Intra-annual variation of soil respiration across four heterogeneous longleaf pine forests in the southeastern United States[☆]

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1 Abstract

2 Soil respiration (R_S) is one of the largest fluxes of net ecosystem exchange and is related
3 to both soil climate and vegetatively driven substrate supply at various spatial and temporal
4 scales. Relationships between the intra-annual variation in R_S and abiotic and biotic variables
5 were examined across diverse longleaf pine (*Pinus palustris* Mill.) forests to better understand
6 factors related to R_S in these low density, spatially heterogeneous forests. Soil respiration, soil
7 temperature, soil moisture, litter mass, size and proximity of nearby trees, understory cover, and
8 root biomass were measured over 13 months in four longleaf pine forests varying in age from 5
9 to 87 years. The exponential relationship between R_S and soil temperature accounted for the
10 majority of the intra-annual variation in R_S with a corresponding temperature sensitivity (Q_{10})
11 of 2.18. Soil moisture affected the R_S -temperature relationship by dampening R_S and Q_{10} during
12 times of extremely dry soil conditions, as defined by soil moisture $\leq 50\%$ of the texture-derived
13 wilting point, but volumetric soil moisture did not directly correlate with R_S . The intra-annual
14 variation in temperature-normalized R_S was negatively related to the distance to nearest tree and
15 positively related to pine root biomass, but not related to litter mass, understory cover, or stand
16 structural variables such as stand age, basal area, or tree density. Annual R_S estimates ranged
17 from 12.0 Mg ha⁻¹ of C in the 5-year-old stand with mostly grass stage seedlings to 13.9 Mg ha⁻¹
18 of C in the dense 21-year-old stand. This study contributes to our understanding of carbon fluxes
19 across diverse longleaf pine ecosystems and indicates the importance of climate in determining the
20 carbon sink potential of southeastern longleaf pine forests.

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21 1. Introduction

22 The efflux of CO₂ from soil, or soil respiration (R_S), is the dominant flux of CO₂ from forests
23 and determines whether forests are carbon sources or sinks (Raich and Nadelhoffer, 1989; Gaumont-
24 Guay et al., 2006). Intra-annual patterns of R_S generally follow soil temperature and the relation-
25 ship between R_S and soil temperature has implications for carbon modeling of forested ecosystems,
26 as it is the most commonly used model to calculate annual R_S (Reichstein and Beer, 2008; Bahn
27 et al., 2010b; Gomez-Casanovas et al., 2013). However, the temperature sensitivity of R_S (Q_{10}) has
28 been shown to vary by forest type and age, latitude, and season (Knorr et al., 2005; Zhou et al.,
29 2009; Mahecha et al., 2010; Subke and Bahn, 2010), and the R_S -temperature relationship may be
30 affected by interactions with other biotic and abiotic factors that directly influence the autotrophic
31 and heterotrophic components of R_S (Chen et al., 2011; Metcalfe et al., 2011). For example, soil
32 moisture may affect R_S in a parabolic manner by limiting root and microbial activity in the soil
33 at low soil moisture levels and restricting CO₂ diffusivity at high soil moisture levels (Orchard and
34 Cook, 1983; Maier et al., 2010); but an effect of soil moisture is often only detected when field
35 studies capture soil moisture levels low enough to be limiting to R_S or when R_S measurements are
36 frequent enough to discern rapid responses of R_S to soil moisture fluctuations (Palmroth et al.,
37 2005; Reichstein and Beer, 2008; Ford et al., 2012). In addition to soil temperature and moisture,
38 R_S may also be affected by the proximity of nearby trees (Clinton et al., 2011), the amount and
39 type of vegetation cover (Ma et al., 2005; Tjoelker et al., 2005; Fleming et al., 2006; Metcalfe et al.,
40 2011), litterfall (Samuelson and Whitaker, 2012; Oishi et al., 2013), and amount and diversity of
41 root functional groups (i.e. mycorrhizae-infected pine roots versus non-pine roots) (Tjoelker et al.,
42 2005; van Hees et al., 2005; Metcalfe et al., 2011). The effect of many biotic variables, such as
43 vegetation cover, litter mass, and root biomass, are coupled with seasonal increases in soil temper-
44 ature; therefore, the temperature-independent influence of these variables on R_S can be difficult
45 to quantify.

46 Soil respiration has been well studied in loblolly pine (*Pinus taeda* L.), the dominant plantation
47 species in the southern United States, on a variety of sites throughout its range and under varying
48 resource availability and forest management regimes (Samuelson et al., 2004; Wiseman and Seiler,
49 2004; Palmroth et al., 2005; Samuelson et al., 2009; Noormets et al., 2010; Oishi et al., 2013;
50 Novick et al., 2014; Tyree et al., 2014; Heim et al., In Press). In contrast, relatively less is
51 known of R_S in longleaf pine (*P. palustris* Mill.) forests. Longleaf pine forests were once common
52 throughout the southeastern United States (Noss, 1988), and are being actively restored throughout
53 their native range (Hendricks et al., 2006; Brockway et al., 2014). In comparison to intensively

54 managed southern pine plantations, longleaf pine forests are typically longer-lived, lower density
 55 stands that support high understory vegetation richness and cover, and are managed with frequent
 56 prescribed burns to reduce hardwood succession, maintain spatial heterogeneity of the canopy, and
 57 promote natural regeneration and native plant diversity (Hedman et al., 2000; Hiers et al., 2003;
 58 Mitchell et al., 2006; Archer et al., 2007; Lavoie et al., 2012). Longleaf pine forests are also unique
 59 in that they have a relatively open coniferous canopy with a diverse grassland-like understory,
 60 and thus may be placed on the nexus between conifer forests, which have relatively lower R_S
 61 than deciduous forests, and grasslands, which have relatively higher R_S than forests (Raich and
 62 Tufekcioglu, 2000). In previous studies of R_S in longleaf pine forests, R_S was shown to be related
 63 to: soil temperature and litterfall in 50-year-old stands varying in basal area (Samuelson and
 64 Whitaker, 2012); irrigation treatments in mature stands on excessively drained xeric soils (Ford
 65 et al., 2012); canopy scorching in a 22-year-old longleaf pine plantation (Clinton et al., 2011);
 66 and soil temperature and soil moisture in juvenile longleaf pine systems grown in control and
 67 elevated CO₂ open-top chambers (Runion et al., 2012). Given the importance of R_S in quantifying
 68 net ecosystem productivity and forest carbon sequestration (Raich and Nadelhoffer, 1989; Lovett
 69 et al., 2006), a better understanding of R_S in longleaf pine forests across a range of site and
 70 stand characteristics would improve efforts to quantify the carbon sink potential in these forests
 71 (Samuelson et al., 2014).

