

**The Effects of 40% Throughfall Reduction on Soil Respiration in a Longleaf Pine  
Plantation**

by

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## Abstract

Longleaf pine (*Pinus palustris*) forests can serve as disturbance-resistant, long-term carbon sinks, but net ecosystem productivity of longleaf pine forests has been shown to be sensitive to drought. Soil respiration (Rs) is often the largest component of ecosystem respiration and can be sensitive to drought. The primary objective of this study is to explore the influence of drought, imposed by a 40% reduction in throughfall (TR<sub>40</sub>), relative to ambient throughfall treatment (TR<sub>0</sub>) on soil respiration (Rs), heterotrophic respiration (Rh) and fine root biomass. The study was conducted in a longleaf pine plantation located in the Chattahoochee Fall Line Region in Georgia. During a naturally occurring severe drought in 2016, soil moisture and Rs declined to near zero in both treatments, and TR treatment had no effect on Rs, soil moisture, or soil temperature. In 2017, TR<sub>40</sub> reduced Rs from 13.8% to 21.6% on six of the 12 measurement dates. Annual Rs ranged from 9.96 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in the TR<sub>0</sub> treatment to 8.70 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in the TR<sub>40</sub> treatment, and Q<sub>10</sub> was reduced from 1.92 to 1.67 by TR<sub>40</sub>. Soil temperature and soil moisture explained the majority of the variation in Rs in 2016 (68% in TR<sub>0</sub> and 68% in TR<sub>40</sub>) and 2017 (54% in TR<sub>0</sub> and 42% in TR<sub>40</sub>). Surrounding tree basal area and distance to nearest tree each accounted for up to 6% of the variation in Rs. Throughfall reduction treatment did not significantly reduce fine root biomass or shift the spatial distribution of fine root biomass in response to TR trays. Heterotrophic respiration accounted for the majority of soil respiration (72.4-89.4%). Throughfall reduction altered the contribution of Rh to Rs in August 2017, suggesting that autotrophic respiration (Ra) was decreased. Results suggest that Ra may be more

sensitive to moderate drought in longleaf pine forests but both Ra and Rh are sensitive to soil moisture below the wilting point.

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## CHAPTER 1 - BACKGROUND

Longleaf pine (*Pinus palustris* Mill.) historically dominated an estimated 37 million hectares ranging from Virginia to Florida and as far west as Texas (Oswalt et al. 2012). Longleaf pine ecosystems were negatively affected by centuries of unregulated harvest, fire suppression, turpentine harvest, and more recently the conversion to loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) plantations (Oswalt et al. 2012). As a consequence, only approximately 1.2 million hectares of longleaf pine forest remain today (Frost 2006). Longleaf pine ecosystems offer many benefits including insect and disease resistance, endangered species habitat, and less susceptibility to wind damage (Johnsen et al. 2009). Prescribed fire is an important management tool in these forests to reduce competition from other woody species, promote understory plant biodiversity, and provide exposed mineral soil for natural forest regeneration (Mitchell 2006). Longleaf pine ecosystems can be an important tool for mitigating climate change because of their role in long-term carbon sequestration. However, drought stress and rising temperatures can cause changes in the ability of an ecosystem to sequester carbon and thus mitigate the effects of climate change.

Projected climate changes include more extreme precipitation events, increased temperatures, and longer periods of drought stress between precipitation events (Borken et al. 2006; IPCC 2013; Wang et al. 2014). Elevated temperatures will likely lead to increased vapor pressure deficits and soil water deficits in southern pine forests (Farjat et al. 2016). Increased temperatures can increase root and soil microbial function as well as decrease C use efficiency

(Li et al. 2016). Drought can affect trees aboveground and reduce carbon sequestration. For example, Maggard et al. (2016) concluded that drought stress can cause reduce photosynthesis and respiration at the leaf level via stomatal closure to conserve water. Belowground, drought stress can lead reduced mobility of soil microbes and reduced diffusion of available nutrients (Susella et al. 2012; Schlesinger et al. 2016). Drought stress can also affect fine root growth as Farrish et al. (1991) observed decreased fine root biomass in areas decreased water availability. Reduced fine root biomass can lead to decreased drought resilience as longleaf pine typically use well-developed root systems to help mitigate the harsh conditions during periods of drought stress.

Drought stress in forested ecosystems is likely to influence global carbon exchange through reduced ecosystem respiration (Knorr et al. 2007; Kopittke et al. 2014). Soil respiration ( $R_s$ ) is the second largest flux of carbon in the global carbon cycle therefore any small change in  $R_s$  could impact the global carbon cycle (Raich and Schlesinger 1992). Anthropocentric sourced greenhouse gas emissions and increased frequency and intensity of seasonal droughts may limit forest growth and the ability of forests to mitigate climate change. Longleaf pine forests have shown potential to help mitigate the effects of greenhouse gases through carbon sequestration (Heath et al. 2011; Samuelson et al. 2014). Longleaf pine aboveground productivity has been shown to decrease with water stress (Runion et al. 1997; Jose et al. 2003), and Ford et al. (2012) concluded that longleaf pine belowground production is more dependent on water availability than temperature or nutrient availability. The response of  $R_s$  to drought stress in longleaf pine forests is not well understood and is important to quantify to better predict the impact of changing climate on forest carbon fluxes.

The primary objective of this study is to better understand the effects of experimental drought on Rs and its components in longleaf pine forests. Future climate change scenarios include increased temperatures, more extreme precipitation events, and longer periods of drought stress between precipitation events (Borken et al. 2006; Wang et al. 2014). Drought stress can impact trees aboveground (Maggard et al. 2016) and causes decreases in available substrate to microbes belowground (Suseela et al. 2012; Schlesinger et al. 2016). Drought can also affect fine root growth. For example, Sword Sayer and Haygood (2006) observed a decrease in fine root elongation in longleaf pine during a naturally occurring three-year drought. Specific objectives are to:

1. Determine the responses of Rs and Rh in a longleaf pine plantation to experimentally induced drought stress imposed by 40% reduction of throughfall.
2. Examine the relationships between Rs and soil temperature, soil moisture, surrounding tree basal area, and distance to nearest tree.
3. Determine if the reduction in soil moisture underneath throughfall reduction trays influences the spatial distribution of Rs and fine root biomass.

## **CHAPTER 2 - THE EFFECTS OF 40% THROUGHFALL REDUCTION ON SOIL RESPIRATION IN A LONGLEAF PINE PLANTATION**

### **2.1 - Introduction**

The terrestrial biosphere is one of the largest carbon (C) reservoirs in the global C cycle (Schimel 1995). Managed U.S. forests sequester approximately 15% of atmospheric CO<sub>2</sub> emissions from fossil fuels (Woodall 2015). Projected atmospheric C increases range from 4 - 5 Pg C yr<sup>-1</sup> due solely to fossil fuel emissions (Lal 2010; IPCC 2013). Soils are the largest C pool in the global C cycle (Schlesinger 1977), and soil respiration (Rs) is the second largest flux of C in the terrestrial biome (Raich and Schlesinger 1992). Therefore, changes in Rs can impact the global C cycle. Soil respiration is the largest C flux in the terrestrial biome (100 Pg C yr<sup>-1</sup>) (Bond-Lamberty and Thomson 2010) and is comprised largely of two major types of fluxes: autotrophic respiration (Ra) and heterotrophic respiration (Rh). Heterotrophic respiration represents CO<sub>2</sub> produced by respiring macro and micro soil fauna that typically decompose dead organic matter in soil and Ra is composed of root tissue respiration and autotrophic bacterial communities in soil (Schlesinger 1977; Raich and Schlesinger 1992; Schlesinger and Andrews 2000; Lovett et al. 2006). Mycorrhizal respiration is combined with Ra due to the difficulty of partitioning mycorrhizal respiration from Ra (Bond-Lamberty et al. 2004; Subke et al. 2006). Increased attention has been placed on managing soils for C storage and more specifically on forest management to help mitigate greenhouse gas emissions through C sequestration in live biomass and soil organic matter (IPCC 2013). Future climate change scenarios include increased

temperatures, more extreme precipitation events, and longer periods of drought stress between precipitation events (Borken et al. 2006; Wang et al. 2014c). The Fifth Assessment Report from the Intergovernmental Panel on Climate Change (IPCC) projects that the southeastern United States will experience a temperature increase of 1.5-3 °C by the end of the century (IPCC 2013). Kunkel et al. (2013) added that in the southeastern United States there has been an increase in the frequency of extremely high temperatures that are often followed by long periods of drought stress. These projected changes in climate could significantly impact the ability of southeastern forests to sequester C (Brantley et al. 2018), primarily due to the high rates of photosynthesis in southeastern forest tree species (Novick et al. 2015). Future climate conditions could dampen the ability of southern forests to store carbon to help mitigate climate change.

A positive exponential relationship exists between soil temperature and  $R_s$  (Fang and Moncrieff 2001; Dilustro et al. 2005; Wang et al. 2014c). This relationship is expressed as the Arrhenius equation or the  $Q_{10}$  function, which demonstrates that for every 10°C increase in soil temperature,  $R_s$  will approximately double ( $Q_{10}=2$ ). As temperature increases, the metabolic reaction rates of plants and soil fauna increase, thereby increasing plant and microbial respiration (Lloyd and Taylor 1994; Pang et al. 2013). Increasing temperatures can affect  $R_s$  and more specifically  $R_h$ , by shifting microbial community structure, microbial metabolic rates, and soil microbial biomass, but the effect of drought stress on  $R_s$  and its components may vary with the ecosystem (Wang et al. 2014a, Wang et al. 2014c). For example, drought stress suppressed  $R_s$  in mesic and xeric ecosystems (Wang et al. 2014a) but stimulated  $R_s$  in hydric ecosystems (Sowerby et al. 2008).

Longleaf pine (*Pinus palustris* Mill.) once spanned 37 million acres throughout its native range but now, longleaf pine occupies less than 5% of its native range which spanned from North

Carolina to Texas and as far south as Florida. Longleaf pine ecosystems offer many benefits including insect and disease resistance, endangered species habitat, and less susceptibility to wind damage (Johnsen et al. 2009). Prescribed fire with frequent return intervals is an important management tool to promote understory plant biodiversity, reduce competition from other woody species, and provide exposed mineral soil for natural forest regeneration (Mitchell 2006). Longleaf pine is typically a slower growing species than the more productive loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) species in the southeastern United States, but longer rotations provide more C sequestration opportunities (Samuelson et al. 2014). Longleaf pine has drawn recent interest due to its possible drought tolerance when compared to other southern pines. For example, Samuelson et al. (2012) found that longleaf pine may possess more efficient hydraulic architecture, when compared to loblolly and slash pine to better withstand lower soil water potentials, which could lead to increased drought tolerance. Longleaf pine has shown the ability to physiologically adapt to xeric soil conditions (Addition et al. 2005; Wright et al. 2013; Whelan et al. 2015).

Throughfall reduction (TR) is a method that has been used to reduce, or in some cases eliminate, throughfall from reaching the soil environment to induce drought-like conditions in various forest types (Talmon et al. 2011; Koptitke et al. 2014; Heim et al. 2015; Will et al. 2015). The effect of experimental drought imposed by TR has shown to decrease  $R_s$  in a variety of ecosystems (Schindlbacher et al. 2012; Borke et al. 2006, Koptitke et al. 2014). Archmiller and Samuelson (2016a) observed a decrease in  $R_s$  during a naturally occurring drought in a longleaf pine forest, but this study allows the investigation of  $R_s$  in response to experimentally imposed drought relative to ambient conditions.



Many variables other than soil temperature and soil moisture have been shown to influence  $R_s$  rates in forest ecosystems. Other variables include: surrounding tree basal area (ArchMiller and Samuelson 2016a; McElligott et al. 2016; Luan et al. 2012; Samuelson and Whitaker 2012), distance from nearest trees (Clinton et al. 2011; ArchMiller and Samuelson 2016a), root biomass (Wang et al. 2017), soil texture (Dilustro et al. 2005), soil bulk density (Vincent et al. 2006; Luan et al. 2012; ArchMiller and Samuelson 2016a), and soil nitrogen content (Zhou et al. 2014). In this study the relationship between  $R_s$ , soil temperature, soil moisture, surrounding basal area, and distance from nearest trees will be explored. Because drought stress may impact fine root biomass and  $R_a$  (Wang et al. 2014b) the influence of TR on the spatial distribution fine roots and  $R_s$  was also examined.

The primary objective of this study was to better understand the effects of experimental drought imposed by 40% TR in longleaf pine forests. I hypothesized that: (1) throughfall reduction treatment will decrease  $R_s$  and  $R_h$ ; (2)  $R_s$  will be negatively correlated to distance from nearest tree and positively correlated to soil moisture, soil temperature, and surrounding basal area; and (3) due to decreased soil moisture availability imposed by throughfall reduction trays, fine root distribution will shift to areas of increased water availability.

## 2.2 - Methods

### 2.2.1 Site Description

The study site is located within the Chattahoochee Fall Line Wildlife Management Area in Marion County, GA (N 32°33.19', W 84°28.61) and owned by the Georgia Department of Natural Resources. Thirty year average (1985-2015) annual precipitation is 1226 mm in Americus, GA (approximately 60 km from site), and mean annual minimum and maximum air temperatures are 11.5°C and 24.6°C, respectfully, (<http://www.ncdc.noaa.gov/cdo-web>). The Palmer Drought Severity Index (PDSI) during 2016 and 2017 was collected for Climate Division 4 in the state of Georgia (<https://www.ncdc.noaa.gov/cag/time-series/us/9/4/pdsi/all/10/2016-2016>, accessed January 2016). The site is located in the Sand Hills Ecoregion, which is characterized by deep, excessively drained, and nutrient poor Entisol sands (Griffith et al. 2001). The entire study site is comprised of Lakeland Series soils (2 to 5% slopes) which are Thermic, coated Typic Quartzipsamments (Soil Survey Staff 2016). The site was planted with longleaf pine seedlings in 2005 at an approximate spacing of 2.6 m x 2.6 m, resulting in an initial planting density of approximately 1479 trees ha<sup>-1</sup>.

### 2.2.2 Experimental Design

The experimental design is a randomized complete block design with two levels of TF treatment, a 40% reduction and an ambient treatment, replicated in three blocks. The throughfall reduction amount was selected because a 40% reduction in average annual precipitation represents the 1<sup>st</sup> percentile of annual precipitation of Americus, GA observed over a hundred-year period and thus represents very low annual precipitation in a typical year for this site. Each treatment plot is 31 m x 21 m (0.0651 ha) with an interior intensive measurement plot 11 m x 21

m (0.0231 ha) in size. Blocking was based on pre-treatment basal area. A minimum 17 m buffer surrounds all plots. The treatment plots contained an average of 72 trees and measurement plots contained an average of 24 trees.

To induce drought and limit above TF by approximately 40%, two TF exclusion trays spanning a total of 1.54 m were installed between rows. The trays were an average height of 1.0 m and separated by a 50 cm gap to minimize soil moisture banding. Each tray spanned a total length of 31 m in each treatment plot. The frames of TF exclusion trays were constructed from pressure treated lumber and steel studded T-Posts. Trays were covered with a bi-layer clear Poly Scrim 12 plastic of U.V. stabilized polyethylene with high strength cord (Americover Inc., Escondido, CA, USA.) Intercepted TF was transported off the plot a minimum of twenty meters away from plots through a series of solid corrugated plastic tubes. Installation was completed on May 12, 2016.

