SOIL CO$_2$ EFFLUX ACROSS FOUR AGE CLASSES OF PLANTATION LOBLOLLY PINE (*Pinus taeda* L.) ON THE VIRGINIA PIEDMONT

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(ABSTRACT)

Soil CO$_2$ efflux resulting from microbial and root respiration is a major component of the forest carbon cycle. We undertook this investigation to better understand the nature of soil CO$_2$ efflux of plantation loblolly pine, an important ecological and economical resource in the southeastern United States. Specifically, we hoped to learn how soil CO$_2$ efflux differs both spatially and temporally for four age classes of plantation loblolly pine on the Virginia piedmont. During a 12-month period, soil CO$_2$ efflux was repeatedly measured for four age classes of plantation loblolly pine using a dynamic, closed-chamber infrared gas analyzer. The age classes examined were 1- to 2-year-old, 4- to 6-year-old, 8- to 12-year-old, and 20- to 25-year-old stands. Mean soil CO$_2$ efflux rates measured during the 12-month study were 1.72, 2.58, 2.84, and 2.90 μmol/m^2/s for 1- to 2-year-old, 4- to 6-year-old, 8- to 12-year-old, and 20- to 25-year-old stands, respectively. Stand age had a significant effect on efflux rate during 10 of the 12 monthly sampling sessions. Additionally, mean efflux rates were consistently higher near the tree and a significant positional difference was detected during 8 of the 12 monthly sampling sessions. Mean soil CO$_2$ efflux rates, by position, for the 12-month study were 2.72 and 2.28 μmol/m^2/s for the near and away measurement positions, respectively. Based on monthly mean soil CO$_2$ efflux rates, annual carbon losses were estimated at 651, 976, 1074, and 1082 g C/m^2/yr for 1- to 2-year-old, 4- to 6-year-old, 8- to 12-year-old, and 20- to 25-year-old stands, respectively. Regression analysis was used to examine the influence of soil and climatic factors on seasonal changes in soil CO$_2$ efflux. The most influential factors affecting soil CO$_2$ efflux during the 12-month study were soil temperature, soil moisture, stand age, and measurement position. We believe respiring roots significantly influence soil CO$_2$ efflux of plantation loblolly pine and account for differences observed between stands of different ages as well as spatial differences observed within a given stand.

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Chapter 1: Introduction

In the last 150 years, several anthropogenic phenomena have contributed to changes in the concentrations of certain atmospheric gases. These phenomena, including a burgeoning human population, changing land-use patterns, and the combustion of fossil fuels, have resulted in elevated concentrations of carbon dioxide, methane, and nitrous oxide in the earth's atmosphere (Houghton *et al*. 1983). These gases are referred to as greenhouse gases due to their ability to trap long-wave radiation radiated from the earth's surface. The result is an overall warming of the earth's climate, potentially affecting the world's weather patterns, sea levels, and floral and faunal distributions.

Carbon dioxide is the most important greenhouse gas produced by human activities (World Resources Institute 2000). From an examination of Antarctic ice core samples, scientists have estimated that atmospheric carbon dioxide levels were relatively stable during the previous millennium at a concentration of 280-ppm (National Research Council 1998). With current atmospheric carbon dioxide concentrations averaging 360-ppm, it is hoped that future levels will be stabilized between 350 and 700-ppm (Sarmiento and LeQuere 1995). Of the 1834 million metric tons carbon equivalent (MMTCE) of greenhouse gases emitted by the United States in 1998, 80% or 1468 MMTCE were carbon dioxide (U.S. Environmental Protection Agency 2000). The chief source of this carbon dioxide emission is fossil fuel combustion for electricity production and for transportation.

In 1997, the parties to the United Nations Framework Convention on Climate Change met in Kyoto, Japan, and negotiated legally binding reductions in six greenhouse gases that result directly from human activities. If ratified, the Kyoto Protocol will require member nations to reduce greenhouse gas emissions to specific levels below 1990 emissions. The United States negotiators agreed to a 7% reduction below its 1990 baseline level of 1650 MMTCE. These binding reductions would have to be attained during the first commitment period between 2008 and 2012. If the United States ratifies the Kyoto Protocol, greenhouse gas emissions will have to be cut by roughly 650 MMTCE per year compared to expected emission rates of 2010 (Laitner 1999). Managing carbon dioxide emissions will require efforts, legislated or voluntary, by

society to reduce the consumption of fossil fuels. Efforts to improve energy efficiency and to develop alternative fuel sources will be necessary to achieve the required reductions.

Another important component in mitigating atmospheric carbon dioxide enrichment is photosynthesis. Photosynthesis is a fundamental physiological process of trees, whereby carbohydrates are synthesized from water, carbon dioxide, and the sun's radiant energy. While this process is vital to the tree's subsistence, it may also prove vital to maintaining earth's climate. Trees can potentially influence climate change through photosynthesis by absorbing large quantities of carbon dioxide from the atmosphere and storing carbon in above and belowground biomass. Trees, their associated organisms, and their environment (collectively known as forests) also act as a source of carbon dioxide to the atmosphere through aerobic respiration, the process whereby carbohydrates are consumed by organisms for energy production. Forest soils, in particular, are an important component in the efflux of carbon to the atmosphere. Soils contain from 50% (tropical) to 80% (boreal) of all carbon in forested ecosystems (Brown 1996). Because forest soils are such a critical component of the forest carbon balance, it is imperative that resource managers understand the components and controls of soil CO_2 efflux. Without a thorough understanding of these components and controls, managing forests for global climate amelioration will prove to be a difficult task.

Soils are but one component of an intricate global carbon cycle, which consists of several large pools between which carbon is constantly moving. The earth contains about 10^8 Pg of carbon (1 Pg C = 10^{15}g C), which is distributed across seven principal pools. Geologic formations in the earth's crust by far represent the largest accumulation of carbon at 90,000,000 Pg. The oceans contain the second largest pool of carbon at 39,973 Pg. The majority of ocean carbon (38,800 Pg) is in dissolved carbonates. Gas hydrates, primarily methane hydrate, contain 10,000 Pg C and fossil fuels account for 4,000 Pg C. Soil, atmospheric, and terrestrial vegetation pools are estimated at 1600, 750, and 610 Pg C, respectively (Rustad *et al*. 2000; Brown 1996; Schimel *et al*. 1995). Brown (1996) estimated that the world's forests contain 340 Pg C in live and dead biomass both above and belowground and 618 Pg C in mineral soil and the O horizon. Accordingly, forests account for about 55% of the terrestrial vegetation carbon pool and about 41% of the soil

carbon pool. Within the forest component, tropical forests possess about 62% of global forest vegetation carbon, while boreal forests possess about 54% of global forest soil carbon. Temperate forests contain about 15% of global forest vegetation carbon and about 11% of global forest soil carbon.

The most significant and active carbon exchange occurs between the atmosphere, the oceans, and terrestrial systems. The ocean and atmosphere currently act as net sinks for carbon at estimated rates of 2.0 and 3.3 Pg C per year, respectively. Fossil fuel burning and land-use changes act as net sources of carbon at estimated rates of 5.4 and 1.6 Pg C per year, respectively (Rustad *et al*. 2000). A comparison of these sinks and sources indicates that an imbalance of 1.7 Pg C per year exists. Brown (1996) surmised that a majority of the imbalance may be due to an actual carbon sink in the tropical latitudes, which has not been captured in theoretical models used to estimate carbon flux for tropical forests. In preparing a global carbon budget, Craig and Holmen (1995) found a similar "missing sink" of 1.7 Pg C per year. However, they attributed the sink to mid-latitude temperate and boreal forests that have undergone enhanced growth due to afforestation, reforestation, nitrogen fertilization, and increased atmospheric carbon dioxide levels.

Intensively managed loblolly pine (*Pinus taeda* L.) stands account for over 13 million hectares of forested land in the southeastern United States (Schultz 1997). Collectively, the southern United States supplies approximately 60% of the nation's total wood production. Due to its significant economic importance, there may be more scientific knowledge of loblolly pine and its stand biology than any other tree species in the world.

The economic importance of southern timber production, especially plantation loblolly pine, is manifest. However, the importance of the extensive ecosystem services that the southern forests provide should not be overlooked. Perhaps one of the most important ecosystem services provided by the southern forests is that of carbon sequestration (Schlesinger 1995). Carbon sequestration, through the process of photosynthesis and wood production, provides a negative feedback to the accumulation of carbon dioxide in the earth's atmosphere due to the combustion of fossil fuels. Birdsey *et al.* (1993) found that carbon stored on U.S. timberland has increased by 38%

since 1952. This increase in carbon sequestration, primarily in the northeastern and southern U.S., can be attributed to the reforestation of approximately 10 million hectares of agricultural lands in these regions. As a result, afforestation and continuous advancements in the pursuit to increase forest ecosystem productivity may result in the sequestration of significant amounts of carbon on the global scale. Furthermore, increasing ambient carbon dioxide concentrations in the atmosphere will result in enhanced carbon sequestration by producing a fertilization effect on forests. Carbon dioxide fertilization results in greater water-use efficiency and decreased photorespiration during gas exchange and carbon fixation (Groninger *et al*. 1999). Increased carbon fixation under increasing ambient carbon dioxide concentrations could further enhance the role of forests as carbon sinks.

   While the accumulation of carbon as aboveground plant biomass is apparent, forest ecosystems also store significant amounts of carbon belowground in the form of root systems and forest litter in various stages of decomposition. Huntington (1995) estimates that soils contain 70% of all carbon in the forest ecosystem. Jobbagy and Jackson (2000) calculated that temperate evergreen forests contain 20.4 kg C/m^2 in the top three meters of soil. The management of forests for timber production can have a significant impact on soil carbon dynamics through the use of management tools such as fertilization, site preparation, vegetation control, and shortened rotation lengths.

   Hoover *et al*. (2000) estimated that 20% of soil carbon is lost during intensive site preparation following harvest of southern pine plantations alone. The accumulated effect of intensive forest management may be elevated rates of soil CO_2 efflux and thus reduced rates of net carbon sequestration. The magnitude of carbon stored in forest soils suggests that a better understanding of the effects of intensive forest management on soil CO_2 efflux rates is necessary. Empirical modeling is an important tool for understanding soil CO_2 efflux and for identifying the environmental factors that influence it. Specifically, modeling soil CO_2 efflux is essential to producing an integrated assessment of net ecosystem productivity (NEP) in the southern pine system. Such knowledge will be essential for facilitating policy and management decisions conducive to maintaining southern forests as overall carbon sinks.

Due to its importance in the southern forest and its simpler biological and physical diversity relative to natural systems, the loblolly pine plantation provides an appropriate medium for modeling soil CO_2 efflux. In this study, we investigated the effect of stand age on temporal and spatial patterns of soil CO_2 efflux for plantation loblolly pine on the Virginia piedmont. Stand age and measurement position were applied as independent variable treatments and the response variables soil CO_2 efflux rate, soil temperature, and volumetric soil moisture content were measured monthly over a 12-month period. Soil temperature and soil moisture were chosen as additional response variables due to the known correlation between these parameters and soil CO_2 efflux. At the end of the 12-month period, an intensive sampling session was conducted to quantify other site parameters thought to be significant variables in predicting soil CO_2 efflux rates. These site parameters included coarse fragment content, coarse woody debris content, litter content, live root biomass, nutrient content, and stem volume.

Specific Objectives

1. Characterize soil CO_2 efflux both spatially and temporally across four age classes of plantation loblolly pine.

2. Examine the effect of stand age on soil CO_2 efflux for plantation loblolly pine.

3. Examine the effect of soil temperature, soil moisture, and other site parameters on soil CO_2 efflux for plantation loblolly pine.

4. Develop empirical models describing the relationship between soil CO_2 efflux and the above parameters for plantation loblolly pine.

Hypotheses

1. As loblolly pine stands mature, soil CO_2 efflux rates will increase significantly due to increasing root biomass and litter inputs.

2. Soil CO_2 efflux rates will be significantly higher near the tree versus away from the tree due to the greater quantity of respiring roots near the tree.

3. As loblolly pine stands mature, the differences in soil CO_2 efflux rates measured near and away from the tree will diminish due to decreasing soil organic matter heterogeneity and decreasing fine root heterogeneity.

4. Soil temperature, soil moisture, and other site parameters will be significant parameters in predicting soil CO_2 efflux rates for plantation loblolly pine.

Chapter 2: Literature Review

2.1: Soil CO_2 Efflux – Components

The majority of soil CO_2 evolves from the metabolic activities of soil organisms (Mielnick and Dugas 1999). Both heterotrophic and autotrophic organisms contribute to soil CO_2 efflux through respiration. An additional, non-metabolic source of soil CO_2 is chemical oxidation of soil minerals. Kelting *et al.* (1998) described the movement of soil carbon between three compartments: plant root tissue, the rhizosphere, and root-free soil. The rhizosphere is the soil matrix in close proximity to plant roots and supports a large microbial community that utilizes root-derived organic matter as its primary energy substrate. Root-free soil supports a smaller microbial community, deriving nourishment via secondary products diffused from soil organic matter.

Photosynthetically fixed carbon accounts for the majority of soil organic matter through litterfall, root exudates, and root mortality (van Veen *et al.* 1991). Faunal mortality also contributes to the organic matter pool. Heterotrophic organisms (microbes and other soil fauna) release CO_2 as they consume soil organic matter. Plant root respiration makes a significant contribution to soil CO_2 efflux when carbon fixed aboveground is assimilated by the plant into root tissue and other compounds belowground.

The contribution of plant roots to overall soil CO_2 efflux varies depending on a myriad of factors including biome, season, stage of succession, and microclimate. In reviewing previous studies, Raich and Tufekcioglu (2000) found that root respiration reportedly accounts for 50-93% of soil CO_2 efflux on the arctic tundra. Estimates for root respiration contribution in grasslands range from 17% to 60% (Kucera and Kirham 1971; Dugas *et al.* 1999). In temperate forests, plant roots produce an estimated 40-50% of total soil CO_2 (Epron *et al.* 1999; Ohashi *et al.* 2000). Maier and Kress (2000) found that root respiration accounted for 52% and 73% of total soil CO_2 efflux in non-fertilized and fertilized loblolly pine stands, respectively. In assessing soil CO_2 efflux for a two-year-old loblolly pine plantation on the Virginia piedmont, Pangle (2000) attributed 30% of total soil CO_2 efflux on an annual basis to root respiration. This estimate was derived through comparison of efflux rates near and away from the pine seedlings. Efflux rates

were on average 39% and 65% higher near the seedlings during the growing season and winter season, respectively. The investigator attributed these differences to the absence of pine roots at the away position, which was confirmed upon seedling root system excavation.

In a recent review of soil respiration studies, Hanson *et al.* (2000) found that as little as 10% to more than 90% of forest soil CO_2 efflux has been attributed to plant roots by various investigators. For pine forests in particular, they found a range of 35-62% contribution by root respiration. They attributed the large range of estimates to variation in forest cover type, the time of year when measurements were taken, and varying methodologies. Quantifying the contribution of roots to soil CO_2 efflux has proven problematic to many researchers. Methods utilized in previous research include component integration, root exclusion, and carbon isotope techniques (Hanson *et al.* 2000). Component integration calculates total soil CO_2 efflux by summing the rate for each soil compartment measured separately. Similarly, root exclusion calculates total soil CO_2 efflux as the difference between fluxes with and without roots in the soil medium. Exclusion techniques include trenching, root removal, and root gap analysis. Carbon isotopes have also been used to follow the movement of carbon through the soil compartments and ultimately as soil CO_2 efflux. These techniques have limitations, however, due to gross soil disturbance, improper extrapolation to larger systems, and inadequate replication of natural conditions. Despite the large range of component contribution estimates, it is apparent that plant roots exert significant influence on soil CO_2 efflux.

2.2: Soil CO_2 Efflux – Temperature and Moisture Dependence

Temperature and precipitation are considered the most influential environmental factors affecting soil CO_2 efflux rates because they interact to influence the productivity of terrestrial ecosystems and the decomposition rate of detritus/soil organic carbon (Schlesinger 1977, Singh and Gupta 1977, Raich and Schlesinger 1992). Reinforcing this notion is the fact that the highest average soil CO_2 efflux rates are usually observed in tropical evergreen forest ecosystems while the lowest rates are usually observed in tundra ecosystems. In tropical forests, primary productivity is high and decomposition rates are

seldom limited by temperature or moisture constraints. In contrast, primary productivity in tundra ecosystems is low and decomposition rates are often constrained by low temperatures and excessive soil moisture.

The response of soil respiration to temperature and moisture content varies with extremities in either factor. According to Schlentner and Van Cleve (1985), temperature increases have little effect on respiration at gravimetric water contents below 75%; however, respiration is quite responsive to temperature changes at higher gravimetric water contents (100-250%). Similarly, changes in moisture content have little effect on respiration at temperatures below 5°C while respiration is quite responsive to moisture changes at temperatures between 10°C and 20°C. Wildung *et al*. (1975) examined the effects of soil temperature and soil moisture content on soil CO_2 efflux rates in arid grassland soils of Washington State. While soil temperature alone was not significantly correlated with efflux changes, they noted that soil temperature and efflux were positively correlated when volumetric soil moisture was greater than 10%. The investigators concluded that soil CO_2 efflux was controlled by the interaction of soil temperature and soil moisture content.

