial scales. In this section, we first describe the response of $F_{\text{soil}}$ to environmental variables, and then examine the sources of variability of annual $F_{\text{soil}}$ among and within stands.

4.3.1 Soil temperature and moisture sensitivity of daily $F_{\text{soil}}$

Between 66 and 82% of variability in daily $F_{\text{soil}}$ under non-limiting REW ($F'_{\text{soil}}$) was explained by exponential function of $T_{10}$ (Eq. 3.2; Table 4.2). At PP, mean $R_{b10}$ values were similar among plots ($P=0.39$), but $Q_{10}$ differed ($P<0.0001$, although some pairs of plots were similar Table 4.2). An inverse relationship was found between $Q_{10}$ and $R_{b10}$...
among plots within PP \( (P=0.09; r^2=0.82) \), resulting in that \( F_{\text{soil}} \) of no plot was consistently higher or lower over the entire \( T_{10} \) range (Fig. 4.1a). However, \( Q_{10} \) and, less significantly, \( R_{b10} \) differed among stands \( (P<0.003; \text{but } P=0.16 \text{ for } R_{b10} \text{ differences between HW and OP; Table 4.2}) \). Overall, PP exhibited the highest \( F_{\text{soil}} \) across the range of temperatures, followed by HW then OP (Fig. 4.1b).

During the growing season, low REW led to reductions in \( F_{\text{soil}} \) in all plots and stands. The soil moisture reduction function \( (f(\text{REW}), \text{Eq. 3}) \) explained approximately 50\% of the variability remaining in daily \( F_{\text{soil}} \) after accounting for \( T_{10} \) (Fig. 1c, Table 4.2). Parameter estimates for REW reduction functions were different among PP plots \( (P<0.003, \text{Table 4.2}) \), resulting in greater reduction in \( F_{\text{soil}} \) with REW in PP8 than PP6, but PP1 and PP5 were not consistently higher or lower than another plot across the range of REW. Among stands, parameters at HW and OP were similar \( (P>0.13) \), but the \( d \) parameter at PP was higher \( (P=0.04) \). The values of \( c \) and \( d \) parameters were positively correlated \( (r^2=0.39, P<0.001) \). An increase in the \( c \) parameter causes \( f(\text{REW}) \) to begin declining at a lower REW while an increase in the \( d \) parameter reduces \( f(\text{REW}) \). The compensatory effect of differences in these parameters resulted in similar sensitivities of \( F_{\text{soil}} \) to soil moisture among stands: \( f(\text{REW}) \) from each stand was within one standard deviation of the other two stands across the range of REW (Fig. 4.1d). Reductions in \( F_{\text{soil}} \) due to soil moisture limitation at HW was within 2\% of PP from REW down to 0.15, at which point PP declined more sharply. Reductions in \( F_{\text{soil}} \) at OP was within 5\% of PP down to REW=0.25. Thus, the frequency of limiting REW conditions largely determines reductions in \( F_{\text{soil}} \). For example, \( F_{\text{soil}} \) was reduced to less than 60\% of non-limited conditions 37 of days during 2005 at PP, compared to about 10 days at HW and OP, or reductions to at least 80\% for 70, 30, and 25 days (Fig. 4.1d inset).
Under soil moisture-limited conditions, $F_{\text{soil}}$ showed a rapid response to precipitation during the growing season (Fig. 4.2), increasing by an average of 20% (SD=34%, $P<0.001$), but only when prior to the event REW was $\leq 0.33$ ($P=0.64$ for REW>$0.33$). As seen in the example figure, precipitation led to a temporary increase in REW but high $F_{\text{soil}}$ persisted as REW declined. The duration of high $F_{\text{soil}}$ following rain was not consistent and could not be adequately assessed given our twice-weekly chamber repositioning. The precipitation-induced increases of $F_{\text{soil}}$ tended to bring drought-period fluxes close to, but rarely above the expected non-drought values. Small precipitation events (<5 mm) were not detected by soil moisture sensors and did not affect $F_{\text{soil}}$ ($P=0.90$); of precipitation $\geq 5$ mm, the amount did not affect the response ($P>0.37$). We did not observe a reduction in $F_{\text{soil}}$ at soil moisture higher than field capacity ($P=0.06$).

Strong seasonal variability was observed in REW, with winter conditions remaining near field capacity (REW=1.0) and progressive drying during much of the growing season (Fig. 4.2b and Appendix Table 4.4). Unlike $T_{10}$, REW showed large interannual variability, depending on the magnitude and frequency of precipitation events during the growing season. Severe drought conditions occurred in 2002, 2007, and 2010 and a moderate drought in 2005; our measurements captured two of these droughts at HW (2002 and 2005) and one at OP (2005). Both annual and growing season REW was highest at HW and lowest at PP.

We examined the synchronicity of the dynamics of daily $F_{\text{soil}}$ variation among chamber locations, plots, and stands using a cross-correlation analysis (Fig. 4.3a). Within-plot comparisons were only possible for PP1, PP5, and PP6, where detailed coordinate data for all equipment was available. Between-plot comparisons were possible only when ACES were running concurrently. Sampling points were generally well-correlated.
within each PP plot, with average $r^2=0.88$ (SD=0.08). Correlations weakened with log-distance between plots and stands from a mean $r^2=0.89$ (SD=0.05) at 1-2 m distances to 0.53 (SD=0.22) at 33 km distances (Fig. 4.3a; $P<0.0001$). Some of the decrease in correlation among stands reflects the difference in soil moisture dynamics among forest types (Fig. 3b). Temperatures were similar among stands during the winter (November – February, $P>0.71$, Fig. 3c), but were higher at HW than PP (1.8 °C) and OP (1.4 °C) during the 2005 growing season ($P<0.04$ comparing HW, $P=0.28$ comparing PP and OP).

### 4.3.2 Sources of variation of annual $F_{soil}$ among plots and years

Annual $F_{soil}$ varied among plots and years (Fig. 4.4a,b). For the four years before ACES were installed in PP1, PP5, and PP6, we estimated $F_{soil}$ using measured $T_{10}$ and REW and mean, plot-level parameters (Table 4.2). Of the PP plots, PP8 generally had the lowest $F_{soil}$ while PP1 and PP6 produced the highest fluxes. At the stand level, PP had the highest $F_{soil}$, followed by HW, then OP.

Interannual variability of $F'_{soil}$ was generally low, with plot-level standard deviations ranging from 64-193 g C m$^{-2}$ y$^{-1}$ (average CV=7.7%) somewhat lower than the range of actual $F_{soil}$ 107-218 g C m$^{-2}$ y$^{-1}$ (average CV=12.2%). Over the study period, mean annual $T_{10}$ showed small variability within each site (see Appendix, Table 4.4), with plot-level interannual standard deviations <0.5 °C or less than 1 °C differences between highest and lowest annual $T_{10}$ (with the exception of 1.5 °C at PP6). Much of the variability in mean annual $T_{10}$ originated from the non-growing season (mean 8.3 °C, SD=0.8 °C), a period of little influence on annual $F_{soil}$. During the growing season, the average $T_{10}$ (=19.2 °C) was associated with small variability (SD=0.4 °C). Thus, inter-annual variability in $F_{soil}$ was dependent on other factors.

Comparing the three stands, PP showed the greatest reductions of $F_{soil}$ from $F'_{soil}$ (i.e. annual $f$(REW), Fig. 4.4c). The lowest annual $f$(REW) occurred during the four
drought years. Under the extreme drought conditions of 2007, $F_{\text{soil}}$ at PP was 73% of potential. Across the study period and stands, annual $f(\text{REW})$ was similarly correlated with mean growing season $\text{REW}$ (Fig. 4.5a; $P<0.0001$). However, because $F_{\text{soil}}$ was gapfilled using REW data, we also compared growing season $f(\text{REW})$ with an independently-measured growing season index of water availability (WAI) defined as precipitation minus pan evaporation (from a nearby NOAA weather station; www.ncdc.noaa.gov) (Fig. 4.5b). Linear regressions for HW and OP were similar ($P=0.85$). Compared to the other stands, the intercept of this relationship was lower at PP ($P=0.01$), owing to higher rainfall interception loses at PP (compare Schäfer et al., 2002 with Oishi et al., 2010) and higher overall evapotranspiration (Stoy et al., 2006). Neither REW nor WAI were related to annual $R_{b10}$ ($P>0.37$), so the primary source of the interannual variability in $F_{\text{soil}}$ was water availability.

### 4.3.3 Relationships between mean inter-annual fluxes and stand and environmental variables

The variation of mean annual $F'_{\text{soil}}$ among the three stands was best explained by leaf litterfall ($P=0.004$; Fig. 4.6a). LAI was not well correlated with litterfall across stands ($P=0.43$), and produced a weaker relationship with $F'_{\text{soil}}$ ($P=0.12$). Assuming that soil $C$ was in near equilibrium over the study period, and subtracting leaf litterfall $C$ from $F'_{\text{soil}}$ gives a rough estimate of total belowground carbon flux (TBCF). The estimates of TBCF also increased with leaf litterfall across stands ($P=0.005$).

Across PP plots, $F_{\text{soil}}$ and TBCF showed weak inverse correlations with leaf litterfall ($P=0.19$ and 0.13, respectively). However, leaf litterfall did not explain the variation in $F_{\text{soil}}$ among years at any of the sites ($P>0.41$; data not shown). Nor was litterfall or LAI related to the parameters of $f(\text{REW})$ across stands ($P>0.61$) or within PP ($P>0.70$). The inter-annual variation of $F_{\text{soil}}$ across all stands and PP plots was explained
to a large extent by the inter-annual variation of WAI (Fig. 4.6b; P=0.004). The relationship was similar among the stands (P>0.42).

We sought a plausible explanation for the contrasting relationships between mean inter-annual $F_{\text{soil}}$ and leaf litterfall among the stands and PP plots (Fig. 4.6a). One obvious candidate was difference in $T_{10}$ within PP and among stands and how it was affected by leaf litterfall and LAI. Although mean non-growing season $T_{10}$ was similar among PP plots and stands (P>0.07), mean growing season $T_{10}$ at PP was 1.8 °C lower than in HW. This indicates that among-stand differences in LAI alone could not explain variation in $T_{10}$ ($r^2=0.04; P=0.87$), which was likely influenced by the more heterogeneous stand structure and thinner growing season litter layer at HW than PP. However, $Q_{10}$ (and $R_{b10}$) increased with leaf litterfall ($P=0.060$ and 0.14, respectively; Fig. 4.7a,b), and the resulting stand differences in the temperature response of $F_{\text{soil}}$ (Fig. 4.3b) more than compensated for differences in $T_{10}$. In contrast, the temperature response of $F_{\text{soil}}$ was similar in all PP plots and unrelated to LAI or leaf litterfall (P>0.86). Leaf litterfall was well-correlated with mean annual LAI (Figure 3.8a; P=0.06), and mean growing-season $T_{10}$ decreased with increasing LAI (ranging 1.2 °C among plots; Fig. 4.8b; P=0.25). Thus, mean annual $F'_{\text{soil}}$ increased with $T_{10}$ (Fig. 4.8c; P=0.14), yet the relationship with LAI was even stronger (Fig. 4.8d; P=0.018). Analyzing the relative contribution of differences in $T_{10}$ among plots versus the plot-specific parameters of the temperature response of $F'_{\text{soil}}$ revealed that $T_{10}$ contributed 55-85% to the difference of $F'_{\text{soil}}$ among plots with the remaining differences explained by between-plot differences in $Q_{10}$ (Table 2).

4.4 Discussion

Two broad classes of factors can contribute to spatial and inter-annual annual variation of $F_{\text{soil}}$: the temperature- and moisture-sensitivity of the flux, reflecting differences in attributes such as litter quality and C availability, and variation in
temperature and moisture, reflecting incoming radiation and water availability, which are related to topography and soil characteristics but also to forest attributes such as LAI. Our study shows that leaf litterfall works as an index of $F_{soil}$ only over a wide range of productivity. However, within narrower productivity ranges such an index fails because it inversely relates to physical and physiological factors driving $F_{soil}$. Our study also makes headway in providing a common soil moisture-based function to account for the inter-annual variation of $F_{soil}$.

4.4.1 Variation in the sensitivity of $F_{soil}$ to soil temperature

In all years, the seasonal dynamics of $F_{soil}$ corresponded to those of $T_{10}$ at all chamber locations and, thus, plots and stands. When soil moisture was non-limiting, increased $T_{10}$ resulted in an exponential rise of $F_{soil}$ (Eq. 2, Fig. 1a,b). Our gap-filling approach of using a constant $Q_{10}$ within each plot (i.e. single slope in the relationship between Log$_e(F_{soil})$ and $T_{10}$ with “year” as a categorical variable) loaded the inter-annual variability in the relationship on $R_{b10}$. Seasonal variation of basal rate of respiration (similar to $R_{b10}$ in this study) has been shown to reflect variation of photosynthesis (Sampson et al., 2007); however, in our study, inter-annual variation of $R_{b10}$ was unrelated to variation in water availability, the resource most dominating the inter-annual variation of net primary production (McCarthy et al., 2010).

Spatially, the sensitivity of $F_{soil}$ to $T_{10}$ was similar among PP plots – the increase of $Q_{10}$ was negated by a decrease in $R_{b10}$ – but differed among stands, with PP showing greatest sensitivity and OP the least (Table 2). Although support for a constant $Q_{10}$ can be found from comparisons of labile and recalcitrant soil carbon pools (Fang et al., 2005) to comparison among ecosystems over the globe (Mahecha et al., 2010), other studies showed a linear increase of root respiration with $T_{soil}$ (i.e. decreasing $Q_{10}$; Drake et al., 2008), and declining $Q_{10}$ after canopy closure (Berhnardt et al., 2006). In our study, $Q_{10}$
increased (and $R_{bl}$ tended to increase) with leaf litterfall across stands, but the variation of these parameters among PP plots was smaller and unexplainable by either leaf litterfall or LAI. We later discuss the implication of these findings to spatial variation of annual $F_{soil}$.

Within plots, variability of daily $F_{soil}$ among chamber locations was large and is impractical to correlate to fine scale variation in temperature, moisture as well as other potential sources, such as root and litter biomass and pools of carbon and nitrogen (Martin and Bolstad, 2009). In this study, we examined only the variation of $F_{soil}$ with distance to nearest tree at PP and OP plots. Although some near-tree locations showed high $F_{soil}$, the trend was weak at both stands ($P>0.1$).

### 4.4.2 Variation in the sensitivity of $F_{soil}$ to soil moisture

All stands in our study showed reductions in $F_{soil}$ from $F_{soil}^*$ (i.e. lower $f(REW)$) under dry conditions. In contrast to the $F_{soil}^*$ response to $T_{10}$, parameters of $f(REW)$ were similar among stands and thus unrelated to either leaf litterfall or LAI despite differences in soil texture (sandy-loam soil of OP versus clay-loam soil of the other two stands) and in deciduous and evergreen growth habits. Although parameters of $f(REW)$ differed among PP plots, there too they were unrelated to leaf litterfall or LAI.

When precipitation was sufficiently large to alleviate REW-limited conditions, it led to significant increases in $F_{soil}$, bringing it to $F_{soil}^*$ controlled only by $T_{soil}$ (Fig. 4.2a). If $F_{soil}$ was limited by carbohydrate supply due to drought-induced decrease of photosynthesis, the recovery of $F_{soil}$ would lag precipitation 2-5 days based on estimated transport times (Stoy et al., 2007; Mencuccini and Hölttä, 2009). The observed rapid recovery (Fig. 4.2b) suggests that, at least initially, much of the recovery of $F_{soil}$ is the result of increased microbial activity with soil hydration (Wu and Lee, 2011).
Cross-correlation analysis of the daily flux time-series showed a weakening relationship with distance amongst measurement positions as distance increased from 1 m to 30 km (Fig. 4.3a). We show strong cross-correlations among mean daily $F_{soil}$ from individual chamber locations within PP plots, suggesting that the variation of driving biophysical variables are synchronized at proximate locations. The decreasing strength of correlations could be due, in part, to a decreased synchrony of environmental variability (e.g., precipitation events) with increasing distance (Fig. 4.3b), amplified partially by the difference in soil texture at OP versus the more proximate HW and PP, responding differently to precipitation, and by difference in drainage patterns and species composition between HW and PP, and among PP plots. In contrast, the dynamics of $T_{soil}$ was similar at all sites (Fig. 4.3c).

### 4.4.3 Spatial and inter-annual variation in $F_{soil}$

Earlier we demonstrated that the parameters capturing $F_{soil}^s$-sensitivity to $T_{soil}$ differed among stands in relations to leaf litterfall, and were insensitive to inter-annual variation in soil moisture or stand variables. Furthermore, the stands shared a similar $f$(REW). In contrast, $F_{soil}^s$ of PP plots showed similar overall sensitivity to $T_{soil}$ but differences in $f$(REW) parameters. These responses interact with stand and plot $T_{10}$ and REW to produce the observed annual $F_{soil}$ and its inter-annual and spatial variation.

Annual and growing season mean $T_{10}$ was nearly invariable at any plot (See Appendix, Table 4.4), pointing to REW as the dominant source of inter-annual variability of $F_{soil}$. Limitations of REW are expected to reduce photosynthesis through stomatal regulation, which will, in turn, likely lead to reductions in both belowground production and respiration. For example, annual fine root respiration at PP was estimated at 645 g C m$^{-2}$ (Drake et al., 2008), a sizable portion of $F_{soil}$ so an observed water availability-induced variation of fine root production at PP (Pritchard et al., 2008)
could cause large variation of $F_{soil}$. Indeed, differences in the drought-related reductions in $F_{soil}$ were driven by the frequency of low soil moisture days (inset in Fig. 4.1d), and resulted in that the inter-annual variation of $F_{soil}$ roughly corresponded to the inter-annual variation in annual f(REW) (Fig. 4c). Thus, greater drought-induced reductions of $F_{soil}$ at PP are less due to its slightly greater sensitivity to soil moisture than to lower REW, owing to a more extended active season than HW and to shallower rooting zone than OP. For these reasons, in addition to greater canopy and litter interception of precipitation, annual f(REW) was lower at a given growing season WAI at PP than in the other stands (Fig. 4.5b), but all stands subscribed to a single relationship when growing season REW was used (Fig. 4.5a). As result, the inter-annual variation of $F_{soil}$ expressed as a difference from the inter-annual mean of each stand, was largely explained by the corresponding variation of WAI (Fig. 4.6b), leaving us with the task of explaining the spatial variation of the inter-annual mean of $F_{soil}$.