72 The overall goal of this study was to examine R_S in longleaf pine forests in order to: (1) quantify
 73 the intra-annual variation of R_S across a range of stand ages and forest structures; and (2) explore
 74 the relationships between R_S and factors related to forest abiotic and biotic factors. Longleaf pine
 75 stands ranging in age from 5 to 87 years were studied and represented a range in soil textures, stand
 76 structures, and management histories and allowed us to explore variation in R_S not possible with a
 77 single study site. Although not a true chronosequence, measurement of R_S in different aged stands
 78 can contribute to identifying broad controls over ecosystem carbon exchange (Ryan and Law,
 79 2005). We expected that soil temperature would account for the most intra-annual variation in R_S
 80 in an exponential manner, but hypothesized that soil moisture would affect the R_S -temperature
 81 relationship when at biologically limiting levels. Because of varying soil textures between stands,
 82 we predicted that the general effect of volumetric soil moisture on R_S may be confounded by soil
 83 textural differences (Balogh et al., 2011; Moyano et al., 2012). Therefore, to test for the limiting
 84 effect of soil moisture on R_S , the influence of both field-measured volumetric soil moisture and
 85 texture-derived soil water potential on the R_S -temperature relationship were explored. We also
 86 examined the relationships between the monthly variation in temperature-normalized R_S (R_{norm})
 87 and biotic factors. Finer scale biotic variables (e.g. litter mass, understory cover) were expected

to vary seasonally and thus account for more variation in R_S than stand structural variables (e.g. stand age, basal area). Specifically, we expected R_{norm} to linearly increase with proximity to adjacent trees and with increasing litter mass, live root biomass, and understory cover.

2. Materials and Methods

2.1. Study sites and stand descriptions

Study sites were located at Fort Benning Military Base near Columbus, Georgia, USA (32.38° N, 84.88° W). The climate at Fort Benning is subtropical with 30-year-average minimum, mean, and maximum temperatures of 12.8 °C, 18.7 °C, and 24.6 °C, respectively (National Climatic Data Center, 2015a). The 30-year-average monthly temperatures range from highest in July (28.1 °C) to lowest in January (8.4 °C). The 30-year-average annual precipitation is 1180 mm, spread evenly throughout the year. The soils at Fort Benning are characteristic of highly weathered Ultisols of the southeastern United States, with sandy and loamy sand soils in upland areas and sandy loam and sandy clay loams in lowland areas (Garten and Ashwood, 2004). Fort Benning is within the Southeastern Mixed Forest Preserve and is specifically positioned along the transition zone between the Southern Appalachian Piedmont Section in the northern two-thirds of the base and the Middle Section of the Coastal Plains in the southern one-third (Bailey, 1994).

Four longleaf pine stands were selected for this study, ranging in age from 5 to 87 years (Table 1). The 5-, 12-, and 21-year-old stands were plantations and the 87-year-old stand was a naturally-regenerated, even-aged forest. Stands were located 1 to 9 km apart and ranged in size from 2.9 ha to 27.3 ha. The 5- and 12-year-old stands were planted at a density of 1494 trees ha⁻¹ with containerized seedlings and the 21-year-old stand was planted at 2235 trees ha⁻¹ with bare root seedlings. No site preparation details or information on genetic material were available. The soil series dominating each stand were Nankin sandy clay loam, Nankin sandy loam, Troup loamy sand, and Troup loamy sand in the 5-, 12-, 21-, and 87-year-old stands, respectively (Soil Survey Staff, 2014). The 5-year-old stand was located in the Middle Section of the Coastal Plains, which is characterized by rolling to hilly topography with variable textured marine-based sediments (McNab et al., 2005). The other three stands were located within the Southern Appalachian Piedmont Section, characterized by highly weathered and eroded deep clayey soils and a mixture of conifer forest cover types. Frequent, unrecorded burns occurred prior to 1981 because of live fire during military training. Stands were last burned before this study in the winter of 2010 and were on a 1-3 year burn cycle since 2002 (Table 1). No other records besides burn history were available for the 87-year-old stand. More specific information about stand characteristics, including total carbon stocks, can be found in Samuelson et al. (2014).

Table 1: The age, location, soil properties, planting density and burn history of four longleaf pine stands in western Georgia.

Stand Age	5 years	12 years	21 years	87 years
Longitude (°W)	-84° 52.265'	-84° 46.622'	-84° 47.550'	-84° 47.112'
Latitude (°N)	32° 23.999'	32° 22.353'	32° 23.373'	32° 21.967'
Size (ha)	5.6	2.9	27.3	20.5
Soil Texture ^a	73, 7, 20	80, 8, 12	85, 7, 8	80, 9, 11
Soil Water Properties ^b	0.13, 0.21, 0.44	0.09, 0.17, 0.41	0.07, 0.16, 0.38	0.09, 0.17, 0.41
Standing Litter Depth ^c	1.6	1.9	2.7	2.2
Soil Carbon ^d	61.0	76.0	52.9	84.8
Planting Density ^e	1494 (CS)	1494 (CS)	2235 (BR)	Natural
Burn History ^f	2007, 2010	2002, 2005, 2008, 2010	1992, 1995, 1998, 2001, 2004 ^g , 2005, 2006 ^g , 2009, 2010 ^g	1981, 1985 ^g , 1990, 1992, 1994, 1998, 2001, 2004, 2006, 2008, 2010

^a Soil texture (%) from 10-20 cm in sand, silt, clay.

