Relationships Between Forest Structure And Soil CO_2 Efflux In 50-Year-Old Longleaf Pine

by

William Bennett Whitaker

A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
May 14, 2010

Keywords: *Pinus palustris* Mill., forest structure, soil CO_2 efflux, annual soil C efflux, forest carbon sequestration, net primary productivity

Approved by

Lisa J. Samuelson, Chair, Professor, School of Forestry and Wildlife Sciences
John S. Kush, Research Fellow IV, School of Forestry and Wildlife Sciences
Dean H. Gjerstad, Professor Emeritus, School of Forestry and Wildlife Sciences

Abstract

Global climate change and the accumulation of the greenhouse gas, carbon dioxide (CO_2), in the atmosphere, may be mitigated by the proper management of soils and forests through carbon (C) sequestration. Longleaf pine (*Pinus palustris* Mill.) forests, which historically dominated the upper and lower Coastal Plain in the southeastern United States, have the potential to sequester large quantities of C through long rotations and temperate climatic conditions. Soils compose the largest C sinks on earth and thus have potential to be the largest contributors of CO_2 to total ecosystem respiration. More knowledge on the effects of stand and community structure on soil CO_2 efflux is needed to understand how forest management influences C cycling. The objective of this study was to examine how forest structure and forest characteristics influence the rate of soil CO_2 efflux to better understand forest management effects on C pools. Soil CO_2 efflux was examined over a 10 month period on the Escambia Experimental Forest near Brewton, AL in response to basal area, root biomass, woody debris in the soil, soil charcoal mass, soil C, litter depth, litter mass, downed woody debris, aboveground and belowground biomass, ground cover, and environmental conditions.

Basal areas ranged from 7 to 36 $m^2 \cdot ha^{-1}$ and ground cover, litter mass, litter depth, soil woody debris, and downed woody debris varied with basal area but soil temperature did not. Mean monthly soil CO_2 efflux ranged from 1.6 μmol $m^{-2} \cdot s^{-1}$ in January to 6.5

μmol $m^{-2} \cdot s^{-1}$ in August 2008. Soil CO_2 efflux increased exponentially with soil temperature and temperature explained 96% of the variation in soil CO_2 efflux. Only 1-11% of the variation in soil CO_2 efflux was explained by soil moisture, litter mass or depth, ground cover, natural log-transformed live coarse roots, downed woody debris C, or natural log-transformed soil charcoal. These results indicate that soil CO_2 efflux can be modeled using soil temperature and that forest management practices that influence soil temperature rather than forest structure or forest characteristics per se will influence soil CO_2 efflux.

Acknowledgments

The author is indebted to all whose support enabled the completion of the research project. Dr. Lisa J. Samuelson provided expertise, guidance, and encouragement during the study. Thomas A. Stokes was enthusiastically present during every aspect of the research. Dr. John S. Kush and Dr. Dean H. Gjerstad offered their expertise and comprehensive working knowledge of the longleaf pine ecosystem as well as guidance during the study. Dr. Ralph S. Meldahl, professor emeritus of Forest Mensuration, granted his excellent services in numerous data analyses and reviews. John Gilbert was also helpful in data analysis and in providing information concerning the Escambia Experimental Forest. Dr. William D. Boyer provided valuable historical information regarding the Escambia Experimental Forest. Marianne Farris was irreplaceable during field collections and in laboratory work. Lacey Avery and Wesley Brown provided help in the laboratory and in the field. Ronnie Tucker, the head forester at the Escambia Experimental Forest, was vital in initiating the experiment, providing historical information for Compartment 135, and for offering his knowledge of forest management. The School of Forestry and Wildlife Sciences and the United States Geological Survey provided funding for the research and the School of Forestry and Wildlife Sciences generously provided a graduate assistantship.

The author wishes to acknowledge Great Uncle John H. Land, Johnny H. Land, Cathy L. Waters, and Uncle Art Miller as they offered more encouragement than they

would accept. To his father and mother, William V. and Virginia M., his brothers, Wilson and Rob, and his grandparents Vernon E. Whitaker and Jane M. Whitaker and the late Mary L. Miller, the author wishes to express his gratitude by recognizing their sincere encouragement through the abundant support and motivation that they put forth during the entirety of the project.

Table of Contents

List of Tables

List of Figures

Figure Page

List of Abbreviations

BA	basal area
C	carbon
CAI	current annual increment
CO_2	carbon dioxide
DBH	diameter at breast height
ha	hectare
Mg	megagram
N	nitrogen
NPP	net primary productivity
Pg	petagram
QMD	quadratic mean diameter
SAS	Statistical Analysis System
SM	soil moisture
Tg	teragram
T_{AIR}	air temperature
T_{SOIL}	soil temperature

CHAPTER 1. INTRODUCTION

Longleaf pine (*Pinus palustris* Mill.) historically inhabited approximately 37 million hectares (ha) of the upper and lower Coastal Plain in the Southeast United States from east Texas to southeast Virginia and into the Piedmont of Alabama and Georgia (Landers et al. 1995). Extensive logging practices, improper regeneration techniques, reforestation with various species of southern yellow pine (*P*. *taeda* L., *P*. *elliottii* Engelm., *P*. *echinata* Mill.), the naval stores industry which utilized pine oleoresin, conversion of forested land to agricultural land, and suppression of natural wildfires all played an important role in the decline of the natural range of the longleaf pine (Wahlenberg 1946). The original longleaf range has been reduced to approximately 1.2 million ha (Landers et al. 1995).

There has been a renewed interest in longleaf pine in recent years. Lands are being reforested with longleaf pine through private landowner interests, governmental cost share programs assisting landowners with reforestation and afforestation, and ecologists seeking to restore native habitat which supports many diverse forms of flora and fauna. With the current concern that anthropogenic increases in carbon dioxide (CO_2) are altering climates globally (Houghton 2005), and because the largest terrestrial carbon (C) sinks are primarily within the soil (Hibbard et al. 2005) and secondarily within trees (Woodbury et al. 2007), an understanding of controls on soil CO_2 efflux in a variety of ecosystems is needed to better model global C budgets and C sequestration. Soil CO_2 efflux is the rate at which CO_2 moves out of the soil and into the atmosphere and is the product and the combination of autotrophic (root) and heterotrophic (microbial) respiration (Janssens et al. 2001). This research investigated how forest structure and forest characteristics were related to soil CO_2 efflux to characterize forest C fluxes and provide a better estimate of forest C sequestration in managed longleaf pine stands.

1.1 Rational and Significance

Longleaf pine ecosystems are able to support an abundance of diverse plant and animal species. Many of these species are threatened, such as the fox squirrel (*Sciurus niger* L.), the gopher tortoise (*Gopherus polyphemus* Daudin), the indigo snake (*Drymarchon couperi* Fitzinger), and pitcher plants (*Sarracenia* spp.). The red-cockaded woodpecker (*Picoides borealis* Vieillot) is on the Endangered Species List. As interest in these species and their supporting ecosystem increases, more land managers are seeking to restore longleaf pine to its native range. Interest in the diverse ecosystem has helped longleaf pine become a conduit through which C credits may be invested. Because forests can be large C banks which are able to reduce the amount of greenhouse gases in the atmosphere by storing C in biomass, their value has risen with increasing focus on a national and global CO_2 cap and trade system. On June 26, 2009 the H.R. 2454 bill sponsored by Henry Waxman and Ed Markey, known as American Clean Energy and Security Act of 2009, passed with a margin of 7 votes in the House of Representatives (Stone and Shaw 2009). Voluntary buying and selling of C credits in the United States has been managed by voluntary C markets such as the Chicago Climate Exchange, Clean

Development Mechanism, Voluntary Carbon Standard, American Carbon Registry, and the Climate Action Reserve, but the H.R. 2454 bill would be the first legislation to put mandatory limits on greenhouse gas production (Ramseur et al. 2009). Passage of this bill by Congress may increase the value of forestland as trees sequester large amounts of C and thus may assist in a solution of greenhouse gas mitigation. United States' forests cover approximately one-third of the area in the United States and 67% of this forestland is classified as timberland with the potential to produce more than 1.4 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ in volumetric growth (Smith et al. 2001).

The Kyoto Protocol meeting in 1997 identified intensely managed forested plantations as a key player in global C sequestration (Kobziar 2007). Because longleaf pine is being planted at a greater frequency, and because it is not usually planted singularly for growing pulpwood and is often balanced with other objectives such as habitat restoration for flora and fauna and for producing wood products, longleaf pine may be a good species for long-term C sequestration. Management objectives to increase C sequestration need to be developed based from scientific studies. Long rotation age in longleaf pine timberlands also has potential to provide long-term C sequestration opportunities, high-quality specialty lumber, diverse recreational activities, and habitat for the threatened and endangered species.

Carbon sequestration at the forest level provides multiple ecosystem services. Managed forests provide an avenue to capture sequestered C more efficiently than unmanaged stands, and managed stands may store more C in forests, forest products, and through the replacement of fossil fuel products (Perez-Garcia et al. 2005). In natural longleaf stands, management often includes prescribed fire on a regular interval between

2 to 5 years and periodic thinning to achieve a targeted basal area depending on management objectives. Meldahl and Kush (2006) speculated that longleaf pine ecosystems in the Southeast United States have great potential for C sequestration in the forest stand and in C storage in forest products such as poles, pilings, and lumber. The benefits of sequestering C in longleaf forests are threefold. Renewable products such as lumber are produced and harvested logs can store C for varying time periods with the longest storage period most commonly attributed to solid wood products used for structural supports. The second benefit is the substitution of renewable products for non-renewable alternatives such as steel, vinyl, concrete, and oil. Gustavsson and Sathre (2006) found in nearly all cases that wood based construction materials were superior to concrete materials when lower energy and CO_2 balances were desired. Residential contractors selecting wood products over non-renewable materials observed a fourfold decrease in emissions when installing walls and flooring according to Lippke and Edmonds (2006). The viable alternatives to wood based products require more inputs during production and produce greater emissions during processing. Buchanan and Levine (1999) stated that the small fossil fuel requirement necessary to process wood products is much more important than the actual C stored in the wood products compared to the large inputs required for C costly materials such as brick, aluminum, steel, or concrete. The final benefit is the preservation of a unique ecosystem accommodating various forms of flora and fauna.

Because a better understanding of forest management effects on C sequestration and C stocks in longleaf pine forests is needed, the objective of this study was to examine C stocks and soil CO_2 efflux rates in relation to forest structure, forest characteristics, and environmental conditions in 50-year-old longleaf pine stands varying in basal area. The study site on the Escambia Experimental Forest has been actively managed for over 60 years and detailed historical records of the past management are available and provide a foundation for this unique research. Study plots have been managed for different densities across a range of basal areas from 7-34 $m^2 \cdot ha^{-1}$, and these target basal areas are often used for different silvicultural objectives such as pinecone production for natural regeneration methods, production of solid wood products, and wildlife management. If land managers are able to utilize a land management plan to produce timber, manage for wildlife, and sequester C simultaneously, economic and intrinsic values increase for the land owner. A second objective was to explore environmental and plant factors related to soil CO_2 efflux. Because soil CO_2 efflux composes the majority of ecosystem respiration (Janssens et al. 2001) with the relative contribution of soil CO_2 efflux to ecosystem respiration estimated between 50-80% (Lavigne et al. 1997; Davidson et al. 1998; Law et al. 1999), factors affecting soil CO_2 efflux influence whether a stand is a source or sink for CO_2. This study examined relationships among soil CO_2 efflux and stand basal area, soil temperature, soil moisture, soil C, soil N, soil charcoal, soil woody debris, ground cover, litter, downed woody debris, and aboveground and belowground biomass.

1.2 Hypotheses

The hypotheses tested by this study were:

1. Soil temperature will explain the majority of variation in soil CO_2 efflux rates in the longleaf pine stands.
2. Soil moisture will be related to soil CO_2 efflux rates.

3. Forest structure defined by basal area will be related to soil CO_2 efflux through effects on forest characteristics including soil temperature, soil moisture, percent ground cover, litter, and above and belowground biomass.

CHAPTER 2. LITERATURE REVIEW

2.1 Forest Carbon Sequestration

Forests are a large component of the C cycle as both sources and sinks for CO_2. Forests in the northern hemisphere during the 1980's and 1990's were estimated to store 0.6-0.7 Pg C·year^{-1} (1 Pg = 10^9 Mg) in the forest with approximately 0.21 Pg C·year^{-1} in live tree biomass (Goodale et al. 2002). Every year, forests in the United States sequester approximately 200 Tg C (1 Tg = 10^6 Mg) from CO_2 in the atmosphere (Heath and Smith 2004). Sources of CO_2 from forests include forest fires, decomposition of leaf matter and woody debris, and autotrophic respiration (Kimmins 2004). The amount of C stored in forests of the United States has increased since 1953 (Birdsey 2006). Currently, the C sequestration rate has slowed because of maturing forests and from increased harvesting operations (Birdsey 2006). In general, as forests mature, the rate at which C is sequestered is reduced because of slower growth rates (Birdsey 2006). Forest C sequestration in the Southeast United States was modeled from historical records of land use transitions from 1900 to 1940 by Woodbury et al. (2006) who determined that there was a net emission of CO_2 because of deforestation and timber maturation, but from 1940 to present there was a net sequestration of C by forests. When timber is harvested for lumber production, the C sequestered during the life span of the trees is stored in the final product. Dimensional lumber stores C for many decades before decomposition occurs

(Birdsey 2006). Ultimately, when wood products are deposited in a landfill, the amount of C released back into the atmosphere as CO_2 is between 0-3% of the C in the wood (Micales and Skog 1997).

The net flux of C in an ecosystem entering through photosynthesis or exiting through respiration is the net ecosystem exchange. Valentini et al. (2000) found that annual ecosystem respiration increased as latitude increased in European forests, even though the mean temperature of the air decreased. While individual site ecosystem respiration rates were well explained by temperature, the relationship between all sites and ecosystem respiration was not significant. This may be an indication that latitude influences length of the growing season, mean soil temperature, precipitation, soil organic matter decomposition, species composition, and site, which may determine soil CO_2 efflux (Valentini et al. 2000). Valentini et al. (2000) suggest that the temperature sensitivity of soil organic matter decomposition is greater in higher latitudes, thus a similar temperature increase across all latitudes would result in greater decomposition rates from the high latitude boreal forests.

Total ecosystem respiration within forests is determined by autotrophic and heterotrophic respiration. Soils are the largest storage bank of C, exceeding aboveground and belowground biomass or atmospheric CO_2 by two to three times (Johnson and Curtis 2001; Post et al. 1982) and therefore soil organic C is equal in importance if not greater to the tree biomass growing in the soil (Chen et al. 2007). Because of the importance of soil C relative to a forest as a C sink, many soil factors influence soil CO_2 efflux including the parent material, texture, depth, forest cover, and past and present forest management practices (Yu et al. 2007). For example, soil CO_2 efflux can be the most significant source of CO_2 emitted from forests and soil CO_2 efflux was found to be between 58% and 76% of total ecosystem respiration in a temperate mixed hardwood and conifer forest in Belgium (Yuste et al. 2005). Goulden et al. (1996) and Longdoz et al. (2000) hypothesized that soil CO_2 efflux in temperate forested ecosystems may compose between 60-90% of total ecosystem respiration. Soil C is difficult to determine because of the non-uniform spatial distribution of C in the soil and limited methods for measurements of the soil C inputs, especially belowground systems (Ebinger et al. 2003). In fact, there is only a partial understanding of the process of C allocation in forests, because there are uncertainties concerning belowground C fluxes and allocation of C through different forested ecosystems (Litton et al. 2007). Soil C has been noted by Birdsey (2006) to change in very small increments that are difficult to quantify over short time scales.

Soil C can be released through disturbances such as fire, pest outbreaks, logging, or through land use changes. Valentini et al. (2000) found that as the use of land changes, there is often a large change in the soil organic matter, which may accumulate within soil stores or decompose and be recycled through the C cycle by increased soil CO_2 efflux rates. Land C storage is composed of plant and soil C sinks. When a C sink is not maintained in the same manner as when C accumulation took place, transformation from a C sink to a C source may occur (Scholes and Noble 2001). For example, land change from forestland to agricultural land results in different cycling patterns of C. A land use change resulting in the transformation of a forest into cropland will lose long term storage ability as woody materials are excluded from the landscape. Land use may alter microclimate which changes the variable residence time of soil organic C. Factors which influence the mean residence time of soil C are the ability of a C source to resist decay as well as the degree of protection C sources have against decomposition (Paul et al. 2003). Both variables influence the storage and respiration of C in soil. Scholes and Noble (2001) stated that C in plant biomass or soil organic C will be released back into the atmosphere with improper management. The transformation of a C sink to a C source can be a very rapid change as a result of disturbances altering the structure of the land. However, the transformation can also be gradual through the process of respiration. Falkowski et al. (2000) state three possible pathways by which C is reintroduced into the atmosphere. These are autotrophic respiration, heterotrophic respiration, and land disturbances such as fire, pests, land use change, deforestation, and aforestation.

2.2 Soil CO_2 Efflux

2.2.1 History

In the 19th century, soil organisms and bacteria were found to produce a majority of the CO_2 efflux from the soil (Pettenkofer 1858). Other early studies found that soil CO_2 rates indicated microbial activity (Hutchinson 1912) and nitrification rates (Russell 1915, Russell and Appleyard 1915) due to the bacteria in the soil. Microbial decomposition of roots was also determined by Potter and Snyder (1916) to be a factor in soil CO_2 production. In contrast, Neller (1918) did not find a relationship between the soil bacteria and soil CO_2 efflux.

Additional studies found that soil CO_2 levels were greater in soils with crops than in bare soil and that CO_2 efflux increased during flowering and fruit production, demonstrating a positive relationship between belowground root activity and soil CO_2

efflux (Russell and Appleyard 1917; Lundegardh 1926). Lundegardh (1926) also found that root respiration accounted for 30% of soil CO_2 efflux when a cropped soil was compared to bare soil. Turpin (1920) compared cropped soil to bare soil and discovered increased CO_2 production within cropped soil, even after oat (*Avena* spp.) and common millet (*Panicum miliaceum* L.*)* harvest. The increase in CO_2 rates following harvesting were possibly from decay of residual plant roots. He also found that during vigorous plant growth soil CO_2 rates were higher and that soil temperature did not influence soil CO_2 rates. In contrast, in the same study bare soil CO_2 rates did fluctuate with soil temperature. Turpin (1920) concluded that plant and soil organisms acted independently in soil CO_2 production and that the soil fauna was a more consistent source of soil CO_2, but plant root systems produced the greatest amount of soil CO_2 when vigorous plant growth was observed. Therefore, Turpin (1920) concluded that during the growing season soil CO_2 production was primarily attributed to root respiration and not to root decomposition or fine root turnover.

Soil conditions have been shown to play a role in the amount of soil CO_2 produced. For instance, in early soil CO_2 efflux studies, soil CO_2 levels were extremely low in a rice (*Oryza sativa* L.) swamp in India, possibly due to low oxygen (O_2) levels and greater methane (CH_4) production (Harrison and Aiyer 1913). High organic matter was also noted to correlate with soil CO_2 levels when studied by Russell and Appleyard (1915). Soil temperature and soil CO_2 levels were positively related in numerous early studies due to the common relationship between rate of reaction and temperature (Russell and Appleyard 1915; Leather 1915). These studies demonstrated the importance of environmental conditions, plant factors and microbes in understanding soil CO_2 efflux.

2.2.2 Autotrophic and Heterotrophic Respiration

Autotrophic (root) respiration and heterotrophic (microbial) respiration are the components that produce the majority of CO_2 in soil CO_2 efflux (Bond-Lamberty et al. 2004; Hanson et al. 2000; Olsson et al. 2005). Autotrophic respiration consists of maintenance and growth respiration (Amthor 1984). Soil CO_2 efflux from autotrophic maintenance respiration is produced from metabolic repairs, protein reconstruction, maintenance of ion gradients, and physiological adaptations (Penning de Vries 1975). Growth respiration is the use of C during the production of biomass (Amthor 1984).

Autotrophic respiration ranges from 10% to 90% of total soil CO_2 efflux (Hanson et al. 2000). Hogberg et al. (2001) performed a phloem girdling study to reduce C transport to roots and to eliminate autotrophic respiration using Scots pine (*Pinus sylvestris* L.) in Sweden and found up to 56% of the soil CO_2 efflux was due to autotrophic respiration. Tree phloem girdling studies prevent the flow of photosynthates to root systems, therefore the reduction in soil CO_2 efflux after phloem girdling may be directly related to autotrophic respiration. In a Central Amazon tropical forest, Chambers et al. (2004) found that approximately 70% of soil CO_2 efflux was due to autotrophic respiration. Andersen et al. (2005) reported that phloem girdling of European beech (*Fagus sylvatica* L.) trees in Germany resulted in a decrease in soil CO_2 efflux by 50% and they attributed the reduction to an absence of autotrophic outputs. In another phloem girdling study using 40-year-old Norway spruce (*Picea abies* (L.) H. Karst) in Sweden, Olsson et al. (2005) reported that the girdled trees had significantly less soil CO_2 efflux than the nongirdled trees. In the same experiment, fertilized trees exhibited lower soil CO_2 efflux rates than the trees receiving no fertilizer even though the aboveground portion of the fertilized trees was two to three times greater than the unfertilized trees. The decrease in soil CO_2 efflux in the fertilized treatment was attributed to less C allocated to fine root production as nutrients became readily available from fertilization, thus resulting in reduced fine root biomass and respiration (Axelson and Axelson 1986). The importance of fine root respiration was demonstrated by Ryan et al. (1997) after determining that fine root respiration was greater than coarse root respiration per unit of root biomass. In another study, fine root respiration was reported to be slightly greater than coarse root respiration and fine root respiration was related to fine root nitrogen deposition, indicating a relationship between photosynthesis, leaf production and litterfall, and respiration (Vose and Ryan 2002).

Litton et al. (2007) found that autotrophic respiration was heavily correlated to both aboveground and belowground biomass production. As biomass grows volumetrically, autotrophic respiration also increases. Carbon allocation to aboveground and belowground biomass production is recognized by many scientists to be directly related to soil CO_2 efflux (Ekblad and Hogberg 2001; Hogberg et al. 2001). As more biomass is produced aboveground or belowground, plant respiration will increase due to the amount of living tissue and its supporting biological processes. Also, the supply of photosynthate and autotrophic respiration are closely related due to metabolic rates, individual and stand growth rates, and stand dynamics (Lambers et al. 1998; Reich et al. 1998; Ekblad and Hogberg 2001). Other factors which influence autotrophic respiration include temperature, moisture, nutrients, and photosynthate supply (Amthor 1994; Sprugel et al. 1995; Lambers et al. 1998; Singh and Shekhar 1986). Cheng et al. (2005) separated rhizospheric respiration from soil CO_2 efflux using buried root chambers within a 21-year-old longleaf pine plantation in Georgia and determined that different tree species had different soil CO_2 efflux rates that varied with soil types.