Inter-annual mean $F_{soil}$ varied among plots and stands and these differences were of similar magnitude to the inter-annual variations at each plot and stand (Fig. 4.4a,b). Among stands, the inter-annual mean $F_{soil}$ increased with leaf litterfall (Fig. 4.6a), as has been reported earlier in this and other sites (Davidson et al., 2002; Palmroth et al., 2006; Chen et al., 2011). A rough estimate of TBCF across our three stands shows that even after subtracting the effect of leaf litterfall (assuming steady-state litter and soil C pools), the flux still increases with leaf litterfall (Fig. 4.6a), which accounts for ~20% of $F_{soil}$. Furthermore, the relationship tended to reverse among plots of PP, showing decreasing $F_{soil}$ (as well as TBCF) with increasing litterfall. These results demonstrate that litterfall is not a unique indicator of stand and site factors controlling TBCF and $F_{soil}$. For example, leaf litterfall was well correlated with LAI among PP plots (Fig. 4.8a) but not among stands. Furthermore, annual litterfall is not sensitive to leaf phenology, yet earlier
budbreak of deciduous trees can reduce springtime $T_{\text{soil}}$ resulting in correlation of $F_{\text{soil}}$ with inter-annual dynamics of LAI (Phillips et al., 2010). This highlights the importance of accounting for LAI dynamics, horizontal heterogeneity in canopy cover, litter quality, and probably soil thermal properties when attempting to explain the variation of $F_{\text{soil}}$ among stands of different attributes. Overall, however, the increased $T_{\text{soil}}$-sensitivity of $F_{\text{soil}}$ with litterfall (Fig. 4.7) suggest that differences in productivity and TBCF among forests under roughly similar climatic forcing dominated over the relatively small differences in $T_{10}$ (e.g., higher in HW) and REW (e.g., lower in PP) in determining among-stand variation of $F_{\text{soil}}$.

Within PP, LAI varied spatially among plots, reflecting nitrogen availability (McCarthy et al., 2007). Higher LAI reduced $T_{10}$ (Fig. 4.8b) by reducing radiation input and, given the similar temperature response (Fig. 4.4, Table 4.2), reduced $F_{\text{soil}}$ (Fig. 4.8c). However, because LAI spatially integrates conditions better than a few point measurements of $T_{\text{soil}}$ among stands of similar attributes, LAI explains the spatial variation of $F_{\text{soil}}$ better than $T_{\text{soil}}$ alone (Fig. 4.8d).

### 4.4.4 Broader context

In a recent global synthesis, Bahn et al. (2010) combined site-specific estimates of base respiration and $Q_{10}$ with mean annual $T_{\text{soil}}$ to calculate $F_{\text{soil}}$ at mean annual $T_{\text{soil}}$ (Fig. 4.9a). As expected, annual $F_{\text{soil}}$ was related to the rate of $F_{\text{soil}}$ at mean annual $T_{\text{soil}}$, but neither $Q_{10}$ nor annual $F_{\text{soil}}$ were related to soil temperature. Using this approach, which explicitly considers $T_{\text{soil}}$, the rank of annual $F_{\text{soil}}$ among our stands was preserved, and our estimates are close to those expected based on the global relationship, averaging 8% higher values (+4% at PP and +10% at HW and OP, Fig. 4.9a).

We also compared our results to a global dataset presented by Bond-Lamberty and Thompson (2010). Our reanalysis shows that the relationship between $F_{\text{soil}}$ and
litterfall does not hold for stands within subcategories of forests (e.g., young or mature, evergreen or deciduous), and among categories within all but boreal forests (Fig. 4.9b). The overall relationship emerges mostly at the scale of biomes. Interestingly, our forests hug the upper range of the temperate data, perhaps reflecting the relatively warm nature of the US southeast (~15 °C versus ~10 °C for many of the other temperate forests) or the inclusion of fine woody material as litterfall by some of these studies (Bond-Lamberty and Thompson, 2010). The relationship clearly does not imply that litterfall controls \( F_{\text{soil}} \), because on average litterfall accounts for roughly a third of the flux; litterfall is but an indicator of stand and site factors controlling TBCF. Another such factor that covaries with overall productivity across biomes is \( T_{\text{soil}} \). It decreases poleward with radiation, and among stands with similar characteristics, it decreases with increasing LAI.

Thus, within a stand, higher LAI can be correlated to two potential mechanisms for reductions in \( F_{\text{soil}} \): lower radiative load heating of the soil and reduced allocation of carbon to belowground uses. However among stands, increased photosynthesis associated with higher LAI or more supportive climate, along with increased decomposable litter appears to lead to increases in \( F_{\text{soil}} \).
Table 4.1: Site characteristics for three Duke Forest stands: pine plantation (PP), hardwood (HW), and old pine (OP).

<table>
<thead>
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<th>Coordinates (Lat, Lon)</th>
<th>PP</th>
<th>HW</th>
<th>OP</th>
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<tbody>
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<td>Coordinates (Lat, Lon)</td>
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**Stand characteristics**

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<th></th>
<th>PP</th>
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<th>OP</th>
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<td>Stand age (years old in 2005)</td>
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<tr>
<td>Stem density (trees ha⁻¹)</td>
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<tr>
<td>Basal area (cm² m⁻²)</td>
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<td>22</td>
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<tr>
<td>Height (m)</td>
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<td>25</td>
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<td><em>Quercus</em> spp.</td>
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<tr>
<td>Other deciduous</td>
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**Soil characteristics**

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<th>Iredell gravelly loam</th>
<th>Durham sandy loam</th>
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<tbody>
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Table 4.2: Parameters for estimating soil CO₂ flux under non-liming soil moisture conditions ($F^\text{soil}$, see Eq. 1,2) and limitations as a function of relative extractable water (REW, see Eq. 1,3). SD in parentheses and superscript letters for parameters represent significant similarities among PP plots ($P>0.05$).

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<th>$Q_{l0}$</th>
<th>$r^2$</th>
<th>$f$(REW)</th>
<th>c</th>
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Table 4.3: Number of operational days for each ACES. Blank cells indicate that no system was installed during that year. Zero values indicate that no useable data was recoverable from that year.

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Table 4.4: Environmental variables

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Table 4.5: Year-specific $R_{\text{bio}}$ coefficients. Mean value for each plot (SD). All units in $\mu$mol m$^{-2}$ s$^{-1}$.

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<td>1.30</td>
<td>(0.51)</td>
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<td>(0.51)</td>
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Figure 4.1: Response of potential soil CO₂ flux under non-limiting soil moisture ($F'_{\text{soil}}$) to soil temperature at 10 cm ($T_{10}$) across all years (a & b) and relative reduction of soil CO₂ efflux ($F_{\text{soil}}$) from $F'_{\text{soil}}$ due to a decrease in relative extractable water ($f(\text{REW})$) as a function of relative extractable water (REW) (c & d). Data from PP plots are presented in (a & c) and for all stands in (b & d), including the mean and S.D. (shaded gray) for the four PP plots. The cumulative effect of $f(\text{REW})$ based on recorded REW values in the drought year of 2005 is presented in the Fig 4d inset.
Figure 4.2: Sample data of response of soil CO$_2$ flux ($F_{\text{soil}}$) to precipitation ($P$) measured at one chamber location during low soil moisture (relative extractable water, REW) conditions. (a) half-hourly values of soil temperature at 10 cm ($T_{10}$) and $F_{\text{soil}}$, triangles are sub-set of data shown in (b), the time series of $F_{\text{soil}}$ before and after precipitation event.
Figure 4.3: (a) Cross-correlation analysis between mean daily fluxes from different sampling locations as a function of distance between locations. Error bars represent SD. Daily environmental data for a sample year 2005 for all sites (b) soil moisture as relative extractable water (REW) and (c) soil temperature at 10 cm ($T_{10}$).
Figure 4.4: Estimated annual soil CO2 flux ($F_{soil}$) at (a) individual PP plots, and (b) the three forest stands. (c) Deviation of $F_{soil}$ from potential $F_{soil}$ ($f(\text{REW})$), estimated $F_{soil}$ from exponential functions under non-limiting soil moisture; Eq. 2). Error bars represent 1 SD. Solid/shaded symbols are estimated annual sums from measurements taken throughout the year and open symbols are modeled based on plot-specific parameters (see Table 2).
Figure 4.5: Proportionate departure of annual soil CO$_2$ flux ($F_{soil}$) from potential $F_{soil}$ due to relative extractable water (REW) reduction function ($f$(REW)) and (a) mean growing season REW and (b) water availability index (WAI, the difference between growing season precipitation and pan evaporation).
Figure 4.6: (a) Annual potential soil CO₂ flux under non-limiting soil moisture conditions ($F_{\text{soil}}^*$, symbols and solid lines) or total belowground carbon flux (TBCF = $F_{\text{soil}}^*$ minus leaf litterfall) as a function of annual leaf litterfall (dashed lines). Black symbols and lines represent PP plots ($n=4$) and gray lines and symbols represent forest stands, including the mean of the four PP plots ($n=3$). An inverse relationships among PP plots were not significant for $F_{\text{soil}}^*$ and TBCF ($r^2=0.65$ and 0.75, $P=0.19$ and 0.13, respectively). (b) Annual difference from mean annual soil CO₂ flux ($F_{\text{soil}}$) as a function of growing season water availability index (WAI, precipitation minus pan evaporation).
Figure 4.7: Stand-level annual leaf litterfall and (a) $Q_{10}$ and (b) basal respiration at 10 °C ($R_{b10}$, $r^2=0.94$, but $P=0.14$). Error bars represent 1 SD.
Figure 4.8: Mean annual leaf area index (LAI) compared to (a) leaf litter and (b) mean annual soil temperature at 10 cm ($T_{10}$; $r^2=0.56$, but $P=0.25$). Potential soil CO$_2$ flux under non-limiting soil moisture conditions ($F_{\text{soil}}$) as a function of (c) mean annual $T_{10}$ ($r^2=0.74$, but $P=0.14$) and (d) mean annual LAI.
Figure 4.9: Global trends in forest soil CO$_2$ flux ($F_{\text{soil}}$) as a function of (a) $F_{\text{soil}}$ at mean annual soil temperature (MAT), separated by mesic and dry (Mediterranean, sub-humid, and semi-arid; data from forests ecosystems from Bahn et al. (2010), averaged over years for a given site) and (b) annual leaf litter from the Global Soil Respiration Database (Bond-Lamberty and Thompson, 2010; version “20110524a”, download date 1/29/2012, http://code.google.com/p/srdb; data from untreated stands, averaged over years for a given site), separated by biome, evergreen/deciduous, and age group (aggrading or mature). Error bars represent 1 SD.
4.5 Appendix

The following information is included as supporting material for Chapter 4.

4.5.1 Soil moisture measurements

Cross-correlation of cleaned data from the two different sensors types installed concurrently at PP8 showed significant linear relationships (P<0.001) in all pairings, and CS-615s were not consistently higher or lower than ML2x probes at shallow or deep depths or averaged across depths. Mean $r^2$ among different sensors was 0.68 (SD=0.11), slightly lower than correlation among ML2x probes ($r^2=0.77$, SD=0.08, t-test P=0.001) and not significantly lower than correlation among CS-615 probes ($r^2=0.75$, SD=0.12, t-test P=0.20). Periods where $\theta$ reached field capacity or the hygroscopic minimum were identified and the recorded values for each sensor were rescaled to match these values. Missing data, due to power outages in one of the plots or sensor failure, were gap-filled using the best linear regressions with other working sensors. The regressions were comprised of data on both sides of the gap, equal to the length of the gap in each direction.

4.5.2 Leaf litter replenishment under soil chambers

Although chambers do temporarily exclude leaf litter, we replenished litter with all biomass components in one of two ways. In PP8 up to 2005, HW, and OP, litter was collected in baskets, harvested weekly during peak litterfall and monthly to bi-monthly the rest of the year, weighed and redistributed at the chamber location to maintain a similar input per unit ground area. After the deployment of ACES in all FACE plots in 2005, the protocol was changed to redistribute litter that accumulated on the chamber top each time location was switched (twice weekly). The revised approach was designed to solve two issues, (1) it immediately replaced litter that had been excluded, preventing
a lag in measurements and drying while the litter remained in the basket, and (2) it provided a more similar quantity and quality of litter that reflected the within-plot species distribution. We assessed the likely effect of the changed approach setting up a study in a 5x5 m plot adjacent to PP6 and compared litter collected in two baskets (0.5 m² each) with 8 “dummy” chambers during the peak of leaf fall, from mid-September through early December. The chamber-top litter approach collected approximately 15% more (SD = 12%) litter than the basket method, but the amount was not significantly different (p >0.05) during 13 out of 17 collection periods. The revised approach has likely resulted in an addition of 50 g C m⁻² y⁻¹ in litter added to the chamber footprint, or less than 5% of previously-reported annual F_soil from this site (1231-1330 g C m⁻² y⁻¹; Palmroth et al. 2005).

### 4.5.3 Temperature response model performance

Data from profile measurements (Daly et al., 2009) revealed that the time of day T_soil reached its peak was similar at all depths and for all months (P>0.06), and that using daily mean T_soil from either 5 or 10 cm depth produced similar estimates of annual F_soil (P=0.32), justifying gap-filling daily F_soil using more consistently available T₁₀.

In order to compare the exponential model with other commonly-used function, we fit location data for PP8 under non-limiting soil moisture conditions (REW>0.33). A modified Arrhenius equation (Lloyd and Taylor 1994) explained only ~1% more of the variation and did not lead to a significant difference in annual numbers (<1%; t-test P = 0.87). We also attempted to test for different temperature sensitivities between winter (where contribution of recently-assimilated carbon is nearly or entirely eliminated) and summer. This approach did not yield useful results because extrapolating exponential function derived based on highly-scattered data outside of the data range led to many unreasonable predictions at higher temperatures. Furthermore, large variability of F_soil
during the growing season (even after filtering out low REW conditions) often did not produce significant fits (P >0.05 32% of growing season fits).
5. Effects of atmospheric [CO2], nitrogen availability and soil moisture on the spatial and temporal variation of forest soil CO2 flux

5.1 Introduction

Carbon dioxide emissions from forest soils are not only a major component of the global atmospheric [CO2] budget, but also reflect how assimilated carbon (C) is allocated by plants under certain biophysical constraints. However, CO2 efflux from soils (\(F_{\text{soil}}\)) integrates both autotrophic and heterotrophic respiration (\(R_A\) and \(R_{Hb}\) respectively), each differentially sensitive to a number of drivers, frustrating the interpretation of the variation of \(F_{\text{soil}}\) in time and space. Here we account for the response of \(F_{\text{soil}}\) to elevated [CO2] and nitrogen (N) fertilization based on variation of stand and site characteristics (leaf area index (LAI), litterfall, and soil N), reflecting both responses to treatments and variation in native conditions, accounting first for the variation caused by soil temperature and moisture. We used a 10-year long, high-frequency dataset collected in four ambient CO2 and four elevated [CO2] plots, half of each fertilized with N. Having four drought years in the time series allows us to assess treatment effects on annual fluxes under varying climate conditions.

Generally, \(F_{\text{soil}}\) tends to increase with productivity within and across biomes (Litton et al. 2007), and has been linked to leaf production (Davidson et al. 2002; Palmroth et al. 2005; Bond-Lamberty & Thomson, 2010; Chen et al. 2011). However, within biomes, and even within stands, \(F_{\text{soil}}\) can change over the course of stand development, often increasing in aggrading stands (Wiseman & Seiler, 2004; although management history may lead to large soil C pools and reverse this trend, e.g., Gough and Seiler, 2004), but eventually declining after canopy closure (Giardina & Ryan, 2002; Drake et al. 2011). Although ecosystem \(R_A\) increases with gross primary productivity (GPP) over a wide
range of forests (DeLucia et al. 2007), the proportion of net primary productivity (NPP = GPP - \( R_A \)) to GPP tends to decrease with nutrient limitation (Vicca et al. 2012).

Furthermore, forests seem to trade off allocating C to aboveground versus belowground depending on resource availability and, thus, \( F_{\text{soil}} \) does not scale proportionately with GPP and may vary inversely with NPP (Palmroth et al. 2006).

The link between productivity and respiration has particular importance in the context of global change. Projected levels of increased atmospheric \([\text{CO}_2]\) have been shown to enhance productivity across a range of systems (Oren et al. 2001; Norby et al. 2005; McCarthy et al. 2006), leading to increased aboveground leaf production and woody biomass (McCarthy et al. 2010, 2007), as well as belowground production of root biomass (Norby et al. 2004; Pritchard et al. 2008a; Jackson et al. 2009), microbial biomass (Bader & Körner, 2010), and soluble C released from roots (Phillips et al. 2011). However there is large uncertainty of estimates of pool size and turnover rate of each C budget component, as well as of how much of the extra C of these pools is retained in ecosystems, particularly in belowground pools. Minor variations in these components can greatly influence conclusions on the impacts of environmental perturbations.

Combining measurements of \( F_{\text{soil}} \) with the balance between total belowground carbon flux (TBCF) and C accumulation in the forest floor and soil (Giardina & Ryan, 2002) sets a boundary to the net treatment effect on these components, constraining estimates of a few commonly available fluxes and simple assumptions used to assess treatment effects on finer-scale flux components.

Elevated \([\text{CO}_2]\) has typically been shown to increase \( F_{\text{soil}} \) (King et al. 2004). Initial findings from the Duke free-air \( \text{CO}_2 \) enrichment (FACE) experiment at a \textit{Pinus taeda} L. (loblolly pine) stand were a 16% increase in \( F_{\text{soil}} \) under elevated \([\text{CO}_2]\) using high-frequency automatic chamber measurements during the growing seasons from 1998-
2000 in the unreplicated Prototype and Reference plots (Butnor et al. 2003; here plots 7 and 8, respectively). Using periodic rather than continuous measurements at Duke FACE, a declining enhancement of \( F_{\text{soil}} \) of the elevated \([\text{CO}_2]\) relative to ambient treatment was found between 1999 and 2003 (Bernhardt et al. 2006), but extending the time series through 2008 deemed to have reversed the trend (Jackson et al. 2009). More recently, a mature broadleaf forest (in a webFACE setting) showed no enhancement of \( F_{\text{soil}} \) under elevated \([\text{CO}_2]\), attributed to interactions between productivity and soil moisture (Bader & Körner, 2010).

