Forest Ecology and Management 408 (2018) 54–66

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tortoise or hare: Will resprouting oaks or reseeding pines dominate following severe wildfire?

Caitlyn E. Cooper[a,*], James P. Muir[b], Cristine L.S. Morgan[a], Georgianne W. Moore[c]

[a] Texas A & M University, Department of Soil and Crop Sciences, 2474 TAMU, College Station, TX 77843, USA
[b] Texas A & M AgriLife Research, 1229 N. US Hwy 281, Stephenville, TX 76401, USA
[c] Texas A & M University, Department of Ecosystem Science and Management, 2138 TAMU, College Station, TX 77843, USA

A R T I C L E I N F O

Keywords:
Loblolly pine
Oak
Wildfire
Gas exchange
Pressure-volume curves

A B S T R A C T

Post-fire shifts in species composition and growth are driven in part by alterations in resource availability. However, less is known about the extent to which differences in fire severity will affect leaf-level physiological responses in co-occurring species. Therefore, this study tested loblolly pine (*Pinus taeda* L.) saplings' and resprouting oaks' (*Quercus stellata* Wangenh. (post oak) and *Q. marilandica* Muenchh. (blackjack oak)) responses to various stresses following a catastrophic wildfire in 2011 that occurred in the Lost Pines region in Texas, USA. General plant responses (height, stem number, and plant density) and leaf-level stress indicators [gas exchange (photosynthesis (*A*), transpiration (*E*) and stomatal conductance (g_s), pressure-volume parameters, and leaf biochemistry] were monitored along resource availability gradients (two burn severities and three soil types) in the summer of 2016. Nearly 5 years after the fire, there were 180% more pines in moderate severity transects than high severity transects. However, pines in high severity areas were similar in height to those growing in moderate severity areas. Pines consistently had low *A*, *E*, and g_s rates when compared to co-occurring oaks. Pine osmotic potential at full turgor (Π_{FT}), turgor loss point (Π_{TLP}), and bulk modulus of elasticity (ε) were 33, 30, and 58% greater, respectively, than those of oaks. Loblolly pine leaf-level gas exchange and pressure-volume results suggest this species adopts a *drought-avoidance* strategy for survival. Low gas exchange rates in pine saplings may reflect greater stomatal control, which could reduce cavitation risks, or may have arisen from reduced access to water resources by saplings' shallow roots. Gas exchange and pressure-volume parameters of the oaks reflect greater *drought tolerance* than pine, with post oak being the more tolerant of the two oak species. Leaf-level gas exchange and pressure-volume measurements were coordinated, and results suggest that post oak utilized osmotic adjustment to maintain gas exchange in the more exposed, high severity areas. Additionally, differences in foliar nutrient and phenolic contents between oaks and pines may reflect differences in their leaf-level gas exchange capabilities. Results suggest loblolly pine regeneration may be slower in high burn-severity areas, and that differences in physiological strategies to cope with water stress among the three species may shift stand composition to oak dominance in parts of this region following wildfire.

1. Introduction

Historically, pines have been favored in environments exposed to repeated fires (Rodríguez-Trejo and Fulé, 2003; Bond and Keeley, 2005; Fulé, 2008; Pausas, 2015). Although perceived as destructive and often portrayed as a negative phenomenon, frequent, low-intensity fire favors the survival and growth of young pines and maintains pine dominance in mixed pine/hardwood stands (Pollet and Omi, 2002; Van Lear, 2005; Mitchell et al., 2006). Alternatively, severe crown-fires in forests occupied by a mixture of pines and oaks may result in a shift from pine- to a more oak-dominated forest, oak-shrubland, or grassland (Barton, 2002; Rodrigo et al., 2004; Savage and Mast, 2005; Strom and Fulé, 2007).