^b Soil water properties (cm^3 water cm^{-3} soil) in wilting point, field capacity, saturation from Oram and Nelson (2014).

^c Mean standing litter depth (cm) includes fine woody debris, understory litter, and canopy litterfall.

^d Soil carbon (Mg ha^{-1}) to 1 m depth from Samuelson et al. (2014).

^e Planting density in trees ha^{-1} ; CS, containerized seedlings; BR, bare root seedlings.

^f Burn records began in 1981.

^g Indicates wildfire.

121 Circular plots one hectare in size were established in each stand. Within each plot, three 25
 122 by 25 m subplots were placed 35 m from plot center to the northeast (45°), south (180°), and
 123 northwest (315°). Plot centroids were 60 m apart and were not considered independent. Only
 124 two subplots (northeast and northwest locations) were created in the 12-year-old stand due to
 125 spacing restrictions from an adjacent study. Stand inventories of each subplot were conducted in
 126 February 2012 and included tree species and diameter at breast height (1.37 m, DBH). Trees were
 127 inventoried if they were taller than 2 m in height with at least 1 cm DBH and classified as saplings
 128 ($\text{DBH} < 10 \text{ cm}$) or mature trees ($\text{DBH} \geq 10 \text{ cm}$). The four stands represented a range in age and
 129 forest structure (Table 2). The youngest stand was a juvenile forest with no mature trees, and a
 130 greater proportion of sapling species other than longleaf pine; the 21-year-old stand had trees of
 131 a similar size as the 12-year-old stand but at a higher density and basal area; and the 87-year-old
 132 stand represented a more mature longleaf pine forest with fewer but larger mature trees and a
 133 large cohort of longleaf pine saplings. Understory longleaf pine seedlings and saplings less than
 134 2 m in height were not recorded in this study, but were cited in a related study at 625, 0, 0,
 135 and 500 trees ha^{-1} in the 5-, 12-, 21- and 87-year-old stands, respectively (Samuelson et al., 2014).
 136 Only one stand inventory was conducted due to limited site access.

137 *2.2. Soil respiration and soil environment*

138 Each 25 by 25 m subplot was evenly divided into 625 1 m^2 sampling plots. Beginning in January
 139 2012, five different sampling plots were randomly chosen from each subplot for measurement of R_S
 140 and related variables (55 randomly chosen 1 m^2 sampling plots per month). Measurements were
 141 conducted monthly from January 2012 through January 2013. Soil respiration, soil temperature,
 142 soil moisture, understory vegetation cover, litter mass, and the distance and DBH of the nearest
 143 tree to R_S collar were measured at each 1 m^2 sampling plot. Soil respiration was measured with
 144 a soil respiration chamber head (LI-6400-09) attached to a portable infrared gas analyzer (LI-
 145 6400, LI-COR Biosciences, Lincoln, NE). Soil respiration collars (PVC, 10 cm diameter, 4.5 cm
 146 height) were installed in each 1 m^2 sampling plot at least 18 hours prior to R_S measurement to
 147 reduce the initial flush of CO_2 that can occur from soil and litter disturbance and root severing.
 148 Collars were inserted in an area free from photosynthetically active vegetation and pushed into
 149 the soil through standing litter with 2.5 cm height remaining above mineral soil. Ambient CO_2
 150 concentration (ppm) was measured at the first 1 m^2 sampling plot within each subplot and used
 151 for the target CO_2 concentration across that subplot. To measure R_S , the chamber was placed on
 152 the collar and CO_2 was scrubbed out of the chamber to a level at least 5 ppm below the target
 153 CO_2 concentration. As soil respiration occurred, chamber CO_2 concentration increased and was

Table 2: Mean stand characteristics of four longleaf pine forests in western Georgia ($n = 2$ to 3).

Stand age (years)	Size class ^a	Species ^b	Basal Area (m ² ha ⁻¹)	Density (trees ha ⁻¹)	DBH (cm)
5	Mature	LLP	0.0	0	-
		other	0.0	0	-
	Sapling	LLP	0.1	123	3.7
		other	0.2	475	1.94
12	Mature	LLP	2.1	176	12.1
		other	2.5	96	16.5
	Sapling	LLP	2.9	768	6.8
		other	0.2	248	1.9
21	Mature	LLP	17.7	1259	13.2
		other	2.2	165	12.9
	Sapling	LLP	2.5	491	7.9
		other	0.6	176	6.7
87	Mature	LLP	9.9	59	46.1
		other	0.8	11	26.0
	Sapling	LLP	0.8	699	3.6
		other	0.0	91	1.2

^a Mature includes trees DBH ≥ 10 cm and saplings include DBH ≥ 1 cm and < 10 cm. Height of all measured trees > 2 m.

^b LLP, longleaf pine.

logged by the LI-COR 6400 console until the CO₂ concentration was at least 5 ppm higher than the target CO₂ concentration. Soil respiration was calculated as the rate of CO₂ efflux at the target CO₂ concentration based on linear regression of the logged data points ($n \geq 33$). Soil temperature was measured concurrently with R_S at a 15 cm depth and within 10 cm of the collars using a soil temperature probe connected to the LI-6400 system. Volumetric soil moisture was measured across 0 to 20 cm depth (Hydrosense II, Campbell Scientific, Inc., Logan, UT) within 10 cm of the collar location at the time of R_S and soil temperature measurement.

2.3. Vegetation and root variables

Subsequent to the installation of the R_S collars, the percent of live vegetation cover (< 1 m in height) was ocularly estimated within the 1 m² sampling plots and included total cover and individual cover classes of woody plants, vines, forbs, legumes, and graminoid species. Because of the overlapping vertical structure of the canopy layers, the cumulative percentage of individual cover classes could exceed total percent cover. The nearest tree (DBH > 1 cm and height > 2 m) to the R_S collar location was identified and its DBH and distance to the collar were recorded. Subsequent to R_S measurement, standing litter down to mineral soil within the R_S collar was collected, dried at 70 °C for 48 hours and weighed. Standing litter mass included fine woody debris, leaf litter from understory species, and litter fall from canopy trees.