Heterotrophic respiration is linked to the rate of litter decomposition as well as photosynthate production and net primary productivity (NPP) (Zak et al. 1994; Gaudinski et al. 2000). Hamer and Marschner (2002) also reported an increase in heterotrophic respiration resulting from the deposition of more organic matter which was likely due to microbial communities flourishing under the nutrient rich conditions accompanying litter and root decomposition. However, the relative contribution of heterotrophic respiration to soil CO_2 efflux is not clearly understood because of difficulty in the separation of autotrophic and heterotrophic respiration (Ekberg et al. 2007). Isotope fractionation, trenching, phloem girdling, and component analyses are approaches used to attempt the separation of autotrophic respiration from heterotrophic respiration, but all methods have drawbacks and limitations (Hanson et al. 2000).

2.3 Factors Influencing Soil CO_2 Efflux

Important biotic, abiotic, and edaphic factors that may influence soil CO_2 efflux include soil temperature, soil moisture, plant cover, litter, and aboveground and belowground biomass. These factors have a large impact on the autotrophic and heterotrophic components of soil CO_2 efflux (Hanson et al. 2000). Biotic and abiotic factors are often autocorrelated. For example, reduced plant cover may alter soil temperature which in turn can increase soil CO_2 efflux rates. Other factors influencing soil CO_2 efflux rates are forest management practices. Intensive silviculture techniques may increase growth and overall productivity with practices such as fertilization, irrigation, and the use of herbicide, pesticide, and fungicide treatments. Intensive culture techniques result in faster growth rates, but these practices can alter fine root production and soil CO_2 efflux rates (Samuelson et al. 2004).

2.3.1 Soil Temperature

The amount of increase in the rate of reaction in response to a 10 ºC increase in temperature is known as the temperature sensitivity or Q_{10} (Winkler et al. 1996). Within a limited range of temperatures, biological and microorganism reactions will behave according to the Van't Hoff and Arrhenius laws by increasing the rate of a chemical reaction by a factor of two with a temperature increase of 10 ºC (Greaves 1922; Waksman 1932; Lloyd and Taylor 1994; Meyer et al. 2001; Winkler et al. 1996; Takahashi et al. 2003). Soil CO_2 efflux reactions are often described by the Q_{10} relationship. However, caution must be used as Fang and Moncrieff (2001) demonstrated that Q_{10} values are not all equal because of multiple Q_{10} equations which may result in different Q_{10} values. Quadratic and first-order exponential Q_{10} models have a fixed Q_{10} value and therefore may underestimate Q_{10} values at low temperatures and overestimate values at high temperatures (Lloyd and Taylor 1994).

The average Q_{10} of soil CO_2 efflux as reported from the literature by Raich and Schlesinger (1992) was 2.4 and ranged from 1.3 to 3.3. Wiant (1967) found a Q_{10} value of 2.0 for soil CO_2 efflux for eastern white pine (*Pinus strobus* L.), black spruce (*Picea mariana* (Mill.) B. S. P.), and northern red oak (*Quercus rubra* L.), and a value of 1.7 for eastern hemlock (*Tsuga canadensis* (L.) Carr.) with temperature ranging from 10 ºC to 40 ºC. When temperature is greater than 50 ºC, microbe and tissue damage may result from protein denaturation and enzyme deactivation, and thus Wiant (1967) and others have found a significant decrease in the amount of soil CO_2 efflux at high temperatures. Reichstein et al. (2000) found Q_{10} values of 2.5 and 2.8 for soil CO_2 efflux in the organic soil layer and the A-horizon in a forest-tundra ecosystem in Switzerland, respectively. Peterjohn et al. (1993) found a Q_{10} of 3.1 for soil CO_2 efflux in a temperate hardwood forest in Massachusetts. Kao and Chang (2009) measured a higher Q_{10} value of 3.5 in a mountainous hemlock (*Tsuga chinensis* var. *formosana* (Bong.) Carr.) forest and noted that the forest soil CO_2 efflux was more sensitive to temperature than a grassland site (Q_{10} of 2.8). Martin et al. (2007) noted temperature to be more significant in controlling belowground soil CO_2 efflux than any other variable, including soil moisture. Gough and Seiler (2004) also found a strong correlation between the rate of soil CO_2 efflux and soil temperature. Soil temperature has been noted to drive soil CO_2 efflux rates more than any other variable (Wang et al. 2007; Wang and Yang 2007).

2.3.2 Soil Moisture

The relationship between soil CO_2 efflux and soil moisture varies with site and species (Davidson et al. 2000). For example, arid soils experiencing drought stress may likely have lower soil CO_2 efflux rates from lack of adequate moisture which may limit microbial and root production (Wildung et al. 1975). Tufekcioglu et al. (2001) observed that soil moisture influenced soil CO_2 efflux rates more in soybean (*Glycine max* (L.) Merr.) and prairie grass (*Panicum* spp.) fields than soil temperature, and the combination of soil temperature and soil moisture explained 69% of the variation in soil CO_2 efflux. Laboratory experiments inducing drought showed that when soil moisture was below field capacity, soil CO_2 efflux was reduced (Doran et al. 1991; Orchard and Cook 1983). Other studies report an increase in soil CO_2 efflux with increased moisture availability (Schmidt et al. 2004; Wan et al. 2007). On the other hand, in soils which are very wet a decrease in moisture may increase soil CO_2 efflux rates. For example, Oberhauer et al. (1992) tested tundra soil in the Arctic and found increasing soil CO_2 efflux rates with decreasing water table levels. Qi and Xu (2001) found a maximum soil CO_2 efflux at 20% soil moisture content in a ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) plantation in California but soil moisture greater than 20% reduced soil CO_2 efflux. Linn and Doran (1984) explained that increased soil CO_2 efflux after drying of regularly inundated soil took place because O_2 diffusion increased enabling respiration to occur. Davidson et al. (2000) observed the general pattern of decreasing soil CO_2 rates with decreasing soil moisture in a forest and pasture in the Amazon Basin in Brazil. However, when soil CO_2 efflux measurements directly followed a precipitation event in Davidson's experiment, soil was nearly saturated (matric potential >-0.005 MPa) and efflux rates were depressed. Saturation of soil pore space limits O_2, reducing respiration (Bouma and Bryla 2000). In contrast, precipitation events can cause water percolation into soil pore spaces which displaces soil pore gas, releasing an intense pulse of soil CO_2 (De Selm 1952).

Other studies have not found significant relationships between soil CO_2 efflux and soil moisture. Edwards (1975) found no statistically significant relationship between soil moisture and soil CO_2 efflux in a 40 to 50-year-old yellow-poplar (*Liriodendron tulipifera* L.) stand. Keith et al. (1997) reported that soil moisture does not have an effect on soil CO_2 efflux rates unless drought conditions occur. Keith et al. (1997)

demonstrated that higher soil temperatures reduced soil moisture in a eucalypt snow gum (*Eucalyptus pauciflora* Sieber ex Spreng.) ecosystem in Australia and reduced soil CO_2 efflux. The interaction between soil temperature and soil moisture can often influence soil CO_2 efflux (Kirschbaum 2000). Martin et al. (2007) reported that when moisture was adequate, there was only a small correlation between soil moisture and soil CO_2 efflux rates in mountain ash (*Eucalyptus regnans* F. Muell.). However, Gough and Seiler (2004) stated that there was no correlation between the soil CO_2 efflux rates and soil moisture in loblolly pine plantations in the upper Coastal Plain of South Carolina. A study at Fort Benning, Georgia in a mixed pine stand reported that soil CO_2 efflux was related to soil moisture in sandy soils when moisture was greater than the wilting point, but was not related to soil moisture in clayey soils with greater moisture holding capacity (Dilustro et al. 2005).

2.3.3 Fire

A native plant restoration study in Northern Arizona reported that reintroduction of prescribed fire into a ponderosa pine stand increased herbaceous fine root biomass and soil moisture, reduced total fine root biomass, and increased soil CO_2 efflux rates (Selmants et al. 2008). Herbaceous fine root biomass may have increased in response to more soil moisture, greater light resources, and additional nutrients. Studies in longleaf pine ecosystems also demonstrate the role of fire in increasing or maintaining an herbaceous layer (Kush et al. 1999; Hiers et al. 2000; Brockway and Lewis 1997) but it is not well understood how the herbaceous layer and fire influence soil CO_2 efflux rates in longleaf pine. Kush et al. (1999) reported that the timing of burning did not influence longleaf overstory basal area but that understory hardwood basal areas were different among burning season treatments, with greater hardwood basal areas in the unburned and winter burn treatments. Additionally, there was a greater amount of total biomass in the unburned plots with the majority of the biomass attributed to accumulation of organic matter in the litter layer over a 34-year duration without prescribed fire (Kush et al. 1999). It may be that unburned longleaf pine forests sequester greater amounts of C due to understory growth and litter accumulation, but these unburned stands increase the risk of severe wildfire and do not provide adequate habitat for certain targeted flora and fauna. Prescribed fire is vital in longleaf ecosystems, but Boyer (1994) found that prescribed fire within longleaf did reduce growth in stands of 24 years and younger. However, Boyer's findings may provide evidence that increased rotation length in longleaf pine stands and use of prescribed fire on a regular interval offer long-term C storage in trees and solid wood products, reduced wildfire hazard, and a valuable ecosystem.

2.3.4 Litter

Reinke et al. (1981) reported that prescribed fire and pine straw removal in a longleaf pine plantation in South Carolina reduced total soil CO_2 efflux, but only by 5% and 6%, respectively. However, the removal of litter, duff, and humus layers decreased soil CO_2 efflux in a longleaf pine plantation by 22% (Reinke et al. 1981). Leaf litter may inhibit soil drying by acting as a natural barrier to evaporation (Ginter et al. 1979), may influence nutrients supplied through organic matter decomposition, and may be a CO_2 source as decomposition occurs thus affecting soil CO_2 efflux. Bowden et al. (1993) and

Edwards and Sollins (1973) reported that litter contributed 37-48% to total soil CO_2 efflux in a mixed hardwood stand.

As litter breaks down and decomposes, organic materials are deposited into soil increasing the soil organic content (Keith et al. 1997). Also, a considerable amount of energy produced during primary production is accumulated in the litter layer and then recycled back into the system through decomposition (Macfadyen 1971). Phillipson et al. (1975) observed that total organic matter (including above and below ground litter) decomposition made up 95% of soil CO_2 efflux rates. Higher rates of litterfall increase the amount of C in the soil as litter breaks down through decomposition (Martin et al. 2007). A mature oak-hickory forest type had greater litterfall than a maturing pine plantation and the decomposition of the hardwood litter was also greater, which increased forest floor CO_2 efflux rates (Palmroth et al. 2005), and the higher rates of litterfall and decomposition resulted in greater soil organic C content. Bolstad et al. (2005) found similar results when comparing pasture land to forested land. The aboveground live biomass was much greater in the forests than in pastures, and the average soil C in the pasture sites was lower than forest sites as the forested sites maintained much higher litter volumes than pastures. The differences between aboveground biomass allocation and litter decomposition resulted in lower soil CO_2 efflux rates in the pasture sites.

Downed woody debris is a significant part of the C cycle, an important structural component of forested ecosystems (Lindenmayer and McCarthy 2002), and composes approximately 18% of the total C within temperate forested ecosystems (Pregitzer and Euskirchen 2004). Liu et al. (2006) observed that 30% of the net ecosystem exchange in the Harvard Forest in Massachusetts was from downed woody debris, and the main factors driving decomposition of downed woody debris were air temperature, sampling temperature, bulk density, and wood moisture. Tate et al. (2006) reported that CO_2 production was significantly higher in treatments containing logging residue than in treatments lacking slash.

2.3.5 Root Biomass

Root biomass contributes to soil CO_2 efflux levels through the autotrophic component of soil CO_2 efflux. King et al. (2000) found a close correlation between soil CO_2 efflux rates and fine root biomass in stands of paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) under conditions of elevated CO_2. However, the stands with greater rates of fine root growth also exhibited a greater fine root turnover rate which in turn may increase heterotrophic respiration as microbial populations decompose root biomass (Badia and Marti 2003). Heterotrophic respiration may increase when microbial communities increase in population size within the bounds of the microbial carrying capacity. Pregitzer et al. (1995) also found that elevated CO_2 levels increased fine root growth and turnover. The mortality of fine roots provides fuel for microbial activity which may increase heterotrophic soil respiration rates (Pregitzer et al. 1995). In an intensively managed loblolly pine plantation in Bainbridge, Georgia, soil CO_2 efflux rates were not correlated with fine root biomass (Samuelson et al. 2004). However, Wiseman and Seiler (2004) and Gough et al. (2005) reported that soil CO_2 efflux rates in loblolly pine plantations in Virginia and South Carolina increased with root biomass and root biomass increased with stand age and proximity to trees.

CHAPTER 3. MATERIALS AND METHODS

3.1 Study Site

The study site is located at the Escambia Experimental Forest, seven miles south of Brewton, Alabama. The USDA-Forest Service maintains this ±1214 ha forest as an experimental study site primarily for natural longleaf pine management. It was established as an Experimental Forest on April 1, 1947 when the T.R. Miller Mill Company leased it without charge for 99 years to the USDA-Forest Service. The 16 ha study site, Compartment 135, was naturally regenerated in 1957-1958 by the shelterwood method. Seedlings from the 1957-1958 seed crop were released from the parent overstory in the winter of 1961. Since regeneration, the stand has been managed with prescribed fire approximately every three years and the last prescribed fire before this experiment began was conducted on January 9, 2007.

Compartment 135 is located in the lower Coastal Plain with the majority of soils of the Troup fine sand type with 0-5% slope. The taxonomic class for Troup fine sand is: loamy, kaolinitic, thermic Grossarenic Kandiodults. All experimental plots are in the Troup fine sand type. Minor soil types bordering Compartment 135 include the Orangburg (taxonomic class: fine-loamy, kaolinitic, thermic Typic Kandiudults) and Dothan (taxonomic class: fine-loamy, kaolinitic, thermic Plinthic Kandiudults).

The study site was established in 1967-1968 in order to examine the relationship between density and stand development. Three replicates (0.08 ha) of five densities includuing 741, 1483, 2224, 2965, and 3707 residual trees·ha^{-1}, were installed through precommercial thinning of seedlings. The average stand density across all plots in 1963 was 14 826 trees·ha^{-1}. Stand density was eventually reassigned from trees·ha^{-1} to basal area·ha^{-1} as trees grew, including residual basal area targets of 7, 14, 21, 28, and 34 m^2·ha^{-1}. Stand inventories were conducted at 2-year intervals through 1978, then in 1981 and 1985. Post 1985, stands were remeasured every five years. These 15 plots were part of a permanent plot Regional Longleaf Growth Study investigating growth and yield in pure, even-aged, longleaf pine stands relative to site, age, and stand density. Plot basal areas were maintained by low thinning and improvement cuts every five years if plot basal area growth exceeded the target basal area by 2 m^2·ha^{-1} (Farrar 1978).

The 15 study plots used for this study ranged in basal area from 7-36 m^2·ha^{-1}. Study plots were 0.04 ha in area and each plot was subdivided into 400 separate 1 m^2 subplots. During the 10 month study from January through October 2008, five different 1 m^2 subplots from each plot were sampled every month. Soil CO_2 efflux, soil temperature, soil moisture, downed woody debris, litter depth, litter mass, live, dead, fine and coarse root biomass, woody debris within the soil (consisting of residual coarse root biomass), soil charcoal mass, and percent ground cover were measured within each subplot. Total soil C and soil N were measured in January 2008.

3.2 Soil CO_2 Efflux Measurements

Soil CO_2 efflux rates were measured in a single location in each 1 m^2 subplot using an infrared gas analyzer (IRGA) (LICOR 6400, Li-Cor, Inc.; Lincoln, Nebraska USA) connected with a soil chamber head attachment (LICOR 6400-09 Soil CO_2 Flux Chamber). Polyvinyl chloride (PVC) soil collars, 10 cm in diameter, were installed into the ground the day prior to measurements in order to avoid the pulse of CO_2 immediately following installation of collars due to soil disturbance and injury to fine roots (Maier and Kress 2000; Law et al. 1999).

Instantaneous soil CO_2 efflux rates were measured monthly so that over the course of 10 months seasonal variations would be observed (Maier and Kress 2000). Measurements were taken before the peak of the diurnal cycle between the hours of 0900 and 1200. The concentration of CO_2 in the air at ground level was determined by placing the soil chamber on its side and monitoring the CO_2 concentration. This concentration was set as the ambient CO_2 concentration used in the efflux calculation. Soil CO_2 efflux rates were measured with the LICOR 6400 using a single measurement cycle set for a delta of 10 parts per million (ppm) above and below the ambient CO_2 concentration unless CO_2 rates were low. In the case when low soil CO_2 efflux rates were observed, a delta of 5 ppm was used. Low rates of soil CO_2 efflux at the Escambia Experimental Forest occurred during cool weather. The LICOR 6400 calculated the flux of CO_2 for the targeted ambient CO_2 level. Concurrent soil temperature measurements were taken adjacent the soil chamber head at a depth of 0-15 cm with a soil temperature probe connected to the IRGA.

3.3 Environmental Measurements

In order to estimate annual soil C efflux from the instantaneous soil CO_2 efflux measurements and soil temperature, soil temperature was continuously measured using HOBO thermocouples (U12) inserted to a depth of 15 cm and recorded using data loggers (U12-008) (Onset Computer Corporation, Pocasset, Massachusetts USA). Sensors were inserted into the soil in four cardinal directions 6.0 m from plot center in five plots selected to represent the range in basal area including 8, 16, 25, 30, and 32 $m^2 \cdot ha^{-1}$. Soil temperatures within the five measurement plots were averaged across plots because soil temperature was similar among varying basal areas. Mean hourly soil temperatures were used to estimate cumulative annual soil CO_2 efflux rates. Soil CO_2 efflux was modeled for each experimental plot from soil temperature using the equation $y = a*e^{(b*x)}$, where y is the soil CO_2 efflux (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) and x is soil temperature (ºC) (see Results). Soil moisture at a depth of 0-10 cm was measured immediately adjacent to soil respiration collars with a time domain reflectometry system (TDR Model 6050X1, Soil Moisture Equipment Corp., Santa Barbara, California USA; Trime-FM Probe P3 SN.:14323, IMKO Micromodultechnik, Ettlingen, Germany) concomitantly with soil respiration measurements.

A HOBO Weather Station (Onset Computer Corporation, Pocasset, Massachusetts USA) measured and recorded photosynthetically active radiation, precipitation, soil moisture, air temperature, relative humidity, wind speed, and wind direction every half hour. The weather station was located in the Escambia Experimental Forest near the USDA-Forest Service office.

3.4 Forest Characteristics

Current annual increment was calculated from diameter at breast height (DBH) (1.37 m) measurements on trees marked at DBH in January 2008 and February 2009. Longleaf pine aboveground biomass was estimated following Mitchell et al. (1999) using allometric equations to estimate stem and branch biomass and total aboveground biomass which included stem, branch, and foliage. Longleaf pine taproot and coarse root biomass for 1 m^2 around each tree was estimated according to Johnsen et al. (2004) using allometric equations for loblolly pine. The amount of C in all biomass was assumed to be 50% of the oven-dried biomass (Pearson et al. 2007). In addition, three site specific longleaf pine biomass equations were used to estimate stem and branch, foliage, and total aboveground biomass including stem, branch, and foliage, from Taras and Clark (1977), Baldwin and Saucier (1983), and Garbett (1977).

Litter depth and litter mass were measured inside the soil collar. Litter depth was measured by inserting a ruler into the litter matter down to the beginning of the soil profile after installation of the soil collar and approximately 24 hours prior to soil CO_2 efflux measurements in order to limit disturbance of CO_2 concentration within soil pore space. Litter was removed after soil CO_2 efflux measurements, placed in a paper bag and transported to the laboratory, where the mass was determined directly following drying in an oven at 75 ºC for at least 96 hours.

Coarse woody debris consisted of downed trees and downed branches. Cubic volume of downed coarse woody debris within subplots was estimated by measuring the mid-diameter and length of the log following Siitonen et al. (2000). The calculation is based on the volume of a cylinder. Decomposition estimation followed the three degrees of decay defined by Heath and Chojnacky (2001). The first class of decay assumed 90% of the oven-dried density of wood from a living tree of the same species, 0.66 g·cm^{-3} for longleaf pine (Brown et al. 1949). The second decay class allocated 70% of the oven dried density of longleaf pine to downed woody debris, and the third decay class allocated 40% of the oven dried density of longleaf pine to downed woody debris. Class I included new downed woody debris. Classes II and III included slightly decomposing and fully decomposed logs, respectively (Stewart et al. 1994).

Soil cores containing the soil horizon from 0-15 cm were removed directly underneath the soil CO_2 efflux measurements each month after completion of soil CO_2 efflux measurements. A cylindrical metal corer 10 cm in diameter by 60 cm in length was used to remove the soil cores. The soil cores were placed in a plastic bag and stored in a cooler during transportation. Samples were stored at 5 ºC to minimize desiccation of live fine roots. Soil was then hand sifted in the laboratory through a No. 10 sieve (2 mm opening) (U.S.A. Standard Testing Sieve, Fisher Scientific Company, Pittsburgh, Pennsylvania USA) and the remaining components were washed, divided into one of the four root categories including live fine (≤ 2 mm), dead fine (≤ 2 mm), live coarse (> 2 mm), and dead coarse (> 2 mm) root biomass. Soil woody debris biomass and soil charcoal biomass were also measured. All biomass components within the soil were oven-dried at 75 ºC until reaching a constant mass. The amount of C in charcoal was assumed to be 80% of the oven-dried charcoal mass (Forbes et al. 2006). January soil samples were used to estimate soil C concentration to a 15 cm depth assuming a bulk density of 1.41 g·cm^{-3} which was measured in the A-horizon in a Troup soil series at the Escambia Experimental Forest by Kush et al. (2004). Total soil C and N concentrations were analyzed in the Soil Testing Laboratory at Auburn University by elemental combustion analysis at approximately 950 ºC in pure oxygen.

On a monthly basis, ground cover was estimated ocularly and included all herbaceous plants and woody stems less than 2.54 cm in DBH within each 1 m^2 subplot. Species with a DBH greater than or equal to 2.54 cm were recorded to estimate basal area ingrowth. To describe the vegetation in the understory in more detail and to examine relationships between soil CO_2 efflux and cover type, in July 2008, woody vegetation less than breast height was identified by genus and counted. Ground cover was sorted into grasses, herbs, vines, woody plants and poison-oak (*Toxicodendron toxicarium* (Salisb.) Gillis.) due to its frequent occurrence. Nomenclature followed Godfrey (1988).

