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

Althea A. ArchMiller *, Lisa J. Samuelson

School of Forestry and Wildlife Sciences, Auburn University, 3301 SFWS Building, Auburn, AL 36849, USA

ABSTRACT

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

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1. Introduction

The efflux of CO$_2$ from soil, or soil respiration (R_S), is the dominant flux of CO$_2$ from forests and determines whether forests are carbon sources or sinks (Raich and Nadelhoffer, 1989; Gaumont-Guay et al., 2006). Intra-annual patterns of R_S generally follow soil temperature and the relationship between R_S and soil temperature has implications for carbon modeling of forested ecosystems, as it is the most commonly used model to calculate annual R_S (Reichstein and Beer, 2008; Bahn et al., 2010b; Gomez-Casanovas et al., 2013). However, the temperature sensitivity of R_S (Q_{10}) has been shown to vary by forest type and age, latitude, and season (Knorr et al., 2005; Zhou et al., 2009; Mahecha et al., 2010; Subke and Bahn, 2010), and the R_S-temperature relationship may be affected by interactions with other biotic

and abiotic factors that directly influence the autotrophic and heterotrophic components of R_S (Chen et al., 2011; Metcalfe et al., 2011). For example, soil moisture may affect R_S in a parabolic manner by limiting root and microbial activity in the soil at low soil moisture levels and restricting CO$_2$ diffusivity at high soil moisture levels (Orchard and Cook, 1983; Maier et al., 2010); but an effect of soil moisture is often only detected when field studies capture soil moisture levels low enough to be limiting to R_S or when R_S measurements are frequent enough to discern rapid responses of R_S to soil moisture fluctuations (Palmroth et al., 2005; Reichstein and Beer, 2008; Ford et al., 2012). In addition to soil temperature and moisture, R_S may also be affected by the proximity of nearby trees (Clinton et al., 2011), the amount and type of vegetation cover (Ma et al., 2005; Tjoelker et al., 2005; Fleming et al., 2006; Metcalfe et al., 2011), litterfall (Samuelson and Whitaker, 2012; Oishi et al., 2013), and amount and diversity of root functional groups (i.e. mycorrhizae-infected pine roots versus non-pine roots) (Tjoelker et al., 2005; van Hees et al., 2005; Metcalfe et al., 2011). The effect of many biotic variables, such as vegetation cover, litter mass, and root biomass, are coupled with seasonal increases in soil temperature; therefore, the

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temperature-independent influence of these variables on R_S can be difficult to quantify.

Soil respiration has been well studied in loblolly pine (*Pinus taeda* L.), the dominant plantation species in the southern United States, on a variety of sites throughout its range and under varying resource availability and forest management regimes (Samuelson et al., 2004; Wiseman and Seiler, 2004; Palmroth et al., 2005; Samuelson et al., 2009; Noormets et al., 2010; Oishi et al., 2013; Novick et al., 2014; Tyree et al., 2014; Heim et al., 2015). In contrast, relatively less is known of R_S in longleaf pine (*Pinus palustris* Mill.) forests. Longleaf pine forests were once common throughout the southeastern United States (Noss, 1988), and are being actively restored throughout their native range (Hendricks et al., 2006; Brockway et al., 2014). In comparison to intensively managed southern pine plantations, longleaf pine forests are typically longer-lived, lower density stands that support high understory vegetation richness and cover, and are managed with frequent prescribed burns to reduce hardwood succession, maintain spatial heterogeneity of the canopy, and promote natural regeneration and native plant diversity (Hedman et al., 2000; Hiers et al., 2003; Mitchell et al., 2006; Archer et al., 2007; Lavoie et al., 2012). Longleaf pine forests are also unique in that they have a relatively open coniferous canopy with a diverse grassland-like understory, and thus may be placed on the nexus between conifer forests, which have relatively lower R_S than deciduous forests, and grasslands, which have relatively higher R_S than forests (Raich and Tufekcioglu, 2000). In previous studies of R_S in longleaf pine forests, R_S was shown to be related to: soil temperature and litterfall in 50-year-old stands varying in basal area (Samuelson and Whitaker, 2012); irrigation treatments in mature stands on excessively drained xeric soils (Ford et al., 2012); canopy scorching in a 22-year-old longleaf pine plantation (Clinton et al., 2011); and soil temperature and soil moisture in juvenile longleaf pine systems grown in control and elevated CO_2 open-top chambers (Runion et al., 2012). Given the importance of R_S in quantifying net ecosystem productivity and forest carbon sequestration (Raich and Nadelhoffer, 1989; Lovett et al., 2006), a better understanding of R_S in longleaf pine forests across a range of site and stand characteristics would improve efforts to quantify the carbon sink potential in these forests (Samuelson et al., 2014).

The overall goal of this study was to examine R_S in longleaf pine forests in order to: (1) quantify the intra-annual variation of R_S across a range of stand ages and forest structures; and (2) explore the relationships between R_S and factors related to forest abiotic and biotic factors. Longleaf pine stands ranging in age from 5 to 87 years were studied and represented a range in soil textures, stand structures, and management histories and allowed us to explore variation in R_S not possible with a single study site. Although not a true chronosequence, measurement of R_S in different aged stands can contribute to identifying broad controls over ecosystem carbon exchange (Ryan and Law, 2005). We expected that soil temperature would account for the most intra-annual variation in R_S in an exponential manner, but hypothesized that soil moisture would affect the R_S-temperature relationship when at biologically limiting levels. Because of varying soil textures between stands, we predicted that the general effect of volumetric soil moisture on R_S may be confounded by soil textural differences (Balogh et al., 2011; Moyano et al., 2012). Therefore, to test for the limiting effect of soil moisture on R_S, the influence of both field-measured volumetric soil moisture and texture-derived soil water potential on the R_S-temperature relationship were explored. We also examined the relationships between the monthly variation in temperature-normalized R_S (R_{norm}) 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 1–9 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).

Circular plots one hectare in size were established in each stand. Within each plot, three 25 by 25 m subplots were placed 35 m from plot center to the northeast (45°), south (180°), and northwest (315°). Plot centroids were 60 m apart and were not considered independent. Only two subplots (northeast and northwest locations) were created in the 12-year-old stand due to spacing restrictions from an adjacent study. Stand inventories of each subplot were conducted in February 2012 and included tree species and diameter at breast height (1.37 m, DBH). Trees were inventoried if they were taller than 2 m in height with at least 1 cm DBH and classified as saplings (DBH < 10 cm) or mature trees (DBH ⩾ 10 cm). The four stands represented a range in age and forest structure (Table 2). The youngest stand was a juvenile forest with no mature trees, and a greater proportion of sapling species