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Annual growth in longleaf (*Pinus palustris*) and pond pine (*P. serotina*) in the Sandhills of North Carolina is driven by interactions between fire and climate

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ABSTRACT

Understory fires are important for the maintenance of pine savanna ecosystems of the southeastern U.S., which contain high biodiversity and numerous federally endangered species. Prescribed burns are administered to maintain the open structure of pine savannas, conserve biodiversity, and to reduce wildfire hazard. However, relatively little research has examined which factors control the effects of prescribed burns on mature trees, and how responses might be altered by changing climate. The impact of prescribed burning on growth responses is likely to vary by tree species and by environmental conditions. To test the importance of these factors, tree cores were taken from mature *Pinus palustris* and *Pinus serotina* individuals at multiple locations across Fort Bragg, NC, a military preserve with detailed records on prescribed burn history dating back to 1991. Individual trees were sampled along the hydrologic gradient from xeric uplands to streamside wetlands. Annual growth was modeled as a function of species identity, hydrologic position, fire history, and climate conditions. We determined that prescribed burning produced a moderate decline in annual growth indicating that stress from prescribed burns outweighs benefits from increased water and nutrient availability. We found that the negative effects from prescribed burning were diminished or reversed during warmer years, and that the model predicts potential increases in growth during burn years under anticipated climate change scenarios. Surprisingly, there were no significant differences in growth rate by species or hydrologic position. Together these findings suggest that while prescribed burns may have minor, short-term impacts on tree growth under most current conditions, these effects are small enough that they are unlikely to outweigh the many benefits of this management technique for other aspects of ecosystem structure.

1. Introduction

After decades of fire exclusion, prescribed burns have become an important part of forest management across the United States (McPherson, 1997; Gilliam and Platt, 1999; Mitchell et al., 2006). Frequent prescribed burns help to maintain biodiversity and reduce combustible material in the forest understory (Gilliam and Platt, 1999; Varner et al., 2005; Mitchell et al., 2006; Noss, 2013). In fire-adapted ecosystems, many species have developed traits that allow them to thrive in frequently-burned habitats, and fire can prevent and reset succession by burning competitors (Komarek, 1974) or improve seedling fitness by germinating or releasing seeds only in the nutrient-rich and competition-free post-burn soil (Wahlenberg, 1946; Bramlett, 1990). However, research on the factors that control the net effect of prescribed burning on growth of mature canopy trees is relatively limited. Understanding the impacts of these burns on tree growth and how these effects vary across complex landscapes, and over time, is necessary for understanding the productivity of forests and their ability to provide ecosystem services such as carbon sequestration (Nave et al., 2011) and biodiversity conservation (Mitchell et al., 2006) under changing climatic regimes (Pederson et al., 2008).

Pine trees in the southeastern U.S. are generally fire-tolerant, with adult pines typically experiencing low mortality and low injury from frequent understory fires (Glitzenstein et al., 1995; Keeley and Zedler, 1998). They are not, however, completely unaffected by fire. A previous study showed that differing prescribed burn regimes had unpredictable effects on the short-term growth of *Pinus palustris* Mill. (longleaf pine) (Glitzenstein et al., 1995). In a more recent study, Ford et al. (2010) showed that prescribed burning inhibited mature tree growth during fire years, though

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trees recovered in non-fire years. In addition, trees experiencing different prescribed burn regimes had similar long-term mean growths rates, as longer intervals between fires result in greater negative impact on growth during fire years. Still other studies have found that frequent fires cause significant loss of productivity in pine trees (Boyer, 1987, 2000; Haywood and Grelen, 2000).

Many studies have documented strong correlations between the growth of Southeastern pines and climate variables such as temperature and precipitation (Coile, 1936; Schumacher and Day, 1939; Meldahl et al., 1999; Bhuta et al., 2009; Henderson and Grissino-Mayer, 2009) and have greatly improved our understanding of the constraints that climate places on pine growth. These studies have generally restricted their focus exclusively to the climatic drivers of pine growth, and largely ignored how the relationship between climate and pine growth is altered by the effects of prescribed burning. We hypothesize that the effect of fire on pine growth will be mediated by climate conditions. For example, dry years have been shown to inhibit recovery of Canadian spruce forests following fire (Hogg and Wein, 2005), and years with higher average temperatures should lead to increased stress through a variety of mechanisms (Rennenberg et al., 2006; Henderson and Grissino-Mayer, 2009), which could lead to increased vulnerability to fires and slower recovery following the burns. Conversely, because burning has been shown to increase soil nutrients (Christensen, 1977; McKee, 1982; Wilbur and Christensen, 1983) and reduce pine competition with the herbaceous understory for water and nutrients (Nambiar and Sands, 1993), favorable rainfall and temperature conditions might allow for enhanced tree growth following a prescribed burn.