### *2.2.3 Climate, Soil Moisture and Soil Temperature*

A weather station was installed approximately 0.55 km from the site in an open field (Vantage Pro2 Plus, Davis Instruments, Hayward, California, USA) to measure precipitation and air temperature. Air temperature and precipitation was measured every minute and the averaged was recorded every thirty minutes on a datalogger (HOBO Micro Station Data Logger, Onset Computer Corp, Bourne, MA, USA).

Soil moisture was continuously measured with soil moisture sensors (10HS, Decagon Devices, Inc., Pullman, WA, USA) at 5 cm, 15 cm, and 50 cm depths in all plots. Sensors were buried in the middle of a row in the center of the measurement plot. In one block, soil moisture at a 100 cm depth was also measured. Soil moisture was measured every minute and the average

was recorded every thirty minutes. Soil temperature was monitored in all plots using thermocouples (TMC20-HD Soil temperature sensor, Onset Computer Corp., Bourne, MA, USA). The thermocouples were buried at a 10 cm depth in all plots in the middle of a row located in the center of the measurement plot. Soil temperature was measured every minute and the average was recorded every thirty minutes. Soil moisture and soil temperature data were stored on data loggers (HOBO Micro Station Data Logger, Onset Computer Corp, Bourne, MA, USA). Sensors were installed in June 2016.

#### *2.2.4 Initial Soil Testing*

Before installing TF exclusion trays, spatial variation in fine (< 2 mm) root biomass, soil texture and soil micronutrients was measured in April 2016. Eight 1 m<sup>2</sup> grid spaces within the 231 m<sup>2</sup> available grid spaces of each measurement plot were randomly selected. Within the selected grids, soil samples were collected with a 10 cm diameter auger at 0.0-0.1 m, 0.1-0.2 m, 0.2-0.5 m and 0.5-1.0 m depths. The selected grids were at least 60 cm from the base of a tree. For the three shallowest depths, the entire soil sample was collected for soil and root measurements. Soil from the deepest depth was well mixed in a bucket and a 3 L subsample was collected for soil analyses. All samples were kept on ice during transport to Auburn University for processing.

Roots from the soil samples to a 0.5 m depth were washed, sieved (through a 2 mm sieve), and then sorted into four size categories (very fine, fine, coarse, and very coarse) based on root diameter (<1mm, ≥1mm to <2mm, ≥2 to <5mm, and ≥5mm, respectively) and live and dead categories. Roots were oven-dried at 70°C and weighed.

Soil bulk density was measured at two random sampling grids per plot using a 5.72 cm diameter core (Soil Moisture Equipment Corp., Goleta, CA, USA) at 0.0-0.1 m, 0.1-0.2 m, 0.3-0.4 m and 0.6-0.7 m depths. Roots and rocks were removed, and soil was dried at 105°C for 96 hours. Bulk density was calculated as the ratio of mass of dry soil to fresh volume ( $\text{g cm}^{-3}$ ) (Law et al. 2008) (Table 2.2.1).

Each air-dried soil subsample (approximately 0.5 L) was sent to USFS-NC (United States Forest Service Southern Research Station, Research Triangle Park, NC, USA) for measurement of soil carbon (C) and nitrogen (N) concentrations and soil texture. Total soil C and N concentrations were determined by dry combustion with detection by thermal conductivity (Flash EA 1112 series CN analyzer, Thermo-Finnigan Instruments, Milan, Italy). We randomly selected soil samples from four locations in each plot at all depths for measurements of pH and cation exchange capacity (CEC) and concentrations of phosphorus (P), potassium (K), magnesium (Mg), and calcium (Ca) by AU Soil Testing Laboratory (Tables 2.2.1 and 2.2.2).

### *2.2.5 Soil Respiration*

Soil respiration, soil moisture, and soil temperature were measured approximately every 3 weeks over 16 months (from July 2016 to December 2018) (Table 2.2.3). Because of low efflux rates in 2016, measurements sometimes required two days to complete. Measurements were conducted by block between 900-1300 hours during a sampling day to minimize diurnal variation. The measurement order of blocks and plots within blocks was randomly selected. Ten 1 m<sup>2</sup> grid spaces within the 231 m<sup>2</sup> possible grid spaces in each measurement plot were randomly selected for each measurement period. All 1 m<sup>2</sup> grid spaces had equal opportunity of being selected at each sampling period, i.e., all grid spaces were available to be sampled again.

Soil respiration was measured with a portable infrared gas analyzer (LICOR 6400, LiCor, Inc., Lincoln, NE, USA) attached to a Rs chamber (LICOR 6200-09 Soil CO<sub>2</sub> Flux Chamber). Temporary polyvinyl chloride (PVC) soil collars 10 cm in diameter were inserted 2 cm into mineral soil without removing leaf litter. It's important to mention that approximately 42% of all Rs collars in TF reduction plots landed directly under the TF reduction tray (Table 2.2.4). The soil collar along with the Rs chamber's Styrofoam gasket provided an air tight seal. Collars were inserted at least 24 hours before measurements to limit CO<sub>2</sub> pulse. Live vegetation in the collar was clipped at time of collar insertion to minimize plant tissue respiration within the soil chamber at time of measurement. Ambient CO<sub>2</sub> concentration (ppm) was measured at each plot by placing the chamber on the ground near the first collar and was used as ambient CO<sub>2</sub> across the plot. Soil temperature was measured to a 15 cm depth concurrently within 10 cm of each collar. Soil moisture was measured to 20 cm depth within 10 cm of the collar directly after Rs measurement using a soil moisture probe (Hydrosense II, Campbell Scientific, Inc., Logan, UT, USA). Distance to nearest tree from the collar, location of sampling point in relation to trays (in open space, directly under TF tray, or in gap between trays), and total tree basal area in a 7 x 7 m area around each 1 m<sup>2</sup> plot was recorded.

#### *2.2.6 Effect of Throughfall Reduction Trays on Fine Root Biomass*

To determine if trays reduced fine root biomass underneath the trays and if Rs was similarly reduced, Rs and fine root biomass were sampled in June 2017 approximately one year after treatment initiation. Sword Sayer et al. (2005) found that longleaf pine fine root length and biomass peaks in June, July, and December at xeric sites. Five trees and two cardinal directions were randomly selected in measurement plots. The east and west direction represented between row positions and north and south within row locations. A temporary Rs collar was installed 60-

80 cm from the tree within the row and between the row. Thus, the between row position fell under a tray in the TF<sub>40</sub> treatment. Soil respiration was measured at least 24 hours after collar insertion and immediately prior to soil core removal.

Root biomass was determined to a 30 cm depth below the Rs collar by removing a soil core using a 10 cm diameter auger. Soil samples were stored in plastic bags and kept on ice during transport to Auburn University for processing. Roots were separated from soil and washed and sorted into four size categories (very fine, fine, coarse, and very coarse) based on root diameter (<1mm, ≥1mm to <2mm, ≥2 to <5mm, and ≥5mm, respectively) and live and dead based on resiliency. Roots were oven dried at 70°C and weighed.

#### *2.2.7 Partitioning Autotrophic and Heterotrophic Respiration*

Heterotrophic respiration (Rh) was measured using root exclusion tubes (10 cm diameter, 30 cm length) as described by McElligott et al. (2016). Four trees were randomly selected in the outside rows of each measurement plot. The four selected trees received one exclusion tube each for each sampling period. One cardinal direction was randomly selected for each tree (east or west represented between row locations, and north or south represented within row locations). One exclusion tube was inserted 60-80 cm from the base of the tree in the selected cardinal direction. Litter was removed, and exclusion tubes were gently pressed into the soil until top of the tube was flush with the surface of the mineral soil. Litter was replaced in original location and any live vegetation was clipped. Tubes remained in soil for approximately 90 days to allow adequate time for root death and to exclude root respiration (McElligott et al. 2016). Soil respiration was measured at 90 days over the tube and over soil at two locations approximately 40 cm from the tube.

Litter covering the tubes and nearby measurement areas was removed 24 hours prior to  $R_s$  measurements. Three total  $R_s$  measurements were taken: two  $R_s$  measurements adjacent (approximately 40 cm) to the exclusion tube and one  $R_s$  measurement directly over the exclusion tube (Rh). All  $R_s$  measurements were made using a portable infrared gas analyzer (LICOR 6400, LiCor, Inc., Lincoln, NE, USA) attached to a soil respiration chamber (LICOR 6200-09 Soil CO<sub>2</sub> Flux Chamber). Soil temperature was integrated along the soil temperature probe to 20 cm depth and was measured concurrently within 10 cm of each adjacent  $R_s$  measurement and directly inside the exclusion tube. Soil moisture was integrated along the soil moisture probe to a 20 cm depth and was measured directly over each measurement area following all measurements using a soil moisture probe (Hydrosense II, Campbell Scientific, Inc., Logan, UT, USA). Each of the two adjacent  $R_s$ , soil moisture and soil temperature measurements were averaged. After all measurements were completed, exclusion tubes were removed and reinserted three additional times. Thus, Rh was measured on February 3, 2017, May 5, 2017, August 15, 2017, and November 14, 2017.

### *2.2.8 Growth*

Annual inventories were conducted to monitor treatment effects on aboveground growth. We measured diameter at breast height (DBH) to the nearest 0.1 cm. Total and live crown heights were measured with a laser hypsometer (TruePulse 200, Laser Technology, Inc. Centennial, Colorado, USA) to the nearest 0.1 m.

### *2.2.9 Data Analyses*

Data were averaged by plot, date of measurement and location where appropriate for repeatedly measured variables. Due to a severe naturally occurring drought in fall 2016, we



separated data analyses by year (2016, 2017.) Main and interactive effects of treatment and date (month for Rh) on repeatedly measured variables were tested using PROC MIXED (SAS Institute Inc., Cary, NC, USA) with block included as a random effect. If an interaction was significant, then the SLICE option of PROC MIXED was used to separate means. The most appropriate covariance structure was chosen based on the lowest Akaike information criterion. The autoregressive structure (AR (1)) was chosen for all repeated measures except for soil moisture inside the tube in which the unstructured (UN) was the most appropriate covariance structure. Treatment effects on variables not measured repeatedly over time were tested using PROC GLM (SAS Institute Inc., Cary, NC, USA). Both main and interactive effects were considered significant at  $\alpha=0.05$ .

Relationships between Rs and soil moisture, soil temperature, distance to nearest tree, and surrounding basal area were tested using stepwise regression analysis (PROC GLM, SAS Institute Inc., Cary, NC, USA). Variables were considered in stepwise selection models at  $\alpha=0.15$ . Relationship between Rs and soil moisture in 2016 was testing using regression analysis (PROC REG, SAS Institute Inc., Cary, NC, USA) along with dummy variable analysis to test for treatment differences via slope coefficients (Draper and Smith 1981.) The temperature sensitivity ( $Q_{10}$ ) of Rs was calculated as  $Q_{10} = e^{10b}$ . The relationship between Rs and soil temperature (Tsoil) on Rs in 2017 for each treatment was tested using the model:

$$Rs = a * e^{(bT_{soil})}$$

The model was fit by plot, and treatment effects on coefficients were tested using ANOVA (PROC GLM, SAS Institute Inc., Cary, NC, USA.)

To estimate annual CO<sub>2</sub> efflux, the model described above fitted to each plot was used to predict Rs for each plot from January-November 2017. Annual soil respiration was predicted for each plot using continuously monitored soil temperature in each plot recorded at 30 minutes intervals. Soil respiration was predicted for each thirty-minute interval and then summed by year (Samuelson and Whitaker 2012). Treatment effects on monthly mean, maximum and minimum soil temperature were tested using PROC MIXED (SAS Institute Inc., Cary, NC, USA) with block included as a random variable.

**Table 2.2.1.** Pre-treatment soil texture and soil properties by depth measured May 12, 2016 in an 11-year-old longleaf pine plantation.

	Sand (%)	Silt (%)	Clay (%)	pH	CEC ( $\text{cmol}_c \text{ Kg}^{-1}$ )	Bulk Density ( $\text{g cm}^{-3}$ )
<b>Depth (m)</b>						
0.0-0.1	92.3 (0.4)	4.6 (0.2)	3.2 (0.3)	5.82 (0.15)	2.82 (0.17)	1.35 (0.03)
0.1-0.2	92.0 (0.3)	4.3 (0.2)	3.8 (0.3)	5.67 (0.14)	2.12 (0.14)	1.43 (0.01)
0.2-0.5	90.8 (0.2)	4.3 (0.2)	4.9 (0.1)	5.63 (0.11)	1.64 (0.04)	1.55 (0.04)
0.5-1	90.8 (0.3)	4.2 (0.3)	5.0 (0.2)	5.19 (0.08)	0.96 (0.03)	1.53 (0.03)

Note: Values are means  $\pm$  standard errors (SEs). Soil properties include pH; CEC, Cation exchange capacity; and soil bulk density.

**Table 2.2.2.** Pre-treatment soil macronutrients by depth measured May 12, 2016 in an 11-year-old longleaf pine plantation.

	C (Mg ha <sup>-1</sup> )	N (Mg ha <sup>-1</sup> )	P (Mg ha <sup>-1</sup> )	K (Mg ha <sup>-1</sup> )	Mg (Mg ha <sup>-1</sup> )	Ca (Mg ha <sup>-1</sup> )
<b>Depth (m)</b>						
0.0-0.1	11.61 (1.97)	0.60 (0.07)	0.37 (0.04)	0.12 (0.02)	0.44 (0.06)	2.19 (0.31)
0.1-0.2	8.16 (0.51)	0.44 (0.04)	0.38 (0.07)	0.09 (0.02)	0.32 (0.04)	1.47 (0.23)
0.2-0.5	17.53 (3.15)	0.91 (0.12)	0.16 (0.04)	0.063 (0.008)	0.27 (0.03)	0.83 (0.08)
0.5-1	9.35 (0.91)	0.98 (0.18)	0.066 (0.005)	0.065 (0.005)	0.13 (0.01)	0.29 (0.03)

Notes: Values are means  $\pm$  standard errors (SEs). C, soil carbon concentration; N, soil nitrogen concentration; P, soil phosphorus concentration; K, soil potassium concentration; Mg, soil magnesium concentration; and Ca, soil calcium concentration.

**Table 2.2.3.** Measurement dates for soil respiration (Rs) by year in an 11-year-old longleaf pine plantation during 2016 and 2017.

	Measurement
<b>2016</b>	Date
	7/9, 7/27, 8/14, 9/10, 10/1, 10/22, 11/21, 12/16
<b>2017</b>	
	1/28, 2/24, 4/2, 4/29, 5/10, 6/14, 6/28, 7/19, 8/18, 9/19, 10/13, 11/16

**Table 2.2.4.** Portion of individual randomly selected sampling points within throughfall treatment plots (TR<sub>40</sub>) by measurement date and mean portion over all measurement dates in an 11-year-old longleaf pine plantation in 2017.

Measurement Date	Measurements Under Tray in TR <sub>40</sub>	Total Measurements in TR <sub>40</sub>	Under Tray in TR <sub>40</sub> (%)
7/8/16	9	30	30.00%
7/28/16	14	30	46.67%
8/14/16	15	30	50.00%
9/10/16	15	30	50.00%
10/1/16	13	30	43.33%
10/22/16	6	20	30.00%
11/21/16	9	20	45.00%
12/16/16	11	30	36.67%
1/28/17	13	30	43.33%
2/24/17	12	30	40.00%
4/2/17	12	30	40.00%
4/29/17	16	30	53.33%
5/10/17	11	30	36.67%
6/14/17	12	30	40.00%
6/28/17	11	30	36.67%
7/19/17	10	30	33.33%
8/18/17	13	30	43.33%
9/19/17	13	30	43.33%
10/13/17	13	30	43.33%
11/16/17	16	30	53.33%
<b>Totals</b>	<b>244</b>	<b>580</b>	<b>42.07%</b>

## 2.3 - Results

### 2.3.1 Climate

In 2016, mean monthly air temperature during the study ranged from 9.1 °C in December to 24.3 °C in July (Figure 2.3.1). In 2017, mean monthly air temperature ranged from 8.0 °C in December to 23.6 °C in July (Figure 2.3.1). Monthly precipitation in 2016 during the study ranged from 0.25 mm month<sup>-1</sup> in October to 144 mm month<sup>-1</sup> in July (Figure 2.3.1). In 2017, monthly precipitation ranged from 39 mm month<sup>-1</sup> in November to 279 mm month<sup>-1</sup> in January (Figure 2.3.1). Based on precipitation and PDSI, the site experienced extreme drought in 2016 (Figure 2.3.1). The PDSI dropped below -4 in October, November, and December in 2016 and did not recover until May 2017.

