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Carbon accumulation in loblolly pine plantations is increased by fertilization across a soil moisture availability gradient

Rosvel Bracho[a,*], Jason G. Vogel[a], Rodney E. Will[b], Asko Noormets[c], Lisa J. Samuelson[d], Eric J. Jokela[a], Carlos A. Gonzalez-Benecke[e], Salvador A. Gezan[a], Daniel Markewitz[f], John R. Seiler[g], Brian D. Strahm[g], Robert O. Teskey[f], Thomas R. Fox[g], Michael B. Kane[f], Marshall A. Laviner[g], Kristin M. McElligot[g], Jinyan Yang[f], Wen Lin[h], Cassandra R. Meek[b], Joshua Cucinella[a], Madison K. Akers[i], Timothy A. Martin[a]

[a] School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611, USA
[b] Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA
[c] Department of Ecosystem Science and Management, Texas A&M University, College Station, TX 77843, USA
[d] School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36840, USA
[e] Department of Forest Engineering, Resources and Management, College of Forestry, Oregon State University, Corvallis, OR, USA
[f] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA
[g] Department of Forest Resources and Environmental Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA
[h] Department of Forestry and Environmental Resources, North Carolina State University, 2820 Faucette Drive, Raleigh, NC 27606, USA
[i] Dougherty & Dougherty Forestry Services, Inc., Wake Forest, NC 27588, USA

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ABSTRACT

Silvicultural practices, particularly fertilization, may counteract or accentuate the effects of climate change on carbon cycling in planted pine ecosystems, but few studies have empirically assessed the potential effects. In the southeastern United States, we established a factorial throughfall reduction (D) × fertilization (F) experiment in 2012 in four loblolly pine (*Pinus taeda* L.) plantations encompassing the climatic range of the species in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA). Net primary productivity (NPP) was estimated from tree inventories for four consecutive years, and net ecosystem productivity (NEP) as NPP minus heterotrophic respiration (R_H). Soil respiration (R_S) was measured biweekly-monthly for at least one year at each site and simultaneous measurements of R_S & R_H were taken five to eight times through the year for at least one year during the experiment. Reducing throughfall by 30% decreased available soil water at the surface and for the 0–90 cm soil profile. Fertilization increased NPP at all sites and D decreased NPP (to a lesser extent) at the GA and OK sites. The F + D treatment did not affect NPP. Mean annual NPP under F ranged from 10.01 ± 0.21 MgC·ha^{-1}·yr^{-1} at VA (mean ± SE) to 17.20 ± 0.50 MgC·ha^{-1}·yr^{-1} at FL, while the lowest levels were under the D treatment, ranging from 8.63 ± 0.21 MgC·ha^{-1}·yr^{-1} at VA to 14.97 ± 0.50 MgC·ha^{-1}·yr^{-1} at FL. R_S and R_H were, in general, decreased by F and D with differential responses among sites, leading to NEP increases under F. Throughfall reduction increased NEP at FL and VA due to a negative effect on R_H and no effect on NPP. Mean annual NEP ranged from 1.63 ± 0.59 MgC·ha^{-1}·yr^{-1} in the control at OK to 8.18 ± 0.82 MgC·ha^{-1}·yr^{-1} under F + D at GA. These results suggest that fertilization will increase NEP under a wide range of climatic conditions including reduced precipitation, but either NPP or R_H could be the primary driver because F can increase stand growth, as well as suppress R_S and R_H. Moreover, D and F never significantly interacted for an annual C flux, potentially simplifying estimates of how fertilization and drought will affect C cycling in these ecosystems.

1. Introduction

Forests of the southeastern United States cover 99 million hectares, almost one third of the forested lands in the contiguous U.S. (Oswalt et al., 2014). About 34% of southeastern forests are pine ecosystems, with 15% originating from natural regeneration and 19% from

* Corresponding author.
E-mail address: rbracho@ufl.edu (R. Bracho).