3.5 Statistical Analysis

The experimental unit was the 0.04 ha plot. Subplot values were averaged by plot and relationships between soil respiration and basal area, current annual increment, soil temperature, soil moisture, aboveground biomass, belowground biomass, litter depth, litter mass and ground cover were explored using stepwise regression analyses, linear regression, and nonlinear regression. All analyses were conducted at the 0.10 level of significance. Residual analyses and tests for normality were performed on regression analyses. Natural log-transformations provided the best outcome when transformations were required. Statistical procedures were performed with SAS (Statistical Analysis Program) version 9.1 (SAS 2003).

CHAPTER 4. RESULTS

4.1 Climate

The 50-year mean annual precipitation for Brewton, Alabama is 1648 mm, with a 50-year average minimum of 89 mm in October and a 50-year average maximum of 176 mm in July (data from National Oceanic and Atmospheric Administration) (Figure 4.1.1). During the experiment, annual precipitation at the EEF was 1292 mm, with a minimum of 16 mm in September and a maximum of 239 mm in July (Figure 4.1.1). The 50-year average minimum and maximum temperatures at Brewton, Alabama were 8.4 ºC and 27.1 ºC, respectively, and the 24 hour mean was 18.4 ºC (Figure 4.1.1). The mean annual minimum and maximum temperatures were 13.3 ºC and 24.2 ºC, respectively, during 2008 at the EEF and the annual mean temperature for 2008 was 19.6 ºC.

4.2 Forest Structure and Forest Characteristics

Stand structure was described by basal area, quadratic mean diameter, current annual increment, ingrowth, mortality, and standing snags (Table 4.2.1). Basal area ranged from 7-36 $m^2 \cdot ha^{-1}$ and quadratic mean diameter was between 18.0-41.7 cm. Longleaf pine density ranged from 49-1334 $trees \cdot ha^{-1}$ (Table 4.2.1). In general, density, current annual increment, mortality, and snag density were higher in plots with higher basal area. Ingrowth was small and was observed in only three plots.

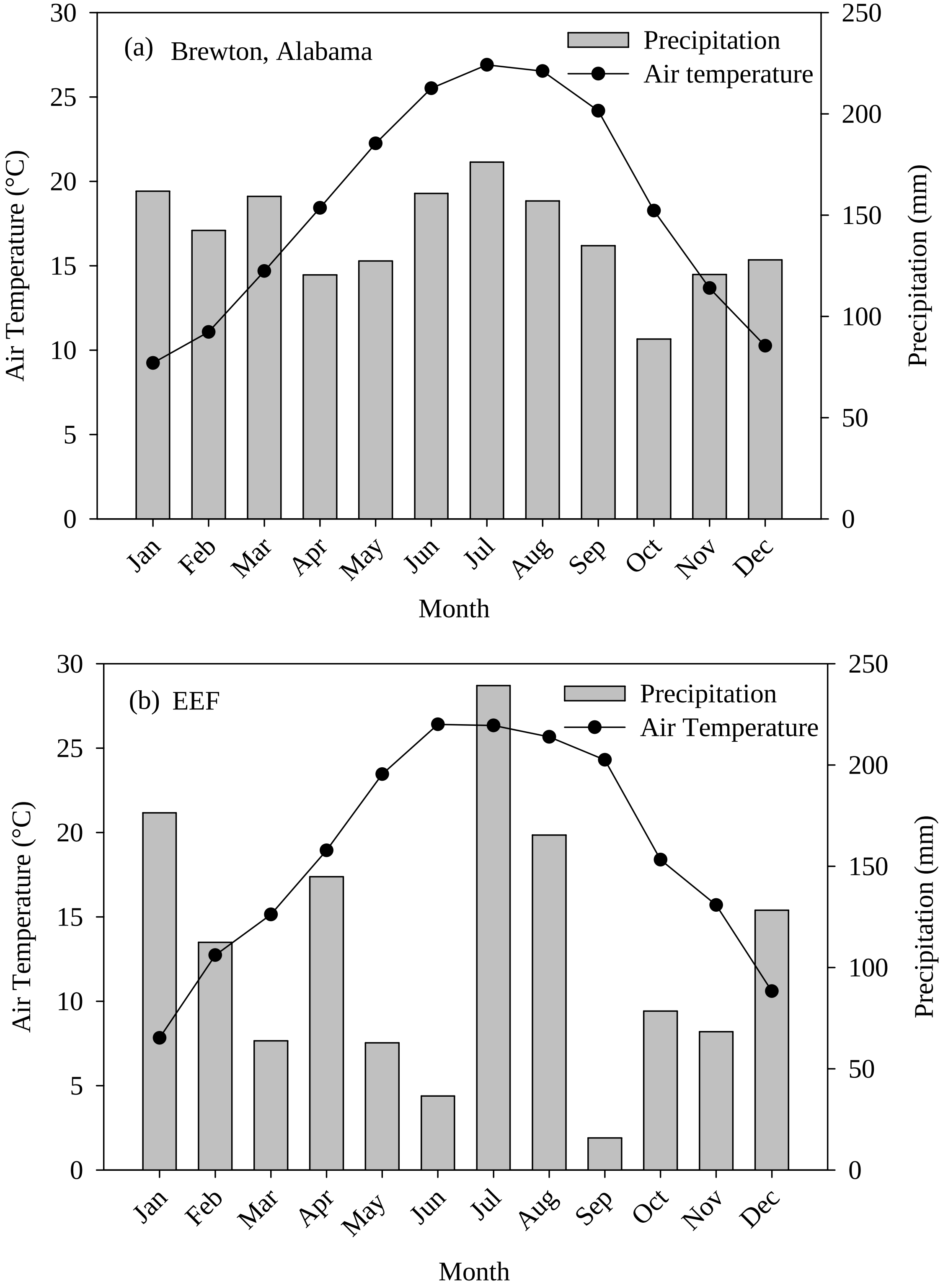

Figure 4.1.1. The 50-year mean monthly 24 hour temperature and monthly precipitation for Brewton, Alabama (NOAA data) (a) and monthly mean 24 hour temperature and monthly precipitation during 2008 measured at the Escambia Experimental Forest (EEF) (b).

Table 4.2.1. Stand characteristics for each 50-year-old longleaf pine measurement plot on the Escambia Experimental Forest in 2008. Ingrowth was defined as longleaf pine or hardwood trees that obtained a DBH of 2.54 cm over 2008.

Plot No.	**Basal Area** ($m^2 \cdot ha^{-1}$)	**Quadratic Mean Diameter** (cm)	**Density** ($trees \cdot ha^{-1}$)	**Current Annual Increment** ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	**Longleaf Ingrowth** ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	**Hardwood Ingrowth** ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	**Mortality** ($trees \cdot ha^{-1} \cdot yr^{-1}$)	**Snags** ($trees \cdot ha^{-1}$)
189	7	41.7	49	0.1	0.1	0.2	0	0
186	8	31.5	99	0.2	0.0	0.0	0	0
190	13	36.3	124	0.4	0.1	0.1	0	0
188	14	37.3	124	0.2	0.1	0.1	0	0
184	15	24.6	321	0.1	0.0	0.0	0	25
182	16	26.2	297	0.4	0.0	0.0	0	0
185	18	30.5	247	0.5	0.0	0.0	0	49
187	18	31.8	222	0.4	0.0	0.0	0	0
179	23	24.9	445	0.6	0.0	0.0	25	74
183	25	25.1	494	0.6	0.0	0.0	0	0
176	29	20.3	865	0.8	0.0	0.0	25	74
180	30	22.4	766	0.6	0.0	0.0	0	0
181	31	24.9	618	0.9	0.0	0.0	25	49
177	32	18.0	1186	0.8	0.0	0.0	49	74
178	36	18.3	1334	0.7	0.0	0.0	49	148

Additional ecosystem variables that were measured to describe forest characteristics included ground cover, shrub biodiversity, litter depth and mass, root biomass, and soil characteristics. Ground cover was generally higher during the growing season and varied from 9 to 93% (Figure 4.2.1). Tables describing the July 2008 understory vegetation by component of ground cover, species richness and Shannon-Weaver diversity index for woody plants, and a species count for woody species are included in the Appendix. The forest floor was described not only by cover but by litter mass which ranged from 1.9-29.4 $\mathrm{Mg{\cdot}ha^{-1}}$ and litter depth which varied from 7-22 mm (Figure 4.2.1). Downed woody debris ranged from 0.0-45.7 $\mathrm{Mg{\cdot}ha^{-1}}$ and soil woody debris was between 0.2-5.5 $\mathrm{Mg{\cdot}ha^{-1}}$ (Figure 4.2.2). Soil charcoal was from 0.02-2.5 $\mathrm{Mg{\cdot}ha^{-1}}$ (Figure 4.2.2). Soil N concentration varied from 0.48 to 0.99 $\mathrm{mg{\cdot}g^{-1}}$ and soil C concentration ranged from 5.39 to 14.32 $\mathrm{mg{\cdot}g^{-1}}$ (Table 4.2.2). In general, no seasonal trends in live fine and coarse root biomass and dead fine and coarse root biomass were observed (Figure 4.2.3).

Relationships between forest characteristics and basal area were examined in order to determine how basal area influenced forest characteristics. Ground cover was significantly and negatively related to basal area (Figure 4.2.4; Table 4.2.3). The arcsine transformation of ground cover did not improve the relationship between basal area and cover therefore the arcsine transformation was not used. Litter mass, litter depth, downed woody debris, and soil woody debris were significantly and positively related to basal area (Figures 4.2.4 and 4.2.5; Table 4.2.3). The wide range in downed woody debris in Figure 4.2.5 is a result of a few large, downed trees in the measurement plots. Frequent prescribed fires in these 50-year-old longleaf pine stands reduced downed woody debris to minimal amounts. Soil charcoal, live fine and coarse root biomass and dead fine and coarse root biomass, total root biomass, soil N, and soil C were not significantly related to basal area (Figures 4.2.5, 4.2.6, 4.2.7, and 4.2.8; Table 4.2.3). Vine and grass cover measured in July was significantly related to basal area (Figure 4.2.9; Table 4.2.3).

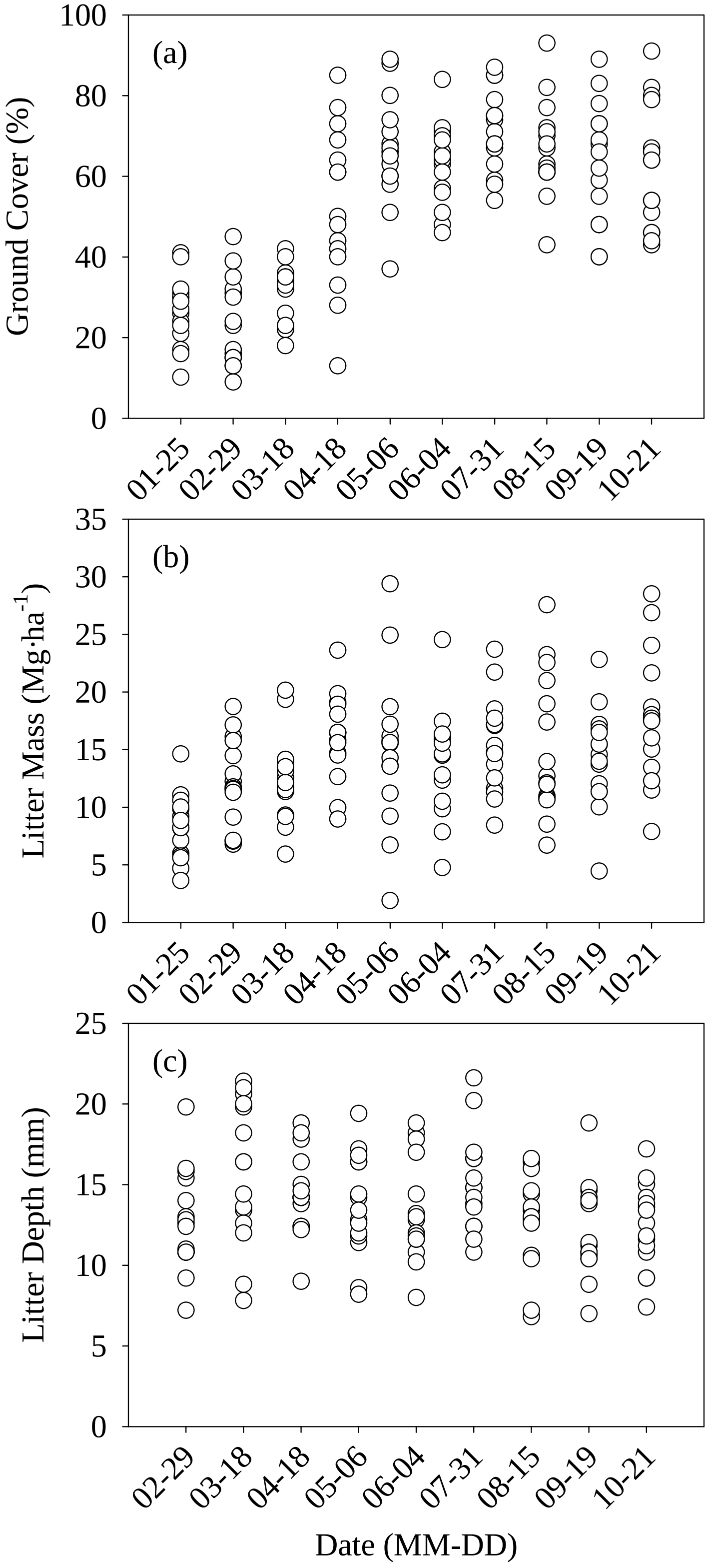

Figure 4.2.1. Total ground cover (a), litter mass (b), and litter depth (c) versus sampling date in 2008 in 50-year-old longleaf pine stands varying in basal area. Each data point represents a plot average of five subplots.

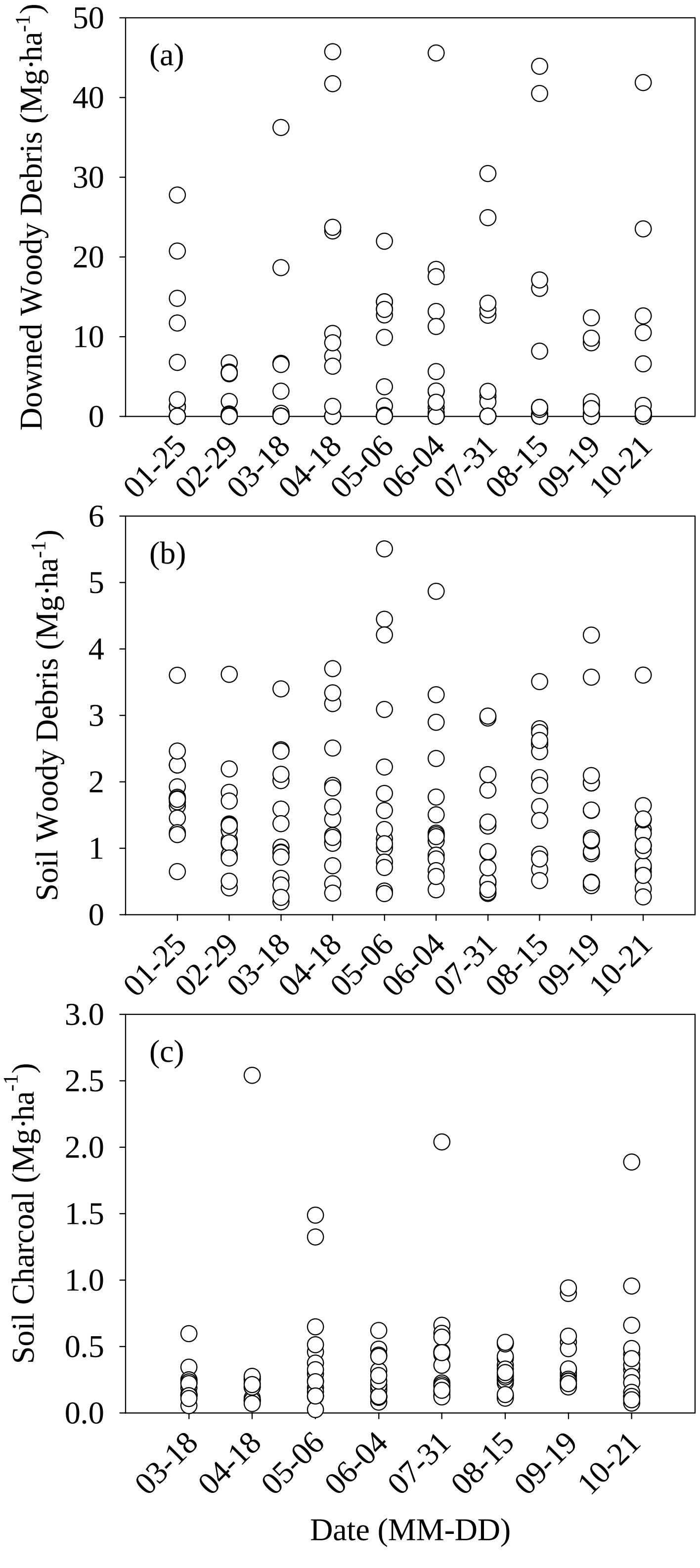

Figure 4.2.2. Downed woody debris (a), soil woody debris (b), and soil charcoal (c) versus sampling date in 2008 in 50-year-old longleaf pine stands varying in basal area. Each data point represents a plot average of five subplots.

Table 4.2.2. Soil nitrogen (N) and carbon (C) concentration measured in January 2008 in longleaf pine stands varying in basal area.

Plot No.	**Basal Area** ($m^2 \cdot ha^{-1}$)	**Soil N** ($mg \cdot g^{-1}$)	**Soil C** ($mg \cdot g^{-1}$)
189	7	0.65	11.55
186	8	0.73	8.51
190	13	0.58	9.34
188	14	0.56	5.39
184	15	0.73	14.32
182	16	0.99	11.17
185	18	0.74	11.74
187	18	0.62	7.47
179	23	0.57	11.37
183	25	0.81	10.77
176	29	0.59	11.97
180	30	0.56	8.73
181	31	0.60	11.26
177	32	0.48	8.22
178	36	0.50	7.24

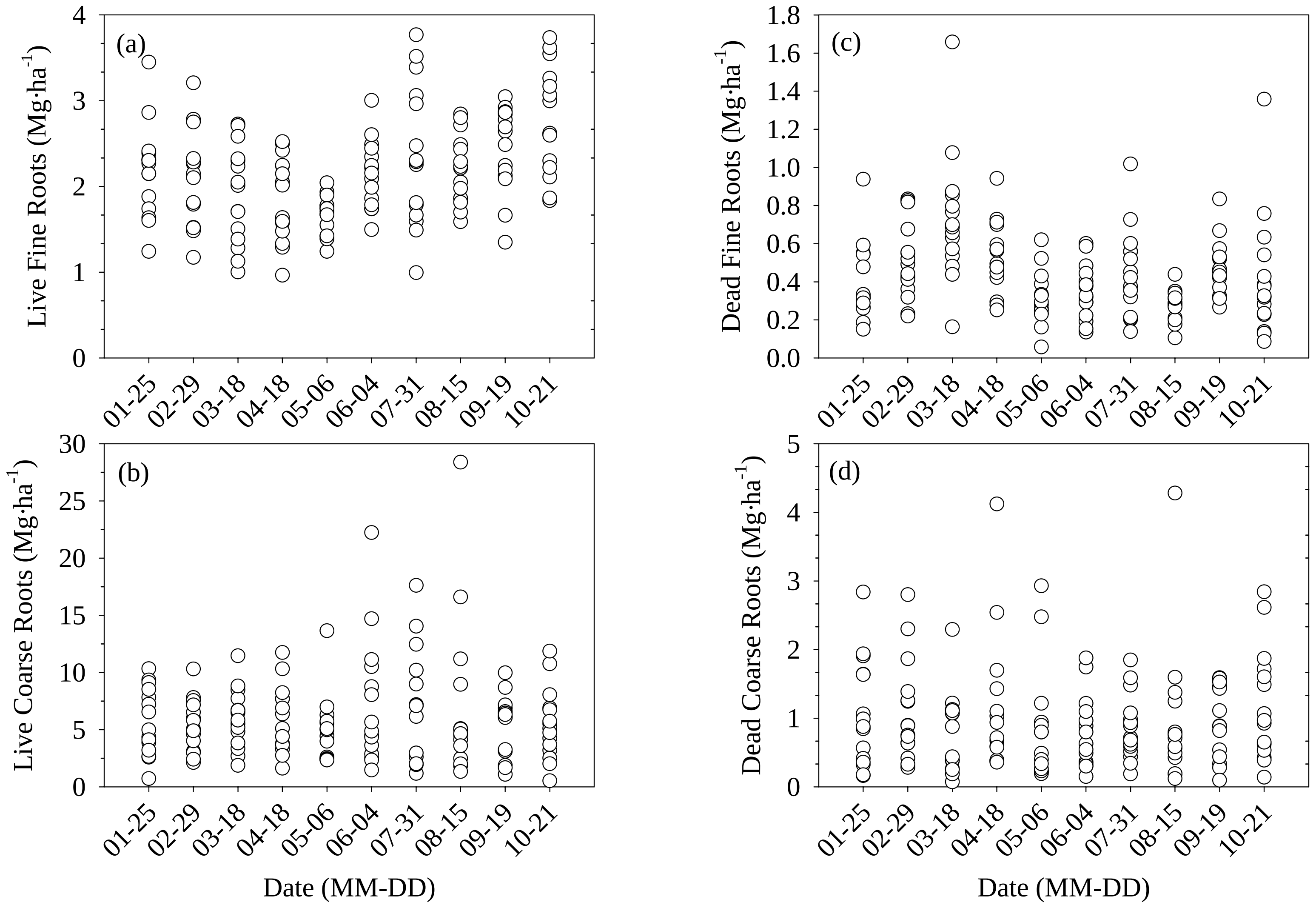

Figure 4.2.3. Live fine (a), live coarse (b), dead fine (c), and dead coarse (d) root mass versus sampling date in 2008 in 50-year-old longleaf pine stands varying in basal area. Each data point represents a plot average of five subplots.