Aerobic respiration is a basic chemical reaction involving enzymatic processes with reaction velocities that vary directly with temperature. As with most metabolic processes, respiration is limited by both minimal and maximal temperature extremes. Temperatures at or below freezing slow enzyme activity and may damage cellular structure. While studying plant cellular processes, Larcher (1995) found that at temperatures above 40°C biochemical reactions proceed so quickly that respiration declines due to a shortage of respiratory substrates. At 50°C and higher, enzyme function and cellular membrane integrity began to fail, causing mitochondrial respiration to cease.

Soil moisture content has a significant impact on microbial populations. Orchard and Cook (1983) investigated the impact of soil drying and rewetting on microbial populations. As soil dries, the relative contribution of bacteria and fungi to soil respiration changes. The investigators found that bacterial activity declines sharply as water potential falls (-0.05 to -0.3 MPa) and is negligible at -1.5MPa. Bacteria live in water films on soil particles. These water films allow diffusion of nutrients toward and waste products away from the bacteria and quickly dissipate at water potentials between

–0.02 and –0.1 MPa. Fungi remain viable at lower water potentials by hyphal extension, bridging air-filled pores and actively exploring for nutrients (Griffin 1969).

As soils near saturation, oxygen availability is generally less than adequate for aerobic respiration. Gaarder (1957) found that aerobic microbial respiration reached maximum values when the moisture content was 30-45% of water holding capacity. Increasing soil moisture beyond that range resulted in decreased microbial activity. Rovira (1953) found a similar trend of increasing soil CO_2 efflux with increasing moisture contents until near saturation at which point microbial activity was depressesed. Furthermore, Howard and Howard (1993) found that organic matter content, which increases the water holding capacity, modified the influence of moisture content on respiration. Soil porosity also modifies the influence of moisture content on respiration. Bouma and Bryla (2000) found that soil efflux from a fine textured soil was more restricted than from a coarse textured soil after watering. The greater macropore density of a coarse textured soil allows drainage to occur more quickly. Furthermore, the transport of gases is greater through a more porous soil and will accelerate CO_2 evolution from the soil surface.

The relationship between soil CO_2 efflux and temperature has been studied in many different terrestrial ecosystems. Lawrence and Oechel (1983) studied root respiration of taiga seedlings under varying soil temperatures. Holding soil moisture near field capacity, the investigators observed a fourfold increase in total root respiration over a temperature range of 5 to 25°C. Zogg *et al*. (1996) studied fine root respiration of sugar maple (*Acer saccharum* Marsh.) under different levels of nitrogen availability in four northern hardwood stands in the Great Lakes region. Live roots were collected from each site and respiration was measured over a 35-minute period using a gas-phase oxygen electrode. Increasing respiration rates corresponded closely to increasing soil temperature.

MacDonald *et al*. (1999) studied the impact of soil warming on carbon loss for a northern hardwood site in Michigan. Surface and subsurface soil cores were incubated at both normal and elevated temperatures and gas samples were analyzed biweekly over a 32-week period. While respiration rates were higher for elevated temperature cores, the difference was not significant. Ewel *et al*. (1987) examined soil CO_2 evolution in Florida

slash pine (*Pinus elliotii* Engelm.) plantations using a portable infrared gas analyzer. Soil CO_2 efflux, soil temperature, and soil moisture were measured in 9-year-old and 29-year-old plantations on a monthly basis for one year. Regression equations showed that the natural logarithm of soil CO_2 evolution was strongly related to soil temperature for both the 9-year-old site (R^2=0.89) and the 29-year-old site (R^2=0.75).

Maier and Kress (2000) examined respiration rates in an 11-year-old loblolly pine plantation in North Carolina for an entire year. Respiration rates were measured for roots as well as mineral soil with and without intact litter horizons. Respiration rates were highest for all three components during the warmest months of the year. The investigators reported a strong correlation (R^2=0.70) between soil CO_2 efflux and soil temperature at a depth of 7 cm. Pangle (2000) studied soil CO_2 efflux response to mulching and fertilization for a 2-year-old loblolly pine plantation on the Virginia piedmont. Soil CO_2 efflux, soil temperature, and soil moisture content were measured on a monthly basis over a 13 month period. Regression analyses were performed to examine significant environmental, soil, and biomass parameters influencing soil CO_2 efflux. For the 13-month sampling period, soil temperature alone explained 42% of soil CO_2 efflux variation.

Popescu (2001) found similar temperature dependence of soil CO_2 efflux for naturally regenerated and planted clear-cuts on the Virginia piedmont. The investigator measured soil CO_2 efflux, soil temperature, and soil moisture for loblolly pine, shortleaf pine (*Pinus echinata* Mill.), and eastern white pine (*Pinus strobus* L.) on a biweekly basis for 7 months. Regression analysis of monthly treatment means (n=96) over the entire sampling period found that soil temperature explained 51% of the variation in soil CO_2 efflux.

While the temperature dependence of soil CO_2 efflux is clear, there has been difficulty in describing the relationship mathematically. Lloyd and Taylor (1994) evaluated the adequacy of various mathematical relationships using 15 data sets collected by various researchers in terrestrial ecosystems around the world. Simple linear, exponential (Q_{10}), and Arrhenius relationships were evaluated for their ability to predict soil respiration rates in the absence of soil moisture limitations. The investigators

rejected a simple linear relationship outright simply by graphing respiration as a function of temperature and observing marked curvilinearity.

According to Lloyd and Taylor (1994), the Q_{10} relationship was first described by van't Hoff in 1898 and applies to many chemical reactions with temperature dependence. The Q_{10} relationship is exponential and is defined as the ratio of the rate of respiration at temperature T to the rate at temperature $T + 10^{o}C$. The investigators found that the best-fit curve for the 15 data sets (n=149) gave a Q_{10} of 2.4 and explained 70% of the variation in respiration as a function of temperature. However, they also found that the exponential form underestimated respiration rates at low temperatures and overestimated at high temperatures. Based on their results, they concluded that the relationship between respiration and temperature is not a simple exponential over the normal range of physiological temperatures.

The investigators also evaluated an Arrhenius type dependence of respiration rate upon temperature. Arrhenius derived his rate equation in 1889 through experimentation with a theoretical equation derived by van't Hoff 14 years earlier. The Arrhenius equation is an exponential function that accounts for activation energy of a chemical process. However, the equation assumes constant activation energy across a range of temperatures and while more predictive than the simple exponential relationship (R^2=0.74), it too is inadequate, similarly underestimating respiration rates at low temperatures and overestimating respiration rates at high temperatures.

The investigators found that the relationship between respiration and temperature was best described by an Arrhenius type equation where the effective activation energy for respiration varies inversely with temperature. The equation produced the best fit for the data set studied with R^2=0.79 and provided an accurate, unbiased estimate of soil respiration rates across a wide range of ecosystem types and soil temperatures.

Yet the empirical convenience of the Q_{10} relationship for examining temperature effects on respiration over a limited temperature range can not be discounted. For this reason, Q_{10} values continue to be reported in the literature and are convenient for comparisons across studies. Q_{10} values cited across a range of studies vary from 1.3 to 3.3 (Raich & Schlesinger 1992). Similarly, Howard and Howard (1993) reported Q_{10} values that ranged from 1.96 to 2.83 over a range of soil types and temperatures. For

loblolly pine, Maier and Kress (2000) reported Q_{10} values of 2.2 and 2.4 in fertilized and non-fertilized stands, respectively.

Several reasons have been proposed for differences in Q_{10} values across different studies. An important consideration is differences in soil moisture content. As alluded earlier, moisture extremes limit the response of respiration to temperature. Another consideration is the use of air temperature versus soil temperature. Air temperature tends to fluctuate more in vegetated sites than soil temperature (Raich and Potter 1995). Also, a decrease in Q_{10} with increasing temperature is a long-known phenomenon (Slator 1906) and is most likely due to different temperature sensitivities of the various contributors to soil CO_2 efflux. Vegetation type may also be responsible for variation in Q_{10} values. Cover types differ in allocation of carbon between above and belowground biomass, quantity and quality of litter, soil floral and faunal diversity, and soil microclimate and structure (Raich and Tufekcioglu 2000).

2.3: Soil CO_2 Efflux – Temporal and Spatial Characteristics

To a large extent temporal and spatial variation in soil CO_2 efflux is driven by the effect of variation in soil temperature and soil moisture on root and microbial respiration. However, we are quickly learning that variation in root biomass distribution significantly explains spatial variation in soil CO_2 efflux as well.

For most ecosystems, a change of the seasons is manifested by a change in precipitation patterns and/or daily average temperatures. Given the temperature and moisture dependence discussed earlier, it is not surprising that soil CO_2 efflux exhibits a seasonal trend. In a study of a 2-year-old loblolly pine plantation on the Virginia piedmont, Pangle (2000) observed a yearlong maximum for mean soil CO_2 efflux rate (2.48 $\mu mol/m^2/s$) when mean soil temperature rose to 21.8^{o}C during the month of September. In contrast, the yearlong minimum for mean soil CO_2 efflux rate (0.14 $\mu mol/m^2/s$) was observed when mean soil temperature fell to a yearlong minimum of 2.7^{o}C during the month of January. Interestingly, the maximum mean soil temperature for the yearlong study was recorded in August (32.8^{o}C), but mean soil CO_2 efflux rate failed to reach a yearlong maximum at that time due to extremely low mean soil moisture

content (8% volumetric). This is yet another example of soil moisture modifying the effect of soil temperature on soil CO_2 efflux.

Popescu (2001) found similar seasonal trends for soil CO_2 efflux in a study of a naturally regenerated and a planted clear-cut on the Virginia piedmont. Soil CO_2 efflux rates varied from a mean high of 4.19 $\mu mol/m^2/s$ at the beginning of September to a mean low of 0.265 $\mu mol/m^2/s$ in December. The mean soil temperature for September was 26.2^{o}C while the mean soil temperature for December was 4.2^{o}C. Ewel *et al*. (1987) found similar seasonal trends in 9- and 29-year-old Florida slash pine plantations. Average CO_2 evolution rates during the summer season were approximately twice as fast as average rates during the winter season.

While short-term (seasonal) temporal variation in soil CO_2 efflux has been well documented, long-term temporal variation has received less attention. Of particular interest is the effect of vegetation succession/maturation over extended periods of time (years). The few studies that have examined the effect of vegetation age on soil respiration suggest that soil respiration increases with age. Soil respiration most likely increases due to an increase in total respiring root biomass (Makkonen and Helmisaari 2001). In studying Florida slash pine plantations, Ewel *et al*. (1987) found soil CO_2 evolution rate for a 29-year-old plantation was 35% higher than for a 9-year-old plantation. The investigators concluded that the increase in soil CO_2 evolution rate for the 29-year-old plantation was due primarily to the nearly threefold increase in live root biomass. Similarly, a 35% increase in soil CO_2 evolution rate was observed in a comparison of young and mature Costa Rican lowland forests (Raich 1983).

Vegetation succession/maturation also spurs an increase in specific microbial respiration (microbial respiration rate/unit microbial biomass). In a study of a southern Australia mixed boreal forest, Bauhus *et al*. (1998) found that specific microbial respiration generally increased with stand age. Mathes and Schriefer (1985) investigated soil respiration from the beginning of secondary succession of a newly exposed rubble-dump in Germany. The investigators found that soil respiration increased during the first three years following reclamation and attributed this increase to the succession of soil microflora. Generally, increases in microbial respiration with vegetation

succession/maturation can be attributed to an increase in organic matter input via litterfall and root mortality.

Spatial variation in soil CO_2 efflux may be explained by variation in root biomass distribution. Pangle (2000) observed that young seedling roots had a consistent, significant influence on soil CO_2 efflux spatial patterns in loblolly pine plantations on the Virginia piedmont. The investigator observed efflux rates near seedlings that were on average 39% and 65% higher during the growing season and winter season, respectively, compared to rates in plots away from the influence of seedling roots. Thomas *et al*. (1996) found similar spatial trends in studying the effect of seasonal root distribution on soil CO_2 efflux for one-year-old *Pinus radiata* trees. The investigators observed that root distribution decreased with horizontal distance from the tree and that 35% of the total root density was concentrated within a 0.15-m radius from the tree stems. Popescu (2001) also found a consistent trend of higher soil CO_2 efflux rates near seedlings in both a naturally regenerated and a planted clear-cut on the Virginia piedmont. Interestingly, the investigator also found higher organic matter contents near seedlings, but determined through analysis of covariance that positional differences still had a significant effect on soil CO_2 efflux rates. The investigator attributed significant correlation between organic matter and seedling proximity to several causes, including rapid turnover of seedling roots, planter bias, and the influence of slope on the interception of eroded organic matter by the seedlings.

These conclusions for the influence of root biomass distribution on soil CO_2 efflux generally assume that microbial respiration does not significantly vary on a spatial basis within a stand. To more completely understand root distribution influence on soil CO_2 efflux, future research should focus on spatial patterns in both root and microbial respiration.

2.4: Soil CO_2 Efflux – Biome Influence

Soil CO_2 efflux has been measured for many biomes on Earth. Quite expectedly, efflux rates vary greatly on a global basis. These differences appear to be driven by the climate and vegetation inherent to a particular biome. Raich and Schlesinger (1992) compiled soil respiration studies from around the globe and summarized their findings by

biome. They reported tropical lowland forests, temperate forests, and tropical grasslands as having the highest annual soil respiration rates, estimated at 1092, 662, and 629 g $C/m^2/year$, respectively. Desert scrub vegetation, swamps and marshes, and tundra had the lowest annual respiration rates at 224, 200, and 60 g $C/m^2/year$, respectively. Intermediate annual respiration rates were found for cultivated lands, temperate grasslands, and boreal forests at 544, 442, and 322 g $C/m^2/year$, respectively.

Raich and Tufekcioglu (2000) investigated the influence of vegetation type on soil respiration rates by analyzing the results from a number of studies. Soil respiration rates measured in forests, grasslands, and cropped fields using similar methods, sampling period, topography, and soil characteristics were analyzed. The investigators found that soil respiration rates on grasslands were approximately 25% higher than nearby cropped fields on average. Similarly, grassland rates were approximately 20% higher than rates observed in nearby forests. The investigators concluded that the higher grassland rates could be attributed to a greater allocation of productivity to belowground biomass.

Jackson *et al*. (1996) investigated the allocation of above/belowground biomass in a review of 250 studies. They found that root to shoot ratios were the highest in tundra, grassland, and cold desert biomes. In contrast, forest biomes were observed to have the lowest root to shoot ratios. These biomass allocations undoubtedly represent survival strategies adapted by plants in their respective biomes. In those biomes where productivity allocation to the root system is greatest (tundra, grassland, desert), soil conditions can see extremes in temperature, moisture, and nutrient quality. The vegetation has a lesser influence on soil microclimate and a well-developed root system is necessary to exploit the often-impoverished soil volume. In contrast, plants in forest biomes face inter/intraspecific competition for light and have adapted (on the most basic level) by being taller than competitors. Height, of course, requires greater productivity allocation to stem biomass, which also results in a more mesic soil environment due to buffering of soil microclimate.

Despite the fact that they have a greater allocation of productivity to aboveground biomass, forests still have the greatest root biomass per unit of land area (Jackson *et al*. 1996). Specifically, tropical forests have the greatest root biomass per unit of land area, followed by other forest biomes and sclerophyllous shrublands, which both possess

similar root biomass averages. Root biomass per unit of land area is lowest in croplands, deserts, grasslands, and tundra.

Biomes also differ in the vertical distribution of soil organic carbon (Jobbagy and Jackson 2000). Tropical deciduous forests, tropical grasslands/savannas, temperate grasslands, sclerophyllous shrublands, and deserts possess a higher percentage of total organic carbon in the second and third meters of soil in comparison to tropical evergreen forests, temperate evergreen/deciduous forests, boreal forests, and tundra. At greater depths, soil carbon is highly decomposed and is less likely to be affected by disturbance resulting from changes in land use or from forest management. In forest biomes, however, a significant portion of soil organic carbon is present in non-decomposed forest floor litter and in surface soil horizons; therefore it is prone to significant losses following disturbance.

Finally, biomes differ in net primary productivity (NPP), which is an important factor in differentiating soil CO_2 efflux patterns across biomes. One method of estimating NPP is by measuring litterfall input. Litter (along with dead roots) serves as the primary substrate for microbial decomposition, which is a primary component of soil CO_2 efflux. Based on these premises, it is surmised that soil CO_2 efflux will be greater for biomes with greater NPP. Raich and Schlesinger (1992) used data from 171 separate studies to model annual NPP and annual soil respiration rates. Regression analysis demonstrated that the two variables were highly correlated (R^2=0.87). In a study of primary productivity allocation to belowground biomass, Raich and Nadelhoffer (1989) analyzed the results from 30 studies for forest biomes. The investigators found that annual litterfall inputs and annual soil respiration rates were well correlated (R^2=0.71).