Following the Bastrop County Complex Fire in the "Lost Pines" region located in Bastrop, Fayette, and Caldwell counties in central Texas, USA, it appears such a situation could occur. The Lost Pines Ecoregion constitutes the western-most range of loblolly pine (*Pinus taeda* L.) in the USA. This unique 34,400-ha patch of pine-dominated forest was isolated from the East Texas Piney Woods ecoregion by over 160 km during the Pleistocene (Bryant, 1977; Al-Rabab'ah and Williams, 2004). Prior to the Bastrop County Complex Fire, the region was dominated by loblolly pine (~75%), but some areas also had a significant

* Corresponding author at: Texas A & M AgriLife Research, 11708 Hwy 70 S, Vernon, TX 76384, USA.
E-mail address: caitlyn.cooper@ag.tamu.edu (C.E. Cooper).

http://dx.doi.org/10.1016/j.foreco.2017.10.044
Received 20 July 2017; Received in revised form 15 October 2017; Accepted 21 October 2017

contribution from various oak species (~24%) (G Creacy, unpublished data). The fire, which ignited on 4 September 2011, burned more than 12,950 ha and 1.8 million trees (Rissel and Ridenour, 2013). In the years following the fire, post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Quercus marilandica* Muenchh.) resprouts have cropped up and are apparently thriving, indicating that some areas that were previously pine-dominated may be on a trajectory toward becoming oak-dominated woodlands or savannas. Loblolly pine as a species is known to have limited tolerance to fire (Schultz, 1997; Shelton and Cain, 2002; Will et al., 2013; Stewart, 2015), but no studies have specifically addressed fire-tolerance or post-fire recovery of the Lost Pines.

Density and size of resprouting or reseeded individuals can provide an immediate visual appraisal of how species appear to be doing in the post-fire environment, but a closer inspection of leaf-level characteristics such as gas exchange rates or nutrient concentrations may provide us with insights into why certain species are responding externally the way they are. For example, differences in gas exchange rates may reflect disparities in water access throughout the soil profile. Resprouts have deep root systems remaining from mature top killed trees. These pre-existing roots systems not only support rapid growth rates through carbohydrate mobilization (Del Tredici, 2001; Kabeya and Sakai, 2005; Wigley et al., 2009; Zhu et al., 2012) but also likely provide greater access to deeper water sources than the shallow roots of pine seedlings regenerating from seed. This may be reflected in greater gas exchange rates and faster rates of growth in resprouts than non-sprouters (Fleck et al., 1996, 1998; Peña-Rojas et al., 2004; Moya et al., 2015).

Inherent species differences in leaf-level responses may also be reflected in density and growth patterns. Many species with the capacity to resprout, including oaks, are classified as drought tolerant (Abrams, 1990; Cavender-Bares and Bazzaz, 2000; David et al., 2007; McCulloh et al., 2010), while many pines, including loblolly, are often thought of as drought avoiders with large hydraulic safety margins (McDowell et al. 2008; McCulloh et al., 2010; Choat et al., 2012). In previous studies, oaks were less sensitive to vapor pressure deficits and decreases in soil moisture (Kolb and Stone, 2000; Stoy et al., 2006; Ford et al., 2010; Meinzer et al., 2013; Renninger et al., 2015; Moya et al., 2015) and had greater leaf-level gas exchange rates (Kolb and Stone, 2000) than pines. Oaks also often exhibit low osmotic potential at full turgor (Π_{FT}), turgor loss points (Π_{TLP}), relative water content at the turgor loss point (RWC_{TLP}), and high capacitance at full turgor (C_{FT}) as well as bulk elastic modulus (ε) (Abrams, 1990; Saito and Terashima, 2004; Aranda et al., 2004), all of which further signify drought tolerance (Corcuera et al., 2002; Dichio et al., 2003; Bartlett et al., 2012, 2016).

Modifications of the physical environment by disturbance may affect regeneration success as well. Fire may alter plant tissue C:N ratios due to changes in nutrient availability in burned soil (Ojima et al., 1994; Nardoto et al., 2006). Nitrogen volatilizes at relatively low temperatures and is therefore lost in greater amounts than P, K and Ca that volatilize at higher temperatures (> 500 °C) (Caldwell et al., 2002; Certini, 2005); however, the availability of N remaining in the soil may be greatly increased following fire (Grogan et al., 2000; Certini, 2005; Turner et al., 2007) which may contribute to enhanced growth after fire (Grogan et al., 2000; Carter and Foster, 2004). Plant secondary compound contents, such as condensed tannins (biologically active condensed tannins can be measured as protein-precipitable phenolics; PPP), may also reflect stress conditions experienced by regenerating and resprouting plants due to photoxidation, high levels of PAR, and UV radiation following canopy removal (Fleck et al., 1998; Close and McArthur, 2002; Turtola et al., 2005; Abdala-Díaz et al., 2006; Mellway et al., 2009). Climatic stress is reported to increase PPP production and reactivity (e.g. protein binding ability) (Tharayil et al., 2011).