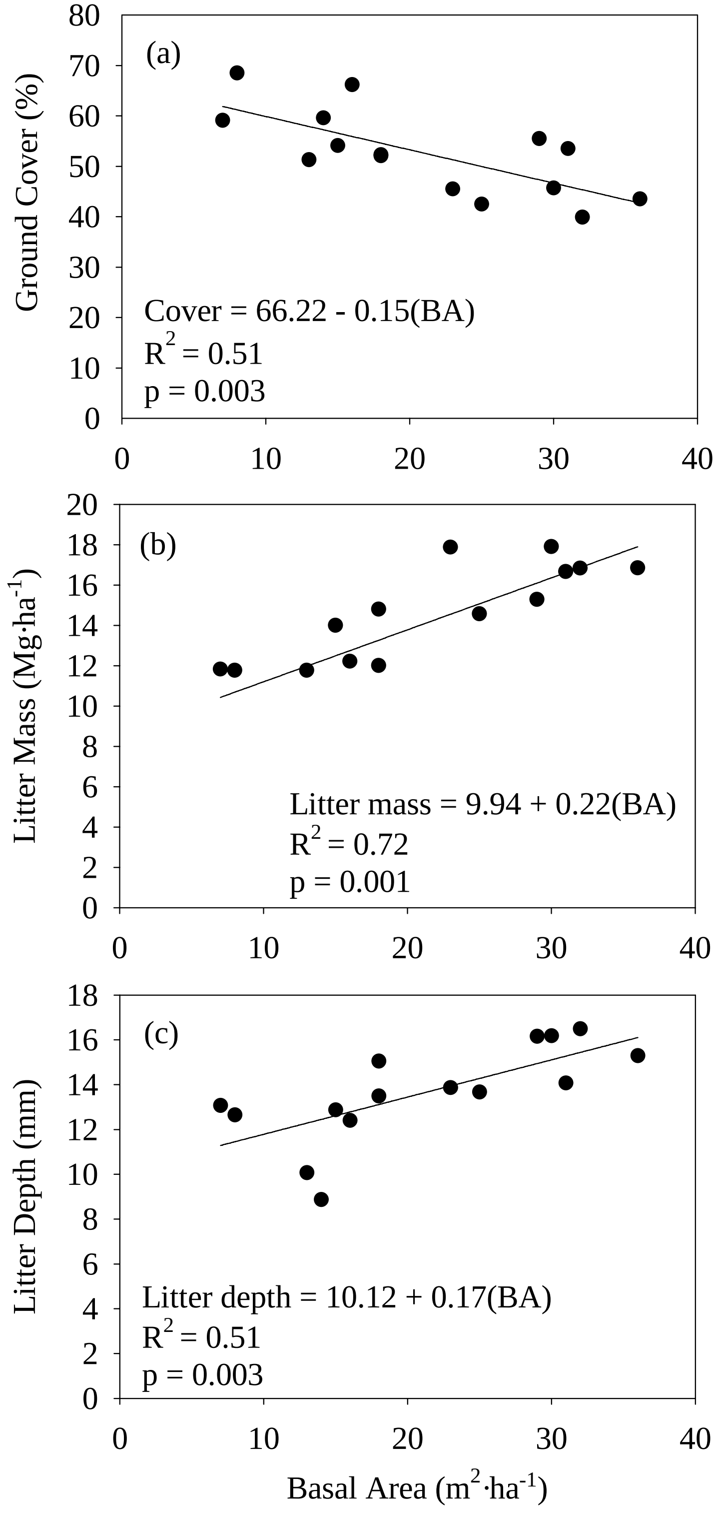

Figure 4.2.4. Total ground cover (a), litter mass (b), and litter depth (c) versus basal area in 50-year-old longleaf pine stands. Each data point represents a plot average across measurements conducted from January through October 2008. Regression equations were included when $p<0.100$.

Table 4.2.3. Observed probability values for significant linear relationships between basal area or annual carbon (C) efflux versus soil CO_2 efflux, forest characteristic variables, and environmental variables in 50-year-old longleaf pine stands.

Source	**Basal Area**	**Annual C Efflux**
Soil CO_2 efflux	0.045	0.077
Soil temperature	0.912	0.345
Air temperature	0.711	0.626
Soil moisture	0.209	0.010
Live fine root biomass	0.991	0.246
Live coarse root biomass	0.126	0.455
Dead fine root biomass	0.678	0.143
Dead coarse root biomass	0.677	0.032
Soil woody debris	<0.001	0.299
Soil charcoal	0.195	0.936
Soil N	0.167	0.564
Soil C	0.695	0.103
Downed woody debris	0.006	0.121
Cover	0.003	0.187
Litter mass	0.001	0.687
Litter depth	0.003	0.015
Aboveground biomass	<0.001	0.064
Belowground biomass	<0.001	0.064
Total biomass	<0.001	0.064
Basal area	-	0.062
Current annual increment	<0.001	0.048
Density	<0.001	0.088
Quadratic mean diameter	<0.001	0.016
Grass	0.007	0.004
Vine	0.015	0.750
Herb	0.512	0.089
Poison-oak	0.369	0.072
Richness	0.111	0.641
Shannon-Weaver diversity index	0.846	0.563

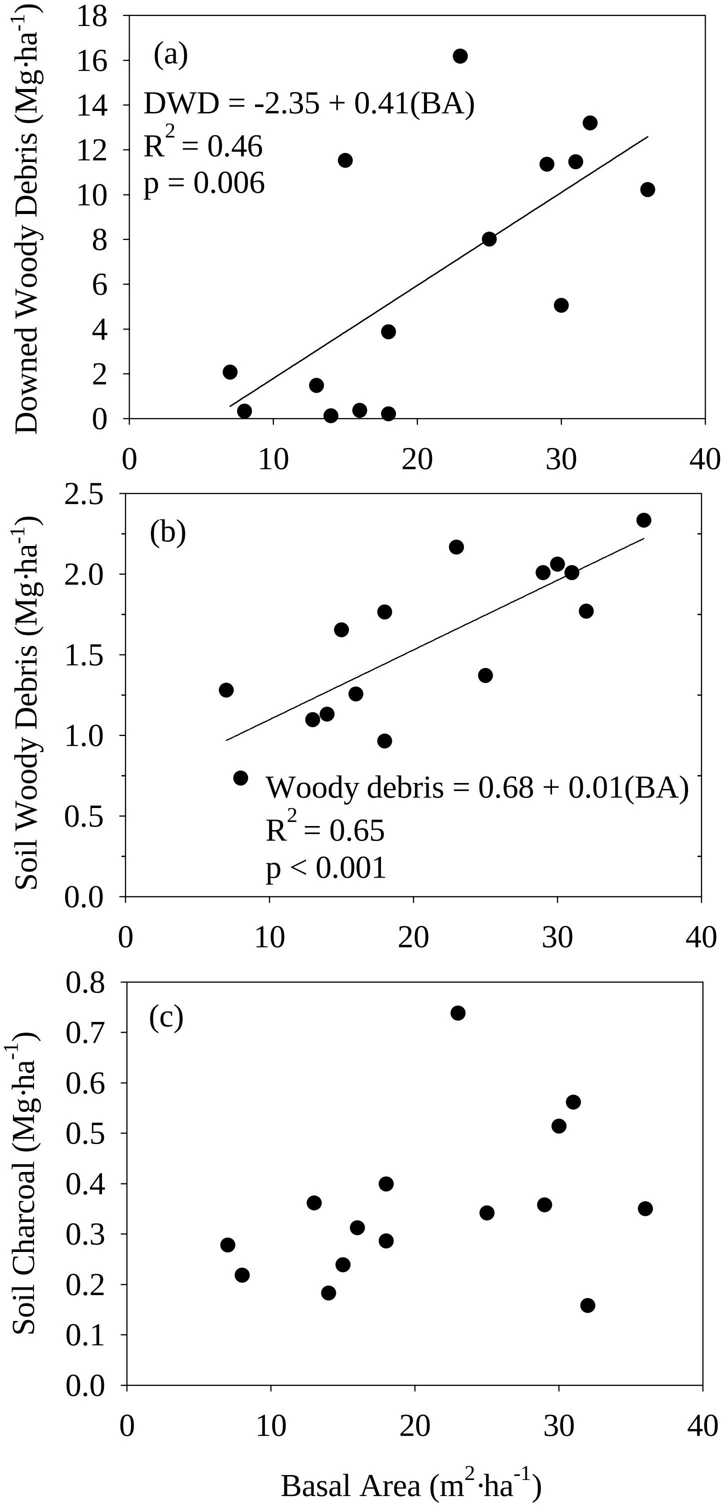

Figure 4.2.5. Downed woody debris (a), soil woody debris (b), and soil charcoal (c) versus basal area in 50-year-old longleaf pine stands. Each data point represents a plot average across measurements conducted from January through October 2008. Regression equations were included when $p<0.100$.

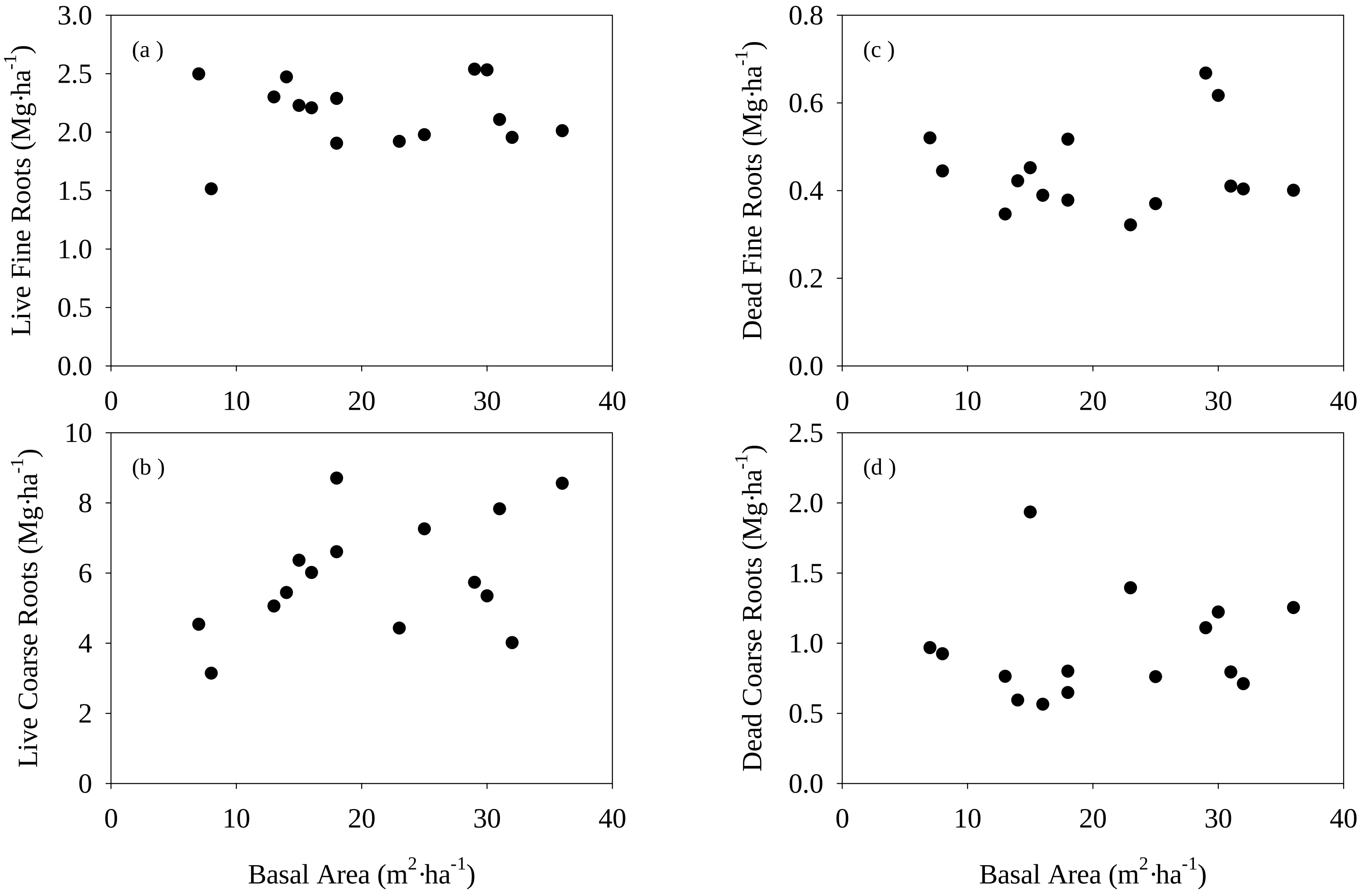

Figure 4.2.6. Live fine (a), live coarse (b), dead fine (c), and dead coarse (d) root mass versus basal area in 50-year-old longleaf pine stands to a 15 cm soil depth. Each data point represents a plot average across measurements conducted from January through October 2008. Regression equations were included when $p<0.100$.

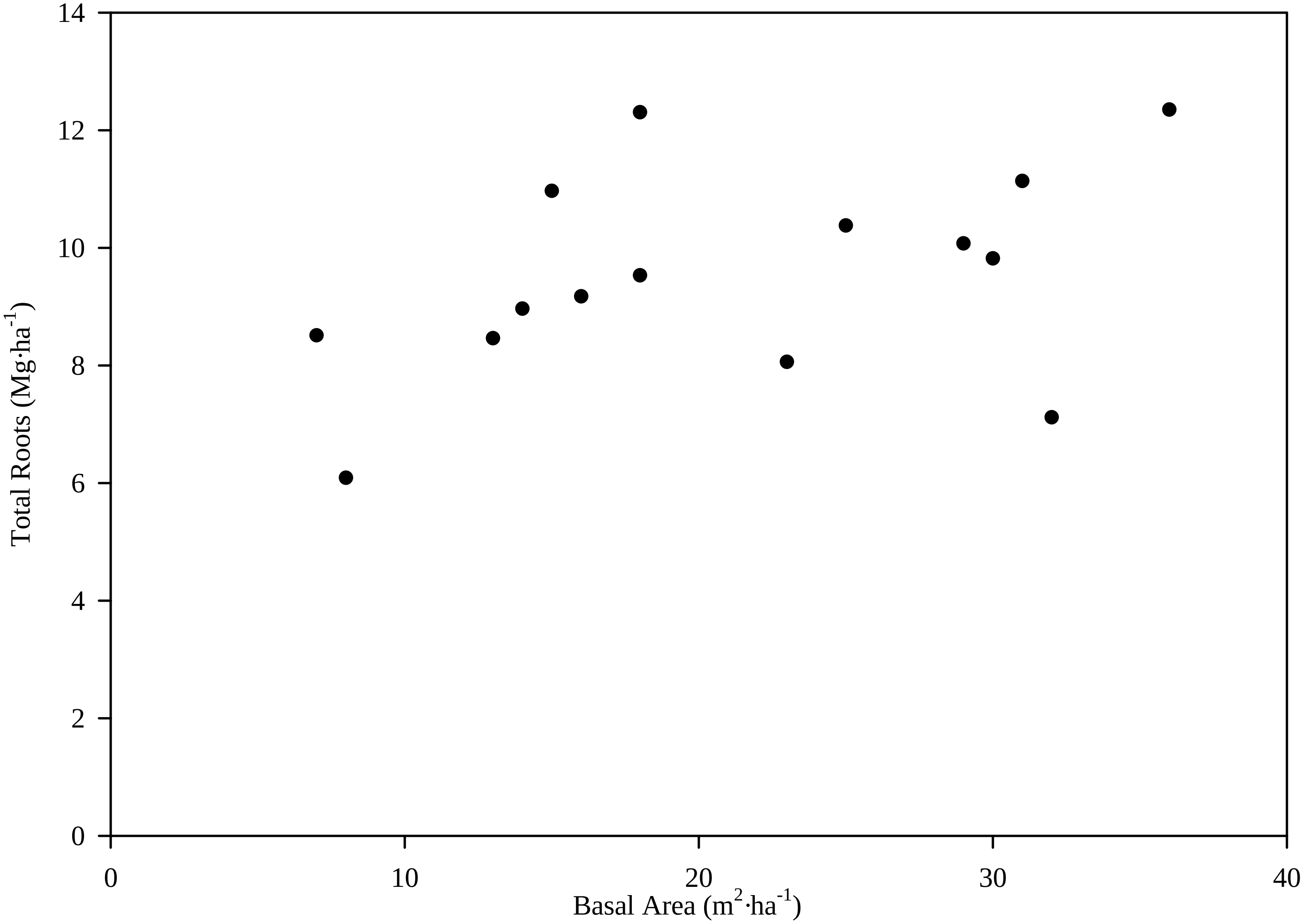

Figure 4.2.7. Live fine and coarse root biomass and dead fine and coarse root biomass to a 15 cm soil depth versus basal area in 50-year-old longleaf pine stands. Each data point represents a plot average across measurements conducted from January through October 2008. Regression equations were included when $p<0.100$.

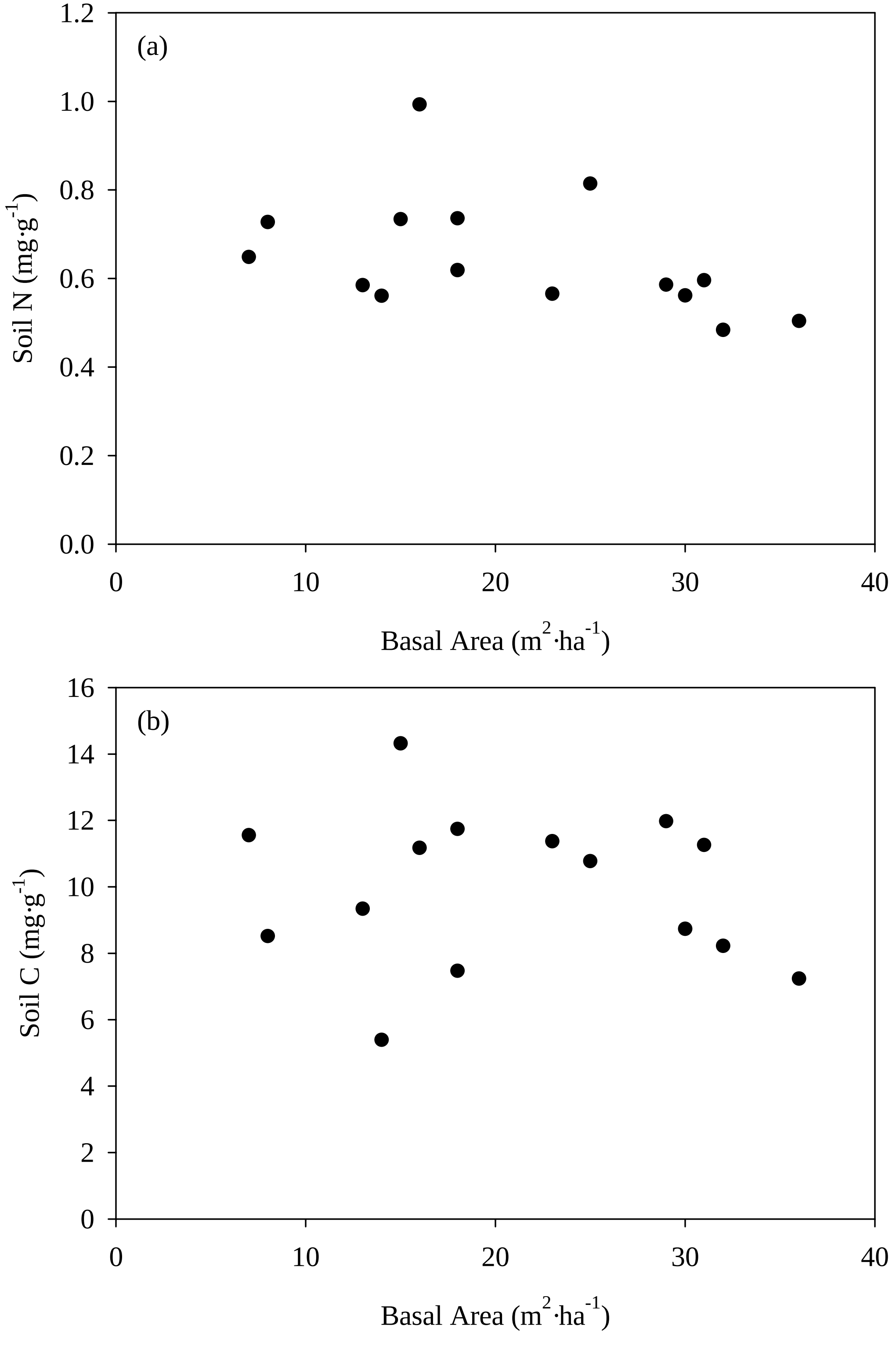

Figure 4.2.8. Soil nitrogen concentration (N) (a) and soil carbon concentration (C) (b) versus basal area in 50-year-old longleaf pine stands. Each data point represents a plot average measured in January 2008.

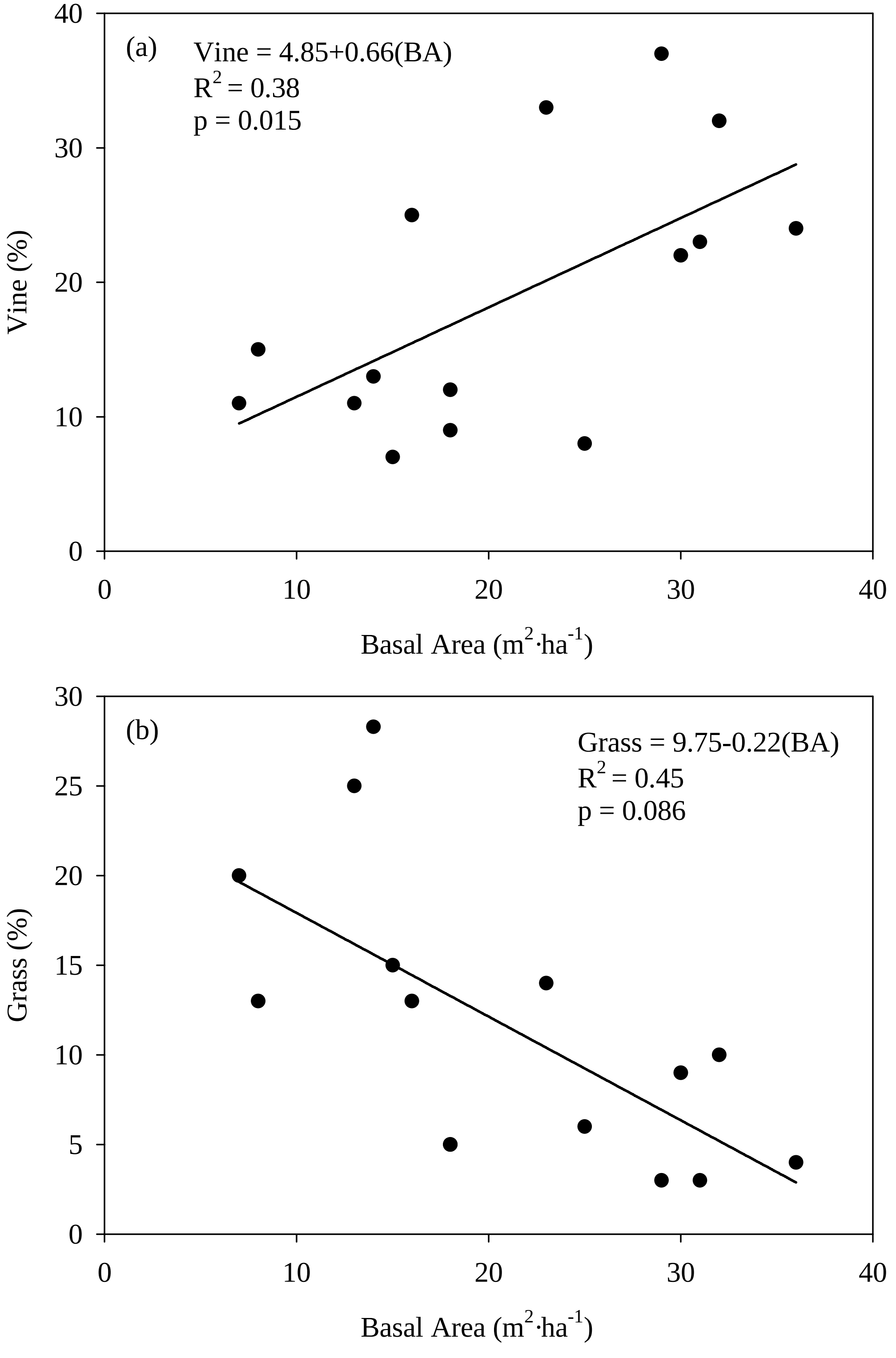

Figure 4.2.9. Ground cover in vines (a) and grasses (b) versus basal area in 50-year-old longleaf pine stands. Each data point represents an average measured in July 2008. Regression equations were included when $p<0.100$.