Another key factor potentially mediating fire impacts on tree growth is the availability of soil water. Two main causes of fire-induced damage and mortality in adult trees are cambium necrosis caused by heat conduction through the bark (Michaletz and Johnson, 2007) and xylem cavitation, which can occur when xylem water potential rapidly drops as heat from fire decreases sap surface tension (Michaletz et al., 2012) or leads to large atmospheric water vapor deficits (Kavanagh et al., 2010). These effects can be mitigated by having thick bark to insulate trees from heat transfer (Brando et al., 2012; Lawes et al., 2013) and also by increased water availability, which can reduce xylem cavitation by increasing soil water potential (Kavanagh et al., 2010) and also prevent xylem cavitation and cambium necrosis by cooling sapwood via convection/advection as unheated water is drawn from the ground (Ryan and Frandsen, 1991; Michaletz et al., 2012). Heat transfer to the soil from fire can also damage the root systems of trees (Varner et al., 2009), but the amount of heat transferred to the soil decreases with soil water content (Michaletz and Johnson, 2007). Water availability can have direct impacts on trees ability to recover from the stress of fire events. For example, *P. palustris* has been shown to have higher growth rates in areas with higher soil moisture (Shoulders and Tiarks, 1980; Foster and Brooks, 2001), potentially allowing for greater regrowth in moister areas following fire damage, although this pattern can be reversed in very saturated soils (Mitchell et al., 1999). Overall, the potential for soil water to mitigate the effects of fire suggests that rainfall and position along the hydrological gradient will affect the response of individual trees to prescribed burning.

Both *P. palustris* and *Pinus serotina* Michx (pond pine) are fire-adapted species that co-occur throughout the pine savanna ecosystem in the Southeastern U.S. Both are shade intolerant, are poor competitors for nutrients, and benefit from fire to remove competitors (Boyer, 1990; Bramlett, 1990). *P. palustris* is found throughout the coastal plains (Boyer, 1990) and requires bare mineral soil, like that found following fire, for seedling establishment (Bruce, 1951). After germination, *P. palustris* exhibits delayed seedling development where it persists in a fire-resistant "grass" stage for many years, during which time drought is the largest cause of seedling mortality (Boyer, 1990). During the grass stage the seedling forms an extensive root system and accumulates carbohydrate stores that it uses for a period of rapid growth (Boyer, 1990; Keeley and Zedler, 1998). Saplings are vulnerable to fire during this rapid growth phase, but become increasingly resistant as they mature, with adult trees possessing several adaptations for surviving the direct effects of low-intensity fire including tufts of long leaves to insulate terminal buds, thick bark to insulate against heat transfer, and self-pruning of lower branches (Boyer, 1990; Keeley and Zedler, 1998).

P. serotina is more restricted in habitat, existing primarily in coastal plains along the eastern coastline in wet or poorly drained areas, where it germinates in peat and organic soils, but also on bare mineral soil following a fire, where its establishment is enhanced by removal of competitors (Bramlett, 1990). Populations of *P. serotina* have several methods of persisting in fire-prone areas, including precocious reproduction, resprouting, and serotinous cones that store up to 10 years of seed production and release them immediately following fire (McCune, 1988; Bramlett, 1990; Keeley and Zedler, 1998). Individuals have moderately thick bark (Keeley and Zedler, 1998), but mature trees have only a modest tolerance of fire (McCune, 1988).

Adaptations of *P. palustris* to resist the direct effects of fire have resulted in its classification as "fire-tolerant" (McCune, 1988) or "fire-resisting" (Fonda, 2001; Fonda and Varner, 2004), while *P. serotina* is classified as "fire-resilient" (McCune, 1988) or as a "fire evader" (Fonda and Varner, 2004) due to its poor tolerance of the direct effects of fire, coupled with its adaptations for re-establishment at a site following a fire. These different strategies for dealing with fire suggest that the potential impacts of prescribed burns on their growth are likely to differ.

Determining the interaction between prescribed burns, hydrology, and climate is important for determining how management regimes developed under current climate conditions might have unanticipated effects as climate change results in increased temperatures and more variable rainfall for this region (Mearns et al., 2003; Christensen et al., 2007) and an increased risk of wildfire (Scholze et al., 2006). While the effects of fire, hydrology, and climate on longleaf pine has been investigated independently, we are unaware of research that investigates their interacting effects on mature trees. The goal of our research was to describe the effect of prescribed burning on the annual growth of two tree species, *P. palustris* and *P. serotina,* at different points along hydrologic gradients across years with variable climate. Specifically, we asked:

(1) Do the effects of prescribed burning on tree growth vary with either climate or position on the hydrologic gradient?
(2) Do the effects of prescribed burning on pine growth vary by species? And
(3) How is pine growth likely to be affected by prescribed burning under conditions predicted by climate change forecasts?

To evaluate these questions we developed a predictive model using tree core, topographic, historical fire and climate data, and then applied the model to explore changes in growth under modified climate scenarios. Our results provide insights on the interactive effects of multiple environmental gradients with prescribed fires commonly used for management of longleaf pine forests in the Sandhills.

2. Methods

2.1. Site description

This study was conducted at the U.S. Army Fort Bragg military installation in the North Carolina Sandhills region near Fayetteville,