Site fertility may affect \( F_{\text{soil}} \) through LAI and C uptake, and by affecting C allocation. These interacting factors may lead to variation of \( F_{\text{soil}} \) depending on native variation of soil nutrient availability, forest nutrient management, as well as atmospheric deposition. In earlier studies at Duke FACE, fertilization has been shown to increase productivity, leading to enhanced aboveground woody biomass, leaf biomass, and coarse root biomass (McCarthy et al. 2007, 2010; Jackson et al. 2009). In the short-term, N fertilization can stimulate microbial activity (Butnor et al. 2003) leading to increases in \( F_{\text{soil}} \) for several days. However, the longer-term effect of fertilization leads to reduction in \( F_{\text{soil}} \) due to a shift in balance between above- and below-ground C partitioning (Butnor et al. 2003; Palmroth et al. 2006), ranging 10-23% (Butnor et al. 2003; Jackson et al. 2009). Yet, fertilization may not always reduce \( F_{\text{soil}} \): in another loblolly pine stand a decrease of fine root biomass with fertilization was counteracted by increased microbial activity, resulting in similar \( F_{\text{soil}} \) to unfertilized plots (Samuelson et al. 2009).

Elevated \([\text{CO}_2]\)-induced enhancement of production can be limited by soil nutrient availability, particularly in N poor soils (Oren et al. 2001). Such limitation was shown to increase the extra flux of C belowground (Norby et al. 2004; Palmroth et al. 2006). The combination of elevated \([\text{CO}_2]\) and N fertilization increased NPP (Palmroth et
al. 2006; McCarthy et al. 2010) and decreased $F_{soil}$ compared to unfertilized elevated treatment, resulting in $F_{soil}$ similar to unfertilized ambient treatment (Butnor et al. 2003; Palmroth et al. 2006; Jackson et al. 2009). However, the longevity and magnitude of these changes is uncertain. For example, as the duration of [CO$_2$] enrichment increased, the extra flux of carbon to some belowground components (e.g., fine roots) can be greatly reduced (Norby et al. 2010), allowing the extra carbohydrates to stimulate microbial biomass and, as microbes search for N, increase the turnover of older soil organic matter (Drake et al. 2011; Ziegler & Billings, 2011).

Treatment differences affecting $F_{soil}$ must be distinguished from direct and indirect effects of highly varying environmental factors. $F_{soil}$ is primarily regulated by soil temperature ($T_{soil}$) through enzyme kinetics and moderated by soil moisture at short time scales (Fang & Moncrieff, 2001; Palmroth et al. 2005; Davidson & Janssens, 2006). $F_{soil}$ is also coupled with GPP due to the supply of recently-assimilated C to the rhizosphere, often lagging behind C uptake only 1-5 days (Johnsen et al. 2007; Högberg et al. 2008; Mencuccini & Höltä, 2010). Thus, some of the variations of $F_{soil}$ may reflect drought-cycle and seasonal-phenological effects on GPP, directly or through stomatal regulation, as well as effects on aboveground production, all of which respond to $T_{soil}$, soil moisture, and other associated resource variables.

Site productivity, driven by either elevated [CO$_2$] or soil fertility can also influence $F_{soil}$ in indirect ways. Higher leaf area generated by either factor (McCarthy et al. 2007) can reduce $T_{soil}$ (and potentially soil moisture) and subsequently $F_{soil}$ both temporally through inter-annual phenological differences (Phillips et al. 2010), and spatially through within-stand variability in fertility (Oishi et al. in review).

In light of previous findings at Duke FACE and elsewhere, we set to test three hypotheses: (1) $F_{soil}$ is driven by variation of soil temperature diurnally and seasonally,
but over drying cycles and inter-annually $F_{\text{soil}}$ is driven by variation of soil moisture. (2) Spatially, the integrated effects of temperature and moisture sensitivities of $F_{\text{soil}}$ reflect greater carbon allocation belowground, positively related to elevated atmospheric [CO$_2$] and negatively related to N amendment and to high native soil N. In addition, (3) spatially, the variation of soil temperature and moisture are driven by LAI and leaf litterfall which, in turn, reflect the effects of [CO$_2$] and N availability.

### 5.2 Materials and Methods

#### 5.2.1 Study site

The study was conducted at the Duke Forest Free Air CO$_2$ Enrichment (FACE) site in central North Carolina, USA (35°58′N, 79°06′W). The *Pinus taeda* L. (loblolly pine) stand was planted in 1983, and has a substantial component broadleaved species. The experiment consists of eight circular plots, four exposed to ambient [CO$_2$] and four receiving 200 ppm [CO$_2$] above ambient. The paired Prototype and Reference plots (plots 7 and 8, respectively) were established in 1993, with enrichment commencing in 1994; enrichment of the adjacent replicates (plots 1-6) began in 1996. In 1998 plots 7 and 8 were divided in half with an impermeable barrier to 70 cm, well below the reach of the fine roots (Matamala and Schlesinger, 2000), and one half received annual N fertilization (11.2 g N m$^{-2}$ y$^{-1}$). This fertilization protocol was established in plots 1-6 beginning in 2005. Native N availability was previously presented in McCarthy et al. (2010) and we assumed that 20% of added N (2.2 g N m$^{-2}$) was available for uptake (Nason & Myrold, 1992).

Terms relating to the spatial aggregation of samples are described as follows: *plot* refers to one of the eight circular FACE rings, *subplot* refers to half of a plot, divided into the fertilized and unfertilized sections, and *treatment* refers to grouped four subplots receiving the same combination of [CO$_2$] and N. Treatment abbreviations are: ambient
[CO₂] unfertilized (AU), elevated [CO₂] unfertilized (EU), ambient [CO₂] fertilized (AF), and elevated [CO₂] fertilized (EF).

5.2.2 Instrumentation

Soil temperature was measured in each FACE plot with a permanently-installed thermistor buried at 10 cm ($T_{10}$). Volumetric soil moisture ($\theta$) was obtained with four Campbell Scientific CS-615 installed at 0-30 cm depth at each plot. Sensors were installed prior to dividing plots for N fertilization, so the four sensors were not always evenly divided among subplots. Soil moisture is expressed in this study as relative extractable water (REW), a percentage of measured water relative to the maximum between the hygroscopic point ($\theta=0.125$ m$^3$ m$^{-3}$) and field capacity ($\theta=0.35$ m$^3$ m$^{-3}$). Incoming precipitation was measured with an above-canopy tipping bucket installed at the top of a walkup tower (TE525M, Texas Electronics, Dallas, TX).

$F_{\text{soil}}$ was measured using the Automated Carbon-dioxide Efflux System (ACES, USDA Forest Service, US Patent 6692970). The system has been described in previous studies (Butnor et al. 2003; Palmroth et al. 2005); briefly, it is an IRGA-based, open system that sequentially samples 15 chambers plus one null chamber (491 cm$^2$ footprint, 10 cm height). Each chamber is sampled for a 10-minute cycle and the final record is accepted if air flow rates and CO₂ concentrations are stable and within a specified range; thus a maximum of 9 measurements for each chamber throughout each day is possible.

Plots 7 and 8 include data from 2001-2010. Additional ACES were added to plots 1 – 4 and 6 in early 2005, and plot 5 in 2006. For each of the ACES, four of the chambers were connected to tree stems and data collected are not used in this study. Six of the soil chambers were positioned in the unfertilized subplots and 5 chambers were positioned in the fertilized subplots. The ACES operation and data analysis in this study follow
Oishi et al. (in review), who analyzed only AU subplots, but we provide a detailed description below.

Each chamber was alternated between one of two fixed locations in the plot and ran in a given position for 3-4 day periods. Chamber movement is intended to minimize chamber effects on the amount of litter and moisture arriving at the monitored surface, and to increase the spatial sampling. Chamber locations were changed several times during the study period, initially to minimize disturbance to a sampling area and later to examine variability with proximity to trees. The chamber bases have a sharp, metal edge that cut into the soil approximately 1 cm, but do not use a permanently-installed collar. Litterfall excluded during measurement cycles was replenished (Oishi et al. in review).

ACES are designed to run continuously; however, several factors reduced the amount of usable data. First, individual measurements are filtered to exclude sampling periods where either air flow or CO\(_2\) concentrations were out of range. Second, systems were offline periodically for general maintenance and recalibration. Third, over the long duration of the study, systems began to breakdown more frequently. Therefore, the measurements were not continuous throughout the study period. Nevertheless, measurements did encompass virtually all of the environmental variability that occurred over the past decade, including several droughts and wet growing seasons.

To fill gaps in data coverage, we utilized the model for \(F_{\text{soil}}\) as a function of \(T_{\text{soil}}\) and REW previously described in Palmroth et al. (2005):

\[
F_{\text{soil}} = F^*_{\text{soil}} \times f(\text{REW})
\]  
Eq. 1

where \(F_{\text{soil}}\) is mean daily soil CO\(_2\) flux (\(\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}\)), \(F^*_{\text{soil}}\) is potential \(F_{\text{soil}}\) for a given \(T_{\text{soil}}\) under non-limiting REW, and \(f(\text{REW})\) is the reduction function for soil moisture limited conditions. Our approach to fit parameters differed as follows. We first estimated \(F_{\text{soil}}\) by fitting measured mean daily \(F_{\text{soil}}\) from each chamber location where >4
daily measurements were available as a function of mean daily $T_{10}$ under non-limiting soil moisture conditions. These conditions were defined as REW>0.33 (Oishi et al. in review; equivalent to the volumetric soil moisture, $\theta>0.20$ m$^3$ m$^{-3}$ in Palmroth et al. 2005). The form used is

$$F_{\text{soil}}^* = R_{b10} e^{b(T_{10}-10)}$$

Eq. 2.

where, $R_{b10}$ is estimated “basal” respiration at 10 °C ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$), and $b$ is the temperature sensitivity parameter ($e^{b\times10} = Q_{10}$). The values of $F_{\text{soil}}$ were natural log-transformed so the data could be fit as a linear function using the ACOTOOL function in Matlab (Version 6.0.1.450, Release 12.1, MathWorks Inc.), with year as a categorical variable. Linear regressions were not possible for all locations in all years due to limitations in data for reasons described previously as well as uneven representation of $T_{10}$ ranges. For example, during the drought year of 2005, there were very few days with temperature above the annual mean while soil moisture was non-limiting. Least squares fitting of these data led to some unreasonable $Q_{10}$ values (e.g. $<0$). Therefore, we constrained each location’s regressions by assuming a constant $Q_{10}$ parameter across years, but allowing for varying $R_{b10}$.

Limitations to $F_{\text{soil}}$ imposed by REW, $f$(REW), were accounted by fitting the proportionate reduction from daily $F_{\text{soil}}^*$ under non-limiting REW using Matlab’s least-squares, nonlinear NLINFIT function for each chamber location:

$$f(\text{REW}) = 1 - e^{-c \times \text{REW} + d}$$

Eq. 3

where $c$ and $d$ are coefficients describing the sensitivity of $F_{\text{soil}}$ to low REW. Because some years experienced few low-REW days, data were pooled across years.

Matlab was also used to process raw data and for linear regressions and statistical tests. SigmaPlot (v8.0.2, SPSS Inc.) was used for additional curve fitting.
N fertilization as split plot), with years as repeated measures were performed to test for treatment effects using SAS (PROC MIXED; Version 9.3, SAS Institute Inc., Cary, NC.)

5.2.3 Leaf litterfall, leaf area index and NPP

Leaf litter was collected periodically throughout the study with an array of baskets in each subplot, oven-dried, separated by pine or deciduous, and weighed. Leaf litter, together with optical and allometric-based approaches, was also used to estimate LAI (McCarthy et al. 2007).

NPP was estimated for foliage, wood (including coarse roots), fine roots, and reproductive organs as in McCarthy et al. (2010; published through 2004, updated here through 2010). Foliage was collected in litter baskets and linked to the year-of-production based on leaf longevity (McCarthy et al. 2010). Coarse root biomass was estimated as a function of aboveground biomass (Johnsen et al. 2004). Fine root production was measured through 2004 and the relationship between fine root and woody production was used for post-2004 estimates. The ratio of fine root:woody production was adjusted to 63% in fertilized treatments (Maier et al. 2004).

5.3 Results

Between 2001 and 2010, we collected a total of 69,996 acceptable individual samples across the 16 subplots. Using these data, and associated environmental variables, we first explain the temperature- and soil moisture-sensitivity of $F_{\text{soil}}$ among treatments. We then estimate annual $F_{\text{soil}}$ and finally attempt to determine the sources of variability within and among treatments.

Results of the ANOVAs testing for treatment effects and N availability on the coefficients of the soil temperature and moisture responses, on the growing season temperature (only whole plot effects) and moisture, and on the products of annual $F_{\text{soil}}$ and $F_{\text{soil}}$ are presented in Table 5.1. None of the variables with significant trends over
time exhibited interaction with year (i.e. [CO₂] × year, N × year), meaning the behavior over time was similar in the four treatment combinations (P>0.56). Over the period 2005-2010, Rₚ坐下 declined and, together with decreases in REW and T坐下, lead to a decline in annual F’soil of 49 g C m⁻² y⁻¹ (~4% per year; P=0.0685) or ~15% decrease in annual F’soil for the period, and a somewhat smaller decline in annual Fsoil.

### 5.3.1 Sensitivity of Fsoil to temperature and soil moisture

Despite the low number of replicates (n=4), there was a strong (P<0.05) N effect on Q₁₀ and Rₚ坐下 and a tendency (P<0.15) for [CO₂] effect on both, as well as a tendency for interaction effects on both soil moisture response parameters (Table 5.1). The mean responses (Fig. 5.1) show [CO₂] and N induced reductions of Q₁₀ such that at EF it was lower than at AU. In contrast, [CO₂] induced enhancement and N induced reductions of Rₚ坐下 such that at AF it was lower than at both elevated [CO₂] treatments. The values of c showed a greater tendency to increase with [CO₂] under native soil N than under fertilized conditions, while d, showed a tendency to decrease with [CO₂] only under fertilized conditions.

The combined effect of the parameters is shown in Fig. 5.2. F’soil increased exponentially with T坐下 for all treatments (Fig 5.2a, Table 5.2). Comparing the two temperature-sensitivity parameters, Q₁₀ decreased slightly with increasing Rₚ坐下 (P=0.062, r²=0.23, data not shown). The relative increase of F’soil with T坐下 was higher in AU than any of the other treatment plots, indicated by the negative slopes in Fig 5.2c. EU had higher F’soil than AU plots up to ~17 °C. However, because lower Q₁₀ compensated for the higher Rₚ坐下 in EU compared to AU (Table 5.1), at higher temperatures, including the mode of T坐下 (Fig. 5.2e), the flux rate in EU was similar to AU (Fig 5.2c). F’soil of AF was similar to AU at T坐下<5 °C, but having similar T坐下-sensitivity to EU, AF dropped...
appreciably below AU at high temperatures. EF was least sensitive to changes in $T_{10}$ crossing from higher to lower $F_{\text{soil}}$ than AU at about the mid-temperature range.

Treatments may affect not only the $T_{10}$ and REW sensitivities but these soil variables as well. Monthly mean $T_{10}$ differed among plots an average of 10 months of each year ($P<0.05$), with approximately 2 °C separating the plots with lowest and highest temperatures. Similar temperatures typically occurred in spring months when soil warmed rapidly. However, among [CO$_2$] treatments, annual $T_{10}$ were similar over all years ($P>0.13$), as were the inter-annual mean (Table 5.1; Fig. 5.1e) and the frequency distributions (Fig. 5.2e).

$F_{\text{soil}}$ decreased with REW in all treatments (Fig. 5.2b, Table 5.2). The $c$ parameter, determining the value below which REW begins to suppress $F_{\text{soil}}$ (lower $c$ leads to decline at higher REW), increased with annual leaf litterfall across treatments ($P=0.0097$, $r^2=0.39$), but $d$ (the rate of decline) was uncorrelated with leaf litterfall or LAI ($P>0.67$). The $c$ and $d$ parameters were not related to each other ($P=0.94$), so the rate of decline did not compensate for the point of REW limitation. Thus, lower litterfall in AU was associated with greater sensitivity to REW.

$F_{\text{soil}}$ of AU decreased the most with REW (Fig. 5.2b, Table 5.2). Despite slight differences among the treated plots, all were increasingly less sensitive than AU to REW as soil dried, averaging ~15% higher $f$(REW) in the driest soil conditions (Fig 5.2d). REW $<0.4$ accounted for 35% of days over the study period (Fig. 5.2f), but as many as 207 days (56%) in the severe drought year 2007. The average difference $f$(REW) between AU and the other treatments over this REW represented a 6% lower $F_{\text{soil}}$. The high frequency of days with high REW represents mostly winter days when $F_{\text{soil}}$ was temperature-limited.

Neither [CO$_2$] nor N affected the inter-annual growing season means of REW (Table 5.1, Fig. 5.1f), nor the frequency distributions (Fig. 5.2f), but there was a tendency
for elevated [CO₂] to reduce REW in N fertilized subplots. However, when observing these differences at monthly time scales, REW at EF was lower than EU only for three of the 120 months in this study (P<0.05), and only one month with mean REW <0.33, where large reductions in F_soil were observed (Fig. 5.2b). Fertilization in ambient plots (AF) reduced REW relative to AU during 12 months (P<0.05); in only two of these months was REW <0.33. Elevated [CO₂] (EU and EF) was associated with lower REW than ambient [CO₂] treatments (AU and AF) during 19 months in the study period (P<0.05), five of which occurred during the growing season and had mean REW <0.33. Thus, regardless of the treatment, subplots experienced similar drought conditions over the study period.

5.3.2 Inter-annual variability in $F_{soil}$

Mean annual $F_{soil}$ and $F_{soil}$ tended to increase with [CO₂] and strongly decreased with N (Table 5.1; Fig. 5.1g,h). Mean annual $F_{soil}$ and $F_{soil}$ showed a tendency to increase more with [CO₂] under fertile conditions. Annual $F_{soil}$ of AU averaged 1383 (SD=152) g C m⁻² y⁻¹, varying between a minimum of 1202 g C m⁻² y⁻¹ and maximum of 1639 g C m⁻² y⁻¹ (Fig 5.3a). Annual $F_{soil}$ of EU averaged $F_{soil}$ of 1471 (SD=153) g C m⁻² y⁻¹, consistently higher than AU (average 7%, SD=5%, Fig 5.3b). AF mean annual $F_{soil}$ was 1085 (SD=101) g C m⁻² y⁻¹, a 21% (SD=2%) reduction from AU, and lower in all years (P<0.05) except the two of the driest years of the study (2005 and 2007). EF led to consistently lower annual $F_{soil}$ than AU, averaging 1271 (SD=121) g C m⁻² y⁻¹, a non-significant 8% reduction (P>0.12). EF averaged 14% lower annual $F_{soil}$ than EU, with a tendency for significant reduction only during two dry years, 2002 and 2007 (P<0.10).

Over the 10-year study period, annual $F_{soil}$ of AF decreased ~28 g C m⁻² y⁻¹ (P=0.028). The other treatments tended to decrease as well, albeit not significantly (P>0.13; Fig. 5.3b). Because the tendency was lesser in EF, the difference in $F_{soil}$ relative to
AU showed convergence from a reduction of ~14% to no reduction in 2010 (P=0.020, P>0.14 for all other treatments).