4.3 Soil CO_2 Efflux

Soil CO_2 efflux ranged from 0.9-8.8 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ and tracked seasonal changes in soil temperature (Figure 4.3.1). Soil temperature ranged from 8.0-26.9º C and soil moisture content ranged from 1.8-16.6 % (Figure 4.3.1). Soil CO_2 efflux increased exponentially with increasing soil temperature and soil temperature explained 96% of the variation in soil CO_2 efflux (Figure 4.3.2). The Q_{10} was 2.7, defined as the change in soil CO_2 efflux with a 10º C change in soil temperature and was calculated using the equation $y=0.4723*e^{(0.0995*x)}$, where y is soil CO_2 efflux and x is soil temperature.

Averaged across all measurement dates, soil CO_2 efflux was significantly and positively related to basal area and basal area explained 29% of the variation in soil CO_2 efflux (Figure 4.3.3). However, averaged across measurement dates, soil temperature was not significantly related to basal area (Figure 4.3.3; Table 4.2.3). In addition, soil moisture averaged across dates was not related to basal area (Figure 4.3.3; Table 4.2.3).

The relationship between air temperature, continuously measured at the Escambia Experimental Forest, and soil temperature, continuously measured in five plots, was examined to determine if air temperature could be used to model soil CO_2 efflux since air temperature is most often measured at weather stations. Soil temperature was measured to a 15 cm depth continuously at four locations in five plots with varying basal areas and data were averaged across the five plots. Air temperature was measured continuously to a 3 m height in one location. Soil temperature and air temperature measured at the Escambia Experimental Forest were similar and air temperature explained 88% of the variation in soil temperature (Figure 4.3.4).

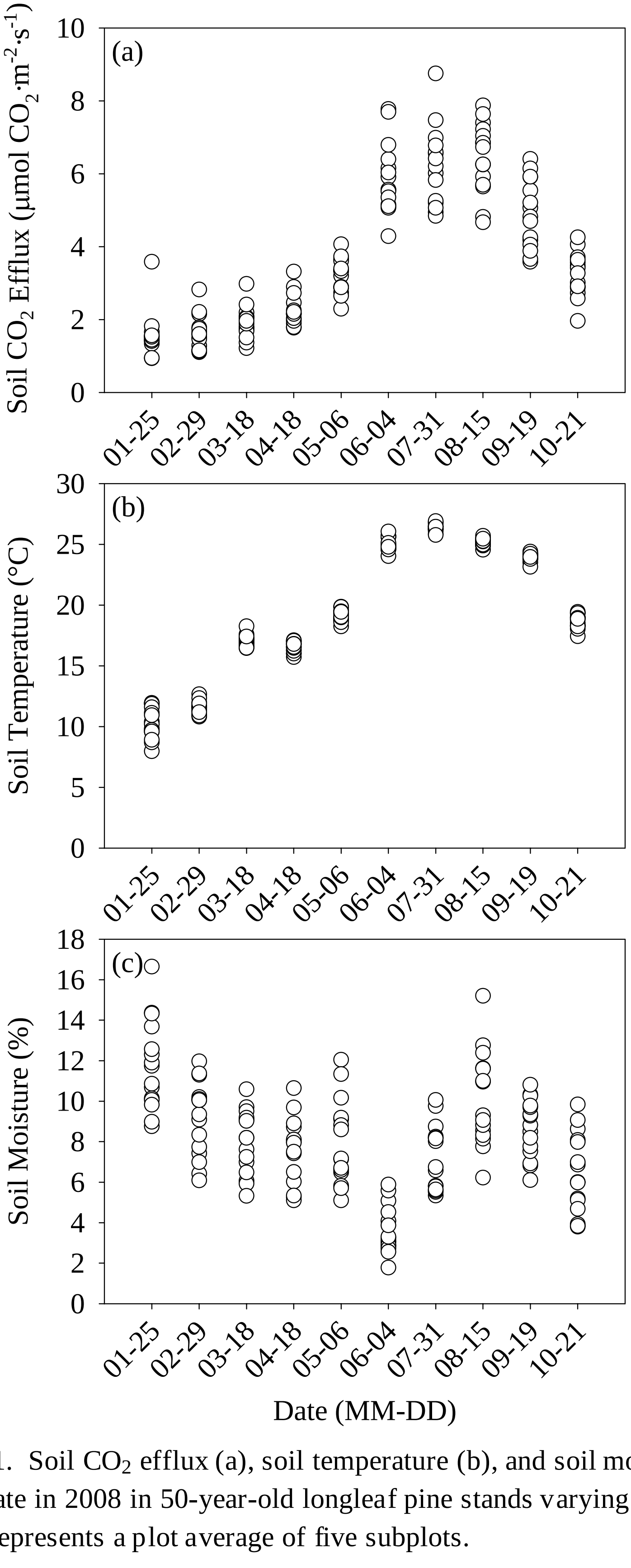

Figure 4.3.1. Soil CO_2 efflux (a), soil temperature (b), and soil moisture (c) versus sampling date in 2008 in 50-year-old longleaf pine stands varying in basal area. Each data point represents a plot average of five subplots.

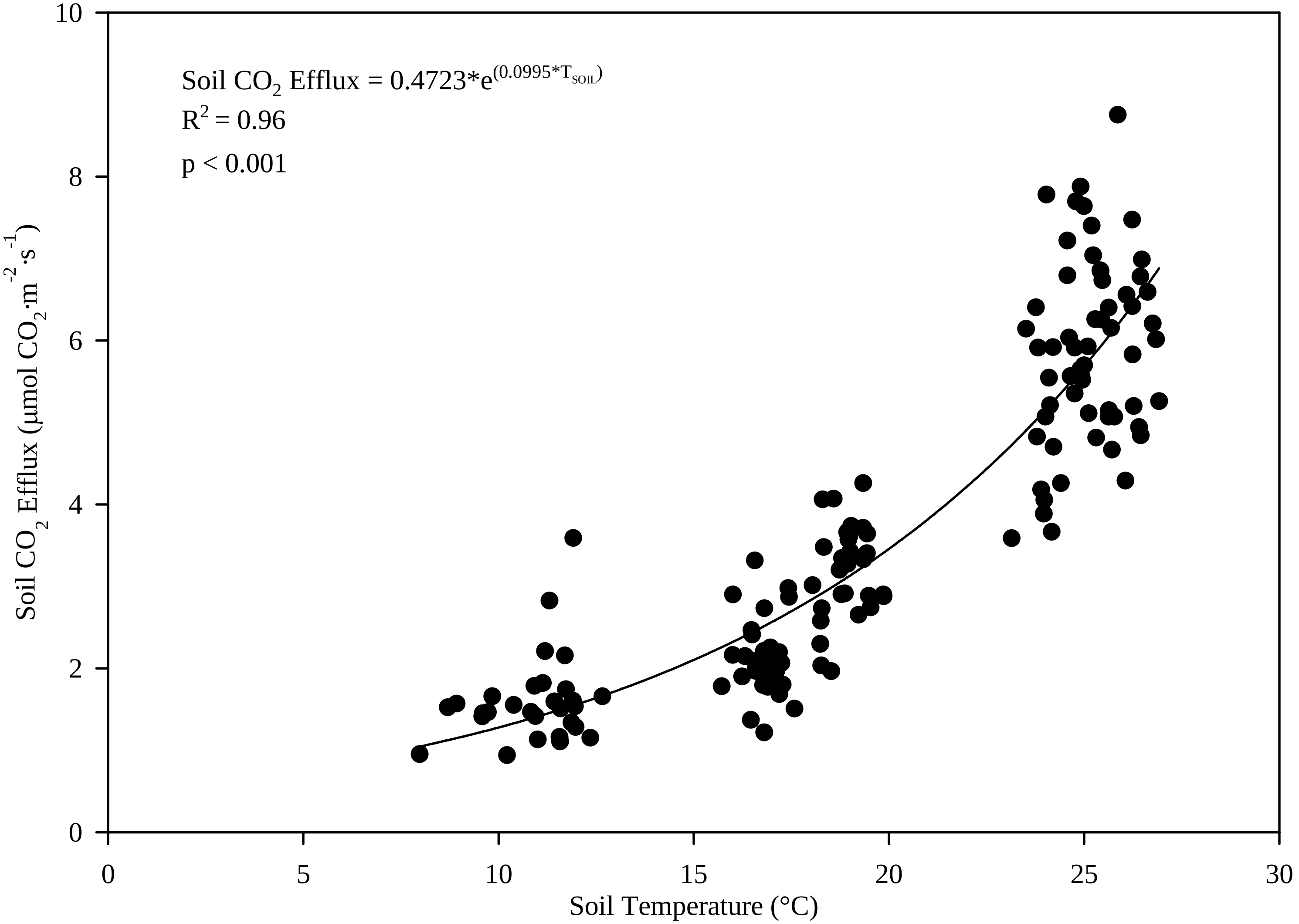

Figure 4.3.2. Soil CO_2 efflux versus soil temperature in 50-year-old longleaf pine stands varying in basal area at the Escambia Experimental Forest in 2008. Each data point represents an average of five subplots.

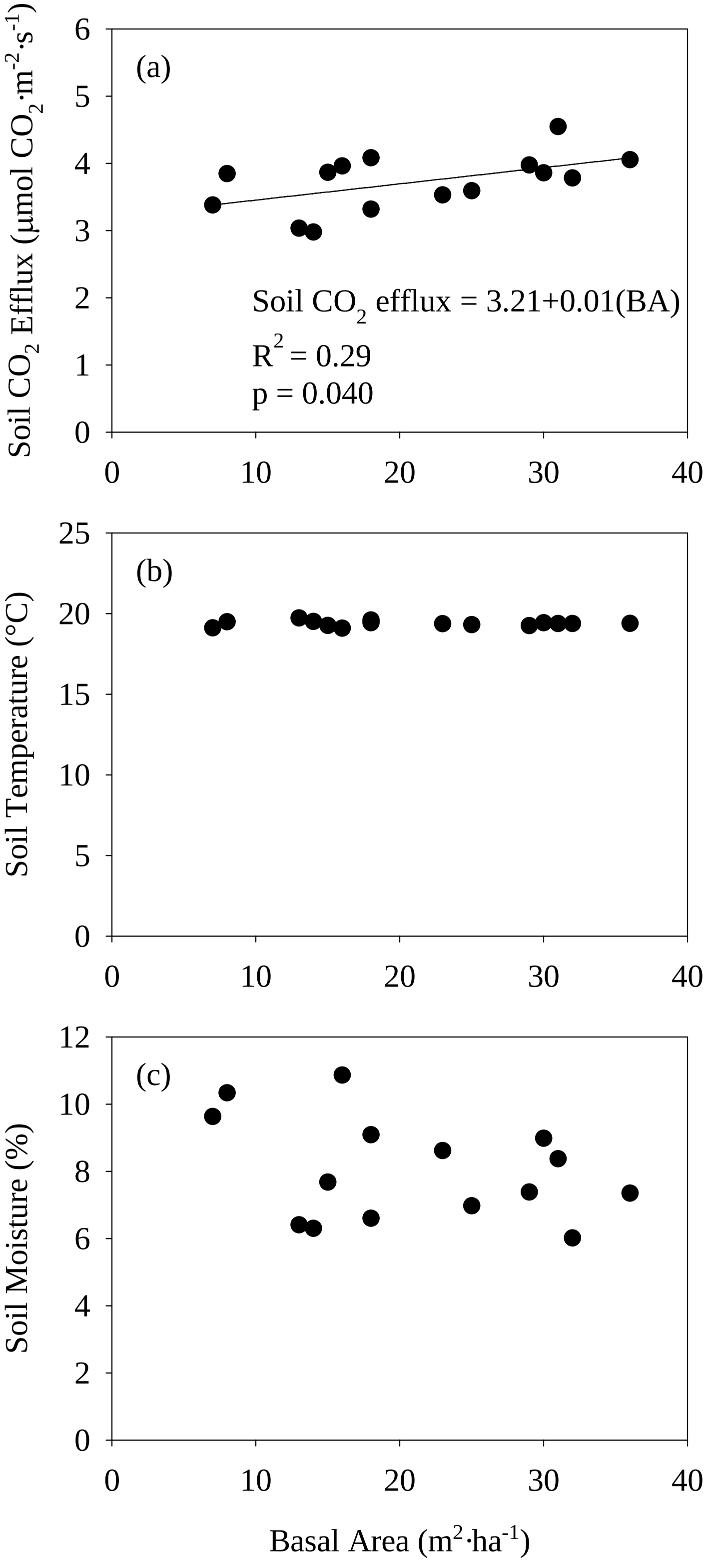

Figure 4.3.3. Soil CO_2 efflux (a), soil temperature (b), and soil moisture (c) versus basal area (BA) in 50-year-old longleaf pine stands. Each data point represents a plot average across measurements conducted from January through October 2008. Regression equations were included when $p<0.100$.

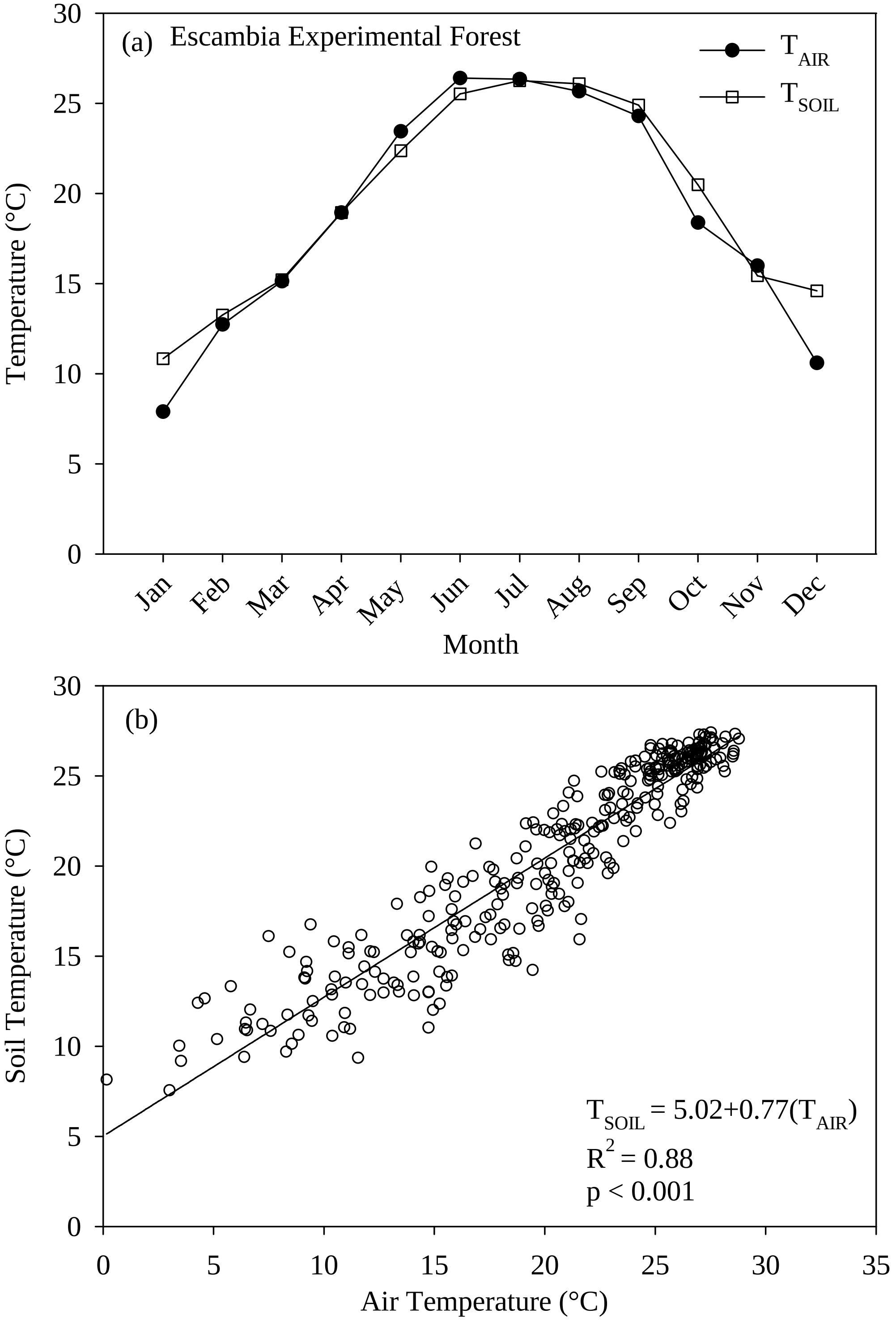

Figure 4.3.4. Monthly average soil temperature and air temperature versus month (a) and soil temperature versus air temperature (b) in 50-year-old longleaf pine stands. Averaged over the five locations, soil temperature was measured to 15 cm continuously at four locations in five plots with varying basal areas. Air temperature was measured continuously to a 3 m height in one location. Regression equations were included when $p<0.100$.

Stepwise regression analysis was used to determine which environmental and forest characteristic variables were related to soil CO_2 efflux. Because of the potential for seasonal hysteresis in the relationship between soil CO_2 efflux and soil temperature, and because factors covarying with soil temperature may vary with seasonality and plant phenology, stepwise regression analysis was separated into two time periods. The first modeling time period began in March and continued to the end of July (March-July period, N=75) and the second modeling period began in August and continued through the completion of the study in October (August-October period, N=45). Soil temperatures were similar between sampling dates, but there was no obvious seasonal hysteresis loop as defined by Kopfova (2006) because soil CO_2 efflux rates were similar for a given temperature across seasons (Figure 4.3.5). However, physiological processes such as flushing, xylem production, and leaf area development may differ over the year and may influence the relationship between soil CO_2 efflux and soil temperature differently in Spring versus Fall. Therefore, stepwise regression was used to determine if there were other predictor variables for soil CO_2 efflux during the two modeling periods.

Stepwise regression analyses for soil CO_2 efflux measured in March-July indicated that soil temperature explained the majority of variation (83%) in soil CO_2 efflux, while litter mass, ground cover, natural log-transformed live coarse root biomass, downed woody debris C, and natural log-transformed soil charcoal were significant variables in the model but explained only a minor amount of the variation (1-2%) in soil CO_2 efflux (Table 4.3.1). In July, the combined effect of litter mass and poison-oak explained the most variation in soil CO_2 efflux (37% and 30%, respectively) (Table 4.3.1). Other significant variables included natural log-transformed live coarse roots, which explained 10% of the variation in soil CO_2 efflux in July, and natural log-transformed soil charcoal, which explained 7% of July's variation in soil CO_2 efflux (Table 4.3.1). Natural log-transformations improved residual plots. During August-October, soil temperature explained 64% of the variation in soil CO_2 efflux and litter depth, ground cover, and soil moisture were significant predictor variables in the model but explained only 2-11% of the variation in soil CO_2 efflux (Table 4.3.1).

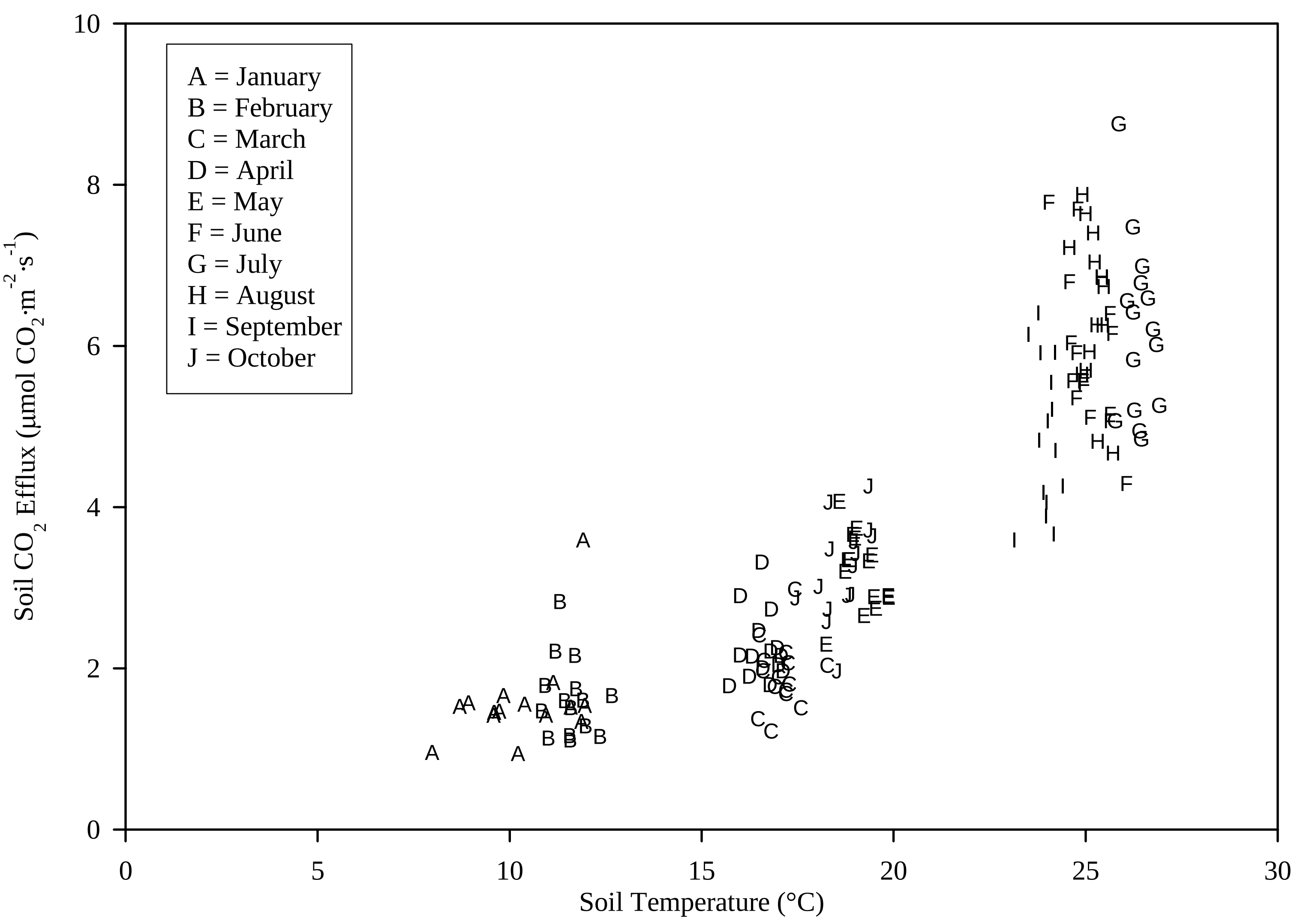

Figure 4.3.5. Soil CO$_2$ efflux versus soil temperature over 10 months with each month differentiated by different letters for 50-year-old longleaf pine stands.