Soil samples (10 cm diameter, 15 cm depth) were removed from directly below the R_S collars in February, May, and September 2012 and January 2013 for measurement of root biomass by type (live pine, live non-pine, and dead) and size class. Live root size classes included very fine (≤ 1 mm), fine (> 1 and ≤ 2 mm), coarse (> 2 and ≤ 5 mm) and very coarse (> 5 mm). Dead root size classes included coarse (≤ 5 mm) and very coarse (> 5 mm). Soil was air dried and sifted through a Number 10 sieve. Roots were removed from the soil, sorted, washed, dried at 70 °C for 72 hours, and weighed. Inventories of soil to 30 cm depth indicated that approximately 80 % of fine root biomass was in the top 15 cm (data not shown).

2.4. Data analysis

Each set of monthly measurements were averaged by subplot ($n = 11$ across all stands per month) and then nonlinear regression and linear mixed-effects analyses were performed to investigate the relationship between R_S and abiotic, biotic, and stand structural variables. All data analysis was completed in SAS (version 9.3, SAS Institute Inc., Cary, NC) with significance level of $\alpha = 0.05$. Since there was no true replication of stand ages, differences between stands were not tested.

186 The relationship between R_S and soil temperature was modeled using a first-order exponential
 187 relationship:

$$R_S = \beta_0 * \exp(\beta_1 T_{\text{soil}}) \quad (1)$$

188 where β_0 and β_1 are the fit parameters and T_{soil} is soil temperature (PROC NLIN). The temper-
 189 ature sensitivity of R_S was calculated as $Q_{10} = e^{10\beta_1}$ and basal R_S was estimated as the intercept
 190 (β_0) at $T_{\text{soil}} = 0^\circ\text{C}$. Annual R_S was calculated for each stand with linear interpolation between
 191 measured daily R_S values (Gomez-Casanovas et al., 2013).

192 To examine the effects of soil moisture (θ) on the relationship between soil temperature and
 193 R_S , we analyzed the change in nonlinear trends between R_S and soil temperature during different
 194 water status periods (e.g. soil moisture at field capacity versus at wilting point). The soil water
 195 categories followed Ma et al. (2005) but were modified to relate volumetric soil moisture to soil
 196 texture properties, including wilting point (WP), field capacity (FC), and saturated soil (SS) from
 197 Table 1 and Oram and Nelson (2014). The final soil categories included: extremely dry soils
 198 ($0 \leq \theta \leq 0.5\text{WP}$); dry soils ($0.5\text{WP} < \theta \leq \text{WP}$); moderate soils ($\text{WP} < \theta \leq \text{FC}$); and wet soils
 199 ($\text{FC} < \theta \leq \text{SS}$). Soils were never measured at levels above saturation, so no soils were considered
 200 extremely wet.

201 To compare trends in Eq. (1) between soil moisture levels, a sum of squares reduction test was
 202 completed using the following test statistic:

$$\text{F-statistic} = \frac{(\text{SSE}_{\text{red}} - \text{SSE}_{\text{full}})/(\text{df}_{\text{red}} - \text{df}_{\text{full}})}{\text{SSE}_{\text{full}}/\text{df}_{\text{full}}} \quad (2)$$

203 where SSE_{red} and SSE_{full} are the error sum of squares and df_{red} and df_{full} are the degrees of
 204 freedom of the reduced and full models, respectively. The full (or saturated) model had individual
 205 β_0 and β_1 parameters fit for each soil moisture category:

$$\theta = \begin{cases} \text{Extremely dry} & : R_S = \beta_{0a} * \exp(\beta_{1a} T_{\text{soil}}) \\ \text{Dry} & : R_S = \beta_{0b} * \exp(\beta_{1b} T_{\text{soil}}) \\ \text{Moderate} & : R_S = \beta_{0c} * \exp(\beta_{1c} T_{\text{soil}}) \\ \text{Wet} & : R_S = \beta_{0d} * \exp(\beta_{1d} T_{\text{soil}}) \end{cases} \quad (3)$$

206 The F-statistic was used to compare reduced models (e.g. Eq. 1) with the saturated model and de-
 207 termine whether parameters varied amongst soil moisture categories. This analysis was completed
 208 with the SSReductionTest macro in PROC NLIN (Larkin et al., 2012).

209 The relationships between R_S and stand structural and other biotic variables were explored after
 210 the data was temperature-normalized. To calculate temperature-normalized R_S (R_{norm}) following

211 Maier et al. (2011), observed R_S was divided by the expected R_S value at that soil temperature,
 212 which was modeled with:

$$\theta = \begin{cases} \text{Extremely dry} & : R_S = \beta_{0a} * \exp(\beta_{1a} T_{\text{soil}}) \\ \text{Not extremely dry} & : R_S = \beta_{0a} * \exp(\beta_{1e} T_{\text{soil}}) \end{cases}$$

213 which was the binary model retained from the sum of squares reduction test.

214 The linear relationship between R_{norm} and stand structural and other biotic variables (Ys)
 215 were tested in the form $R_{\text{norm}} = \beta_2 + (\beta_3 Y)$ with random coefficients model analyses using PROC
 216 MIXED (Littell et al., 2006). Stand structural variables, including subplot basal area, mean DBH,
 217 quadratic mean diameter or QMD, tree density, Reineke's stand density index or SDI, and soil
 218 sand and clay percentages, were measured once for each subplot. These variables were modeled
 219 with the population mean regression intercept (β_2) and coefficient (β_3) as fixed effects and each
 220 month's intercept and coefficient (β_{2i} and β_{3i}) as random effects, where i represents each month.
 221 Reineke's stand density index was calculated following VanderSchaaf (2013). This analysis had no
 222 repeated factors.