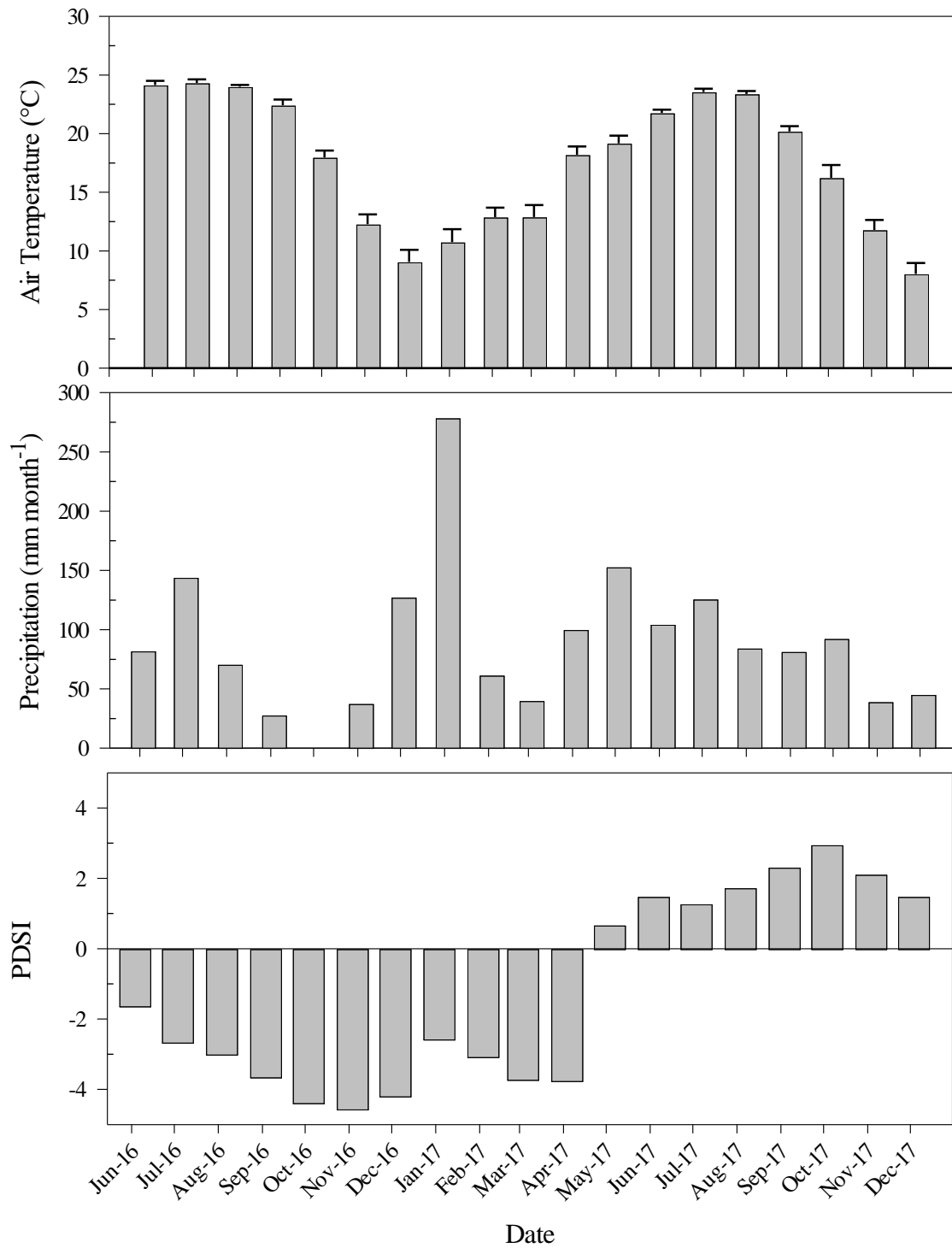
### 2.3.2 Soil Temperature and Soil Moisture

In 2016, mean daily soil temperature ranged from 9.4 °C in December to 28.0 °C in June in the TR<sub>0</sub> treatment and from 9.3 °C in December to 28.6 °C in June in the TR<sub>40</sub> treatment (Figure 2.3.2). In 2017, mean daily soil temperature ranged from 6.2 °C in January to 26.5 °C in August in the TR<sub>0</sub> treatment and from 6.5 °C in January to 26.7 °C in August in the TR<sub>40</sub> treatment (Figure 2.3.2).

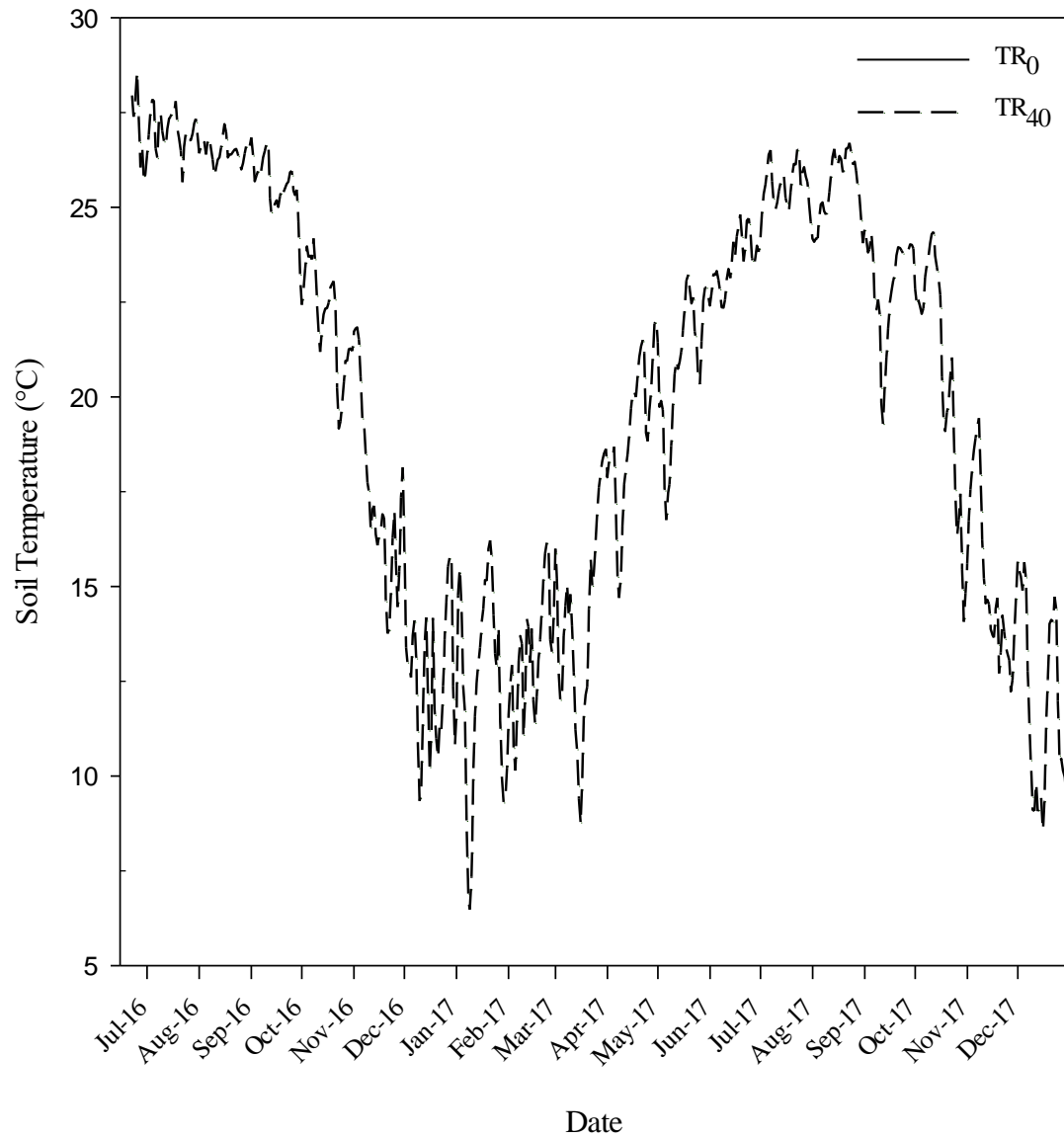
In 2016, daily precipitation ranged from 0 mm day<sup>-1</sup> on various days to 60 mm day<sup>-1</sup> in July (Figure 2.3.3A). From September 12 to November 28 2016, the site did not experience any appreciable rainfall (<1 mm day<sup>-1</sup>) (Figure 2.3.3A). In 2017, daily precipitation was as high as 68 mm day<sup>-1</sup> (Figure 2.3.3A). Peaks in soil moisture generally followed patterns in daily precipitation, particularly at the shallow depth (Figure 1.5.3). At the 5 and 15 cm depths, the effect of TR treatment appeared to reduce

soil moisture whereas the 50 cm (Figure 1.5.3C) depth did not show as strong of a response to the TR treatment (Figure 1.5.3C). In 2016, during the 79-day extended period without precipitation, soil moisture at all depths declined to near 2% then increased with precipitation events in late November (Figure 1.5.3).

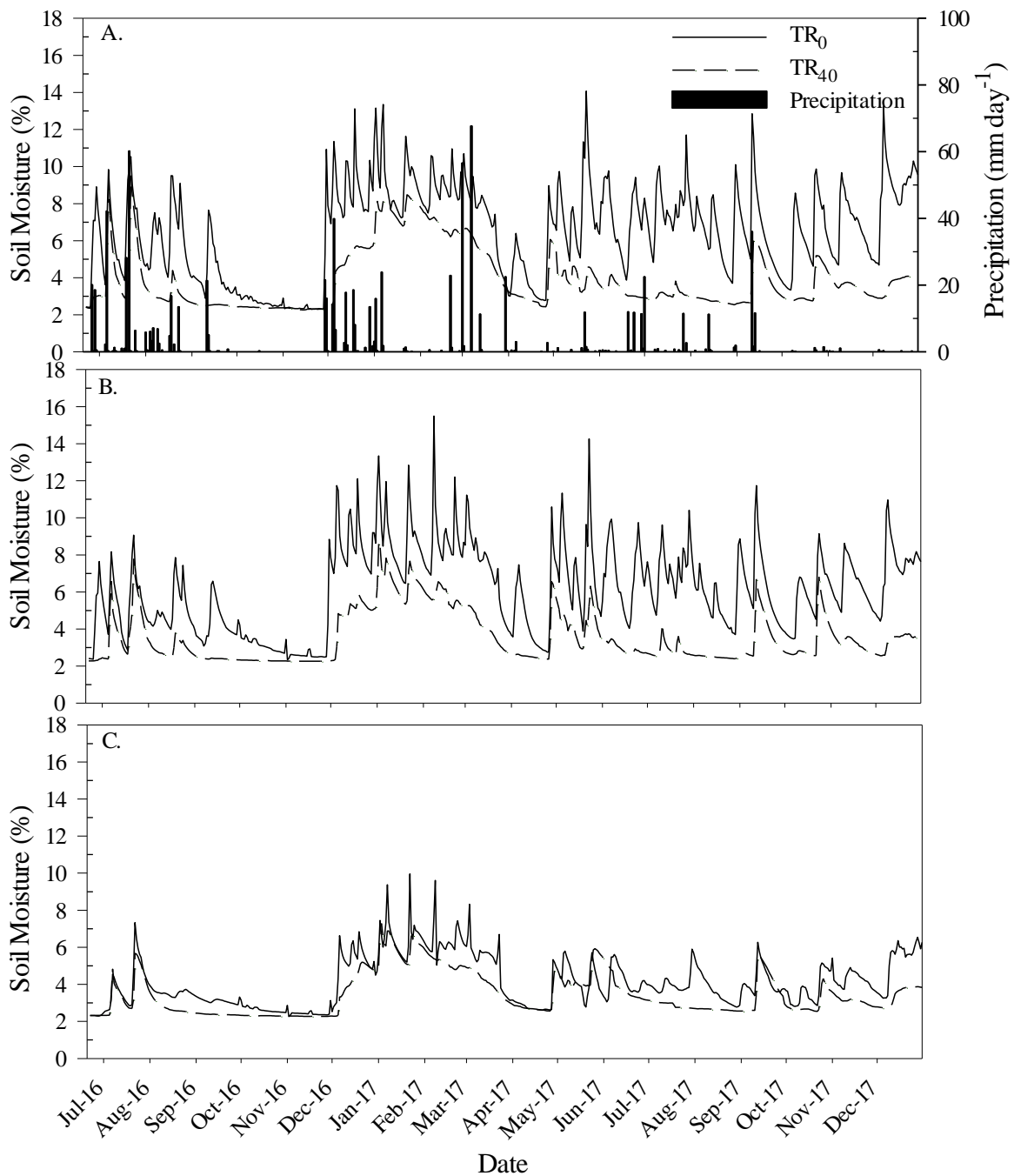




**Figure 2.3.1.** Average monthly 24-hour air temperature, the Palmer Drought Severity Index (PDSI), and monthly precipitation measured from June 2016 to December 2017.



**Figure 2.3.2.** Daily average 24-hour soil temperature measured at 10 cm depth in response to throughfall treatment (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub>, throughfall reduction) measured from June 2016 to December 2017.



**Figure 2.3.3.** Average 24-hour soil moisture content measured at 5 cm (A), 15 cm (B) and 50 cm (C) depths in response to throughfall treatment (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub>, throughfall reduction) measured from June 2016 to December 2017. Daily precipitation is shown in panel A.

### 2.3.3 Growth

Growth varied with year, but no main or interactive effects of TR treatment were observed for DBH, height, or basal area (Table 2.3.1). No significant main or interactive effects of the TR treatment were observed for density (Table 2.3.1). Diameter at breast height averaged across both treatments increased from 15.4 cm in 2016 to 16.1 cm in 2017 (Table 2.3.1). Height averaged across both treatments increased from 10.3 m in 2016 to 10.9 m in 2017 (Table 2.3.1). Basal area increased from 19.2 m<sup>2</sup> ha<sup>-1</sup> in 2016 to 20.6 m<sup>2</sup> ha<sup>-1</sup> in 2017 (Table 2.3.1).

### 2.3.4 Pre-Treatment Root Biomass

Fine root (0.1-0.99 mm diameter) biomass varied by depth with 73.1% represented in top 0.2 cm of the soil profile (Table 2.3.2). These results indicated that sampling to the 30 cm depth as described in section 3.6 should capture the majority of the fine root biomass. All fine root biomass (0.1-1.99 mm diameter) was greater at 0.0-0.01 m depth than at 0.2-0.5 m depth (Table 2.3.2). Coarse root (2-4.99 mm diameter) biomass was lowest in the 0.0-0.01 m depth and similar between the two deepest depths (Table 2.3.2). Coarse root (>5 mm diameter) biomass was lowest in the 0.0-0.1 m depth and similar between the two deepest depths (Table 2.3.2). The effect of depth was not significant for fine root (1-1.99 mm diameter) biomass (Table 2.3.2).