5.3.3 Sources of spatial variation of $F_{soil}^*$

Within treatments, $Q_{10}$ and $R_{b10}$ were weakly related to leaf litterfall only in EF ($P=0.099$ and 0.069, respectively); otherwise the parameters were unrelated to either LAI or leaf litterfall ($P>0.13$). Across treatments, $Q_{10}$ was weakly related to LAI ($P=0.072$); otherwise the parameters were unrelated to either LAI or leaf litterfall ($P>0.16$). However, the product of $R_{b10}$, $Q_{10}$ and $T_{10}$ might still be affected by these stand characteristics. We related estimates of $F_{soil}^*$ at 21 °C, the peak frequency of $T_{10}$ (Fig 5.2e), to mean annual LAI and annual leaf litterfall (Fig 5.4a,b). Although for a given treatment, $F_{soil}^*$ at 21 °C was unrelated to LAI or litterfall ($P>0.11$), significant relationships emerged across fertilization treatments within each [CO$_2$] treatment as N fertilization increased LAI and litterfall extending the range of each variable. Under elevated [CO$_2$], $F_{soil}^*$ at 21 °C was unrelated to LAI ($P=0.53$). We note that one EF subplot, the long-running FACE prototype plot (plot 7), exhibited a much lower $F_{soil}^*$ than would be expected based on its LAI and litterfall and the data from other elevated [CO$_2$] plots (circled in Fig. 5.4), and was excluded from the analyses described above.

Estimates of annual $F_{soil}^*$ also decreased with increasing LAI and leaf litterfall (Fig. 5.4d,e) and the relationships were slightly to appreciably better than those with $F_{soil}^*$ at 21 °C. Again, only leaf litterfall produced significant regressions with both [CO$_2$] treatments. However, replacing LAI and annual leaf litterfall with N availability reduced the separation between [CO$_2$] treatments in $F_{soil}^*$ at 21 °C ($P=0.035$ for differences in populations, Fig. 5.4c) and resulted in the four treatment combinations behaving as a single population of annual $F_{soil}^*$ ($P=0.078$, Fig. 5.4f), without a need to exclude any data point as an outlier. We tested N availability as a covariate with the treatment effects on
temperature- and soil moisture-sensitivity parameters (see Table 5.1), but it was not significant ($P>0.13$) and fundamentally did not change the results.

5.3.4 REW control over inter-annual variation of $F_{soil}$

Because inter-annual variability of $T_{10}$ was generally small, inter-annual variability of $F_{soil}$ was driven by REW. However, since REW was very similar among treatments (Fig. 5.2f), differences in the REW-sensitivity among treatments also contributed to treatment-level differences in $F_{soil}$ (Fig. 5.2b,d). The annual proportionate reduction from $F_{soil}^*$ increased with decreasing growing season REW (Fig. 5.5a). AU followed a quadratic function that reflected a greater sensitivity than other treatments to soil drought. In turn, REW was related similarly in all treatments to an independently-derived water availability index (WAI), defined as precipitation minus potential evaporation from pan measurements (NOAA weather station Chapel Hill, www.ncdc.noaa.gov; Fig. 5.6). Although annual $f(REW)$ decreased more sharply with decreasing growing season mean REW in AU than the other treatments, the treatment response relative to AU departed linearly (Fig. 5.5b), resulting in up to $\sim5\%$ higher annual $f(REW)$ and annual $F_{soil}$ than AU in the driest years of the study.

5.4 Discussion

Recent publications, both based on monthly measurements of $F_{soil}$ from Duke FACE experiment describe some inconsistent patterns. In Bernhardt et al. (2006), annual $F_{soil}$ from 1997-2003 averaged 16% higher in EU than AU, but the difference decreased from about 300 (19% in 1999) to 100 (10% in 2003) g C m$^{-2}$ y$^{-1}$. In contrast, Jackson et al. (2009) found that monthly rates of $F_{soil}$ from 1997-2008 averaged 23% higher in EU, increasing in the latter years to 30% along with increases in fine root biomass. Our results show that EU tended to increase annual $F_{soil}$ (Table 5.1, Fig. 5.1 & 5.3), averaging 6.5% (SD=4.7%) over the study period, even lower than Bernhardt et al. (2006) and more
similar to the uncertain response of a mature, mixed-deciduous forest (webFACE experiment, Bader and Körner, 2010). However, in contrast to both earlier studies, there was no trend towards either increasing or decreasing [CO₂]-induced response of Fₘₐₜ.

We contribute two additional findings: First, consistent with our hypothesized controls of variability and the findings of Oishi et al. (in review) on three forest types, we find that seasonal variation of Fₘₜ is driven mostly by soil temperature, while drying cycles, which tend to congregate in dry years, control the daily and inter-annual variation by reducing Fₘₜ from its temperature-controlled potential. Thus variation of annual Fₘₜ are mostly explainable by soil moisture (Fig. 5.5), an opportune outcome considering that soil moisture is highly correlated to easily obtained climatic data (Fig. 5.6). Relative to AU, the three treatments showed slightly less sensitivity as reflected in the response of daily Fₘₜ to REW (Fig. 5.2b,d). Daily variation in canopy photosynthesis is reflected in fine root respiration after one day (Drake et al. 2011), indicating that water limitations can have a significant and immediate impact on Fₘₜ. In addition, prolonged droughts also reduce fine root production (Pritchard et al. 2008a), and microbial respiration (Drake et al. in review). It seems that both [CO₂] and N offer some protection from drought effects, such that during two dry years (2005 and 2007), the greater REW-sensitivity of AU appeared to reduce its annual Fₘₜ to levels similar to AF (Fig 5.3).

Second, consistent with Palmroth et al. (2006) and our second hypothesis, Fₘₜ decreased along with TBCF as productivity (indicated by LAI and leaf litterfall) increased; the [CO₂] level separated the subplots into two, largely overlapping populations, within which native fertility and N-fertilized subplots form a continuum of response (Fig. 5.4d,e). However, we found that replacing these indices of productivity with available soil N, blurred the difference between the two populations, indicating that the effect of both treatments on Fₘₜ was mediated through soil N (Fig. 5.4f). Indeed,
even the outlier in the former relationships was no longer distinguishable when soil N was used. Because, in contrast to our third hypothesis, soil temperature and moisture responded only marginally to treatments, it seems that the spatial variation in $F_{\text{soil}}$ was controlled by processes related to belowground C partitioning. Thus, the spatial variation of annual $F_{\text{soil}}$ was best explained across the four $[\text{CO}_2] \times N$ treatments with available soil N (Fig. 5.4f), while the inter-annual reductions from this potential was best explained with relative extractable soil moisture (Fig. 5.5).

Similar to most earlier studies, we also find that the N-induced depression of $F_{\text{soil}}$ was ~20% in both $[\text{CO}_2]$ treatments (Butnor et al. 2003; Palmroth et al. 2006; Jackson et al. 2009). However, our analysis seems to contradict earlier findings of Palmroth et al. (2006) from a small subset of the plots used here: the decrease in TBCF with N-fertilization was not a compensation for increased aboveground net primary production (ANPP′, which includes construction respiration), but rather indicated a large suppression of $F_{\text{soil}}$, which should result in a large accumulation of soil C. To date, no data have been published on soil C in the fertilized treatment plots.

Qualitatively, the $[\text{CO}_2] \times N$ treatment-induced patterns observed in the parameters of the $F_{\text{soil}}$ response to temperature and $F_{\text{soil}}$ response to moisture, and thus in annual $F_{\text{soil}}$ and $F_{\text{soil}}$, reflect published observations on $F_{\text{soil}}$ (Butnor et al. 2003; Bernhardt et al. 2006; Jackson et al. 2009), as well as fine root respiration (Drake et al. 2008), fine root biomass (Pritchard et al. 2008a; Jackson et al. 2009), forest floor C and heterotrophic respiration (Lichter et al. 2008), root exudation rates (Phillips et al. 2011), rhizomorphs (Pritchard et al. 2008b), as well as fungal and microbial activity (Billings & Ziegler, 2008), all showing greater pools or fluxes under high $[\text{CO}_2]$, with decreases following fertilization. However, despite the matching of patterns, it is difficult to quantitatively account for treatment-induced changes in $F_{\text{soil}}$ based on the fluxes from
these pools. For example, fine root biomass in the upper 15 cm increased 24% under elevated \([\text{CO}_2]\), but this change accounted for increased \(F_{\text{soil}}\) of only 26 g C m\(^{-2}\) y\(^{-1}\) (Jackson et al. 2009). Although potentially physiologically significant, this amount had a small influence on annual \(F_{\text{soil}}\).

To examine the treatment effects of elevated \([\text{CO}_2]\) and N fertilization on \(F_{\text{soil}}\) in the context of the stand C budget, we compared the differences in aboveground and belowground fluxes of C. Total belowground C flux (TBCF) was estimated based on Giardina and Ryan (2002) and Palmroth et al. (2006), such that

\[
\text{TBCF} = F_{\text{soil}} + F_{\text{tr}} - F_{\text{H,litter}} + \Delta C, \quad \text{Eq. 4}
\]

where \(F_{\text{tr}}\) is C transport off site from the rooting zone, assumed negligible (Palmroth et al. 2006), \(F_{\text{H,litter}}\) is heterotrophic respiration associated with litter decomposition, assumed equal to litterfall C if the litter pool is at steady state, and \(\Delta C\) represents the change in C pools of roots, litter, and soil (\(\Delta C_{\text{root}} + \Delta C_{\text{litter}} + \Delta C_{\text{soil}}\)). Lichter et al. (2008) reported a 30 g C m\(^{-2}\) y\(^{-1}\) enhancement in forest floor C under elevated \([\text{CO}_2]\), equal to approximately 50% of the difference in annual litterfall between AU and EU. Because no forest floor data were available for AF or EF, we assumed that \(\Delta C\) was 50% of the difference between litterfall in AU and these treatment plots (20 and 35 g C m\(^{-2}\) y\(^{-1}\), respectively). This, however, would be somewhat counterbalanced by the shrinking fine root pool under fertilization (Table 5.3). Aboveground NPP (ANPP) was estimated to include construction respiration (\(R_C = 0.25 \times \text{ANPP}, \text{ and ANPP}' = \text{ANPP} + R_C\)).

Differences between ANPP’ and TBCF in AU as a reference state and the other treatments are presented in Fig. 5.7 and Table 5.3. Previous analysis performed on data from the prototype and its reference plot showed that an increased ANPP’ with N fertilization was accompanied by a similar decrease in TBCF, indicating that additional N did not change GPP but altered C partitioning in favor of wood and foliage.
production (Palmroth et al. 2006). Based on the current analysis it would appear that N
addition decreased the observed total C by ~200 – 250 g C m$^{-2}$ y$^{-1}$. However, there is no
reason for our N fertilization to lower GPP, an assertion supported by LAI, gas-
exchange, and NPP data (McCarthy et al. 2007, 2010; Maier et al. 2008). Indeed, it would
take only a relatively small underestimation of ANPP’ (10% or less, Table 5.3) and
relaxing the assumptions made in calculating TBCF to reestablish the previously
observed pattern.

Increases in coarse root biomass (diameter ≥2 mm, Jackson et al. 2009; Table 5.3)
add to soil C, but only little to autotrophic respiration. These roots represent an
intermediate class, not estimated as a part of the tap and sinker root system, commonly
obtained from allometric relationships (McCarthy et al. 2010), and largely missed in soil
cores or minirhizotron measurements. The amount of C added to this component over
the first three years of fertilization would reduce by nearly a fifth the underestimation of
TBCF in AF, and over a third in EF (Table 5.3), thus moving the forest towards
reestablishing the simple replacement between ANPP’ and TBCF observed earlier.
Moreover, it is possible that as the stand aged, especially under elevated [CO$_2$], N
became progressively limiting, thus forcing microorganisms to mine soil organic matter
for N, in the process releasing CO$_2$ from older material (Drake et al. 2011). Indeed, in
comparing soil from EU and EF, shifts in microbial and fungal communities resulted in
increased activity of organisms that can decompose more recalcitrant soil organic matter
in the N-limited, unfertilized treatments (Billings & Ziegler, 2008). Based on $^{13}$C tracer,
root respiration accounted for 14-37% of daytime $F_{\text{soil}}$ of EU, whereas soil carbon fixed
prior to CO$_2$ fumigation in 1996 accounted for 10-19% of $F_{\text{soil}}$ (Taneva & Gonzalez-Meler,
2011), contributing an estimated 100 g C m$^{-2}$ y$^{-1}$ to $F_{\text{soil}}$ but not to TBCF. Mining of soil
organic matter might also be occurring, albeit to a lesser extent, under ambient [CO$_2$] where N was not added.

The preponderance of evidence, including ours, indicates that fertilization generally decreased $F_{\text{soil}}$ without reducing GPP. However, our analysis does not indicate the expected increase in ANPP' with reductions in TBCF. Based on the analyses above, we suggest that a combination of overestimation of TBCF under unfertilized conditions, a result of not having data needed for accounting for decomposition of older soil organic matter, and underestimation of TBCF under fertilized conditions, a result of not having enough data on coarse root C pools and litter accumulation may have contributed to a lack of complimentary changes in ANPP' and TBCF observed with N fertilization (Fig. 5.7).
Table 5.1: *P*-values for significance of treatment effects on temperature- and soil moisture-sensitivity parameters, growing season environmental variables, and annual soil CO$_2$ fluxes. ANOVAs were performed to test for treatment effects as a blocked, split-plot experiment with repeated measures. Single values were used for all years for $Q_{10}$, $c$, and $d$. Sub-plot $T_{10}$ was not available, so N effects could not be tested. We discuss responses where significant (*P*<0.05; in bold) or if there is a tendency (*P*<0.15; in italic). We do not discuss single factors effect if the interaction is significant.

<table>
<thead>
<tr>
<th></th>
<th>CO$_2$</th>
<th>N</th>
<th>CO$_2$×N</th>
<th>Year</th>
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<tr>
<td>$T_{10}$ parameters</td>
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<tr>
<td>$R_{p10}$</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$f$(REW) parameters</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>$c$</td>
<td>0.241</td>
<td>0.307</td>
<td><strong>0.145</strong></td>
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<tr>
<td>$d$</td>
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<td>0.580</td>
<td><strong>0.116</strong></td>
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<td></td>
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<tr>
<td>Growing season variables</td>
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<td></td>
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<tr>
<td>$T_{10}$</td>
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<td>n/a</td>
<td>&lt;0.0001</td>
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<tr>
<td>REW</td>
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<td><strong>0.133</strong></td>
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</tr>
<tr>
<td></td>
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<td></td>
</tr>
<tr>
<td>Annual Fluxes</td>
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<td></td>
</tr>
<tr>
<td>$F^*$ soil</td>
<td>0.102</td>
<td>&lt;0.0001</td>
<td>0.004</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$F^*$ soil</td>
<td>0.109</td>
<td>&lt;0.0001</td>
<td><strong>0.073</strong></td>
<td>&lt;0.0001</td>
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Table 5.2: Parameters for temperature sensitivity of soil CO$_2$ flux under non-limiting soil moisture conditions ($F_{\text{soil}}^\alpha$; Eq. 2) and for sensitivity $F_{\text{soil}}$ to relative extractable water (REW) ($f(\text{REW})$; Eq. 3) presented as mean (with SD) by plot and treatment. $R_{\text{bl0}}$ is in µmol CO2 m$^{-2}$ s$^{-1}$, all other parameters are unitless.

<table>
<thead>
<tr>
<th>Ring</th>
<th>$Q_{\text{bl0}}$</th>
<th>$F_{\text{soil}}^\alpha$</th>
<th>$R_{\text{bl0}}$</th>
<th>c</th>
<th>d</th>
</tr>
</thead>
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<td>AU</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>3.24 (1.09)</td>
<td>0.713 (0.277)</td>
<td>5.35 (0.98)</td>
<td>-0.421 (0.180)</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>3.81 (1.10)</td>
<td>0.612 (0.204)</td>
<td>4.41 (1.45)</td>
<td>-0.708 (0.251)</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>3.46 (1.18)</td>
<td>0.587 (0.434)</td>
<td>11.06 (6.06)</td>
<td>-0.264 (0.332)</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>2.97 (1.16)</td>
<td>0.742 (0.156)</td>
<td>7.55 (2.54)</td>
<td>-0.083 (0.471)</td>
<td></td>
</tr>
<tr>
<td>EU</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>2</td>
<td>2.77 (1.11)</td>
<td>0.981 (0.077)</td>
<td>7.09 (2.25)</td>
<td>-0.492 (0.379)</td>
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</tr>
<tr>
<td>3</td>
<td>3.06 (1.13)</td>
<td>0.669 (0.123)</td>
<td>19.98 (13.89)</td>
<td>-0.646 (0.351)</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2.87 (1.08)</td>
<td>0.816 (0.099)</td>
<td>10.47 (3.02)</td>
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<tr>
<td>7</td>
<td>3.09 (1.17)</td>
<td>0.754 (0.178)</td>
<td>11.18 (13.94)</td>
<td>-0.271 (0.874)</td>
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</tr>
<tr>
<td>AF</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>2.85 (1.09)</td>
<td>0.493 (0.260)</td>
<td>5.67 (1.77)</td>
<td>-0.581 (0.265)</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>3.59 (1.11)</td>
<td>0.371 (0.121)</td>
<td>6.69 (2.10)</td>
<td>-0.676 (0.134)</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>2.98 (1.19)</td>
<td>0.528 (0.160)</td>
<td>8.20 (2.95)</td>
<td>-0.360 (0.239)</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>2.50 (1.13)</td>
<td>0.651 (0.223)</td>
<td>9.86 (4.19)</td>
<td>-0.250 (0.494)</td>
<td></td>
</tr>
<tr>
<td>EF</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>2.60 (1.06)</td>
<td>0.805 (0.268)</td>
<td>6.96 (1.26)</td>
<td>-0.295 (0.108)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>2.86 (1.10)</td>
<td>0.630 (0.198)</td>
<td>14.33 (5.51)</td>
<td>-0.523 (0.169)</td>
<td></td>
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<tr>
<td>4</td>
<td>2.60 (1.06)</td>
<td>0.837 (0.114)</td>
<td>10.10 (1.92)</td>
<td>-0.276 (0.144)</td>
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</tr>
<tr>
<td>7</td>
<td>2.58 (1.12)</td>
<td>0.641 (0.188)</td>
<td>7.08 (2.65)</td>
<td>-0.297 (0.439)</td>
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Table 5.3: Comparison of differences between treatment-level aboveground net primary productivity (including construction respiration; $\Delta$ANPP') and total belowground C flux ($\Delta$TBCF; Fig. 7). Departure from the 1:1 replacement ratio for the addition of N between $\Delta$ANPP' and $\Delta$TBCF. Total leaf litterfall and change in fine root and coarse root NPP. All units g C m$^{-2}$ y$^{-1}$ unless otherwise noted.