223 Biotic variables (i.e. litter mass, understory cover, distance to and diameter of nearest tree,
 224 and root biomass) were measured at each 1 m² subplot per stand per month. These variables were
 225 modeled with the population mean regression intercept (β_2) and coefficient (β_3) as fixed effects.
 226 The subplot and the regression coefficients for each subplot (β_{2i} and β_{3i}) were considered random
 227 factors, where i represents each subplot. The 13 monthly measurements were used as repeated
 228 measures for this analysis.

229 In both analyses, covariance structures were chosen by minimizing corrected Akaike informa-
 230 tion criteria (AICC) for each model individually. The random coefficients were modeled with an
 231 unstructured covariance structure including the covariance estimate, a banded covariance structure
 232 with the covariance estimate set to zero, or a variance components structure. The repeated factors
 233 were modeled with either an autoregressive covariance structure or an autoregressive covariance
 234 structure with a moving average.

235 **3. Results**

236 *3.1. Variation in abiotic and biotic variables in longleaf pine stands*

237 Mean monthly air temperature at Columbus, Georgia ranged from 9.9 °C to 28.8 °C over the
 238 measurement period with the highest temperature in July and lowest in January 2012 (Fig. 1A)
 239 (National Climatic Data Center, 2015b). Mean soil temperature exhibited typical seasonal pat-
 240 terns, closely paralleled with air temperature, with an average of 19.1 °C across stands and over

the measurement period (Fig. 1B). Total monthly precipitation ranged from 12.4 mm month⁻¹ to 138.7 mm month⁻¹ (Fig. 1A) (National Climatic Data Center, 2015b). Palmer Drought Severity Index (PDSI) values were above severe drought only during two months, December 2012 and January 2013 (PDSI ranged from -5.23 to 0.26) (National Climatic Data Center, 2014), and monthly precipitation was below the 30-year-average monthly precipitation rates during every month except January, May, September, and December 2012 (data not shown) (National Climatic Data Center, 2015a). Mean monthly volumetric soil moisture varied from a low of 1.30 % in May 2012 to a high of 24.57 % in February 2012 and was generally lower in the 21-year-old stand (Fig. 1C). Within each soil moisture category, mean volumetric soil moisture was generally higher in the 5-year-old stand and lower in the 21-year-old stand relative to the other stands (Table 3).

The mean DBH of the nearest trees to R_S collars was in general smaller in the 5-year-old stand (range of 2.7 cm to 4.3 cm; Fig. 2A). The widest range in DBH and the largest trees were in the 87-year-old stand (range 2.4 cm to 18.7 cm). The mean distance to nearest trees was from 0.8 m to 1.1 m in the dense 21-year-old stand, and from 1.3 m to 3.7 m and 1.6 m to 3.7 m in the 5- and 87-year-old stands, respectively (Fig. 2B). The mean DBH and distance to the nearest tree in the 12-year-old stand ranged from 4.9 cm to 12.2 cm and 1.2 m to 1.9 m, respectively. Mean monthly litter mass was in general higher in the two oldest stands than in the two youngest stands and ranged from 3.0 Mg ha⁻¹ to 15.2 Mg ha⁻¹ across stands (Fig. 2C).

Seasonal variation in total percent vegetation cover was evident in all stands but less pronounced in the denser 21-year-old stand (Fig. 3). In the 21-year-old stand, peak total vegetation cover was generally lower than in the other stands and its understory was dominated by forb cover, such as *Pityopsis graminifolia* (Michx.) Nutt., and woody cover (mainly *Toxicodendron* spp.). Grasses dominated the understory of the other three stands, followed by woody cover in the 12- and 87-year-old stands and woody and forb cover in the 5-year-old stand. Across all stands, annual mean vine and legume percent cover were 8.0 % and 3.8 %, respectively.

Mean root biomass values by type, size class, and sampling month are shown in Figure 4. Total live root biomass was as high as 20.4 Mg ha⁻¹ in the 21-year-old stand, but in the other stands did not exceed 15.2 Mg ha⁻¹. In the 5-year-old stand, non-pine root biomass was greater than pine root biomass during each sampling month, and in the 21-year-old stand, pine root biomass was greater than non-pine root biomass during each sampling month. In the 12-year-old stand, the relative contribution of pine and non-pine roots varied by sampling month, and in the 87-year-old stand, non-pine and pine roots had similar biomass quantities. On average, very fine, fine, coarse, and very coarse roots comprised 61, 16, 16, and 7 % of total non-pine root biomass, respectively, and 40, 17, 15, and 28 % of total pine root biomass, respectively.

Figure 1: (A) Mean air temperature and total precipitation by month at a Columbus, Georgia weather station (National Climatic Data Center, 2015b). (B) Mean soil temperature and (C) soil moisture during soil respiration measurements in four longleaf pine stands varying in age and structure. Triangles represent dates of root biomass sampling and error bars are $\pm$ SE.

Table 3: Mean volumetric soil moisture (%) by soil moisture status in four longleaf pine stands varying in age and structure. Soil moisture status categories included: extremely dry soils ($0 \leq \theta \leq 0.5\text{WP}$); dry soils ($0.5\text{WP} < \theta \leq \text{WP}$); moderate soils ($\text{WP} < \theta \leq \text{FC}$); and wet soils ($\text{FC} < \theta \leq \text{SS}$), where WP is the permanent wilting point, FC is field capacity, and SS is saturated soil (Table 1).