**Table 2.3.1.** Influence of year and throughfall treatment on tree and stand growth of a longleaf pine plantation.

	DBH (cm)	Height (m)	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Density (stems ha <sup>-1</sup> )
<b>Year</b>				
2016	15.4 (0.3)	10.3 (0.1)	19.2 (0.9)	1000 (32)
2017	16.1 (0.3)	10.9 (0.2)	20.6 (0.8)	978 (33)
<b>Throughfall treatment</b>				
TR <sub>0</sub>	15.8 (0.4)	10.8 (0.2)	20.9 (1.1)	1029 (35)
TR <sub>40</sub>	15.7 (0.2)	10.4 (0.1)	19 (0.3)	949 (18)
<b>P &gt; F</b>				
Year	<0.001	<0.001	0.002	0.228
TR	0.867	0.157	0.288	0.221
Year*TR	0.265	0.316	0.898	0.670

Note: Values are means ± standard errors. TR<sub>0</sub>, no throughfall treatment; TR<sub>40</sub>, throughfall reduction; DBH, diameter at breast height.

**Table 2.3.2.** Pre-treatment mean root biomass by depth and root diameter class measured on May 12, 2016 in a longleaf pine plantation. Roots were collected from eight random locations in each of the six plots. Lowercase letters denote significant differences among depths.

	Fine Roots (0.1-0.99 mm) (Mg ha <sup>-1</sup> )	Fine Roots (1-1.99 mm) (Mg ha <sup>-1</sup> )	Fine Roots (0.1-1.99 mm) (Mg ha <sup>-1</sup> )	Coarse Roots (2-4.99 mm) (Mg ha <sup>-1</sup> )	Coarse Roots (>5 mm) (Mg ha <sup>-1</sup> )
<b>Depth (m)</b>					
0.0-0.1	1.90 (0.15) a	0.54 (0.05)	2.44 (0.16) a	0.33 (0.07) b	0.33 (0.09) b
0.1-0.2	1.40 (0.10) b	0.67(0.06)	2.08 (0.15) ab	0.81 (0.12) a	2.12 (0.43) a
0.2-0.5	0.94 (0.12) c	0.71 (0.04)	1.66 (0.11) b	1.01 (0.13) a	1.64 (0.66) a
<b>P&gt;F</b>	0.010	0.065	0.008	0.004	0.028

Note: Values are means ± standard errors.

### 2.3.5 Soil Respiration

In 2016, no interactions between date and TR treatment were detected for Rs, and soil temperature and soil moisture measured at the time of Rs measurement (Table 2.3.3). Soil respiration, soil temperature, and soil moisture varied significantly by date in 2016. Mean Rs was highest on July 7 ( $4.09 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and varied significantly throughout 2016 (Table 2.3.3). Mean soil moisture was also highest on July 7 (7.5%) and lowest (<1%) on October 22 and November 21 (Table 2.3.3). Mean soil temperature was highest from July to September and varied significantly decreased October to December (Table 2.3.3). The TR treatment had no significant effect on Rs, soil temperature, or soil moisture (Table 2.3.3).

In 2017, significant interactions between date and TR treatment were detected for Rs and soil moisture measured during Rs measurements (Figure 2.3.4). The TR treatment significantly reduced Rs on six of the 12 measurements dates and the reduction ranged from 13.8% to 21.6% (Figure 2.3.4). Throughfall reduction significantly reduced soil moisture on seven dates and the reduction ranged from 18.7% to 40.2% (Figure 2.3.4). Soil temperature during Rs measurement varied significantly by date but not treatment (Figure 2.3.4).

### 2.3.6 Factors Controlling Soil Respiration

In 2016, stepwise linear regression analysis indicated that soil temperature, soil moisture, and distance from nearest tree accounted for 70% of the variation in Rs in the TR<sub>0</sub> treatment and 71% of the variation in Rs in the TR<sub>40</sub> treatment (Table 2.3.4). Soil moisture explained 38% of the variation in Rs in the TR<sub>0</sub> treatment and 34% in the TR<sub>40</sub> treatment (Table 2.3.4). Dummy variable analysis of treatment effects on Rs response to soil moisture in 2016 indicated no

significant differences in slopes ( $p=0.673$ ) or intercepts ( $p=0.382$ ) of the regression so one regression function was fit to data pooled across treatments (Figure 2.3.5).

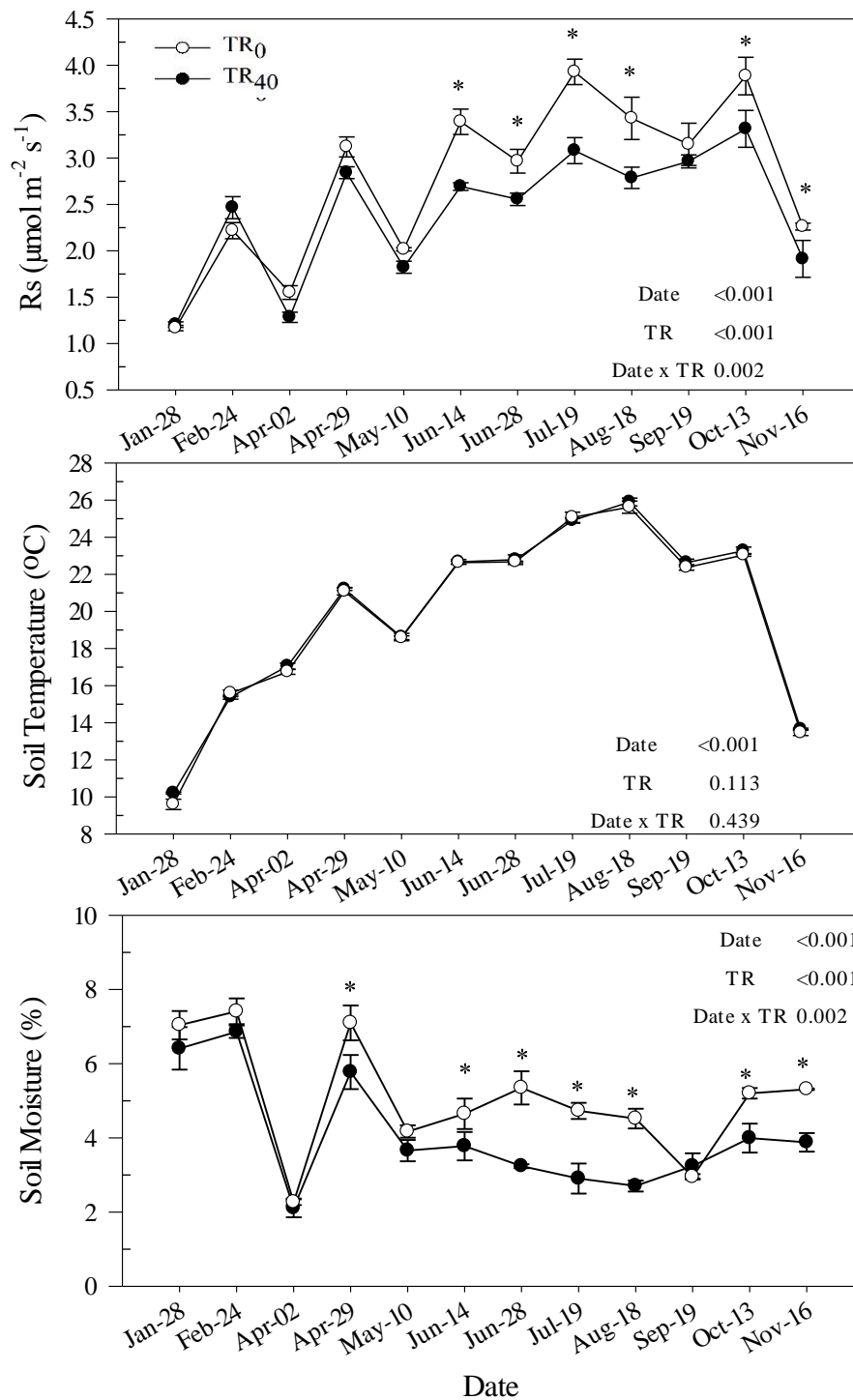
In 2017, stepwise linear regression analysis indicated that soil temperature, soil moisture, distance to nearest tree, and surrounding basal area (only in TR<sub>40</sub>) accounted for 56% of the variation in  $R_s$  in TR<sub>0</sub> treatment and 48% in TR<sub>40</sub> treatment (Table 2.3.4). Soil temperature explained the majority of the variation in  $R_s$  in both treatments with the other variables explaining from 1 to 8% of the variation in  $R_s$  (Table 2.3.4). A nonlinear function ( $R_s = a * e^{(bT_{soil})}$ ) was fit to the  $R_s$ -temperature responses by plot and coefficients were tested between treatments. Analysis of variance indicated a significant treatment difference in the  $b$  coefficient ( $p=0.019$ ) but not the  $a$  coefficient ( $p=0.086$ ) (Table 2.3.5, Figure 2.3.6). Throughfall reduction treatment significantly decreased the  $Q_{10}$  from 1.92 in TR<sub>0</sub> treatment to 1.67 for TR<sub>40</sub> treatment ( $p=0.016$ ) (Table 2.3.5, Figure 2.3.6).



**Table 2.3.3.** Influence of date (D) and throughfall treatment (TR) on soil respiration (Rs), soil temperature, and soil moisture measured at the time of Rs measurement in a longleaf pine plantation in 2016. Lowercase letters denote significant differences among dates.

	Rs ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Soil Temperature ( $^{\circ}\text{C}$ )	Soil Moisture (%)
<b>Date</b>			
7-Jul-16	4.09 (0.08) a	25.4 (0.3) b	7.5 (0.2) a
27-Jul-16	3.61 (0.09) b	26.1 (0.2) a	4.2 (0.2) c
14-Aug-16	2.74 (0.15) c	26.0 (0.2) a	1.8 (0.1) d
10-Sep-16	1.30 (0.03) de	25.7 (0.1) ab	1.5 (0.2) de
1-Oct-16	1.11 (0.05) ef	21.5 (0.2) c	1.1 (0.1) e
22-Oct-16	0.89 (0.04) fg	20.0 (0.1) d	0.4 (0.1) f
21-Nov-16	0.71 (0.02) g	13.5 (0.2) e	0.4 (0.1) f
16-Dec-16	1.37 (0.09) d	9.8 (0.1) f	6.5 (0.3) b
<b>Throughfall treatment</b>			
TR <sub>0</sub>	2.14 (0.27)	21.3 (1.3)	3.2 (0.6)
TR <sub>40</sub>	2.02 (0.27)	21.5 (1.3)	3.1 (0.6)
<b>P &gt; F</b>			
D	<0.001	<0.001	<0.001
TR	0.114	0.201	0.786
D x TR	0.707	0.708	0.790

Note: Values are means  $\pm$  standard errors (SEs). TR<sub>0</sub>, no throughfall treatment; TR<sub>40</sub>, throughfall reduction.

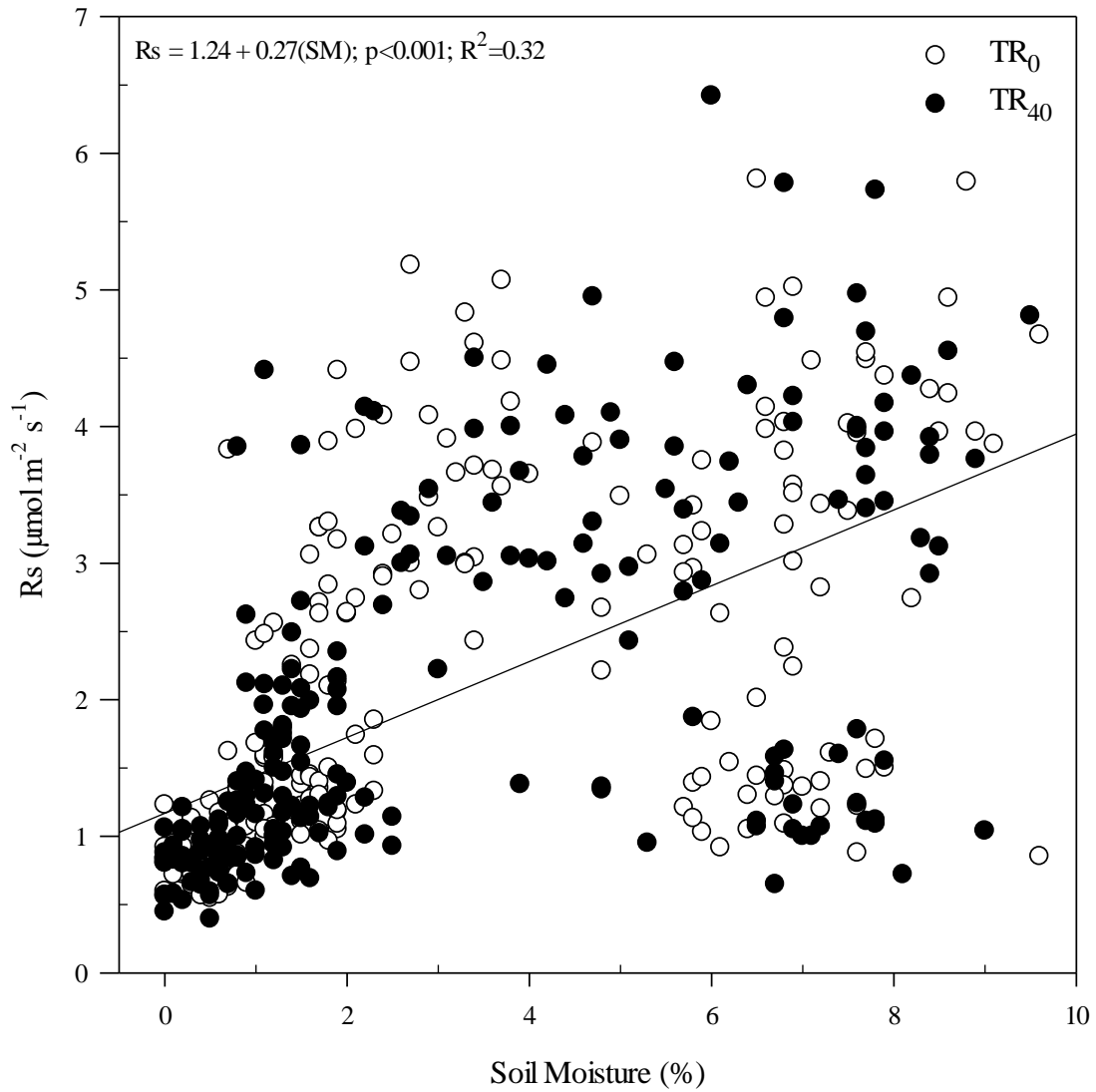


**Figure 2.3.4.** Mean ( $\pm$ SE) soil respiration (Rs), and soil temperature, and soil moisture measured during Rs measurements in response to throughfall treatment (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub>, throughfall reduction) by date in 2017 in a longleaf pine plantation. Asterisks indicate a significant treatment effect within a date. Observed probability values for the effects of date and throughfall treatment (TR) are indicated.

