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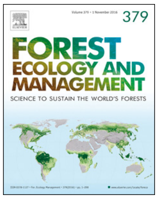

Soil heterotrophic respiration: Measuring and modeling seasonal variation and silvicultural impacts

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ABSTRACT

To determine the effectiveness of forests in sequestering atmospheric carbon (C), we must know the amount of fixed carbon dioxide (CO_2) that is subsequently lost due to heterotrophic microbial activity in the soil. Furthermore, the heterotrophic proportion of total soil respiration (R_s) must be quantified as it changes between different physiographic regions, seasons, and silvicultural treatments. This research quantified heterotrophic contributions to R_s in loblolly pine (*Pinus taeda*) plantations in the Piedmont ($n = 3$) and Upper Coastal Plain ($n = 3$) of the Southeastern USA under control, fertilized, and herbicide treatments over an annual cycle. Heterotrophic respiration (R_h) was separated in the field from autotrophic root respiration (R_a) using metal root-excluding collars. The R_h proportion of R_s was not significantly different between regions or treatments, but demonstrated some seasonal variance. The average R_h proportion across the study was found to be ~73 ± 2% but ranged from ~70% in winter, spring, and summer to 82% in the fall. Statistical models using microbial biomass, temperature, moisture, and other soil characteristics explained 82% and 75% of R_s and R_h variability, respectively. In contrast, the process based DAYCENT model, parameterized for each site to model R_s, R_h, and R_h proportion compared poorly to field measurements. Model predicted mean seasonal R_h proportions also extended beyond the range of those measured (65–88%) from 61 ± 1.3% to 94 ± 0.4%. DAYCENT performed slightly better (i.e., lower root mean square error) for Piedmont than Coastal Plain sites. DAYCENT does not simulate CO_2 fluxes below 20 cm and may be missing substantial fluxes from deeper roots and microbial activity. The results from this study suggest that statistical models such as multiple regression may provide more accurate estimates of R_h proportion for regional extrapolation than the current formulation of the process based DAYCENT model. It is unclear, however, if either approach captures seasonal variation in R_h or how strongly R_h varies with season. Finally, the empirical field data suggest the use of fertilizer and herbicides in these ecosystems increases ecosystem productivity without increasing R_h, which results in an increase in net ecosystem productivity that may lead to greater rates of C sequestration.

1. Introduction

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

Investigations into the factors that affect R_a and R_h have been performed at the regional or ecosystem level, and a few have specifically examined the vast acreage of managed pine plantations of the southeastern United States (Maier and Kress, 2000; Wiseman and Seiler, 2004; Gough et al., 2005; Tyree et al., 2006; Templeton et al., 2015;

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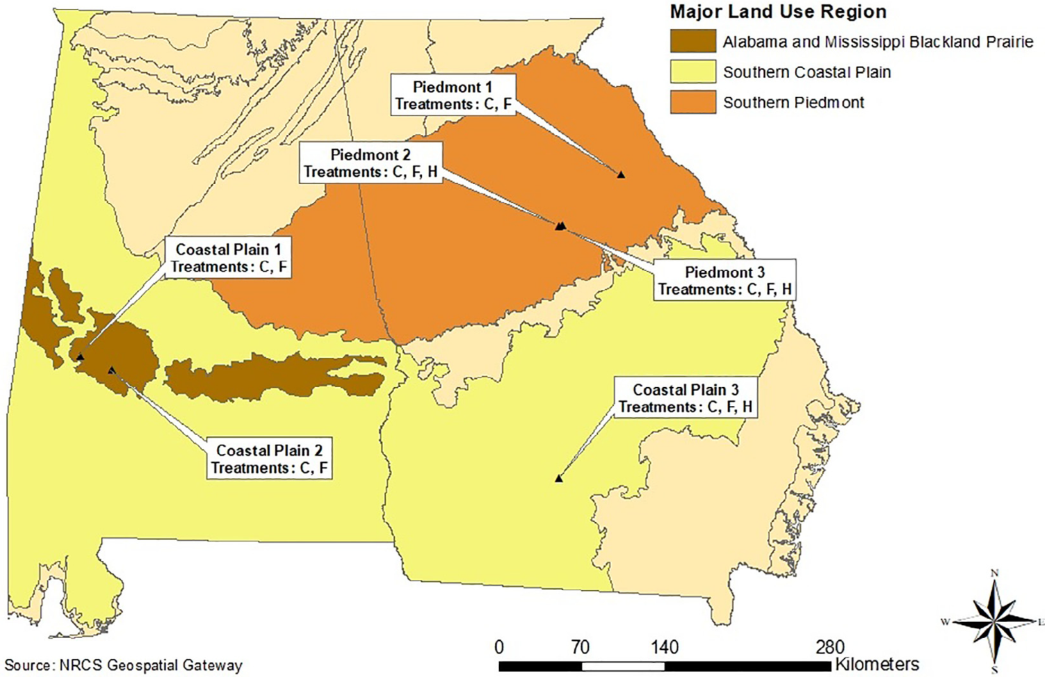

Source: NRCS Geospatial Gateway

Fig. 1. Study site locations and physiographic regions in Georgia and Alabama. Piedmont 2 and 3 are 2.5 kms apart and Coastal Plain 1 and 2 are just outside the map delineation of the Blackland Prairie. Treatments: C = Control, F = Fertilize, H = Herbicide.