<table>
<thead>
<tr>
<th></th>
<th>$\Delta$ANPP'</th>
<th>$\Delta$TBCF</th>
<th>Total</th>
<th>Departure from 1:1</th>
<th>Departure % of ANPP'</th>
<th>Departure % of TBCF</th>
<th>Leaf litterfall</th>
<th>$\Delta$C in fine roots</th>
<th>$\Delta$C in coarse roots</th>
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</thead>
<tbody>
<tr>
<td>EU - AU</td>
<td>+344</td>
<td>+128</td>
<td>473</td>
<td>161</td>
<td>+10</td>
<td>-12</td>
<td>+42</td>
<td>-15</td>
<td>+30</td>
</tr>
<tr>
<td>AF - AU</td>
<td>+84</td>
<td>-311</td>
<td>-227</td>
<td>136</td>
<td>+9</td>
<td>-13</td>
<td>+10</td>
<td>-20</td>
<td>+55</td>
</tr>
<tr>
<td>EF - EU</td>
<td>+30</td>
<td>-222</td>
<td>-192</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

$\Delta$ANPP', leaf litterfall, and fine root data from McCarthy et al. (2010), updated in this study. Coarse root (diameter \(\geq 2 \) mm) data adapted from Jackson et al. (2009) by averaging change in biomass between the start of fertilization in 2005 and sampling in 2008.
Figure 5.1: Treatment mean of temperature-response parameters for soil CO$_2$ flux ($F_{soil}$, see Eq.2), (a) $Q_{10}$, (b) $R_{b10}$, parameters for the $F_{soil}$ sensitivity to relative extractable water (REW; $f$(REW), see Eq. 3) (c) $c$, and (d) $d$, mean growing season environmental variables (e) soil temperature at 10 cm ($T_{10}$), (f) REW, and annual sums of (g) potential $F_{soil}$ under non-limited REW ($F'_{soil}$) and (h) $F_{soil}$. Variables are expressed in relation to fertilization treatment on the x-axis. Open and closed symbols represent ambient and elevated [CO$_2$] plots and circles and triangle represent unfertilized and fertilized plots, respectively. Letters indicate similar means (Tukey’s least significant difference, $P<0.05$). Error bars represent 1 SE.
Figure 5.2: (a) Potential soil CO$_2$ flux under non-limiting soil moisture ($F'_{\text{soil}}$) as a function of soil temperature at 10 cm ($T_{10}$) and (b) limitation of soil CO$_2$ flux ($F_{\text{soil}}$) by relative extractable water content of soil (REW; $f(\text{REW})$, see Eq. 1 & 3). Treatment responses (c) $F'_{\text{soil}}$ and (d) $f(\text{REW})$ relative to control plots, expressed as a proportion. Frequency distribution of (e) $T_{10}$ and (f) REW. Gray areas in (a-d) represent 1 SE around the control plots.
Figure 5.3: (a) Annual soil CO$_2$ flux ($F_{\text{soil}}$) by treatment and (b) treatment response of $F_{\text{soil}}$ as a proportion of control plot. Only one plot ambient and elevated CO$_2$ received nitrogen fertilization prior to 2005 (FACE Reference and Prototype plots), so stand level estimates were scaled based on the relationship between these two plots and the other six plots using data from 2005-2010 (gray symbols). Asterisks indicate significant differences between N and Control ($P<0.05$). Error bars represent 1 SE.
Figure 5.4: Potential soil CO$_2$ flux under non-limiting soil moisture conditions ($F_{\text{soil}}^-$) at 21 °C (a,b,c) and as a yearly sum (d,e,f) as a function of mean annual leaf area index (LAI, a & d), leaf litterfall (b & e), and N availability (c & f). Lines represent linear fits by CO$_2$ level (solid are significant). Data from plot 7 (elevated [CO$_2$] with fertilization; circled) were not used in the regressions for (a, b, d & e) (see text for details). Error bars represent 1 SE.
Figure 5.5: Mean growing season relative extractable water content (REW) compared to (a) annual reduction of soil CO$_2$ flux due to soil moisture limitation ($f$(REW)) and (b) treatment response of annual $f$(REW) relative to control (AU) plots.
Figure 5.6: Growing season water availability index (WAI; precipitation minus pan evaporation) versus mean growing season relative extractable water (REW).
Figure 5.7: Treatment-induced change in change in annual total belowground carbon flux ($\Delta$TBCF) compared to annual aboveground net primary productivity (including construction respiration; $\Delta$ANPP'). Dotted 1:1 Replacement lines represent theoretical change associated with a balanced change in allocation between ANPP' and TBCF. Error bars represent 1 SE.
6. Carbon use efficiency of a mature deciduous forest and response to drought

6.1 Introduction

Forests play an important role in the global carbon cycle, contributing to a large sink of atmospheric [CO$_2$] as well as sequestering an enormous pool of carbon. The processes regulating carbon (C) uptake through photosynthesis, and ultimately the fate of that C in the ecosystem are needed in any application requiring quantification of C accumulation in the form of plant biomass, also known as net primary productivity (NPP). Estimating NPP based using environmental variables is, logically, a desirable approach but may pose additional challenges. NPP is the difference between carbon gains (gross primary productivity, GPP) and losses (autotrophic respiration $R_A$) and these variables respond differently to environmental conditions. Although some respiration is coupled with GPP at short time scales (Johnsen et al., 2007; Högberg et al., 2007; Mencuccini & Hölttä, 2010), other respiratory fluxes associated with biomass construction may be seasonal and out of phase with GPP (Arneth et al., 1998). From a global perspective, a wide variety of forest stands have a similar carbon use efficiency (CUE); the proportion of NPP:GPP (Waring et al., 1998). However, there is considerable variability in CUE among stand ages (DeLucia et al., 2007) and across fertility gradients (Vicca et al., 2012). Additionally, growth in a given year may be dependent on the previous year’s environmental conditions (Arneth et al., 1998; Zweifel et al., 2006; Noormets et al., 2008), so environmental drivers of GPP may be temporally decoupled from observed NPP. In addition to spatial and long-term temporal variability in CUE, it may also vary interannually since the responses of GPP, NPP, and $R_A$ to environmental drivers may not be proportionate, or even in the same direction. However, studies that
have examined interannual trends in CUE appear to support a consistent value (Curtis et al., 2005, Schwalm et al., 2007).

Mature forests in temperate climates provide an interesting ecosystem to address tradeoffs between NPP and $R_A$ under GPP constraints. These systems contain large pools of C, both as living biomass and potentially in soils that have built-up over stand development. Large amounts of standing biomass supports high leaf area index (LAI) for photosynthesis; however, it also represents a large respiratory cost to support. Furthermore, stand height has often reached its peak, and may be exhibiting hydraulic limitations. Such hydraulic limitations associated with stand height may drive age-related decline in CUE (Drake et al., 2010) even when the photosynthetic apparatus and water transporting system do not vary appreciably with age. If this is the case, GPP in mature forests should be particularly vulnerable to drought stress. On the other hand, trees in mature stands may have access to deeper sources of water, making them more tolerant to drought (Leuzinger et al., 2005, Oishi et al., 2010).

We apply the analysis described above to a temperate, mature, mixed-species broadleaf deciduous in the Piedmont region of North Carolina, USA. This stand includes drought-sensitive species, but has shown conservative interannual water use (Oishi et al., 2010). Based on recently-revised eddy covariance data (Novick et al., in prep. and presented here), this mature stand also represents a sizable C sink for its age.

Our analysis addresses the following questions: quantify how C is allocated within the components of the ecosystem, and (3) examine how interannual variability in environmental conditions affects uptake and allocation. Data to construct independent carbon budgets are used to address the following questions: (1) How is C allocated in this system, both between NPP and $R_A$, as well as by individual components of these larger fluxes? (2) Based on expected hydraulic limitations of GPP and the fact that much
of NPP occurs prior to drought, do drought conditions affect GPP more strongly than NPP, leading to increases in CUE with decreasing water availability (i.e. greater interannual variability in $R_e$)? (3) Based on small interannual variability in transpiration at this site (Oishi et al., 2010), does water use efficiency (WUE) decline with water availability? (4) At what time scales are mature stands sensitive to environmental variability?

To accomplish these objectives, the main components of the C budget for this system are explored. This study analyzes data from biometric estimates of NPP, measured and modeled respiratory fluxes, modeled GPP based on sap flux-derived canopy conductance, and eddy covariance data collected over a four year period, including one severe and one moderate drought, as well as an abnormally wet year.

6.2 Materials and methods

6.2.1 Research site

The HW site is located at the Duke Forest Ameriflux Hardwood site, Orange County, North Carolina (36°58′41.430″N, 79°05′39.087″W). Long-term (115-year) mean annual precipitation ($P$) for the area is 1146 (±166) mm, with 630 (±133) mm occurring between April and September (www.ncdc.noaa.gov/). The forest stand is comprised of approximately 80-100 year-old mixed hardwood species. Mean canopy height is 25 m with emergent crown tops extending above 35 m and is dominated by hickories (Carya tomentosa (Poir.) Nutt., C. glabra (P.Mill). Sweet.), yellow poplar (Liriodendron tulipifera L.), sweetgum (Liquidambar styraciflua L.), and oaks (Quercus alba L., Q. michauxii Nutt., Q. phellos L.). Other species that contribute to the mid- and under-story include Carpinus caroliniana Walt., Ostrya virginiana (P. Mill.) K. Koch., Ulmus sp., Cornus florida L., and Cercis canadensis L. Coniferous species including Pinus taeda L. and Juniperus virginiana L. make up a minor component of the over and understory, respectively. The soil is an
Iredell gravelly loam with <4% slope. The upper 35 cm is a clay loam with a porosity of 0.54 m\(^3\) m\(^{-3}\). A clay pan with low hydraulic conductivity limits the majority of the rooting zone to approximately 35 cm. Soil depth can be as deep as 2 m (D. Richter, unpublished data), which overlays bedrock (Oren et al. 1998). The HW stand has also been included in previous studies involving sap flux (Oren and Pataki 2001; Pataki and Oren 2003).

6.2.2 Environmental and canopy flux measurements

The Duke Forest Hardwood Ameriflux tower was instrumented with an above-canopy photosynthetically active radiation (PAR) sensor (Li-Cor Li-190) and precipitation tipping bucket (Texas Electronics). A combined air temperature (\(T_{\text{air}}\)) and relative humidity (RH) probe (Vaisala HMP-35) was positioned at 2/3 canopy height and used to estimate vapor pressure deficit (\(D\)). Soil moisture was measured with 12 ThetaProbe sensors (ML2x, Delta-T Devices; see Oishi et al., 2008 for details). Soil moisture was converted to relative extractable water (REW), a percentage of water ranging from 0 at the hygroscopic point (0.125 m\(^3\) m\(^{-3}\)) and 1.0 at field capacity (0.35 m\(^3\) m\(^{-3}\)).

Eddy covariance measurements of H\(_2\)O and CO\(_2\) fluxes, along with wind speed, were reported previously in Stoy et al. (2006), but have been reprocessed using the Online Eddy Covariance Gap-filling and Partitioning Tool (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php; Novick et al., in prep). Outputs from these measurements are (1) net ecosystem exchange (NEE), assumed to approximate net ecosystem productivity (NEP), which consists of NPP minus \(R_{\text{H}}\), and (2) total ecosystem respiration (\(R_{\text{eco}}\)), derived from extrapolations of measured nighttime NEE under well developed turbulence, which includes \(R_{\text{A}}\) and \(R_{\text{H}}\). The sum of these two fluxes is estimated gross ecosystem productivity (GEP), which is theoretically equal to GPP. We
have not used eddy covariance conventions for the direction of these fluxes, but instead all fluxes appear as positive numbers.

6.2.3 Net primary productivity

6.2.3.1 Litter production

Leaf litter collection and analysis protocol was described previously in Oishi et al. (2008), but briefly, leaf litter was collected in an array of 0.5 m² baskets at intervals ranging from weekly during peak litterfall to bi-monthly during low-litterfall. Leaves were oven-dried, sorted by species, and weighed. Specific leaf area (surface area / mass) for a subsample of individual leaves was estimated using a light-table and camera (Decagon Devices). Branch biomass and reproductive structures were also collected and weighed.

6.2.3.2 Aboveground woody biomass

Aboveground NPP was estimated as the change between annual estimates of aboveground woody biomass ($B_A$). $B_A$, including stems and branches was estimated for all trees with species-specific allometric equations (Clark et al., 1986) with the form

$$B_A = a \times (DBH^2)^b$$

Eq. 1.

These allometric equations were generated from data collected in the Piedmont region of the southeastern US, which encompasses our study site, and included a total of 773 hardwood trees, separated by species and into size classes <27.9 cm and ≥27.9 cm (Clark et al., 1986). Annual changes in DBH were estimated using tree cores taken from five sap flux trees of each species in 2008. Radial increments over the past 10 years were measured using a digital scanner.
6.2.3.3 Belowground woody biomass

Three soil pits with dimensions of 40×40×40 cm were excavated in 2004, and standing total root biomass was found to be 1156 g C m\(^{-2}\) (SD=732 g C m\(^{-2}\)) based on a root carbon content of 43.7% (SD=1.2%) (K. Johnsen, unpublished data). This analysis did not differentiate between coarse and fine roots, nor does it account for the total root C pool since taproots were not extracted. Therefore, we separated root biomass from pits into fine and coarse with the following approach. Coarse root biomass, including the stump, was assumed to be 22% of aboveground woody biomass, based on the proportions from a mature Quercus forest Oak Ridge, Tennessee, with the stump and taproots equal to 10.8% of aboveground biomass and other coarse roots comprising 11.8% (Hanson et al., 2003). Since the soil pits did not account for stump and taproots, we then estimated fine roots as the difference between sampled total root biomass and estimated coarse root biomass. We assumed that fine root production (NPP\(_{fr}\)) was equal to annual turnover of standing fine root stock, which was estimated to be 0.45 y\(^{-1}\) in a northern mixed-hardwood forest (Gough et al., 2008). Since interannual measurements of root biomass were not made, we use the same value of NPP\(_{fr}\) for all years.

6.2.4 Components of ecosystem respiration

Soil CO\(_2\) flux (\(F_{soil}\)), including both autotrophic respiration from roots and heterotrophic respiration from microbes and fungi were presented in Oishi et al. (in review). The approach used the Automated CO\(_2\) Efflux System (ACES, US Patent 6692970, Butnor et al. 2003), an IRGA-based open system that sequentially samples 15 chambers (491 cm\(^2\) footprint, 10 cm high) by circulating air through a chamber and comparing input and output CO\(_2\) concentrations. Each chamber is sampled for a 10-minute cycle to allow for [CO\(_2\)] equilibration. Daily mean \(F_{soil}\) from each chamber was used to establish exponential temperature-response functions with soil temperature at
10 cm \((T_{10})\) during non-limiting soil moisture conditions and the deviation from
temperature-response estimates were used to estimate soil moisture limitation functions.
The combined equation was adapted from Palmroth et al. (2005):

\[
F_{soil} = R_{b10}e^{b(T_{10} - 10)} \times (1 - e^{-c \times REW + d})
\]

Eq. 2

where \(T_{10}\) is soil temperature at 10 cm, \(R_{b10}\) is basal respiration at 10 °C and \(b, c, \) and \(d\) are
fitted parameters (Oishi et al., in review). For each chamber each of the \(b, c, \) and \(d\)
parameters were consistent among years, but \(R_{b10}\) was allowed to vary to capture
interannual variability. These equations were used to gapfill days when no data were
available (due to system maintenance, equipment failure, and power outages).

The ACES was also used to measure CO\(_2\) flux from the stems \((F_{stem})\) with
customized chambers. The stem chambers have been previously described in Maier &
Clinton (2006), but briefly, are constructed of a flexible plastic enclosure encircling the
entire stem at breast height (~1.3 m). These enclosures are permanently installed with
weatherstripping and caulk, creating an air-tight seal. These chambers were installed on
four trees throughout 2004, as well as 10 additional trees for several 2-week periods
representing the most abundant species in the stand (see Table 1 for details). Since \(F_{stem}\)
from tree trunks include locally respired CO\(_2\), as well as CO\(_2\) transported in sap from the
rooting zone (Teskey et al., 2008), we are cautious not to assume that this flux represents
exclusively stem respiration. Exponential temperature-response functions were
estimated using an analogous approach to \(F_{soil}\) (Oishi et al., in review):

\[
F_{stem} = R_{b10}e^{b(T_{10} - 10)}
\]

Eq. 3

where \(R_{b10}\) is the basal respiration at 10 °C and \(b\) represents the increase in \(F_{stem}\) with \(T_{air}\)
\((Q_{10} = e^{10b})\).

\(F_{stem}\) was scaled to the stand-level as flux per unit sapwood volume \((V_s)\).

Sapwood volume within the chamber \((V_{S, \text{chamber}})\) as
where \( h_{\text{chamber}} \) is the vertical dimension of the stem chamber, DBH is diameter at breast height (both in cm), and \( a \) and \( b \) are empirical parameters for estimating cross-sectional sapwood area previously published for this stand in Oishi et al. (2008). Total aboveground \( V_s \) was estimated for each tree using species-specific allometric equations collected for this region (Martin et al., 1998) with the format

\[
\log_{10}(V_{s,\text{tree}}) = a + b \times \log_{10}(\text{DBH})
\]

Eq. 5

where DBH is in cm and \( V_{s,\text{tree}} \) is in m\(^3\). \( F_{\text{stem}} \) per unit \( V_s \) was estimated daily for each species and applied to total \( V_{s,\text{tree}} \) for the entire stand.

Coarse root respiration was estimated with the same temperature response parameters as \( F_{\text{stem}} \), but scaled to total stump/coarse root biomass substituting \( T_{10} \) for \( T_{\text{air}} \). Fine root respiration (\( R_f \)) was estimated using parameters for a \( Q_{10} \) function (log-transformed) from a mature southeastern Quercus forest

\[
R_f = M_f \times e^{(0.088T_{\text{soil}} - 0.419)}
\]

Eq. 6

where \( M_f \) is dry weight of fine roots, \( T_{\text{soil}} \) is soil temperature (Burton et al., 2002). For \( T_{\text{soil}} \), we used temperature measurements at 10 cm, a depth that included 93% of the root mass.