Stand	Extremely dry soils		Dry soils		Moderate soils		Wet soils	
Age	Mean $\pm$ SE	n(%)	Mean $\pm$ SE	n(%)	Mean $\pm$ SE	n(%)	Mean $\pm$ SE	n(%)
5	3.9 $\pm$ 0.5	8(22)	10.9 $\pm$ 0.6	11(31)	16.6 $\pm$ 0.5	11(31)	25.9 $\pm$ 1.3	6(17)
12	2.4 $\pm$ 0.5	6(23)	–	0(0)	13.9 $\pm$ 0.8	7(27)	19.7 $\pm$ 0.6	13(50)
21	2.0 $\pm$ 0.1	12(32)	5.9 $\pm$ 0.2	21(57)	10.2 $\pm$ 0.9	4(11)	–	0(0)
87	3.1 $\pm$ 0.3	10(26)	7.5 $\pm$ 0.5	6(15)	12.9 $\pm$ 0.4	21(54)	19.5 $\pm$ 1.1	2(5)

Figure 2: (A) Mean diameter at breast height (DBH) of the nearest tree to soil respiration (R_S) collars, (B) mean distance to nearest tree from R_S collars, and (C) litter mass by date in four longleaf pine stands varying in age and structure. Triangles represent dates of root biomass sampling and error bars are $\pm$ SE.

Figure 3: Mean total vegetation cover and proportions of individual cover classes to total cover by date in four longleaf pine stands varying in age and structure.

Figure 4: Mean root biomass for each root type by sampling month and size class in four longleaf pine stands varying in age and structure. Sampling months include February 2012 (F), May 2012 (M), September 2012 (S), and January 2013 (J). Size classes were determined by root diameter and include very fine roots (≤ 1 mm), fine (> 1 and ≤ 2 mm), coarse (> 2 and ≤ 5 mm), and very coarse (> 5 mm).

Figure 5: (A) Mean monthly soil respiration (R_S) by date in four longleaf pine stands varying in age and structure. Triangles represent dates of root biomass sampling and error bars are $\pm$ SE. (B) Soil respiration versus soil temperature for two soil moisture (θ) categories. Ext Dry, extremely dry soils ($\theta \leq 0.5$ WP); Not Ext Dry, dry, moderate, or wet soils ($\theta > 0.5$ WP), where WP is wilting point.

3.2. Relationships between R_S and abiotic and biotic variables in longleaf pine stands

With all stands and seasons pooled together, mean monthly R_S ranged from 1.18 to 5.94 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 5A). Soil respiration generally followed the seasonal trend in soil temperature and increased exponentially with increasing soil temperature (Figs. 1B and 5A). Across all the stands and on an annual basis, the temperature sensitivity (Q_{10}) of R_S was 2.18 (AICC = -66.43) and the relationship, as modeled with Eq. (1), was $R_S = 0.680 \cdot \exp(0.079 T_{\text{soil}})$. Annual R_S calculated from linear interpolation across individual measurement periods was 12.0 ± 0.9 , 12.3 ± 0.7 , 13.9 ± 0.7 , and $12.34 \pm 1.0 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in the 5-, 12-, 21-, and 87-year-old stands, respectively.

Categorization of soil moisture measurements based on stand-specific soil water status suggested

Table 4: The probabilities of the linear relationships between temperature-normalized soil respiration (R_{norm}) and the stand structural variables of each subplot ($n = 138$) in four longleaf pine stands varying in age and structure. Unstructured covariance structures were used to model the random coefficients.

Variable ^a	DBH	BA	QMD	Dens. ^b	SDI	Age	Sand	Clay
df	12	12	12	–	12	12	12	12
<i>t</i> -value	2.02	1.96	0.88	–	2.04	-1.09	1.96	-1.82
<i>p</i> -value	0.07	0.07	0.40	–	0.06	0.30	0.07	0.09
AICC	-32.3	-18.8	-8.0	–	-16.0	-4.8	-30.1	-24.8

^a DBH, mean diameter at breast height; BA, subplot basal area; QMD, quadratic mean diameter; Dens., subplot tree density; SDI, Reineke’s stand density index; Age, stand age; Sand, soil sand percentage; Clay, soil clay percentage.

^b Tree density model did not converge regardless of covariance structure.

that soil moisture limited R_S at levels below half the wilting point (extremely dry conditions, Fig. 5B). When the parameters for Eq. (1) were compared between soil moisture categories, Q_{10} was significantly reduced under extremely dry soil conditions ($Q_{10} = 1.90$) compared to all other soil moisture conditions ($Q_{10} = 2.14$), while basal R_S was the same under all soil moisture conditions:

$$\theta = \begin{cases} \text{Extremely dry} & : R_S = 0.767 * \exp(0.064T_{\text{soil}}) \\ \text{Not extremely dry} & : R_S = 0.767 * \exp(0.076T_{\text{soil}}) \end{cases}$$

Based on the sum of squares reduction test (Eq. 2), this model accounted for the same variation as the full model (Eq. 3; $F_{5,130} = 1.57$, $p = 0.17$), and was a better fit for the data compared to Eq. (1) based on minimizing corrected AIC (-97.75).

The linear relationships between R_{norm} and stand structural variables were not significant (Table 4). The linear relationships between R_{norm} and distance to nearest tree, fine pine root biomass, and coarse pine root biomass were significant (Tables 5 and 6). Distance to nearest tree was negatively related with R_{norm} , and fine and coarse pine root biomass were positively related with R_{norm} (Fig. 6). When the distance to the nearest tree was farther than 1.7 m, observed R_S was lower than expected based on observed soil temperature (Fig. 6A). When fine and coarse pine root biomass was higher than 1.2 and 1.1 Mg ha^{-1} , respectively, observed R_S was higher than expected based on soil temperature (Figs. 6B and 6C).

Table 5: The probabilities of the linear relationships between temperature-normalized soil respiration (R_{norm}) and biotic variables measured each month ($n = 138$) in four longleaf pine stands varying in age and structure. The covariance structures for the random coefficients and repeated factors (Rnd. CS and Rpt. CS, respectively) include: UN, unstructured; UN(1), banded; and AR(1), autoregressive covariance structures. Significant p -values at $\alpha = 0.05$ are bolded.