McElligot et al., 2016). There are an estimated 13 million hectares of planted pine in the South, which offer many ecological services, including atmospheric C sequestration (Wear and Greis, 2002). Southern forests including managed pine have been shown to be strong C sinks, primarily accumulating C in aboveground biomass and the forest floor, and to a lesser extent mineral soil (Richter et al., 1999). However, pine plantations and forests in general also release a substantial amount of CO_2, most of which is via R_s (Tyree et al., 2006). In order to determine the effectiveness of southern forests and pine plantations, in particular, in sequestering atmospheric C, we must know the amount of fixed CO_2 that is subsequently lost due to heterotrophic microbial activity in the soil. Furthermore, this heterotrophic proportion of total soil respiration must be quantified as it changes between different physiographic regions, seasons, and silvicultural treatments. These proportions are necessary to accurately determine NEP from NPP, thus helping to estimate the amount of C accumulated by the ecosystem. An understanding of what factors have the greatest influence over R_h and NEP in individual ecosystem types is essential to provide "bottom-up" derived data for large-scale extrapolation (Bond-Lamberty et al., 2016).

The most common silvicultural treatments used to enhance growth (i.e., NPP) in southern pine plantations, in addition to enhanced genetics, are fertilizer and herbicide application (Borders and Bailey, 2001; Jokela et al., 2004). Fertilization, besides increasing aboveground NPP, has been shown to decrease soil microbial biomass C (MBC), increase soil C, and either decrease or not affect R_s (Lee and Jose, 2003; Maier et al., 2004; Rifai et al., 2010; Templeton et al., 2015). Understory vegetation control using herbicide also increases stand level NPP but has also been found to suppress R_s, decrease MBC, as well as decrease soil C (Shan et al., 2001; Li et al., 2004; Busse et al., 2006; Rifai et al., 2010). Additionally, decreases in fine root biomass have been associated with both fertilizer and herbicide application in loblolly pine stands (Colbert et al., 1990; Albaugh et al., 1998; Shan et al., 2001). Quantifying how these physical and chemical changes, particularly fine roots and MBC, may affect R_h and the R_h proportion of R_s at the stand level throughout the year is necessary to better calculate NEP.

Quantitative modeling, including statistical and process models, will be necessary to understand and extrapolate R_h and the R_h proportion of R_s regionally and potentially to other forest ecosystems. Further, using field-based empirical data to parameterize or constrain model estimates can greatly decrease model uncertainty for C flows and stocks (Carbone et al., 2016). The DAYCENT biogeochemical model, as well as its predecessor CENTURY, have been used extensively to model trace gas fluxes, nutrient cycling, and land-use effects on agricultural soils, but have limited practice in forested areas (Del Grosso et al., 2005; Fenn et al., 2008; Kim et al., 2009; van Oijen et al., 2011; Gathany and Burke, 2012; Bonan et al., 2013). Few studies have validated DAYCENT R_s estimates using soil efflux measurements taken at the associated research site being simulated (Kelly et al., 2000; Del Grosso et al., 2005; Yeluripati et al., 2009; Chang et al., 2013). Of these studies, two have directly evaluated R_h estimates (Del Grosso et al., 2005; Chang et al., 2013), and one has included a forested site in the evaluation (Del Grosso et al., 2005). A comparison of predicted R_h proportions versus measurements taken seasonally across multiple sites would provide valuable insight into the ability of DAYCENT to estimate this large and complex C flux under varying forest management scenarios and thus its potential for regional extrapolation.

By providing simultaneous estimates of R_s and R_h across multiple sites over an annual cycle, we can refine C budget estimates, and adjust for changes in R_h due to environmental variables and silvicultural treatments. If certain combinations of variables decrease the R_h proportion of R_s, then we can assume an increase in NEP in that area if NPP inputs stay constant. Alternatively, if R_h remains constant under silvicultural treatments that increase NPP (fertilizer and herbicide), we can also assume an increase in NEP. An increase in NEP means more C is being stored in above or belowground components resulting in