Table 4.3.1. Stepwise regression analysis for significant relationships between monthly soil CO_2 efflux or annual soil C efflux and forest characteristic variables by sampling period.

Sampling Period	**Parameter**	**Parameter Estimate**	**Partial R^2**	**F-value**	**P>F**
March-July	Soil temperature	0.4075	0.83	279.19	<0.001
	Litter mass	0.0467	0.02	5.64	0.009
	Ground cover	0.0139	0.01	6.68	0.085
	Log(Live coarse roots)	0.2681	0.01	3.71	0.093
	Downed woody debris C	0.0382	0.01	5.28	0.069
	Log(Soil charcoal)	-0.2374	0.01	4.01	0.049
July	Litter mass	0.1903	0.37	7.98	0.017
	Poison-oak	0.1155	0.30	6.8	0.007
	Log(Live coarse roots)	-0.5756	0.10	2.54	0.049
	Log(Soil charcoal)	0.4015	0.07	1.14	0.065
August-October	Soil temperature	0.3643	0.64	68.00	<0.001
	Litter depth	0.2197	0.11	28.31	<0.001
	Ground cover	0.0196	0.05	4.91	0.003
	Soil moisture	0.1177	0.02	4.46	0.041
Annual soil C efflux	Log(Soil charcoal)	11.8213	0.17	68.58	0.046
	Litter depth	0.7457	0.14	64.19	0.041
	Log(Dead fine roots)	2.7436	0.05	19.86	0.098
	Log(Soil woody debris)	-1.9772	0.07	14.88	0.013
	Current annual increment	1.9095	0.03	4.26	0.069

Note: N=75 for March-July, N=15 for July, N=45 for August-October, and N=15 for annual soil C efflux

A fourth stepwise regression was performed to examine variables related to annual soil C efflux. Annual soil C efflux was significantly related to natural log-transformed soil charcoal, litter depth, natural log-transformed dead fine root mass, natural log-transformed soil woody debris, and current annual increment (Table 4.3.1). These variables explained between 3-17% of the variation in the annual soil C efflux. Annual soil C efflux modeled from soil temperature and air temperature varied from 11.0-17.9 Mg C·ha^{-1}·yr^{-1} and 10.6-18.9 Mg C·ha^{-1}·yr^{-1}, respectively (Table 4.3.2).

Table 4.3.2. Annual soil C efflux for longleaf pine plots varying in basal area modeled using soil (T_{SOIL}) or air temperature (T_{AIR}).

Plot No.	**Basal Area** (m^2·ha^{-1})	**Annual soil C efflux** T_{SOIL} (Mg C·ha^{-1}·yr^{-1})	T_{AIR}
189	7	13.22	13.90
186	8	14.90	14.84
190	13	11.16	11.23
188	14	11.04	10.59
184	15	14.82	14.49
182	16	15.72	15.18
185	18	15.73	16.07
187	18	12.50	12.61
179	23	13.55	13.67
183	25	13.63	12.89
176	29	15.68	15.97
180	30	14.90	14.57
181	31	17.93	18.88
177	32	14.42	14.92
178	36	15.67	15.65

Note: The general formula $y = e*a^{(b*x)}$ was used for annual soil C efflux estimates where y was soil CO_2 efflux and x was soil temperature or air temperature.

4.4 Carbon Sequestration

Longleaf pine aboveground biomass (stem plus branch and foliage) was estimated using allometric equations developed by Mitchell et al. (1999) from natural, uneven-aged longleaf pine in Georgia across three different sites and longleaf pine belowground biomass (taproot and coarse roots) was estimated using relationships between DBH and woody root biomass reported for loblolly pine (Johnsen et al. 2004). Aboveground standing stock biomass in longleaf pine stem and branch biomass ranged from 27.3-107.8 Mg C·ha^{-1} and from 1.2-5.5 Mg C·ha^{-1} for foliage. Depending on plot basal area, belowground standing stock biomass estimates varied from 7.2-25.5 Mg C·ha^{-1} (Table 4.4.1). Standing C stocks in longleaf pine trees, composed of stem plus branch, foliage, taproot, and coarse root biomass ranged from 35.7-138.8 Mg C·ha^{-1} (Table 4.4.1). Total stand C stocks, which included litter, soil woody debris, soil charcoal, soil C, live and dead fine roots, live and dead coarse roots, downed woody debris, and aboveground and belowground longleaf biomass, ranged from 66.3-183.7 Mg C·ha^{-1} (Table 4.4.2).

In addition to Mitchell et al. (1999) biomass equations, three other site specific longleaf pine biomass equations were applied to the longleaf pine stands at the Escambia Experimental Forest using 2005 Regional Longleaf Pine Growth Study diameter and height data (Kush, unpublished data). Using Mitchell et al. (1999) biomass equations and 2005 inventory data, aboveground woody biomass was between 24.4-103.8 Mg C·ha^{-1}, foliage biomass was 1.1-5.9 Mg C·ha^{-1}, and total tree biomass was from 25.5-109.1 Mg C·ha^{-1} (Figure 4.4.1). Taras and Clark (1977) developed biomass equations at the Escambia Experimental Forest for natural, uneven-aged sawtimber which ranged from 15.2-46.0 cm in DBH. Aboveground woody biomass ranged from 21.1-107.5 Mg

$C \cdot ha^{-1}$, foliage biomass ranged from 0.9-5.3 Mg $C \cdot ha^{-1}$, and total tree biomass was from 22.0-112.8 Mg $C \cdot ha^{-1}$ using allometric equations from Taras and Clark (1977) (Figure 4.4.1). Baldwin and Saucier (1983) developed biomass equations in 10 unthinned longleaf pine plantations in Texas and Louisiana for trees ranging in DBH from 2.5-53.0 cm. Using Baldwin and Saucier (1983) equations, aboveground woody biomass was from 13.0-92.7 Mg $C \cdot ha^{-1}$, foliage biomass ranged from 1.3-7.8 Mg $C \cdot ha^{-1}$, and total tree biomass was from 14.4-98.5 Mg $C \cdot ha^{-1}$ (Figure 4.4.1). In an uneven-aged Florida flatwoods slash-longleaf pine forest, Garbett (1977) developed biomass equations using longleaf pine trees which ranged in DBH from 12.0-42.0 cm. Estimated aboveground woody biomass ranged from 23.1-118.8 Mg $C \cdot ha^{-1}$, foliage biomass was from 0.8-3.0 Mg $C \cdot ha^{-1}$, and total tree biomass ranged from 23.9-121.8 Mg $C \cdot ha^{-1}$ using Garbett (1977) allometry (Figure 4.4.1).

Longleaf pine current annual growth increment ranged from 0.1 to 0.9 $m^2 \cdot ha^{-1} \cdot yr^{-1}$ (Table 4.2.1). Longleaf pine aboveground NPP ranged from 0.4-4.2 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ and belowground NPP ranged from 0.1-0.9 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ (Table 4.4.3). Annual soil C efflux was on average 8.3 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ higher than total NPP and ranged from 3.1 to 30.0 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ higher than total NPP (Table 4.4.3).

Table 4.4.1. Standing C in longleaf pine biomass for 50-year-old longleaf pine stands varying in basal area.

		----------------------------------Standing C----------------------------------			
Plot No.	**Basal Area**	**Stem/Branch**	**Foliage**	**Tap/Coarse Roots**	**Total Standing C**
	($m^2 \cdot ha^{-1}$)	------------------------------($Mg\ C \cdot ha^{-1}$)-----------------------------			
189	7	27.3	1.2	7.2	35.7
186	8	29.6	1.4	7.7	38.7
190	13	50.3	2.3	12.4	65.0
188	14	53.6	2.5	13.1	69.2
184	15	54.3	2.8	13.3	70.4
182	16	57.6	2.9	14.1	74.6
185	18	68.3	3.3	16.5	88.1
187	18	67.6	3.2	16.3	87.1
179	23	78.9	4.0	19.0	101.9
183	25	87.5	4.4	20.9	112.8
176	29	90.4	5.0	21.6	117.0
180	30	101.5	5.4	24.1	131.0
181	31	107.8	5.5	25.5	138.8
177	32	91.8	5.5	22.1	119.4
178	36	101.0	6.1	24.2	131.3

Table 4.4.2. Carbon in forest components in 50-year-old longleaf pine stands with varying basal area. Longleaf C included aboveground and belowground biomass. Understory vegetation is not included.

Plot No.	**Basal Area**	**Longleaf C**	**Litter**	**Soil Woody Debris**	**Soil Charcoal**	**Soil C**	**Live Fine Roots**	**Dead Fine Roots**	**Live Coarse Roots**	**Dead Coarse Roots**	**Downed Woody Debris**	**Total C**
	($m^2 \cdot ha^{-1}$)	---($Mg\ C \cdot ha^{-1}$)--										
189	7	35.7	5.9	0.6	0.2	24.4	1.2	0.3	2.2	0.5	1.0	72.2
186	8	38.7	5.9	0.4	0.2	18.0	0.8	0.2	1.6	0.5	0.2	66.3
190	13	65.0	5.9	0.5	0.3	19.7	1.2	0.2	2.5	0.4	0.7	96.4
188	14	69.2	3.1	0.6	0.1	11.4	1.2	0.2	2.8	0.3	0.1	89.0
184	15	70.4	7.0	0.8	0.2	30.3	1.1	0.2	3.2	1.0	5.8	120.0
182	16	74.6	6.1	0.6	0.2	23.6	1.1	0.2	3.0	0.3	0.2	110.0
185	18	88.1	7.4	0.9	0.3	24.8	1.1	0.3	4.4	0.4	1.9	129.6
187	18	87.1	6.0	0.5	0.2	15.8	1.0	0.2	3.3	0.3	0.1	114.5
179	23	101.9	9.0	1.1	0.6	24.0	1.0	0.2	2.2	0.7	8.1	148.7
183	25	112.8	7.3	0.7	0.3	22.8	1.0	0.2	3.6	0.4	4.0	153.0
176	29	117.0	7.7	1.0	0.3	25.3	1.3	0.3	2.9	0.6	5.7	162.0
180	30	131.0	9.0	1.0	0.4	18.5	1.3	0.3	2.7	0.6	2.5	167.2
181	31	138.8	8.3	1.0	0.4	23.8	1.1	0.2	3.9	0.4	5.7	183.7
177	32	119.4	8.4	0.9	0.1	17.4	1.0	0.2	2.0	0.4	6.6	156.4
178	36	131.3	8.4	1.2	0.3	15.3	1.0	0.2	4.3	0.6	5.1	167.7

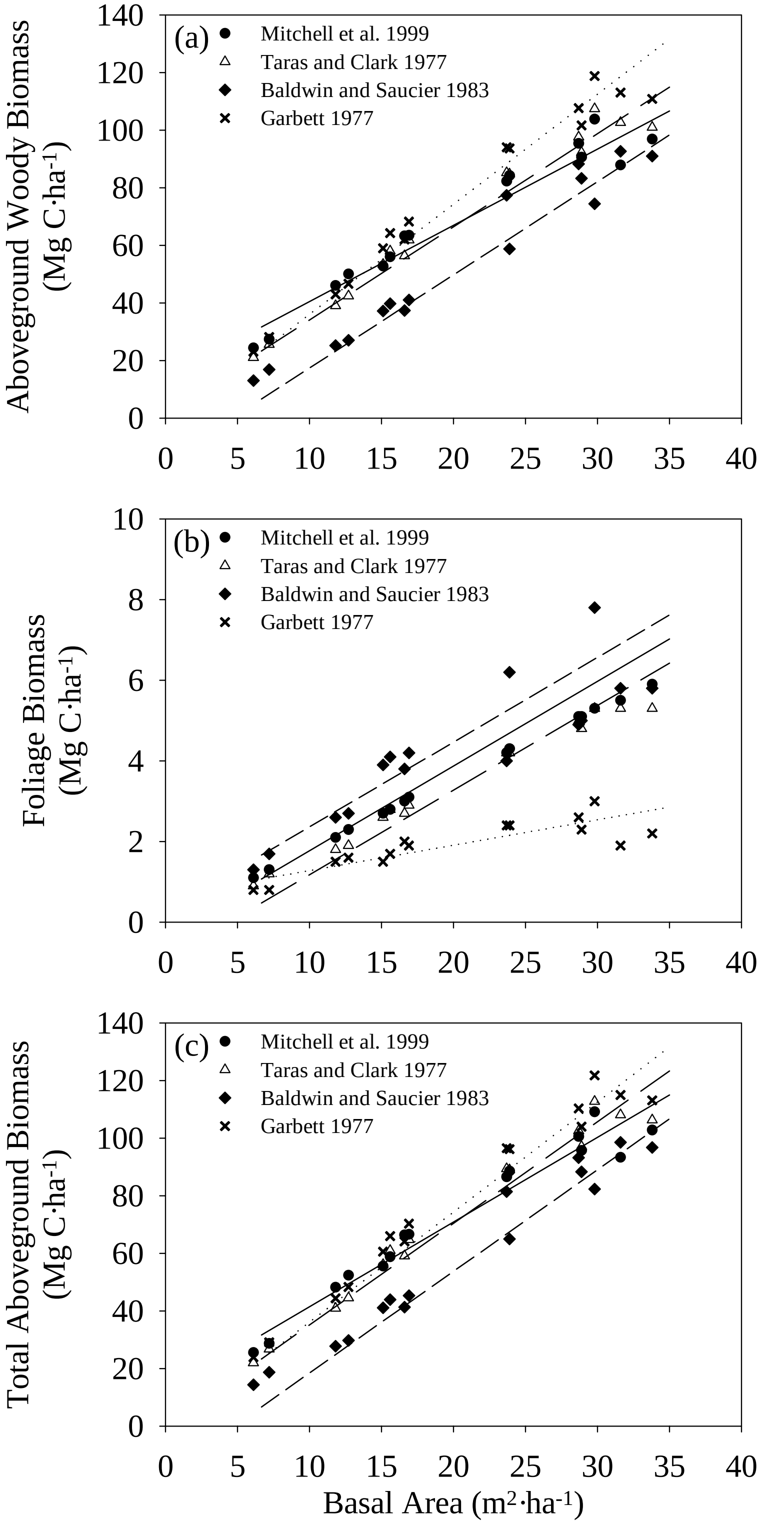

Figure 4.4.1. Site specific longleaf pine biomass equations applied to the longleaf pine stands in the Escambia Experimental Forest from 2005 inventory data for aboveground woody (a), foliage (b), and total aboveground (c) biomass (——— = Mitchell et al. 1999, — — — = Taras and Clark 1977, --------- = Baldwin and Saucier 1983, and …….. = Garbett 1977).

Table 4.4.3. Annual C fluxes for longleaf pine stands varying in basal area.

Plot No.	**Basal Area**	**Soil C Efflux**	**Longleaf NPP_{AG}**	**Longleaf NPP_{BG}**	**Longleaf NPP_{TOTAL}**
	($m^2 \cdot ha^{-1}$)	--------------------Mg $C \cdot ha^{-1} \cdot yr^{-1}$--------------------			
189	7	13.22	0.4	0.1	0.4
186	8	14.90	0.9	0.2	1.1
190	13	11.16	1.9	0.4	2.3
188	14	11.04	1.1	0.2	1.3
184	15	14.82	0.6	0.1	0.7
182	16	15.72	1.8	0.4	2.2
185	18	15.73	2.2	0.5	2.7
187	18	12.50	1.7	0.4	2.1
179	23	13.55	2.6	0.6	3.2
183	25	13.63	2.6	0.6	3.1
176	29	15.68	3.6	0.8	4.4
180	30	14.90	2.6	0.6	3.2
181	31	17.93	4.2	0.9	5.2
177	32	14.42	3.8	0.8	4.6
178	36	15.67	3.3	0.7	4.0

Note: NPP=net primary productivity, AG=aboveground,

CHAPTER 5. DISCUSSION

The research at the Escambia Experimental Forest is unique in that soil C fluxes were measured over the course of 10 months in naturally regenerated, even-aged, fire maintained, 50-year-old longleaf pine stands varying in basal area. There have been multiple studies which have measured C fluxes in both young and mature loblolly pine plantations to determine the effectiveness with which vigorous plantations can sequester C (Samuelson et al. 2004; Gough and Seiler 2004; Wiseman and Seiler 2004; Maier and Kress 2000). However, information on C fluxes in longleaf pine ecosystems is limited. Of the available literature on soil CO_2 efflux in longleaf pine stands, Cheng et al. (2005) observed that longleaf soil CO_2 efflux rates were significantly higher in wiregrass soil than in prairie soil or a sand/vermiculite mixture. Another experiment investigated the influence of litter on soil CO_2 efflux in a 20-year-old longleaf plantation in South Carolina and reported that different levels of litter removal resulted in varying soil CO_2 efflux rates, with the greatest reduction in soil CO_2 efflux following total litter removal (Reinke et al. 1981). Tobert et al. (2004) modeled a regenerating longleaf community treated with ambient and elevated atmospheric CO_2 concentrations and found a decrease in soil CO_2 efflux in response to elevated atmospheric CO_2 although longleaf pine biomass significantly increased. Soil C mineralization rates and C turnover rates were lower for elevated CO_2 conditions suggesting that soil C sequestration will increase under elevated CO_2 levels (Torbert et al. 2004).

Soil CO_2 efflux ranged from 0.9-8.8 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ over the 10 month experiment. These rates are similar to values reported for other Coastal Plain sites with various southern pine species. For example, soil CO_2 efflux ranged from 0.8-7.0 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in natural mixed pine and pine-hardwood stands at Fort Benning, Georgia (Dilustro et al. 2005). Moncrieff and Fang (1999) reported soil CO_2 efflux rates ranging from 1.5-7.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in a mature slash pine stand in Gainesville, Florida. In a 23-year-old slash pine plantation in Gainesville, soil CO_2 efflux rates were between 0.7-5.8 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Fang et al. 1998). On the Virginia Piedmont, varying age classes of loblolly pine produced soil CO_2 efflux rates between 0.3-6.5 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Wiseman and Seiler 2004).

Annual soil C efflux estimates ranged between 11.0-17.9 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ and this range is similar to other southern pine species and sites in the Coastal Plain region. For example, Moncrieff and Fang (1999) estimated an annual sum of 14.0 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ for a mature slash pine stand in Florida. Ewel et al. (1987) estimated 13.0 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ in a mature 29-year-old slash pine plantation located in Florida. A 20-year-old longleaf pine plantation in South Carolina with 1100 $trees \cdot ha^{-1}$ and a mean DBH of 15 cm had a lower estimate of 5.1 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ perhaps due to the underestimation by the static alkali technique used to measure soil CO_2 efflux (Reinke et al. 1981). Gough et al. (2005) observed annual soil C efflux rates in 20-year-old loblolly pine stands of 12.3 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ in Virginia and 13.2 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ in South Carolina. In an 11-year-old loblolly pine stand with a density of 1260 $trees \cdot ha^{-1}$ in North Carolina, mean annual soil

C efflux was 14.1 Mg C$\cdot$ha$^{-1}\cdot$yr^{-1} (Maier and Kress 2000), which was similar to the soil C efflux rate of 14.4 Mg C$\cdot$ha$^{-1}\cdot$yr^{-1} from Plot 177 on the Escambia Experimental Forest with similar tree density (1186 trees$\cdot$ha^{-1}). Raich and Schlesinger (1992) determined that the average annual soil C efflux in temperate coniferous forests was 7.0 Mg C$\cdot$ha$^{-1}\cdot$yr^{-1} and the average ranged between 2.5-13.0 Mg C $\cdot$ha$^{-1}\cdot$yr^{-1}, with a maximum of 26.0 Mg C$\cdot$ha$^{-1}\cdot$yr^{-1} on a recently clearcut slash pine plantation.

Soil temperature was hypothesized to explain the majority of variation in soil CO_2 efflux rates in the 50-year-old longleaf pine stands in this study. Soil CO_2 efflux was exponentially related to soil temperature, and soil temperature explained 96% of the variability in the soil CO_2 efflux rates. Gough and Seiler (2004) explained 26% of soil CO_2 efflux variation with soil temperature over a range of different ages in loblolly pine plantations with a nonlinear model. Pangle and Seiler (2002) explained 42% of the variation in soil CO_2 efflux in a 2-year-old loblolly stand using soil temperature in a linear model. Butnor et al. (2006) used soil temperature as the predictor variable in an exponential model and explained 40-66% of the variability in soil CO_2 efflux in a loblolly pine plantation. Maier and Kress (2000) explained 70% of the variation in soil CO_2 efflux in 11-year-old loblolly stands with soil temperature using a similar exponential model. Borken et al. (2002) explained 68-86% of the variation in soil CO_2 efflux in two Scots pine forests using soil temperature modeled from the Arrhenius function. Carlyle and Than (1988) modeled soil CO_2 efflux in an 18-year-old Monterey pine (*Pinus radiat*a D. Don) stand with a nonlinear model that included interaction terms between soil temperature and soil moisture and accounted for 85% of variation in soil CO_2 efflux. Winter soil CO_2 efflux was modeled with a nonlinear function in a ponderosa pine-bunchgrass system and soil temperature explained 43% of the variation in soil CO_2 efflux (Kaye and Hart 1998).