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plantations (Wear and Greis, 2012). Loblolly pine (*Pinus taeda* L.) is the dominant planted species, and occupies more than 13 million hectares (69% of total planted pine) (Wear and Greis, 2012; Oswalt et al., 2014). Because of their extent and high productivity, southern pine plantations are important economic and ecological resources. For example, this region produces about 60% of the nation's timber (Prestemon and Abt, 2002), and generates more wood than any country (Wear and Greis, 2012). Southeastern forests annually sequestered 176 Tg C from 2000 to 2005, far more than any other forested region in the continental United States, an amount sufficient to offset 42% of the region's anthropogenic CO_2 emissions (Lu et al., 2015).

The implementation of coordinated, intensive silvicultural treatments across the region has substantially increased pine productivity. Southern pine plantations established in the 2000s can produce up to 16 $Mg{\cdot}ha^{-1}{\cdot}yr^{-1}$ of above ground biomass, four times more than forests planted in the 1950s and 1960s (Jokela et al., 2004; Fox et al., 2007), and up to six times more than extensively managed naturally-regenerated pine forests (Cubbage et al., 2007). Much of this increased productivity can be attributed to the alleviation of nutrient deficiency through fertilizer application (Fox et al., 2007; Jokela et al., 2010). The area of southern pine plantation fertilized annually increased from 1×10^5 ha in the mid 1990s to more than 6×10^5 ha in the early 2000s in the region (Albaugh et al., 2012), resulting in not only increased productivity, but also increased sequestered C (Markewitz, 2006; Vogel et al., 2011; Albaugh et al., 2012). For example, mid rotation fertilization increased stem C sequestration by 19.2 Mg CO_{2eq} in a loblolly pine plantation managed on a 25 year rotation (Albaugh et al., 2012).

During this and the next century, climate change may be an important factor affecting C cycling of pine plantations. Air temperatures are expected to increase between 2.5 °C and 4.0 °C across the region by the end of the 21st century (Collins et al., 2013; Walsh et al., 2014). Annual precipitation may slightly increase, but extreme rainfall events and more frequent drought periods during the growing season are expected within the next two decades (Christensen et al., 2007; Li et al., 2011; Dai, 2012). These expected climatic changes most likely will change plant species productivity and range (Noormets et al., 2010; Wear and Greis, 2012; Johnson et al., 2014; Gonzalez-Benecke et al., 2017) and survival (Berdanier and Clark, 2016). The southeastern United States has already experienced multiyear droughts in the last two decades (Crosby et al., 2015), that reduced productivity and C sequestration in planted pines (Bracho et al., 2012).

The positive effects of fertilization on the productivity of planted pines is well documented (Jokela and Martin, 2000; Jokela et al., 2004; Fox et al., 2007; Samuelson et al., 2008; Will et al., 2015), while results for the effect of water availability on productivity are mixed. Irrigation, when combined with fertilization in loblolly pine plantations, has caused relatively small increases in pine productivity above fertilization alone (Albaugh et al., 2004; Samuelson et al., 2008), no increases (Coyle et al., 2008), or relatively large increases (Campoe et al., 2013). Simulations have also indicated that net canopy assimilation is increased by 10% or less across the natural growth range of loblolly pine when the effects of water limitation are removed (Sampson and Allen, 1999). In contrast, natural drought has had a negative effect on loblolly pine stand growth (Ellsworth, 2000; Amateis et al., 2008; Domec et al., 2009). However, the interaction of fertilization and drought on loblolly pine has rarely been tested experimentally. The positive effects of nutrient amendments on pine productivity may be constrained by drought (Tang et al., 2004), or fertilization may enhance growth even under moderate drought (Samuelson et al., 2014; Maggard et al., 2016).