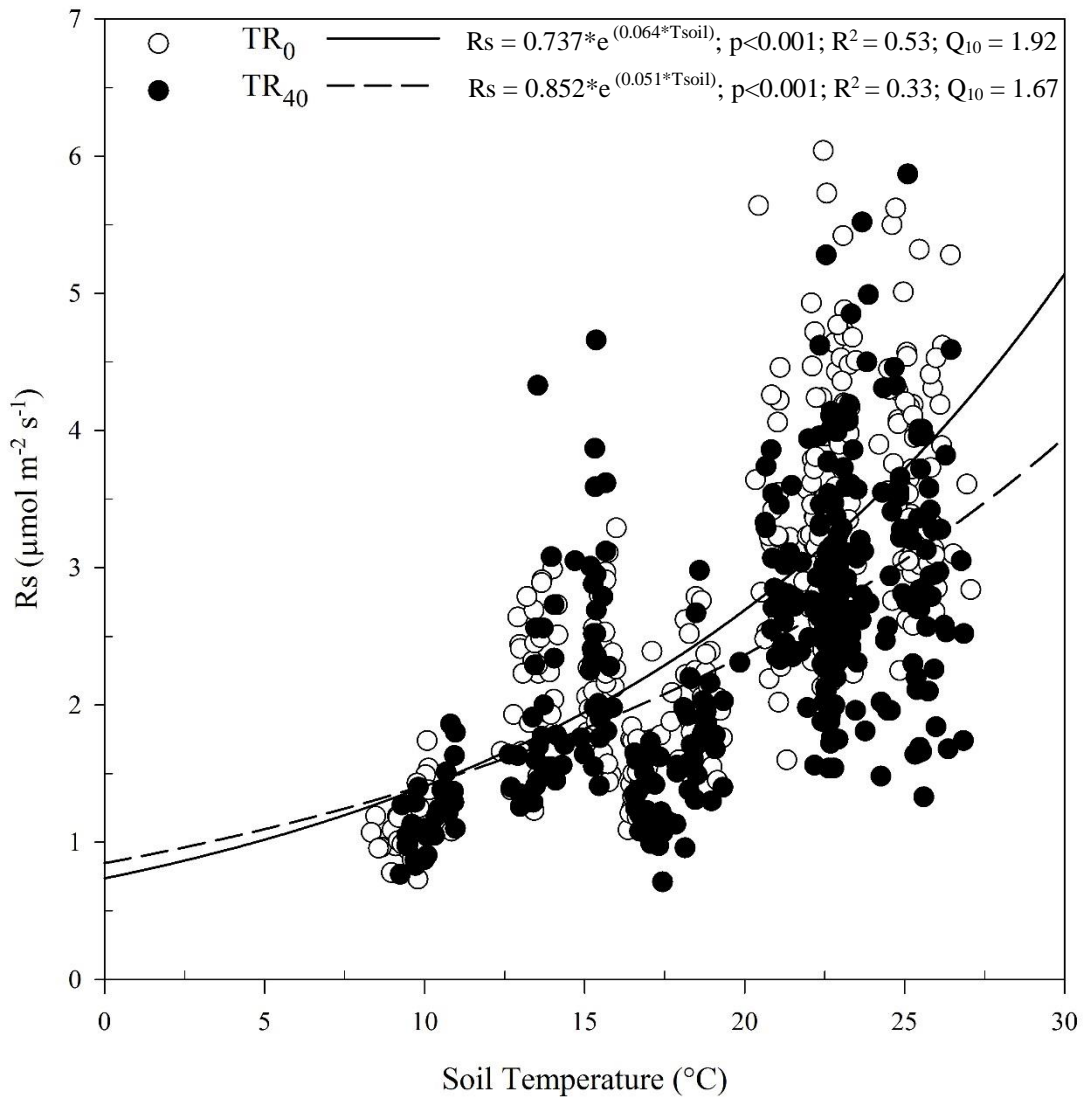
**Table 2.3.4.** Parameter estimates and partial  $R^2$  for models describing relationships between soil respiration and soil temperature (Tsoil), soil moisture (SM), distance from nearest tree (DNT) and surrounding basal area (BA) by year and treatment in a longleaf pine plantation.

<b>2016</b>				<b>2017</b>			
	Estimate	Partial $R^2$	P>F		Estimate	Partial $R^2$	P>F
<b>TR<sub>0</sub></b>				<b>TR<sub>0</sub></b>			
Intercept	-1.426			Intercept	-0.663		
Tsoil	0.139	0.30	<0.001	Tsoil	0.171	0.52	<0.001
SM	-0.003	0.38	<0.001	SM	0.091	0.02	<0.001
DNT	0.302	0.02	<0.001	DNT	-0.004	0.02	<0.001
BA	N.S.	N.S.	N.S.	BA	N.S.	N.S.	N.S.
<b>TR<sub>40</sub></b>				<b>TR<sub>40</sub></b>			
Intercept	-1.242			Intercept	-1.002		
Tsoil	0.130	0.34	<0.001	Tsoil	0.149	0.34	<0.001
SM	0.306	0.34	<0.001	SM	0.167	0.08	<0.001
DNT	-0.004	0.03	<0.001	DNT	-0.004	0.05	<0.001
BA	N.S.	N.S.	N.S.	BA	3.602	0.01	0.010

Note: TR<sub>0</sub>, no throughfall treatment; TR<sub>40</sub>, throughfall reduction. N.S., not significant.



**Figure 2.3.5.** Soil respiration (Rs) in response to soil moisture (SM) in the throughfall treatments (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub>, throughfall reduction) in a longleaf pine plantation in 2016. Each data point represents an individual measurement.



**Figure 2.3.6.** Soil respiration (Rs) versus soil temperature (Tsoil) in response to throughfall treatment (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub>, throughfall reduction) in a longleaf plantation in 2017. Each data point represents an individual measurement. Solid line represents the relationship of Rs versus Tsoil in TR<sub>0</sub> plots whereas the dashed line represents the relationship of Rs versus Tsoil in TR<sub>40</sub> plots.

### 2.3.7 Annual Soil Respiration

Throughfall reduction treatment reduced annual Rs by 12.6%, from 9.96 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in the TR<sub>0</sub> treatment to 8.70 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in the TR<sub>40</sub> treatment (Table 2.3.5). Monthly minimum, maximum, and/or mean continuously measured T<sub>soil</sub> did not vary due to TR treatment in 2017 (Table 2.3.5).

### 2.3.8 Effect of Throughfall Reduction Trays on Fine Root Biomass

There were no interactive or main effects of TR treatment and location (within row versus between rows) on Rs, soil temperature, and fine root biomass (0.1-1.99 mm diameter) one year after initiation of TR treatment (Table 2.3.6). A significant interaction between TR treatment and location for soil moisture was observed (Table 2.3.6); an effect of location was observed only in the TR<sub>40</sub> treatment with lower soil moisture between rows (under trays) than within rows. (Figure 2.3.7).

### 2.3.9 Heterotrophic Respiration

Soil respiration near tubes, Rh, Rh:Rs, soil temperature, and soil moisture (both inside and outside the tube) all varied significantly by month (Table 2.3.7). Soil respiration was highest in August (2.93 μmol m<sup>-2</sup> s<sup>-1</sup>) and ranged from 2.20 μmol m<sup>-2</sup> s<sup>-1</sup> -1.22 μmol m<sup>-2</sup> s<sup>-1</sup> in all other months (Table 10). Heterotrophic respiration was highest in August (2.19 μmol m<sup>-2</sup> s<sup>-1</sup>) and lowest in February (1.09 μmol m<sup>-2</sup> s<sup>-1</sup>) (Table 2.3.7). The ratio of Rh to Rs was highest in February (89.4%) and ranged from 77.8-72.4% in all other months (Table 2.3.7).

There were no main effects of TR treatment on soil temperature (inside or outside the tube), Rh, or Rh:Rs (Table 2.3.7). Interactive effects of month and TR treatment were observed for Rs and Rh:Rs. A significant effect of treatment on Rs and Rh:Rs was observed in August when

TR<sub>40</sub> treatment increased Rh:Rs by 22% and decreased Rs by 27% (Table 2.3.7, Figure 2.3.8.) Main effects of location were observed for Rs and Rh where Rs decreased by 9% and Rh decreased by 11.6% between rows versus within rows (Table 2.3.7). A significant three-way interaction between month, TR treatment and location indicated that soil moisture within the tube decreased between rows but not within rows only in TR<sub>40</sub> ranging from 28.5% to 56.0 % in May, August, and November (Table 2.3.7, Figure 2.3.9A). An interaction between TR treatment and location indicated that soil moisture outside the exclusion tube was decreased by TR<sub>40</sub> between rows but not within rows from 5.8 % to 3.8% (Table 2.3.7, Figure 2.3.9B).

**Table 2.3.5.** Throughfall (TR) treatment effects on annual soil CO<sub>2</sub> efflux, coefficients *a* and *b* of the nonlinear function describing soil respiration response to soil temperature ( $R_s = a * e^{(bT_{soil})}$ ), and minimum (Tsoil-min), maximum (Tsoil-max), and mean soil temperature (Tsoil) measured continuously in a longleaf pine plantation in 2017.

	Annual Soil Efflux (Mg C ha <sup>-1</sup> yr <sup>-1</sup> )	Coefficient <i>a</i>	Coefficient <i>b</i>	Q <sub>10</sub>	Tsoil-min (°C)	Tsoil-max (°C)	Tsoil (°C)
<b>TR<sub>0</sub></b>	9.96 (± 0.16)	0.734 (± 0.01)	0.065 (±0.002)	1.92 (±0.04)	15.2 (±1.0)	21.5 (±0.7)	18.8 (±0.8)
<b>TR<sub>40</sub></b>	8.70 (± 0.12)	0.852 (±0.07)	0.051 (±0.005)	1.67 (±0.05)	15.2 (±1.0)	21.5 (±0.7)	18.8 (±0.8)
<b>P&gt;F</b>							
Month	N.A.	N.A.	N.A.	N.A.	<0.001	<0.001	<0.001
TR	0.008	0.086	0.019	0.016	0.933	0.974	0.959
Month x TR	N.A.	N.A.	N.A.	N.A.	0.798	0.0279	0.363

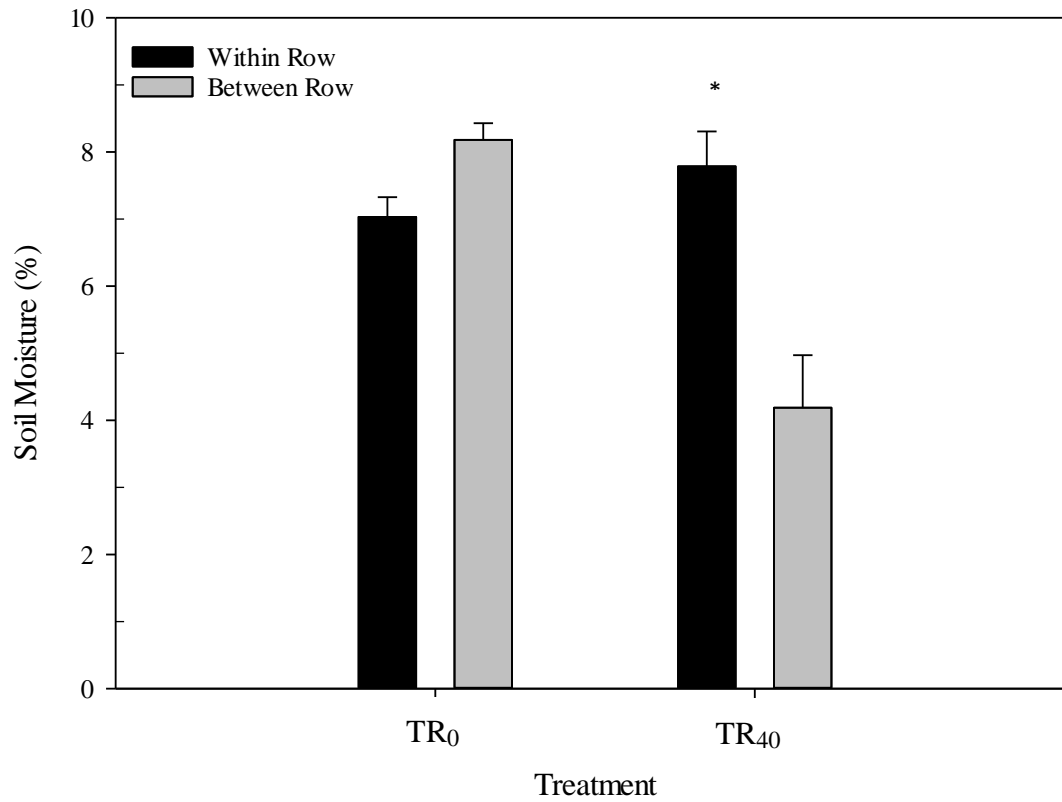
Note: Values are means ± standard errors (SEs). TR<sub>0</sub>, no throughfall treatment; TR<sub>40</sub>, throughfall reduction. N.A., Not Applicable.



**Table 2.3.6.** Influence of throughfall reduction treatment (TR) and location (LOC) on soil respiration (Rs), soil temperature, soil moisture, and fine roots by diameter class in a longleaf pine plantation measured in June 2017 approximately one year after throughfall treatment initiation.

	Rs ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Soil Temperature ( $^{\circ}\text{C}$ )	Soil Moisture (%)	Fine Roots (0.1-1.99 mm) ( $\text{Mg ha}^{-1}$ )
<b>Throughfall treatment</b>				
TR <sub>0</sub>	2.63 (0.08)	21.6 (0.1)	7.6 (0.3)	1.37 (0.11)
TR <sub>40</sub>	2.54 (0.09)	21.5 (0.1)	6.0 (0.9)	1.52 (0.13)
<b>Location</b>				
Within Row	2.51 (0.04)	21.5 (0.1)	7.4 (0.3)	1.37 (0.11)
Between Row	2.67 (0.09)	21.6 (0.7)	6.2 (0.1)	1.52 (0.13)
<b>P &gt; F</b>				
TR	0.498	0.178	0.003	0.256
LOC	0.223	0.419	0.012	0.236
TR x LOC	0.207	0.585	<0.001	0.634

Note: Values are means  $\pm$  standard errors. TR<sub>0</sub>, no throughfall treatment; TR<sub>40</sub>, throughfall reduction.