The Q_{10} of 2.7 for soil CO_2 efflux was slightly higher than the average of 2.4 reported in the literature but was within the range of 1.3-3.3 reported by Raich and Schlesinger (1992) and was consistent with other Q_{10} values reported for southern pines. For example, Pangle and Seiler (2002) observed a Q_{10} of 2.3 for soil CO_2 efflux with soil temperatures ranging from 5-35° C in a loblolly stand. In a naturally regenerated slash and longleaf stand in Florida, the Q_{10} for soil CO_2 efflux varied between 2.0 in soil with a water content greater than 5.5% and 1.4 for soils with a water content less than 5.5% (Powell et al. 2008). Fang et al. (1998) calculated a Q_{10} of 2.5 for soil CO_2 efflux in a mature, Florida slash pine plantation. The Q_{10} value is useful as a modeling tool in predicting soil CO_2 efflux at varying spatial and temporal scales (Carlyle and Than 1988; Qi and Xu 2001).

An objective of the study was to identify environmental and plant variables in addition to soil temperature that may be related to soil CO_2 efflux. In the March-July and August-October modeling periods, soil temperature demonstrated the strongest relationship with soil CO_2 efflux and soil temperature explained 83% of the variation in soil CO_2 efflux during March-July and 64% of variation during August-October. Dilustro et al. (2005) also used stepwise regression analyses to examine relationships between environmental variables and soil CO_2 efflux, and soil temperature was the strongest explanatory variable explaining 24-51% of the variation in soil CO_2 efflux in natural mixed pine and pine-hardwood stands at Fort Benning, Georgia. In the study at the Escambia Experimental Forest, soil moisture was expected to be related to soil CO_2

efflux rates only when moisture became a limiting factor. Monthly soil moisture content varied during the 10 month experiment and was greatest in January 2008 at 11.8% and lowest in June at 3.6%. Extremely dry conditions can limit microbial activity, heterotrophic respiration, and fine root production (Wildung et al. 1975; Raich and Tufekcioglu 2000), but soil CO_2 efflux was not apparently limited by soil moisture during our measurements. Edwards (1975) and Keith et al. (1997) also reported no influence of soil moisture content on soil CO_2 efflux in 50-year-old yellow-poplar (*Liriodendron tulipifera* L.) and eucalypt snow gum forests. Gough and Seiler (2004) did not find a relationship between soil moisture content and soil CO_2 efflux in loblolly pine on soils of the upper Coastal Plain in South Carolina. Furthermore, Gough et al. (2005) did not find a correlation between soil moisture content which ranged from 2-69% and soil CO_2 efflux in loblolly pine in South Carolina. The range in soil moisture at the Escambia Experimental Forest was within the range reported by Gough et al. (2005). Another study reported that when soil moisture content was adequate for microbial and root growth and maintenance, only a small correlation was observed between soil CO_2 efflux and soil moisture content (Martin et al. 2007). Fang and Moncrieff (2001) also found no relationship between soil moisture content and soil CO_2 efflux with three different moisture regimes in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Scotland. Soil moisture was measured to 10 cm at the Escambia Experimental Forest and it is possible that greater depths had higher soil water available for root uptake.

Basal area is often utilized as a forest management decision making tool and variation in forest structure, primarily in basal area, was hypothesized to be related to soil CO_2 efflux through basal area effects on forest characteristics including soil temperature, soil moisture content, ground cover, litter mass and depth, and above and belowground biomass. Soil CO_2 efflux, ground cover, litter mass, litter depth, downed woody debris C, soil woody debris, and cover in vines and grasses varied significantly with basal area. Variables that were related to basal area and were significantly but weakly related to soil CO_2 efflux in the March-July modeling period included litter mass, ground cover, and downed woody debris C. Log-transformed live coarse roots and log-transformed soil charcoal were not related to basal area but were weakly related to soil CO_2 efflux. However, these variables explained only 1-2% of the variation in soil CO_2 efflux. In the August-October modeling period, litter depth and ground cover were related to soil CO_2 efflux. Soil moisture was not related to basal area in this period but was weakly related to soil CO_2 efflux. Litter depth, ground cover, and soil moisture explained between 2-11% of soil CO_2 efflux variability in the August-October modeling period. Therefore, in both modeling periods, only a minor portion of the variation in soil CO_2 efflux was explained by variables other than soil temperature which suggests that soil CO_2 efflux can be modeled by soil temperature and is not as responsive to forest characteristics. However, variation in soil CO_2 efflux between stand ages may be significant based on Reinke et al. (1981) experiment in 20-year-old longleaf pine.

Cumulative annual soil C efflux was expected to be positively related to belowground biomass because greater root biomass may increase the contribution of autotrophic respiration to soil CO_2 efflux rates. Belowground live fine root biomass ranged from 0.76-1.27 Mg $C{\cdot}ha^{-1}$, live coarse root biomass ranged from 1.57-4.35 Mg $C{\cdot}ha^{-1}$, dead fine root biomass ranged from 0.16-0.33 Mg $C{\cdot}ha^{-1}$, and dead coarse root biomass ranged from 0.28-0.97 Mg C·ha^{-1}. There was no significant relationship between cumulative annual soil C efflux and root biomass.

Aboveground C stocks in leaf and branch plus stem biomass ranged from 28.5-113.3 Mg C·ha^{-1}. This range is similar to other southern pines in the Coastal Plain. For example, Ryan et al. (1995) reported 59.5 Mg C·ha^{-1} for aboveground branch plus stem stocks in a 24-year-old slash pine plantation in Florida in stands with a basal area of 26.1 m^{2}·ha^{-1}. Gholz et al. (1991) and Cropper and Gholz (1991) estimated an average 53 Mg C·ha^{-1} for aboveground C stocks in a 24-year-old slash pine in Florida with basal areas varying from 18.6-30.4 m^{2}·ha^{-1}. Kinerson (1975) reported 57.8 Mg C·ha^{-1} aboveground biomass in 12 to 16-year-old loblolly pine plantations with a mean DBH of 17.2 cm and a density of 1445 trees·ha^{-1} in North Carolina. The comparison between the four different site specific longleaf pine biomass equations developed by Mitchell et al. (1999), Taras and Clark (1977), Baldwin and Saucier (1983), and Garbett (1977) in the 50-year-old stands suggests that site specific equations may be needed for aboveground biomass estimates and in particular for foliage estimates. In this study, longleaf pine aboveground NPP was between 0.4-4.2 Mg C·ha^{-1}·yr^{-1} and was similar to the range including 0.6-5.2 Mg C·ha^{-1}·yr^{-1} and the average of 4.1 Mg C·ha^{-1}·yr^{-1} in unfertilized 24-year-old slash pine plantation stands varying in basal area from 18.6-30.4 m^{2}·ha^{-1} in north Florida (Gholz et al. 1991). Teskey et al. (1994) reported NPP between 2.0-2.9 Mg C·ha^{-1}·yr^{-1} in a 23-year-old fertilized slash pine plantation with 25.9 m^{2}·ha^{-1} of basal area in Florida.

Soil C stocks in the top 0-15 cm of soil were between 11.4-30.3 Mg C·ha^{-1} which is less than other longleaf pine studies perhaps due to the regular prescribed burning in the Escambia Experimental Forest. For example, Kalisz and Stone (1984) reported a soil

C content of 56.6 Mg C·ha^{-1} in the top 0-60 cm of soil and 31.9 Mg C·ha^{-1} at 0-15 cm for soil C in a naturally regenerated, 40 to 50-year-old longleaf pine stand in central Florida. Similarly, Brinkley et al. (1992) found that soil C was 41 Mg C·ha^{-1} at a 0-10 cm depth and 20 Mg C·ha^{-1} at a 10-20 cm depth in a 31-year-old longleaf-loblolly pine stand in a South Carolina managed for 30 years with prescribed fire at three year intervals. Markewitz et al. (2002) reported that soil C in Southwest Georgia was 26.7 Mg C·ha^{-1} in 0-10 cm of soil in a mature, natural, untilled longleaf pine stand with tree ages as great as 200 years, which is similar to the upper range measured at the Escambia Experimental Forest. Schlesinger and Lichter (2001) found that soil C was between 19-22 Mg C·ha^{-1} in the top 0-15 cm of soil in a 16-year-old loblolly pine plantation in North Carolina and Turner et al. (1995) estimated that soil C was 17.0 Mg C ·ha^{-1} in a longleaf-slash pine ecosystem. Soil C is the largest terrestrial C sink, but the accumulation rate of soil C is lower than the accumulation rate of C within vegetation in the temperate zone.

Relative C stocks at the Escambia Experimental Forest were dominated by longleaf C which made up 49-78% of the total C. Soil C and litter C were between 9-34% and 3-9% of total C, respectively. Other components, such as live fine root C, live coarse root C, dead coarse root C, and downed woody debris C only constituted between 1-5% of total C. Carbon sequestration was clearly dominated by longleaf pine in these stands.

5.1 Conclusions

The study at the Escambia Experimental Forest tested three hypotheses. The first hypothesis tested if soil temperature would explain the majority of variation in soil CO_2 efflux. Ninety-six percent of the variability in soil CO_2 efflux was explained by soil temperature using a nonlinear model. In stepwise regression analyses, 64-83% of soil CO_2 efflux variability was explained by soil temperature during the March-July and August-October modeling periods. The second hypothesis tested that soil CO_2 efflux would be related to soil moisture. However, soil moisture was not related to soil CO_2 efflux even during a minor drought in June when soil moisture reached the minimum monthly average of 3.6%. The third hypothesis tested by this study was that forest structure would influence soil CO_2 efflux through effects on forest characteristics including soil temperature, soil moisture, ground cover, litter, and fine root biomass. Basal area was not related to soil temperature; however, basal area was significantly related to soil CO_2 efflux, ground cover, litter mass, litter depth, downed woody debris C, soil woody debris, and cover in vines and grasses. Nonetheless, only 1-2% of the variation in soil CO_2 efflux was explained by litter mass, ground cover, log-transformed live coarse roots, downed woody debris C, and log-transformed soil charcoal in the March-July modeling period and 2-11% of the soil CO_2 efflux variability was explained by litter depth, ground cover, and soil moisture in the August-October modeling period.

The study emphasizes the need for a better understanding of net ecosystem productivity and subsequent C sequestration in longleaf pine ecosystems. Higher annual soil C efflux estimates relative to NPP suggest that the 50-year-old longleaf pine stands were a source of C rather than a sink. However, a better understanding of the C pools contained in snags and residual stumps, fine root production and turnover, tap root biomass, and the contribution of heterotrophic respiration to ecosystem respiration is needed to estimate net ecosystem productivity and determine whether stands are sinks for C in this longleaf pine ecosystem.

In conclusion, soil CO_2 efflux in 50-year-old longleaf pine stands varying in basal area was measured for 10 months in 2008, and soil temperature explained the majority of variation in soil CO_2 efflux. This is in accordance with other experiments which examined soil CO_2 efflux and found a strong influence of soil temperature on soil CO_2 efflux in forests in the Southeast United States (Gough and Seiler 2004; Pangle and Seiler 2002; Butnor et al. 2006). The value of forest stand component separation is important in determining C stocks and provides a better understanding of the distribution of C stocks in 50-year-old longleaf pine stands. Variation in stand structure was only weakly related to soil CO_2 efflux. The strong relationship between soil temperature and soil CO_2 efflux indicates that soil CO_2 efflux can be modeled in longleaf pine ecosystem C models. Data from this experiment are useful in estimating C fluxes in mature longleaf pine ecosystems over a range of basal areas and in developing forest management plans that include C budgeting.

REFERENCES

Amthor, J.S. 1984. The role of maintenance respiration in plant growth. Plant, Cell, and Environment 7: 561-569.

Amthor, J.S. 1994. Plant respiratory responses to the environment and their effects on the carbon balance. In: Wilkerson, R.E. (ed.) Plant-environment interactions. Marcel Dekker, New York, pp. 501-554.

Andersen, C.P., I. Nikolov, P. Nikolova, R. Matyssek, and K.H. Haberle. 2005. Estimating "autotrophic" belowground respiration in spruce and beech forests: decreases following girdling. European Journal of Forest Resources 124: 155-163.

Axelson, E., and B. Axelson. 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. Tree Physiology 2: 189-204.

Badia, D. and C. Marti. 2003. Effect of simulated fire on organic matter and selected microbiological properties of two contrasting soils. Arid Land Research and Management 17: 55-69.

Baldwin, V.C., Jr., and J.R. Saucier. 1983. Aboveground weight and volume of unthinned, planted longleaf pine on West Gulf forest sites. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA, Research Paper, SO-191: 25 pp.

Birdsey, R.A. 2006. Carbon accounting rules and guidelines for the United States Forest Sector. Journal of Environmental Quality 35: 1518-1524.

Bolstad, P.V., and J.M. Vose. 2005. Forest and pasture carbon pools and soil respiration in the southern Appalachian mountains. Forest Science 51: 372-383.

Bond-Lamberty, B., C. Wang, and S.T. Gower. 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration? Global Change Biology 10: 1756–1766.

Borken, W., Y. Xu, E.A. Davidson, and F. Beese. 2002. Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. Global Change Biology 8: 1205-1216.

Bouma, T.J., and D.R. Bryla. 2000. On the assessment of root and soil respiration for soils of different textures: interactions with soil moisture contents and soil CO_2 concentrations. Plant Soil 227: 215-221.

Bowden, R.D., K. L. Nadelhoffer, R.D. Boone, J.M. Melillo, and J.B. Garrison. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Canadian Journal of Forest Research 23: 1402-1407.

Boyer, W.D. 1994. Eighteen years of seasonal burning in longleaf pine: effects on overstory growth. *In* Proceedings of the 12th International Conference on Fire and Forest Meteorology, 26-28 Oct. 1993, Jekyll Island, Ga. Society of American Foresters, Bethesda, MD. pp 602-610.

Brinkley, D., D. Richter, M.B. David, B. Caldwell. 1992. Soil chemistry in a loblolly/longleaf pine forest with interval burning. Ecological Applications 2: 157-16.

Brockway, D.G., and C.E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management 96: 167-183.

Brown, H.P., A.J. Panshin, and C.C. Forsaith. 1949. Textbook of wood technology: Structure, identification, defects, and uses of the commercial woods of the United States. McGraw-Hill Book Company, Inc.: New York, NY, 652 pp.

Buchanan, H. A., and S. B. Levine. 1999. Wood-based building materials and atmospheric carbon emissions. Environmental Science and Policy 2: 427-437.

Butnor, J.R., K.H. Johnsen, and F.G. Sanchez. 2006. Whole-tree and forest floor removal from a loblolly pine plantation have no effect on forest floor CO_2 efflux 10 years after harvest. Forest Ecology and Management 227: 89-95.

Carlyle, J.C., and U.B. Than. 1988. Abiotic controls of soil respiration beneath an eighteen-year-old *Pinus radiata* stand in south-eastern Australia. Journal of Ecology 76: 654-662.

Chambers, J.Q., E.S. Tribuzy, L.C. Toledo, B.F. Crispim, N. Higuchi, J.D. Santos, A.C. Araujo, B. Kruijt, A.D. Nobre, and S.E. Trumbore. 2004. Respiration from a tropical forest ecosystem: Partitioning of sources and low carbon use efficiency. Ecological Applications 14: 72-88.

Chen, J.M., S.C. Thomas, Y. Yin, V. Maclaren, J. Liu, J. Pa, G. Liu, Q. Tian, Q. Zhu, J.-J. Pan, X. Shi, J. Xue, and E. Kang. 2007. Enhancing forest carbon sequestration in China: toward an integration of scientific and socio-economic perspectives. Journal of Environmental Management 85: 515-523.

Cheng, W., F. Shenglei, R.B. Susfalk, and R.J. Mitchell. 2005. Measuring tree root respiration using ^{13}C natural abundance: rooting medium matters. New Phytologist 167: 297-307.

Cropper, W.P. Jr., and H.L. Gholz. 1991. *In situ* needle and fine root respiration in mature slash pine *(Pinus elliottii)* trees. Canadian Journal of Forest Research 21: 1589-1595.

Davidson, E.A., E. Belk, R.D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology 4: 217-227.

Davidson, E.A., L.V. Verchot, J.H. Cattanio, I.L. Ackerman, and J.E.M. Carvalho. 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry 48: 53-69.

De Selm, H.R. 1952. Carbon dioxide gradients in a beech forest in central Ohio. Ohio Journal of Science 52: 187-198.

Dilustro, J.J., B. Collins, L. Duncan, and C. Crawford. 2005. Moisture and soil texture effects on soil CO_2 efflux components in southeastern mixed pine forests. Forest Ecology and Management 204: 85-95.

Doran, J.W., I.N. Mielike, and J.F. Power. 1991. Microbial activity as regulated by soil water-filled pore space. In: Ecology of soil microorganisms in the microhabital environments, pp. 94-99. Tranactions of the 14th Int. Congress of Soil Science Symposium III-3.

Ebinger, M.H., M.L. Norfleet, D.D. Breshears, D.A. Cremers, M.J. Ferris, P.J. Unkefer, M.S. Lamb, K.L. Goddard, and C.W. Meyer. 2003. Extending the applicability of laser-induced breakdown spectroscopy for total soil carbon measurement. Soil Science Society of America Journal 67: 1616-1619.

Edwards, N.T. 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Scientific Society of America 39: 361-365.

Edwards, N.T., and P. Sollins. 1973. Continuous measurement of carbon dioxide evolution from partitioned forest floor components. Ecology 54: 406-412.

Ekberg, A., N. Buchmann, and G. Gleixner. 2007. Rhizoshperic influence on soil respiration and decomposition in a temperate Norway spruce stand. Soil Biology and Biogeochemistry 39: 2103-2110.

Ekblad, A., and P. Hogberg. 2001. Natural abundance of 13C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. Oecologia 127: 305–308.

Ewel, K.C., W.P. Cropper Jr., and H.L. Gholz. 1987. Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. Canadian Journal of Forest Research 17: 325-329.

Falkowski, P., R.J. Scholes, E. Boyle, J. Canadell, D. Canfield, J. Elser, N Gruber, K. Hibbard, P. Hogberg, S. Linder, F.T. Mackenzie, B. Moore III, T. Pederson, Y. Rosenthal, S. Seitzinger, V. Smetacek, and W. Steffen. 2000. The global carbon cycle: a test of our knowledge of earth as a system. Science 290: 291-296.

Fang, C., and J.B. Moncrieff. 2001. The dependence of soil CO_2 efflux on temperature. Soil Biology and Biochemistry 33: 155-165.

Fang, C., J.B. Moncrieff, H.L. Gholz, and K.L. Clark. 1998. Soil CO_2 efflux and its spatial variation in a Florida slash pine plantation. Plant and Soil 205: 135-146.

Farrar, R.M. 1978. Silvicultural implications of the growth response of naturally regenerated even-aged stands of longleaf pines (*Pinus palustris* Mill.) to varying stand age, site quality, and density and certain stand structure measures. Unpublished Ph.D. Dissertation, University of Georgia. 132 pp.

Forbes, M.S., R.J. Raison, and J.O. Skjemstad. 2006. Formation, transformation, and transport of black carbon (charcoal) in terrestrial and aquatic ecosystems. Science of the Total Environment 370: 190-206.

Garbett, W.S. 1977. Aboveground biomass and nutrient content of a mixed slash-longleaf pine stand in Florida. Unpublished master of forestry thesis, University of Florida. 88 pp.

Gaudinski, J.B., S.E. Trumbore, and E.A. Davidson. 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. Biogeochemistry 51: 33–69.

Gholz, H. L., S.A. Vogel, W.P. Cropper Jr., K. McKelvey, K.C. Ewel, R.O. Teskey, and P.J. Curran. 1991. Dynamics of canopy structure and light interception in *Pinus elliottii* stands of north Florida. Ecological Monograms 61: 33-51.

Ginter, D.L., K.W. McLeod, and C. Sherrod, Jr. 1979. Water stress in longleaf pine induced by litter removal. Forest Ecology and Management 2:13-20.

Godfrey, R.K. 1988. Trees, shrubs, and woody vines of northern Florida and adjacent Georgia and Alabama. The University of Georgia Press: Athens, GA, 734 pp.

Goodale, C.L., M.J. Apps, R.A. Birdsey, C.B. Field, L.S. Heath, R.A. Houghton, J.C. Jenkins, G. H. Kohlmaier, W. Durz, S. Liu, G.-J. Nabuurs, S. Nilsson, and A.Z. Shvidenko. 2002. Forest carbon sinks in the northern hemisphere. Ecological Applications 12: 891-899.

Gough, C.M., and J.R. Seiler. 2004. The influence of environmental, soil carbon, root and stand characterstics on soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations located on the South Carolina Coastal Plain. Forest Ecology and Management 191: 353-363.

Gough, C.M., J.R. Seiler, P.E. Wiseman, and C.A. Maier. 2005. Soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations on the Virginia Piedmont and South Carolina Coastal Plain over a rotation-length chronosequence. Biogeochemistry 73: 127-147.

Goulden, M.L., J.W. Munger, S.M. Fan, B.C. Daube, and S.C. Wofsy. 1996. Measurements of carbon sequestration by longterm eddy covariance: methods and a critical evaluation of accuracy. Global Change Biology 2: 169-182.

Greaves, J.S. 1922. Agricultural bacteriology. Lea and Febiger, Philadelphia and New York. 437 pp.

Gustavsson, L., and R. Sathre. 2006. Variability in energy and carbon dioxide balances of wood and concrete building materials. Building and Environment 41: 940-951.

Hamer, U., and B. Marschner. 2002. Priming effects of sugars, amino acids, organic acids and catechol on the mineralization of lignin and peat. Journal of Plant Nutrition and Soil Science 165: 261–268.

Hanson, P.J., N.T. Edwards, C.T. Garten, and J.A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48: 115–146.

Harrison, W.H., and P.A.S. Aiyer. 1913. The gases of swamp rice soils: their composition and relationship to the crop. Memoirs of the Department of Agriculture in India, Chemical Series 3: 65-106.

Heath, L.S., and D.C. Chojnacky. 2001. Down dead wood statistics for Maine timberlands, 1995. Resource Bulletin NE-150. Newton Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station, 80 p.

Heath, L.S., and J.E. Smith. 2004. Criterion 5, Indicator 27: Contribution of forest ecosystems to the total global carbon budget, including absorption and release of carbon (Standing biomass, coarse woody debris, peat and soil carbon). Pp. 1-7. *In* D.R. Darr (ed.) A supplement to the national report on sustainable forests 2003. FS-766A. USDA. Washington, DC.

Hibbard, K.A., B.E. Law, M. Reichstein, and J. Sulzman. 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. Biogeochmistry 73: 29-70.

Hiers, J.K., R. Wyatt, R.J. Mitchell. 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: is a season selective? Oecologia 125: 521-530.

Hogberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M.N. Hogberg, G. Nyberg, M. Ottosson-Lofvenius, and D.J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411: 789–792.

Houghton, J. 2005. Global warming. Reports on Progress in Physics 68: 1343-1403.