Variable ^a	LM	DBH	TD	TC	WC	FC	LC	VC	GC
df	10	10	10	10	10	10	10	10	10
t -value	1.19	2.15	-5.20	1.01	0.23	-1.28	0.52	0.74	1.43
p -value	0.26	0.06	< 0.01	0.33	0.82	0.23	0.61	0.48	0.18
AICC	-14.5	-17.0	-33.9	-20.7	-16.6	-13.0	-19.0	-15.1	-13.8
Rnd. CS	UN	UN	UN	UN	UN	UN	UN	UN	UN(1)
Rpt. CS	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)

^a LM, litter mass; DBH, diameter at breast height of nearest tree; TD, distance to nearest tree; TC, total cover; WC, woody cover; FC, forb cover; LC, legume cover; VC, vine cover; GC, graminoid cover.

Table 6: The probabilities of the linear relationships between temperature-normalized soil respiration (R_{norm}) and root variables ($n = 39$) in four longleaf pine stands varying in age and structure. The covariance structures for the random coefficients and repeated factors (Rnd. CS and Rpt. CS, respectively) include: UN, unstructured; UN(1), banded; and AR(1), autoregressive covariance structures. Significant p -values at $\alpha = 0.05$ are bolded.

Variable ^a	VFNP	FNP	CNP	VCNP	VFP	FP	CP	VCP	CD	VCD
df	10	10	10	9	10	10	9	9	10	9
t -value	-2.09	-0.97	-1.49	-0.76	-1.07	2.69	2.55	1.81	1.01	-2.08
p -value	0.06	0.36	0.17	0.47	0.31	0.02	0.03	0.10	0.34	0.07
AICC	11.4	11.6	10.6	15.5	13.9	11.2	8.1	3.2	13.1	10.1
Rnd. CS	UN(1)	UN	UN(1)	UN	UN	UN(1)	UN(1)	UN	UN	UN(1)
Rpt. CS	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)	AR(1)

^a VFNP, FNP, CNP, VCNP, very fine, fine, coarse, and very coarse non-pine root biomass; VFP, FP, CP, VCP, very fine, fine, coarse, and very coarse pine root biomass; CD and VCD, coarse and very coarse dead root biomass.

Figure 6: Temperature-normalized soil respiration (R_{norm}) versus (A) distance to nearest tree from R_{S} collar, (B) fine pine root biomass, and (C) coarse pine root biomass. Individual subplot regression lines shown in grey and mean regression line shown in black. TD, tree distance; FP, fine pine root biomass; CP, coarse pine root biomass.

4. Discussion

Over the 13-month study period and across four heterogeneous longleaf pine stands, the Q_{10} of R_S was 2.18. Our results suggest that the apparent temperature response of R_S was significantly lower during periods of drought-like soil conditions than during periods of non-limiting soil moisture. Soil moisture has also been shown to affect the Q_{10} of R_S in laboratory incubations (Reichstein et al., 2005c) and in experimental drought studies in mixed deciduous forests (Borken et al., 2006) and old-field grasslands (Chen et al., 2011). Georgia was under drought stress for most months of this study, and 2012 was cited as the tenth driest year on record for Georgia (National Climatic Data Center, 2012). However, low soil moisture modified the R_S -temperature model only when soil temperature was relatively high, as evidenced by changes to the Q_{10} parameter but not the basal R_S parameter of Eq. (1). This finding agrees with Concilio et al. (2006), who found that soil moisture limited R_S only during periods of high soil temperature and low soil moisture in a fire-dependent old-growth mixed forest of the Sierra Nevada Mountains, and work by Davidson et al. (2006), who concluded that drought can reduce R_S during the growing season in temperate ecosystems when evapotranspiration may exceed precipitation, as it did in our study (i.e. negative 3-month Standardized Precipitation Evapotranspiration Index for May through August 2012; National Climatic Data Center, 2014).

Limitations to estimating the apparent Q_{10} from empirical models based on observational field data are well documented (e.g. Reichstein et al., 2005a,b; Davidson et al., 2006; Reichstein and Beer, 2008; Bahn et al., 2010b). Specifically, estimating Q_{10} based on a first-order exponential function simplifies the phenological effects of substrate supply on R_S (Davidson et al., 2006; DeForest et al., 2006) and ignores the diurnal hysteresis between R_S and soil temperature (Reichstein et al., 2005c). Estimating Q_{10} values based on the first-order exponential function may also result in a wide range of apparent Q_{10} values between ecosystem types due to the correlation between the parameters (Reichstein et al., 2005b). These limitations of Q_{10} reduce the utility of comparing Q_{10} values between studies, however, Eq. (1) has also been shown to be adequate for evaluating the apparent temperature response of R_S over a normal temperature profile (Reichstein and Beer, 2008; Lellei-Kovács et al., 2011), which was the case in 2012 during this study (the range of monthly air temperature was similar to the 30-year-average air temperature range) (National Climatic Data Center, 2015a,b). Although the first-order exponential model is used in this study primarily to highlight the threshold-like interaction between soil moisture and Q_{10} , comparing Q_{10} across studies or ecosystems and drawing conclusions about the physiological response of R_S to temperature from simplified Q_{10} parameters is not recommended (Reichstein et al., 2005c;

333 Reichstein and Beer, 2008).

334 Previous studies have stressed the importance of empirical models that describe the interactive
335 roles of soil temperature and moisture on R_S (Dilustro et al., 2005; Lellei-Kovács et al., 2011;
336 Moyano et al., 2012), and our results indicate the importance of relating volumetric soil moisture to
337 soil-specific, texture-derived soil water potential, particularly when R_S is compared across a range
338 of soil textures. Although the influence of soil moisture on R_S was evident at high soil temperatures
339 when related to the wilting point properties of the various soil textures across these stands, no
340 linear relationship was detected when volumetric soil moisture was regressed directly against R_S .
341 Volumetric soil moisture is easy to measure with portable devices and is more commonly researched
342 in relation to R_S than is texture-derived soil water potential (e.g. Borken et al., 2006; Reichstein
343 and Beer, 2008; Balogh et al., 2011; Ceccon et al., 2011; Lellei-Kovács et al., 2011; Barron-Gafford
344 et al., 2014), but water availability for root, mycorrhizae, and microbial uptake is dependent not
345 only on the volumetric quantity of soil water, but also upon its sorption to soil particles (Saxton
346 and Rawls, 2006). For instance, almost twice the volumetric soil moisture must be present in
347 the relatively clay-rich 5-year-old stand to reach wilting point (13 %) compared to the sandier
348 21-year-old stand (7.0 %; Table 1).