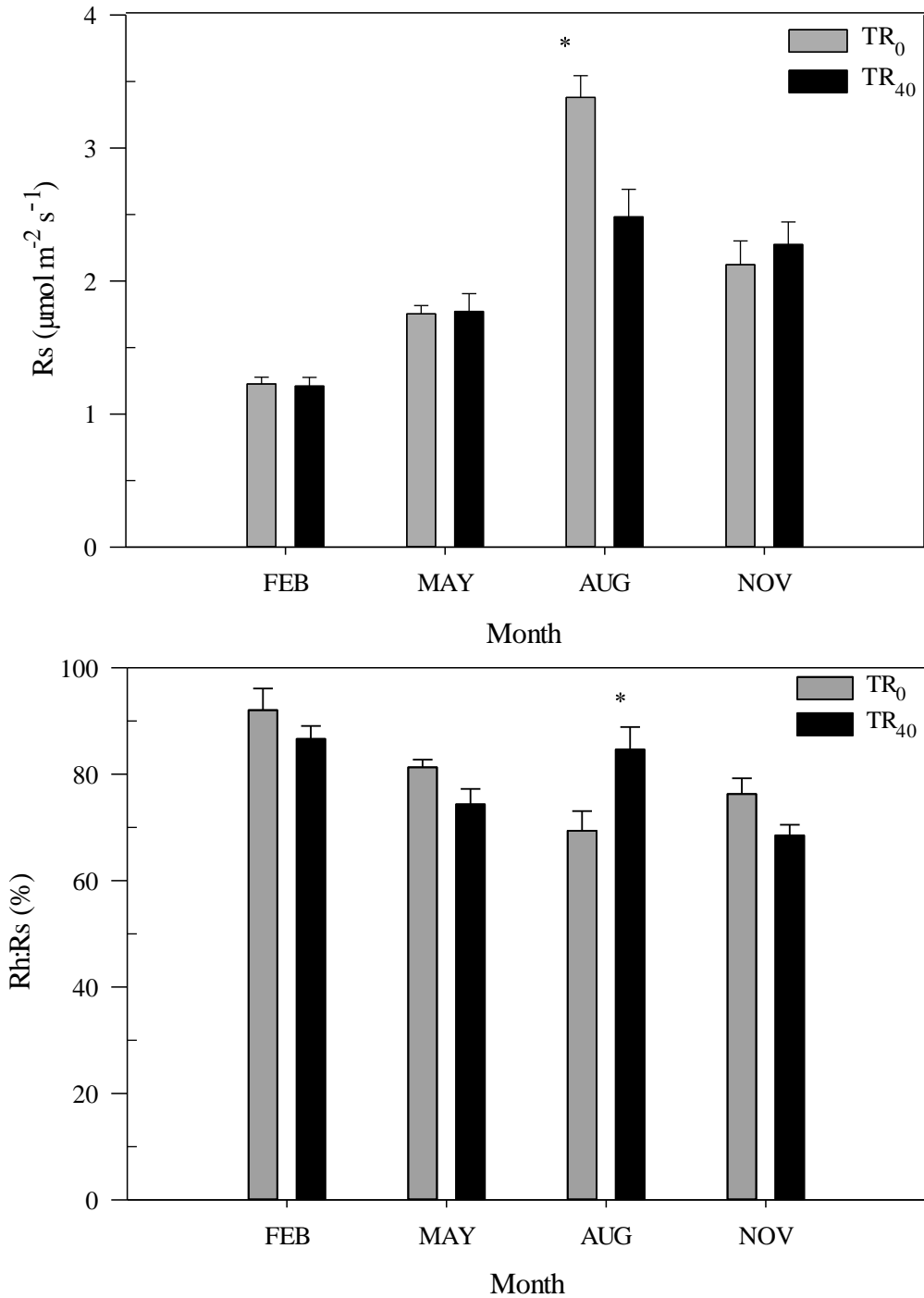


**Figure 2.3.7.** Mean soil moisture by throughfall reduction treatment (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub> throughfall reduction) in response to location in 2017 in a longleaf pine plantation. Asterisks indicate a significant location effect within treatment.

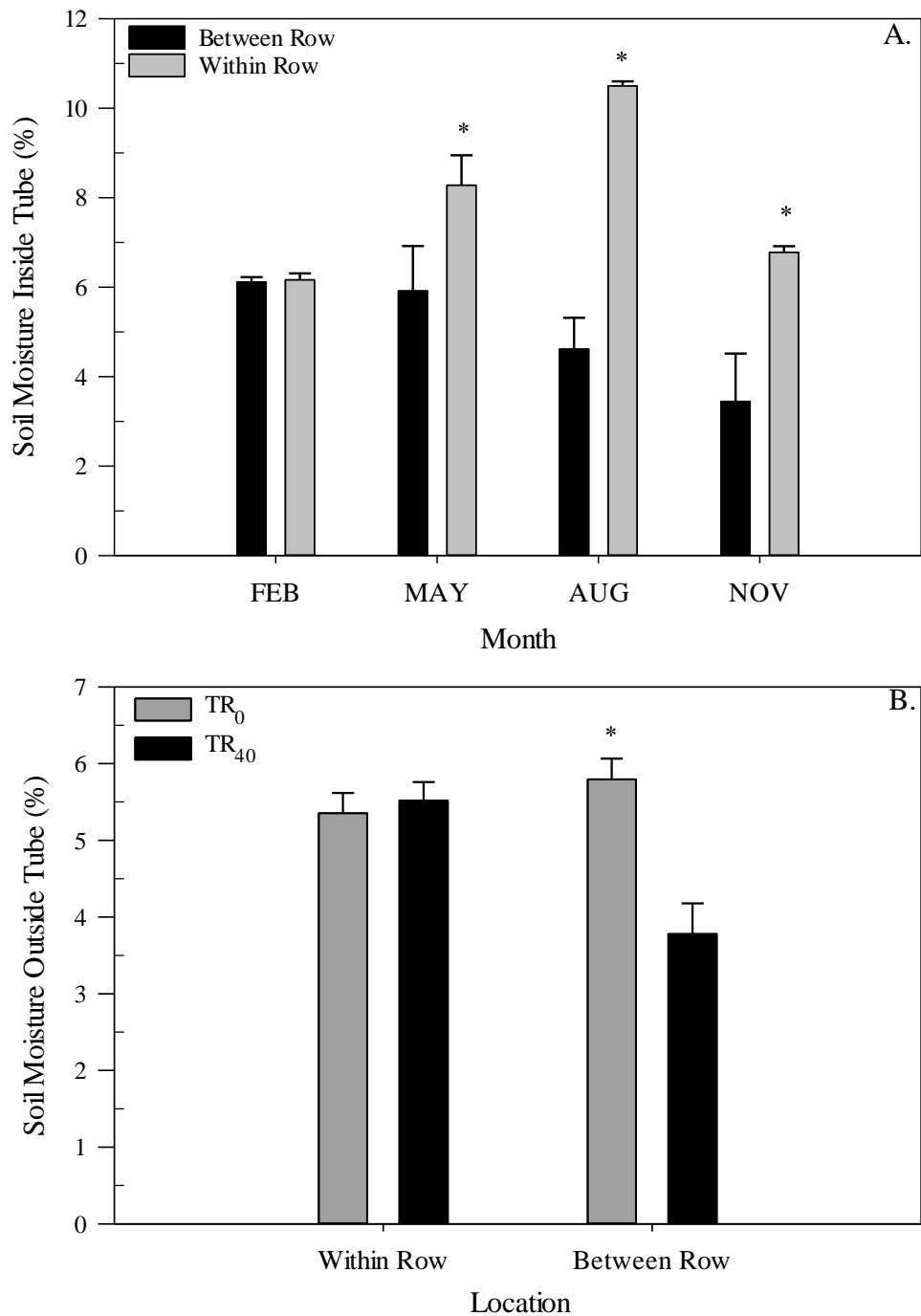
**Table 2.3.7.** Influence of month (M), throughfall treatment (TR), and location (LOC), on soil respiration (Rs), heterotrophic respiration (Rh), the ratio of Rh to Rs (Rh:Rs), soil temperature (Tsoil), and soil moisture (SM) within and outside the exclusion tube in a longleaf pine plantation in 2017. Lowercase letters denote significant differences among months.

	Rs	Rh	Rh:Rs	Tsoil outside tube	SM outside tube	Tsoil within tube	SM within tube
	( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	(%)	( $^{\circ}\text{C}$ )	(%)	( $^{\circ}\text{C}$ )	(%)
<b>Month (2017)</b>							
FEB	1.22 (0.04) c	1.09 (0.06) d	89.4 (3.0) a	13.1 (0.4) d	4.7 (0.1) b	13.2 (0.0) d	6.2 (0.9) c
MAY	1.76 (0.07) bc	1.37 (0.09) c	77.8 (2.0) b	17.3 (0.1) b	6.0 (0.4) a	17.6 (0.2) b	7.6 (0.4) ab
AUG	2.93 (0.18) a	2.19 (0.10) a	76.9 (3.3) bc	25.4 (0.1) a	4.9 (0.4) b	25.6 (0.2) a	9.2 (0.9) a
NOV	2.20 (0.12) b	1.53 (0.07) b	72.4 (2.3) c	15.1 (0.2) c	4.7 (0.4) b	15.4 (0.1) c	6.4 (0.7) bc
<b>Throughfall treatment</b>							
TR <sub>0</sub>	2.12 (0.18)	1.61 (0.10)	79.7 (2.2)	17.7 (0.1)	5.6 (0.2)	17.9 (1.0)	8.3 (0.4)
TR <sub>40</sub>	1.94 (0.12)	1.48 (0.10)	78.5 (2.4)	17.8 (0.1)	4.6 (0.3)	18.0 (1.0)	6.4 (0.7)
<b>Location</b>							
Within Row	2.12 (0.16)	1.64 (0.10)	80.5 (2.5)	17.7 (0.1)	5.4 (0.2)	17.9 (1.0)	8.0 (0.5)
Between Row	1.93 (0.15)	1.45 (0.10)	77.7 (2.0)	17.8 (0.1)	4.8 (0.3)	18.0 (1.0)	6.8 (0.5)
<b>P &gt; F</b>							
M	<0.001	<0.001	<0.001	<0.001	0.003	<0.001	<0.001
TR	0.028	0.115	0.652	0.414	0.001	0.325	0.004
LOC	0.023	0.027	0.280	0.510	0.013	0.650	0.006
M x TR	0.001	0.790	0.001	0.220	0.129	0.888	0.002
M x LOC	0.204	0.906	0.086	0.912	0.564	0.239	0.001
TR x LOC	0.805	0.126	0.104	0.669	0.001	0.362	0.001
M x TR x LOC	0.137	0.436	0.207	0.936	0.093	0.564	0.020

Note: Values are means  $\pm$  standard errors. TR<sub>0</sub>, no throughfall treatment; TR<sub>40</sub>, throughfall reduction.



**Figure 2.3.8.** Mean soil respiration (Rs) and the ratio of Rs to Rh (Rh:Rs) in response to throughfall treatment (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub>, throughfall reduction) by month in 2017 a longleaf pine plantation. Asterisks indicate a significant treatment effect within a month.



**Figure 2.3.9.** Mean soil moisture inside the exclusion tube in the TR<sub>40</sub> treatment in response to location effects by month (A) and soil moisture outside the tube in response to throughfall reduction (TR<sub>0</sub>, no throughfall reduction; TR<sub>40</sub> throughfall reduction) by location (B) in 2017 in a longleaf pine plantation. Asterisks indicate a significant location by month interaction in soil moisture inside the exclusion tube (A) and a significant treatment by position interaction in soil moisture outside the exclusion tube (B).

## 2.4 - Discussion

I hypothesized that  $R_s$  would decrease in response to drought imposed by TR. In support of this hypotheses,  $TR_{40}$  significantly decreased  $R_s$  during some months in 2017 and decreases ranged from 13.8% to 21.6%. These results agree with other studies that demonstrated decreased  $R_s$  in a variety of forests (Schindlbacher et al. 2012; Borken et al. 2006, Koptitike et al. 2014; Brando et al. 2008). For example, Schindlbacher et al. (2012) found that 100% summer TR in Norway spruce (*Picea abies* L.) stands decreased  $R_s$  by 50%. Borken et al. (2006) observed a 10-30% decline in  $R_s$  in response to 100% TR in a maple/oak forest. In *Calluna* spp. dominated shrub lands in the Netherlands, 100% TR decreased  $R_s$  by 42-45% (Kopittke et al. 2014). Conversely, in an Amazonian rainforest, Brando et al. (2008) found no significant response to 40% TR, and attributed the lack of  $R_s$  response to large pulses in  $R_s$  after rewetting in TR plots compared to the control plots. In 2017,  $TR_{40}$  reduced annual  $R_s$  in this study by 12.6%. Annual  $R_s$  was 9.96 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in the  $TR_0$  treatment and 8.70 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in the  $TR_{40}$  treatment and similar to the range reported for other southern pine forests. For example, Palmroth et al. (2005) reported that annual  $R_s$  decreased from 13.3 Mg C ha<sup>-1</sup> yr<sup>-1</sup> to 12.3 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (7.5%) in response to a severe drought in a loblolly pine (*Pinus taeda* L.) plantation. Our annual  $R_s$  values are somewhat lower than rates reported by ArchMiller and Samuelson (2016a) for longleaf pine forests ranging from 5 to 87-years-old (12.0-13.9 Mg C ha<sup>-1</sup> yr<sup>-1</sup>). Samuelson and Whitaker (2012) reported a slightly higher range for a 50-year-old longleaf pine forest of varying basal areas (11.0-17.9 Mg C ha<sup>-1</sup> yr<sup>-1</sup>). However, none of the longleaf studies mentioned were conducted on Lakeland soils. Our range is higher than Hendricks et al. (2006) who compared  $R_s$  from longleaf pine forests on xeric soils and hydric soils and reported annual  $R_s$  from 4.6 Mg C

ha<sup>-1</sup> yr<sup>-1</sup> to 6.9 Mg C ha<sup>-1</sup> yr<sup>-1</sup>. However, Hendricks et al. (2006) used a different technique to measure soil CO<sub>2</sub> which may account for their lower rates.

No effect of TR on Rs were observed in 2016 during extreme natural drought when Rs in both treatments were reduced to near zero. Although TR had no influence on Rs in 2016, soil moisture explained 32% of the variation in Rs across treatments. Often in xeric soils, rewetting after a period of prolonged drought can cause a pronounced release of CO<sub>2</sub> from the soil caused by diffusion of water into pore space, increased active decomposition of dead soil microbes, and increased root maintenance respiration (Brando et al. 2008; Schindlbacher et al. 2012; Vicca et al. 2014). The effects of soil moisture on Rs are often interrelated with soil temperature, as described later in this discussion. A large pulse in Rs when soil moisture recovered in late 2016 was not observed perhaps because of seasonally low soil temperature in December 2016.

In both years, Rs was significantly related to soil temperature. As my results suggest, there is a significant reduction in the response of Rs to soil temperature when soil moisture is limited. Throughfall reduction treatment reduced Q<sub>10</sub> by 13% in 2017, from 1.92 in TR<sub>0</sub> to 1.67 in TR<sub>40</sub>. Others have also observed a reduction in Q<sub>10</sub> with reduced soil moisture. For example, Wang et al. (2014a) observed a decrease in Q<sub>10</sub> in a desert shrub ecosystem following a decrease in soil moisture. A reduction in Q<sub>10</sub> in response to drought stress has been reported in a tropical forest (Goodrick et al. 2016) and a temperate forest (Subke and Bahn 2010.) Whitaker and Samuelson (2012) observed a slightly higher Q<sub>10</sub> of 2.81 in a 50-year-old longleaf pine forest but did not encounter drought stress. ArchMiller and Samuelson (2016a) found that drought stress reduced Q<sub>10</sub> from 2.18 to 1.94 when soil moisture was extremely limited during a naturally occurring drought in a longleaf pine forest. Powell et al. (2008) observe a significant reduction in Q<sub>10</sub> from 2.0 when soil water content was above 5.5% to 1.4 when soil water content was below 5.5% in a

longleaf pine forest. A possible explanation of the reduction in  $Q_{10}$  is that drought stress can limit: (1) the diffusion of nutrients to plants and microbes, (2) physiological performance in plants, and (3) extracellular enzymes in soil that aid in the degradation of available substrate (Wang et al. 2014c). The results from the Rh study suggest that the reduction in  $Q_{10}$  in response to TR<sub>40</sub> could be due to a reduction in Ra rather than Rh. Others have observed similar reductions in Ra but not Rh. For example, Nikolova et al. (2009) suggested that Ra was more responsive to changes in soil temperature and soil moisture than Rh in a Norway spruce (*Picea abies* L.) forest. Similarly, Hinko-Najera (2015) observed in a Eucalyptus (*Eucalyptus* sp.) forest that Rh was more sensitive to changes in soil temperature but Ra was more sensitive to changes in soil moisture in response to 40% TR.