Hutchinson, C.M. 1912. Report of the Imperial Agricultural Bacteriologist. Report of the India Agricultural Research Institution and College, Pusa 1911-12: 78-83.

Janssens, I.A., H. Lankreijer, G. Matteucci, A.S. Kowalski, N. Buchmann, D. Epron, K. Pilegaard, W. Kutsch, B. Lobgdoz, T. Grunwald, L. Montagnani, S. Dore, C. Rebmann, E.J. Moors, A. Grelle, U. Rannik, K. Morgenstern, S. Oltchev, R. Clement, J. Gudmundsson, S. Minerbi, P. Berbigier, A. Ibrom, J. Moncrieff, A. Aubinet, C. Bernhoffer, N.O. Jensen, T. Vesala, A. Granier, E. -D. Schulze, A. Lindroth, A.J. Dolman, P.G. Jarvis, R. Ceulemans, And R. Valentini. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology 7: 269-278.

Johnsen, K.H., R. Teskey, L. Samuelson, J. Butnor, C. Maier, D. Sampson, and S. McKeand. 2004. Carbon sequestration in loblolly pine plantations: methods, limitations and research needs for estimating storage pools. *In*: Southern Forest Science: past, present, and future. *Edited by* M.H.M. Rauscher and K.H. Johnsen. USDA For. Serv. Gen. Tech. Rep. SRS-75. pp 373-382.

Johnson, D.W., and P.S. Curtis. 2001. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management 140: 227-238.

Kalisz, P.J., and E. L. Stone. 1984. The longleaf pine islands of the Ocala National Forest, Florida: A soil study. Ecology 65: 1743-1754.

Kao, W., and K. Chang. 2009. Soil CO_2 efflux from a mountainous forest-grassland ecosystem in central Taiwan. Botanical Studies 50: 337-342.

Kaye, J.P., and S.C. Hart. 1998. Restoration and canopy-tree effects on soil respiration in a Ponderosa pine-bunchgrass ecosystem. Soil Scientific Society of America Journal 62: 1062-1072.

Keith, H., K.L. Jacobsen, and R.J. Raison. 1997. Effects of soil phosphorus availability, temperature and moisture on soil respiration in *Eucalyptus pauciflora* forest. Plant and Soil 190: 127–141.

Kimmins, J.P. 2004. Forest ecology: a foundation for sustainable forest management and environmental ethics in forestry. Pearson/Prentice Hall, Upper Saddle River, NJ, 611 pp.

Kinerson, R.S. 1975. Relationships between plant surface area and respiration in loblolly pine. Journal of Applied Ecology 12: 965-971.

King, J.S., K.S. Pregitzer, D.R. Zak, J. Sober, J.G. Isebrands, R.E. Dickson, G.R. Hendrey, and D.F. Karnosky. 2000. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO_2 and tropospheric O_3. Oecologia 128: 237-250.

Kirschbaum, M.U.F. 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48: 21–51.

Kobziar, L.N. 2007. The role of environmental factors and tree injuries in soil carbon respiration response to fire and fuels treatments in pine plantations. Biogeochemistry 84: 191-206.

Kopfova, J. 2006. Hysteresis in biological models. Journal of Physics 55: 130-134.

Kush, J.S., R.S. Meldahl, and W.D. Boyer. 1999. Understory plant community response after 23 years of hardwood control treatments in natural longleaf pine (*Pinus palustris*) forests. Canadian Journal of Forest Research 29: 1047-1054.

Kush, J.S., D.G. Pitt, P.J. Craul, and W.D. Boyer. 2004. Quantifying forest soil physical variables potentially important for site growth analyses. Southern Journal of Applied Forestry 28: 5-11.

Lambers, H, F.S. Chapin III, and T.L. Pons. 1998. Plant Physiological Ecology. Springer-Verlag, New York. 540 pp.

Landers, J.L., D.H. Van Lear, and W.D. Boyer. 1995. The longleaf pine forests of the Southeast: Requiem or Renaissance? Journal of Forestry 93: 39-44.

Lavigne, M.B., M.G. Ryan, and D.E. Anderson. 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. Journal of Geophysical Research 102: 28 977-28 985.

Law, B.E, M.G. Ryan, and P.M. Anthoni. 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biology 5: 169-182.

Leather, J.W. 1915. Soil gases. Memoirs of the Department of Agriculture in India, Chemical Series 4: 85-134.

Lindenmayer, D.B., and M.A. McCarthy. 2002. Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. Forest Ecology and Management 155: 319-335.

Linn, D.M., and L.W. Doran. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. Soil Scientific Society of America Journal 48: 1267-1272.

Lippke, B., and L. Edmonds. 2006. Environmental performance improvements in residential construction: the impact of products, biofuels, and processes. Forest Products Journal 56: 58-63.

Litton, C.M., J.W. Raich, and M.G. Ryan. 2007. Carbon allocation in forest ecosystems. Global Change Biology 13:2089-2109.

Liu, W.H., D.N. Bryant, L.R. Hutrya, S.R. Saleska, E. Hammond-Pyle, D. Curran, and S.C. Wofsy. 2006. Wood debris contribution to the carbon budget of selectively logged and maturing mid-latitude forests. Oecologia 148: 108-117.

Lloyd, J., and J.A. Taylor. 1994. On the temperature dependence of soil respiration. Functional Ecology 8: 315-323.

Longdoz, B., M. Yernaux, and M. Aubinet. 2000. Soil CO_2 efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. Global Change Biology 6: 907-917.

Lundegardh, H. 1926. Carbon dioxide evolution of soil and crop growth. Ecological Station of Hallands Vadero, Sweden and Central Experimental Station, Stockholm. Soil Science 13: 417-453.

Macfadyen, A. 1971. The soil and its total metabolism. In: Methods of study in quantitative soil ecology, J. Phillipson, ed. P.1-13. IBP Handbook No. 18, Oxford: Blackwell.

Maier, C.A., and L.W. Kress. 2000. Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Canadian Journal for Forest Research 30: 347-359.

Markewitz, D., F. Sartori, and C. Craft. 2002. Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. Ecological Applications 12: 1276-1285.

Martin, D., J. Beringer, L.B. Hutley, and I. McHugh. 2007. Carbon cycling in a mountain ash forest: analysis of belowground respiration. Agricultural and Forest Meteorology 147:58-70.

Meldahl, R.S., and J.S. Kush. 2006. Carbon sequestration and natural longleaf pine ecosystems. *In* Proceedings of the 13th Biennial Southern Silvicultural Research Conference. General Technical Report SRS–92. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 640 pp.

Meyer, C.P., I.E. Galbally, Y. Wang, I.A. Weeks. 2001. Two autotrophic chamber techniques for measuring soil-atmosphere exchange of trace gases and results of their use in the OASIS Field Experiment. AGO/CSIRO Atmospheric Research, Victoria.

Micales, J.A., and K.E. Skog. 1997. The decomposition of forest products in landfills. International Biodeterioration and Biodegradation 39: 145-158.

Mitchell, R.J., L.K. Kirkman, S.D. Pecot, C.A. Wilson, B.J. Palik, and L.R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas: I. aboveground net primary productivity. Canadian Journal of Forest Research 29: 743-751.

Moncrieff, J.B., and C. Fang. 1999. A model for soil CO_2 production and transport 2: Application to a Florida *Pinus elliottii* plantation. Agricultural and Forest Meteorology 95: 237-256.

Neller, J.R. 1918. Studies on the correlation between the production of carbon dioxide and the accumulation of ammonia by soil organisms. Soil Science 5: 225-241.

Oberhauer, S.F., C.T. Gillespie, W. Cheng, R. Gebauer, A. Sala Serra, and J.D. Tenhunen. 1992. Environment effects on CO_2 efflux from riparian tundra in the northern foothills of the Brooks Range, Alaska, U.S.A. Oecologia 92: 568-577.

Olsson, P., S. Linder, R. Giesler, and P. Hogberg. 2005. Fertilization of boreal forest reduces both autotrophic and heterotrophic respiration. Global Change Biology 11: 1745-1753.

Orchard, V.A., and F. Cook. 1983. Relationship between soil respiration and soil moisture. Soil Biology and Biochemistry 15: 477-453.

Palmroth, S., C.A. Maier, H.R. McCarthy, A.C. Oishi, H.-S. Kim, K.H. Johnson, G.G. Katul, and R. Oren. 2005. Contrasting response to drought of forest floor CO_2 efflux in a loblolly pine plantation and a nearby oak-hickory forest. Global Change Biology 11: 421-434.

Pangle, R.E., and J. Seiler. 2002. Influence of seedling roots, environmental factors and soil characteristics on soil CO_2 efflux rates in a 2-year-old loblolly pine (*Pinus taeda* L.) plantation in the Virginia Piedmont. Environmental Pollution 116: 85-96.

Paul, E.A., S.J. Morris, J. Stix, K. Paustian, and E.G. Gregorich. 2003. Interpretation of soil carbon and nitrogen dynamics in agricultural and afforested soils. Soil Science Society of America Journal 67: 1620-1628.

Pearson, T.R.H., S.L. Brown, and R.A. Birdsey. 2007. Measurement guidelines for the sequestration of forest carbon. USDA General Technical Report NRS-18. USDA Forest Service.

Penning de Vries, F.W.T. 1975. The cost of maintenance processes in plants. Annals of Botany 39: 77-92.

Perez-Garcia, J., B. Lippke, J. Comnick, and C. Manriquez. 2005. An assessment of carbon pools, storage, and wood products market substitution using life-cycle analysis results. Wood and Fiber Science 37: 140-148.

Peterjohn, W.T., J.M. Melillo, F.P. Bowles and P.A. Steudler. 1993. Soil warming and trace gas fluxes: experimental design and preliminary flux results. Oecologia 93**:** 18-24.

Pettenkofer, M. 1858. Volumetric estimation of atmospheric carbonic acid. Quarterly Journal of the Chemical Society of London 10: 292-297.

Phillipson, J., J. Putman, J. Steel, and S.R.J. Woodell. 1975. Litter input, litter decomposition and the evolustion of carbon dioxide in a beech woodland-Wytham Woods, Oxford. Oecologia 20: 203-217.

Post, W.M., W.R. Emanuel, P.J. Zinke, and A.G. Stangenberger. 1982. Soil carbon pools and world life zones. Nature 298: 156-159.

Powell, T.L., H.L. Gholz, K.L. Clark, G. Starr, W.P. Cropper, Jr., and T.A. Martin. 2008. Carbon exchange of a mature, naturally regenerated pine forest in north Florida. Global Change Biology 14: 2523-2538.

Potter, R.S., and R.S. Snyder. 1916. Carbon dioxide production in soil and carbon and nitrogen changes in soils variously treated. Iowa Agricultural Experimental Station Research Bulletin 39: 249-309.

Pregitzer, K.S., and E.S. Euskirchen. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10: 2052-2077.

Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri, and C.S. Vogel. 1995. Atmospheric CO_2, soil nitrogen and turnover of fine roots. New Phytologist 129: 579-585.

Qi, Y., and M. Xu. 2001. Separating the effects of moisture and temperature on soil CO_2 efflux in a coniferous forest in the Sierra Nevada mountains. Plant and Soil 237: 15-23.

Raich, J.W., and A. Tufekcioglu. 2000. Vegetation and soil respiration: correlations and controls. Biogeochemistry 48: 71-90.

Raich, J. W., and W. H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B: 81-99.

Ramseur. J.L., L. Parker, and B.D. Yacobucci. Congressional Research Service Report for Congress, Order Code R40556, Market-based greenhouse gas control: selected proposals in the 111th Congress, May 27, 2009. http://www.nationalaglawcenter.org/assets/crs/R40556.pdf.

Reich, P.B., M.B. Walters, and M.G. Tjoelker. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Functional Ecology 12: 395-405.

Reichstein, M., F. Bednorz, G. Broll, and T. Kätterer. 2000. Temperature dependence of carbon mineralization: conclusions from a long-term incubation of subalpine soil samples. Soil Biology and Biochemistry 32: 947–958.

Reinke, J.J., D.C. Adriano, and K.W. McLeod. 1981. Effects of litter alteration on carbon dioxide evolution from a South Carolina pine forest floor. Soil Scientific Society of America Journal 45: 620-623.

Russell, E.J. 1915. Recent investigations on the production of plant food in the soil. Journal of the Royal Horticultural Society 41: 173-187.

Russell, E.J., and A. Appleyard. 1915. The atmosphere of the soil: its composition and causes of variation. Journal of Agricultural Science 7: 1-48.

Russell, E.J., and A. Appleyard. 1917. The influence of soil conditions on the decomposition of organic matter in the soil. Journal of Agricultural Science 8: 385-417.

Ryan, M.G., S.T. Gower, R.M. Hubbard, R.H. Waring, H.L. Gholz, W.P. Cropper Jr., and S. W. Running. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. Biomedical and Life Sciences 101: 133-140.

Ryan, M.G., M.B. Lavigne, and S.T. Gower. 1997. Annual carbon costs of autotrophic respiration in boreal forest ecosystems in relation to species and climate. Journal of Geophysical Research 102: 28,871-28,883.

Samuelson, L.J, K. Johnsen, T. Stokes, and W. Lu. 2004. Intensive management modifies soil CO_2 efflux in 6-year-old *Pinus taeda* L. stands. Forest Ecology and Management 200: 335-345.

SAS Institute Inc., 2003. Version 9.1, Cary, NC: SAS Institute Inc.

Schlesinger, W.H., and J. Lichter. 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature 411: 466-469.

Schmidt, I.K., A. Tietema, D. Williams, P. Gundersen, C. Beier, B.A. Emmett, and M. Estiarte. 2004. Soil solution chemistry and element fluxes in three European heathlands and their responses to warming and drought. Ecosystems 7: 638-649.

Scholes, R.J., and I.R. Noble. 2001. Climate change: storing carbon on land. Science 294: 1012-1013.

Selmants, P.C., S.C. Hart, S.I. Boyle, C.A. Gehring, and B.A. Hungate. 2008. Restoration of a ponderosa pine forest increases soil CO_2 efflux more than either water or nitrogen additions. Journal of Applied Ecology 45: 913-920.

Siitonen, J., P. Martikainen, P. Punttila, and J. Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management 128: 211-225.

Singh, K.P., and C. Shekhar. 1986. Seasonal pattern of total soil respiration, its fractionation and soil carbon balance in a wheat–maize rotation cropland at Varanasi. Pedobiologia 29: 305-318.

Smith, W.B., J.S. Vissage, D.R. Darr, and R.M. Sheffield. 2001. Forest Resources in the United States, 1997. USDA Forest Service, North Central Research Station, NC-GTR-219, St. Paul, MN, 198 pp.

Sprugel, D.G., M.G. Ryan, and J.R. Brooks. 1995. Respiration from the organ level to the stand. In: Resource Physiology of Conifers (eds. Smith, W.K., and T.M. Hinckley), pp. 255-299. Academic Press, San Diego, CA.

Stewart, G.H., and L.E. Burrows. 1994. Coarse woody debris in old-growth temperate beech (*Nothofagus*) forests of New Zealand. Canadian Journal of Forest Research 24: 1989-1996.

Stone, S. and H. Shaw. Executive Summary. Center of Budget and Policy Priorities, July 10, 2009. http://www.cbpp.org/cms/index.cfm?fa=view&id=2871.

Takahashi, A., T. Hiyama, H. Takahashi, and Y. Fukushima. 2003. Analytical estimation of the vertical distribution of CO_2 production within soil: application to a Japanese temperate forest. Agricultural and Forest Meteorology 126: 223-235.

Taras, M.A., and A. Clark III. 1977. Aboveground biomass of longleaf pine in a natural sawtimber stand in southern Alabama. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC, Research Paper, SE-162: 32 pp.

Tate, K.R., D.J. Ross, N.A. Scott, N.J. Rodda, J.A. Townsend, G.C. Arnold. 2006. Post-harvest patterns of carbon dioxide production, methane uptake, and nitrous oxide production in a *Pinus radiata* D. Don plantation. Forest Ecology and Management 228: 40-50.

Teskey, R.O., H.L. Gholz, and W.P Cropper, Jr. 1994. Influence of climate and fertilization on the net photosynthesis of mature slash pine. Tree Physiology 14: 1215-1227.

Torbert, H.A., S.A. Prior, G.B. Runion, M.A. Davis, S.G. Pritchard, H.H. Rogers. 2004. Nitrogen and carbon cycling in a model longleaf pine community as affected by elevated atmospheric CO_2. Environmental Management 33: 132-138.

Tufekcioglu, A., J.W. Raich, T.M. Isenhart, and R.C. Schultz. 2001. Soil respiration within riparian buffers and adjacent crop fields. Plant and Soil 229: 117-124.

Turner, D.P., G.J. Koerper, M.E. Harmon, and J.J. Lee. 1995. A carbon budget for forests of the conterminous United States. Ecological Applications 5: 421-436.

Turpin, H.W. 1920. The carbon dioxide of the soil air. Cornell University Agricultural Experimental Station. Memoir 32: 318-362.

Valentini, R., G. Matteucci, A.J. Dolman, E.D. Schulze, C. Rebmann, E.J. Moors, A. Granier, P. Gross, N.O. Jensen, K. Pilegaard, A. Lindroth, A. Grelle, C. Bernhofer, T. Grunwald, M. Aubinet, R. Ceulemns, A.S. Kowalske, T. Vesala, U. Rannik, P. Berbigier, D. Loustau, J. Guomundsson, H. Thorgeirsson, A. Ibrom, K. Morgenstern, R. Clement, J. Moncrieff, L. Martin, D., J. Beringer, L.B. Hutley, and I. McHugh. 2000. Respiration as the main determinant of carbon balance in European forests. Nature 20:861-865.

Vose, J.M, and M.G. Ryan. 2002. Seasonal respiration of foliage, fine roots, and woody tissues in relation to growth, tissue N, and photosynthesis. Global Change Biology 8: 182-193.

Wahlenberg, W.G. 1946. Longleaf pine: its use, ecology, regeneration, protection, growth, and management. Charles Lathrop Pack Forestry Foundation, Washington, DC: 429 pp.

Waksman, S.A. 1932. Principles of soil microbiology. 2nd ed. Williams and Wilkins Co., Baltimore, MD. 894 pp.

Wan, S., R.J. Norby, J. Ledford, and J.F. Weltzin. 2007. Responses of soil respiration to elevated CO_2 air warming, and changing soil water availability in a model old-field grassland. Global Change Biology 13: 2411-2424.

Wang, W., J. Guo, and T. Oikawa. 2007. Contribution of root to soil respiration and carbon balance in disturbed and undisturbed grassland communities, northeast China. Journal of Biosciences 32: 375-384.

Wang C., and J. Yang. 2007. Rhizospheric and heterotrophic components of soil respiration in six Chinese temperate forests. Global Change Biology 13: 123-131.

Wiant, H.V. 1967. Influence of temperature on the rate of soil respiration. Journal of Forestry 65: 489–490.

Wildung, R.E., T.R. Garland, and R.L. Buschbom. 1975. The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soils. Soil Biology and Biochemistry 7: 373-378.

Winkler, J.P., R.S. Cherry, and W.H. Schlesinger. 1996. The Q_{10} relationship of microbial respiration in a temperature forest soil. Soil Biology and Biochemistry 28: 1067-1072.

Wiseman, P.E., and J.R. Seiler. 2004. Soil CO_2 efflux across four age classes of plantation loblolly pine (*Pinus taeda* L.) on the Virginia Piedmont. Forest Ecology and Management 192: 297-311.

Woodbury, P.B., J.E. Smith, and L.S. Heath. 2006. Land use change effects on forest carbon cycling throughout the southern United States. Journal of Environmental Quality 35: 1348-1363.

Woodbury, P.B., J.E. Smith, and L.S. Heath. 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. Forest Ecology and Management 241: 14-27.

Yu, D., X. Shi, H. Wang, W. Sun, J.M. Chen, Q. Liu, and Y. Zhao. 2007. Regional patterns of soil organic carbon storages in China. Journal of Environmental Management 85: 680-689.

Yuste, J.C., M. Nagy, I.A. Janssens, A. Carrara, and R. Ceulemans. 2005. Soil respiration in a mixed temperate forest and its contribution to total ecosystem respiration. Tree Physiology 25: 609-619.

Zak, J.C., M.R. Willig, D.L. Moorhead and H.G. Wildman. 1994. Functional diversity of microbial communities: a quantitative approach. Soil Biology and Biochemistry 26: 1101–1108.

APPENDICES

Table A.1.1. Ground cover in vines, grasses, herbaceous plants, and poison-oak (*Toxicodendron toxicarium* (Salisb.) Gillis.) for each longleaf pine measurement plot sampled in July 2008.

Plot No.	**Basal Area**	**Ground Cover** Vine	Grass	Herb	Poison-oak
	($m^2 \cdot ha^{-1}$)	(%)			
189	7	9	9	8	2
186	8	32	7	15	3
190	13	5	11	11	0
188	14	11	29	17	2
184	15	4	9	10	4
182	16	3	3	2	2
185	18	4	3	6	9
187	18	9	4	11	4
179	23	13	5	8	0
183	25	7	5	10	1
176	29	23	2	13	9
180	30	11	4	4	3
181	31	9	1	6	3
177	32	20	6	8	0
178	36	13	2	13	8

Table A.1.2. Woody plant biodiversity of plants less than 2.54 cm in diameter at 1.37 m and of plants less than 1.37 m height by longleaf pine measurement plot measured July 2008.

Plot No.	**Basal Area** ($m^2 \cdot ha^{-1}$)	**Species Richness** ($number \cdot plot^{-1}$)	**Shannon-Weaver Diversity Index**
189	7	11	1.8
186	8	6	0.6
190	13	5	1.3
188	14	5	1.1
184	15	7	1.2
182	16	8	1.7
187	18	5	1.3
185	18	10	1.5
179	23	9	1.2
183	25	5	1.3
176	29	5	1.0
180	30	5	1.3
181	31	7	1.1
177	32	6	1.4
178	36	4	1.3

Table A.1.3. Number of woody species less than 2.54 cm in diameter at 1.3 m height on the longleaf pine measurement plots measured July 2008.

Latin name	**Number**
Callicarpa americana L.	30
Cornus florida L.	27
Diospyrus virginiana L.	1
Ilex glabra L.	29
Ilex vomitoria Ait.	8
Licania michauxii Prance.	121
Osmanthus americanus (L.) Gray	1
Pinus palustris Mill.	28
Prunus serotina Ehrh.	5
Quercus alba L.	17
Quercus falcata Michx.	36
Quercus incana Bartr.	12
Quercus laevis Walt.	1
Quercus nigra L.	15
Quercus margaretta Ashe	113
Rhus copallina L.	15
Sassafras albidum (Nutt.) Nees	75
Vaccinium arboreum Marsh.	9
Vaccinium spp.	339

Note: Nomenclature follows Godfrey (1988).