Nighttime leaf maintenance respiration (\( R_{\text{leaf}} \)) was estimated with species-specific exponential parameters based on leaf mass and canopy position (Bolstad et al., 1999). We assumed that all Quercus species behaved like \( Q. \) alba, all Carya species behaved like \( C. \) glabra, and understory species behaved like Fraxinus spp. (use of Cornus florida resulted in 15% higher \( R_{\text{leaf}} \) in mixed species, but <5% increase in annual \( R_{\text{leaf}} \)). No parameters were available for \( L. \) styraciflua, so we assumed that these trees behaved like the other shade-intolerant species, \( L. \) tulipifera.
Daytime leaf respiration ($R_{\text{leaf}}$) was estimated using the approach described in (Kim et al., 2008), where

$$R_{\text{leaf}} = 0.015 \times V_{\text{cmax}}$$  \hspace{1cm} \text{Eq. 7}$$

where $V_{\text{cmax}}$ at 25 °C ($V_{\text{cmax,25}}$) varied seasonally and half-hourly with $T_a$ as

$$V_{\text{cmax}}=V_{\text{cmax,25}} \times \exp \left( 26.35 \right) - \left( \frac{65.33}{(R(T_{air}+273))} \right)$$  \hspace{1cm} \text{Eq. 8},

where $R$ is the universal gas constant (Bernacchi et al., 2001).

Construction respiration ($R_C$) was estimated for each component of NPP as 1.4 g glucose per g dry weight (Wullschleger et al., 1997).

### 6.2.5 Net carbon assimilation

We estimated net C assimilation ($A_{\text{net}}$) using the Canopy Conductance Constrained Carbon Assimilation (4C-A) model (Kim et al., 2008, Schäfer et al., 2003). The model estimates direct and diffuse light along a 1-dimension canopy profile based on plant area characteristics (Table 2). Light levels reaching eaves at each canopy layer are used to partition mean canopy conductance ($G_c$) among leaf levels based leaf level light-response curves (Pataki & Oren, 2003).

$A_{\text{net}}$ was estimated at each canopy level for sun and shade leaves of each species based on estimated light and a Farquhar-type photosynthesis model with the following equation

$$A_{\text{net}} = \min(W_{\text{rub}} W_i) - R_{\text{leaf,day}} = g_c(C_a - C_i)$$  \hspace{1cm} \text{Eq. 9}$$

where $W_{\text{rub}}$ and $W_i$ are the Rubisco-limited and electron transport limited rates of ribulose-1,5-biphosphate regeneration and min() identifies the minimum of these two values, $g_c$ is leaf canopy conductance and $C_i$ and $C_a$ are concentrations of CO$_2$ at the leaf surface and in leaf intercellular space, respectively (Kim et al., 2008).

Leaf area profiles were constructed by comparing the change in LAI during senescence from litter baskets and from optical plant canopy measurements (Li-Cor LAI-
2000) taken along a vertical gradient from the eddy covariance tower. Relative changes in the optically-based vertical profile were distributed among the area of leaves collected for each weekly collection period. The understory was dominated by different species than the canopy (i.e. “mixed” species as opposed to the four genera used in sap flux measurements), so mixed species were preferentially assigned to the lowest canopy layers first.

$G_c$ was estimated at 30-minute intervals based on sap flux-scaled transpiration estimates taken at this stand (Oishi et al., 2008). These estimates were made for the four dominant genera and two classes encompassing all other species, divided into mixed canopy and understory classes and adjusted per unit leaf area. For times when $D<0.6$ kPa, $G_c$ was estimated using boundary line analysis for 5 light classes.

### 6.3 Results

#### 6.3.1 Environmental variability

The 2002 and 2005 growing seasons were marked with low $P$, leading to low REW through much of the growing season (Table 3). REW was reduced below 0.33, a value that marks declines in $F_{soil}$ (Palmroth et al., 2005; Oishi et al., in review) and $E_C$ (Oishi et al., 2010), for 95 and 91 days in 2002 and 2005, respectively, compared to fewer than 20 in the other years. However, among dry years, 2002 was marked by higher mean growing season daytime PAR, day and night $T_{air}$ and day-length-normalized vapor pressure deficit ($D_Z$, Table 3). In contrast, 2003 was marked by higher than average precipitation, leading to high REW but also reflected in lower PAR due to cloud cover. This site also experienced a severe ice storm in December of 2002, which occurred after the end of leaf senescence, but did result in some branch damage. Total branch and debris biomass accumulated in litter baskets in 2002 was 120 g C m$^{-2}$, exceeding the following three years, which accumulated 87, 72, and 69 g C m$^{-2}$, respectively.
Comparing the combination of daily environmental factors occurring at this site, days with low REW occurred during the growing season and were correlated by high daily PAR (i.e. the absence of many low-PAR days), high $T_{\text{air}}$ and high $D_z$ (Fig. 1).

6.3.2 Net primary productivity

Annual increases in DBH tended to increase with size for all species except for $L. styraciflua$ (Table 6.4; estimates resulting in negative numbers were set to zero growth). We compared current and previous growing season REW with estimated annual growth increment for the median DBH of each genera: $L. tulipifera$, $L. styraciflua$, Carya spp., Quercus spp., and other mixed species were 28.0, 34.2, 29.9, 23.8, and 5.2 cm, respectively. Growth increment was not related to current or previous growing season precipitation for any species ($P>0.51$). For current growing season REW, only $L. tulipifera$ exhibited a significant increase in growth increment with REW ($P=0.0549$, all others $P>0.54$) and for REW of the previous growing season, growth increment of $L. styraciflua$ showed a tendency to decrease ($P=0.100$, $P>0.74$ for all other species; data not shown). Scaled to the stand level, annual changes in aboveground biomass resulted in an average NPP of 172 g C m$^{-2}$ y$^{-1}$ (Table 6.5).

The greatest amount of NPP was devoted to leaf production, which accounted for nearly 40% of total NPP at this site (Table 6.5). Leaf NPP also showed the greatest absolute interannual variability, 54 g C m$^{-2}$ y$^{-1}$ between the highest and lowest years. Estimates of fine root NPP were held as a constant proportion of standing fine root biomass so did not vary interannually. Despite large differences in absolute values, all components, except for seeds, showed similar interannual (CV~10%). Overall, aboveground NPP was accounted for 75% of total NPP.
6.3.3 Respiration

\( F_{\text{stem}} \) increased exponentially with \( T_{\text{air}} \) in all species (Table 6.1). For species with more than one individual measured, we used an average of the \( Q_{10} \) and \( R_{\text{bi10}} \) parameters. Since these measurements were made over the entire year, \( F_{\text{stem}} \) should include both growth and maintenance respiration. We did not detect a difference temperature-sensitivity between spring and fall for any of the four, continuously monitored trees (\( P>0.13 \)). The measurement period for \( F_{\text{stem}} \) did not include the drought periods, so we were not able to test for soil moisture sensitivity of this flux. Thus, given the limited interannual variability in \( T_{\text{air}} \) variability in \( F_{\text{stem}} \) was low (Table 6.5).

Respiration from fine roots dominated the autotrophic C losses in this system comprising approximately 50\% of \( R_A \) (Table 6.5). \( R_{\text{leaf,day}} \) was the greatest single component of aboveground \( R_A \) driven by substantial LAI and exceeding \( R_{\text{leaf,night}} \) due to higher daytime temperatures and more daylight hours when temperatures were greatest. For comparison, \( R_{\text{leaf,day}} \) estimated using as a function of \( V_{\text{Cmax}} \) was on average 8\% lower than daytime estimates made with temperature response parameters we used for \( R_{\text{leaf,night}} \) (Bolstad et al., 1999).

The cumulative totals of annual aboveground and belowground \( R_A \) and NPP are presented in Figure 6.2. Of these fluxes, aboveground \( R_A \) showed the greatest interannual variability in absolute and proportionate terms (SD=89 g C m\(^{-2}\) y\(^{-1}\), CV=12\%), due to interannual variability in leaf biomass, whereas all other fluxes were more consistent (CV<8\%; Table 6.5).

6.3.4 Net photosynthesis

Canopy LAI profiles illustrate that Carya spp. comprise the majority of leaf area in this upper canopy, followed by Quercus spp. (Fig. 6.3). As opposed to those shade-tolerant species, the shade-intolerant L. tulipifera and L. styraciflua produced
comparatively lower LAI. Although the previous four tree genera represented the 80% of the sapwood area in this stand (Oishi et al., 2008), other species contributed a large amount of leaf area to the canopy, primarily in the understory. The profile of stem and branch biomass constructed from winter measurements when trees were leafless added 0.70 m² m⁻² of plant area. Daily vertical profiles of LAI (Fig. 6.4a) show strong seasonal patterns, with peak leaf area in the upper canopy. High upper canopy LAI led to rapid attenuation of absorbed PAR (aPAR) below 25 m after full leaf expansion in the spring (Fig. 6.4b).

\( G_C \) was reduced in all species under low REW (Fig. 6.5), resulting in reductions in photosynthesis during drought conditions. However, variability in LAI among years also led to differences in species-level and stand-level \( A_{\text{net}} \). *Carya* spp. accounted for 26% of stand level \( A_{\text{net}} \) on average, followed by *Quercus* spp. (20%), *L. styraciflua* (18%), and *L. tulipifera* (10%). All other species made up for the remaining 26% of \( A_{\text{net}} \). Over the study period, \( A_{\text{net}} \) ranged from 1271 to 1628 g C m⁻² y⁻¹ (Table 6.6, Fig. 6.2). Most \( A_{\text{net}} \) occurred in the upper canopy, following the vertical distribution of leaf area (Fig. 6.4c).

On average the two shade-tolerant species *Carya* spp. and *Quercus* spp. had the lowest average leaf \( C_i/C_a \) ratio estimated from the 4C-A model, approximately 0.70 compared to 0.80 and 0.78 for shade-intolerant *L. tulipifera* and *L. styraciflua*, respectively (Table 6.7). \( C_i/C_a \) tended to increase with leaf biomass and over the four-year period. Modeled \( C_i/C_a \) for each genera were not correlated with independent estimates from \( \delta^{13}C \) analysis of leaf tissue sampled in 2002 (D. Ellsworth and K. Schäfer, unpublished; \( P=0.66 \) comparing modeled versus \( \delta^{13}C \) estimates among genera); however, \( \delta^{13}C \) estimates were within the range of modeled \( C_i/C_a \) 0.67-0.75.
6.3.5 Carbon budget closure

To estimate GPP, we added $R_{\text{leaf,day}}$ which increased $A_{\text{net}}$ by ~20% ($\text{GPP}_{\text{modelled}}$; Table 6.6; Fig. 6.2). $\text{GPP}_{\text{modelled}}$ was lower than the sum of NPP and $R_A$ components ($\text{GPP}_{\text{comp}}$) by an average of 22%.

Total belowground respiration, expressed as $F_{\text{soil}}$ was estimated at this site by Oishi et al. (in review), averaged 1231 g C m$^{-2}$ y$^{-1}$, varying interannually in response to soil moisture limitations and annual changes in estimated temperature sensitivity parameters. Thus, despite the fact that 2002 had the lowest mean growing season REW, 2005 actually exhibited lower annual $F_{\text{soil}}$ due to the combination of moderate drought and a lower basal respiration rate. Annual $F_{\text{soil}}$ was on average 15% higher (182 g C m$^{-2}$ y$^{-1}$; SD=128) than belowground RA plus turnover of fine root NPP and leaf litterfall, but the two fluxes were nearly equal in 2005.

Since many of our components of NPP are estimated at annual time steps, we compared daily estimated GPP with GEP (Fig. 6.6a). Both estimates followed similar seasonal patterns and despite larger daily variability in GEP; however, differences in annual numbers appeared to diverge with time (Fig. 6.2 & 6.6b).

6.3.6 Variability in fluxes

To assess the sources of interannual variability in C fluxes, we analyzed our results across the range of mean growing season REW. $\text{GPP}_{\text{modeled}}$, GEP, $\text{NPP}_{\text{comp}}$, and NEP appeared to show lower fluxes at the lowest REW but also the highest REW values, with comparatively higher annual fluxes at intermediate REW. Overall none followed a linear trend ($P>0.40$; data not shown). However, when we compared C fluxes with the previous growing season’s mean REW, $\text{GPP}_{\text{modeled}}$ and GEP tended to be higher following wetter years (Fig. 6.7a). $\text{GPP}_{\text{modeled}}$ increased with lagged REW ($P=0.051$). Although other fluxes did not show significant relationships ($P>0.15$), fluxes appeared fall into wet and
dry classes. NEP did show a significant tendency to decrease with REW ($P=0.085$; Fig. 6.7b), whereas the response of NPP$_{\text{comp}}$ showed a more muted response ($P=0.31$). These two sets of fluxes resulted in diverging CUEs (Fig. 6.7c). The NPP:GPP ratio increased with decreasing REW ($P=0.036$), while no trend in NEP:GPP with REW was observed ($P=0.14$). As expected, whole-ecosystem CUE ratio (i.e. NEP:GEP) was lower since it also incorporates turnover of some components of annual NPP as $R_{\text{H}}$. Interestingly, NPP:GPP fell very close to the predicted CUE for a 100-year old stand (DeLucia et al., 2007), particularly in years following drought.

LAI increased with the previous year’s growing season REW for the dominant canopy genera, Carya spp. ($P=0.027$), with weaker increasing tendencies for L. styraciflua and Quercus spp. ($P=0.093$ and 0.058, respectively, $P>0.29$ for all other genera, Fig. 6.8a). However, high LAI of mixed species in 2003 (the year with lowest lagged REW) led to relationship in total LAI with lagged REW ($P=0.127$, Fig. 6.8c). In contrast, current growing season REW was unrelated to LAI for all genera or total LAI ($P>0.24$, Fig. 6.8b,d).

Transpiration ($E_C$) showed little interannual variability (Fig. 6.9a), so water use efficiency (WUE) followed the trends of GPP$_{\text{modeled}}$ and NPP$_{\text{comp}}$ with previous growing season REW (Fig. 6.9c,e). Interannual variability in annual absorbed PAR (aPAR) increased with decreasing current-year REW (data not shown); however, the magnitude of this difference did not affect the general trends in LUE with either GPP and NPP along the range of past or current WUE (Fig. 6.9d,f).

We did observe an increase in GPP$_{\text{modeled}}$ and NPP with time ($P=0.048$ and 0.038; Fig. 6.10a,b). Although GPP$_{\text{comp}}$ showed higher annual fluxes in the two latter years than the two earlier years, it did not show a linear increase ($P=0.153$). $R_A$ showed no consistent trend over time ($P=0.33$; Fig. 6.10c), but similar to GPP$_{\text{comp}}$, the latter two years
were higher than the earlier two. Eddy covariance data also showed increases in all C fluxes over time, which was emphasized when we included data from 2001 through 2008. Driven by increased $R_{\text{eco}}$ ($P=0.0052$), GEP increased with time ($P=0.0034$), including a rapid rise in 2006, after our study had ended. Excluding the dip in 2003, NEP also showed a tendency to increase over time ($P=0.090$), but our biometric estimate of NEP (NPP minus turnover of leaf litterfall and fine roots) showed no trend ($P=0.35$).

We also observed strong correlations between leaf biomass and productivity. Annual GPP$_{\text{modeled}}$ increased with LAI for most species, with the exception of the mixed species (Fig. 6.11a). Species were grouped in distinct clusters, with the shade-intolerant $L.~tulipifera$ and $L.~styraciflua$ showing slightly lower GPP for a given LAI. However, when we compared leaf litterfall with $A_{\text{net}}$, a single linear fit described all species over all years (Fig. 6.11b). Thus, interannual variability in a primary productivity is highly dependent on leaf mass, seemingly regardless of species composition.

Examining the source of the consistent trend between leaf biomass and GPP, we compared GPP by species, normalized by LAI, with leaf mass per area (LMA; average leaf mass divided by one-sided surface area). The ratio of GPP/LAI increased linearly with LMA in the major canopy species and as a quadratic function if we include the mixed species which include a large proportion of understory species with high leaf area, but low mass and low overall productivity due to light limitations ($P<0.0001$).

6.4 Discussion

In addressing our initial questions, we observed that (Q1) C allocation in this stand is weighted more heavily toward respiration than NPP. CUE in this stand was lower than the global mean of 0.45 (Waring et al., 1998), but instead fell along the predicted line for mature forests, $-0.37$ (DeLucia et al., 2007). (Q2) Among years, changes in water availability led to seasonal reductions in $G_{\text{C}}$ and thus $A_{\text{net}}$; however, GPP was
reduced when REW was low the previous growing season. Changes in NPP were less variable interannually proportionate to GPP and thus, CUE increased slightly with previous year’s water availability. (Q3) Although NPP and GPP varied more than $E_C$ among years, neither of these C fluxes followed a linear trend with current or previous year water availability resulting in no consistent trend in WUE. (Q4) While water availability affects GPP immediately, it does not result in a consistent effect on annual NPP or GPP. Instead GPP, and to a lesser extent NPP, appear to be influenced by the previous growing season’s water availability. Furthermore, this stand may be undergoing a longer-term transition toward greater GPP, possibly in response to a recent history of droughts and severe storms.

6.4.1 Lagged climate effects

In a mature forest such as this, we predicted that NPP and GPP could be variable, but did not expect to see steady increases over time (Ryan et al., 1997). Instead, both NPP and GPP modeled increased over the study period, similar to eddy covariance estimates (Fig. 6.10). One possible explanation of this trend is carryover effects from the ice storm of late-2002, potentially exacerbated by a mild drought in 2001 and a severe drought in 2002. This storm reduced woody biomass production in an adjacent loblolly pine stand by $\sim 56$ g C m$^{-2}$ y$^{-1}$ the following year and reductions in LAI took several years to recover (McCarthy et al., 2006). Since ice damage to pines is probably more severe than broadleaf trees since our broadleaf species have more extensive branching whereas loss of pine tops increased mortality. Furthermore, the weight of ice removed living needles from the pine, while no viable leaves were present in the broadleaf stand and this disturbance would not have increased total annual leaf litterfall. Even if productivity reduction in our stand was roughly equal to the pine stand, a reduction of
56 g C m\(^{-2}\) y\(^{-1}\) in NPP would not explain the large decline in NEP (~150 g C m\(^{-2}\) y\(^{-1}\)) in 2003.

However, the impact of these disturbances could have resulted in a longer-term influence of the C budget at this site. Since GEP is estimated as the sum of NEP and \(R_{eco}\) and since \(R_{eco}\) showed a more significant increase over time than GEP, it is possible that the primary driver of these increases was added decomposable biomass to the forest floor carbon pool. Litter baskets received an additional 45 g C m\(^{-2}\) y\(^{-1}\) of branch and debris in 2002, representing a non-trivial additional flux of C to the forest floor. Since this estimate only captures biomass that lands in baskets, it does not include standing or hanging dead biomass that will also contribute to \(R_{eco}\). However, the increase in both GEP and GPP\(_{modeled}\) along with NEP, suggests that the increase in fluxes is due in part to added photosynthesis.