A shift to an oak-dominated stable state could have substantial effects on ecosystem functions (Strom and Fulé, 2007). Although there have been several oak and pine forest studies, very few natural sites have had the opportunity to be immediately studied for the physiological effects of fire on multiple species and their survival strategies at different burn severities. Therefore, the goal of this study was to evaluate how ecological biotic and abiotic legacies might affect loblolly pine recovery following the Bastrop County Complex Fire. As an early indicator of post-fire success, we compared differences in size (heights) and density among loblolly pine, post oak, and blackjack oak individuals along with leaf-level stress response indicators across soil type and burn severity gradients. The stress response indicators evaluated included gas exchange rates, pressure-volume parameters, and leaf biochemistry. We used soil type as a surrogate for soil water and nutrient limitation, as well as burn severity, which correlates strongly with loss of topsoil and associated nutrients (Neary et al., 1999; González-Pérez et al., 2004; Shakesby, 2011).

Hypotheses addressed in this study were: (1) resprouting oaks act as the proverbial "hare" and have greater initial advantages over pine saplings, the "tortoise" in this case, in areas with greater resource limitations (i.e. high severity sites, shallow soils). We expected pines to be smaller, less dense, and display greater stress in leaf-level responses in these areas. (2) Post oak was expected to be a better competitor than blackjack oak in the preliminary stages of regrowth, which may indicate its potential for species dominance over time. As such, we expected post oak individuals to be larger than blackjack oak with greater gas exchange rates. Our specific objectives were to: (1) quantify the number and size of loblolly pine saplings and oak resprouts in various burn severity by soil type combinations. (2) Based on sizes and numbers of individuals, identify areas where natural pine regeneration may be limited and oaks may become dominant. (3) Compare leaf-level gas exchange rates, pressure-volume parameters, and leaf/needle chemical composition among loblolly pine, post oak, and blackjack oak. (4) Use these leaf-level characteristics to help us understand species responses to current growing conditions and future stress events. We envision that our findings will provide insight into loblolly pine and oak responses to severe fires and help guide replanting and vegetation management decisions in the Lost Pines region and other mixed pine/oak forests following fire. Our results should be of interest to forest researchers, stakeholders, and managers in general, not only in the study region.

2. Materials and methods

2.1. Site description

This study was conducted within Bastrop State Park (N30°6′43.992″, W97°15′38.016″) in Bastrop County, Texas, USA. Dominant overstory species in this region include loblolly pine, post oak, blackjack oak, and eastern red cedar (*Juniperus virginiana* L.). Yaupon holly (*Ilex vomitoria* Sol. ex Aiton), American beautyberry (*Callicarpa americana* L.), and farkleberry (*Vaccinium arboreum* Marshall) are common understory species. Soils in the study area consist of fine sand and fine sandy loam surfaces with argillic horizons below (Alfisols) with some exposed areas of gravel or clay on steep, eroded slopes (Soil Survey Staff, 2016). The three soil types focused on in this study included Edge (fine, mixed, active, thermic Udic Paleustalf), Jedd (fine, mixed, semiactive, thermic Ultic Paleustalf), and Padina (loamy, siliceous, active, thermic Grossarenic Paleustalf). The Padina series is characterized by very deep fine sand (165 to over 250 cm), while the Edge and Jedd sandy loams are typically shallower, approximately 150 and 75 cm deep, respectively. Sites in the Padina soil type were selected for further leaf gas exchange and pressure-volume comparisons due to its prevalence throughout the area; Padina comprises approximately one-third of the area of Bastrop State Park. Temperatures in the area typically range from 12.7 to 26.5 °C annually, and the region receives around 820 mm of annual precipitation on average. However, Bastrop received more than this annual total in only 6 months (January through June) in both 2015 (910 mm) and 2016 (865 mm) (Fig. 1) (SRCC, 2017).

Following the Bastrop County Complex Fire, the Texas Parks and Wildlife Department (TPWD) mapped burn severities in Bastrop State