2.5: Soil CO_2 Efflux – Harvest and Site Preparation Influences

Timber harvest and site preparations have a profound effect on the physical and chemical properties of forest soil. Significant changes are observed in soil temperature, soil moisture, soil organic matter content, soil strength, and soil aeration depending on the method of harvest and intensity of site preparation. As a result, immediate changes are seen in soil CO_2 efflux as well.

Harvesting and site preparation have been observed to both increase and decrease soil CO_2 efflux compared to undisturbed sites (Edwards and Ross-Todd 1983, Ewel *et al*. 1981, Toland and Zak 1994). The efflux response seems to be rather site specific and depends heavily on how the above soil parameters are changed by disturbance. A fairly predictable outcome following harvest is an increase in soil temperature due to removal of the forest canopy and to disturbance of the litter layer. Another predictable outcome is root mortality.

However, post-harvest response of soil moisture is less predictable. Some post-harvest sites experience decreases in moisture in soil surface horizons (0-15 cm), some experience increases, and others experience increased moisture at depth with pronounced drying at the soil surface (Edwards and Ross-Todd 1983, Ewel *et al*. 1981, Londo *et al*. 1999). Soil microbe response to harvesting and site preparation also appears to be site-specific. Lundgren (1982) noted that clear-cutting of a 120-year-old Scots pine (*Pinus sylvestris* L.) forest in Sweden initially resulted in increases in bacterial biomass, but by the third year, bacterial biomass had decreased to levels lower than the uncut control plots. On the same site, Sohlenius (1982) observed a temporary increase in nematode populations during the second year following clear-cut harvest. In contrast, microarthropod populations were approximately 50% lower one year after clear-cutting of a southern Appalachian watershed (Seastedt and Crossley 1981). Hendrickson *et al*. (1985) also observed that microbial respiration was significantly lower during the first year following harvest of a mixed conifer and hardwood forest in Ontario. However, they observed that bacterial populations increased in both the forest floor and mineral soil of harvested plots compared to controls. Apparently, the microbial response depends heavily on the level of disturbance of the forest floor as well as the intensity of the harvest and the resultant effect on soil microclimate and organic matter inputs. As can be seen in the following citations, the response of soil CO_2 efflux to harvesting and site preparation varies across sites and the causes for change in efflux are usually attributed to changes in the above soil parameters.

Nakane *et al*. (1986) attributed significantly lower soil respiration rates one year after clear-felling in a Japanese red pine (*Pinus densiflora* Sieb. & Zucc.) forest to a lack of root respiration and decreased microbial respiration. Similarly, Mattson and Swank

(1989) observed significantly lower efflux rates in a clear-cut mountain watershed of western North Carolina compared to an uncut control watershed. They, too, attributed the lower efflux rates to less live root biomass and slower rates of decomposition of soil detrital carbon pools. Striegl and Wickland (1998) also cited root death and reduction in microbial activity as the cause of a 40% decrease in efflux rate one year after clear-cutting of jack pine (*Pinus banksiana* Lamb.) woodland in Saskatchewan, Canada. In addition, Popescu (2000) found a 27% decrease in efflux rate after clear-cutting of a Virginia pine (*Pinus virginiana* Mill.)/mixed hardwood forest on the Virginia piedmont and cited the same factors as above for this reduction.

Ewel *et al.* (1987) examined soil CO_2 efflux in a clear-cut, 9-year-old, and 29-year-old Florida slash pine plantation. The highest annual efflux rate was observed in the clear-cut followed by the 29- and 9-year-old plantations. The investigators rationalized the elevated clear-cut efflux rate as a short-term response to fresh organic matter (branches, needles, and roots incorporated into the soil during the harvest operation) and to higher observed soil temperatures, both of which spurred microbial activity. Londo *et al.* (1999) also observed elevated soil CO_2 efflux rates in clear-cut plots during the first 16 months following harvest of a 65-year-old bottomland hardwood forest in Texas. Clear-cut efflux rates were higher than both partial harvest plots and non-harvest control plots and all efflux rates were significantly different than one another. The investigators attributed the higher clear-cut efflux rates to increased microbial activity, decaying root biomass, and a substantial increase in herbaceous species germination and rooting activity.

Lytle and Cronan (1998) examined the effects of clear-cutting on soil CO_2 efflux in a spruce-fir forest growing on poorly drained soils in Maine. The investigators attributed higher efflux rates in harvested plots to decomposition of elevated root necromass due to the fact that litter decomposition rates did not differ between harvested and unharvested plots. Furthermore, the investigators concluded that soil CO_2 efflux on the harvested sites was not as heavily influenced by root respiration losses as is typically observed in other studies.

Still other researchers have observed little or no effect on soil CO_2 efflux from harvesting and site preparation. Toland and Zak (1994) observed very little difference in

annual efflux rates between clear-cut and unharvested hardwood stands in northern Michigan one year after harvest. The investigators concluded that a decrease in root respiration in the harvested plots was offset by an increase in microbial respiration. Marra and Edmonds (1996) also observed little effect on soil CO_2 efflux from clear-cutting western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)/Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands on the Olympic Peninsula of Washington State. The investigators reported that over a 13-month period, average efflux rates on the clear-cut site differed little from rates in a nearby old growth stand. Seasonal differences were noted, however, with higher efflux rates on the clear-cut site during the summer months and higher efflux rates in the old growth stand during the winter months. The investigators attributed these seasonal efflux differences to soil temperature variation because the clear-cut stand had a higher average summer temperature and a lower average winter temperature. Furthermore, coarse woody debris decomposition did not significantly differ between the clear-cut and old growth stands for any of five different decay classes examined.

2.6: Soil CO_2 Efflux – Measurement Techniques

Many different techniques have been used for measuring soil CO_2 efflux. Choosing an appropriate technique is made difficult by the fact that there is often a trade-off between accuracy and feasibility (Janssens *et al*. 2000). Furthermore, accuracy concerns are confounded due to the lack of a true standard or reference for measuring soil CO_2 efflux. As a result, all measurement techniques harbor considerable uncertainty (Lund *et al*. 1999).

Soil CO_2 efflux measurement techniques are broadly divided into two categories (Singh and Gupta 1977). Indirect methods use other measured parameters to estimate soil CO_2 efflux. Examples include weight loss of litter, change in tensile strength of cotton cloth, and soil ATP levels (Witkamp and Van Der Drift 1961, Latter and Howson 1977, Vogt *et al*. 1980). Direct methods quantify soil CO_2 efflux by measuring changes in CO_2 concentration (Schlentner and Van Cleve 1985). Direct methods typically incorporate chambers covering an area of the soil surface. Depending on the absence or presence of air circulation, direct methods are further categorized as static or dynamic. A

traditional static sampling method incorporates soda lime adsorption of CO_2. A tray of soda lime is placed on the ground and covered with a chamber that seals to the soil surface. After a period of time, the soda lime is removed from the chamber and weighed. The increase in weight, after correction for the chemical release of water when soda lime reacts with CO_2, corresponds to the soil CO_2 efflux during that time period (Janssens *et al*. 2000).

Dynamic systems circulate air from a soil chamber to an infrared gas analyzer (IRGA). The gas analyzer measures CO_2 concentration by passing infrared light through a cylinder containing an air sample collected by the chamber and circulated to the analyzer. The impedance of infrared light transmission by CO_2 in the cylinder is used to calculate CO_2 concentration. By computing the change in CO_2 concentration over a specific time period, a soil CO_2 efflux rate is derived.

Dynamic systems are further characterized as closed-chamber or open-chamber. In closed-chamber systems, sampled air circulates from the chamber to an external IRGA, and then back to the chamber (Rochette *et al*. 1997). In the open-chamber system, sampled air is vented to the atmosphere instead of being returned to the chamber (Rayment and Jarvis 1997).

Direct measurement not utilizing a soil chamber includes an array of micrometeorological methods. Examples include the eddy correlation technique, the flux-gradient method, the Bowen ratio/energy balance method, and the aerodynamic method (Janssens *et al*. 2000). Basically, all micrometeorological methods measure CO_2 concentration by sampling eddies that displace air parcels from the soil to the measurement height (Mosier 1990). The eddy correlation technique, for example, uses a sonic anemometer in conjunction with an IRGA. The anemometer is mounted above the soil surface and a sample intake for the IRGA is positioned directly adjacent. During a specified time frame, air turbulence and CO_2 concentration are monitored and used to compute soil CO_2 efflux.

Janssens *et al*. (2000) compared techniques for measuring forest soil CO_2 efflux. They compared three chamber techniques (the soda lime method and two dynamic closed-chamber IRGA systems) and the eddy correlation technique. Among the three chamber methods, large and systematic differences in soil CO_2 efflux estimates were

found; however, they also found that *in situ* cross-calibration made it possible to calibrate the different chamber techniques to one standard. In addition, the eddy correlation technique was found to be unsuitable for estimating soil CO_2 efflux in forest ecosystems due to the technique's integration of under story gas exchange and bole respiration into the estimates.

While the authors cautioned that no reference soil CO_2 efflux data exist to test accuracy, they were able to identify limitations of each technique. Chamber techniques in general have several limitations. Chamber limitations include soil disturbance, alteration of the CO_2 concentration gradient, pressure differences between the chamber and the atmosphere, and reduction of mass flow of CO_2. The soda lime method has the tendency to overestimate small fluxes due to the enhanced concentration gradient within the static chamber. The soda lime method also has the tendency to underestimate large fluxes due to diminished mass flow within the static chamber. Soda lime flux estimation is also highly dependent on the purity and surface area of the soda lime substrate and thus requires meticulous attention to measurement protocol.

Dynamic chambers can also underestimate fluxes due to disruption of airflow at the soil surface. Mass flow is a driving mechanism for CO_2 transport at the soil surface. Without turbulence inside the chamber, the viscous boundary layer at the soil surface thickens, retarding diffusion into the chamber and instead forcing the movement of CO_2 into the surrounding soil. The chamber flux, therefore, will be diminished. Introducing chamber fans may help to induce turbulence, but often at elevated levels, thus excessively disturbing the viscous boundary layer. As a result, the use of fans often results in overestimation of chamber flux.

Chapter 3: Materials and Methods

3.1: Study Site

Our investigation of the temporal and spatial patterns of soil CO_2 efflux of plantation loblolly pine was performed on industrial forestland in Buckingham County, Virginia ($37^o34'56"$N, $78^o26'55"$W). The area of concentration was approximately 1,000 acres of forestland owned by the Westvaco Corporation and located in the western part of the county, approximately 5 miles southeast of the James River. Buckingham County is located on the Virginia piedmont and averages 106.7 cm of precipitation per year. The average growing season temperature (April through September) is 20.7^o C and the average winter temperature (December through February) is 3.3^o C. A frost-free period lasts on average 180 days beginning in mid-April and lasting through early October (Westvaco Corporation, unpublished data).

Soils in the investigation area are predominantly derived from stratified, metasedimentary bedrock of the Western Piedmont geologic formation. Typical mineral content is metagraywacke, quartzose schist, and mélange. Landform is typically broad ridges with slopes ranging from 5% to 25%. Soil texture is typically a gravelly loam to gravelly sandy loam over 1:1 nonsticky clay to clay loam subsoil. Soil thickness averages 63 cm to 127 cm and site index averages 17.7 m (58 ft) at 25 years for loblolly pine (Westvaco Corporation, unpublished data).

In cooperation with the Westvaco Corporation, suitable loblolly pine stands were identified based on age, geographical proximity between stands, and accessibility. Stands chosen for investigation had all received similar management treatments in accordance with Westvaco's timber and fiber production objectives. Management practices used on these stands included site preparation with varying intensities of broadcast burning, chopping, and raking. All stands were established within two years of conventional harvesting of loblolly or Virginia pine plantations. Most stands were established by hand planting and all received herbicide treatment for control of herbaceous and hardwood competition at or shortly after establishment. Neither fertilization nor mid-rotation thinning had been performed on these stands.

Four age classes of plantation loblolly pine were chosen for this research. Classes were based on the age of stands during the 2000 growing season. These included 1- to 2-year-old stands, 4- to 6-year-old stands, 8- to 12-year-old stands, and 20- to 25-year-old stands (hereafter referred to as age classes one, two, three, and four, respectively). These age classes were chosen to allow soil CO_2 efflux comparisons across an average rotation length on the Virginia piedmont. After identifying appropriate age classes, inventory maps were used to locate geographical blocks that contained all four age classes. Important considerations during this process were that the stands within a block be grouped closely together and be easily accessible. These considerations were important for executing an appropriate error control design and the respective sampling within the time constraint of one day.

3.2: Study Installation

In March 2000, the study plots were installed. Three co-dominant trees were randomly chosen within each age replication. This process was repeated for each of the four geographical blocks, giving a total of 48 sample trees. Trees manifesting poor form, storm damage, disease, or pest infestations were omitted from the selection process. Sample trees were selected well within the borders of each stand to minimize any edge effects. At each sample tree, a pair of 1-m^2 plots was established. One plot was located at the base of the sample tree and the other plot was located midway (approximately 1.5 m) across the planting row. A pair of stainless steel rods, each measuring 0.32-cm by 30 cm, was inserted into the ground at each plot center. These rods were used throughout the study to quantify volumetric soil moisture using time domain reflectrometry. An herbicide consisting of Sulfometuron methyl (Oust®, DuPont, Wilmington, DE) and Isopropylamine salt of Imazapyr (Arsenal®, American Cyanamid Co., Wayne, NJ) was applied to the plots at rates of 2 oz/acre and 4 oz/acre, respectively. Spot-treatment using Glyphosphate (Round-Up Pro®, Monsanto Co., St. Louis, MO) at a 6.25% volumetric concentration was also applied to the plots in May 2000. Herbicide applications were made to control competing woody and herbaceous vegetation within the plots.

3.3: Experimental Design

The experiment was designed as a randomized complete block with a split-plot. Within each of four geographical blocks, the four age classes were replicated once. The whole-plot treatment was stand age class and the sub-plot treatment was measurement position (near or away from the tree). Three sub-samples were taken in each treatment x block combination. The three sub-samples were averaged for each replication and the average used as the experimental unit in statistical analyses. Within a given day, 96 measurements were made (4 blocks x 4 age classes x 3 sub-samples x 2 positions). Measurements were taken one day per month from April 2000 to April 2001. The monthly measurement day usually occurred during the last two weeks of the month, but varied within this time frame depending on weather conditions. Measurements were only taken on days devoid of precipitation and/or high winds to avoid equipment damage and/or measurement error.

3.4: Soil CO_2 efflux rate, temperature, and moisture measurements

During each monthly measurement cycle, soil CO_2 efflux rate, soil temperature, and soil moisture were measured at each plot, beginning shortly after sunrise and continuing until late afternoon when all plots were complete. Measurements were made on a block-by-block basis to minimize the effect of time of day on the measured parameters. Soil CO_2 efflux was measured using a Licor® 6250 (Lincoln, NE) infrared gas analyzer linked to a Licor® 6200 portable photosynthesis console. The control console was programmed to calculate CO_2 efflux rate using the equation:

CO_2 efflux rate ($\mu mol\ m^{-2}\ s^{-1}$) = $[(dC/dt)(PV_t/RT)]$ / soil surface area
where dC = change in CO_2 concentration, dt = change in time, P = atmospheric pressure, V_t = system volume, R = universal gas constant, and T = temperature.

A dynamic closed cuvette chamber was used to capture CO_2 diffusing from the soil surface and to circulate the gas to and from the gas analyzer. The cuvette chamber was constructed using a 20.3 cm inside diameter PVC pipe end-cap. A 0.32 cm thick Plexiglas ring with a 21.6 cm inside diameter and 29.6 cm outside diameter was cemented to the lip of the end-cap. A 1.6 cm thick closed-cell foam gasket of the same diameters was cemented to the Plexiglas ring. The foam gasket provided a reliable seal

between the chamber and the soil surface. The total system volume was 4103 cm^3 and the soil diffusive area enclosed by the chamber was 368 cm^2. Before each day of measurements, the gas analyzer was span-calibrated using a reference gas of known CO_2 concentration. The zero-calibration was reset before each measurement block by using an internal CO_2 scrubbing mechanism. Upon arriving at each measurement plot, the chamber was allowed to equilibrate with the ambient CO_2 concentration near the soil surface. Then the chamber was pressed firmly on the ground at the plot center. After CO_2 concentration was observed to be rising steadily, a 30-second sampling period was initiated. The gas analyzer then calculated a flux rate based on the increase in CO_2 over time, the volume of the entire system, and the enclosed soil surface area (Janssens *et al.* 2000).

As mentioned earlier, there is much debate and concern over the ability to accurately measure soil CO_2 efflux. In an effort to gauge the robustness of our dynamic closed cuvette chamber, Virginia Tech collaborated with the USDA Forest Service to compare efflux measurements made with our system against measurements made with the Forest Service ACES system. The ACES system has been found to be extremely accurate in measuring soil CO_2 efflux based on experimentation with artificial fluxes under laboratory conditions. The ACES and dynamic closed cuvette systems were tested on bedded sites on the South Carolina Coastal Plain during June 2000 and quite similar results were found over a two-day sampling period (Table 1).

Table 1: Comparison of ACES and dynamic closed cuvette system on bedded sites on the South Carolina coastal plain, June 2000.

	Mean Soil CO_2 Efflux Rate ($\mu mol/m^2/s$)			
	On Top Of Bed		Between Beds	
	ACES	Dynamic System	ACES	Dynamic System
Day 1, AM	8.68	6.86	4.96	4.83
Day 1, PM	8.32	8.15	4.66	5.02
Day 2, AM	6.70	5.53	3.27	3.45

Soil temperature and volumetric soil moisture were measured in conjunction with soil CO_2 efflux rate. Soil temperature was measured for each plot at a depth of 15 cm using a soil probe attached to a Digi-Sense® thermocouple thermometer (Cole-Parmer, Vernon Hills, IL). Soil moisture was measured using a Trase® 6050X1 time domain reflectometer (Soil Moisture Equipment Corp., Golena, CA) to a depth of 30 cm (Topp and Davis 1985). A pair of rods was installed at each plot as discussed earlier and remained *in situ* for the entire length of the study.

3.5: Final Intensive Sampling

At the end of the study period in May 2001, intensive sampling was performed at each of the 96 plots. The normal regime of soil CO_2 efflux rate, soil temperature, and soil moisture measurements was made. In addition, litter samples and mineral soil samples were collected from each plot center. The entire O horizon (litter, fragmented, and humus layers) was collected from beneath the cuvette chamber location (an area of 368 cm^2) and placed in a paper bag. A sample was then collected from the now-exposed mineral soil at the center of the litter collection site. The mineral sample was collected by driving a section of 6.9 cm diameter galvanized conduit into the soil to a depth of 10.2 cm. The 382 cm^3 of mineral soil were then placed in a paper bag. Live roots, coarse woody debris, and coarse fragments were captured in the mineral soil sample as well. A $1/20^{th}$-acre plot was centered at the near plot of one sub-sample within each replicate. Within this plot, all woody stems over 2.5 cm ground-line diameter were counted. Hardwoods and pines were counted separately. Height and stem diameter (ground-line diameter for age class one and DBH for age classes two, three, four) were recorded for each of the three loblolly pines at the near plots for each replicate.

3.6: Laboratory Analysis

Litter samples were oven-dried at 65° C until weight stabilization to correct for moisture content at the time of sampling. Each sample was then placed in a muffle furnace at 380° C for 24 hours to correct for mineral soil contamination. Corrected litter weight was calculated as oven dried weight minus ash weight and recorded. Each of the mineral soil samples was passed through 0.64 cm meshing to separate the soil from live

roots, coarse woody debris, and coarse fragments. The soil was passed through an additional 2 mm sieve, packaged, and sent to the USDA Forest Service, Research Triangle Park, North Carolina, for carbon and nitrogen analysis. Analysis was performed with a Carlo Erba Nitrogen and Carbon Series II analyzer (CE Elantech Inc., Lakewood, NY) according to the machine's standard operating procedures. Coarse fragments greater than 0.64 cm diameter were collected and weights recorded for each sample. Coarse woody debris greater than 0.64 cm diameter was collected and a corrected weight was derived for each sample using the same technique used for the litter samples.

Live root samples were thoroughly washed and then digitally scanned using a flatbed scanner. WinRhizo® 5.0A software (Regent Instruments Inc., Quebec, Canada) was used to analyze the digital images and quantify various root parameters, including total length, surface area, projected area, volume, and average diameter. The root samples were also divided into fine (< 2 mm), medium (2-5 mm), and coarse (> 5 mm) diameter classes utilizing the software. No attempt was made to separate pine roots from other roots. Very few non-pine roots were expected in the samples due to effective herbicide control of non-pine vegetation within the plots. After scanning, root samples were oven-dried at 65° C to correct for moisture content and then weighed.

3.7: Statistical Analysis

All statistical analyses were performed using SAS© software (SAS Institute, Cary, NC). The effect of stand age and measurement position on soil CO_2 efflux rate, soil temperature, and soil moisture for plantation loblolly pine was analyzed for each month separately using the general linear model (GLM) procedure of SAS. The data were analyzed as a randomized complete block with split-plot design. In the GLM procedure, block, stand age, the block x age interaction, measurement position, and the age x position interaction were identified as the independent variables. The stand age variable had four treatment levels (the four age classes) and the measurement position variable had two treatment levels (near versus away from the tree). Soil CO_2 efflux rate, soil temperature, and soil moisture were identified as the dependent variables within the GLM procedure. Treatment effects and the interaction between treatments were tested against the null hypothesis at the $\alpha = 0.05$ significance level. Differences in treatment

means for each dependent variable were tested using Tukey's studentized range test (HSD) at the $\alpha = 0.05$ significance level. The slicing option within the GLM procedure was used to test for differences between measurement positions within each age class at the $\alpha = 0.05$ significance level.

Multiple linear regression analysis was used to determine the significance of the relationship between soil CO_2 efflux rate and various site parameters measured during the study. A seasonal model was developed to predict soil CO_2 efflux using soil temperature, soil moisture, coarse fragments, stand age, and measurement position as regressors. The data set for the entire 12-month period was used for this analysis. A stand-level model was also developed to predict soil CO_2 efflux using soil temperature, soil moisture, pine volume, and measurement position data from the entire investigation as regressors. Finally, a soil CO_2 efflux model was developed using root volume, soil carbon, soil temperature, soil moisture, stand age, and measurement position data collected during the final intensive sampling session in May 2001.

Chapter 4: Results

4.1: Treatment effects on soil CO_2 efflux, temperature, and moisture

Stand age class had a significant treatment effect ($p = 0.05$) on soil CO_2 efflux rate on 10 of the 12 monthly sampling dates (Table 2). Mean soil CO_2 efflux rate by age class ranged from a high of 6.50 μmol/m^2/s for age class four (20- to 25-years-old) during June 2000 to a low of 0.314 μmol/m^2/s for age class one (1- to 2-years-old) during December 2000 (Table 3). There was never a significant difference between mean efflux rates for age classes two, three, and four. However, age class one was significantly different from the other age classes on a consistent basis. These trends are further discernable in a time series graph of soil CO_2 efflux rates for the four age classes (Figure 1). Age class one consistently had the lowest mean efflux rate. Another clear trend is the ranking of the age classes during the period from June through September 2000. During this time frame, when efflux rates were at their highest for the entire investigation, the age classes were clearly ordered from youngest to oldest in efflux rate magnitude. At other times during the investigation, the three older age classes changed ranking with no discernible trend. All four age classes follow a similar pattern of changing efflux rates during the year. As expected, efflux rates are highest during the growing season and lowest during the winter months. An interesting dip occurred in the efflux rates during July 2000. This drop occurred due to extremely low soil moistures following a period of prolonged drought.

Mean soil CO_2 efflux rates were higher at the near position during the entire investigation, but were significantly higher ($p = 0.05$) on only 8 of the 12 sampling dates (Tables 2 & 3). Efflux rates ranged from 77% higher during January 2001 to 9% higher during July 2000 at the near position. There was a significant treatment interaction ($p = 0.05$) between stand age and measurement position for soil CO_2 efflux rate during August, September, and December 2000 (Table 2).

Table 2: Treatment effects and interactions (p-values from ANOVA) of stand age and measurement position for soil CO_2 efflux rates measured in loblolly pine plantations on the Virginia piedmont over a 12-month period. Measurement position refers to near or away from the tree base.

	Soil CO_2 Efflux Rate		
Measurement Date	Stand Age Treatment (p > F)	Position Treatment (p > F)	Treatment Interactions (p > F)
April 2000	0.0227	0.0430	0.5959
May 2000	0.1609	0.1589	0.9035
June 2000	0.0037	0.0135	0.1643
July 2000	0.0899	0.1752	0.1044
August 2000	0.0432	0.0302	0.0181
September 2000	0.0014	0.2232	0.0180
October 2000	0.0384	0.4387	0.1723
November 2000	0.0081	0.0098	0.6367
December 2000	0.0256	0.0017	0.0074
January 2001	0.0105	0.0002	0.1559
February 2001	0.0080	0.0106	0.4213
March 2001	0.0296	0.0075	0.4656

Table 3: Monthly mean soil CO_2 efflux rate by stand age and measurement position for plantation loblolly pine on the Virginia piedmont. Monthly means are based on 24 observations per age class and 48 observations per measurement position.

	Mean Soil CO_2 Efflux Rate ($\mu mol/m^2/s$) By Treatment[1]					
	Stand Age Class				Position	
Measurement Date	1	2	3	4	Near	Away
April 2000	0.378 b	0.749 a	0.675 ab	0.633 ab	0.703 a	0.514 b
May 2000	3.933 a	5.562 a	6.038 a	4.836 a	5.529 a	4.655 a
June 2000	3.757 b	4.911 ab	5.938 a	6.499 a	5.714 a	4.839 b
July 2000	3.265 a	3.391 a	3.923 a	4.654 a	3.973 a	3.643 a
August 2000	3.352 b	4.103 ab	4.840 ab	5.706 a	4.798 a	4.203 b
September 2000	1.967 b	4.115 a	4.170 a	4.503 a	3.846 a	3.531 a
October 2000	1.148 b	2.694 a	2.186 ab	2.085 ab	2.156 a	1.900 a
November 2000	0.405 b	0.860 ab	1.365 a	1.174 a	1.121 a	0.780 b
December 2000	0.314 b	0.457 ab	0.586 a	0.589 a	0.588 a	0.385 b
January 2001	0.323 b	0.692 a	0.692 a	0.784 a	0.782 a	0.443 b
February 2001	0.793 b	1.709 a	1.830 a	1.469 ab	1.678 a	1.223 b
March 2001	1.022 b	1.694 ab	1.801 a	1.368 ab	1.742 a	1.200 b

[1]Treatment-specific means with different letters within a given month are significantly different using Tukey's HSD at the 0.05 level.
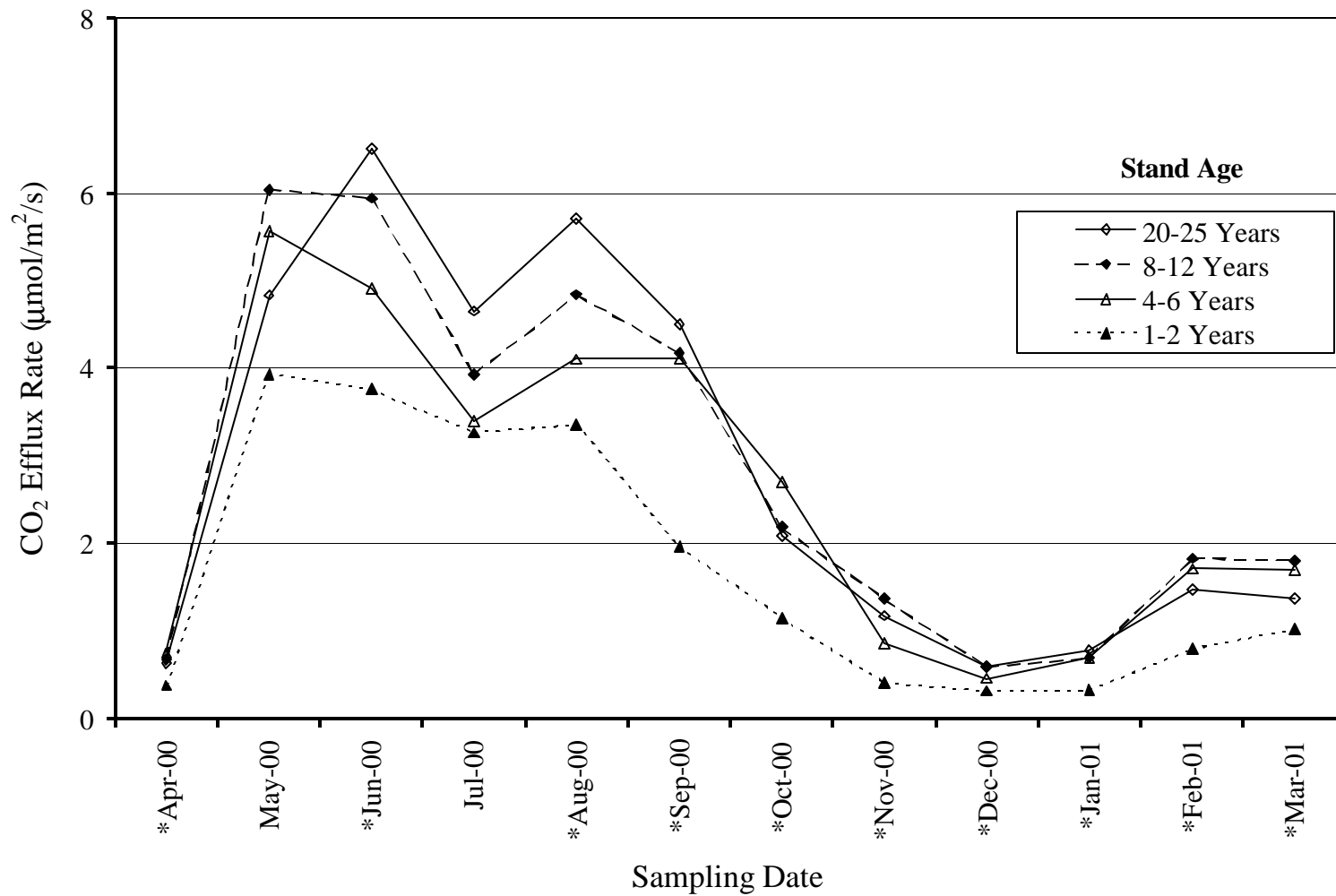
Figure 1: Time series of mean soil CO_2 efflux rates measured in four age classes of plantation loblolly pine on the Virginia piedmont during a 12-month period. A significant age effect was detected during months with an asterisk (*) in the x-axis.

Time series graphs of mean efflux rates were constructed for each of the four age classes (Figure 2). These graphs compare mean efflux rate at the near and away measurement positions for each age class. With the exception of age class two (4- to 6-years-old), the trend of higher mean efflux rates near the tree held for every age class during the entire investigation. From June through October 2000, age class two had higher mean efflux rates away from the tree (Figure 2b). The difference in mean efflux rates by position was not always statistically significant ($p = 0.05$) within a given age class. In fact, there was never a significant difference between the near and away positions for age class one (Figure 2a). In contrast, position difference was significant on 9 of 12 sampling dates for age class three (Figure 2c).

Stand age class had a significant treatment effect ($p = 0.05$) on soil temperature on 9 of the 12 monthly sampling dates (Table 4). Mean soil temperature ranged from a high of 27.2 $^{\circ}$C for age class one during July 2000 to a low of 0.5 $^{\circ}$C for age class one during December 2000. Several trends are discernable with respect to soil temperature (Table 5). Age class one tended to have the highest soil temperatures during the growing season and lowest soil temperatures during the winter months. Age class four tended to have the lowest soil temperatures during the growing season and highest soil temperatures during the winter months. Soil temperatures were significantly different between age classes one and four on 8 of the 12 sampling dates. In contrast, soil temperatures were never significantly different between age classes three and four and were only significantly different between age classes one and two on two sampling dates.
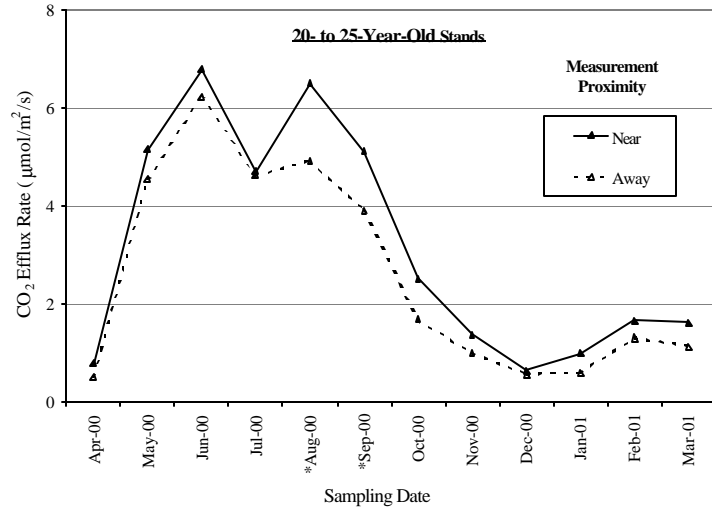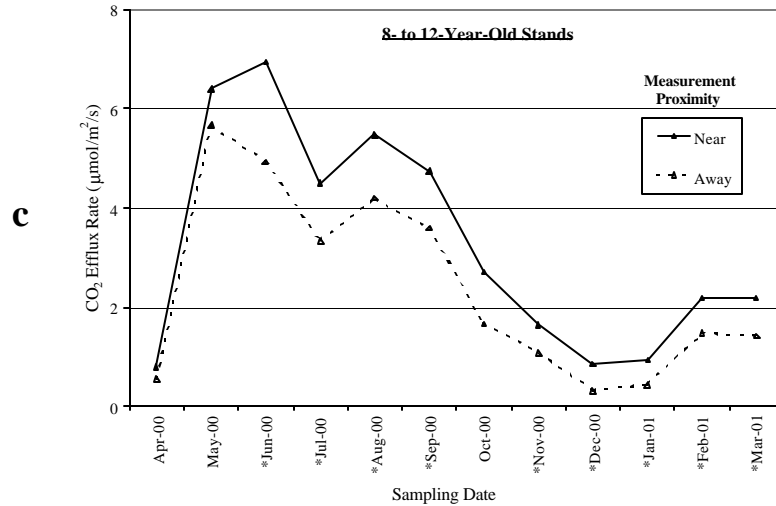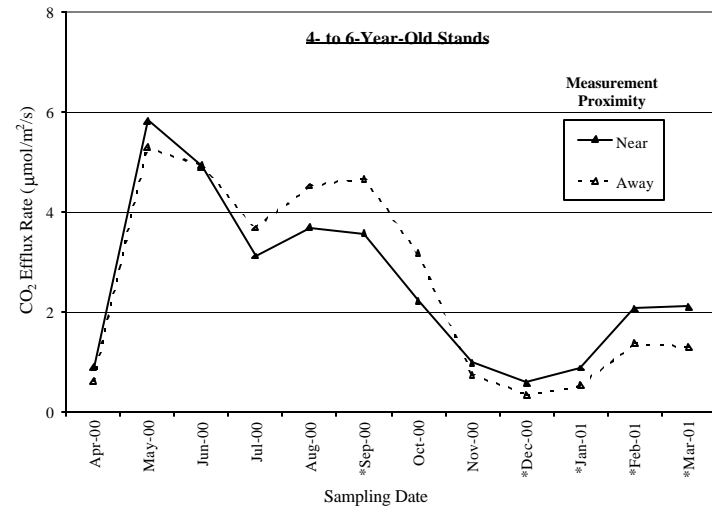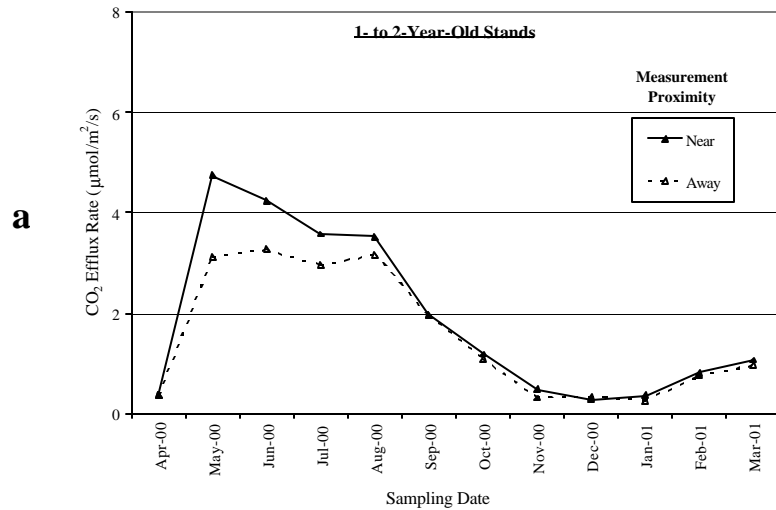
Figure 2: Time series of mean soil CO_2 efflux rates, by position, measured in four age classes of plantation loblolly pine on the Virginia piedmont over a 12-month period. A significant difference was detected during months denoted with an asterisk (*) in the x-axes. Measurement proximity refers to near or away from the tree base.

Table 4: Treatment effects and interactions (p-values from ANOVA) of stand age and measurement position for soil temperature measured in loblolly pine plantations on the Virginia piedmont over a 12-month period. Measurement position refers to near or away from the tree base.

	Soil Temperature		
Measurement Date	Stand Age Treatment $(p > F)$	Position Treatment $(p > F)$	Treatment Interactions $(p > F)$
April 2000	0.0233	0.2299	0.1890
May 2000	<.0001	0.7887	0.7999
June 2000	0.0010	0.7893	0.2013
July 2000	<.0001	0.7222	0.6111
August 2000	0.0008	0.2543	0.2112
September 2000	0.5338	0.3265	0.6586
October 2000	0.0512	0.0256	0.3370
November 2000	<.0001	0.0757	0.4730
December 2000	<.0001	0.1325	0.1426
January 2001	0.0001	0.0898	0.5370
February 2001	0.5436	0.1818	0.8917
March 2001	0.0069	0.0595	0.3180

Table 5: Monthly mean soil temperature by stand age and measurement position for plantation loblolly pine on the Virginia piedmont. Monthly means are based on 24 observations per age class and 48 observations per measurement position.

	Mean Soil Temperature (°C) By Treatment[1]					
	Stand Age Class				Position	
Measurement Date	1	2	3	4	Near	Away
April 2000	10.5 ab	10.8 a	10.0 b	10.1 ab	10.3 a	10.4 a
May 2000	22.5 a	21.9 a	18.5 b	17.8 b	20.1 a	20.2 a
June 2000	24.3 a	23.1 a	20.5 b	19.8 b	21.9 a	21.9 a
July 2000	27.2 a	26.9 a	22.5 b	21.5 b	24.6 a	24.5 a
August 2000	25.1 a	24.3 a	21.3 b	21.0 b	22.8 a	23.0 a
September 2000	16.8 a	17.5 a	16.4 a	16.5 a	16.8 a	16.7 a
October 2000	11.9 a	13.5 a	13.1 a	13.5 a	13.2 a	12.8 b
November 2000	5.2 c	7.1 b	8.2 a	9.0 a	7.4 a	7.3 a
December 2000	0.5 b	1.3 b	2.8 a	3.4 a	2.2 a	2.0 a
January 2001	1.8 d	3.4 bc	4.5 ab	5.0 a	3.7 a	3.5 a
February 2001	7.3 a	7.9 a	7.5 a	7.6 a	7.7 a	7.5 a
March 2001	8.7 a	8.6 ab	7.9 bc	7.7 c	8.2 a	8.2 a

[1]Treatment-specific means with different letters within a given month are significantly different using Tukey's HSD at the 0.05 level.

Measurement position had a significant treatment effect (p = 0.05) on soil temperature only during the October 2000 sampling period, at which time the near position was higher (Tables 4 & 5). Mean soil temperatures at the near and away positions differed by less than 0.3 $^{\circ}$C on 11 of the 12 sampling dates. There was never a significant treatment interaction (p = 0.05) between stand age and measurement position for soil temperature throughout the investigation (Table 4).

Stand age class had a significant treatment effect (p = 0.05) on volumetric soil moisture on 8 of the 11 monthly sampling dates (Table 6). Volumetric soil moisture was not measured on the April 2000 sampling date due to equipment malfunction. The highest mean soil moisture, by age, was 28.1% for both age classes one and two during May 2000 and March 2001, respectively (Table 7). The lowest mean soil moisture was 8.8% for age class three during July 2000. Age class one had the highest soil moistures during the growing season (May through October 2000) while age class two had the highest soil moistures during the winter (November 2000 through March 2001). However, there was never a significant difference (p = 0.05) in soil moistures between age classes one and two. Likewise, age classes three and four consistently had the lowest soil moistures with age class three being lowest 5 months and age class four being lowest 6 months. Once again, there was never a significant difference (p = 0.05) in soil moistures between age classes three and four. In fact, there was no significant difference in soil moistures across all age classes on 5 of the 11 sampling dates. Four of these five dates were during the winter months from December 2000 through March 2001.

Mean volumetric soil moisture was lower at the near position during the entire investigation, but was significantly lower (p = 0.05) on only 6 of the 11 sampling dates (Tables 6 & 7). Three of these dates occurred consecutively from July through September 2000. Soil moisture at the near position ranged from 11% lower during July 2000 to 2% lower during November 2000. There was never a significant treatment interaction (p = 0.05) between stand age and measurement position for soil moisture throughout the investigation (Table 6).

Table 6: Treatment effects and interactions (p-values from ANOVA) of stand age and measurement position for volumetric soil moisture measured in loblolly pine plantations on the Virginia piedmont over a 12-month period. Measurement position refers to near or away from the tree base.

	Volumetric Soil Moisture		
Measurement Date	Stand Age Treatment $(p > F)$	Position Treatment $(p > F)$	Treatment Interactions $(p > F)$
April 2000	No Data[1]	No Data	No Data
May 2000	0.0013	0.0233	0.2188
June 2000	0.0078	0.0548	0.3222
July 2000	0.0065	0.0100	0.2235
August 2000	0.0276	0.0358	0.4252
September 2000	0.0096	0.0032	0.4247
October 2000	0.0012	0.0559	0.5674
November 2000	0.0029	0.6239	0.4551
December 2000	0.3142	0.1412	0.7157
January 2001	0.0954	0.1912	0.2408
February 2001	0.0465	0.0112	0.1191
March 2001	0.0869	0.0190	0.1920

[1]Soil moisture measurements were not taken during April 2000 due to equipment malfunction.

Table 7: Monthly mean volumetric soil moisture by stand age and measurement position for plantation loblolly pine on the Virginia piedmont. Monthly means are based on 24 observations per age class and 48 observations per measurement position.

| | Mean Soil Moisture (% Volume) By Treatment[1] | | | | | |
| | Stand Age Class | | | | Position | |
Measurement Date	1	2	3	4	Near	Away
April 2000	No Data[2]	No Data	No Data	No Data	No Data	No Data
May 2000	28.1 a	25.8 ab	21.3 c	22.3 bc	23.6 b	25.2 a
June 2000	25.1 a	22.8 ab	17.3 b	16.8 b	19.8 a	21.2 a
July 2000	18.0 a	15.2 ab	8.8 b	9.6 b	12.2 b	13.6 a
August 2000	18.6 a	16.7 a	11.8 a	11.7 a	14.1 b	15.3 a
September 2000	26.1 a	24.3 ab	21.4 b	21.2 b	22.4 b	24.1 a
October 2000	20.2 a	16.4 ab	9.7 c	10.3 bc	13.6 a	14.7 a
November 2000	24.4 a	20.5 ab	15.4 b	15.6 b	18.8 a	19.2 a
December 2000	22.1 a	23.3 a	20.0 a	20.5 a	20.8 a	22.2 a
January 2001	25.2 a	25.6 a	21.8 a	22.5 a	23.4 a	24.3 a
February 2001	26.8 a	27.3 a	23.1 a	21.9 a	24.0 b	25.6 a
March 2001	27.5 a	28.1 a	24.2 a	23.8 a	25.3 b	26.4 a

[1]Treatment-specific means with different letters within a given month are significantly different using Tukey's HSD at the 0.05 level.

[2]Soil moisture measurements were not taken during April 2000 due to equipment malfunction.

4.2: Regression analysis

Multiple linear regression analysis was used to examine the relationship between soil CO_2 efflux rate and various site parameters measured during the study. Based on these analyses, models were developed for predicting soil CO_2 efflux for plantation loblolly pine. The above parameters, their interactions, and specific parameter transformations were tested at the $p = 0.05$ significance level. Stepwise, forward, and backward selection options were used within the regression procedure of SAS to identify models with the greatest predictive power.

A seasonal model was developed for soil CO_2 efflux using soil temperature, soil moisture, stand age, measurement position, and coarse fragment weight as independent variables. A data set of 1152 observations collected over the 12-month study was used. Seven significant variables were identified, explaining 55.3% of soil CO_2 efflux variation across the 12-month study (Table 8). Soil temperature proved to be the most influential parameter tested for the data set. Six of the seven variables contain temperature as a transformation or interaction term. The most significant variable in the model, explaining 23.2% of efflux variation, was the interaction polynomial soil temperature*soil moisture*stand age. As a monomial, soil temperature was the second most significant variable, explaining 14.0% of efflux variation. The natural log and second power transformations of soil temperature combined to explain 8.8% of efflux variation. The three remaining variables in the model were interaction polynomials, accounting for 9.3% of efflux variation combined.

Table 8: Significant parameters influencing soil CO_2 efflux rates measured in loblolly pine plantations on the Virginia piedmont over a 12-month period. The regression model includes data from 96 plots located both near and away from the base of loblolly pine trees in four age classes (1152 total observations).

Parameter	Soil CO_2 Efflux (μmol/m^2/s)			
	Parameter Estimate	[1]Partial R^2	F value	p > F
Soil Temperature*Soil Moisture*Stand Age	0.00038	0.232	82.18	<.0001
Soil Temperature	0.44652	0.140	49.70	<.0001
Soil Moisture*Stand Age*Measurement Position	-0.00133	0.049	17.33	<.0001
Soil Temperature^2	-0.00625	0.047	16.71	<.0001
Natural Log Soil Temperature	-0.73176	0.041	14.55	0.0001
Soil Temperature*Soil Moisture*Coarse Fragments	-0.000008	0.026	9.12	0.0026
Soil Temperature*Measurement Position	-0.01739	0.018	6.53	0.0108
Model	Intercept = -0.05195	Total R^2=0.553	175.23	<.0001

[1]Partial R^2 values are calculated from the ANOVA table as the ratio of the partial sum of squares for the parameter to the corrected total sum of squares.

The effects of stand age and soil temperature on soil CO_2 efflux are well demonstrated in Figure 3. Using the seasonal model, predicted values for soil CO_2 efflux rate were computed across a range of observed soil temperatures. All other variables in the model were held constant at mean values for the 12-month study period. Predicted curves were computed for each stand age class. As soil temperature increases, predicted soil CO_2 efflux rate also increases; furthermore, at a given soil temperature, predicted efflux rate increases with increasing stand age. Also, the magnitude of difference in efflux rates between stand age classes increases as soil temperature increases. The shape of the predicted efflux curves suggests that extremely high soil temperatures, which slow the respiratory function of soil microbes and plant roots, inhibited soil CO_2 efflux rate.

To demonstrate the effect of measurement position on soil CO_2 efflux rate, separate graphs were constructed for each age class using the seasonal model (Figure 4). Predicted soil CO_2 efflux rates were computed across a range of expected temperatures while all other variables in the model were held constant. Within a given age class, separate curves were computed for the near and away measurement positions. For each age class, soil CO_2 efflux rate increases as soil temperature increases. The divergent nature of the near and away position curves suggests two notable phenomena. Within a given age class, the effect of position on soil CO_2 efflux rate increases as soil temperature increases. Also, this position effect appears to increase with stand age, i.e., the difference between the near and away position curves becomes stronger as stand age increases.
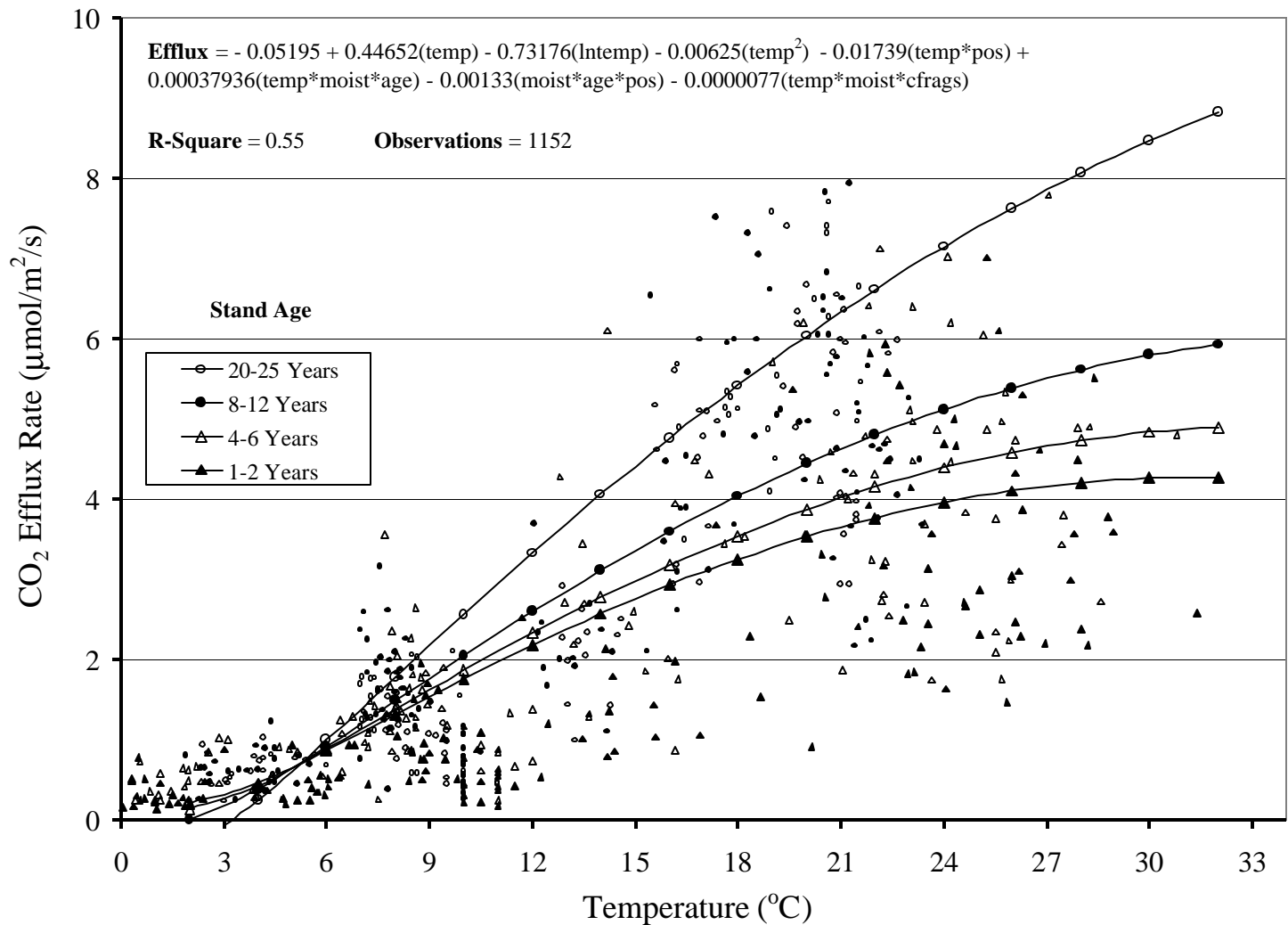
Figure 3: Comparison of actual and predicted soil CO_2 efflux rates over a range of observed soil temperatures for four age classes of plantation loblolly pine on the Virginia piedmont. Observations were collected from April 2000 to April 2001. Predicted rates were calculated using an empirical model and mean parameter values for the 12-month study.
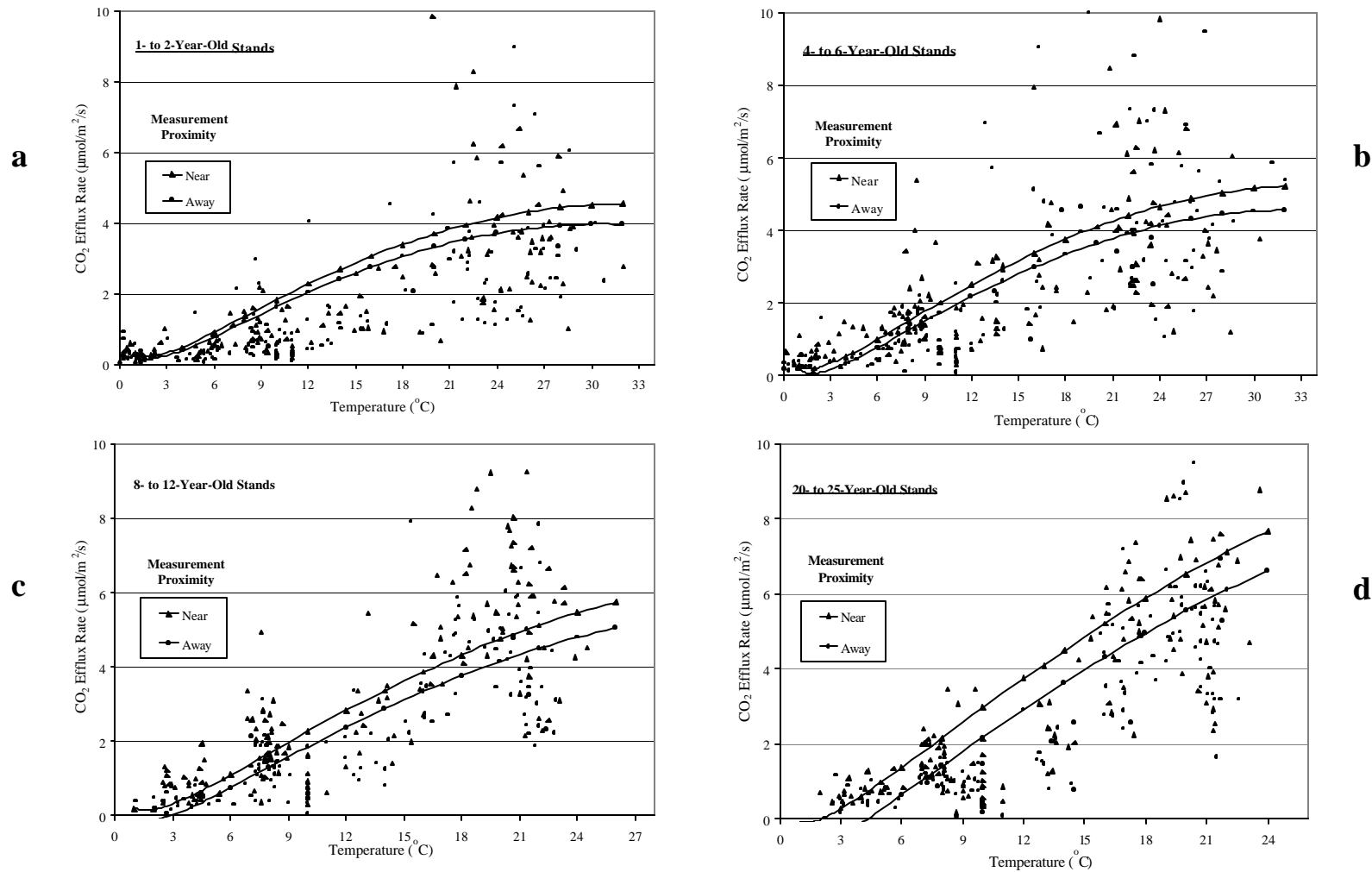
Figure 4: Comparisons of actual and predicted soil CO_2 efflux rates, by position, over a range of observed soil temperatures for four age classes of plantation loblolly pine on the Virginia piedmont. Observations were collected from April 2000 to April 2001. Predicted rates were calculated using an empirical model and mean parameter values for the 12-month study. Measurement proximity refers to near or away from the tree base.

The relationship between aboveground pine volume and soil CO_2 efflux was examined in further regression analysis. Soil temperature, soil moisture, and coarse fragment measurements taken during the 12-month investigation were used in conjunction with stem count and stem volume measurements made during the intensive sampling session in May 2001. While stem counts and stem volume measurements were not made throughout the 12-month study, it is assumed that end-of-study values for these parameters are reasonable for making comparisons across age classes for the entire year. It is assumed that stem count and stem volume at any time during the study is highly correlated with values acquired in May 2001. Stem volume estimates for age classes two, three, and four were computed using the equation:

$$\text{Stem Volume (cubic feet)} = 0.21949 + 0.00238D^2H$$

where D = diameter at breast height in inches and H = total tree height in feet (Tasissa et $al.$ 1997). Stem volume estimates for age class one were computed using the common estimator:

$$\text{Stem Volume (cubic feet)} = D^2H$$

where D = diameter at ground line in inches and H = total tree height in feet. Stem volume was estimated for each sub-sample and the sub-samples were then averaged for each replicate. Mean stem volume was then multiplied by stem count to obtain stand volume on a per acre basis for each replicate. Because stem count was estimated for only one sub-sample per replicate, a total of 384 pine volumes were calculated (4 blocks x 4 stand age classes x 2 measurement positions x 12 months). To insure conformity, the sub-samples for the other parameters were averaged for each replicate. Accordingly, a data set of 384 observations was used for the analysis. Pine volume along with the above parameters, their interactions, and specific parameter transformations were tested at the p = 0.05 significance level.

For the stand-level model, six significant regressors were identified, explaining 75.1% of soil CO_2 efflux variation across the 12-month study (Table 9). Neither coarse fragments nor coarse fragment interactions with other parameters proved to be significant regressors. Again, soil temperature was a highly influential parameter, appearing in 5 of the 6 variables. The interaction polynomial, soil temperature*soil moisture*pine volume, was the most significant parameter, explaining 40.5% of efflux variation. As a

monomial, soil temperature was the second most significant variable, explaining 13.2% of efflux variation. The interaction polynomial, pine volume*measurement position, was also highly significant, explaining 11.0% of efflux variation. The natural log and second power transformations of soil temperature combined to explain 8.1% of efflux variation. The interaction polynomial, soil temperature*measurement position, accounted for the remaining 2.3% of explainable efflux variation.

The effects of pine volume and soil temperature on soil CO_2 efflux are well demonstrated in Figure 5. For each age class, an average pine volume per acre was calculated from the field data. Using the stand-level model, predicted soil CO_2 efflux rates were computed across a range of observed soil temperatures. As before, all other variables in the model were held constant at mean values for the 12-month study. Separate curves were computed for four pine volumes corresponding with the stand age classes. Trends similar to those in the earlier age class comparisons were found for the pine volume comparisons as well. These similarities were both expected and reassuring due to the dependence of pine volume on stand age. Predicted soil CO_2 efflux rate increases as soil temperature increases for all stand volumes. Furthermore, the magnitude of difference in soil CO_2 efflux rates between stand volumes increases as soil temperature increases. Again, a curvilinear relationship between soil temperature and soil CO_2 efflux rate is observed.

To investigate the relationship between soil/root parameters and soil CO_2 efflux of plantation loblolly pine, regression analyses were performed using data collected during intensive sampling in May 2001. Parameters evaluated were soil temperature, soil moisture, stand age, mineral corrected litter weight, mineral corrected coarse woody debris weight, coarse fragment weight, soil carbon content, soil nitrogen content, dry root weight, root length, root volume, average root diameter, root surface area, root surface area by diameter class, and root length by diameter class. All root parameters pertain to pine specifically and were tested at the $p = 0.05$ significance level. While no attempt to separate pine roots from non-pine roots was made, the contribution of non-pine vegetation to the root samples was assumed to be negligible due to herbicide applications during study installation. A data set of 95 observations was evaluated (one extreme observation was removed).

Table 9: Significant parameters influencing soil CO_2 efflux rates measured in loblolly pine plantations on the Virginia piedmont over a 12-month period. The regression model uses pine volume in lieu of stand age and includes data from 96 plots located both near and away from the base of loblolly pine trees in four volume classes (384 total observations).

Parameter	Parameter Estimate	[1]Partial R^2	F value	$p > F$
	Soil CO_2 Efflux (μmol/m^2/s)			
Soil Temperature*Soil Moisture*Pine Volume	0.000002	0.405	100.65	<.0001
Soil Temperature	0.43425	0.132	32.79	<.0001
Pine Volume*Measurement Position	-0.00017	0.110	27.35	<.0001
Natural Log Soil Temperature	-0.76571	0.041	10.15	0.0016
Soil Temperature^2	-0.00585	0.040	9.90	0.0018
Soil Temperature*Measurement Position	-0.01815	0.023	5.81	0.0165
Model Intercept = -0.03162		Total R^2=0.751	163.00	<.0001

[1]Partial R^2 values are calculated from the ANOVA table as the ratio of the partial sum of squares for the parameter to the corrected total sum of squares.
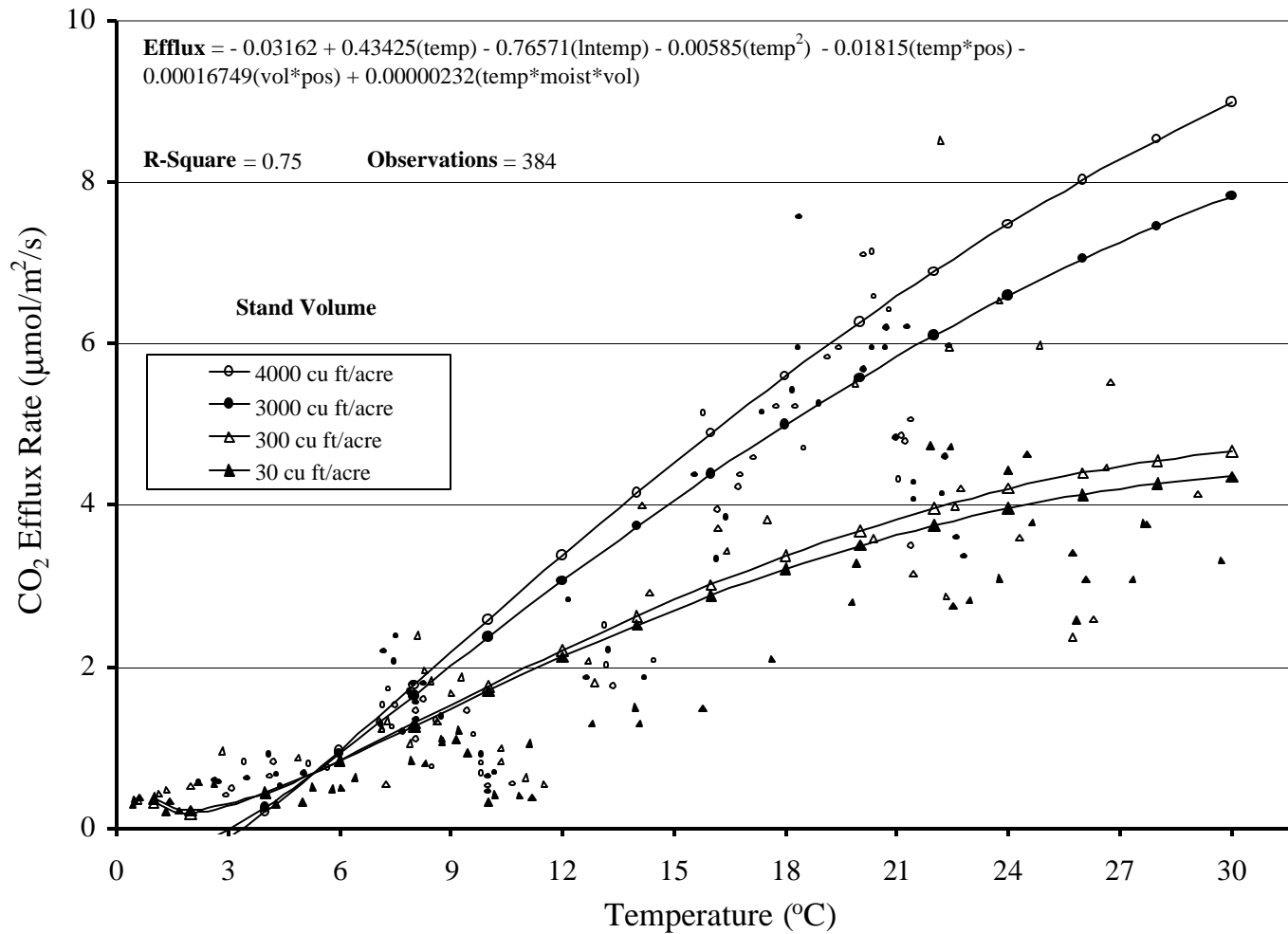
Figure 5: Comparison of actual and predicted soil CO_2 efflux rates over a range of observed soil temperatures for four stand volume classes of plantation loblolly pine on the Virginia piedmont. Observations were collected from April 2000 to April 2001. Predicted rates were calculated using an empirical model and mean parameter values for the 12-month study.

For the soil/root model, eight significant regressors were identified, explaining 43.9% of soil CO_2 efflux variation during the intensive sampling of May 2001 (Table 10). Unlike the full-year models discussed earlier, soil temperature was not as significant in predicting soil CO_2 efflux during May 2001. However, soil temperature is a significant parameter with a natural log transformation and in four interaction parameters (20.1% total variation explanation).

For this data set, soil moisture proved to be very significant in predicting soil CO_2 efflux. While soil moisture alone is not a significant parameter, it appears in 4 of the 8 significant parameters as an interaction term. Those parameters are soil moisture*stand age (7.7%), soil moisture*measurement position (5.0%), soil temperature*soil moisture*stand age (8.7%), and soil temperature*soil moisture*measurement position (5.3%). The significance of soil moisture may be attributed to several causes. In the earlier full-year models, soil temperature accounted for a majority of explainable variation. This is not surprising because temperature is well documented as the most significant driver of soil CO_2 efflux. During the intensive sampling of May 2001, the influence of soil temperature was diluted due to extremely low soil moistures, which averaged 15.1% across all age classes. In comparison, soil moisture averaged 20.4% during the 12-month investigation. Due to the drought conditions, soil CO_2 efflux was more greatly constrained by soil moisture than by soil temperature. In addition, soil moisture showed much greater variation (CV=12%) than soil temperature (CV=2%) during the intensive sampling session. As a result, temperature's predictive power for soil CO_2 efflux was greatly diminished compared to full year models. Of the soil and root parameters tested, only soil carbon content and total root volume proved to be significant regressors, explaining 6.4% and 4.8% of efflux variation, respectively.

Figures 6 and 7 demonstrate the predictive ability of the soil/root model for soil CO_2 efflux. In Figure 6, soil CO_2 efflux is predicted across a range of observed soil carbon contents. All other variables in the model are held constant at mean values (including age) for the May 2001 data set. Intuitively, as soil carbon content increases, soil CO_2 efflux also increases. In Figure 7, soil CO_2 efflux is predicted across a range of observed root volumes. While not as strong as the relationship with soil carbon content, soil CO_2 efflux also shows a positive response to root volume.

Table 10: Significant parameters influencing soil CO_2 efflux rates measured in loblolly pine plantations on the Virginia piedmont during May 2001. The regression model includes data from 96 plots located both near and away from the base of loblolly pine trees in four age classes (96 total observations).

Parameter	Parameter Estimate	[1]Partial R^2	F value	$p > F$
		Soil CO_2 Efflux (μmol/m^2/s)		
Soil Temperature*Soil Moisture*Stand Age	0.00332	0.087	13.37	0.0004
Soil Moisture*Stand Age	-0.04664	0.077	11.77	0.0009
Soil Carbon Content	0.34565	0.064	9.75	0.0024
Soil Temperature*Soil Moisture*Measurement Position	0.01331	0.053	8.07	0.0056
Soil Moisture*Measurement Position	-0.24091	0.050	7.73	0.0067
Root Volume	0.32983	0.048	7.32	0.0082
Soil Temperature*Stand Age	-0.00543	0.031	4.78	0.0314
Natural Log Soil Temperature	-6.61599	0.030	4.60	0.0347
Model	Intercept = 20.12534	Total R^2=0.439	8.42	<.0001

[1]Partial R^2 values are calculated from the ANOVA table as the ratio of the partial sum of squares for the parameter to the corrected total sum of squares.
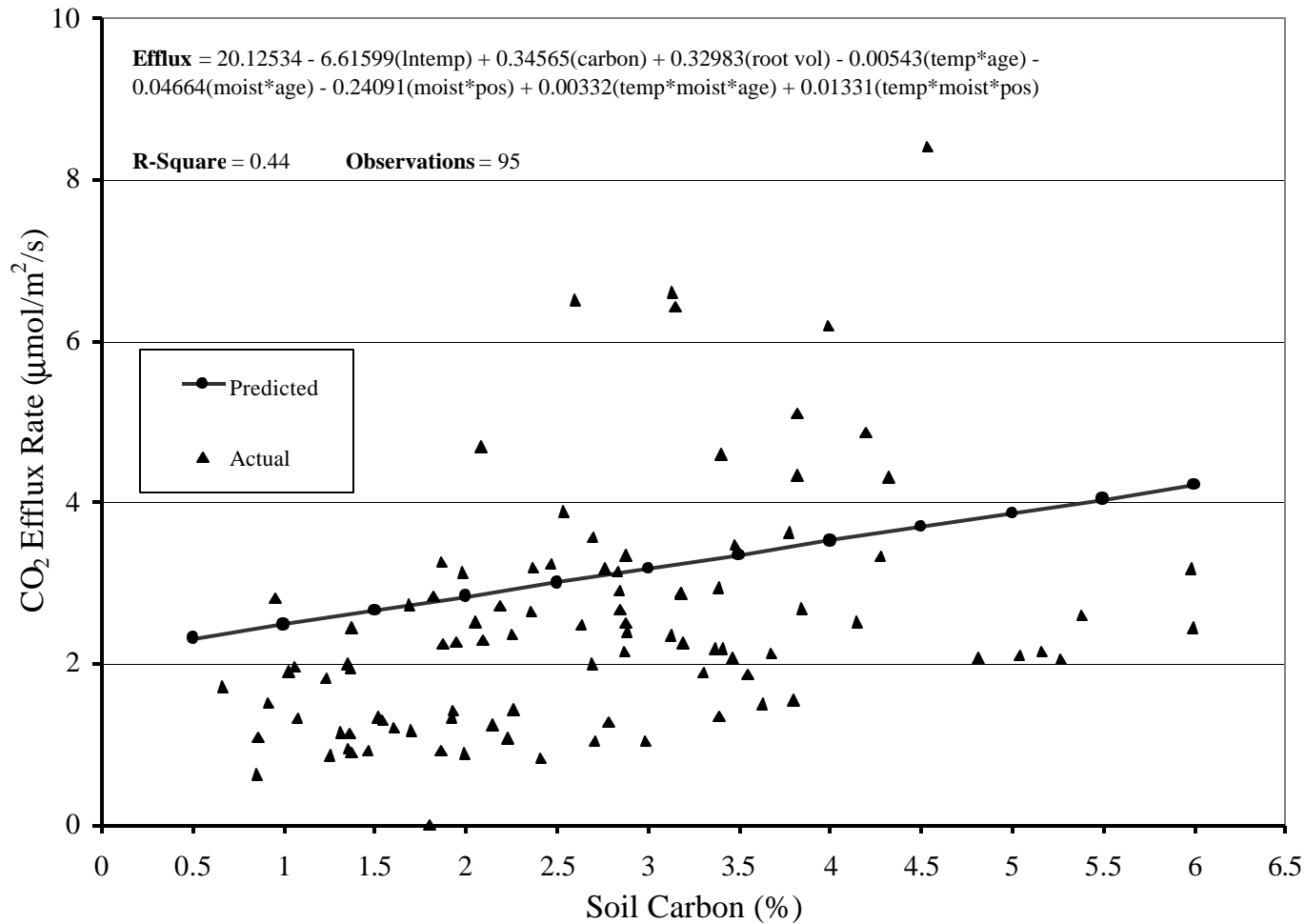
Figure 6: Comparison of actual and predicted soil CO_2 efflux rates over a range of observed soil carbon contents for plantation loblolly pine on the Virginia piedmont. Observations were collected during May 2001. Predicted rates were calculated using an empirical model and mean parameter values for May 2001. Soil carbon content refers to the carbon contained in a soil core collected from the upper 10.2 cm of the A horizon.
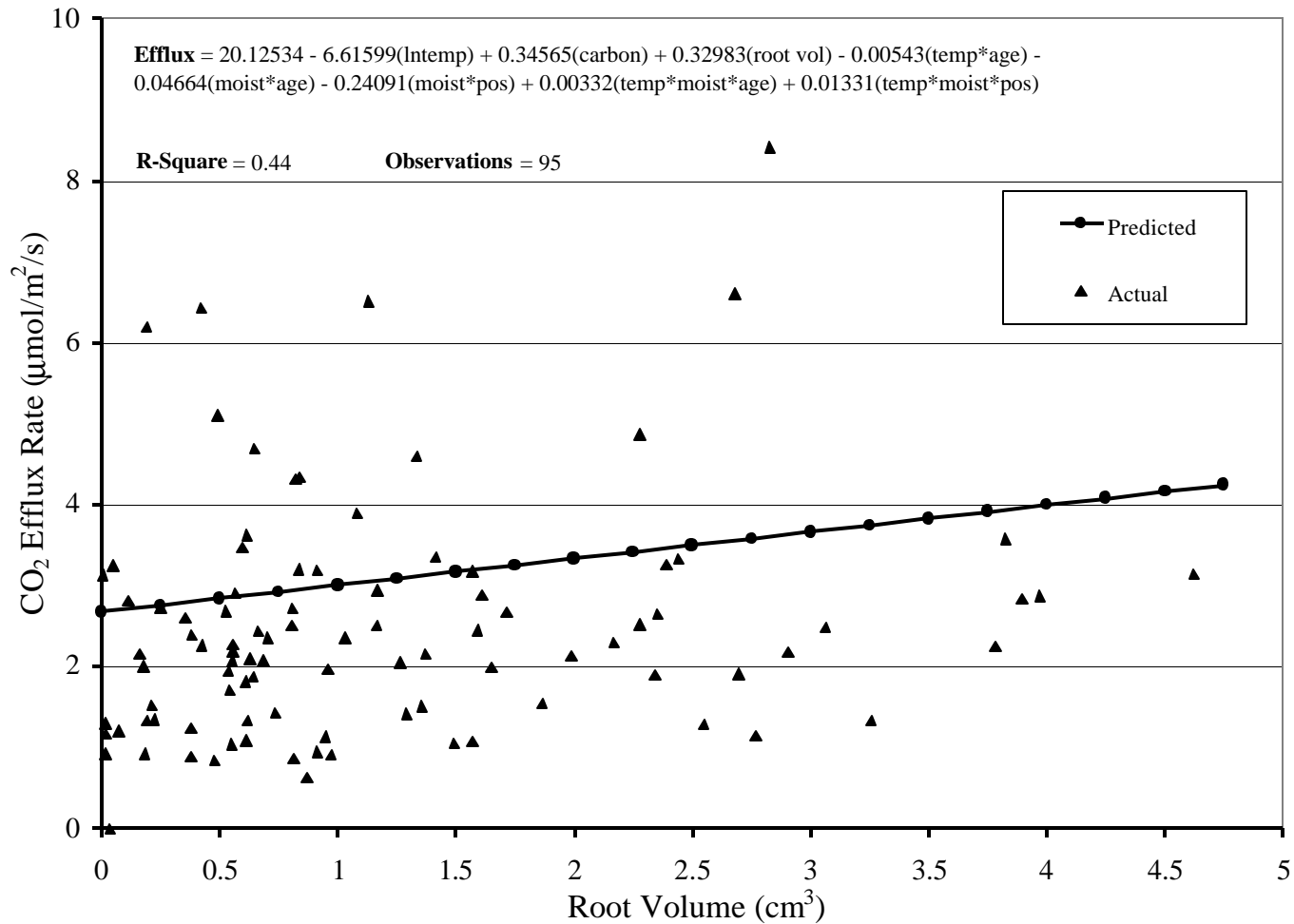
Figure 7: Comparison of actual and predicted soil CO_2 efflux rates over a range of observed root volumes for plantation loblolly pine on the Virginia piedmont. Observations were collected during May 2001. Predicted rates were calculated using an empirical model and mean parameter values for May 2001. Root volume refers to the quantity of pine roots contained in a soil core collected from the upper 10.2 cm of the A horizon.

Chapter 5: Discussion

5.1: Stand age influence on soil CO_2 efflux

Based on the results of our investigation, soil CO_2 efflux increases with stand age for plantation loblolly pine on the Virginia piedmont. This observation is in agreement with our hypothesis proposed at the beginning of the investigation. The overall mean efflux rates for the four age classes were 1.72, 2.58, 2.84, and 2.90 μmol/m^2/s for 1- to 2-year-old stands, 4- to 6-year-old stands, 8- to 12-year-old stands, and 20- to 25-year-old stands, respectively. These averages were calculated from data collected over a 12-month period from April 2000 to April 2001. A comparison of monthly efflux means for the four age classes revealed that stand age had a significant treatment effect ($p = 0.05$) on 10 of the 12 monthly sampling dates.

Furthermore, stand age was a significant parameter in regression analysis. Empirical modeling demonstrated that at a given soil temperature and moisture level, soil CO_2 efflux rate will be higher in older stands than in younger stands. Empirical modeling also demonstrated that the magnitude of difference between efflux rates observed in age class one and those observed in age class four were actually "dampened" during the summer months due to ambient temperature buffering in mature stands. Earlier we showed that soil temperature is consistently cooler in mature stands during the summer months due to radiation interception by the forest canopy. Because soil CO_2 efflux is largely driven by temperature, the cooler soil in mature stands is not respiring at maximum rates. Using our seasonal model, we can demonstrate the dampening of summer efflux rates in mature stands.

Predicted annual efflux rate, using age-specific mean values for all parameters in the model, is 2.51 μmol/m^2/s for age class one. In the same manner, predicted annual efflux rate is 3.54 μmol/m^2/s for age class four. Under this scenario, efflux rate for age class four is 41% higher than the rate for age class one. If we then hold temperature constant between the two age classes and use age-specific mean values for all other parameters in the model, predicted annual efflux rates are 2.42 and 3.68 μmol/m^2/s for age classes one and four, respectively, and represent a 52% difference.

We believe that the increase in soil CO_2 efflux with increasing stand age is due, in part, to increasing pine root biomass. We base this conclusion on the results of previous studies of soil CO_2 efflux in pine plantations and on root volume data collected from our study sites during May 2001. In an investigation of an 11-year-old loblolly pine plantation in North Carolina, Maier and Kress (2000) found that root respiration accounted for 52% and 73% of total soil CO_2 efflux in non-fertilized and fertilized loblolly pine stands, respectively. In addition, Ewel *et al*. (1987) found soil CO_2 evolution rates for a 29-year-old Florida slash pine plantation were 35% higher than the observed rates for a 9-year-old plantation. The investigators attributed the higher evolution rate to the nearly threefold increase in live root biomass observed in the older plantation. Based on these studies, it is clear that pine root respiration makes a significant contribution to total soil CO_2 efflux and that pine root respiration increases as the stand matures, presumably due to increasing live root biomass.

In an analysis of variance of our data, stand age was shown to have a significant effect (p=0.0169) on root volume. Furthermore, mean root volumes show a clear ranking by age for the four age classes. The mean volume of roots captured in a 382 cm^3 soil core collected from the A horizon was 0.66, 1.03, 1.40, and 1.73 cm^3 for stand age classes one, two, three, and four, respectively. Oddly, the root volume estimates do not correspond with the ranking of soil CO_2 efflux rates measured during May 2001. Yet this is not surprising due to the fact that the efflux rates measured during May 2001 exhibit a ranking inconsistent with trends observed throughout the prior twelve months of data collection. Mean soil CO_2 efflux rates for May 2001 were 3.88, 2.42, 2.02, and 1.74 $\mu mol/m^2/s$ for age classes two, three, one, and four, respectively. This ranking clearly differs from the overall ranking observed for the yearlong means. This is likely due to the fact that mean soil moisture content across all age classes during May 2001 was extremely low (15.1%) due to a period of prolonged drought. In comparison, mean soil moisture content across all age classes for the previous 12 months was 20.4%. By using the predictive model developed from the May 2001 data set, we can further solidify the fact that soil moisture deficiency contributed to the anomalous ranking of the soil CO_2 efflux rates. If soil moisture is held constant at the mean value of all age classes for the previous 12 months (20.4%) and all other model parameters are held constant at mean

values for the May 2001 measurement period, an interesting result occurs. The normally observed chronological ranking appears in the predicted soil CO_2 efflux rates. Specifically, rates are predicted as 1.44, 1.88, 2.60, and 4.63 μmol/m^2/s for age classes one, two, three, and four, respectively. It is apparent that soil CO_2 efflux rates observed in May 2001 were suppressed and most likely not representative of typical efflux patterns.

We can not attribute increasing soil CO_2 efflux with stand maturation solely to the proliferation of pine roots due to our inability to partition efflux between root and microbial respiration. Our sampling design and procedures were not developed to measure the contribution of these components to total soil CO_2 efflux. Likewise, no sampling procedure was utilized to quantify microbial biomass. Based on a review of the literature, it is difficult to surmise whether microbial activity increases or decreases with stand maturation/succession (Mathes and Schriefer 1985; Hendrickson *et al*. 1985). Most likely, microbial activity shows a short-term decrease immediately following disturbance due to the sudden change in soil temperature and moisture patterns and then shows a steady increase with stand maturation/succession as the forest floor redevelops and the soil microclimate becomes more hospitable. It would be expected that both root and microbial biomass increase with stand maturation/succession and that respiration from both components would increase; however, we can only conclude from our observations that root biomass increases, resulting in a greater respiring biomass.

5.2: Spatial trends of soil CO$_2$ efflux

We also conclude that there is significant spatial heterogeneity in soil CO_2 efflux of plantation loblolly pine on the Virginia piedmont and that roots exert significant influence on these spatial patterns. Again, this conclusion is in agreement with our hypothesis set forth at the beginning of the investigation. The overall mean efflux rates for the near and away measurement positions were 2.72 and 2.28 μmol/m^2/s, respectively. These averages were calculated using data collected over a 12-month period from April 2000 to April 2001. A comparison of monthly efflux means for the near and away measurement positions revealed significant differences ($p = 0.05$) on 8 of the 12 monthly sampling dates. Furthermore, measurement position was a significant

parameter in regression analysis. Empirical modeling demonstrated that at a given soil temperature and moisture level, soil CO_2 efflux rate will be higher near the tree. We believe that roots account for positional differences in soil CO_2 efflux for several reasons.

From our intensive sampling in May 2001, we found that root volume in a 382 cm^3 soil core collected from the A horizon averaged 1.42 cm^3 at the near position and 0.99 cm^3 at the away position. Based on the analysis of variance, there was not a significant interaction between age and measurement position for root volume (p=0.6103). The significance level of the positional difference was estimated at p = 0.0649, indicating a strong probability of difference in root volume near and away from the tree. Also, regression analysis showed that root volume was a significant parameter in predicting soil CO_2 efflux, explaining 4.8% of efflux variation. As further evidence, previous studies on the Virginia piedmont have observed a similar spatial relationship between root biomass and soil CO_2 efflux. In an investigation of soil CO_2 efflux in a 2-year-old loblolly pine plantation on the Virginia piedmont, Pangle (2000) found that root biomass was positively correlated with soil CO_2 efflux rates when differences in efflux rates between plots both near and away from seedlings were examined. In a similar study of soil CO_2 efflux in newly established pine plantations on the Virginia piedmont, Popescu (2001) attributed observed differences in the spatial pattern of soil CO_2 efflux to root biomass as well.

A simple explanation exists for the spatial distribution of roots in loblolly pine plantations. Following harvest, site preparation, and replanting, a new plantation can be visualized as a clean slate with an orderly arrangement of young seedlings. Assuming herbicide is applied for control of herbaceous and woody competition, the main sources of roots proliferating in the new plantation are the young seedlings. As the developing root system of a young seedling grows to exploit the soil volume, a radial gradient of root biomass develops around the seedling in the upper soil horizon. A greater quantity of root biomass exists close to the seedling because, quite obviously, this is where the root system originates.

While the findings of Pangle and Popescu suggest that fine root biomass differs between locations near the seedling and away from the seedling, positional differences for fine root biomass should diminish with time. Although fine root biomass becomes

homogeneous with stand maturation, coarse root biomass remains concentrated near the stem. At maturity, the contribution of fine root respiration to total root respiration most likely is similar near the tree and away from the tree. However, root respiration is intensified near the tree due to the presence of the taproot and large lateral roots, which are absent away from the tree. Several studies have demonstrated that a large proportion of total root biomass exists in the taproot and large lateral roots residing at the base of loblolly pines. Van Lear and Kapeluck (1995) investigated above- and below-stump biomass of a mature loblolly pine plantation in the upper piedmont of South Carolina. The investigators observed that 75% of below-stump biomass was contained in the taproot and lateral roots larger than 2.5 cm in diameter. The majority of roots in this size class are located near the base of the tree. Wells *et al*. (1975) reported similar findings for a 16-year-old loblolly pine plantation on the North Carolina piedmont. These investigators estimated that the taproot and lateral roots greater than 4 cm in diameter accounted for approximately 74% of total root biomass. While the distribution of fine root biomass may become homogeneous with stand maturity, clearly a large proportion of root biomass remains concentrated near the stem of the tree. It is apparent from our research and the research cited above that a radial gradient in root biomass persists at least through a typical timber management rotation.

An interesting caveat to our discussion on the spatial distribution of soil CO_2 efflux for plantation loblolly pine is the observation of highly probable positional differences in soil carbon content. During May 2001, we sampled the upper 10.2 cm of the A horizon at all plots across the study site and analyzed the soil for carbon content. In an analysis of variance, soil carbon showed a high probability for positional difference (p=0.0830) with an overall mean carbon content of 2.84% at the near position and 2.55% at the away position. Furthermore, soil carbon content was found to be a significant parameter in regression analysis of the May 2001 data, explaining 6.4% of efflux variation. It is difficult to surmise whether this positional difference in soil carbon content is attributable to fine root turnover, litter input, microbial biomass or a combination of all three. Most likely, the positional difference in soil carbon content is a reflection of both greater root density and initially greater litter input near the tree, which may lead to greater microbial activity as dead roots and litter are decomposed.

Interestingly, Popescu (2001) found soil organic matter and measurement position (near or away) to be collinear parameters for soil CO_2 efflux in newly established pine plantations. Popescu found that organic matter averaged 108.4 g/m^2 near seedlings and 74.2 g/m^2 away from seedlings, but could only speculate as to the cause of this phenomenon. In addition to fine root turnover, the investigator speculated that planter bias could result in the establishment of seedlings in locations where the soil appears to afford a better chance of establishment, i.e., a soft, duff location (high organic matter content). The investigator also speculated that the seedlings may act as traps for organic matter eroding from higher up the slope. However, the influence of slope and planter bias on the spatial distribution of soil carbon at stand rotational maturity should diminish. Thus we dismiss these items as explanations for positional differences in carbon content for older age classes.

While the observation of spatial differences in soil CO_2 efflux in recently established plantations is expected, the fact that differences exist throughout the length of a timber management rotation is both surprising and contradictory to our initial hypothesis. Based on previous studies and our understanding of root system development, we initially hypothesized that observed spatial differences in soil CO_2 efflux would diminish with stand maturity due to both decreasing organic matter heterogeneity and decreasing fine root heterogeneity. That is, we believed both the forest floor and pine root system would be so well developed and homogenous at rotation maturity that spatial differences in soil CO_2 efflux would be negligible. In our investigation, we found that soil CO_2 efflux is consistently higher when measured near a loblolly pine than when measured a short distance away. This phenomenon was observed in stands within two years of establishment as well as in 25-year-old stands near harvest age. Additionally, this spatial pattern was consistent during both the growing season and the dormant season.

The only observed inconsistency in the spatial pattern of soil CO_2 efflux occurred in age class two (4- to 6-year-old stands) during a 4-month time frame from July 2000 through October 2000. During this period, observed efflux rates were actually higher at the away position. A possible explanation for this change in efflux pattern may be a short-term change in the distribution of fine root biomass and/or specific root respiration

rate. This short-term change could be a natural occurrence in root system development of young loblolly pines; conversely, it could also be a response to limited resources in the rhizosphere. A consistent trend observed throughout the study was lower soil moisture near the tree. For each monthly data set from July 2000 through October 2000, a significant positional difference was detected in soil moisture content between the near and away positions for age class two, with the away position consistently having greater soil moisture. Undoubtedly, this is due to increased water demand by a greater root density near the tree. Perhaps the root system was depleting soil moisture near the tree to the point of limiting root respiration. (This undoubtedly was the case in July 2000 when overall soil CO_2 efflux rates experienced a distinct slump in response to a period of prolonged drought.) Meanwhile, root respiration was continuing at a higher rate further away from the young tree where soil moisture had not reached a critical minimum. Although root biomass may well have been higher near the tree, the few roots at the away position were respiring at a faster rate and thus producing an overall greater CO_2 efflux. The only flaw in this reasoning is the fact that this phenomenon was not observed in other age classes despite similar soil moisture trends. However, this fact does not discredit the assertion because this may well have been the response of the root system at a very specific point of maturation. The root densities at the near and away positions for this specific age class are different than those for all other age classes and may well have exhibited a unique response to the emerging soil conditions.

5.3: Parameters influencing soil CO_2 efflux

We observed a strong seasonal pattern in soil CO_2 efflux across all four age classes of plantation loblolly pine. The mean soil CO_2 efflux rate for June 2000 was a yearlong high of 5.28 $\mu mol/m^2/s$ while the mean soil CO_2 efflux rate for December 2000 was a yearlong low of 0.487 $\mu mol/m^2/s$. As expected, soil temperature was the main driver of seasonal variation in soil CO_2 efflux. Regression analysis yielded a significant, seven-parameter model explaining 55.3% of seasonal variation in soil CO_2 efflux for plantation loblolly pine. Soil temperature was present in six of the seven parameters as either an interaction term or transformation. Soil temperature, the second power

transformation, and the natural log transformation accounted for a total of 23% of efflux variation.

Soil moisture also exhibited significant influence on seasonal variation in soil CO_2 efflux for plantation loblolly pine, but to a lesser extent than soil temperature. In the previously mentioned regression analysis, soil moisture was present in three significant parameters as an interaction term. Two of these parameters explain a combined 7.5% of efflux variation. These observations are in agreement with the findings of Raich and Potter (1995) whom concluded that temperature is the single most important variable for predicting soil CO_2 efflux. The investigators also noted that while soil moisture is an important environmental variable affecting soil respiration, it generally has little influence on efflux rates when moisture levels are adequate for the physiological needs of plants and soil organisms. We observed this exact phenomenon when mean efflux rates failed to reach a yearlong maximum when soil temperature did achieve a yearlong maximum in July 2000. Suppressed efflux rates were the result of soil moisture constraining respiration during a protracted drought.

Stand age also proved to be a significant variable in the seasonal model. Stand age is present as an interaction term in two of the seven parameters. One of these parameters is the most significant of the seven parameters in the model. It is a trinomial variable, soil temperature*soil moisture*stand age, and explains 23.2% of the variation observed in soil CO_2 efflux during the 12-month study. This fact should lend further credence to our assertion that soil temperature, soil moisture, and stand age have a significant influence on soil CO_2 efflux.

In addition to using environmental parameters, we also used pine volume estimates to model soil CO_2 efflux. We took this approach with the hope of being able to apply stand-level models across geographic regions in the future. On the Virginia piedmont, loblolly pine productivity is much lower than on other sites across the southeast. For this reason, a 12-year-old loblolly pine on the Virginia piedmont is both physiologically and physically different than a 12-year-old loblolly pine on the South Carolina coastal plain. Due to these differences it may be difficult (if not inappropriate) to apply models across geographic regions. By developing a model using pine volume rather than age, we hope to be able to predict soil CO_2 efflux across geographic regions

and to make appropriate comparisons across regions. While two stands of the same age may not have the same level of root system development, forest floor development, or micro-climate characteristics, two stands of the same pine volume should be fairly similar in these respects. In this manner we could use a model developed for loblolly pine on the Virginia piedmont to predict soil CO_2 efflux for much more productive sites farther south. Of course, this approach would assume that the same variables influence soil CO_2 efflux for plantation loblolly pine from region to region.

Regression analysis of pine volume estimates and other environmental data yielded a significant model of soil CO_2 efflux for plantation loblolly pine. This stand-level model is quite similar to the seasonal model discussed earlier. In fact, the stand-level model was developed using the same data set as the seasonal model except pine volume data were used in place of stand age data. A notable difference between the models is that the stand-level model used a data set of 384 observations while the seasonal model used a data set of 1152 observations. This is simply due to averaging of the three sub-samples for the stand-level model because stem count was estimated for only one sub-sample per replication. Also, coarse fragment volume did not prove to be a significant variable in the stand-level model where as it was a significant variable in the seasonal model. Pine volume proved to be a significant variable in predicting soil CO_2 efflux for plantation loblolly pine, appearing as an interaction term in two parameters that explain 51.5% of efflux variation. While this model remains untested across geographic regions, it does prove that soil CO_2 efflux can be modeled using pine volume in conjunction with other environmental variables.

A myriad of soil and root parameters were measured near the conclusion of this investigation with the hope that they would prove useful in characterizing soil CO_2 efflux for plantation loblolly pine. Of those parameters measured, three proved to have a significant influence on soil CO_2 efflux. They were soil carbon content, root volume, and coarse fragment content.

Using regression analysis, a significant, eight-parameter model was developed from data collected during intensive sampling of May 2001. Soil carbon content and root volume were among the eight significant parameters, explaining 6.4% and 4.8% of efflux variation, respectively. Both were positive parameters, which makes sense in light of our

previous discussion. An increase in soil CO_2 efflux would be expected with an increase in either of these parameters. Increasing soil carbon could be indicative of either an increase in microbial biomass or detrital substrate, both of which would result in increased microbial respiration. Likewise, an increase in root volume equates to a larger respiring biomass. As for soil coarse fragment content, it was not a significant variable in the eight-parameter model. However, coarse fragment content was a significant variable in the previously mentioned seasonal model. In the seasonal model, it acts as an interaction term in the parameter soil temperature*soil moisture*coarse fragments. This trinomial variable explains 2.6% of efflux variation and is a negative parameter. Being a negative parameter, a decrease in soil CO_2 efflux would be expected with an increase in coarse fragment content at a given soil temperature and moisture. This is an important observation because a negative relationship has been reported between coarse fragment content and soil CO_2 efflux in previous studies. Studies by Jobbagy and Jackson (2000), Pietikainen *et al*. (1999), and Trumbore (2000) all noted that a significant portion of the soil organic carbon with short turnover periods resides in the top 10-20 cm of the soil profile. Our sampling of coarse fragment content was for the upper 10.2 cm of the A horizon. As coarse fragment content increases in this portion of the A horizon, available volume for water, soil organic matter, and roots is diminished. With less water, fewer roots, and a smaller detrital substrate, soil CO_2 efflux will be suppressed. On an extremely rocky site (15-35% coarse fragments by volume) on the Virginia piedmont, Pangle (2000) found a significant negative relationship between coarse fragment content and soil CO_2 efflux for a 2-year-old loblolly pine plantation. Regression analysis showed that 21.7% of efflux variation could be explained by coarse fragment content alone.

5.4: Annual Soil Carbon Losses

Annual carbon loss estimates were derived using both our seasonal model and actual monthly mean effluxes. Carbon losses predicted using the seasonal model were 856, 949, 960, and 1223 g $C/m^2/yr$ for stand age classes one, two, three, and four, respectively. These carbon losses were calculated by first entering observed monthly means for each parameter into the model to obtain an average efflux rate for the month. The monthly mean efflux rates were then converted to monthly carbon losses through

cross-multiplication. The 12 months were then totaled for each age class to derive an annual carbon loss.

Annual carbon losses were also estimated using actual monthly mean effluxes. Carbon losses calculated using the monthly means were 651, 976, 1074, and 1082 g $C/m^2/yr$ for stand age classes one, two, three, and four, respectively. These carbon losses were calculated by first averaging the 12 monthly efflux means to derive an annual mean efflux rate for each age class. The annual mean efflux rate was then converted to an annual carbon loss for each age class through cross-multiplication.

The estimates for annual carbon loss using the predictive model and actual efflux measurements were quite similar. The model estimates for annual carbon loss were 31% and 13% higher for age classes one and four, respectively, and were 3% and 12% lower for age classes two and three, respectively. Similar carbon loss estimates were expected because the model was developed using empirical data. Regardless of estimation technique, the magnitude of difference between annual carbon losses for age class one and age class four is dampened in a manner similar to that described for soil CO_2 efflux earlier. In the absence of ambient temperature buffering, we would expect the magnitude of difference between annual carbon losses for age class one and age class four to be greater.

Annual soil carbon loss varies significantly across major vegetation biomes (Raich and Schlesinger 1992). Much of the observed variability among sites may be attributed to methodological differences among investigators and has created difficulties in comparing data. In an exhaustive review of published estimates of annual soil CO_2 efflux for major vegetation biomes around the world, Raich and Schlesinger (1992) used only those data based on most or all of one full year of efflux measurements. Furthermore, they excluded data obtained from soil cores and from alkali absorption techniques if the surface area of the absorbent was less than 5% of the surface area of the covered ground. Using data collected from 171 studies in 13 major terrestrial and wetland ecosystems around the globe, the investigators estimated global soil carbon loss at 68 Pg C/yr. Annual soil carbon loss by vegetation type ranged from 60 g $C/m^2/yr$ for tundra to 1260 g $C/m^2/yr$ for tropical moist forests. Annual soil carbon loss for temperate coniferous forests averaged 681 g $C/m^2/yr$. While our annual soil carbon loss estimates

are a bit higher than those reported by Raich and Schlesinger, they compare rather favorably to those reported by Ewel *et al.* (1987) for Florida slash pine plantations. They reported annual soil carbon losses for 29-year-old and 9-year-old plantations at 1300 and 850 g C/m^2/yr, respectively. Similarly, Nakane *et al.* (1984) reported annual soil carbon loss for *Pinus densiflora* in Japan at 987 g C/m2/yr. Conversely, Reinke et al. (1981) reported annual soil carbon loss for 20-year-old *Pinus palustris* in South Carolina at 509 g C/m^2/yr and Weber (1985) reported annual soil carbon loss for 19-year-old *Pinus banksiana* in Quebec at 250 g C/m^2/yr. While much of the variation in annual soil carbon losses is attributable to site-specific differences, assumptions made in calculations may also contribute to variation.

A major assumption in calculating our annual soil carbon losses is that the efflux rate observed during our one-day measurement session each month was indeed representative of the efflux rate for the entire month. Annual carbon losses could be quite skewed if monthly means were not based on representative measurements. A given day could be unusually hot, cold, wet, or dry and may not be representative of overall conditions for the entire month. Daily observations for soil temperature and soil moisture at our study site would allow a more accurate estimate of annual carbon loss . However, precise estimation of annual carbon loss was not one of our specific objectives and we present the above estimates simply as an aside to our discussion of soil CO_2 efflux.

Chapter 6: Conclusion

In this investigation, we have demonstrated that stand age has a significant, positive influence on soil CO_2 efflux of plantation loblolly pine on the Virginia piedmont. Specifically, we observed that soil CO_2 efflux increases with stand maturation and can be attributed, in part, to increasing root biomass. We have also demonstrated that significant spatial patterns exist for soil CO_2 efflux of plantation loblolly pine on the Virginia piedmont. Observed efflux rates were consistently higher when measured near a tree than when measured a short distance away. We attributed this spatial difference in efflux to differences in root biomass. Specifically, we assert that a radial gradient in root biomass exists around a tree and expands outward through the upper soil horizon. Within this radial gradient, greater root biomass exists near the tree than away from the tree. Initially, this gradient is driven by the near absence of fine root biomass away from the seedling. As the tree matures, however, positional differences in fine root biomass diminish and greater taproot and lateral root biomass near the tree drives the radial gradient. This radial gradient appears to persist through time due to the observation of higher efflux rates near the tree across all age classes.

Soil temperature, soil moisture, stand age, and measurement position are variables that explain a large percentage of the observed variation in soil CO_2 efflux for plantation loblolly pine on a seasonal and annual basis. Observations of these variables and other site parameters were utilized in developing empirical models for soil CO_2 efflux of plantation loblolly pine. Pine volume was also observed to be a significant variable for predicting efflux. Using pine volume in lieu of stand age allows more appropriate modeling of soil CO_2 efflux across geographic regions due to volume's direct dependence on site-specific productivity. Soil carbon content and root volume were found to exert a minor, but significant, influence on soil CO_2 efflux. Based on our observations, an increase in soil carbon or root volume results in an increase in soil CO_2 efflux.

This research demonstrates that future efforts to predict carbon losses from intensively managed loblolly pine plantations will have to give consideration to the spatial and temporal trends of soil CO_2 efflux. Empirical modeling has proven that we can accurately describe the spatial and temporal characteristics of soil CO_2 efflux and

their interaction with specific environmental/site variables. Yet the limited predictive ability of our models also shows that there is more to be learned about soil CO_2 efflux and the parameters that influence it. Greater confidence in soil CO_2 efflux models will be gained as larger data sets are compiled across regions of varying productivity, soil type, climate, and management intensity.

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Vita

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