349 In addition to soil temperature and moisture, substrate supply (i.e. quality, quantity and timing
350 of carbon sources allocated to roots and microbes through photosynthesis, root exudation, and
351 litter) is a large contributor to variation observed in R_S , and the effect of substrate supply on R_S
352 is often evaluated through relationships between R_S and biotic variables (Davidson et al., 2006).
353 Our second hypothesis that biotic variables would account for variation in R_S beyond the seasonal
354 influence of soil temperature was supported by the relationships with R_{norm} and distance to nearest
355 tree and pine root biomass. Isolating the direct influence of stand structural variables (e.g. age,
356 basal area) on R_S is challenging in longleaf pine forests because of covarying ecological factors,
357 and our results indicated no significant relationship between temperature-normalized R_S and stand
358 structural variables. However, fine pine root mass was significantly related to pine basal area in
359 these stands in another study (Samuelson et al., 2014). So, although no direct relationship was
360 found between R_{norm} and stand structural variables, the relationships between R_{norm} and pine root
361 biomass and distance to nearest tree may be indirectly related to the influence of stand structure
362 on R_S . Similarly, distance to nearest tree was negatively related to R_S in a 22-year-old longleaf
363 pine forest (Clinton et al., 2011), and R_S was significantly higher closer to the base of loblolly
364 trees in plantations varying in age (Wiseman and Seiler, 2004). Total root volume, although not
365 root biomass, positively related to temperature-normalized R_S in the same study (Wiseman and
366 Seiler, 2004). Root biomass was also related to R_S in a slash pine (*P. elliottii* Engelm.) plantation

367 (Fang et al., 1998) and in 50-year-old longleaf pine stands varying in basal area (Samuelson and
368 Whitaker, 2012).

369 On the other hand, we expected that litter mass and understory cover would positively relate to
370 R_{norm} , but this was not supported. Soil respiration has been shown to be positively related to litter
371 mass and understory ground cover (e.g. Ma et al., 2005; Fleming et al., 2006; Oishi et al., 2013).
372 But, in longleaf pine forests (Samuelson and Whitaker, 2012) and slash pine forests (Fang et al.,
373 1998), the effects of these vegetation variables on R_S were relatively small compared to the influence
374 of soil temperature. Litter mass, understory cover by class, and non-pine roots were not related to
375 R_{norm} in this study, but were all significantly correlated with soil temperature (data not shown).
376 This suggests that the seasonal variation of R_S may be captured with a simple exponential model
377 in these stands. So, despite variability in age, forest structure, soil textures, ground cover, and
378 root biomass observed among stands, relationships between R_S and biotic variables were marginal
379 after first isolating the seasonal influence of soil temperature, which is perhaps a function of tight
380 coupling between the seasonal availability of substrate and soil temperature (Davidson et al., 2006;
381 Bahn et al., 2010a).

382 To our knowledge, no other study has comprehensively quantified R_S in longleaf pine ecosystems
383 across such a range in stand structures. We found that annual R_S varied at most 14 % between
384 stands (5- and 21-year-old stands) and was 12.6 Mg ha⁻¹ year⁻¹ of C on average across stands. Our
385 annual R_S values are within the range of 11.0 to 17.9 Mg ha⁻¹ year⁻¹ of C reported for 50-year-old
386 longleaf pine stands in southern Alabama varying in basal area from 7 to 36 m² ha⁻¹ (Samuelson
387 and Whitaker, 2012), but higher than those estimated for longleaf pine forests across an edaphic
388 gradient (4.6 to 6.8 Mg ha⁻¹ year⁻¹ of C) (Hendricks et al., 2006) and for 85 to 95-year-old longleaf
389 pine savannas under control and irrigation treatments on xeric soils (6.5 to 7.1 Mg ha⁻¹ year⁻¹
390 of C) (Ford et al., 2012). In contrast to our results, Samuelson and Whitaker (2012) found that
391 annual R_S across stands related positively with mean annual litter mass, which varied from 6 to
392 18 Mg ha⁻¹ compared to the smaller range observed in our study (5.6 to 9.5 Mg ha⁻¹). Respiration
393 from the litter layer of the forest floor has been found to be 22 % of R_S in 20-year-old South
394 Carolina longleaf pine stands (Reinke et al., 1981) and up to 26 % of R_S in North Carolina loblolly
395 pine plantations (Taneva and Gonzalez-Meler, 2011). In both Ford et al. (2012) and Hendricks
396 et al. (2006), which were completed at the same research center in southwest Georgia, lower annual
397 R_S was likely due to negligible litter mass because of frequent, 2 year burn intervals.

398 In conclusion, the goal of this study was to explore the intra-annual variation in R_S and
399 related abiotic and biotic variables across four diverse longleaf pine stands. Mean monthly R_S
400 was related most strongly to soil temperature and reduced during periods of drought stress, but

drought stress was only detected when volumetric soil moisture was related to texture-derived water potential. Longleaf pine forests occupy a wide edaphic range (Burns and Honkala, 1990) and thus consideration of soil texture in future longleaf pine R_S studies is warranted. Longleaf pine restoration efforts require plantation establishment to achieve the goal to increase the area of longleaf pine to 5.2 million ha by 2027 (America's Longleaf Restoration Initiative, 2014). Longleaf pine is typically planted at a lower density than other southern pine species, and when coupled with moderate survival forms a mosaic of tree spacing and tree sizes. Accordingly, broad scale stand structural variables such as age and basal area were not related to R_{norm} , but the distance to nearby trees and pine root biomass did relate to R_{norm} when measured concurrently with R_S measurements. The dampening of R_S at high soil temperature by low soil water availability indicates that temperature and precipitation will be important in understanding the contribution of R_S to ecosystem respiration and the carbon sink potential of longleaf pine forests.

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