Productivity in loblolly pine is strongly related to leaf area index (LAI) (Sampson and Allen, 1999; Burkes et al., 2003; Jokela et al., 2004; Martin and Jokela, 2004). However, changes in growth in relation to LAI (growth efficiency) do occur and may reflect changes in stand development or response to environmental stress. For example, growth efficiency may be affected by stem density (Burkes et al., 2003) or age (Will et al., 2002), while for environmental factors, diverse results have been found in relation to nutrient and water availability (Sampson and Allen, 1999; Samuelson et al., 2001, 2004; Albaugh et al., 2004). Others have found growth efficiency is maintained at low to intermediate LAI under a range of silvicultural treatments at different sites (Jokela et al., 2004), suggesting the potential of growth efficiency to change in planted loblolly pine in response to fertilization and water availability requires further clarification.

Net ecosystem productivity (NEP) is a measure of the amount of C potentially available for accumulation in an ecosystem during a given time (Lovett et al., 2006), reflecting the difference between NPP and R_H. Fertilization causes an increase in whole ecosystem C accumulation in pine plantations (Shan et al., 2001; Vogel and Jokela, 2011; Vogel et al., 2011), mostly because of increased tree biomass and forest floor pools. Less certain are fertilization effects on soil C (Vogel et al. 2011), which does not directly follow trends in aboveground productivity (Vogel et al., 2015). Autotrophic (R_A) and R_H are the primary C fluxes out of the soil. Both fluxes often decrease as nitrogen limitation is reduced (Ramirez et al., 2010; Kamble et al., 2013; Sun et al., 2014; Zhong et al., 2016), an effect previously observed in loblolly pine plantations (Maier and Kress, 2000; Butnor et al., 2003; Lee and Jose, 2003; Tyree et al., 2006; Zhang et al., 2016). These results could be associated with less belowground carbon allocation with fertilization (Haynes and Gower, 1995; Maier et al., 2004; Janssens and Luyssaert, 2009), resulting in lower fine root biomass (Giardina et al., 2003; Janssens et al., 2010), root exudates, and rhizosphere microbial biomass (Janssens et al., 2010). Increases in soil moisture by irrigation have increased soil respiration and microbial activity in loblolly pine plantations (Samuelson et al., 2009), and total below ground C allocation in a fire maintained longleaf pine (Ford et al., 2012). In contrast, reductions in soil moisture have reduced soil microbial and macroinvertebrates activity (Sardans and Penuelas, 2005; Zhang et al., 2016). We are not aware of any studies in southern pine that have examined the effects of reduced moisture availability and fertilization simultaneously with an explicit separation of plant productivity and soil respiration fluxes.

The objective of this study was to quantify the effects of fertilizer additions, decreased soil moisture due to throughfall reduction, and their interaction on productivity and C accumulation potential of loblolly pine plantations. Replicated experiments were installed in four locations spanning the natural climatic growing range of loblolly pine in the southeastern United States. We expected an increase in NPP from fertilization and a decrease with reduced soil water availability through changes in leaf area index. Consequently, growth efficiency was expected to be unchanged under different treatments but to change among sites because of differences in site characteristics or stand development. Total and heterotrophic soil respiration also were expected to decrease as a result of fertilization and soil water reduction. Testing these predictions allows for an estimate of NEP response to a key silvicultural and climatic variable in the region, while providing insights on the causes of variation in the primary drivers (NPP, Rs, and R_H) of the NEP response.

2. Materials and methods

2.1. Sites description and experimental design

This project was executed within a regional integrated research network, known as PINEMAP (Pine Integrated Network: Education, Mitigation, Adaptation Project, www.pinemap.org), that focused on loblolly pine productivity in relation to changing climate. The effects of reduced soil water and increased nutrient availability on carbon dynamics were examined using a throughfall exclusion (D) x fertilization (F) network of experiments installed at four different sites: McCurtain County (34°01′47″N, 94°49′23″W), Oklahoma; Taylor County (30°12′22″N, 83°52′12″W), Florida; Taliaferro County (33°37′35″N, 82°47′54″W), Georgia; and Buckingham County (37°27′37″N,