I hypothesized that Rs would be negatively correlated to distance from the nearest tree and positively correlated to soil moisture, soil temperature, and surrounding tree basal area. Surrounding tree basal area was only positively correlated with Rs in TR<sub>40</sub> plots in 2017 and was non-significant in 2016 models in both treatments. Distance from nearest tree only explained a maximum of 5% of the variation in Rs in 2017 in the TR<sub>40</sub> and 3% in 2016 in the TR<sub>40</sub>. A positive relationship between surrounding tree basal area and Rs and a negative relationship between Rs and distance from nearest tree was observed in a variety of forest types. For example, Ohashi et al. (2016) explored the spatial variability of Rs during short-term severe experimental drought and found that distance from nearest tree correlated negatively with Rs in a Mylasiatic tropical forest. ArchMiller et al. (2016a) found that Rs was positively related to surrounding tree basal area and negatively related to distance from nearest tree in a mature, natural longleaf pine forest. However, Samuelson and Whitaker et al. (2012) found that stand basal area was only weakly related to Rs in a 50-year-old longleaf pine forest.



I hypothesized that TR trays would alter soil moisture dynamics and thus influence the spatial distribution of fine roots. Essentially, I hypothesized that fine root mass would increase within row compared to between rows (directly under TR trays in TR<sub>40</sub> treatment) to compensate for reduced fine root biomass below TR trays. This hypothesis was based on root hydrotropism: the ability of a plant to direct growth in response to a hydrologic vector (Eapen et al. 2005; McElrone et al. 2013). Positive hydrotropism occurs when the root cap is stimulated, and cell elongation occurs on the drier side of the root leading to root growth towards the damper soil patch (Takahashi et al. 1994). Guevara and Giordano (2015) observed positive hydrotropism in desert plants when studying the direction of fine root growth in a water limited ecosystem. Kanber et al. (1999) observed a decrease in root biomass as the distance from the irrigation source increased in grapefruit (*Citrus paradise*) trees. Results suggest that TR trays (location) or treatment had no effect on fine root biomass and associated Rs. Others have reported a positive relationship with Rs and fine root biomass in longleaf pine forests (Archmiller and Samuelson 2016a; Samuelson and Whitaker 2012), but I did not observe a significant reduction in fine root biomass in the TR<sub>40</sub> treatment. An interactive effect of location within the TR treatment on soil moisture was observed, suggesting that the TR trays acted as a barrier to limit throughfall from reaching the soil below, thus decreasing soil moisture in TR<sub>40</sub> directly below TR trays. In contrast to these results, others have observed decreases in root biomass and changes in root morphology in response to reduced soil moisture. For example, in a Chinese oak forest, Liu et al. (2017) observed a decrease in fine root biomass in response to ~50% TR reduction and soil warming. Brunner et al. (2015) found that that reduced soil moisture tended to decrease root tip frequency and overall root length leading to decreased fine root biomass in many forested species. Similarly, Nikolova et al. (2009) observed decreased fine root production in Norway

spruce in response to extreme drought. Decreases in fine root biomass with reduced soil moisture may be caused by decreased root growth (Sword-Sayer et al. 2005) or increased fine root mortality and turnover (Brunner et al. 2015; Nikolova et al. 2009; Gual et al. 2008). Sword Sayer and Haygood (2006) observed a decrease in fine root elongation in longleaf pine during a naturally occurring three-year drought. The relatively low sample size and low sampling frequency likely did not capture fine root dynamics. Sword Sayer et al. (2005) found that longleaf pine fine root biomass peaks in June, July, and December. Additional sampling could have provided a better insight how fine root production and mortality respond to drought.

No significant effect of TR on Rh was observed, although soil moisture inside tubes and under trays was reduced by TR<sub>40</sub> treatment. Similarly, Nina Hinko-Najera et al. (2015) found no significant response of Rh to 40% TR treatment in an Australian eucalyptus (*Eucalyptus* sp.) forest. Conversely, in a Norway spruce (*Picea abies* L.) forest (Muhr and Borken 2009) and in mixed deciduous forest (Borken et al. 2006) Rh decreased in response to 100% TR. Therefore, the significant decrease in Rs in response to TR<sub>40</sub> in August associated with the Rh measurement could be attributed to decreased Ra. However, Wang et al. (2014c) proposed that Rh is more sensitive to drought stress than Ra. Heterotrophic respiration can be more sensitive to drought stress because drought limits soil organic matter decomposition, limits the physiological ability of soil microbes, limits the diffusion of nutrients to soil microbes, and may shift microbial communities to less productive, drought tolerant fungal and microbe populations (Wang et al. 2014c). Although Rh constituted the majority of Rs in this study, our results suggest that Ra could be more sensitive to drought stress in longleaf pine forests, at least above the soil wilting point, suggesting decreases in photosynthesis or root biomass in TR<sub>40</sub> treatment (Wang et al. 2014b). The decrease in Ra in the TR<sub>40</sub> treatment could be attributed to a decrease in leaf-level

net photosynthesis, which was detected in a companion study in 2017 at our site (personal communication, Caren Custodio Mendonca). The contribution of Rh to Rs (Rh:Rs) ranged from 72-89%. Hanson et al. (2000) in a synthesis on Rh reported a wide range in Rh, from 10-90% of Rs. Heim et al. (2015) found that Rh accounted for 79% of Rs annually in a 9-year-old loblolly pine plantation in Virginia. However, they found that 30% TR had no effect on Rh:Rs. In another loblolly pine study, McElligott et al. (2016) found that Rh accounted for 50-82% of Rs. In a 26-year-old longleaf pine forest, Rh accounted for 61-82% of total Rs (ArchMiller and Samuelson 2016b). Collins (2005) reported that Rh ranged from 85-88% in longleaf pine forests on clayey soils and 90- 96% in forests on sandy soils.

The wilting point for soils at the study site is 3.3% based on the soil moisture sensors installed permanently in the plots (personal communication, Tom Stokes). An equation: ( $y = 1.080x + 0.743$ ;  $p = <0.001$ ;  $R^2 = 0.63$ ) was developed using regression analysis to relate soil moisture measured directly following Rs measurement using time domain reflectometry (x) to the continuously measured soil moisture using capacitance and frequency domain (y). The wilting point for Rh to based on time domain reflectometry was 2.3%. The TR<sub>40</sub> failed to decrease soil moisture in the tubes and adjacent to the tubes to this extent in 2017, thus suggesting the reductions in soil moisture did not physiologically stress soil microbial population enough to detect a reduction in Rh. Other methods exist to partition Ra and Rh from Rs. For example, the trenching method requires excavating a small trench around plots to exclude roots and the autotrophic component of Rs (Vogel et al. 2005). Tree girdling is used to restrict photosynthate from reaching roots (Högberg 2001). I used root exclusion tubes to limit residual damage to surrounding trees (McElligot et al. 2016) compared to other, more destructive methods mentioned above.

## 2.5 - Conclusions

In summary, drought stress reduced  $R_s$  and its components. Extreme drought stress in 2016 reduced  $R_s$  and soil moisture to near zero, and  $TR_{40}$  reduced  $R_s$  up to 21.6% in 2017. Soil temperature and soil moisture explained the majority of the variation in  $R_s$  in both years, but drought stress reduced the response of  $R_s$  to soil temperature. Heterotrophic respiration accounted for the majority of  $R_s$  (79-82%), but the effect of drought stress may be more apparent on  $R_a$  in longleaf pine forests under moderate drought. Under severe drought, both  $R_a$  and  $R_h$  are greatly reduced. Decreases in  $R_a$  without reduction of fine root biomass in response to drought stress could be an indicator of decreased photosynthesis which could ultimately lead to decreased carbon sequestration. Although longleaf pine forests offer carbon storage benefits compared to other southern pine species, based on their longevity, increasing temperatures and longer periods of drought stress could significantly decrease their physiological ability to store carbon and help mitigate climate change. Decreases in soil respiration due to drought could be an indicator of drought stress effects on soil health leading to decreased nutrient uptake and nutrient processing in plant roots and soil microbes.

## REFERENCES

- Addington, R.N., L.A. Donovan, R.J. Mitchell, J.M. Vose, S.D. Picot, S.B. Jack, U.G. Hacke, J.S. Sperry, and R. Oren. 2006. Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats. *Plant Cell Environment* 29: 535-545
- ArchMiller, A.A., and L.J. Samuelson. 2016a. Intra-annual variation of soil respiration across four heterogeneous longleaf pine forest in the southeastern United States. *Forest Ecology and Management* 359: 370-380.
- Archmiller, A.A., and L.J. Samuelson. 2016b. Partitioning longleaf pine soil respiration into its autotrophic and heterotrophic components through root exclusion. *Forests* 7: 39.
- ArchMiller, A.A., L.J. Samuelson, and Y. Li. 2016. Spatial variability of soil respiration in a 64-year-old longleaf pine forest. *Plant and Soil* 403: 419-435.
- Bond-Lamberty, B., and A. Thomson. 2010. Temperature-associated increases in the global soil respiration record. *Nature* 464: 579-582.
- Bond-Lamberty, B., C. Wang, and S.T. Gower. 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology* 1: 1756-1766.
- Borken, W., K. Savage, E.A. Davidson, and S.E. Trumbore. 2006. Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Global Change Biology* 12: 177-193.
- Brando, P.M., D.C. Nepstad, E.A. Davidson, S.E. Trumbore, D. Ray, and P. Camargo. 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. *Philosophical Transactions of the Royal Society B* 363: 1839-1848.
- Brantley, S.T., Vose, J.M., Wear, D.N. and Band, L., 2018. Planning for an uncertain future: Restoration to mitigate water scarcity and sustain carbon sequestration. In: Kirkman, L. Katherine; Jack, Steven B., eds. *Ecological restoration and management of longleaf pine forests*. Boca Raton, FL: CRC Press: 291-309.
- Brunner, I. C. Herzog, M.A. Dawes, M. Arend, and C. Sperisen. 2015. How tree roots respond to drought. *Frontiers in Plant Science* 6: 547.
- Carmi, A., Z. Plaut, and M. Sinai. 1993. Cotton root growth as affected by changes in soil water distribution and their impact on plant tolerance to drought. *Irrigation Science* 13: 177-182.
- Clinton, B.D., C.A. Maier, C.R. Ford, and R.J. Mitchell. 2011. Transient changes in transpiration, and stem and soil CO<sub>2</sub> efflux in longleaf pine (*Pinus palustris* Mill.) following fire-induced leaf area reduction. *Trees* 25: 997-1007.

- Collins, B. 2005. Thresholds of Disturbance: Land Management Effects on Vegetation and Nitrogen Dynamics; Technical Report. Oak Ridge National Laboratory: Oak Ridge, TN, USA. pp. 1–63.
- Coutts, M.P. 1989. Factors affecting the direction of growth of tree roots. *Annals of Forest Science* 46: 277-287.
- Dilustro, J., B. Collins, L. Duncan, and C. Crawford. 2005. Moisture and soil texture effects on soil CO<sub>2</sub> efflux components in southeastern mixed pine forest. *Forest Ecology and Management* 204: 85-95.
- Dilustro, J.J., B. Collins, L. Duncan, and C. Crawford. 2005. Moisture and soil texture effects on soil CO<sub>2</sub> efflux components in southeastern mixed pine forests. *Forest Ecology and Management* 204: 87-97.
- Draper, N.R and Smith, E. 1981. *Applied Regression Analysis*. 2nd Edition, John Wiley & Sons Inc., New York.
- Eapen, D., M.L. Barroso, G. Ponce, M.E. Campos, and G.I. Cassab. 2005. Hydrotropism: root growth responses to water. *Trends in Plant Science* 10: 44-50.
- Fang, C., and J.B. Moncrieff. 2001. The dependence of soil CO<sub>2</sub> efflux on temperature. *Soil Biology & Biochemistry* 33: 155-165.
- FAO. 2011. *State of the World's Forests 2011*. Technical report, Food and Agriculture Organization of the United Nations.
- Farjat. A.E., F. Isik, B.J. Reich, R.W. Whetten, and S.E. McKeand. 2015. Modeling climate change effects on the height growth of loblolly pine. *Forest Science* 61: 703-715.
- Farrish, K.W. 1991. Spatial and temporal fine root distribution in three Louisiana forest soils. *Soil Science Society of America* 55: 1752-1757.
- Ford, C.R., J. McGee, F. Scandellari, E.A. Hobbie, and R.J. Mitchell. 2012. Long- and short-term precipitation effects on soil CO<sub>2</sub> efflux and total belowground carbon allocation. *Agricultural and Forest Meteorology* 156: 54-64.
- Frost, C. 2006. *History and Future of the Longleaf Pine Ecosystem*. Springer, New York. pp. 3-9.
- Gaul, D. D. Hertel, W. Borke, E. Matzner, and C. Leuschner. 2008. Effects of experimental drought on the fine root system of mature Norway spruce. *Forest Ecology and Management* 256: 1151-1159.
- Goodrick, I., S. Connor, M.I. Bird, and P.N. Nelson. 2016. Emission of CO<sub>2</sub> from tropical riparian forest soil is controlled by soil temperature, soil water content and depth to water table. *Soil Research* 54:311-320.
- Gomez-Casanovas, N., R. Matamala, D.R. Cook, and M.A. Gonzalez-Meler. 2012. Net ecosystem exchange modifies the relationship between the autotrophic and heterotrophic components of soil respiration with abiotic factors in prairie grasslands. *Global Change Biology* 18:2532-2545.

- Griffith, G.E., J.M. Omernik, J.M. Comstock, J.A. Lawrence, S. Martin, G. Goddard, V. J. Hulcher, and T. Foster, 2001. Ecoregions of Alabama and Georgia. Map, U.S. Geological Survey, Reston, Virginia.
- Guevara, A. and C. V. Giordano. 2015. Hydrotropism in lateral but not in pivotal roots of desert plant species under simulated natural conditions. *Plant and Soil* 389:257-272.
- Hanson, P.J., N.T. Edwards, C.T. Garten, and J.A. Andrews. 2000. Separating root and soil microbial contribution to soil respiration: A review of methods and observations. *Biogeochemistry* 48: 115-146.
- Heath, L.S., J.E. Smith, K.E. Skog, D.J. Nowak, and C.W. Woodall. 2011. Managed forest carbon estimates for the US greenhouse gas inventory, 1990-2008. *Journal of Forestry* April/May 167-173.
- Heim, B. C., J.R. Seiler, B.D. Strahm. 2015. Loblolly pine heterotrophic and autotrophic soil respiration as influenced by fertilization and reduced throughfall. Proceedings of the 17<sup>th</sup> Biennial Southern Silvicultural Research Conference. General Technical Report SRS-203. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 2 p.
- Hendricks, J.J., R.L. Hendrick, C.A. Wilson, R.J. Mitchell, S.D. Pecot, and D. Guo. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology* 94: 40-57.
- Heyward, F. 1933. The root system of longleaf pine on the deep sands of western Florida. *Ecology* 14: 136-148.
- Hinko-Najera, N., B. Fest, S.J. Livesley and S.K. Arndt. 2015. Reduced throughfall decreases autotrophic respiration, but not heterotrophic respiration in a dry temperate broadleaved evergreen forest. *Agricultural and forest meteorology*, 200: 66-77.
- Högberg, P. A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekbald, M.N. Högberg, G. Nyberg, M. Ottosson- Lövvenius, and D.J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411: 789-792.
- IPCC (2013) Annex I: Atlas of global and regional climate projections. In: Stocker T, Qin D, Plattner G-K et al (eds) *Climate change 2013: the physical science basis*. Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 1311–1393.
- Johnsen, K.H., J.R. Butnor, J.S. Kush, R.C. Schmidtling, and C.D. Nelson. 2009. Longleaf pine displays less wind damage than loblolly pine. *Southern Journal of Applied Forestry* 33:178-181.
- Jose, S., S. Merritt, and C.L. Ramsey. 2003. Growth, nutrition, photosynthesis, and transpiration responses of longleaf pine seedlings to light, water and nitrogen. *Forest Ecology and Management* 180: 335-344.