Many regional deciduous species may be well suited to buffer against drought. Under a precipitation manipulation experiment in a forest with similar species composition, only \(Acer\ rubrum\), \(A.\ saccharum\) and \(L.\ tulipifera\) showed reduction in dormant season total non-structural carbohydrates [TNC] after a drought year due to depletion of carbohydrate reserves (Tschaplinski & Hanson, 2003). No carryover effect in [TNC] was noted in subsequent years. However, an early season drought was shown to reduce leaf area and subsequently GEP in a temperate \(Quercus\) forest (Noormets et al., 2008). Therefore, environmental factor affecting leaf production are likely to have a significant impact on photosynthesis.

It is not surprising to see GPP increase with leaf area and litterfall (Fig. 6.11) given that these structures are the site of photosynthesis. However, given the high leaf area at this stand, the relationships observed in Fig. 6.11 are partially due to interannual tradeoffs among species and their proportion of total leaf area, such that LAI of mixed
species tended to increase in years when the dominant canopy species tended to decline (Fig 6.8).

Interannual variability in leaf biomass also plays an important role in NPP since it comprises 50% of aboveground NPP. The relationship between litterfall and NPP could potentially be enhanced, given the correlation between litter biomass and fine root production (Raich & Nadelhoffer, 1989); however, our approach lacked interannual information on fine root production and turnover and thus we assumed constant fine root NPP. Much of fine root growth occurs in the spring in deciduous species (Norby et al., 2004), in sync with leaf growth. Similarly in an adjacent pine stand, peak fine root growth occurred in spring and early summer (Pritchard et al., 2008); however, it was also shown that growth was reduced with drought. Thus, if leaf and fine root production are relying on similar stored C sources at the start of a growing season, annual NPP from both of these components may be correlated (Litton et al., 2007).

In contrast to litter biomass, we did not see a correlation with DBH growth and \( P \), lagged or current, nor previous year’s REW. Only \( L. \) tulipifera increased with current growing season REW and since this species only accounted for 23% of total basal area, interannual variability in aboveground woody NPP was not related to water availability. Rocha et al. (2006) found no correlation in NPP and water stress, even after accounting for time lags; however, as with leaf and fine root production, timing of dry periods often impacts stem growth, particularly if drought is early in the growing season (Leuzinger et al., 2005, Zweifel et al., 2006). Our limited number of growth cores per species \( (n=5) \) may have been inadequate to accurately characterize growth increment and resampling is recommended.
6.4.2 Components of NPP

As expected, $NPP_{comp}$ exceeded NEP since NPP should capture all of the components of NEP as well as material that turns over within the year, namely leaf litterfall and new fine root biomass. Subtracting litter and fine root NPP from $NPP_{comp}$ as an independent estimate of NEP was on average 213 g C m$^{-2}$ y$^{-1}$ lower than annual NEP (Fig. 6.10b, Table 6.6). One potential source of these differences is that the eddy covariance footprint extends beyond our study plot. Matching ground-based estimates of water fluxes with eddy covariance data requires scaling to an appropriate footprint (Oishi et al., 2008); however, the limited spatial scope of our biometric data presents a challenge for upscaling NPP. These two fluxes do not follow a similar trend, suggesting error in one, or both of the approaches.

Our aboveground NPP estimates were roughly 100 g C m$^{-2}$ y$^{-1}$ lower than a mature *Quercus* stand in Tennessee (Hanson et al. 2003; Table 6.5). The species-specific parameters we used were developed in the same region as our research site, included a large number of trees sampled, and spanned the DBH classes at our site (Clark et al., 1986), and thus, were the most reliable allometric equations to use for our study.

Estimates of the proportion of coarse root biomass to aboveground woody biomass in mature deciduous forests ranged from 22% (Vande Walle et al., 2001) to 38% (Monk & Day, 1985), so our assumption that coarse roots were 22% of aboveground biomass may have been on the conservative side. However, compared to the latter study, from Coweeta, NC, the standing stock of root mass from soil pits at our site was nearly half, 1156 vs 2250 g C m$^{-2}$ (Monk & Day, 1985), suggesting that the lower above-to below-ground biomass ratio may suit our site better. Still, coarse root NPP is generally small so a large proportionate change in this amount would not change total NPP greatly.
6.4.3 Estimated Respiration

Much of our analysis has focused on GPP and NPP, but it is also important to address respiratory costs in this system, as well as the lack of closure among our estimates of these fluxes. Given these uncertainties in the respiratory components, we focused on quantifying the range of likely values among years. We estimated 90% confidence intervals using nonparametric Monte Carlo simulations for the components of $R_A$ and $F_{soil}$. Estimates of annual respiration were generated using measured environmental variables at either the half-hourly or daily time scale, depending on the model form, and parameters with an added a normally distributed random “noise”, plus or minus one standard deviation. This process was repeated 100,000 times to generate confidence intervals for each flux. Reported standard deviations of the parameter estimates were available for $R_{leaf,night}$ (Bolstad et al., 1999), $F_{soil}$ (Oishi et al., in review) and $F_{stem}$ (this study). $F_{stem}$ parameters were applied to coarse root $R$ estimates. No variability estimates were available for $R_{leaf,day}$; however, since the approach for estimating $R_{leaf,night}$ yielded similar results to the approach for $R_{leaf,day}$, we used these published values for daylight hours. We also allowed for variation in annual total LAI based on the standard deviation among years for a given species.

$F_{soil}$ showed the widest confidence intervals, with approximately a ten-fold increase between the lower and upper bounds (Table 6.8). We resampled annual components of these values to estimate distributions for $R_E$. We assumed that simulated $R_{leaf}$ and $R_{stem}$ comprised the majority of C respired aboveground as well as the majority of the variability. For the other components of aboveground $R_A$, we used the average annual flux (assumed a constant 79 g C m$^{-2}$ y$^{-1}$). Simulated $F_{soil}$ was used to capture total of the belowground $R$. The lower boundary of the 90% confidence interval was typically
higher than $R_{ec0}$, which suggests that even after accounting for the wide variability in $F_{soil}$, $R_{ec0}$ may be low.

Although we estimated $F_{stem}$ from measured fluxes (Table 6.1), the total contribution to stand level $R_A$ is highly dependent on appropriate scaling. Our estimates were somewhat lower than other broadleaf forests (Table 6.5); however, our lower estimates could correspond with comparatively lower NPP in this stand. Our sampling period did not include either of the drought periods, so we were unable to test for changes in $F_{stem}$ with low REW. Therefore, $F_{stem}$ varied only with $T_a$ (Table 6.1) and showed little interannual variability (CV=3%, Table 6.5). Furthermore, since we did not make flux measurements on branches, we did not account for potentially higher branch respiration (Maier *et al.*, 2004).

Fine root maintenance respiration was estimated using an exponential ($Q_{10}$) function from a mature *Quercus* forest within a similar region but further south in Georgia (Burton *et al.*, 2002), scaled based on root biomass. Uncertainty in our estimates of fine root biomass can introduce large uncertainty to our fine root respiration estimates. However, Burton *et al.* (2008) also demonstrate that although annual fine root $R$ tends to increase with mean annual temperature (MAT), the respiration rate at a given temperature tends to decrease with MAT. Therefore, since many temperature-sensitivity parameters for estimating fine root respiration in forests with similar species are from either more northern latitudes or higher elevation forests in the same region, these parameters combined with our estimated fine root biomass led to unreasonably high fine root respiration, exceeding $R_{ec0}$ and $F_{soil}$.

We assumed that 45% fine roots turnover within a year (Gough *et al.* 2008), so any change in this estimate would increase NPP, but would not influence NEP. On the other hand, additional fine root turnover would help to explain the large difference
between estimates of total belowground $R$. Previous estimates of $F_{\text{soil}}$ (Oishi et al., in review) exceeded estimates of belowground $R_A$ plus litter and fine root turnover. Sources of respired C from this stand are predominantly from soil, rather than foliage (Mortazavi et al., 2004), which corresponds with our high fine root respiration and $F_{\text{soil}}$ values.

Given that eddy covariance-derived $R_{\text{eco}}$ was lower than $F_{\text{soil}}$, this provides some additional evidence of overestimation of $F_{\text{soil}}$. However, eddy covariance systems can underestimate nighttime $R$ by around 25% (Juang et al., 2006). In another mature Quercus forest in the same region, Hanson et al. (2004) found that biometric NEE, estimated as $\text{NPP} - 0.5F_{\text{soil}}$ was \( \sim \frac{1}{3} \) of eddy covariance NEP. $F_{\text{soil}}$ was \( \sim 1200 \text{ g C m}^{-2} \text{ y}^{-1} \), on the higher end of compiled data from mature, temperate, broadleaf forests, which averaged 848 g C m\(^2\) y\(^{-1}\) (SD=261; Table 6.5) (Bond-Lamberty & Thomson, 2010). Although our site was among the lower latitudes of these sites, we still have a lack of closure between the components of soil respiration and chamber-based estimates of $F_{\text{soil}}$.

Improving the closure of the respiration budget, particularly belowground $R$ will help to clarify the amount and the variability of C allocation to root growth and maintenance, especially given the variability in $F_{\text{soil}}$ with soil moisture and the potential for C loss from soil during drought periods (Palmroth et al., 2005).

### 6.4.4 Unresolved issues

This analysis demonstrates that variability in the major C fluxes, GPP, NPP, and $R_A$, are governed by environmental drivers acting concurrently at multiple time scales, ranging from hourly to interannually. However, the lack of agreement among different approaches for estimating these fluxes poses an important obstacle in interpreting the response of forests to water stress. Therefore, we present several key unresolved methodological issues and possible approaches to refine our estimates.
6.4.4.1 Net primary productivity

Leaf biomass was collected in an array of baskets covering the majority of the stand within the eddy covariance footprint (Oishi et al., 2008), so we believe that these data provide a solid foundation for stand-level estimates. The current analysis only focused on a one-hectare area within the 6.25 ha eddy covariance footprint so comparison of fluxes will require upscaling to the larger area. Such upscaling can utilize kriged LAI across the footprint, as well as relationships between LAI and sapwood area (Oishi et al. 2008) to upscale not only leaf biomass, but also aboveground woody biomass. The current analysis assumed uniform specific leaf area (SLA; one-sided leaf area divide by mass) to estimate annual LAI from dry leaf biomass. Given the strong relationship between LAI and GPP, accounting for potential interannual variability is an important consideration.

Allometric equations for estimating aboveground woody biomass were generated from forests throughout this region, although not at this specific site (Clark et al., 1986). We are unlikely to find better published allometric relationships, nor will we be able to undertake a comprehensive harvest of trees. Estimates of aboveground woody NPP could be vastly improved by a more comprehensive approach to diameter growth increment. Growth cores are frequently used to estimate interannual variability in tree growth and if our sample size is increased, so will the confidence in our estimates.

Belowground NPP in this site is an area of substantial uncertainty. Coarse root NPP is typically low in mature hardwood forests compared to belowground or total NPP (Hanson et al., 2003), so improving our estimates of fine root biomass, growth, and turnover should be the priority. New research commencing at this site focused on tree hydrology will be sampling roots and could help to provide data to partition root biomass into size classes. Fine root production in a neighboring *Pinus taeda* stand has
been shown to decrease in drought-stressed conditions (Pritchard et al., 2008), so identifying an approach to account for variability will also be of importance.

### 6.4.4.2 Autotrophic respiration

All of our estimates of \( R_A \) are scaled from biomass, so the proposed improvements to these methods described in the previous section will improve confidence in our respiration estimates.

Leaf respiration estimates consume a large amount of C and are require reevaluation. Nighttime \( R_{\text{leaf}} \) was estimated with parameters from northern hardwood forests (Bolstad et al. 1999) and may not be appropriate for the warmer climate at our site. Alternative approaches for estimating daytime \( R_{\text{leaf}} \) must also be considered (Villar et al., 1994; Tcherkez et al., 2005).

In this study, \( F_{\text{stem}} \) was based on measurements made at this site with automated chambers and scaled as a function of sapwood area. It is worth comparing estimates using surface area and adjusting for differential respiration rates in branches as opposed to the stem.

Fine root \( R \) is the largest respiratory flux and perhaps the most uncertain. As mentioned previously, improved estimates of standing root biomass will greatly improve our confidence in this value. Furthermore, since frequent root biomass and/or growth sampling is not scheduled, it will be useful to develop a model for root production from published responses to environmental parameters. Data of \( F_{\text{soil}} \) from the ACES can help to constrain total \( R_A \) from soil and it can potentially be used as an input to a root respiration model if we can make reasonable assumptions about the partitioning of \( R_A \) and \( R_H \) across the range of environmental variability.
6.4.4.3 Net carbon assimilation

GPP\textsubscript{modeled} was consistently lower than GPP\textsubscript{comp} (Fig. 6.2, Table 6.5), indicating a possible underestimation of GPP\textsubscript{modeled}. Underestimation of GPP\textsubscript{modeled} is also supported by modeled C\textsubscript{i}/C\textsubscript{a} ratios that were lower than δC\textsubscript{13} measurements (Table 6.7). Several potential sources could be responsible for this underestimation. Based on the modeled vertical canopy light profile (Fig. 4b) and subsequent $A_\text{net}$ profile (Fig. 4c), it appears that estimated light reaching the middle to lower canopy is not sufficient for C uptake necessary to sustain the leaves at these levels. Therefore, canopy structural parameters, primarily crown height and width, must be examined with a sensitivity analysis. Ongoing modifications with the 4C-A software is also affecting canopy light calculations and must also be resolved before $A_\text{net}$ can be fully resolved. Additionally, any changes to LAI based on variability in SLA describe previously would produce changes in the light environment.

Changes in LAI due to variability in SLA would also affect $G_\text{C}$ and thereby, $A_\text{net}$. And finally, we relied on published values of photosynthetic parameters ($V_{\text{Cmax}}$ and $J_{\text{max}}$) which may not be ideal for this site. A more comprehensive review of photosynthetic parameters and sensitivity analysis of these values and how they change over time will be explored.

6.4.4.4 Eddy covariance fluxes

Assessing nocturnal canopy C fluxes with eddy covariance systems are notoriously challenging and can lead to widely divergent estimates of $R_{\text{eco}}$ and subsequently GEP. While the current approach employs a widely-used method for processing data and improves on systematic overestimation of GPP during winter months (Stoy \textit{et al.}, 2006) alternative approaches should be considered. We will continue collaborating with eddy covariance experts to help examine why GEP is consistently
lower than $\text{GPP}_{\text{mod elo}}$ and $\text{GPP}_{\text{com p}}$. This analysis should also help to explain the remarkably large increase in $R_{\text{eco}}$ and GEP starting in 2006 (Fig. 6.10).

Addressing these issues in NPP, $R_{\text{A}}$, $A_{\text{net}}$, and canopy C fluxes will help explain the discrepancies between GPP estimates and identify specific sources of greatest uncertainty.

6.5 Conclusions

These results indicate that drought effects appears to have led to small changes in growing season GPP and NPP; however, potential carry-over effects of reduced carbohydrate storage may result in lower NPP the following year, particularly in the form of leaf biomass, creating a lagged constraint on photosynthetic capacity of the forest. This mature stand had a consistent CUE over our four-year study period, but may be in the process of a longer-term change in productivity, possibly as recovery from droughts combined with storm damage.
Table 6.1: Stem CO$_2$ flux ($F_{stem}$) tree information and estimated temperature sensitivity parameters.

<table>
<thead>
<tr>
<th>Species</th>
<th>DBH (cm)</th>
<th>$Q_{10}$</th>
<th>$R_{b10}$ (g C m$^{-3}$ d$^{-1}$ sapwood)</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>6.8</td>
<td>1.42</td>
<td>3.64E-05</td>
<td>0.32</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>47.9</td>
<td>1.94</td>
<td>1.44E-05</td>
<td>0.74</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>51.7</td>
<td>1.74</td>
<td>5.06E-06</td>
<td>0.60</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>44.2</td>
<td>1.46</td>
<td>6.94E-06</td>
<td>0.68</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>12.6</td>
<td>1.90</td>
<td>1.55E-05</td>
<td>0.78</td>
</tr>
<tr>
<td>Fraxinus americana</td>
<td>13.0</td>
<td>2.18</td>
<td>1.35E-05</td>
<td>0.64</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>9.4</td>
<td>2.21</td>
<td>2.55E-05</td>
<td>0.76</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>13.0</td>
<td>2.84</td>
<td>1.51E-05</td>
<td>0.66</td>
</tr>
<tr>
<td>L. styraciflua</td>
<td>44.2</td>
<td>2.14</td>
<td>5.52E-06</td>
<td>0.50</td>
</tr>
<tr>
<td>L. tulipifera</td>
<td>42.4</td>
<td>1.75</td>
<td>1.53E-05</td>
<td>0.79</td>
</tr>
<tr>
<td>L. tulipifera</td>
<td>23.5</td>
<td>2.42</td>
<td>1.02E-05</td>
<td>0.72</td>
</tr>
<tr>
<td>Q. alba</td>
<td>37.4</td>
<td>2.86</td>
<td>1.78E-05</td>
<td>0.75</td>
</tr>
</tbody>
</table>
Table 6.2: Input parameters for 4C-A model.

<table>
<thead>
<tr>
<th>Species</th>
<th>Density trees ha(^{-1})</th>
<th>Average height m</th>
<th>Crown length m</th>
<th>Crown width m</th>
<th>Peak (V_{\text{max}}) µmol CO(_2) leaf m(^{-2}) s(^{-1})</th>
<th>Peak (J_{\text{max}}) m(^2) m(^{-2}) s(^{-1})</th>
<th>Peak LAI m(^2) m(^{-2})</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. tulipifera</td>
<td>69</td>
<td>25.3</td>
<td>20</td>
<td>3</td>
<td>47.3</td>
<td>23.6</td>
<td>107.2</td>
<td>57.4</td>
<td>0.32</td>
<td>0.31</td>
<td>0.33</td>
</tr>
<tr>
<td>L. styraciflua</td>
<td>52</td>
<td>26</td>
<td>25</td>
<td>2.5</td>
<td>70.4</td>
<td>35.2</td>
<td>179.6</td>
<td>95.9</td>
<td>0.59</td>
<td>0.45</td>
<td>0.76</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>66</td>
<td>28.3</td>
<td>25</td>
<td>4</td>
<td>62.4</td>
<td>41.6</td>
<td>160.5</td>
<td>111</td>
<td>0.93</td>
<td>0.84</td>
<td>1.20</td>
</tr>
<tr>
<td>Quercus spp.</td>
<td>59</td>
<td>24.1</td>
<td>19</td>
<td>4</td>
<td>90.5</td>
<td>60.3</td>
<td>227.5</td>
<td>155.7</td>
<td>0.67</td>
<td>0.66</td>
<td>1.12</td>
</tr>
<tr>
<td>Mix Canopy</td>
<td>174</td>
<td>14.1</td>
<td>12</td>
<td>3.5</td>
<td>80.5</td>
<td>60.3</td>
<td>203.6</td>
<td>155.7</td>
<td>1.48</td>
<td>1.89</td>
<td>1.45</td>
</tr>
<tr>
<td>Mix Understory</td>
<td>493</td>
<td>8</td>
<td>7</td>
<td>3</td>
<td>25.1</td>
<td>20.1</td>
<td>71.9</td>
<td>60</td>
<td>1.22</td>
<td>1.56</td>
<td>1.19</td>
</tr>
<tr>
<td>Canopy Total</td>
<td>420</td>
<td></td>
<td></td>
<td></td>
<td>3.99</td>
<td>4.15</td>
<td>4.86</td>
<td>4.84</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stand Total</td>
<td>913</td>
<td></td>
<td></td>
<td></td>
<td>5.21</td>
<td>5.71</td>
<td>6.05</td>
<td>6.00</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
Table 6.3: Growing season environmental variables. Mean daytime photosynthetically active radiation (PAR), day and night mean air temperature ($T_{air}$), mean day-length-normalized vapor pressure deficit ($D_Z$), total precipitation ($P$), and mean relative extractable soil water (REW).

