SOIL HETEROTROPHIC RESPIRATION IN LOBLOLLY PINE PLANTATIONS: MEASURING AND MODELING SEASONAL VARIATION AND SILVICULTURAL IMPACTS

by

ROBERT MASON BROWN

(Under the Direction of Daniel Markewitz)

ABSTRACT

Changes in the heterotrophic (R_h) proportion of total soil respiration (R_s) due to silvicultural treatments and seasonal variation across an annual cycle were measured in six loblolly pine (*Pinus taeda*) plantations in the Piedmont and Coastal Plain of Georgia and Alabama. Silvicultural treatments included fertilizer and herbicide application, and measurements were taken every three months to assess seasonality. Soil respiration was measured with (R_h) and without (R_s) root exclusion collars. Soil characteristics were used to predict the R_h proportion, and to parameterize the DAYCENT biogeochemical model. No significant differences in the R_h proportion were detected between treatments, while fall values were significantly higher than other seasons. R_s and R_h were well predicted (R^2 of ~60 and 70%) using moisture, temperature, and soil attributes but R_h proportion was not. DAYCENT reproduced seasonal patterns of R_s but did not reproduce patterns of the R_h proportion.

INDEX WORDS: Heterotrophic Respiration, Soil Respiration, Loblolly Pine, DAYCENT, Biogeochemical Models, Silviculture

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B.S., University of Georgia, 2011

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2016

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May 2016

ACKNOWLEDGEMENTS

Firstly I need to thank my advisor Daniel Markewitz for his consistent guidance, acceptance of my lack of laboratory skills, and unwavering assistance in the field. Without his help I couldn't have achieved this significant milestone in my life, and would never have known what heterotrophic respiration is. I also want to thank my committee members for their help in the thesis process and for the knowledge I've gained from their classes.

I also want to thank Madison Akers, Brandon Crouch, George Matthew, Lori Sutter, Brandon Varner, and Greg Ward for their help in the field and lab, especially those that helped man the Dynadigger. Additionally I want to thank my office-mates Karla Gann and Jenna Stockton for their continued help over the last couple of years.

Finally I must thank my family, as a constant source of support and advice. Most especially my wife Rachel, who has been amazing from the start. With supporting the move back to Athens, listening to and reading my science jargon, calming my stress, and even helping in the field and lab.

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CHAPTER I

INTRODUCTION

Every year, soil respiration (R_s) releases 6-7 times more carbon dioxide (CO_2) into the atmosphere than anthropogenic CO_2 (Rustad *et al.*, 2000; Le Quéré *et al.*, 2013). Soil respiration includes two components: autotrophic root respiration (R_a), and heterotrophic respiration (R_h). R_a is the CO_2 released by the roots during tree growth while R_h is the CO_2 released by microorganisms in the soil (Raich and Nadelhoffer, 1989; Kelting *et al.*, 1998). Forests cover approximately 30% of the Earth's surface and thus contribute significantly to global R_s. Studies report a wide-range of 10-90% of forest R_s is produced via microbial processes (Hanson *et al.*, 2000; Subke *et al.*, 2006; Bonan, 2008). This variability in estimates can be attributed to the strong correlation between R_h and changes in soil temperature and moisture, as well as vegetation type and partitioning method bias (Subke *et al.*, 2006). Unfortunately, the large variance in estimates of R_h limits our ability to accurately estimate components of the carbon (C) budget (i.e., net primary productivity, NPP, and net ecosystem productivity, NEP) and determine whether forests are mitigating or exacerbating climate change (Maier *et al.*, 2004; Kuzyakov, 2006).

Investigations into the factors that affect R_a and R_h are typically performed at the regional or ecosystem level, and few have examined loblolly pine (*Pinus taeda*) plantations of the southeastern United States (Maier and Kress, 2000; Wiseman and Seiler, 2004; Gough *et al.*, 2005; Tyree *et al.*, 2006; Templeton *et al.*, 2015). There are an estimated 13 million hectares of planted pine in the South, which offer many ecological services, including atmospheric C sequestration (Wear and Greis, 2002). Southern pine forests have been shown to be strong C sinks, primarily accumulating C in aboveground biomass and the forest floor, and to a lesser extent mineral soil (Richter *et al.*, 1999). However, pine plantations and forests in general also release a substantial amount of CO_2, most of which is via R_s (Tyree *et al.*, 2006). In order to determine the effectiveness of southern pine plantations in sequestering atmospheric C, we must know the amount of fixed CO_2 that is subsequently lost due to heterotrophic microbial activity in the soil. Furthermore, this heterotrophic proportion of total soil respiration must be quantified as it changes between different operational treatments, physiographic regions, and seasons. These proportions are necessary to accurately determine NEP from NPP, thus helping to estimate the amount of C accumulated by the ecosystem.

Productivity in southern pine plantations, especially loblolly pine, has continually increased with enhancements in genetics as well as refinements in silvicultural methods. The most common methods to enhance growth (or increase NPP) are fertilizer and herbicide application (Borders and Bailey, 2001). Fertilization has been shown to decrease soil microbial biomass C (MBC), increase soil C, and either decrease or not effect R_s in loblolly pine plantations (Lee and Jose, 2003; Maier *et al.*, 2004; Rifai *et al.*, 2010; Templeton *et al.*, 2015). Understory control using herbicide has also been found to suppress R_s, decrease MBC, as well as decrease soil C (Shan *et al.*, 2001; Li *et al.*, 2004; Busse *et al.*, 2006; Rifai *et al.*, 2010). Additionally, decreases in fine root biomass have been associated with both fertilizer and herbicide application in loblolly pine stands (Colbert *et al.*, 1990; Albaugh *et al.*, 1998; Shan *et* *al.*, 2001). These physical and chemical changes may affect R_h at the stand level and could change throughout the year, particularly fine roots and MBC.

Quantitative modeling, including statistical and process models, can be valuable tools when evaluating complex systems, such as ecosystem C cycling. The DAYCENT biogeochemical model, as well as its predecessor CENTURY, have been used extensively to model trace gas fluxes, nutrient cycling, and land-use effects on agricultural soils, but have limited practice in forested areas (Del Grosso *et al.*, 2005; Fenn *et al.*, 2008; Kim *et al.*, 2009; van Oijen *et al.*, 2011; Gathany and Burke, 2012; Bonan *et al.*, 2013). Few studies have validated DAYCENT R_s estimates using soil efflux measurements taken at the associated research site being simulated (Kelly *et al.*, 2000; Del Grosso *et al.*, 2005; Yeluripati *et al.*, 2009; Chang *et al.*, 2013). Of these studies, two have directly evaluated R_h estimates (Del Grosso *et al.*, 2005; Chang *et al.*, 2013), and one has included a forested site in the evaluation (Del Grosso *et al.*, 2005). A comparison of predicted R_h proportions versus measurements taken regularly across multiple sites would provide valuable insight into the model's ability to estimate this large and complex C flux under varying forested scenarios.

This thesis focuses on quantifying the R_h proportion of R_s in southern loblolly pine plantations in the Piedmont and Upper Coastal Plain regions under fertilizer and herbicide treatments over an annual cycle. Measurements were made monthly at six experimental field sites in Georgia and Alabama for one year. In Chapter II of this thesis I review studies that have utilized the root-excluding collar method used in my field study, as well as previously observed R_h and microbiological responses to fertilizer, herbicide, and seasonality. I also discuss previous literature that has tested DAYCENT in forested scenarios. In Chapter III I discuss the use of the root-excluding collar method to partition R_s, and its effects on soil microbial biomass. Changes in the R_h proportion are quantified between treatments and seasons, and measured soil physical and chemical characteristics are used to predict the R_h proportion via multiple regression. In Chapter IV the DAYCENT model is parameterized for each field study site using measured soil data. Predicted R_s, R_h, and R_h proportion values are compared to field measured data to assess the model's ability to simulate these fluxes in loblolly pine plantations. In Chapter V I briefly discuss the importance of this thesis, in that I am providing R_h proportion values necessary for determining levels of C sequestration in southern loblolly pine plantations, as well as insight into the most accurate way to model these values in the future.

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CHAPTER II

LITERATURE REVIEW

Soil Heterotrophic Respiration

Separation of R_h from R_s by root exclusion

There have been numerous techniques developed to separate R_h from R_s in the field, as summarized by Hanson *et al.* (2000). A common method used by researchers is generally termed the “trenching” method. This method consists of digging a trench to a specific depth around an area that is kept free of vegetation and installing a plastic barrier to prevent root intrusion. This severs all roots within the plot eliminating further transfer of photosynthates into the area. A short (usually shorter than 10 cm) polyvinyl chloride (PVC) collar is placed in the plot center for measurements. After a certain amount of time (generally 90-days) carbohydrates from the severed roots are considered to have been consumed by microbes and all resulting respiration is assumed to be the baseline R_h. Bond-Lamberty *et al.* (2011) summarized criticisms of this method, noting its high level of disturbance and potential impacts to soil water and temperature dynamics. Díaz-Pinés *et al.* (2008) studied the impacts of trenching on soil water and microbial biomass in a temperate forest in Austria. They found that while microbial biomass was not significantly different between trenched and un-trenched plots, fine-roots decayed slower than assumed, which may bias R_h proportions to be higher than actual. However, all existing techniques for partitioning soil respiration have compromises, and the most common method used thus far in forest soils has been versions of the trenching technique (Subke *et al.*, 2006).

The trenching method is simple and cheap when compared to other partitioning methods, such as isotope labeling. It requires minimal labor when few plots are being installed, but becomes very labor-intensive when a large number of sites and plots are to be considered (Bond-Lamberty *et al.*, 2011). Thus, the deep root-excluding collar method was developed to save significant installation time. Furthermore, Vogel and Valentine (2005) suggested that the collar method could effectively separate R_h from R_a in a shorter time than trenching, in as little as 22 days. However, to be effective at partitioning soil respiration in forests, the collars must be installed at least 30 cm deep (Bond-Lamberty *et al.*, 2011). Kelting *et al.* (1998) found that root carbon fractions had been fully decomposed three months following root severing using steel cylinders 5.1 cm in diameter by 30 cm long. However, other studies suggest that root decomposition effects will persist longer than one season after severing (Díaz-Pinés *et al.*, 2008).

Measuring R_s and R_h in southern loblolly pine plantations

Total soil respiration and R_h have been measured and modeled across the range of loblolly pine by Templeton *et al.* (2015). While this study incorporated many sites (154 plots) across the "managed range" of loblolly, plots were sampled only once or twice and R_h was estimated using root-free soil incubations rather than the root-excluding collar method. Furthermore, fertilization and thinning treatments were tested, but variables including herbicide and seasonality were not included. They found that a model incorporating soil moisture, temperature, percent coarse fragments, and elevation best predicted the R_h proportion (however with only an $R^2 = 0.45$). Wiseman and Seiler (2004) examined how R_s changes with stand age and within-plot heterogeneity, but did not partition R_h and limited site selection to the Virginia Piedmont. Changes in R_s were evaluated using monthly measurements over an annual cycle along a chronosequence by Gough *et al.* (2005), but R_h was not partitioned from R_s. Intraannual changes in R_s were found (R_s increases during growing season due to increase in R_a), as well as significant effects of stand age (particularly related to canopy closure and soil temperature), region (positive age effect in Piedmont, no effect in Coastal Plain), and site preparation (bedding in Coastal Plain). Tyree *et al.* (2006) intended to see if there are lingering effects of site preparation, initial fertilization, or mid-rotation fertilization in a mature loblolly plantation on R_s and R_h. They found R_s remained low relative to control plots following bedding and ditching, and increased following application of nitrogen, phosphorus, and lime. However, no treatment effects on R_h were found.

Effects of nitrogen fertilization on R_h

In their region-wide evaluation of soil respiration in loblolly plantations, Templeton *et al.* (2015) found R_h to be negatively affected by fertilization, while positively affected by thinning. Tyree *et al.* (2008) found a decrease in R_h in 2 year-old loblolly clones, and an inconsistent decrease in R_s. Conversely, Tyree *et al.* (2006) found that in 33 and 24-year-old loblolly stands, R_s increased following application of nitrogen (N), phosphorus, and lime at early mid-rotation. However, R_h was estimated only once in July using root-free incubations, and within treatment heterogeneity did not allow for significant treatment effects on R_h to be elucidated. Bowden *et al.* (2004) tested the effects of low and high N rates (50 and 150 kg N/ha, respectively) applied annually on R_s and R_h. They used a 55-year-old mixed hardwood stand and a 75-year-old red pine (*Pinus resinosa*) stand fertilized annually in the Harvard forest for approximately 16 years. Heterotrophic respiration was found to be significantly lower in both fertilized pine plots, and in the high-N hardwood plot using root-free soil incubations in the laboratory. The same trends were seen in R_s. Maier *et al.* (2004) developed a carbon budget for 12-year-old loblolly stands following 5-years of fertilization and irrigation using their own previously acquired data as well as existing literature. While they did not make soil respiration measurements in the field for their study, they used derivatives of equations used to calculate NPP and NEP to estimate R_h in mid-rotation loblolly plantations. Their calculations showed that while R_s did not vary with fertilization, R_h was significantly lower in fertilized plots versus control. Furthermore, they stated that R_h was the largest component of R_s in all treatments.

In contrast to the findings mentioned above, in an Alaskan boreal forest, Allison *et al.* (2008) did not find a significant change in R_h in fertilized plots by measuring the ^{14}C isotopic composition of the soil respiration. They did find R_s had decreased by the end of the growing season, but was not a significant treatment effect in their analysis of variance (ANOVA).

Effects of herbicide on R_h

Few studies have directly assessed herbicide effects on R_h, however, we can surmise treatment effects on R_h by examining herbicide effects on R_s and microbial biomass (Shan *et al.*, 2001; Rifai *et al.*, 2010) . Rifai *et al.* (2010) found in multiple mid-rotation loblolly plantations in Georgia decreases of approximately 20% and 25% in R_s and microbial biomass, respectively, in herbicide plots versus control. A portion of the decrease in R_s is due to the lack of understory roots, however, the slightly larger decrease in microbes suggests a decrease in the R_h proportion of total soil respiration. Equivalent changes in R_s were observed in herbicide plots of 17-year-old slash pine (*Pinus elliottii*) plantations in northern Florida flatwoods by Shan *et al.* (2001). Total understory-elimination using herbicide significantly decreased fine root production, as well as R_s in four out of the five months measured.

Effects of root-exclusion on microbial communities

In a 130-year-old temperate mixed Norway spruce (*Picea abies*) forest in Austria, Díaz-Pinés *et al.* (2008) found little and insignificant variation in total microbial biomass between trenched and un-trenched plots. Siira-Pietikäinen *et al.* (2001) and Siira-Pietikäinen *et al.* (2003) also did not detect a change in microbial biomass after trenching in a mixed Norway spruce and Scots pine (*Pinus sylvestris*) forest in Finland. Ross *et al.* (2001) did find a significant decrease in microbial biomass following trenching in the upper 20-cm of soil in a mature radiata pine (*Pinus radiata*) forest in Australia. However, they reported no change in the metabolic quotient (amount of CO_2 released per unit of microbial biomass) as a result of trenching. No known studies have examined effects of root-excluding collars on microbial biomass.

DAYCENT

DAYCENT simulations of forests

DAYCENT has been used extensively for modeling agricultural systems, while far fewer studies have utilized the model for forested systems. Fenn *et al.* (2008) used DAYCENT to calculate historical nitrogen (N) deposition in forests of the Sierra Nevada mountains in California in order to develop new critical N deposition loads. Model output was not being tested in the study, but was simply used to provide historical estimates for N cycling calculations and critical load estimates for the ecosystem. Soil N was also assessed by Gathany and Burke (2012) by simulating a ponderosa pine (*Pinus ponderosa*) forest and the effects of fire on N biogeochemistry and trace gas fluxes. They found that the model followed pre and post-fire trends seen in the field for CH_4 uptake, nitrification, and N gas fluxes. They also found that DAYCENT predictions for trace gas fluxes fell within the range of field-based measurements.

Soil C was evaluated by Kim *et al.* (2009), who modeled changes in soil organic carbon (SOC) after forest and grassland areas were converted to corn fields for ethanol production. While the model did show a longer time period for converted forests to provide greenhouse gas benefits than converted grasslands, the researchers noted that DAYCENT underestimated temperate forest SOC (84 ± 15 Mg C per hectare) compared to what they found in the literature of approximately 107 Mg C per hectare.

Accurate decomposition rates are necessary for understanding forest biogeochemistry, therefore Cotrufo *et al.* (2010) tested DAYCENT's accuracy in determining aboveground leaf-litter decomposition rates when compared to four other commonly used methods, including litterbags. They found that when accurately parameterized, DAYCENT simulated decomposition was very similar to the established field methods. Bonan *et al.* (2013) compared DAYCENT and the Community Land Model (CLM) in their ability to model decomposition using a large dataset spanning North and Central America. Field data included measurements from boreal, conifer, deciduous, and tropical forests, along with different grassland types. They found that DAYCENT performed better than CLM, producing close matches with the field data for C and N dynamics. They noted that certain biomes performed better than others, with the greatest error produced for tropical and deciduous forests.

DAYCENT estimates of R_s

Reliable model simulations of R_s would provide substantial time and cost savings compared to field measurements. These simulations would also enable different conditions to be modeled once the model was shown to provide accurate estimates. Kelly *et al.* (2000) attempted to validate DAYCENT output on a Colorado shortgrass steppe for daily, biweekly, monthly, seasonal, and annual outputs of major ecosystem processes. These included CO_2 flux, trace gasses, NEP, NPP, and others. However, they were not able to make direct comparisons between simulated versus observed CO_2 flux data because the DAYCENT version used only modeled soil respiration, while the measured efflux included soil and live-shoot respiration. Therefore, they compared observed respiration values at night to DAYCENT output in order to decrease the R_a influence. They found that simulated CO_2 flux agreed with observed data on a daily timestep ($R^2 = 0.47$), and increased when taken as a monthly average ($R^2 = 0.53$). Seasonal patterns also matched those observed. Overall they determined DAYCENT to be a strong model for simulating CO_2 flux and soil water dynamics, and that modeled CO_2 flux is more sensitive to changes in soil water than temperature.

Yeluripati *et al.* (2009) developed a Bayesian calibration technique for DAYCENT in order to more accurately initialize the soil C pools. They applied the model to a grassland in Switzerland, and had three years of daily R_s taken using a static chamber technique. However, for the model calibration they used only R_s in winter in an attempt to account for the high SOC decomposition (i.e. R_h). They found that the data did not correlate very well, likely because of a greater contribution of R_a to winter respiration than anticipated. van Oijen *et al.* (2011) compared model output versus daily NO_2, NO, and CO_2 measurements taken from 1994-2003 in a Norway spruce (*Picea abies*) forest in Germany. They also used a Bayesian framework to improve parameterization of DAYCENT along with three other process-based biogeochemical models. In their sensitivity analysis, they found that no individual parameter was strongly correlated with any of the three outputs evaluated. They found very good correlation between model output and measured values for CO_2 flux, with values for r varying from 0.87 to 0.90 depending on their parameterization. Overall they found DAYCENT to perform very well, producing output very similar to measured data. However, they did identify a large phase shift for some of the predictions, where the rate of soil fluxes were relatively accurate, but the timing of fluxes were missed.

DAYCENT for partitioning soil respiration

Chang *et al.* (2013) assessed the ability of DAYCENT to simulate changes in SOC dynamics, including R_h, in response to tillage using nine years of data for validation. Field data used included eddy covariance measurements, harvested biomass, soil moisture, and soil temperature. Using a 5000 year equilibrium block (i.e., spin up), SOC values reached steady state by the time the study simulation was to begin, with values within the range (5200-5400 g C/m^2) of those observed in the field (5205 g C/m^2). They found that R_h was enhanced by tillage, as well as increasing soil temperature and moisture. However, they did not have field-measured R_h values to validate the model estimates. Del Grosso *et al.* (2005) developed, calibrated, and tested a new R_h sub-model for DAYCENT in order to improve its ability to model decomposition. They used gas flux, soil temperature, and soil moisture data from one site to calibrate, and similar measurements from multiple other sites to validate. Data used to parameterize the model were obtained by the researchers from grasslands or agricultural fields in Colorado and Wyoming. Data used to validate the model included these sites, along with measurements found in the literature from various other sites. Most of these sites were prairie or agricultural fields, but some came from an alpine forest in Wyoming, a mixed deciduous forest in Massachusetts, and a beech forest in Germany. The R_h dataset consisted of CO_2 efflux measurements from plots deemed to be vegetation free, either by herbicide applied during fallow season, vegetation control by plowing, or 15 m gaps cut in the beech forest and maintained vegetation free. Efflux data obtained for the calibration dataset was measured using permanent PVC gas flux chambers. The equation for R_h developed using the calibration dataset is:

$$R_h = F(T_{soil}) * F(RWC)$$

where $F(T_{soil})$ is the temperature effect normalized to 1 at 30^0C, and $F(RWC)$ is the moisture effect (measured soil relative water content) normalized to 1 at RWC = 100%. Both of these functions utilize arctangent equations (see paper for full equations), which reportedly "allows for varying sensitivity of the response variable (respiration) to the independent variable (temperature or water)". Measured VWC was converted to RWC to account for water stress associated with varying soil properties. This interaction equation was found to correlate well ($R^2 = 0.47$) with observed efflux data from their native grassland dataset. The model estimated soil efflux better outside the growing season, suggesting a weakness when simulating R_a.

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CHAPTER III

SOIL HETEROTROPHIC RESPIRATION IN SOUTHERN PINE PLANTATIONS CHANGES WITH SEASON AND SILVICULTURAL MANAGEMENT

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[1] Brown, R.M. and Markewitz, D. 2016. To be submitted to *Forest Ecology and Management*.

Abstract

To determine the effectiveness of southern pine plantations in sequestering atmospheric carbon (C), we must know the amount of fixed carbon dioxide (CO_2) that is subsequently lost due to heterotrophic microbial activity in the soil. Furthermore, the heterotrophic proportion of total soil respiration (R_s) must be quantified as it changes between different operational treatments, physiographic regions, and seasons. This research quantified heterotrophic contributions to R_s in loblolly pine (*Pinus taeda*) plantations in the Piedmont and Upper Coastal Plain of the southeastern US under control, fertilized, and herbicide treatments over an annual cycle. Heterotrophic respiration (R_h) was separated in the field from autotrophic root respiration (R_a) using metal root-excluding collars. Soil R_s and R_h were correlated with measures of fine root mass and microbial biomass. The R_h proportion of R_s was not significantly different between regions or treatments. It was found to be significantly higher in the fall (~80±6%) than in all other seasons (69±3%). Root exclusion significantly reduced microbial biomass carbon (MBC) and nitrogen (MBN) in most seasons, and reduced root mass in spring. Levels of MBC and MBN in root-excluding collars was greater in winter than all other seasons. Microbial biomass, temperature, moisture, and other soil characteristics explained 82 and 75% of R_s and R_h variability, respectively. These results suggest that the use of fertilizer and herbicides in these ecosystems increases ecosystem productivity without increasing R_h (i.e., an increase in net ecosystem productivity) that may lead to greater rates of C sequestration and climate change mitigation.

Introduction

Every year, soil respiration (R_s) releases 6-7 times more carbon dioxide (CO_2) into the atmosphere (~60 Pg C/yr) than anthropogenic CO_2 emission from fossil fuel combustion (~9 Pg C/yr) (Rustad *et al.*, 2000; Le Quéré *et al.*, 2013). Soil respiration includes two components: autotrophic root respiration (R_a), and heterotrophic respiration (R_h). R_a is the CO_2 released by the roots during tree growth while R_h is the CO_2 released by microorganisms in the soil (Raich and Nadelhoffer, 1989; Kelting *et al.*, 1998). Forests cover approximately 30% of the Earth's surface and thus contribute significantly to global R_s. Studies report a wide-range of 10-90% of forest R_s is produced via microbial processes (Hanson *et al.*, 2000; Subke *et al.*, 2006; Bonan, 2008). This variability in estimates can be attributed to the strong correlation between R_h and changes in soil temperature and moisture, as well as vegetation type and partitioning method bias (Subke *et al.*, 2006). Unfortunately, the large variance in estimates of R_h limits our ability to accurately estimate components of the carbon (C) budget (i.e., net primary productivity, NPP, and net ecosystem productivity, NEP) and determine whether forests are mitigating or exacerbating climate change (Maier *et al.*, 2004; Kuzyakov, 2006).

The world's forests are generally considered to be C sinks; however, increases in R_s with warming temperatures, and particularly R_h, may result in the associated forests becoming a smaller C sink if NPP remains constant, thus exacerbating the recent rise in atmospheric CO_2 concentrations (Rustad *et al.*, 2000). These large-scale implications create a need for a greater understanding of the processes affecting R_h in forested ecosystems (Templeton *et al.*, 2015).

Investigations into the factors that affect R_a and R_h are typically performed at the regional or ecosystem level, and few have examined loblolly pine (*Pinus taeda*) plantations of the southeastern United States (Maier and Kress, 2000; Wiseman and Seiler, 2004; Gough *et al.*, 2005; Tyree *et al.*, 2006; Templeton *et al.*, 2015). These ecosystem are important in the US as there are an estimated 13 million hectares of planted pine in the South, which offer many ecological services, including atmospheric C sequestration (Wear and Greis, 2002). Southern pine forests have been shown to be strong C sinks, primarily accumulating C in aboveground biomass and the forest floor, and to a lesser extent in the mineral soil (Richter *et al.*, 1999). However, pine plantations and forests in general also release a substantial amount of CO_2, most of which is via R_s (Tyree *et al.*, 2006).

In order to determine the effectiveness of southern pine plantations in sequestering atmospheric C, we must know the amount of fixed CO_2 that is subsequently lost due to heterotrophic microbial activity in the soil. Furthermore, this heterotrophic proportion of total soil respiration must be quantified as it changes between different operational treatments, physiographic regions, and seasons. These proportions are necessary to accurately determine NEP from NPP, thus helping to estimate the amount of C accumulated by the ecosystem. Net ecosystem productivity can be considered synonymous with C sequestration, and is calculated by subtracting R_h from NPP (Smith *et al.*, 2010):

$$NEP = NPP - R_h \tag{1}$$

As such, R_h has a direct impact on the amount of C accumulated by the ecosystem.

Productivity in southern pine plantations, especially loblolly pine, has continually increased with enhancements in genetics as well as refinements in silvicultural methods. The most common methods to enhance growth (or increase NPP) are fertilizer and herbicide application (Borders and Bailey, 2001). Fertilization has been shown to decrease soil microbial biomass C (MBC), increase soil C, and either decrease or not effect R_s in loblolly pine plantations (Lee and Jose, 2003; Maier *et al.*, 2004; Rifai *et al.*, 2010; Templeton *et al.*, 2015). Understory control using herbicides has also been found to suppress R_s, decrease MBC, as well as decrease soil C (Li *et al.*, 2004; Busse *et al.*, 2006; Rifai *et al.*, 2010). Additionally, decreases in fine root biomass have been associated with both fertilizer and herbicide application in loblolly pine stands (Colbert *et al.*, 1990; Albaugh *et al.*, 1998; Shan *et al.*, 2001). These physical and chemical changes may affect R_h at the stand level and could change throughout the year, particularly with respect to fine roots and MBC.

This research aims to quantify heterotrophic contributions to R_s in southern loblolly pine plantations in the Piedmont and Upper Coastal Plain regions under fertilizer and herbicide treatments over an annual cycle. Heterotrophic respiration has been found to be a significant portion of R_s in different forest types worldwide, however, relatively few studies have focused specifically on the R_h proportion in loblolly pine plantations in the southeastern United States (Hanson *et al.*, 2000; Subke *et al.*, 2006; Templeton *et al.*, 2015). Furthermore, of these studies, none have examined interacting effects of region, silvicultural treatment, and season through a full annual cycle using *in situ* measurements.

Many C cycling models and eddy flux tower estimates do not partition R_a and R_h, and may not effectively account for seasonal changes (Lavigne *et al.*, 1997). Eddy flux towers, in particular, calculate net ecosystem exchange (NEE), which is similar to NEP in that it is a net balance of C in to and out of the ecosystem. However, NEE lacks an estimation of R_h, so it cannot partition NPP from NEP (Kirschbaum *et al.*, 2001; Curtis *et al.*, 2002). Comparisons between NEP and NEE provide valuable insight into processes of ecosystem-C sequestration, with R_h representing a critical process.

By providing estimates of R_h across the various scenarios being tested, we can refine C budget estimates, and adjust for changes in R_h due to the above variables being tested. If certain combinations of variables decrease the R_h proportion of R_s, then we can assume an increase in NEP in that area if NPP inputs stay constant. Alternatively, if R_h remains constant under silvicultural treatments that increase NPP (fertilizer and herbicide), we can also assume an increase in NEP. An increase in NEP means more C is being stored in above or belowground components, i.e. increased C sequestration and climate change mitigation.

Our hypotheses are that the R_h proportion will: 1) increase with fertilization due to a decline in fine root production, 2) decrease with herbicide application due to a reduction in available C substrate and 3) decrease during the growing season because of a relative increase in fine root production and respiration.

Methods

Study Sites

Samples and measurements for this study were taken at six planted loblolly pine experimental sites in the Piedmont and Upper Coastal Plain of Georgia and Alabama (Figure 3.1). Treatment plots ranged from 400-1000 m^2 in size. Three sites (Piedmont 1, Coastal Plain 1 & 2) were part of the PINEMAP Tier II network, which is a region-wide study that consists of active experimental plots maintained within existing cooperative field studies throughout the range of loblolly pine (www.pinemap.org). The PINEMAP sites were established and are maintained as part of the North Carolina State University Forest Productivity Cooperative, Regionwide 18 study (http://forestproductivitycoop.net/). Three additional sites were incorporated from the Consortium for Accelerated Pine Production Studies (CAPPS) network (see Borders *et al.* (2002) and Borders and Bailey (2001) for a more detailed description). The CAPPS sites used (deemed Piedmont 2 &3, Coastal Plain 3 here) were chosen based on stand age and physiographic region to most closely match those of the PINEMAP sites. In all cases for this study, Coastal Plain refers to the Upper Coastal Plain physiographic region; the Lower Coastal Plain was not evaluated. See Table 3.1 for additional site information.

Fertilized plots in the PINEMAP study received 268 kg N/ha at planting and every six years, as well as phosphorus (P) and boron (B). Information on the application rate of nutrients other than N at PINEMAP sites was not available. Sites in the CAPPS study received varying amounts of fertilizer from years 1-12, ranging from 59-118 kg N/ha applied yearly, and 118 kg N/ha every year after age 12. They also received 56 kg P/ha in years 1 and 2 in the form of diammonium phosphate, 28 kg P/ha in year 11 as triple super phosphate, and 56 kg K/ha in years 1 and 2 in the form of KCl. Herbicide plots received periodic non-soil active herbicides (e.g., glyphosate) as necessary for complete vegetation control (Kinane, 2014). Basal area for each site in 2014 was obtained from PINEMAP and CAPPS data (Table 3.4).

Soil Sampling

Soil samples for site description were collected once from each plot between 2014-2015. Eight random subsample locations within each plot were used to collect forest floor with a 0.35 x 0.35 m square. The interior of the square was cut with a knife, and the O_a layer was separated from the O_i and O_e. Within each plot two composite samples, subsamples 1-4 and 5-8, were retained for O_a, and O_i and O_e combined. Below these forest floor collection points mineral soil samples were collected using a 6.5-cm diameter, open-bucket hand auger. Mineral soils were sampled at four different depths: 0-10, 10-20, 20-50, and 50-100 cm. Within each plot, samples were similarly composited at each depth for laboratory analysis (total of 120 samples).

Bulk density (BD) samples were also collected between 0-10, 10-30, and 30-60 cm in each plot (Blake and Hartge, 1986).

Soil Analysis

Samples were air-dried before being crushed and sieved through a 2-mm sieve. A moisture correction factor was determined for each air-dried soil sample by placing 3-6 g in tin cups and dried until a constant weight at 105^0C. Forest floor samples were oven dried at 65^oC, weighed, and ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ). A portion of each ground forest floor sample was combusted in a Thermolyne Type 30400 muffle furnace (Thermo Scientific) for ash correction (Nelson and Sommers, 1996).

Soils were analyzed for pH, macro and micro nutrients, C and nitrogen (N), particle size distribution, and exchangeable acidity. Soil pH_{H_2O} and pH_{CaCl_2} were measured using a 2:1 ratio of soil and deionized (DI) water or 0.01 M $CaCl_2$ following Thomas (1996). Macro and micro nutrients (P, K, Mg, Ca, B, Na, Al, Mn, Mo, and Cu) were determined using the Mehlich 1 Extraction (Mehlich, 1953). Extracts were frozen until analysis could be performed by inductively coupled plasma - mass spectrometry (ICP-MS). Carbon and N concentrations were obtained from a Flash EA 1112 Series CN soil analyzer (CE Elantech, Lakewood, NJ). Particle size distribution was measured using the hydrometer method (Gee and Bauder, 1986). Exchangeable acidity values were obtained by shaking 5 g of soil with 50 mL of 1 M KCl and filtering through a Whatman 42 filter. Extracts were frozen until titrated to a pH of 8.2 with 0.02 M NaOH using an auto-titrator (Mettler-Toledo, Columbus, OH) (Bertsch and Bloom, 1996).

Root-excluding Collar Installation and CO_2 Efflux Measurements

Collars for CO_2 efflux measurements were first installed during July-August 2014. These installations included Piedmont 1-3 and Coastal Plain 1-2 (Coastal Plain 3 was added in spring 2015). Two types of collars were utilized: non-root-excluding (NRE) and root-excluding (RE). Non-root-excluding collars consisted of short (5-10 cm) PVC rings 10.16 cm in diameter that did not sever roots and were installed by hand. Efflux measurements from these collars represented R_s. Root-excluding collars were made of steel electrical conduit 10.16 cm in diameter and cut to 35 cm in length. Several small holes were drilled 2 cm from the upper end to prevent ponding. The RE collars were driven into the ground using a Dynadigger (Swannanoa, NC) with a retrofitted steel cup at the tip that fit around the circumference of the RE. When additional force was needed to drive through roots or dry soil, a sledgehammer and round piece of steel were used. Best efforts were given to drive the RE collars in until the drainage holes were approximately level with the soil surface. During the summer 2015 installation of Piedmont 2 & 3, RE collars were not able to be installed as normal due to extremely dry soil and rocky conditions. A hand auger was then used to break up the uppermost soil layer to allow installation.

Within each treatment plot, three subplot locations were randomly selected. Each of these subplots consisted of one NRE collar and one RE collar. Subplot locations directly adjacent to trees (~60 cm) were not included in order to avoid large lateral roots that would inhibit RE collar installation. Prior to the installation of either type collar at a subplot, a square portion of the forest floor was carefully cut along three sides with a knife and peeled back to expose mineral soil. Soil efflux measurements were made using a Licor 6400 infrared gas analyzer with a LI-6400-09 soil chamber attachment (Licor, Lincoln, NE) by placing the chamber on the exposed mineral soil and taking duplicate measurements at three locations within the subplot. The two most similar efflux values were used as the locations for the collar installations.

To avoid bias the first measurement point of each chosen pair was always the NRE collar. Following installation of a NRE and RE collar at a subplot, the forest floor was carefully folded back over the collars.

At the time of efflux measurement, a 10 cm long soil temperature probe on the Licor was placed in the soil directly next to the measurement locations and volumetric water content (VWC) was measured adjacent to this measurement using a HydroSense soil water measurement probe with 12 cm rods (Campbell Scientific, Logan, UT)

Monthly CO_2 Measurements and Collar Soil Sampling

Efflux, temperature, and moisture measurements were made at each collar approximately every 30 days following installation using the same instruments. Forest floor material was cut from around the edge of the collar as needed to provide a good seal with the chamber head. A foam ring was placed on the chamber head where it joined with the collar to further minimize CO_2 leakage.

Efflux measurements taken three months after collar installation were used to calculate R_h proportions (Kelting *et al.*, 1998). On these measurement dates, efflux from the RE collars was considered to be only R_h, while the NRE collars were R_s. Following efflux measurements, VWC inside the RE collars was recorded, and a soil punch tube (3.5 cm diameter) was used to collect a sample of the upper 10 cm of soil at the center of each collar. An open-bucket hand auger (6.5 cm diameter) was then used to collect soil to 30 cm at each efflux measurement location. Samples collected with the soil punch tube were analyzed for microbial biomass, while samples collected with the auger were processed for total root mass. Microbial biomass samples were kept at approximately 4^0C and processed as soon as possible with the longest delay being two weeks. Root mass samples were air-dried before being processed.

After soil samples for microbial biomass and root mass were collected, the RE collars were removed, scraped of remaining soil, and reinstalled at a new randomly selected location within the plot to start the next three-month cycle. This process was repeated five times to capture seasonal differences, with the first cycle eventually being discarded due to sampling issues.

Microbial Biomass and Root Mass Analysis

Microbial biomass samples were analyzed using the fumigation-extraction technique (Brookes *et al.*, 1985; Vance *et al.*, 1987; Horwath and Paul, 1994). For every 24 samples (i.e. samples for two plots), three were randomly chosen to be run in triplicate for both fumigated and un-fumigated assays to assess variability. A moisture correction factor for each soil was performed as previously described. Filtrates were collected in plastic scintillation vials and frozen until analysis. Filtrate samples were analyzed for non-purgeable organic C and total N using a Shimadzu TOC-V CSN Total Organic Carbon Analyzer with a TNM Total Nitrogen Measuring Unit (Shimadzu, Kyoto, Japan). Prior to analysis samples were diluted 20 times with DI water to limit salt buildup in the instrument. A value of 0.45 was used for K_{EC} and K_{EN} to convert results to MBC and MBN (Joergensen *et al.*, 1996; Rifai *et al.*, 2010).

Soil samples collected for root mass were air dried and crushed. Soil was passed through a 2 mm sieve and roots removed by hand for approximately five minutes per sample. Roots were then dried at 65^{0}C for approximately 48 hours and weighed.

Data Analysis

Differences in R_h proportions were compared at the plot-level by taking the mean R_h proportion of each sub-plot pair. Prior to averaging, sub-plot pair values that produced a proportion greater than 1.0 were excluded. This removed 51 of the 161 partitioned efflux values measured across the study (31.6%). Results were analyzed as a randomized block design, with R_h proportion comparisons made between Treatment, Season, and Region, with Site treated as the blocking factor. Means were compared using a full interaction analysis of variance (ANOVA) including Site, Treatment, and Season for each region individually as well as regions combined. Pairwise comparisons were tested for significant difference at $p<0.05$ using Tukey's Honestly Significant Difference (HSD).

Multiple regression was used with both the sub-plot level (i.e., individual collars) and the plot level data to test the ability of measured variables to predict R_s, R_h, and the R_h proportion. The first regression applied measurements made at the sub-plot pair level, which included soil temperature, VWC, microbial biomass, and root mass. The second regression applied the mean values for those parameters for each plot, along with the physical and chemical soil characteristics described above and plot basal area. In all tests, transformations were performed as necessary to adjust for normality using the Shapiro-Wilk test. Final regression models were chosen by best subsets regression using *regsubsets* in the "leaps" package in *R*. Potential models provided by the software were compared by adjusted R^2 and Mallow’s Cp values. Statistical tests were performed using *R* software version 3.2.3.

Results

Soil Analysis

Soil physical and chemical characteristics were compared between treatments and regions (Tables 3.2, 3.3, and 3.4). Soil C was ~32% lower in herbicide plots than control and fertilized (p=0.03 and 0.05, respectively) in the upper 10 cm, but was not significantly different at deeper depths. Piedmont soils contained ~18% more C at 20-50 cm than Coastal Plain soils. Soil N was lower by ~22% in herbicide plots than control and fertilized (p=0.03 each) in only the upper 10 cm. Extractable soil P was higher in fertilize than herbicide plots from 0-10 cm by ~95% and 20-50 cm by ~98% (p=0.0006 and 0.03, respectively).

Monthly R_s and R_h Measurements

Total soil respiration and R_h showed strong seasonal and treatment effects in the Piedmont and Coastal Plain (Figure 3.2). Both R_s and R_h declined substantially during the winter (December-February), and began to climb with rising temperatures around March. Control plots in the Piedmont had ~28% higher R_s and ~61% higher R_h than herbicide plots (*p*=0.03 and 0.001, respectively), and were generally higher than fertilized plots, although not statistically significant. Fertilized plot R_h was also significantly higher than herbicided plots by ~54% (*p*=0.03). This trend in treatment differences continued in the Coastal Plain with control and fertilized R_s significantly higher than herbicided (*p*=0.02 and 0.05, respectively).

Soil R_h Partitioning with Root-Excluding Collars

ANOVA was initially evaluated by region. There were no significant differences in R_h among the Coastal Plain sites (see Figure 3.3), however, there was a marginal site × season interaction (p=0.05) with Coastal Plain 2 being slightly smaller in summer than fall (p=0.07). In the Piedmont there were significant seasonal (p=0.02) and treatment (p=0.01) effects. The R_h proportion was significantly greater in the fall than the summer (p=0.02), and herbicide significantly decreased the R_h proportion compared to fertilized plots (p=0.03). There was also a marginal decrease with herbicide when compared to control plots (p=0.05). No other within-region differences were detected.

When the R_h proportion was compared across the entire dataset (Figure 3.4), there was no significant difference between Piedmont and Coastal Plain. There was a significant main effect of season (p=0.03), an interaction effect of site and season (p=0.03), and a marginal treatment effect (p=0.08). Proportions were smaller in summer than in fall (p=0.04), with values of 0.73 and 0.80, respectively. Finally, the R_h proportion was found to be ~80% in the fall and ~69% for the rest of the year (Table 3.11).

R_s, R_h, and R_h Proportion Models

The strongest predictors to estimate R_h proportion at the sub-plot pair-level included interactions of the five predictors (Table 3.5). With multiple interactions included all parameters were significant, however, the model still only explained approximately 18% of the variability in the R_h proportion. There were no significant main effects for any parameters in the R_h proportion model. Models for R_s (Table 3.6) and R_h (Table 3.7) efflux were much more informative with R^2 values of 0.65 and 0.63, respectively.

The most significant soil characteristics for estimating mean plot-level R_h proportion included sand (%), C (%), and P (kg/ha) in the upper soil layers (Table 3.8). However, the model only explained ~22% of the variation in R_h proportion. Models for plot-level R_s (Table 3.9) and R_h (Table 3.10) again had higher R^2 values than the R_h proportion model, explaining ~82 and ~75% of the variation, respectively. These models were best explained by soil temperature, MBC, soil P contents (kg P/ha), and BD, with the addition of exchangeable acidity for R_s.

Microbial Biomass and Root Mass

Root exclusion had a significant effect on MBC and MBN in most seasons, as well as root mass in spring (Figure 3.5). Levels of MBC in RE collars was ~29% smaller in fall than winter (p=0.03), but unaffected by treatment (Figure 3.6). In NRE collars MBC varied by site (p<0.001), was ~10% smaller in fertilized plots than in control plots (p=0.029), but was not significantly affected by season.

Microbial biomass N in both RE and NRE collars varied among sites (p<0.001 each), but was not significantly affected by treatment. Winter values were significantly greater than all other seasons for MBN in RE collars by an average of ~46%, but no seasonal differences were detected in NRE collars.

Root mass did not change significantly between seasons or treatments among the NRE collars. However, root mass was significantly greater by ~49% in the spring than in the fall among the RE collars (p=0.03). No significant differences in root mass were detected between treatments in RE collars, however, herbicide marginally reduced root mass compared to fertilized plots (p = 0.09).

Discussion

Application of N fertilizer in loblolly pine ecosystems has had contradictory effects on R_s and R_h among previous studies. In their region-wide study across the Southeast, Templeton *et al.* (2015) found R_h to be negatively affected by high application rates of fertilizer, with no significant changes in R_s. Tyree *et al.* (2008) also found a decrease in R_h following fertilization of 2 year-old clones with an inconsistent decrease in R_s. However, Tyree *et al.* (2006) found an increase in R_s following fertilization of mid-rotation loblolly pine stands, and did not find a change in R_h. Fertilization studies in other forest types have also found decreases in R_h and/or R_s (Lee and Jose, 2003; Bowden *et al.*, 2004; Olsson *et al.*, 2005), while others have found no change (Allison *et al.*, 2008). As mentioned by Templeton *et al.* (2015), the influence of R_h on R_s may decrease with stand age as rooting mass increases. Considering that stands in the current study ranged from 17-26 years old, this could at least partially explain the lack of a difference in the R_h proportion between control and fertilized plots. Moreover, absence of a significant difference in rooting mass between control and fertilized plots (Figure 3.6) may further substantiate the idea of rooting mass, thus R_a contribution, becoming relatively static with maturity.

Few studies have directly assessed herbicide effects on R_h in forests, however, we might infer treatment effects on R_h by examining herbicide effects on R_s and microbial biomass (Shan *et al.*, 2001; Busse *et al.*, 2006; Rifai *et al.*, 2010) . Rifai *et al.* (2010), working in multiple mid-rotation loblolly pine plantations in Georgia, found decreases of approximately 20 and 25% in R_s and microbial biomass, respectively, in herbicide plots versus control. A portion of the decrease in R_s is due to the lack of understory roots; however, the slightly larger decrease in microbial biomass suggests a possible decrease in the R_h proportion of R_s. Similar decreases in R_s with herbicide treatments were observed in other loblolly pine stands (Li *et al.*, 2004; Busse *et al.*, 2006) as well as slash pine (*Pinus elliottii*) plantations by Shan *et al.* (2001). We found the R_h proportion in herbicided plots smaller than in fertilized plots in the Piedmont, but this did not apply in the Coastal Plain or when the regions were analyzed as a whole. However, R_s was consistently smaller with treatment throughout the study without a significant decrease in rooting mass. Competition-control has been shown to reduce rooting mass as well as R_s in pine plantations (Shan *et al.*, 2001). While we did not detect a significant reduction in fine root mass due to treatment, undetected changes may have been sufficient to lower R_a, thus the lowering of R_s that we detected. The significantly greater fine root mass within RE collars in spring can likely be attributed to moister conditions within the RE pipes, slowing root decomposition.

Seasonal fluctuations in R_s are typically seen in forests, with photosynthesis (i.e. R_a) slowing down in the winter months along with lower temperatures, and ramping back up in the growing season (Gough and Seiler, 2004; Palmroth *et al.*, 2005; Tyree *et al.*, 2008). We found these trends for R_s and R_h, with a concurrent increase in the R_h proportion in fall. Fall measurements were taken in October and November, when R_s begins to decline back to winter lows (Figure 3.2). At the same time, heterotrophic microbes probably still have an abundant C food source as suggested by MBC not decreasing in the fall (Figure 3.5). With R_a beginning to decline for the year and soil microbes still metabolizing and respiring at a high rate, it is logical that the R_h proportion would be higher in the fall than in other seasons. The general decrease in MBN every season from winter through fall may indicate microbes transitioning from C-deficient to N-deficient with the growing season flush of root exudates. This could further indicate their continued activity into the fall versus slowing R_a, resulting in a greater R_h proportion.

No known studies have assessed the effects of the RE collar method on microbial communities. This method has become increasingly popular among forest soil scientists for partitioning R_s (Kelting *et al.*, 1998; Hanson *et al.*, 2000; Dilustro *et al.*, 2005; Vogel and Valentine, 2005; Bond-Lamberty *et al.*, 2011) without full consideration of its microbiological impacts. The trenching method is similar (see a review by Bond-Lamberty *et al.* (2011)) and has been found to decrease (Ross *et al.*, 2001) or not affect (Siira-Pietikäinen *et al.*, 2003; Díaz-Pinés *et al.*, 2008) MBC levels. Previous studies have found decreases in MBC due to fertilizer and herbicide application, as well as differences among soil textures (Lee and Jose, 2003; Li *et al.*, 2004; Dilustro *et al.*, 2005; Busse *et al.*, 2006; Ratcliff *et al.*, 2006; Rifai *et al.*, 2010). Any change in MBC due to fertilization or herbicide application in forests has generally been attributed to changes in fine root production and not direct-effects of the chemical on the microbes. We found significant decreases of MBC and MBN in RE collars across multiple seasons and among control plots. This would suggest a decrease in available substrate within the collars and subsequent microbial deaths. Significant microbial deaths would lead to a pulse of CO_2 efflux, which may explain the number of sub-plot collar pairs that exhibited an R_h proportion greater than 1. These instances occurred most often during the very hot and dry summer month measurements. The significance of MBC and MBN in our regression models for predicting R_s and R_h further supports the importance of considering microbial communities when partitioning R_s (Tables 3.5, 3.6, 3.7, 3.9, and 3.10).

Measurements of soil characteristics (i.e., pH, exchange cations, etc.) and conditions (i.e., temperature and moisture) were not strong predictors of the R_h proportion, whether at the individual-measurement or plot-level (Tables 3.5 and 3.8, respectively). However, they do appear to explain a large amount of the variability in R_s and R_h individually and at the plot-level

($R^2 = 0.82$ and 0.75, respectively), which would allow one to subsequently calculate the R_h proportion. It is surprising that despite clear evidence that fertilizer and herbicide treatments alter soil C, N, P, and microbial biomass, which are important predictors of R_h, that no subsequent influence on R_h proportion is observed.

Conclusion

We hypothesized that the R_h proportion would increase with fertilizer use and decline with herbicide use, neither of these hypotheses were supported. In contrast, we hypothesized that the R_h proportion would increase in the fall as R_a declines, which was observed.

If application of fertilizer and herbicide increase NPP, as is commonly observed in southern loblolly pine plantations, but has a negligible effect on the R_h proportion, we can presume that these common silvicultural practices increase C sequestration (i.e., NEP). The R_h proportion was not well estimated directly from soil measures but might be estimated by modeling R_s and R_h, as long as microbial characteristics are also considered at the time of sampling. Finally, the time of year needs to be considered when incorporating the R_h proportion into NEP calculations. The R_h proportion in fall may be greater if soil temperatures are warm while trees begin to slow photosynthesis for the winter. Ignoring these seasonal changes may lead to overestimates of annual NEP. Across the Upper Coastal Plain and Piedmont, the R_h proportion was ~80% in the fall and ~69% during the rest of the year.

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Table 3.1: General site descriptions and locations.

Site Name	State	County	Physiographic Region	Soil Series	Associated Study	[1]Treatments Evaluated	Site Prep	Genetic Family	Year Planted
Piedmont 1	GA	Wilkes	Piedmont	Pacolet	PINEMAP	C, F	Unknown	Unknown	1997
Piedmont 2	GA	Putnam	Piedmont	Appling	CAPPS	C, F, H	Shear, rake, pile, disk	10-25	1995
Piedmont 3	GA	Putnam	Piedmont	Davidson	CAPPS	C, F, H	Shear, rake, pile, disk	10-25	1995
Coastal Plain 1	AL	Marengo	Upper Coastal Plain	Savannah	PINEMAP	C, F	Unknown	Unknown	1998
Coastal Plain 2	AL	Marengo	Upper Coastal Plain	Brantley	PINEMAP	C, F	Unknown	Unknown	1996
Coastal Plain 3	GA	Tift	Upper Coastal Plain	Tifton	CAPPS	C, F, H	Shear, rake, bed	7-56	1988

[1] Silvicultural treatment (C = Control, F = Fertilize, H = Herbicide)

Table 3.2: Site soil characteristics (mean ± 1 SE) by region, treatment, and depth sampled in 2014.

Region	[1]Treatment	Depth (cm)	[2]$\text{pH}_{\text{CaCl}_2}$	Texture	[3]O-Hor Mass (kg/m^2)	Carbon (%)	Nitrogen (%)	[4]Ex.Ac. (cmol+/kg soil)	[5]BD (g/cm^3)
Piedmont	Control	O-Hor			6.6 ±0.9	40.6 ±1.90	0.85 ±0.05		
		0-10	4.46 ±0.20	Sandy Loam		1.51 ±0.42	0.095 ±0.022	0.32 ±0.09	1.37
		10-20	4.63 ±0.15	Sandy Clay Loam		0.66 ±0.06	0.052 ±0.013	0.27 ±0.09	1.55
		20-50	4.65 ±0.14	Clay Loam		0.34 ±0.02	0.031 ±0.004	0.31 ±0.10	1.51
		50-100	4.45 ±0.17	Clay Loam		0.20 ±0.05	0.022 ±0.006	0.69 ±0.23	1.47
	Fertilize	O-Hor			7.3 ±0.5	42.1 ±1.60	1.13 ±0.10		
		0-10	3.75 ±0.16	Sandy Clay Loam		1.07 ±0.42	0.064 ±0.009	1.55 ±0.29	1.42
		10-20	3.92 ±0.12	Sandy Clay Loam		0.47 ±0.07	0.037 ±0.003	2.26 ±0.74	1.45
		20-50	4.17 ±0.06	Clay		0.35 ±0.13	0.032 ±0.002	1.29 ±0.35	1.40
		50-100	4.24 ±0.18	Clay		0.11 ±0.02	0.023 ±0.005	1.65 ±0.76	1.40
	Herbicide	O-Hor			6.3 ±0.4	45.0 ±1.20	0.96 ±0.09		
		0-10	4.00 ±0.13	Sandy Clay		0.55 ±0.01	0.041 ±0.009	0.86 ±0.10	1.48
		10-20	4.23 ±0.08	Clay		0.40 ±0.05	0.041 ±0.000	0.80 ±0.08	1.40
		20-50	4.46 ±0.02	Clay		0.26 ±0.03	0.023 ±0.003	0.51 ±0.26	1.39
		50-100	4.30 ±0.08	Clay		0.26 ±0.00	0.025 ±0.002	0.79 ±0.45	1.39
Coastal Plain	Control	O-Hor			5.2 ±0.7	25.6 ±4.30	0.57 ±0.07		
		0-10	3.77 ±0.10	Loamy Sand		1.09 ±0.21	0.064 ±0.005	0.78 ±0.17	1.15
		10-20	4.00 ±0.05	Loamy Sand		0.54 ±0.16	0.036 ±0.004	0.75 ±0.13	1.43
		20-50	4.00 ±0.02	Sandy Loam		0.24 ±0.05	0.025 ±0.006	1.45 ±0.31	1.51
		50-100	3.86 ±0.06	Sandy Clay Loam		0.21 ±0.10	0.024 ±0.006	3.53 ±1.74	1.46
	Fertilize	O-Hor			5.9 ±0.4	31.3 ±3.90	0.90 ±0.08		
		0-10	3.55 ±0.18	Sandy Loam		1.41 ±0.41	0.090 ±0.010	1.75 ±0.45	1.38
		10-20	3.70 ±0.12	Sandy Loam		0.54 ±0.14	0.039 ±0.010	2.22 ±0.92	1.50
		20-50	3.76 ±0.09	Sandy Clay Loam		0.30 ±0.06	0.030 ±0.009	3.59 ±0.95	1.46
		50-100	3.77 ±0.08	Sandy Clay Loam		0.20 ±0.03	0.026 ±0.009	5.91 ±2.22	1.41
	Herbicide	O-Hor			4.9 NA	30.0 *NA	0.80 NA		
		0-10	3.67 NA	Sand		0.74 NA	0.054 NA	0.571 NA	1.20
		10-20	3.99 NA	Sand		0.44 NA	0.042 NA	0.495 NA	1.39
		20-50	4.03 NA	Sandy Loam		0.27 NA	0.038 NA	0.823 NA	1.66
		50-100	3.99 NA	Sandy Loam		0.11 NA	0.034 NA	1.172 NA	1.51

[1] Silvicultural treatment

[2] pH measured in a 0.01 M $CaCl_2$ slurry

[3] O-horizon (O_i, O_e, and O_a combined), values include ash correction

[4] Exchangeable acidity

[5] Bulk density

* Only one herbicide plot included in Coastal Plain so SE could not be assessed

Table 3.3: Site soil particle size distribution (mean ± 1 SE) by region, treatment, and depth sampled in 2014.

Region	[1]Treatment	Depth (cm)	Clay %	Sand %	Silt %
Piedmont	Control	0-10	19.5 ±7.2	64.0 ±8.6	16.6 ±2.2
		10-20	28.0 ±10.5	56.0 ±9.6	15.9 ±1.1
		20-50	37.9 ±11.5	44.4 ±8.3	17.7 ±3.2
		50-100	36.9 ±6.5	43.5 ±6.6	19.6 ±0.1
	Fertilize	0-10	26.0 ±3.1	57.9 ±2.1	16.1 ±1.0
		10-20	33.2 ±2.8	51.2 ±1.7	15.5 ±2.6
		20-50	41.8 ±6.1	42.1 ±2.9	16.2 ±3.9
		50-100	43.9 ±6.1	38.9 ±2.1	17.2 ±5.4
	Herbicide	0-10	36.4 ±7.5	51.3 ±6.3	12.3 ±1.2
		10-20	47.8 ±8.4	40.1 ±4.5	12.1 ±3.8
		20-50	53.3 ±5.5	34.5 ±2.4	12.2 ±3.0
		50-100	49.2 ±5.0	35.3 ±0.6	15.5 ±4.4
Coastal Plain	Control	0-10	5.3 ±0.8	86.1 ±4.4	8.6 ±3.8
		10-20	6.1 ±0.7	83.7 ±3.8	10.2 ±3.4
		20-50	13.8 ±0.7	76.0 ±3.8	10.2 ±3.6
		50-100	21.3 ±5.9	70.4 ±7.0	8.3 ±2.2
	Fertilize	0-10	10.7 ±4.5	79.2 ±4.5	10.1 ±2.2
		10-20	14.1 ±5.8	75.8 ±6.1	10.1 ±4.2
		20-50	21.9 ±4.9	67.7 ±7.1	10.5 ±4.4
		50-100	29.7 ±4.1	61.5 ±8.0	8.8 ±4.1
	Herbicide	0-10	3.8 *NA	90.9 NA	5.4 NA
		10-20	5.0 NA	92.2 NA	2.8 NA
		20-50	12.8 NA	86.8 NA	0.4 NA
		50-100	20.8 NA	77.9 NA	1.3 NA

[1] Silvicultural treatment

* Only one herbicide plot included in Coastal Plain so SE could not be assessed

Table 3.4: Select mineral soil nutrients and plot basal area (mean ± 1 SE).

Region	Treatment	Depth (cm)	Phosphorus (µg/ g soil)	Potassium (µg/ g soil)	Magnesium (µg/ g soil)	Calcium (µg/ g soil)	Basal Area (m^2/ha)
Piedmont	Control	0-10	3.3 ±1.0	79.8 ±11.7	83.6 ±32.9	483.122 ±190.3	34.3 ±7.5
		10-20	1.3 ±1.1	54.3 ±6.2	68.8 ±22.9	294.754 ±89.9	
		20-50	0.6 ±0.4	44.1 ±5.5	89.8 ±13.3	219.069 ±29.1	
		50-100	0.7 ±0.4	45.9 ±8.7	114.8 ±20.7	167.098 ±17.7	
	Fertilize	0-10	20.9 ±13.8	48.2 ±8.1	21.9 ±9.1	139.069 ±64.4	30.5 ±7.8
		10-20	2.0 ±0.8	42.6 ±13.2	27.9 ±21.7	146.974 ±51.9	
		20-50	0.9 ±0.4	45.5 ±13.8	88.7 ±24.6	177.508 ±35.7	
		50-100	0.8 ±0.4	50.7 ±14.7	112.9 ±20.7	126.980 ±30.3	
	Herbicide	0-10	1.1 ±0.7	54.1 ±14.7	39.5 ±37.4	213.733 ±116.3	43.7 ±1.0
		10-20	1.1 [1]NA	65.5 ±52.5	42.8 ±40.1	199.663 ±94.2	
		20-50	0.6 [1]NA	41.4 ±18.4	94.6 ±9.2	160.858 ±80.0	
		50-100	0.9 ±0.5	160.6 ±6.2	100.8 ±2.3	87.687 ±41.9	
Coastal Plain	Control	0-10	6.7 ±5.2	47.7 ±23.6	28.3 ±21.3	170.432 ±64.9	29.1 ±9.6
		10-20	7.7 ±6.4	30.6 ±7.6	18.5 ±14.2	122.786 ±59.5	
		20-50	8.5 ±7.6	32.7 ±9.6	47.4 ±12.4	182.393 ±77.9	
		50-100	9.0 ±8.3	46.1 ±18.8	86.2 ±36.5	185.107 ±63.9	
	Fertilize	0-10	6.7 ±3.0	34.4 ±21.9	66.6 ±61.2	271.413 ±234.7	25.2 ±3.9
		10-20	1.9 ±1.5	28.1 ±19.7	73.2 ±70.6	296.990 ±267.2	
		20-50	2.6 ±1.4	34.3 ±8.71	90.4 ±49.7	311.006 ±238.7	
		50-100	2.3 ±1.7	43.0 ±6.28	125.8 ±18.8	320.734 ±214.2	
	Herbicide	0-10	0.6 *NA	63.8 NA	4.9 NA	50.424 NA	52.1 NA
		10-20	0.1 NA	14.3 NA	1.8 NA	33.430 NA	
		20-50	0.1 NA	16.9 NA	12.1 NA	33.849 NA	
		50-100	0.2 NA	15.0 NA	26.1 NA	70.535 NA	

* Only one herbicide plot included in Coastal Plain so SE could not be assessed

[1] Error could not be assessed because value for Piedmont 3 was below detection limit

Table 3.5: Model parameters for predicting square-transformed R_h proportion of R_s (µmol CO_2/m^2/second) using sub-plot measurements only, n=109.

Parameter	β	Std. Error	*t* value	*p*
Intercept	1.1730	0.2276	5.155	<0.001
([1]Soil temp × [2]Root mass)	0.0012	3.741e-04	3.336	0.001
([3]VWC × Root mass)	-0.7816	0.1848	-4.230	<0.001
(VWC × [4]MBC)	-0.0388	0.0146	-2.660	0.009
(Root mass × MBC)	-0.1163	0.0435	-2.674	0.009
(VWC × Root mass × MBC)	0.1757	0.0415	4.235	<0.001
(Soil temp × Root mass × [5]MBN)	-0.0002	5.257e-05	-2.922	0.004
Model *p* = 0.002				
Model R^2 = 0.184				
Model adjusted R^2 = 0.135				

[1] Soil temperature square transformed
[2] Root mass log(1+X) transformed
[3] Soil volumetric water content (VWC) log transformed
[4] Microbial biomass carbon (MBC) log transformed
[5] Microbial biomass nitrogen (MBN) square-root transformed

Table 3.6: Model parameters for predicting square-root-transformed R_s (µmol CO_2/m^2/second) using sub-plot measurements only, n = 109.

Parameter	β	Std. Error	*t* value	*p*
Intercept	-0.5909	0.3229	-1.830	0.070
[1]Soil temp	0.0016	0.0001	13.670	< 0.001
[2]Root mass	0.1088	0.0414	2.627	0.009
[3]MBC	0.2338	0.0557	4.196	< 0.001

Model p = < 0.001
Model R^2 = 0.653
Model adjusted R^2 = 0.643

[1] Soil temperature square transformed
[2] Root mass log(1+X) transformed
[3] Microbial biomass carbon (MBC) log transformed

Table 3.7: Model parameters for predicting square-root-transformed R_h (μmol CO_2/m^2/second) using sub-plot measurements only, n = 109.

Parameter	β	Std. Error	*t* value	*p*
Intercept	-0.3283	0.3533	-0.929	0.355
[1] Soil temp	0.0013	0.0001	10.216	<0.001
[2] VWC	-0.0867	0.0402	-2.153	0.034
[3] Root mass	0.0841	0.0400	2.103	0.038
[4] MBC	0.2131	0.0542	3.934	<0.001
Model p = <0.001				
Model $R^2 = 0.629$				
Model adjusted $R^2 = 0.614$				

[1] Soil temperature square transformed
[2] Soil volumetric water content (VWC) log transformed
[3] Root mass log(1+X) transformed
[4] Microbial biomass carbon (MBC) log transformed

Table 3.8: Model parameters for predicting the R_h proportion of R_s (µmol CO_2/m^2/second) using plot-averaged measurements, n=47.

Parameter	β	Std. Error	*t* value	*p*
Intercept	0.1303	0.1970	0.662	0.512
[1] %Sand 0-10 cm	0.0034	0.0017	2.081	0.044
[2] %Carbon 10-20 cm	0.4570	0.1755	2.604	0.013
[3] kg P/ha 0-10 cm	0.0530	0.0239	2.214	0.032
[4] kg P/ha 10-20 cm	-0.0446	0.0206	-2.165	0.036
Model p = 0.028				
Model R^2 = 0.223				
Model adjusted R^2 = 0.149				

[1] %Sand in upper 10 cm of soil
[2] %Carbon in upper 10-20 cm of soil square root transformed
[3] kg phosphorus/kg soil in upper 10 cm soil log(1+X) transformed
[4] kg phosphorus/kg soil in upper 10 cm soil square root transformed

Table 3.9: Model parameters for predicting R_s (µmol CO_2/m^2/second) using plot-averaged measurements, n=47.

Parameter	β	Std. Error	*t* value	*p*
Intercept	1.4051	0.1998	7.031	<0.001
[1] Soil temp	0.0015	0.0001	11.847	<0.001
[2] MBC	0.0006	0.0002	2.702	0.01
[3] kg P/ha 0-10 cm	0.0749	0.0216	3.470	0.001
[4] BD deep	-1.3792	0.3220	-4.284	<0.001
[5] Exch. Acidity 0-10 cm	-0.1977	0.0745	-2.652	0.011
Model *p* = <0.001				
Model R^2 = 0.819				
Model adjusted R^2 = 0.797				

[1] Soil temperature square transformed
[2] Microbial biomass carbon (MBC) log transformed
[3] kg phosphorus/kg soil in upper 10 cm soil log(1+X) transformed
[4] Bulk density deep (~35 cm deep) $\frac{1}{X^2}$ transformed
[5] Exchangeable acidity (cmol charge/kg soil) of upper 10 cm soil square root transformed

Table 3.10: Model parameters for predicting R_h (µmol CO_2/m^2/second) using plot-averaged measurements, n=47.

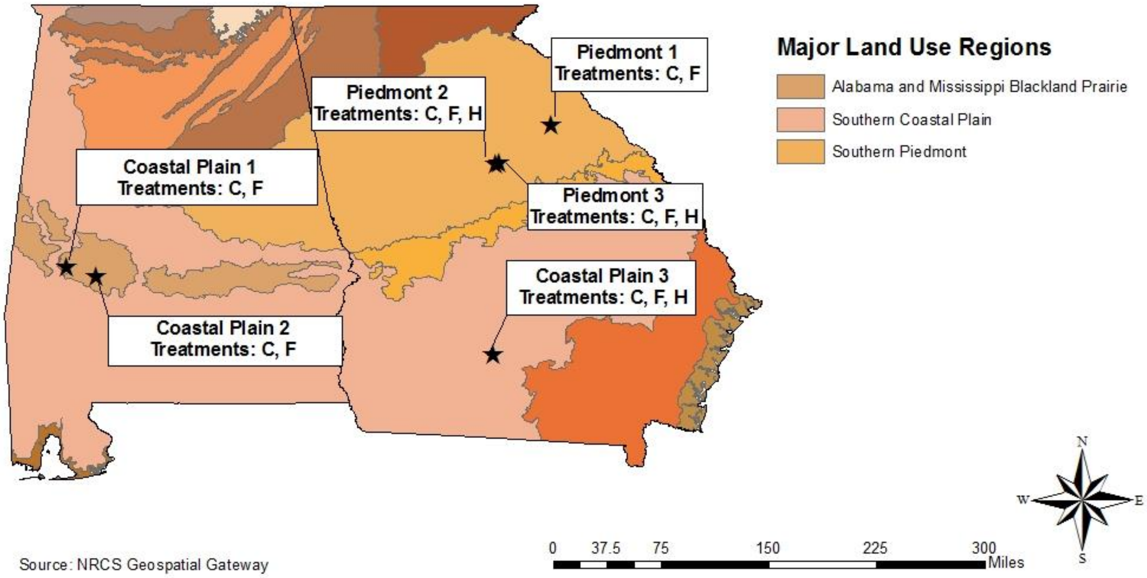
Parameter	β	Std. Error	*t* value	*p*
Intercept	1.1332	0.1984	5.712	<0.001
[1] Soil temp	0.0013	0.0001	9.364	<0.001
[2] MBC	0.0008	0.0002	3.268	0.002
[3] kg P/ha 0-10 cm	0.0442	0.0220	2.004	0.051
[4] BD deep	-1.4959	0.3500	-4.274	<0.001
Model p = <0.001				
Model R^2 = 0.752				
Model adjusted R^2 = 0.728				

[1] Soil temperature square transformed
[2] Microbial biomass carbon (MBC) log transformed
[3] kg phosphorus/kg soil in upper 0-10 cm log(1+X) transformed
[4] Bulk density deep (~35 cm deep) $\frac{1}{x^2}$ transformed

Table 3.11: Average Piedmont and Coastal Plain R_h proportions across seasons and treatments (mean ± 1SE), n=6.

Season	Treatment	R_h Proportion by Treatment	Seasonal R_h Proportion
Winter^{AB}	Control	0.72 ±0.05	
	Fertilize	0.74 ±0.06	
	Herbicide	0.58 ±0.08	0.68 ±0.05
Spring^{AB}	Control	0.65 ±0.04	
	Fertilize	0.75 ±0.07	
	Herbicide	0.61 ±0.04	0.67 ±0.05
Summer^{A}	Control	0.73 ±0.08	
	Fertilize	0.65 ±0.05	
	Herbicide	0.88 ±0.10	0.73 ±0.08
Fall^{B}	Control	0.83 ±0.03	
	Fertilize	0.87 ±0.03	
	Herbicide	0.68 ±0.10	0.80 ±0.03

* Upper case letters designate significant main effect differences ($p \leq 0.05$)



Source: NRCS Geospatial Gateway

Figure 3.1: Study site locations and physiographic regions in Georgia and Alabama.

*Treatments: C = Control, F = Fertilize, H = Herbicide

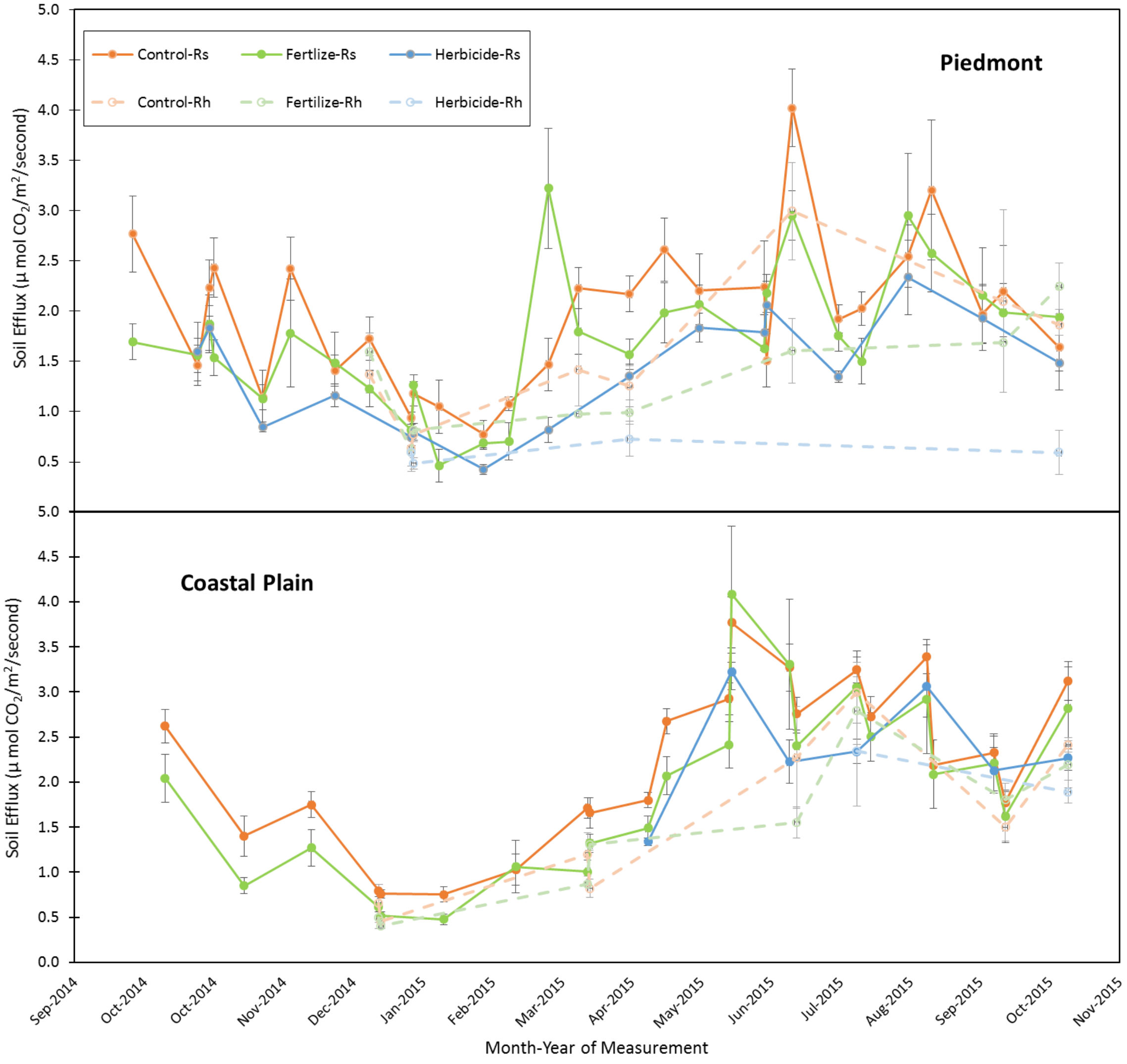


Figure 3.2: Monthly total (R_s) and heterotrophic (R_h) soil respiration (mean ± 1SE) across three Piedmont and three Coastal Plain study sites.

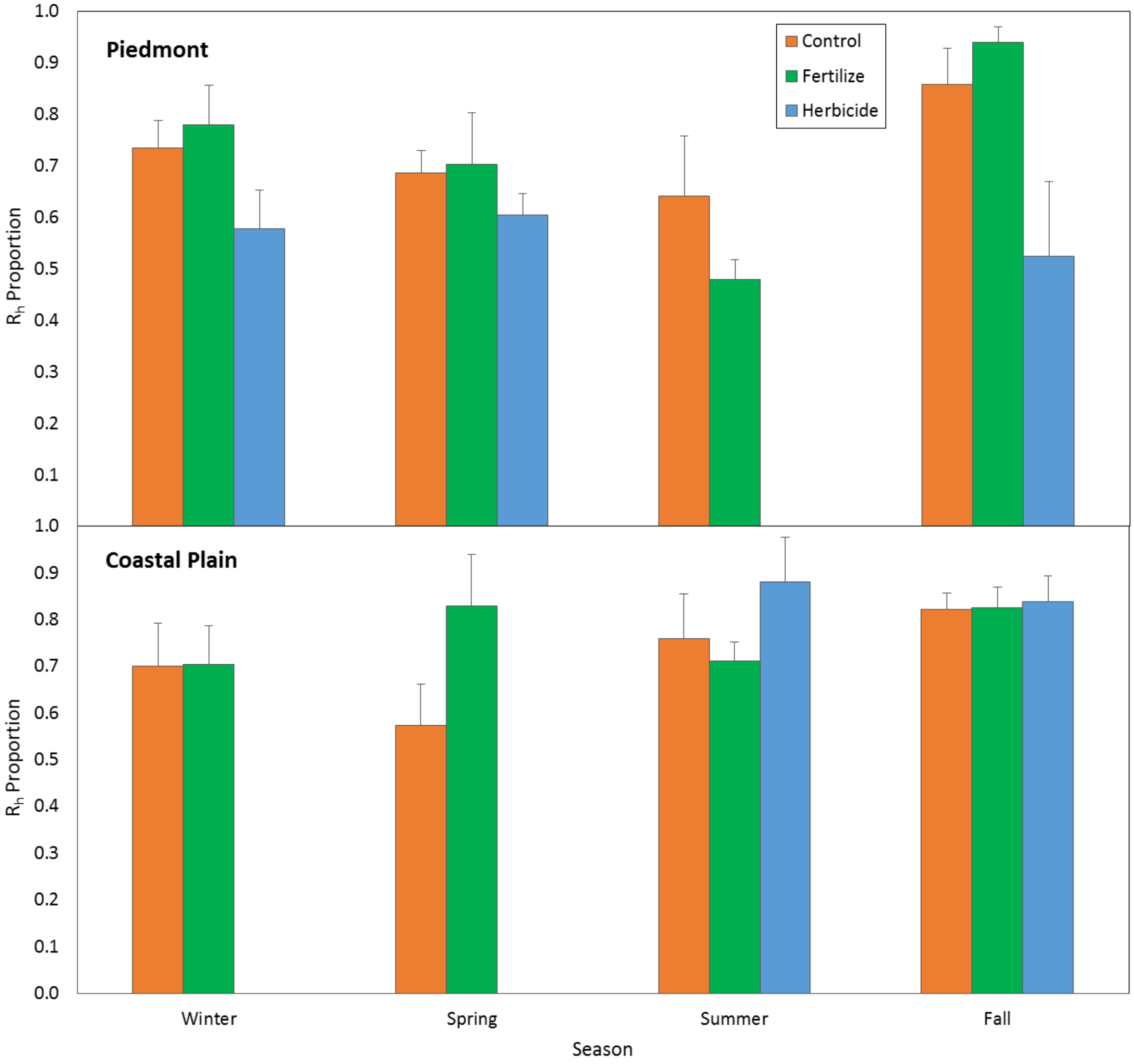


Figure 3.3: Proportion of R_s as R_h by season and silvicultural treatment between the Piedmont and Coastal Plain (mean ± 1 SE), n=6.

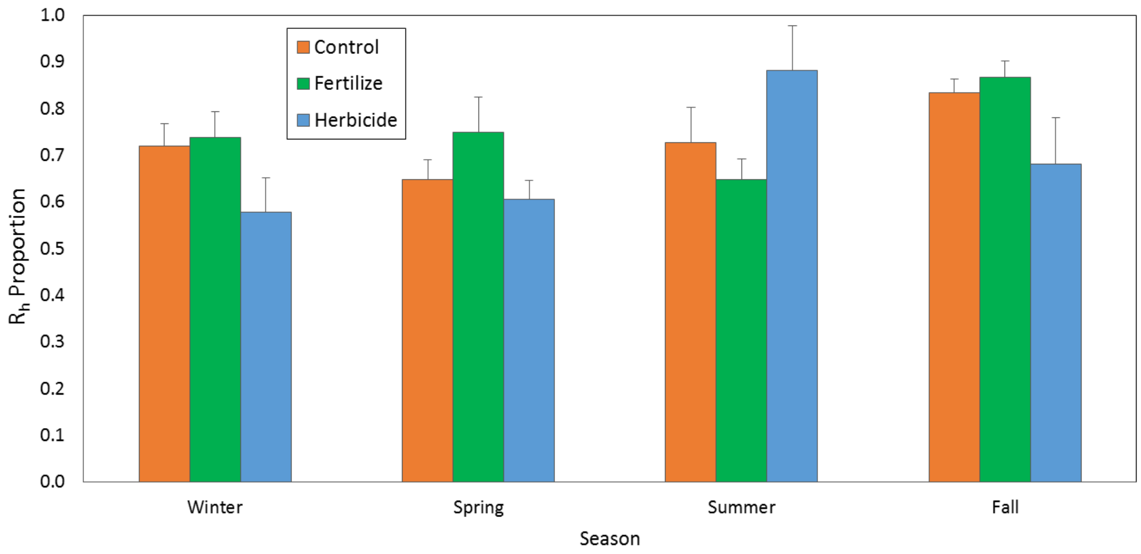


Figure 3.4: Proportion of R_s as R_h by season and silvicultural treatment for Piedmont and Coastal Plain combined (mean ± 1 SE), n=6.

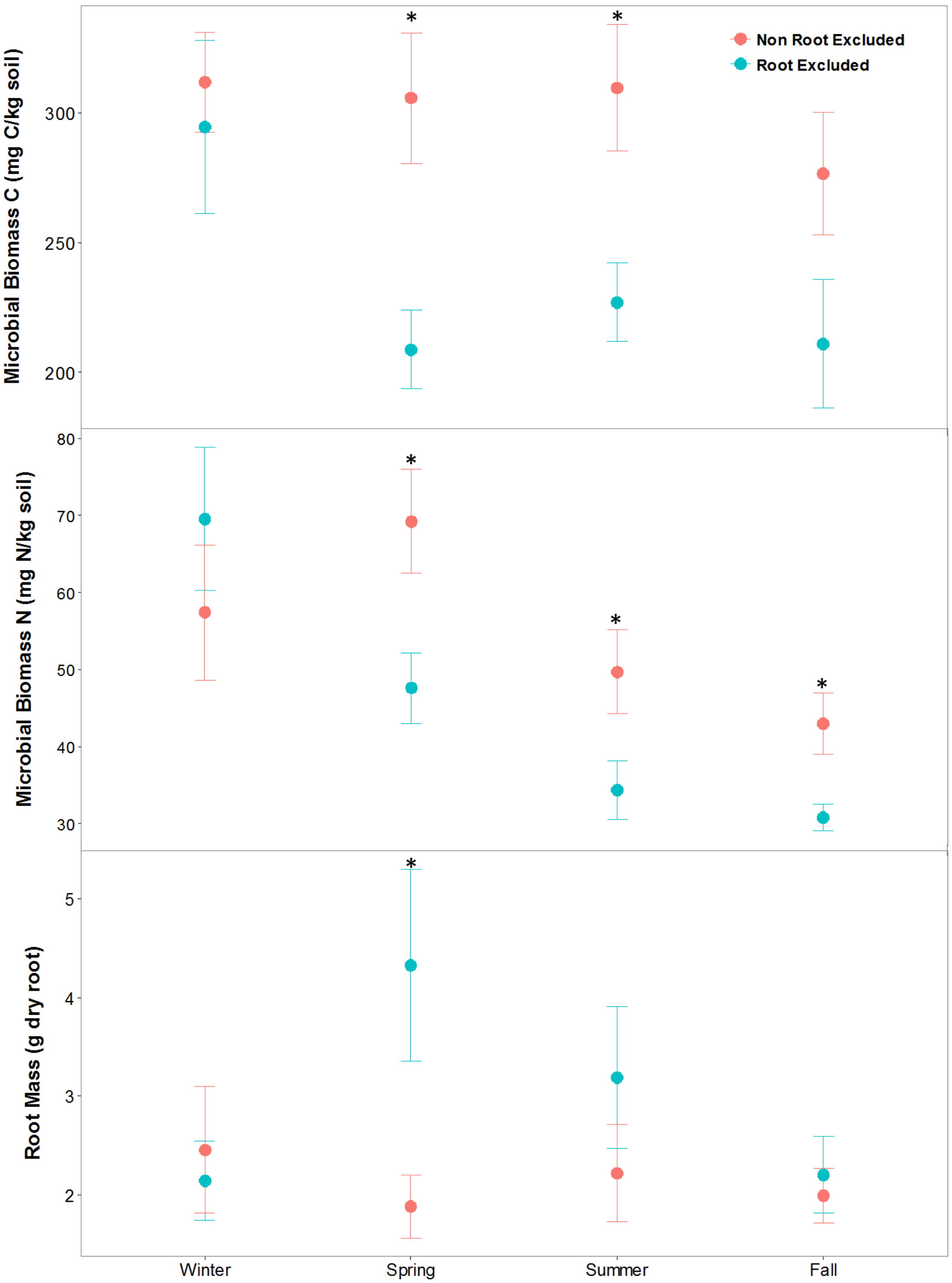


Figure 3.5: Microbial biomass C, N, and root mass from root excluding and non-root excluding collars used for soil efflux measurements by season (mean ± 1 SE). Root mass taken from 33 cm^2 area to a depth of 30 cm. * Designate significant difference between root excluding and non-root excluding collars within season.

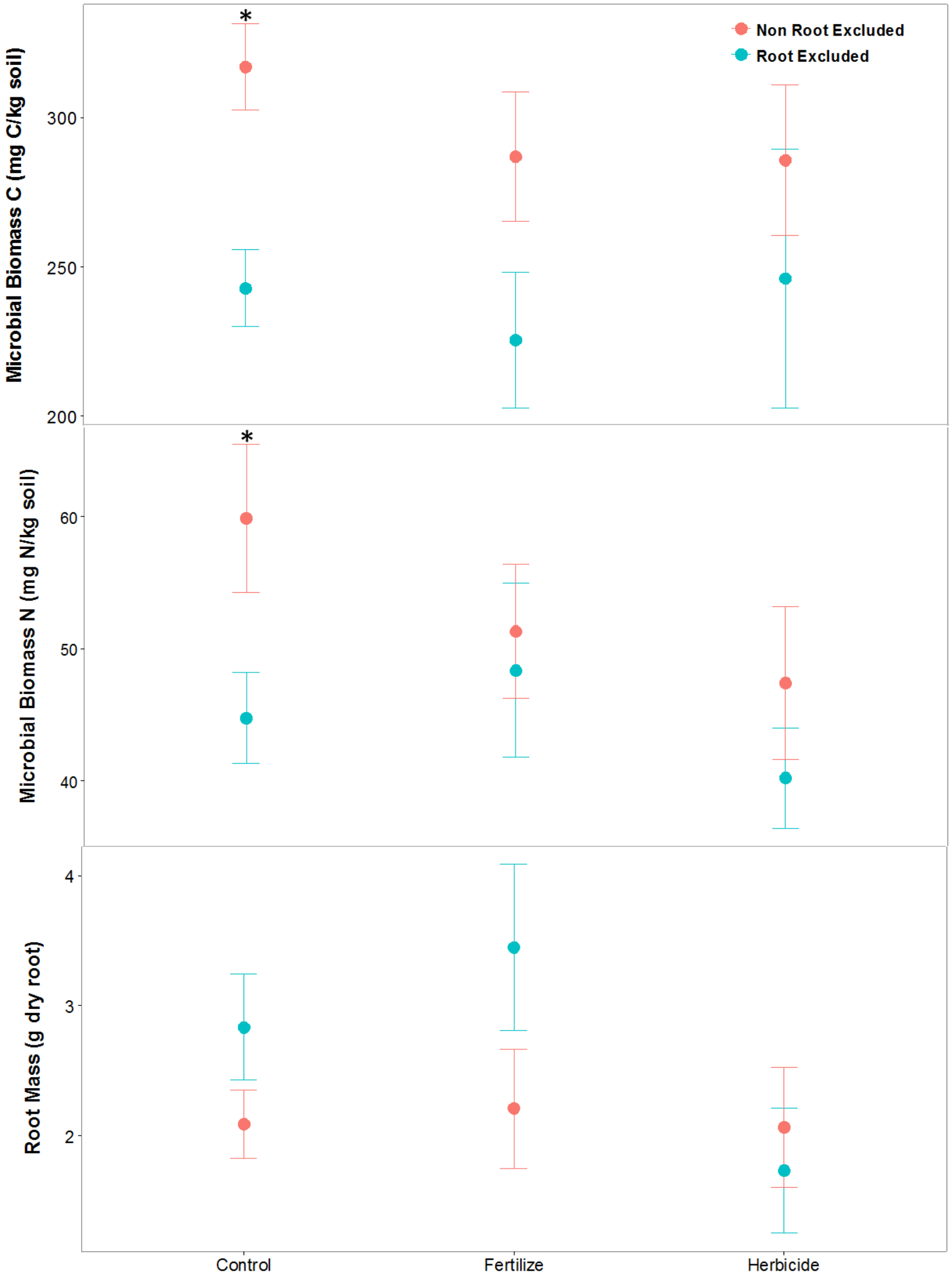


Figure 3.6: Microbial biomass C, N, and root mass from root excluding and non-root excluding collars used for soil efflux measurements by treatment (mean ± 1 SE). Root mass taken from 33 cm^2 area to a depth of 30 cm. * Designate significant difference between root excluding and non-root excluding collars within season.

CHAPTER IV

EVALUATION OF THE DAYCENT MODEL FOR ESTIMATING SOIL HETEROTROPHIC RESPIRATION IN LOBLOLLY PINE PLANTATIONS

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[1] Brown, R.M. and Markewitz, D. 2016. To be submitted to *Forest Ecology and Management*.

Abstract

Quantitative process-based models can provide valuable insights into complex ecosystem processes, such as carbon (C) cycling, and allow for extrapolation across broad regions. An important component of the C cycle is the return of carbon dioxide (CO_2) to the atmosphere via soil respiration (R_s). Furthermore R_s can be partitioned into root autotrophic respiration (R_a) and microbial heterotrophic respiration (R_h). The proportion of R_s comprised of R_h is subtracted from net primary productivity (NPP) to determine net ecosystem productivity, or C sequestration. The DAYCENT model was used to estimate the R_h proportion in six loblolly pine (*Pinus taeda*) plantations located in the Piedmont and Coastal Plain of Georgia and Alabama. Soil and forest floor samples were collected at each site to parameterize the model, and R_s and R_h were measured in the field over one year for model validation. Differences in R_s and R_h were compared between silvicultural treatments of control, fertilizer, and herbicide, as well as seasonally. Model predictions of R_s, R_h, and R_h proportion were compared to observed values using coefficient of determination (R^2) and root mean square error (RMSE). With regions compared separately and combined, R^2 values ranged from 0.01-0.12, 0.24-0.40, and 0.001-0.02 for R_s, R_h, and R_h proportion, respectively. Mean predicted seasonal R_h proportions extended beyond the range of those measured (65-88%) to 61% (±1.3) and 94% (±0.4). Lower RMSE values were observed for Piedmont than Coastal Plain sites. Simulated average annual NPP was consistent with typical southern loblolly pine values, but tended to decline below average as sand content increased for Coastal Plain sites. DAYCENT does not simulate CO_2 fluxes below 20 cm and may be missing substantial fluxes from deeper roots and microbial activity. Statistical models such as multiple regression may provide more accurate estimates of R_h proportion for regional extrapolation.

Introduction

The consistent rise in atmospheric carbon dioxide (CO_2) in recent history and its direct impact on climate change has led to a pulse of research into the ability of forest ecosystems to sequester atmospheric C (Lal, 2005; Canadell and Raupach, 2008; Pan *et al.*, 2011). Managed loblolly pine plantations are a significant portion of forest ecosystems in the southeastern United States, covering 13 million hectares, and accumulate large amounts of C in the aboveground biomass, forest floor, and mineral soil (Richter *et al.*, 1999; Wear and Greis, 2002). However, a substantial amount of the C accumulated is subsequently lost due to R_s (Tyree *et al.*, 2006). The R_h proportion of R_s is subtracted from net primary productivity (NPP) in order to calculate NEP, which in turn allows us to determine if the ecosystem is a source or sink of atmospheric C (Smith *et al.*, 2010).

Accurate values for soil respiration (R_s) and its components are critical for calculating forest carbon (C) pools and fluxes, but field measurements tend to be expensive, labor intensive, and infrequent (Hanson *et al.*, 2000; Bond-Lamberty *et al.*, 2011). In particular, the proportion of R_s that is composed of heterotrophic respiration (R_h) is difficult to partition using existing field methods, and is generally measured at most only several times in a year. The R_h proportion of R_s is necessary to determine net ecosystem productivity (NEP), which is synonymous with C sequestration.

Quantitative process-based models can be invaluable tools when evaluating complex systems, such as ecosystem C cycling. The DAYCENT biogeochemical model, as well as its predecessor CENTURY, have been used extensively to model carbon and nutrient cycling, trace gas fluxes, and land-use effects on agricultural soils, but have limited practice in forested areas (Del Grosso *et al.*, 2005; Fenn *et al.*, 2008; Kim *et al.*, 2009; van Oijen *et al.*, 2011; Gathany and

Burke, 2012; Bonan *et al.*, 2013). Few studies have validated DAYCENT R_s estimates using soil efflux measurements taken at the research site being simulated (Kelly *et al.*, 2000; Del Grosso *et al.*, 2005; Yeluripati *et al.*, 2009; Chang *et al.*, 2013). Of these studies, two have directly evaluated R_h estimates (Del Grosso *et al.*, 2005; Chang *et al.*, 2013), and one has included a forested site in the evaluation (Del Grosso *et al.*, 2005). A comparison of predicted R_h proportions versus measurements taken regularly across multiple sites would provide valuable insight into the model's ability to estimate this large and complex C flux under varying forested scenarios. Accurate estimates of the R_h proportion at high-resolution timesteps using minimal site-specific parameters would greatly enhance C budget and sequestration determinations. Therefore, the objective of this study is to validate the DAYCENT model's predicted R_s, R_h, and R_h proportion to measurements taken seasonally over one year from six loblolly pine plantations using site-specific soil, forest floor, land-use, and climate data.

Methods

Description of Study Sites

Samples and measurements for this study were taken at six planted loblolly pine experimental sites in the Piedmont and Upper Coastal Plain of Georgia and Alabama (See Chapter III, Figure 3.1). Three sites (Piedmont 1, Coastal Plain 1 & 2) were part of the PINEMAP Tier II network, which is a regionwide study that consists of active experimental plots maintained within existing cooperative field studies throughout the range of loblolly pine (www.pinemap.org). The PINEMAP sites were established and are maintained as part of the North Carolina State University Forest Productivity Cooperative, Regionwide 18 study (http://forestproductivitycoop.net/). Three additional sites were incorporated from the

Consortium for Accelerated Pine Production Studies (CAPPS) network (see Borders *et al.* (2002) and Borders and Bailey (2001) for a more detailed description). The CAPPS sites used (deemed Piedmont 2 &3, Coastal Plain 3 here) were chosen based on stand age and physiographic region to most closely match those of the PINEMAP sites. In all cases for this study, Coastal Plain refers to the Upper Coastal Plain physiographic region; the Lower Coastal Plain was not evaluated.

Fertilized plots in the PINEMAP study received 268 kg N/ha at planting and every six years, as well as phosphorus (P) and boron (B). Information on the application rate of nutrients other than N at PINEMAP sites was not available. Sites in the CAPPS study received varying amounts of fertilizer from years 1-12, ranging from 59-118 kg N/ha applied yearly, and 118 kg N/ha every year after age 12. They also received 56 kg P/ha in years 1 and 2 in the form of diammonium phosphate, 28 kg P/ha in year 11 as triple super phosphate, and 56 kg K/ha in years 1 and 2 in the form of KCl. Herbicide plots received periodic non-soil active herbicides (e.g., glyphosate) as necessary for complete vegetation control (Kinane, 2014).

Model Description

The DAYCENT model is a process-based biogeochemical model that has expanded on the CENTURY model to simulate a range of processes at a daily rather than monthly time step, among other additional features (Parton *et al.*, 1998). Several researchers (Mosier *et al.*, 1996; Parton *et al.*, 1996a; Parton *et al.*, 1996b) determined that the land surface sub-model needed to simulate trace gas fluxes at a daily time step to accurately account for rapid spatial and temporal changes in soil water and temperature (Parton *et al.*, 1998). Model parameterization includes creating several site-specific files: 1) a historical weather file including daily rainfall and temperature; 2) a site characteristics file (SITE.100) which includes measured soil data; 3) a historical land-use and management events file (EVENT100); and 4) a vegetative species file (CROP.100 and TREE.100) which includes data specific to the crop, grass, or tree of interest. Parameterization of the SITE.100 file includes soil pH, C, N, and texture. Forested scenarios also include forest floor C, N, and total mass. The soil profile is grouped into ten layers: 0-2, 2-5, 5-10, 10-20, 20-30, 30-45, 45-60, 60-75, 75-90, and 90-105 cm. The user can select to model C, N, P, and sulfur (S) cycles through the simulated ecosystem from the past through future scenarios.

Soil respiration is simulated as total R_s, as well as partitioned into R_h and autotrophic respiration (R_a). The R_h sub-model includes both direct rhizosphere microbial respiration as well as soil organic carbon (SOC) decomposition by the microbial community (Chang *et al.*, 2013). Decomposition of soil C follows first-order kinetics, and is grouped into active (0.5-1 year residence time), slow (10-50 year residence time), and passive (1000-5000 year residence time) pools (Parton *et al.*, 1987; Paustian *et al.*, 1992). The calculation for R_h is described by Chang *et al.* (2013):

$$R_h = C_{flow} f(r_{resp}) \tag{1}$$

where C_{flow} is a function of the quantity of soil organic matter, effects of any cultivation, and the microbial decomposition rate. The microbial decomposition rate is affected by soil temperature and water content, clay content, and pH. The C_{flow} is multiplied by $f\left(r_{resp}\right)$, which is a constant parameter altered by clay content that regulates C flow from SOC pools to CO_2.

Soil Sampling

Soil samples were collected once from each plot between 2014-2015. Eight random subsample locations within each plot were used to collect forest floor with a 0.35 x 0.35 m square. The interior of the square was cut with a knife, and the O_a layer was separated from the O_i and O_e. Within each plot two composite samples, subsamples 1-4 and 5-8, were retained for O_a, and O_i and O_e. Below these forest floor collection points mineral soil samples were collected using a 6.5 cm diameter open-bucket hand auger. Mineral soils were sampled at four different depths: 0-10, 10-20, 20-50, and 50-100 cm. Within each plot, samples were similarly composited at each depth for laboratory analysis (total of 120 samples). Bulk density (BD) samples were also collected between 0-10, 10-30, and 30-60 cm in each plot (Blake and Hartge, 1986).

Soil Analysis

Samples were air-dried before being crushed and sieved through a 2-mm sieve. A moisture correction factor was determined for each air-dried soil sample by placing 3-6 g in tin cups and dried until a constant weight at 105°C. Forest floor samples were oven dried at 65°C, weighed, and ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ). A portion of each ground forest floor sample was combusted in a Thermolyne Type 30400 muffle furnace (Thermo Scientific) for ash correction (Nelson and Sommers, 1996).

Soils were analyzed for pH, C and nitrogen (N), and particle size distribution. Soil pH_{H_2O} and pH_{CaCl_2} were measured using a 2:1 ratio of soil and deionized (DI) water following Thomas (1996). Carbon and N concentrations were obtained from a Flash EA 1112 Series CN soil analyzer (CE Elantech, Lakewood, NJ). Particle size distribution was measured using the hydrometer method (Gee and Bauder, 1986).

Root-excluding Collar Installation and CO_2 Efflux Measurements

Collars for CO_2 efflux measurements were first installed during July-August 2014. These installations included Piedmont 1-3 and Coastal Plain 1-2 (Coastal Plain 3 was added in spring 2015). Two types of collars were utilized: non-root-excluding (NRE) and root-excluding (RE). Non-root-excluding collars consisted of short (5-10 cm) PVC rings 10.16 cm in diameter that did not sever roots and were installed by hand. Efflux measurements from these collars represented R_s. Root-excluding collars were made of steel electrical conduit 10.16 cm in diameter and cut to 35 cm in length. Soil efflux measurements were made using a Licor 6400 infrared gas analyzer with a LI-6400-09 soil chamber attachment (Licor, Lincoln, NE) by placing the chamber on the exposed mineral soil. Collar installation and CO_2 efflux measurements are described in further detail in Brown, Chapter III (2016).

Monthly CO_2 Measurements

Efflux, temperature, and moisture measurements were made at each collar approximately every 30 days following installation using the same instruments. Efflux measurements taken three months after collar installation were used to calculate R_h proportions (Kelting *et al.*, 1998). On these measurement dates, efflux from the RE collars was considered to be only R_h, while the NRE collars were R_s. After final measurements, RE collars were removed, scraped of remaining soil, and reinstalled at a new randomly selected location within the plot to start the next three-month cycle. This process was repeated five times to capture seasonal differences, with the first cycle eventually being discarded due to sampling issues.

Simulation Procedure

A total of 15 simulations were run to represent each treatment plot. Model simulations began with producing the local weather file mentioned above. Daily historical precipitation and temperature data for 1980-2013 was obtained from the online Daymet meteorological tool (https://daymet.ornl.gov/). Daymet is a model managed by NASA that provides weather estimates based on meteorological observations across most of North America at a 1 km resolution (Thornton *et al.*, 1997; Thornton *et al.*, 2014). Data for 2015 was not yet available from Daymet, so nearby weather stations were utilized for the final two years (2014-2015) of the simulation (www.wunderground.com). Precipitation and air temperature for each site over the course of the field study are shown in Figure 1. Next the site characteristics file (SITE.100) was parameterized using data collected from each plot, and a loblolly pine species profile was added to the TREE.100 routine using data from the scientific literature (Wade Ross, UFL, personal communication). This profile includes growth and allometric values such as maximum gross forest production, C:N:P:S ratios for various tree components, maximum decomposition rates, and lignin fractions. Soil layer depths used by DAYCENT did not exactly match those sampled in the field. Therefore, measured values were applied to DAYCENT soil depths that coincided with measured depths or sampled depths were averaged to accommodate DAYCENT depths as necessary.

The simulation components mentioned are incorporated into a site history routine called EVENT100. In EVENT100 previous land-use history can be simulated thousands of years in the past, including vegetation or crops, site disturbances, and soil amendments such as fertilizer, herbicide, or organic matter. Time periods are separated into “blocks”, where each block represents a different vegetation type or management action. The events simulated for each site and treatment plot are shown in Table 1. Blocks for each current stand were modeled to match known planting dates, site preparation techniques, and fertilizer or herbicide use (if applicable). Historical land-use scenarios were estimated using aerial photographs and practices typical to the area during each time period (Larry Morris, UGA, personal communication). An equilibrium block representing these historical land-use scenarios was included from year -3000 until planting of the current stands to allow SOC, the soil water flow sub-model, and other parameters to equilibrate in the simulated ecosystem. The model was initialized for each site using a mixed hardwood/pine forest until subsistence agriculture likely began with European settlers in the 18th century. Common agricultural practices such as plowing, disking, and herbicide application are included in the cultivation subroutine (CULT.100) and were applied when applicable for each crop. The clearcut option in the tree removal subroutine (TREM.100) was utilized for each harvest (Table 4.2).

Model Evaluation

Simulated annual NPP for each stand was evaluated relative to typical trajectories for loblolly pine as an initial model assessment. Daily simulated R_s was also qualitatively evaluated for expected seasonal trends. Model output of daily R_s, R_h, and the R_h proportion was compared to measured field data for each date field measurements were taken. Predicted values were analyzed against observed values by coefficient of determination (R^2) as well as root mean square error (RMSE) (Janssen and Heuberger, 1995). Regression revealed fall measurements at Coastal Plain 3 to be outliers, therefore these values were removed from the regression analysis.

Based on the field experiment there was a particular interest in seasonality of the R_h proportion. As such, model error was further analyzed by subtracting observed values from predicted values for each season to assess seasonal trends of over-and-underestimation. Furthermore, since DAYCENT had daily outputs, predicted seasonal R_h proportions were compared among three averaging techniques: 1) season average (includes month of field measurement and both adjacent months), 2) month average, and 3) week average (date of field measurement used as final day of week), along with the individual day's value. These four groups were compared to observed R_h proportions using RMSE to find the most accurate group averaging method. Pairwise comparisons were tested for significant difference at $p<0.05$ using Tukey's Honestly Significant Difference (HSD). Statistical tests were performed using *R* software version 3.2.3.

Finally, to compare simulated results to the field experiment, simulated R_h proportions were analyzed using a full interaction analysis of variance (ANOVA) including Site, Treatment, and Season for each region individually as well as regions combined; the same as was done with field observations. Normality was tested using Shapiro's Test, and transformations were applied as necessary.

Results

Annual NPP

All simulated sites showed a substantial increase in NPP with fertilization, with the exception of Piedmont 1 which showed no increase (Figure 4.2). Coastal Plain 3 consistently showed the lowest NPP across treatments, with Piedmont sites primarily the highest. Control plots peaked during the first six years of growth at ~ 5-9 Mg C/ha/year in the Piedmont and ~4-6 Mg C/ha/year in the Coastal Plain, with the exception of Coastal Plain 3 which remained at ~1-2 Mg C/ha/year throughout the simulation. Fertilized plots remained elevated at ~8-14 Mg

C/ha/year in the Piedmont, except for Piedmont 1 which remained similar to its control. Coastal Plain sites ranged from ~3-9 Mg C/ha/year with fertilization. Plots receiving herbicide showed an annual increase of approximately 1 Mg C/ha/year over control plots, except Coastal Plain 3 which showed no change.

Annual R_s Trends

Piedmont sites showed typical seasonal trends in R_s, decreasing during winter and reaching maximum values at the height of the growing season (Figure 4.3). Average values ranged from ~0.05-1.5 g C/m^2/day in the winter and ~1-4 g C/m^2/day in the summer with high daily fluctuations due to rainfall. Average R_s was similar in control and herbicide plots, while fertilized plots showed an average increase of ~1 g C/m^2/day. Coastal Plain sites showed similar seasonal trends, but with less contrast between seasons and much more fluctuation due to rain events. All sites showed a reduction in R_s moving from May to June 2015 corresponding to rainfall inputs (Figure 4.1).

Predicted versus Observed R_s, R_h, and R_h Proportion

Predicted values most closely matched observed values for R_h in the Coastal Plain with $R^2 = 0.40$, followed by R_h in the Piedmont with $R^2 = 0.35$ (Table 4.3). Predicted R_s values were also most highly correlated in the Coastal Plain with $R^2 = 0.12$. Predictions for R_s (Figure 4.5) and R_h (Figure 4.6) were more accurate when efflux was low in the winter than for high values during the growing season. The model was particularly weak when predicting the R_h proportion, with plots showing little-to-no correlation and the maximum R^2 reaching 0.02 (Figure 4.7). Model comparisons between R_s, R_h, and R_h proportion using RMSE was not effective due to the smaller sample size for R_h and R_h proportion. However, comparisons between regions indicated that predictions in the Piedmont were slightly closer to observed values, producing smaller RMSE values than the Coastal Plain or when regions were combined (Table 4.3).

Correlation between predicted and observed values was also tested by season (Table 4.3). DAYCENT values for R_s and R_h were most correlated with observed values in winter with R^2 values of 0.16 and 0.40, respectively. The model was again very weak when predicting the R_h proportion, with R^2 values ranging from 0.003-0.06 across seasons. The difference in predicted minus observed values showed DAYCENT simulated R_s and R_h to be consistently lower than observed values, especially during summer months, and the R_h proportion to be consistently over-predicted (Figure 4.8).

DAYCENT R_h Proportion by Treatment, Region, and Season

DAYCENT simulated R_h proportions averaged by season, month, and week were not significantly different, but season and week were significantly lower than single day estimates (*p* = 0.001 and 0.03, respectively). DAYCENT predicted R_h proportion values averaged by season produced the lowest RMSE in two out of the three regions (Coastal Plain and Regions Combined), and was therefore used to assess any significant differences between seasons (Table 4.4). None of the four group average methods revealed a significant silvicultural treatment effect.

The simulated R_h proportion was significantly higher during winter than all other seasons in the Piedmont, Coastal Plain, and with regions combined (Figure 4.9). Spring values were significantly higher than summer in the Coastal Plain and with regions combined (*p* = 0.007 and 0.01, respectively). There was no significant difference between summer and fall when regions were combined. With regions combined, the average R_h proportion was 94% (±0.4) in the winter, 76% (±3.4) in the spring, and 61% (±1.3) in the summer and fall.

Discussion

Soil R_h is a complex C flux to model as it is simultaneously affected by multiple parameters including soil temperature, moisture, pH, SOC quantity and quality, and microbial community dynamics (Del Grosso *et al.*, 2005). This modeling effort showed that even with site-specific parameterization, simulations at a daily time step may not match values measured in the field on any particular day.

In general, annual NPP and R_s seasonality simulated by DAYCENT were within expectations. Average annual NPP values for loblolly pine plantations are generally 5-8 Mg C/ha/year in control plots and 10-13 Mg C/ha/year in fertilized plots (Maier *et al.*, 2004; Samuelson *et al.*, 2009). These values are within the range of those estimated by DAYCENT for Piedmont sites, but NPP estimations tended to decrease for Coastal Plain sites, which is not characteristic for pine in the region. DAYCENT decreased NPP as sand content increased (see Table 4.2 and Figure 4.2), which may be realistic for un-irrigated row crops but is not appropriate for loblolly pine. This low growth could partially explain the error observed with R_s and R_h predictions for the Coastal Plain sites.

To test sensitivity of R_s, R_h, and the R_h proportion to growth, simulations were re-run with fine root production doubled in the TREE.100 file. Model predictions were compared between normal and doubled fine root production by t-tests. Doubling fine root production caused an average 0.2, -0.3, and -6.9% change in R_s, R_h, and the R_h proportion, respectively, when compared to original model runs. None of the changes were statistically significant. A calibration and sensitivity analysis of DAYCENT were previously performed by van Oijen *et al.* (2011) for a Norway spruce (*Picea abies*) forest in Germany. In their sensitivity analysis, they found that no individual parameter was strongly correlated with CO_2, NO, or NO_2 output.

The associated field study that generated the validation data for this test of DAYCENT (Brown, Chapter III) found the R_h proportion in the Piedmont to be significantly higher in the fall than summer ($p = 0.02$), herbicide plots lower than fertilize plots ($p = 0.03$), and herbicide plots lower than control plots ($p = 0.05$). No significant differences were detected in the Coastal Plain, and there was no significant difference between regions. When the regions were combined, summer was significantly lower than fall ($p = 0.04$).

These field results were quite different than simulated results that found the greatest R_h proportion to be in winter rather than fall. DAYCENT also overestimated the average R_h proportion in winter, and underestimated it during summer and fall. Field-observations found the proportion to be ~82% in the fall (as opposed to 61% in DAYCENT) and ~70% the rest of the year (94, 74, or 61% for winter, spring, or summer, respectively, in DAYCENT). It is possible that DAYCENT underestimates microbial biomass, which was elevated in the field experiment during the summer and remained elevated into October and November (Brown, Chapter III). With persistent warm weather in the fall, microbial biomass and R_h persisted while trees and R_a were beginning to senesce, leading to a higher R_h proportion. A similar persistence of microbial biomass into the fall in southern pine plantations was also observed by Rifai *et al.* (2010).

Across sites, differences in substrate quality and quantity will affect microbial community composition, which is largely unaccounted for in the DAYCENT model (Del Grosso *et al.*, 2005). Correlation coefficients for R_s in agricultural and forested areas using DAYCENT were previously found as low as 0.13-0.32 by Del Grosso *et al.* (2005), which they partially attributed to likely differences in SOC and microbial communities.

One additional relevant short-coming of DAYCENT is its treatment of belowground respiration. DAYCENT only models CO_2 efflux from the upper 20 cm of soil and it is not accounting for R_a from roots below 20 cm (Yeluripati *et al.*, 2009). This may be logical for agricultural systems but is certainly not the case for forested ecosystems or mid-rotation pine plantations (Richter and Markewitz, 1995). This deficiency likely partly explains the model simulating a greater R_h contribution to R_s than observed values, and weak correlation with observed values.

Conclusions

Validation of DAYCENT using measurements from six loblolly pine plantation sites over one year revealed that the model underestimates daily R_s and R_h, while overestimating the R_h proportion. This was most prevalent when efflux rates were high, and for sandier Coastal Plain sites. This was most likely due to the model ignoring fluxes below 20 cm, and the inherent difficulties of simulating soil microbial community dynamics. Seasonally predicted R_h proportions ranged from ~61-94%, extending beyond measured seasonal averages. Given the extensive parameterizations required for DAYCENT, other approaches, such as multiple regression models (see Brown, Chapter III), may provide more accurate predictions of R_s, R_h, and the R_h proportion for extrapolation in southern loblolly pine plantations.

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Table 4.1: Land management activities used in the DAYCENT scheduling program for six sites.

Site	[1]Treatment Plot	Time Period Modeled	Land Management Applied
Piedmont 1	C/F	−3000-1740	Mixed forest
		1741	Clear forest
		1742-1785	Corn
		1786-1920	Cotton
		1921-1935	Pasture
		1936-1946	Abandon pasture
		1947	Harvest forest regrowth, burn
		1948	Plant loblolly stand #1
		1972	Harvest stand #1, plow*
		1973	Plant loblolly stand #2
		1983	Thin
		1995	Burn
		1996	Harvest stand #2, plow
		1997	Plant current stand
		2008	Thin
	F	1997, 2003, 2009	Apply fertilizer
Piedmont 2 & 3	C/F/H	−3000-1992	*Same as Piedmont 1*
		1993-1994	Harvest loblolly stand #2, plow
		1995	Plant current stand
	F	1995-2015	Apply fertilizer
	H	1995-2015	Apply herbicide
Coastal Plain 1	C/F	−3000-1989	*Same as Piedmont 1*
		1990	Burn
		1991	Harvest stand #2
		1992-1997	Natural regeneration, harvest, plow
		1998	Plant current stand
		2007	Thin
	F	1998, 2002, 2008, 2014	Apply fertilizer
Coastal Plain 2	C/F	−3000-1994	*Same as Piedmont 1*
		1995	Harvest loblolly stand #2, plow
		1996	Plant current stand
		2005	Thin
	F	1996, 2000, 2006, 2012	Apply fertilizer
Coastal Plain 3	C/F/H	−3000-1785	*Same as Piedmont 1*
		1786-1960	Cotton
		1961	Plow for stand #1
		1962	Plant stand #1
		1987	Harvest stand #1, plow
		1988	Plant current stand
	F	1988-2015	Apply fertilizer
	H	1988-2015	Apply herbicide

[1] Silvicultural treatment (C = Control, F = Fertilize, H = Herbicide)

* Plow command in the cultivation subroutine (CULT.100) used to simulate soil disturbance associated with silvicultural site prep activities such as chopping, ripping, and bedding.

Table 4.2: Measured input parameters for the DAYCENT model from six research sites.

	-----Piedmont 1-----		-----------Piedmont 2-----------			-----------Piedmont 3-----------			--Coastal Plain 1--		--Coastal Plain 2--		---------Coastal Plain 3---------		
Parameter	Control	Fertilize	Control	Fertilize	Herbicide	Control	Fertilize	Herbicide	Control	Fertilize	Control	Fertilize	Control	Fertilize	Herbicide
Latitude	33.8045	33.8057	33.4123	33.4118	33.4121	33.4249	33.4252	33.4254	32.3718	32.3714	32.2810	32.2808	31.4962	31.4960	31.4961
Longitude	-82.9620	-82.9622	-83.5260	-83.5263	-83.5264	-83.4936	-83.4933	-83.4936	-87.8408	-87.8410	-87.5516	-87.5508	-83.5449	-83.5442	-83.5446
Sand Proportion	0.78	0.55	0.48	0.52	0.40	0.55	0.57	0.51	0.78	0.75	0.84	0.70	0.93	0.88	0.92
Silt Proportion	0.15	0.19	0.15	0.13	0.10	0.19	0.15	0.15	0.16	0.17	0.09	0.08	0.03	0.06	0.04
Clay Proportion	0.07	0.26	0.38	0.35	0.50	0.26	0.28	0.34	0.06	0.08	0.07	0.23	0.04	0.06	0.04
Bulk Density (g/cm^3)	1.69	1.51	1.33	1.42	1.39	1.37	1.39	1.49	1.11	1.56	1.47	1.45	1.30	1.32	1.35
pH	4.41	4.11	4.32	3.73	4.22	4.90	3.66	4.00	3.78	3.82	4.05	3.75	3.83	3.32	3.86
Total Forest Floor C (g/m^2)	3735	3409	1982	3016	3009	2790	2981	2761	1792	2043	2139	2184	975	2145	1470
Total Mineral Soil C 0-20 cm (g/m^2)	4363	3697	1894	1596	1281	3167	1196	1474	2493	2026	1901	4245	1501	2015	2403
Total Forest Floor N (g/m^2)	69.1	64.4	49.1	95.4	55.4	46.3	77.9	63.8	35.8	61.1	38.1	48.7	27.3	71.5	39.2
Total Mineral Soil N 0-20 cm (g/m^2)	208.9	173.2	141.2	143.3	99.5	274.7	110.1	138.7	121.9	165.0	125.1	203.9	123.2	177.9	170.7
Forest Floor C/N Ratio	54	53	40	32	54	60	38	44	50	33	56	45	36	30df	38
Soil C/N Ratio	21	21	13	11	13	12	11	11	20	12	15	21	12	11	14
Total C/N Ratio	75	74	54	43	67	72	49	54	70	46	71	66	48	41	52
Mineral Soil N by Layer:															
g N/m^2 0-2 cm	31.4	23.6	13.3	16.1	8.8	34.2	13.1	16.0	14.0	25.3	16.3	31.0	13.0	18.7	20.5
g N/m^2 2-5 cm	47.1	35.4	20.0	24.2	13.3	51.3	19.6	24.0	21.1	38.0	24.4	46.5	19.5	28.0	30.7
g N/m^2 5-10 cm	78.5	59.0	33.3	40.4	22.1	85.6	32.7	40.0	35.1	63.3	40.7	77.5	32.5	46.7	51.3
g N/m^2 10-20 cm	51.8	55.0	74.4	62.3	55.0	103.4	44.5	58.5	51.6	38.3	43.5	48.8	58.1	84.3	68.0
g N/m^2 20-30 cm	39.0	38.8	51.3	46.3	36.6	47.9	50.0	27.9	29.0	31.7	24.2	25.4	63.1	79.2	63.4
g N/m^2 30-45 cm	58.6	58.2	77.0	69.5	55.0	71.9	75.1	41.9	43.5	47.5	36.3	38.1	94.6	118.8	95.1
g N/m^2 45-60 cm	41.7	41.3	63.4	63.7	50.5	68.9	69.1	50.9	51.5	46.9	31.1	29.4	85.9	108.4	90.6
g N/m^2 60-75 cm	25.7	24.6	49.8	57.8	46.0	65.8	63.2	59.9	59.5	46.4	25.8	20.7	77.7	98.5	86.2
g N/m^2 75-90 cm	25.7	24.6	49.8	57.8	46.0	65.8	63.2	59.9	59.5	46.4	25.8	20.7	77.7	98.5	86.2
g N/m^2 90-105 cm	25.7	24.6	49.8	57.8	46.0	65.8	63.2	59.9	59.5	46.4	25.8	20.7	77.7	98.5	86.2

Table 4.3: Coefficient of determination for linear regression of predicted vs observed and root mean square error for R_s, R_h, and R_h proportion values using DAYCENT by region and season.

Region	Parameter	R^2	*p*	[a]d.f.	*RMSE
Piedmont	R_s	0.078	0.069	100	1.107
	R_h	0.358	0.002	23	0.638
	R_h Proportion	0.015	0.555	23	0.235
Coastal Plain	R_s	0.124	0.002	68	1.560
	R_h	0.402	0.003	17	1.091
	R_h Proportion	0.023	0.531	17	0.234
Regions Combined	R_s	0.050	0.003	170	1.329
	R_h	0.247	<0.001	42	0.863
	R_h Proportion	0.002	0.769	42	0.237
Winter	R_s	0.156	0.005	46	0.878
	R_h	0.400	0.027	10	0.508
	R_h Proportion	0.064	0.425	10	0.275
Spring	R_s	0.114	0.022	34	0.784
	R_h	0.014	0.712	10	0.501
	R_h Proportion	0.087	0.349	10	0.194
Summer	R_s	0.034	0.219	44	1.793
	R_h	<0.001	0.989	7	1.359
	R_h Proportion	0.038	0.613	7	0.221
Fall	R_s	0.049	0.157	40	1.519
	R_h	0.154	0.060	9	0.957
	R_h Proportion	0.003	0.864	9	0.246

* Root mean square error

[a] Degrees of freedom

Table 4.4: Root mean square error of DAYCENT predicted R_h proportion of R_s compared to observed values by daily output and averaged by season, month, and week.

Region	Season	Month	Week	Day
	n=90	n=30	n=7	n=1
Piedmont	0.260	0.240	0.241	0.238
Coastal Plain	0.252	0.275	0.298	0.296
Regions Combined	0.256	0.257	0.269	0.267

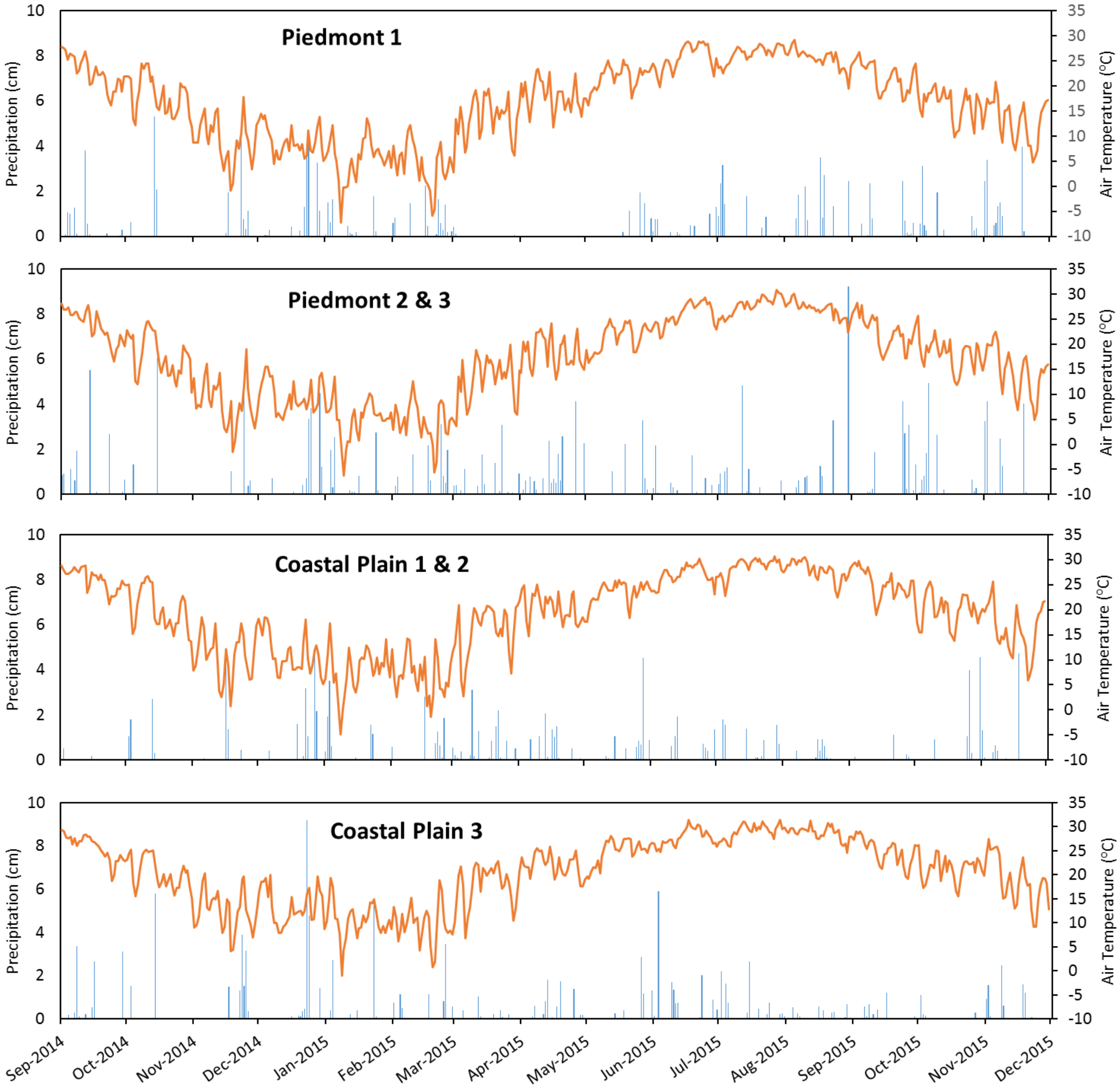

Figure 4.1: Precipitation and average temperature at six research sites during associated field measurement period.

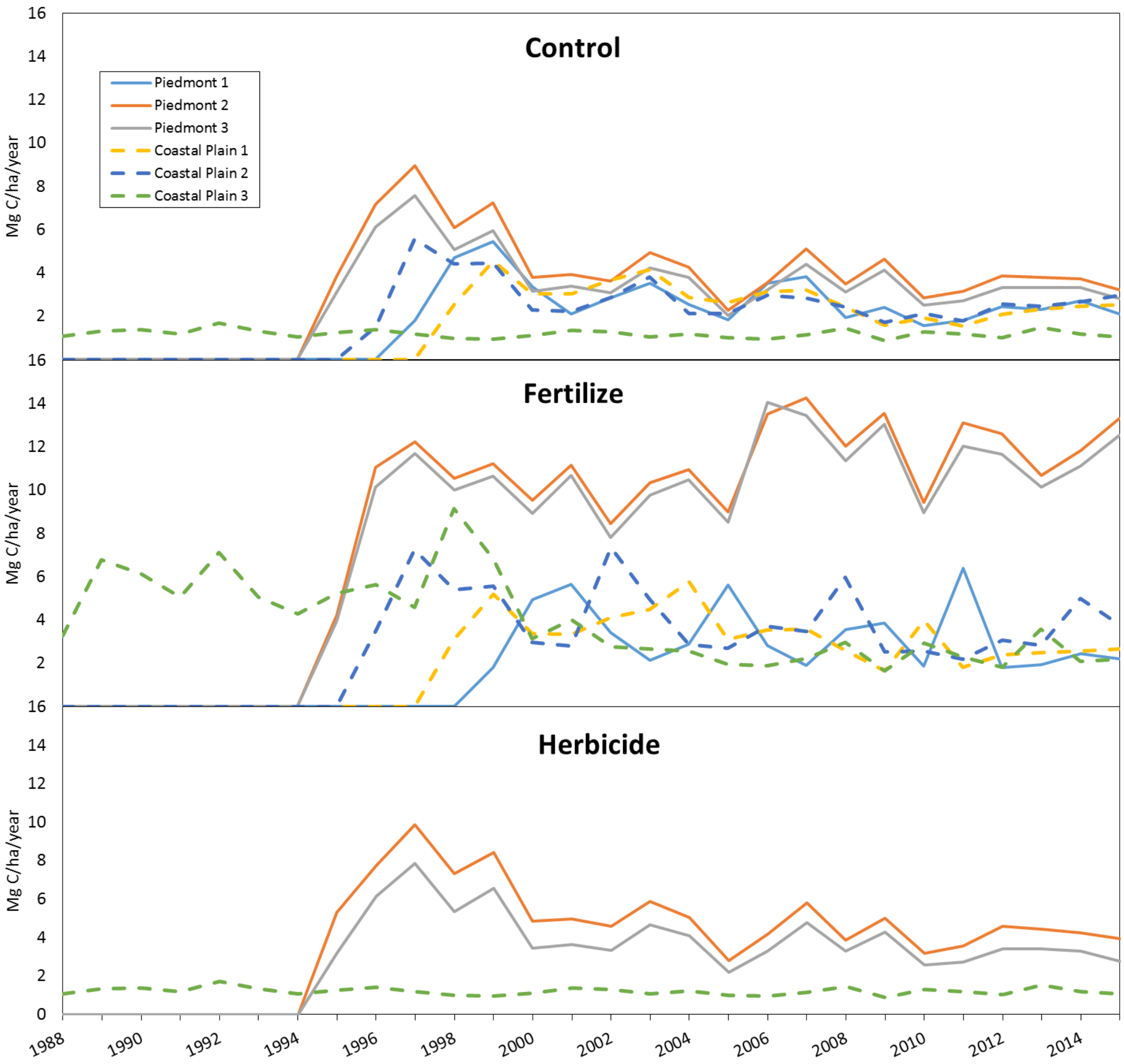

Figure 4.2: DAYCENT simulated annual NPP for six study sites by silvicultural treatment. Simulated values begin at year planted for each plot, starting with Coastal Plain 3 in 1988.

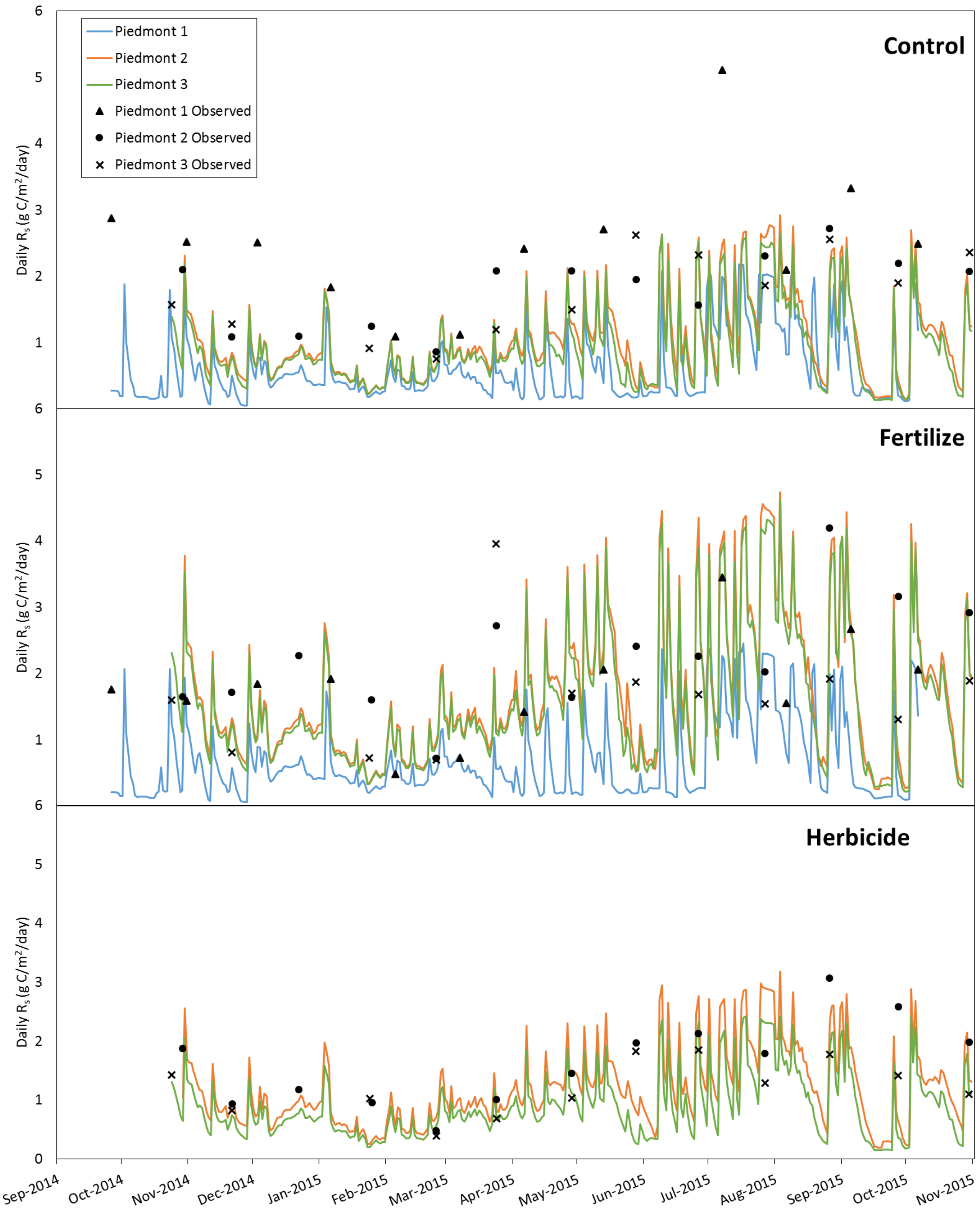

Figure 4.3: DAYCENT simulated daily R_s and measured R_s for Piedmont study sites by silvicultural treatment across accompanied field study measurement dates.

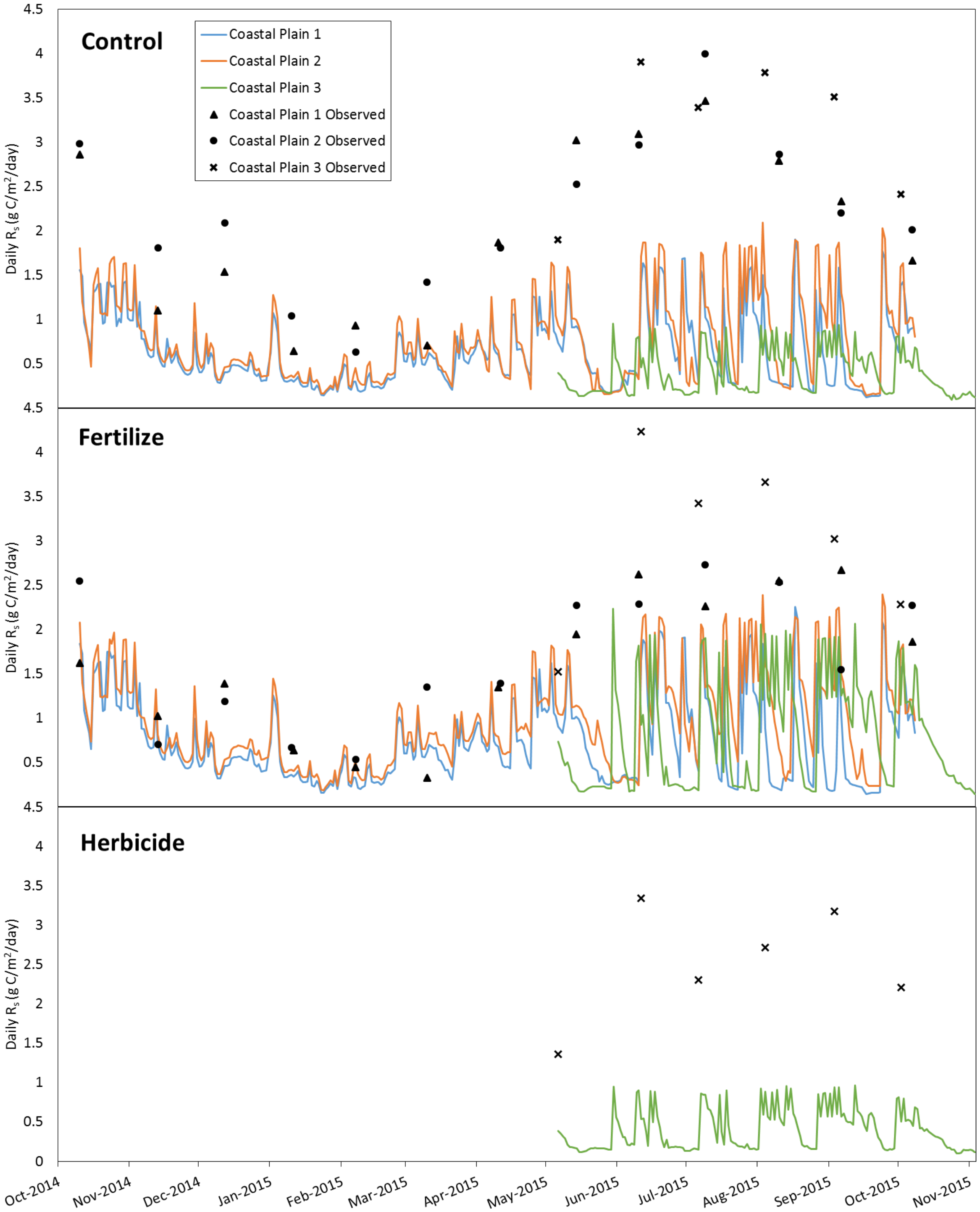

Figure 4.4: DAYCENT simulated daily R_s and measured R_s for Coastal Plain study sites by silvicultural treatment across accompanied field study measurement dates.

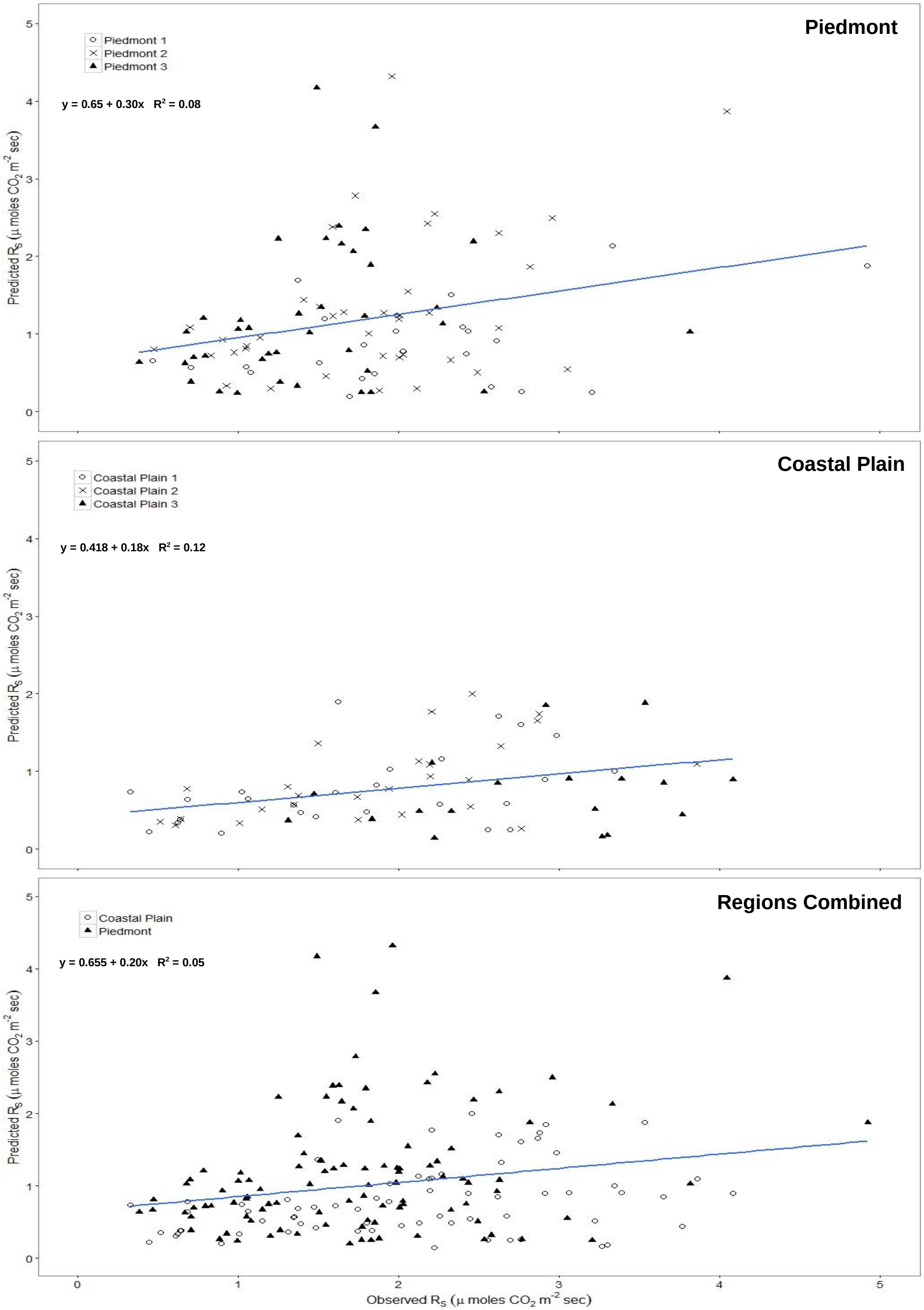

Figure 4.5: Observed versus predicted R_s using DAYCENT for Piedmont, Coastal Plain, and regions combined. Blue line represents best fit using linear regression.

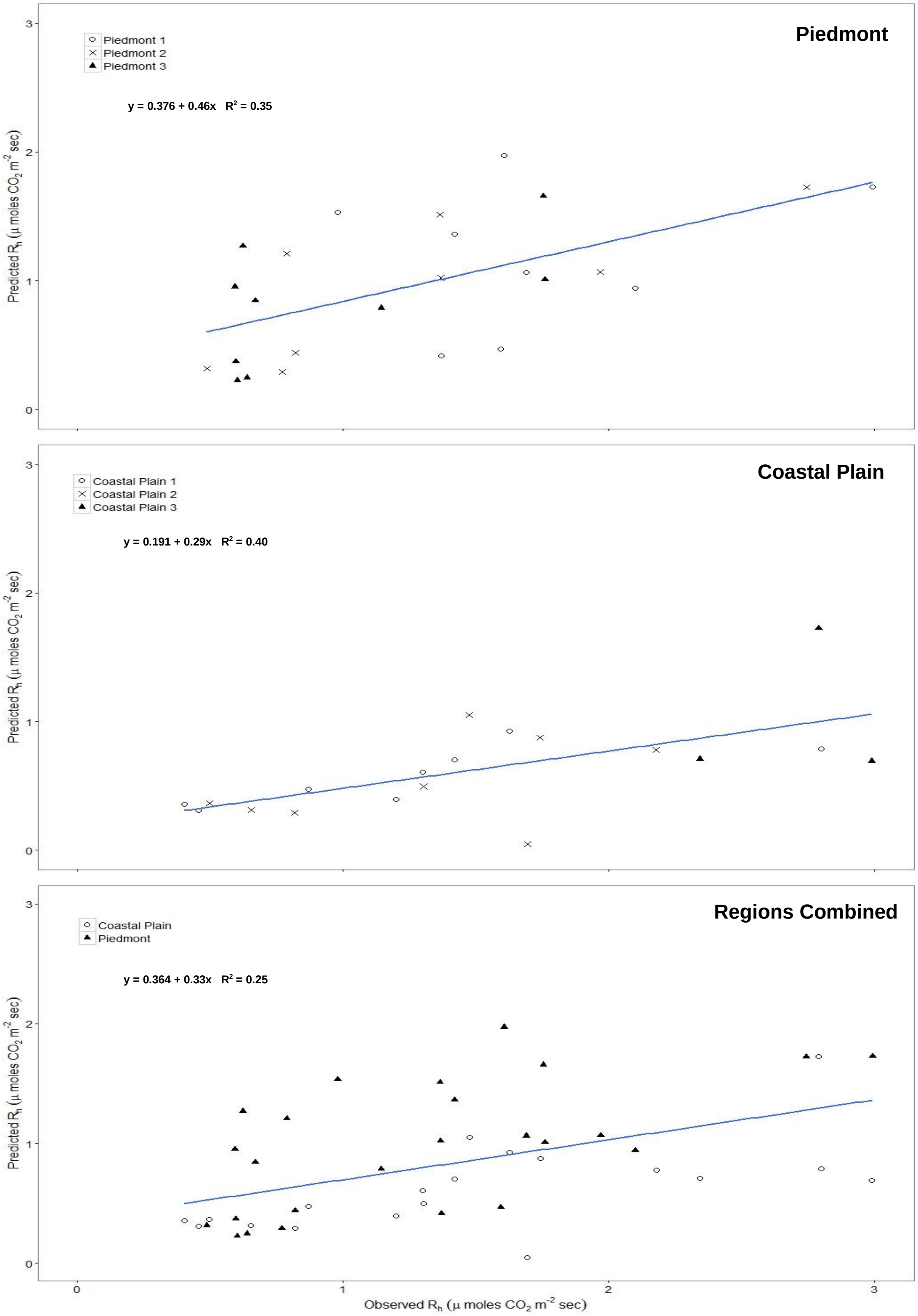

Figure 4.6: Observed versus predicted R_h using DAYCENT for Piedmont, Coastal Plain, and regions combined. Blue line represents best fit using linear regression.

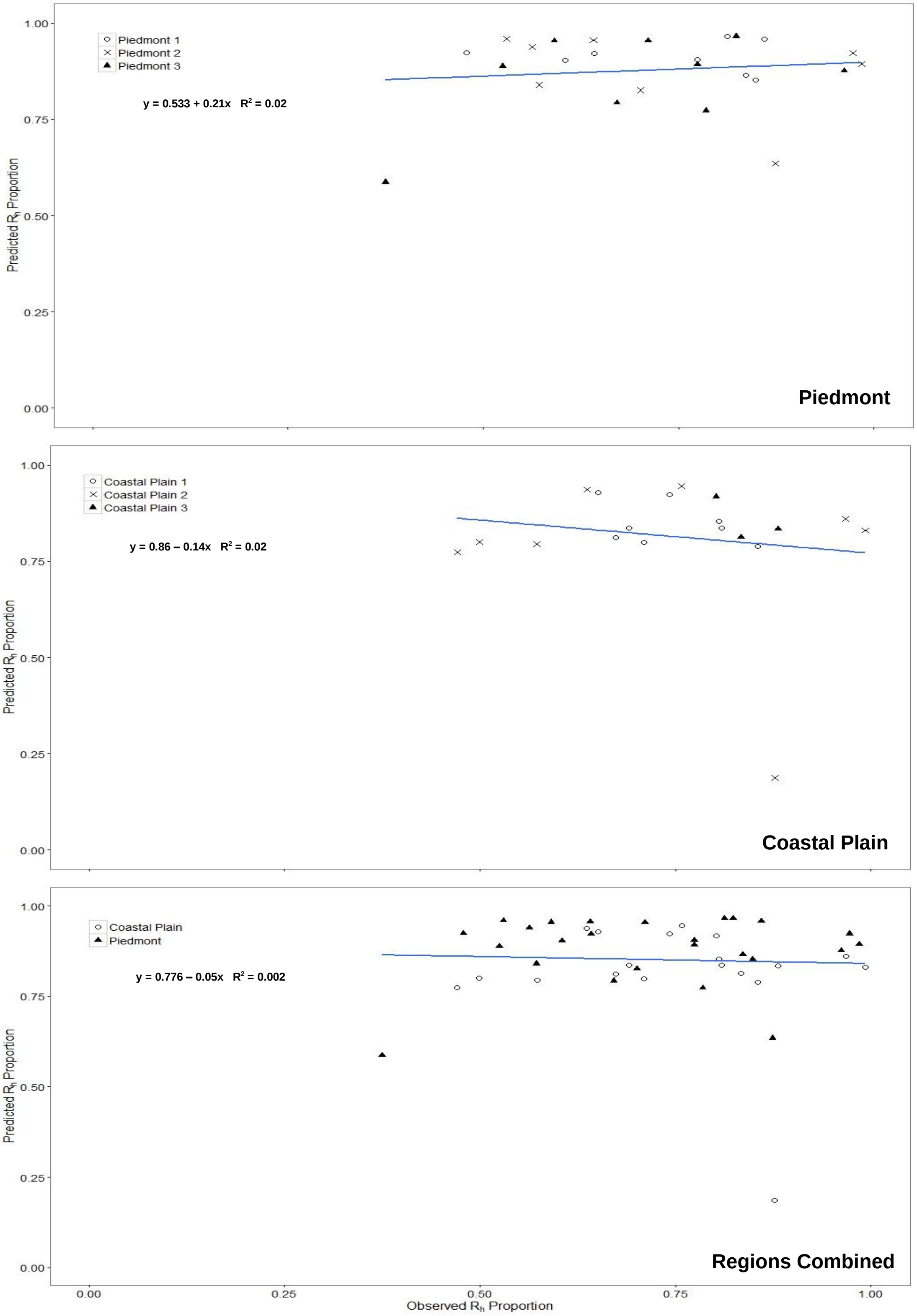

Figure 4.7: Observed versus predicted R_h proportion of R_s using DAYCENT for Piedmont, Coastal Plain, and regions combined. Blue line represents best fit using linear regression.

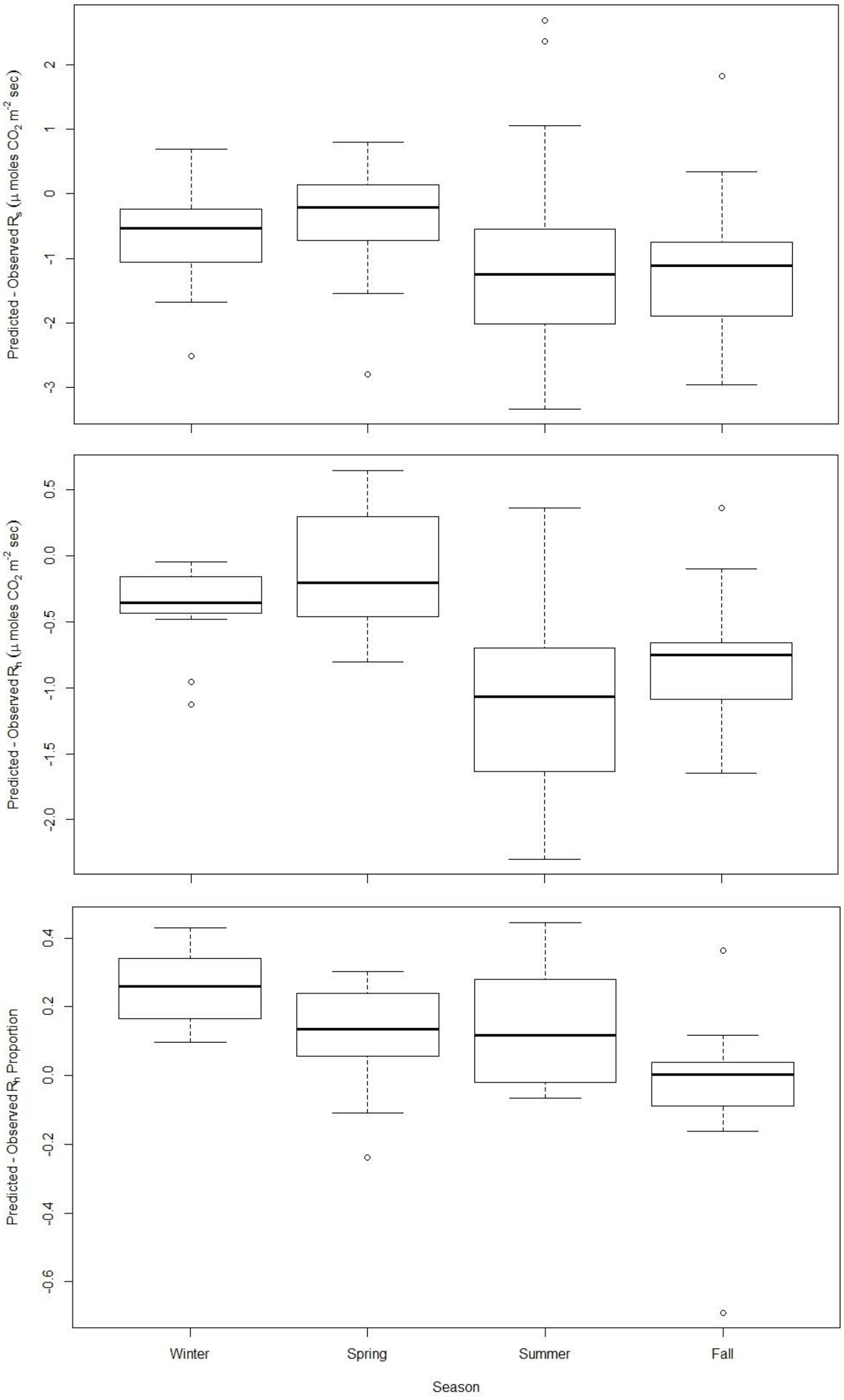

Figure 4.8: DAYCENT predicted minus observed values for R_s, R_h , and the R_h proportion by season.

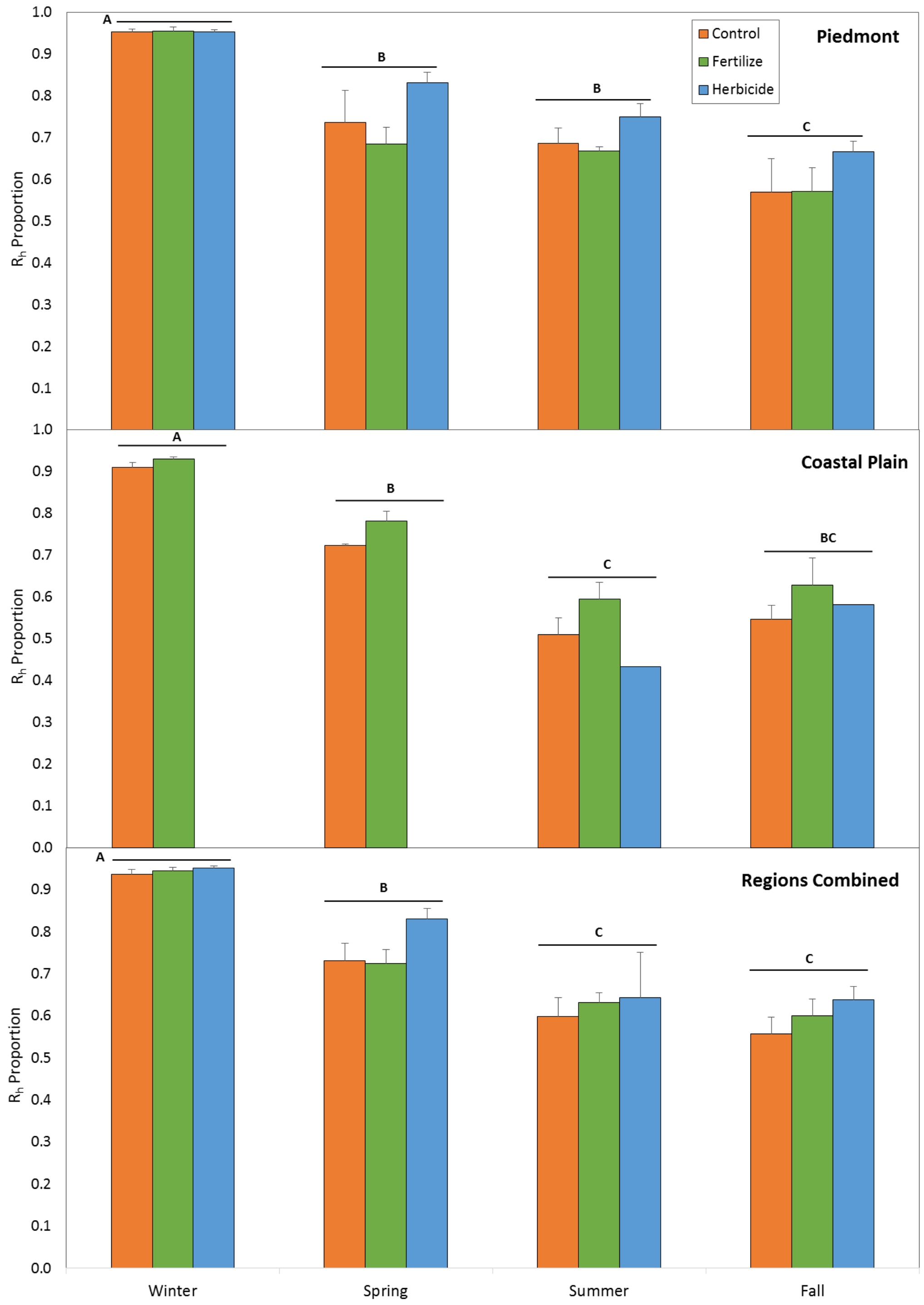

Figure 4.9: DAYCENT predicted seasonal R_h proportion (mean ± SE) by treatment and region. There are no SE bars for Coastal Plain herbicide due to only one plot being included. Letters indicate significant seasonal differences ($p \leq 0.05$).

CHAPTER V

CONCLUSION

Accurate estimates of the R_h proportion of R_s are critical for calculating NEP. Discrepancies in the R_h proportion may lead to substantial under or overestimations of C sequestered by ecosystems. As previously mentioned, the land area covered by loblolly pine plantations is expansive, therefore inaccurate NEP estimates for this ecosystem are nontrivial in terms of understanding the Southeast's role in global climate change. Field measurements revealed that two of the most common silvicultural treatments, fertilizer and herbicide application, do not significantly affect the R_h proportion. When we combine these findings with known increases in NPP associated with fertilizer and herbicide application, we can assume NEP increases with these treatments, i.e. increased C sequestration. The R_h proportion did, however, show a seasonal pattern, being significantly higher in the fall (~80%) than the rest of the year (~69%). This is important because again, if one was to calculate annual NEP using one of these values for the entire year, values may be substantially under or overestimated.

The R_h proportion was not well estimated in regression efforts using site stand and soil characteristics whether using individual subplot values or plot averages ($R^2 = 0.18$ and 0.22, respectively). However, when estimated separately, R_s and R_h were much more informative using plot averages ($R^2 = 0.82$ and 0.75, respectively). Estimating R_s and R_h separately, then calculating the R_h proportion from these estimates, may be more accurate than modeling the R_h proportion directly. While most of the parameters used in the regressions are common soil measurements, quantifying MBC is relatively less common and more difficult. However, the significance of MBC in both the R_s and R_h regressions demonstrates the importance of considering the soil microbial community when estimating soil respiration.

DAYCENT proved to be a reasonable model for predicting NPP when compared to the literature, and produced expected seasonal patterns in R_s and R_h. However, the model was weak when predicting site specific R_s, R_h, and particularly the R_h proportion. Model parameterization was thorough, using soil values measured in each plot rather than soil survey estimates, along with precise site management histories. Even so, predicted efflux values showed little correlation with observed values, with R^2 ranging from 0.40 to as low as 0.01. Furthermore, average seasonal estimates of the R_h proportion were beyond those measured in the field.

Although there is no shortage of models that simulate soil R_s with confidence, the proportion of R_s from R_h is a complex C flux to predict. DAYCENT and its predecessor CENTURY were originally developed for agricultural systems, which generally have shallower rooting depths than forests, and live roots do not persist from year to year. As such, DAYCENT only models R_s and R_h in the upper 20 cm of soil. The majority of fine roots in loblolly pine forests exist in the upper 30 cm, with additional fine and coarse roots extending deeper. Therefore, DAYCENT is not accounting for R_a fluxes and microbial activity at depth in forested scenarios, which likely partly explains the weak correlations with measured field data.

By providing the R_h proportion values measured during this research project, future researchers will be able to more accurately calculate C budgets and sequestration in southern loblolly pine ecosystems. Soil R_s, R_h, and the R_h proportion can be predicted with some confidence using several common soil measurements, as long as the microbial community is also considered. This research also demonstrates that process-based models such as DAYCENT may not adequately capture the complexity of R_h in forests. These findings will benefit the scientific community by providing a critical piece of the C cycle in loblolly pine plantations, and further our understanding of this ecosystem's role in the climate change discussion.