- Kanber, R., H. Koksal, A. Yazar, B. Ozekici, and S. Onder. 1999. Effects of different irrigation programs on fruit, trunk growth rates, quality and yield of grapefruit trees. *Turkish Journal of Agriculture and Forestry* 23: 401-411.
- Knorr, W., N. Gobron, M. Scholze, T. Kaminski, R. Schnur, and B. Pinty. 2007. Impact of terrestrial biosphere carbon exchanges on the anomalous CO<sub>2</sub> increase in 2002-2003. *Geophysical Research Letters* 34: 703.
- Kopittke, G.R., A. Tietema, E.E. van Loon, and D. Asscherman. 2014. Fourteen annually repeated droughts suppressed autotrophic soil respiration and resulted in an ecosystem change. *Ecosystems* 17: 242-257.
- Kunkel, K. E., Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., and Dobson, J. G. (2013). Regional climate trends and scenarios for the U.S. National Climate Assessment: Part 2. Climate of the Southeast U.S. NOAA Technical Report 142– 2 Washington D.C., National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service 103.
- Kuster, T.M, M. Arend, M.S. Gunthardt-Goerg, and R. Schulin. 2013. Root growth of different oak provenances in two soils under drought stress and air warming conditions. *Plant and Soil* 369:61-71.
- Lal, R. 2010. Managing soils and ecosystems for mitigating anthropogenic carbon emissions and advancing global food security. *BioScience* 60: 708-721.
- Law, B. E., T. Arkebauer, J. L. Campbell, J. Chen, O. Sun, M. Schwartz, C. van Ingen, and S. Verma, 2008. Terrestrial carbon observations: protocols for vegetation sampling and data submission. Available from <http://www.fao.org/gtos>, Global Terrestrial Observing System, Rome, Italy.
- Li, Y. G. Zhou, W. Huang, J. Liu, and X. Fang. 2016. Potential effects of warming on soil respiration and carbon sequestration in a subtropical forest. *Plant and Soil* 409: 247-257.
- Liu, Y., S. Liu, S. Wan, J. Wang, H. Wang, and K. Liu. 2017. Effects of experimental throughfall reduction and soil warming on fine root biomass and its decomposition in a warm temperate oak forest. *Science of The Total Environment* 574: 1448-1455.
- Lloyd, J. and J.A. Taylor. 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8: 315-323.
- Loudermilk, E.L., J.K. Hiers, S. Pokswinski, J.J. O'Brien, A. Barnett, and R.J. Mitchell. 2016. The path back: oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. *Ecosphere* 7: e011361.
- Lovett, G.M., J.J. Cole, and M.L. Pace. 2006. Is net ecosystem production equal to ecosystem carbon accumulation? *Ecosystems* 9: 152-155.
- Luan, J., S. Liu, X. Zhu, J. Wang, and K. Liu. 2012. Roles of biotic and abiotic variables in determining spatial variation of soil respiration in secondary oak and planted pine forest. *Soil Biology and Biochemistry* 44: 143-150.



- Maggard, A., R. Will, D. Wilson, and C. Meek. 2016. Response of mid-rotation loblolly pine (*Pinus taeda* L.) physiology and productivity to sustained, moderate drought on the western edge of the range. *Forests* 7:203.
- Mainiero, R. and M. Kazda. 2006. Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. *Forest Ecology and Management* 237: 135-142.
- Manzoni, S., J.P. Schimel, and A. Porporato. 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. *Ecology* 93: 930-938.
- McElligott, K.M., J.R. Seiler, and B.D. Strahm. 2016. Partitioning soil respiration across four age classes of loblolly pine (*Pinus taeda* L.) on the Virginia Piedmont. *Forest Ecology and Management* 378: 173-180.
- McElrone, A.J., B. Choat, G.A. Gambetta, and C.R. Broderson. 2013. Water uptake and transport in vascular plants. *Nature Education Knowledge* 4:6.
- Meir, P., Wood, T.E., Galbraith, D.R., Brando, P.M., Da Costa, A.C., Rowland, L. and Ferreira, L.V., 2015. Threshold responses to soil moisture deficit by trees and soil in tropical rain forests: insights from field experiments. *BioScience*, 65: 882-892.
- Mekonnen, Z.A., R.F. Grant, and C. Schwalm. 2017. Carbon sources and sinks of North America as affected by major drought events during the past 30 years. *Agricultural and Forest Meteorology*. 244-245: 42-56.
- Mitchell, R., J.K. Hiers, J.J. O'Brien, S.B. Jack, and R.T. Engstrom. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forest of the southeastern United States. *Canadian Journal of Forest Research* 36: 2724-2736.
- Muhr, J.A.N., W. Borken and E. Matzner. 2009. Effects of soil frost on soil respiration and its radiocarbon signature in a Norway spruce forest soil. *Global Change Biology*, 15: 782-793.
- Nikolova, P.S., S. Raspe, C.P. Andersen, R. Mainiero, H. Blaschke, R. Matyssek, and K.H. Häberle. 2009. Effects of the extreme drought in 2003 on soil respiration in a mixed forest. *European Journal of Forest Research*, 128: 87-98.
- Novick, K.A., Oishi, A.C., Ward, E.J., Siqueira, M., Juang, J.Y. and Stoy, P.C., 2015. On the difference in the net ecosystem exchange of CO<sub>2</sub> between deciduous and evergreen forests in the southeastern United States. *Global Change Biology* 21: 827-842.
- Ohashi, M., T. Kume, N. Yoshifuji, L.k. Kho, M. Nakagawa, and T. Nakashizuka. 2016. The effects of an induced short-term drought period on the spatial variations in soil respirations measured around emergent trees in a typical Bornean tropical forest, Malaysia. *Plant and Soil* 387: 337-349.
- Oswalt, C.M., J.A. Cooper, D.G. Brockway, H.W. Brooks, J.L. Walker, K.F. Connor, S.N. Oswalt, R.C. Conner. 2012. History and current condition of longleaf pine in the Southern United States. U.S. Forest Service General Technical Report SRS-166, pp. 4-8.

- Palmroth, S., C.A. Maier, H.R. McCarthy, A.C. Oishi, H.S. Kim, K.H. Johnsen, G.G. Katul, and R. Oren. 2005. Contrasting responses to drought of forest floor CO<sub>2</sub> efflux in a loblolly pine plantation and a nearby Oak-Hickory forest. *Global Change Biology* 11: 421-434.
- Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P.E. Kauppi, W.A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J.G. Canadell, P. Ciais, R. B. Jackson, S.W. Pacala, A. D. McGuire, S.Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A large and persistent carbon sink in the world's forest. *Science* 333: 988-993.
- Pang, X. W. Bao, B. Zhu, and W. Cheng. 2013. Responses of soil respiration and its temperature sensitivity to thinning in a pine plantation. *Agricultural and Forest Meteorology* 171-172: 57-64.
- Powell, T.L., Gholz, H.L., Clark, K.L., Starr, G., CROPPER, W.P. and Martin, T.A., 2008. Carbon exchange of a mature, naturally regenerated pine forest in north Florida. *Global Change Biology*, 14: 2523-2538.
- Prior, S.A. G.B. Runion, R.J. Mitchell, H.H. Rogers, and J.S. Amthor. 1997. Effects of atmospheric CO<sub>2</sub> on longleaf pine: productivity and allocation as influenced by nitrogen and water. *Tree Physiology* 17:397-405.
- Raich, J.W., and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B: 81-99.
- Runion, G.B., R.J. Mitchell. H.H. Rodgers., S.A. Prior, and T.K. Counts. 1997. Effects of nitrogen and water limitation and elevated atmospheric CO<sub>2</sub> on ectomycorrhizal of longleaf pine. *New Phytologist* 137: (681-689).
- Samuelson, L.J., and W.B. Whitaker. 2012. Relationships between soil CO<sub>2</sub> efflux and forest structure in 50-year-old longleaf pine. *Forest Science* 58: 472-484.
- Samuelson, L.J., T.A. Stokes, and K.H. Johnsen. 2012. Ecophysiological comparison of 50-year-old longleaf pine, slash pine and loblolly pine. *Forest Ecology and Management* 274: 108-115.
- Samuelson, L.J., T.A. Stokes, J.R. Butnor, K.H. Johnsen, C. A. Gonzalez-Benecke, P. Anderson, J. Jackson, L. Ferrari, T.A. Martin, and W.P. Cropper Jr. 2014. Ecosystem carbon stocks in *Pinus palustris* forests. *Canadian Journal of Forest Research* 44: 476-486.
- Schimel, D.S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biology* 1: 77-91.
- Schindlbacher, A., S. Wunderlich, W. Borken, B. Kitzler, S. Zechmeister-Boltenstern, and R. Jandl. 2012. Soil respiration under climate change: prolonged summer drought offsets soil warming effects. *Global Change Biology* 18: 2270-2279.
- Schlesinger, W.H. 1977. Carbon balance in terrestrial detritus. *Annual Review of Ecology and Systematics* 8:51-81.
- Schlesinger, W.H., and J. A. Andrews. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48: 7-20.

- Schlesinger, W.H., M.C. Dietez, R.B. Jackson, R.P. Phillips, C.C. Rhoades, L.E. Rustad, and J.M. Vose. 2016. Forest biogeochemistry in response to drought. *Global Change Biology* 22: 2318-2328.
- Soil Survey Staff, 2016. Web soil survey. Online. <http://websoilsurvey.nrcs.usda.gov>. Accessed August 1, 2016.
- Sowerby, A., Emmett, B.A., Tietema, A. and Beier, C., 2008. Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils. *Global Change Biology* 14: 2388-2404.
- Subke, J.A., and M. Bahn. 2010. On the 'temperature sensitivity' of soil respiration: Can we use the immeasurable to predict the unknown? *Soil Biology and Biochemistry* 42: 1653-1656.
- Subke, J.A., I. Inglema, M.F. Cotrufo. 2006. Trends and methodological impacts in soil CO<sub>2</sub> efflux partitioning: A metaanalytical review. *Global Change Biology* 12:921-943.
- Suseela, V. and J.S. Dukes. 2013. The responses of soil and rhizosphere respiration to simulated climatic changes vary by season. *Ecology* 94: 403-413.
- Suseela, V.A., R.T. Conant, M.D. Wallenstein, J.S. Dukes. 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biology* 18: 336-348.
- Sayer, M.A.S., J.C. Brissette and J.P. Barnett. 2005. Root growth and hydraulic conductivity of southern pine seedlings in response to soil temperature and water availability after planting. *New Forests* 30: 253-272.
- Sword Sayer, M.A., and J.D. Haywood. 2006. Fine root production and carbohydrate concentration of mature longleaf pine (*Pinus palustris* P. Mill.) as affected by season of prescribed fire and drought. *Trees* 20: 165-170.
- Takahashi, H. 1994. Hydrotropism: The current state of our knowledge. *Journal of Plant Research* 110: 163.
- Talmon, T. M. Sternberg, and J.M. Grunzweig. 2011. Impact of rainfall manipulation and biotic control on soil respiration in Mediterranean and desert ecosystems along an aridity gradient. *Global Change Biology* 17: 1108-1118.
- Vicca, S., M. Bahn, M. Estiarte, E.E. van Loon, R. Vargas, G. Alberti, P. Ambus, M.A. Arain, C. Beier, L.P. Bentley, W. Borken, N. Buchmann, S.L. Collins, G. de Gato, J.S. Dukes, C. Escolar, P. Fay, G. Guidolotti, P.J. Hanson, A. Kahmen, G. Kroel-Dulay, T. Ladreiter-Knauss, K.S. Larsen, E. Lellei-Kovacs, E. Lebrija-Trejos, F.T. Maestre, S. Marhan, M. Marshall, P. Meir, T. Miao, J. Muhr, P.A. Niklaus, R. Ogaya, J. Penuelas, C. Poll, L.E. Rustad, K. Savage, A. Schindlbacher, I.K. Schmidt, A.R. Smith, E.D. Sotta, V. Susella, A. Tietema, N. van Gestel, O. van Straaten, S. Wan, U. Weber, I.A. Janssens. 2014. Can current moisture responses predict soil CO<sub>2</sub> efflux under altered precipitation regimes? A synthesis of manipulation experiments. *Biogeosciences* 11: 2991-3013.

- Vincent, G., A.R. Shahriari, E. Lucot, P-M. Badot, and D. Epron. 2006. Spatial and seasonal variation in soil respiration in a temperate deciduous forest with fluctuating water table. *Soil Biology and Biochemistry* 38: 2527-2535.
- Vogel, J.G. and D.W. Valentine. 2005. Small root exclusion collars provide reasonable estimates of root respiration when measured during the growing season of installation. *Canadian Journal of Forest Research* 35: 2112-2117.
- Wang, B. T.S. Zha. X. Jia, B. Wu, Y.Q. Zhang, and S.G. Qin. 2014a. Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem. *Biogeosciences* 11: 259-268.
- Wang, C., Y. Ma, S. Trogisch, Y. Huang, T. Geng, M. Scherer-Lorenzen, J-S. He. 2017. Soil respiration is driven by fine root biomass along a forest chronosequence in subtropical China. *Journal of Plant Ecology* 10: 36-46.
- Wang, X. L. Liu, S. Piao, I.A. Janssens, J. Tang, W. Liu, Y. Chi, J. Wang, and S. Xu. 2014b. Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration. *Global Change Biology* 20: 3229-3237.
- Wang, Y. Y. Hao, X.Y. Cui, H. Zhao, C. Xu, X. Zhou, and Z. Xu. 2014c. Responses of soil respiration and its components to drought stress. *Journal of Soil Sediments* 14: 99-109.
- Whelan, A., G. Starr, C.L. Staudhammer, H.W. Loescher, and R.J. Mitchell. 2015. Effects of drought and prescribed fire on energy exchange in longleaf pine ecosystems. *Ecosphere* 6:128.
- Will, R.E., T. Fox, M. Akers, J.C. Domec, C. Gonzalez-Benecke, E.J. Jokela, M.Kane, M.A. Laviner, G. Lokuta, D. Markewitz, M.A. McGuire, C. Meek, A. Noormets, L. Samuelson, J. Seiler, B. Strahm, R. Teskey, J. Vogel, E. Ward, J. West, D. Wilson, and T.A. Martin. 2015. A range-wide experiment to investigate nutrient and soil moisture interaction in loblolly pine plantations. *Forest* 6: 2014-2028.
- Woodall, C.W., J.W. Coulston, G.M. Domke, B.F. Walters, D.N. Wear, J.E. Smith, H.E. Anderson, B.J. Clough, W.B. Cohen, D.M. Griffith, S.C. Hagan, I.S. Hanou, M.C. Nichols, C.H. Perry, M.B. Russell, J.A. Westfall, B.T. Wilson. 2015. The US Forest Carbon Accounting Framework: Stocks and Stock Change, 1990– 2016. US Forest Service General Technical Report NRS-GTR- 154.
- Wright, J.K., M. Williams, G. Starr, J. McGee, R.J. Mitchell. 2013. Measured and modelled leaf and stand-scale productivity across a soil moisture gradient and a severe drought. *Plant, Cell and Environment* 36: 467-483.
- Zhou, L., X. Zhou, B. Zhang, M. Lu, Y. Luo, L. Liu, and B. Li. 2014. Different response of soil respiration and its components to nitrogen addition among biomes: a meta-analysis. *Global Change Biology* 20: 2332-2343.