<table>
<thead>
<tr>
<th>Year</th>
<th>PAR $\mu$mol m$^{-2}$ s$^{-1}$</th>
<th>Day $T_{air}$ °C</th>
<th>Night $T_{air}$ °C</th>
<th>$D_Z$ kPa</th>
<th>$P$ mm</th>
<th>REW</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>790</td>
<td>24.6</td>
<td>19.8</td>
<td>0.518</td>
<td>367</td>
<td>0.28</td>
</tr>
<tr>
<td>2003</td>
<td>733</td>
<td>23.0</td>
<td>18.9</td>
<td>0.299</td>
<td>637</td>
<td>0.74</td>
</tr>
<tr>
<td>2004</td>
<td>747</td>
<td>23.8</td>
<td>19.5</td>
<td>0.328</td>
<td>652</td>
<td>0.57</td>
</tr>
<tr>
<td>2005</td>
<td>748</td>
<td>23.9</td>
<td>19.2</td>
<td>0.385</td>
<td>331</td>
<td>0.43</td>
</tr>
</tbody>
</table>
Table 6.4: Diameter growth parameters by year and species. When linear relationships between radial increment and diameter at breast height (DBH; both in cm) were significant ($P<0.05$), growth increment was estimated with a linear equation, otherwise the mean growth is listed as the intercept.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. tulipifera</em></td>
<td>2002</td>
<td>0.0060</td>
<td>-0.0397</td>
<td>0.83</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>0.0059</td>
<td>0.0297</td>
<td>0.82</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>0.0032</td>
<td>0.0733</td>
<td>0.44</td>
<td>0.004</td>
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<tr>
<td></td>
<td>2005</td>
<td>0.0032</td>
<td>0.0752</td>
<td>0.48</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>L. styraciflua</em></td>
<td>2002</td>
<td>0.1761</td>
<td>0.00</td>
<td>0.9705</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>0.1843</td>
<td>0.01</td>
<td>0.5703</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>0.0038</td>
<td>-0.0272</td>
<td>0.28</td>
<td>0.0082</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>0.1664</td>
<td>0.00</td>
<td>0.8773</td>
<td></td>
</tr>
<tr>
<td><em>Carya spp.</em></td>
<td>2002</td>
<td>0.1031</td>
<td>0.00</td>
<td>0.7546</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>-0.0007</td>
<td>0.1363</td>
<td>0.18</td>
<td>0.0375</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>-0.0011</td>
<td>0.1416</td>
<td>0.25</td>
<td>0.0136</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>-0.0016</td>
<td>0.1705</td>
<td>0.44</td>
<td>0.0004</td>
</tr>
<tr>
<td><em>Quercus spp.</em></td>
<td>2002</td>
<td>0.0041</td>
<td>0.0508</td>
<td>0.38</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>0.0029</td>
<td>0.0916</td>
<td>0.22</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>0.0032</td>
<td>0.078</td>
<td>0.21</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>0.0034</td>
<td>0.1159</td>
<td>0.15</td>
<td>0.0007</td>
</tr>
<tr>
<td>Mixed species</td>
<td>2002</td>
<td>0.0029</td>
<td>0.0659</td>
<td>0.22</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>0.0020</td>
<td>0.1103</td>
<td>0.11</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>0.0016</td>
<td>0.1071</td>
<td>0.07</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>0.0017</td>
<td>0.1334</td>
<td>0.05</td>
<td>0.0057</td>
</tr>
</tbody>
</table>
Table 6.5: Components and totals of annual net primary productivity (NPP), respiration, including growth (G) and maintenance (M), and gross primary productivity (GPP) from Duke Forest and other mature, temperate broadleaf forests. All units in g C m\(^{-2}\) y\(^{-1}\) except CV (%).

<table>
<thead>
<tr>
<th></th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
<th>Mean</th>
<th>SD</th>
<th>CV</th>
<th>Oak Ridge</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPP</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Branch and stem</td>
<td>155</td>
<td>182</td>
<td>158</td>
<td>194</td>
<td>172</td>
<td>19</td>
<td>11%</td>
<td>284(^A)</td>
<td>200(^F)</td>
</tr>
<tr>
<td>Leaf</td>
<td>214</td>
<td>205</td>
<td>258</td>
<td>236</td>
<td>228</td>
<td>24</td>
<td>10%</td>
<td>240</td>
<td></td>
</tr>
<tr>
<td>Seeds</td>
<td>33</td>
<td>60</td>
<td>49</td>
<td>53</td>
<td>49</td>
<td>12</td>
<td>24%</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Coarse root</td>
<td>34</td>
<td>40</td>
<td>35</td>
<td>43</td>
<td>38</td>
<td>4</td>
<td>11%</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Fine root</td>
<td>120</td>
<td>120</td>
<td>120</td>
<td>120</td>
<td>120</td>
<td>--</td>
<td>--</td>
<td>153</td>
<td>269(^K), 515-1095(^I)</td>
</tr>
<tr>
<td>NPP above</td>
<td>402</td>
<td>448</td>
<td>465</td>
<td>484</td>
<td>450</td>
<td>35</td>
<td>8%</td>
<td>565(^*)</td>
<td>420(^D), 717(^K)</td>
</tr>
<tr>
<td>NPP below</td>
<td>154</td>
<td>160</td>
<td>155</td>
<td>163</td>
<td>158</td>
<td>4</td>
<td>3%</td>
<td>165</td>
<td>300(^D), 177(^K)</td>
</tr>
<tr>
<td>TOTAL</td>
<td>556</td>
<td>608</td>
<td>620</td>
<td>646</td>
<td>608</td>
<td>38</td>
<td>6%</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

|       |      |      |      |      |      |    |    |           |       |
| Respiration |      |      |      |      |      |    |    |           |       |
| Branch and stem |      |      |      |      |      |    |    |           |       |
| M     | 181  | 168  | 174  | 177  | 175  | 5  | 3% | 95\(^B\)  | 200\(^F\), 233\(^E\) |
| G     | --   | --   | --   | --   | --   | -- | -- | 156       |       |
| Leaf  |      |      |      |      |      |    |    |           |       |
| M (light) | 306  | 245  | 352  | 353  | 314  | 51 | 16%| 389       |       |
| M (dark) | 166  | 149  | 212  | 209  | 184  | 32 | 17%| 49        |       |
| G     | 54   | 51   | 64   | 59   | 57   | 6  | 10%| 49        |       |
| Seeds | 8    | 15   | 12   | 13   | 12   | 3  | 24%|           |       |
| Coarse Root |      |      |      |      |      |    |    |           |       |
| M     | 37   | 37   | 38   | 37   | 37   | 0  | 1% |           |       |
| G     | 9    | 10   | 9    | 11   | 9    | 1  | 11%|           |       |
| Fine Root |      |      |      |      |      |    |    |           |       |
| M     | 698  | 682  | 707  | 699  | 696  | 11 | 2% |           |       |
| G     | 30   | 30   | 30   | 30   | 30   | 0  | 0% |           |       |
| R above | 714  | 629  | 815  | 812  | 742  | 89 | 12%|           |       |
| R below | 774  | 758  | 783  | 777  | 773  | 11 | 1% |           |       |
| TOTAL  | 1488 | 1387 | 1598 | 1588 | 1515 | 99 | 7% | 929\(^C\) |       |

GPP\(_{comp}\)  2044  1995  2218  2235  2123  121  6%

A: Hanson et al., 2003a; B: Edwards & Hanson, 2003; C: Hanson et al., 2003b; D: Monk & Day, 1985; E: Bolstad & Vose, 2005; F: Drake et al., 2011 (100 year old pine-dominated stand); G: Drake et al., 2008 (Duke FACE); H: Bader et al., 2009; I: Davis et al. 2004 (Quercus stands, Coweeta, NC); J: Magill et al., 2004 (Harvard Forest, MA); K: Gough et al., 2008 (northern hardwood, U. of Michigan Biological Station)
Table 6.6: Estimated annual net assimilation ($A_{\text{net}}$) from the 4C-A model, daytime leaf maintenance respiration ($R_{\text{leaf,day}}$), gross primary productivity as the sum of $A_{\text{net}}$ and $R_{\text{leaf,day}}$ ($\text{GPP}_{\text{modeled}}$), GPP estimates based on sum of components ($\text{GPP}_{\text{comp}}$, see Table 6.5), and the difference between GPP estimates. All units in g C m$^{-2}$ y$^{-1}$ except CV (%).

<table>
<thead>
<tr>
<th></th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
<th>Mean</th>
<th>SD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{\text{net}}$</td>
<td>1271</td>
<td>1379</td>
<td>1528</td>
<td>1572</td>
<td>1438</td>
<td>138</td>
<td>10%</td>
</tr>
<tr>
<td>$R_{\text{leaf,day}}$</td>
<td>306</td>
<td>245</td>
<td>352</td>
<td>353</td>
<td>314</td>
<td>51</td>
<td>16%</td>
</tr>
<tr>
<td>$\text{GPP}_{\text{modeled}}$</td>
<td>1577</td>
<td>1625</td>
<td>1880</td>
<td>1925</td>
<td>1752</td>
<td>176</td>
<td>10%</td>
</tr>
<tr>
<td>$\text{GPP}_{\text{comp}}$</td>
<td>2044</td>
<td>1995</td>
<td>2218</td>
<td>2235</td>
<td>2123</td>
<td>121</td>
<td>6%</td>
</tr>
<tr>
<td>$\text{GPP}<em>{\text{comp}}$ - $\text{GPP}</em>{\text{modeled}}$</td>
<td>467</td>
<td>371</td>
<td>338</td>
<td>310</td>
<td>371</td>
<td>69</td>
<td>18%</td>
</tr>
</tbody>
</table>
Table 6.7: Mean growing season $C_i/C_a$ estimated through the 4C-A model and with $\delta^{13}C$ analysis (leaves sampled in June 2002; D. Ellsworth & K. Schäfer, unpublished).

<table>
<thead>
<tr>
<th>Year</th>
<th>L. tulipifera</th>
<th>L. styraciflua</th>
<th>Carya spp.</th>
<th>Quercus spp.</th>
<th>Mixed species</th>
</tr>
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<tbody>
<tr>
<td>2002</td>
<td>0.707</td>
<td>0.729</td>
<td>0.665</td>
<td>0.684</td>
<td>0.745</td>
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<tr>
<td>2003</td>
<td>0.803</td>
<td>0.767</td>
<td>0.686</td>
<td>0.665</td>
<td>0.761</td>
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<tr>
<td>2004</td>
<td>0.837</td>
<td>0.800</td>
<td>0.704</td>
<td>0.727</td>
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</tr>
<tr>
<td>2005</td>
<td>0.839</td>
<td>0.805</td>
<td>0.724</td>
<td>0.735</td>
<td>0.828</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>L. tulipifera</th>
<th>L. styraciflua</th>
<th>Carya spp.</th>
<th>Quercus spp.</th>
<th>Mixed species</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>0.726</td>
<td>0.740</td>
<td>0.747</td>
<td>0.729</td>
<td>0.734</td>
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Table 6.8: Lower and upper 90% confidence intervals for estimated with Monte Carlo simulations of annual respiritory fluxes of stem CO$_2$ flux ($F_{stem}$), daytime leaf respiration ($R_{leaf,day}$), nighttime leaf respiration ($R_{leaf,night}$), soil CO$_2$ flux ($F_{soil}$), and combined confidence intervals for total ecosystem respiration. All units in g C m$^{-2}$ y$^{-2}$.

<table>
<thead>
<tr>
<th>Year</th>
<th>$F_{stem}$</th>
<th>$R_{leaf,day}$</th>
<th>$R_{leaf,night}$</th>
<th>$F_{soil}$</th>
<th>Combined</th>
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<tbody>
<tr>
<td>2002</td>
<td>139</td>
<td>395</td>
<td>338</td>
<td>481</td>
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<td></td>
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<td>1069</td>
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<td></td>
<td></td>
<td>2982</td>
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<tr>
<td>2003</td>
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<td>383</td>
<td>329</td>
<td>461</td>
<td>175</td>
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<td>248</td>
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<td></td>
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<td></td>
<td>2131</td>
</tr>
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</table>
Figure 6.1: Daily mean photosynthetically active radiation (PAR), air temperature ($T_{air}$), and day length-normalized vapor pressure deficit ($D_z$) binned by relative extractable soil water (REW). Boxes represent the upper and lower quartile with means and dots represent the 95% range.
Figure 6.2: Annual totals from individual flux components of gross primary production (GPP). For each year, the first bar represents the component-based approach, the sum of autotrophic respiration \( (R_A) \) and net primary productivity \( (NPP) \) from above and belowground sources. The second bar represents estimates from the 4C-A model, the sum of net assimilation \( (A_{net}) \) and daytime leaf respiration \( (R_{leaf,day}) \).

The third bar represents eddy covariance estimates, the sum of net ecosystem productivity \( (NEP) \) and total ecosystem respiration \( (R_{eco}) \).
Figure 6.3: Vertical profile of peak annual leaf area index (LAI) by species.
Figure 6.4: Vertical profiles of daily (a) leaf area index (LAI), (b) absorbed photosynthetically active radiation (aPAR), and (c) net carbon assimilation ($A_{net}$).
Figure 6.5: Mean half-hourly estimates of sap flux scaled canopy conductance over daylight hours for wet and dry conditions defined by relative extractable water (REW) $>0.33$ or $\leq 0.33$. Bars represent one standard error.
Figure 6.6: Daily and cumulative annual totals of gross ecosystem productivity from the eddy covariance system (GEP) and gross primary productivity modeled from 4C-A (GPP\textsubscript{modeled}).
Figure 6.7: Annual fluxes of (a) of gross primary productivity (GPP) modeled from 4C-A and gross ecosystem productivity (GEP) estimated from eddy covariance measurements, (b) net primary productivity (NPP) estimated from components and net ecosystem productivity (NEP) from eddy covariance measurements, and (c) carbon use efficiency (CUE) in relation to mean growing season relative extractable water (REW) from the previous growing season. Dashed line in (c) represents estimated CUE for a 100 year-old stand (DeLucia et al., 2005).
Figure 6.8: Annual maximum leaf area index (LAI) by species (a & b) and total (c & d) compared with mean relative extractable water (REW) for the previous growing season (a & c) and current growing season (b & d).
Figure 6.9: Comparison of mean annual relative extractable soil water (REW) from the previous growing season and: (a) Annual water flux as canopy transpiration ($E_c$) and total evapotranspiration (ET). (b) Annual photosynthetically active radiation absorbed by leaf area (aPAR). Water use efficiency (WUE) as ratios of (c) modeled gross primary productivity (GPP) and eddy covariance-estimated gross ecosystem productivity (GEP) and of (e) component-based net primary productivity (NPP) and eddy covariance-estimated net ecosystem productivity (NEP). Light use efficiency (LUE) as ratios of (d) GPP and GEP and (f) NPP and NEP.
Figure 6.10: Annual fluxes of (a) of gross primary productivity modeled from 4C-A (GPP\text{modeled}) and as the sum of components (GPP\text{comp}), and gross ecosystem productivity (GEP) estimated from eddy covariance measurements, (b) net primary productivity (NPP) estimated from components, net ecosystem productivity (NEP) from eddy covariance measurements, and NEP estimated as NPP minus annual turnover of leaf litterfall and fine roots, and (c) estimated autotrophic respiration ($R_A$) as a sum of individual components, soil CO$_2$ flux, and eddy covariance-derived ecosystem respiration ($R_{eco}$).
Figure 6.11: Modeled annual gross primary productivity (GPP) as a function of (a) leaf area index (LAI) and (b) leaf biomass. Solid lines indicate $P<0.05$, dashed line indicates $P<0.10$, and dotted line indicates $P>0.20$. 
Figure 6.12: Leaf mass area (LMA) versus gross primary production modeled with 4C-A (GPP_{modeled}) divided by annual leaf area index (LAI).
References


Daly, E. et al., 2009. The effects of elevated atmospheric CO2 and nitrogen amendments on subsurface CO2 production and concentration dynamics in a maturing pine forest. Biogeochemistry, 94(3): 271-287.


Drake, J.E. et al., in review. Root removal reduces soil heterotrophic activity in a loblolly pine (Pinus taeda) forest exposed to elevated atmospheric [CO2] and N-fertilization. Agricultural and Forest Meteorology.


Hanson, P.J. et al., 2004. Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. Ecological Monographs, 74: 443-489.


King, J.S. et al., 2004. A multiyear synthesis of soil respiration responses to elevated atmospheric CO2 from four forest FACE experiments. Global Change Biology, 10: 1027-1042.


Mortazavi, B. et al., 2004. Temporal variability in \(^{13}\)C of respired CO\(_2\) in a pine and a hardwood forest subject to similar climatic conditions. Oecologia, 142: 57-69.


Schwalm, C.R., Black, T.A., Morgenstern, K. and Humphreys, E.R., 2007. A method for deriving net primary productivity and component respiratory fluxes from tower-


Stoy, P.C. et al., 2006b. Separating the effects of climate and vegetation on evapotranspiration along a successional chronosequence in the southeastern US. Global Change Biology, 12(11): 2115-2135.


Biography

Andrew Christopher Oishi was born in Los Gatos, California, February 13, 1975.

He received his B.A. in Environmental Science and Policy from Duke University, Durham, North Carolina in 1997 and his M.E.M. from the School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut in 2001.

Primary authored publications are:
