

Project Title: Fire-based management for promoting drought resistance of woody seedlings in a changing climate

Final Report: JFSP Project Number 14-3-01-16

Principal Investigator:

Dr. Jennifer Fraterrigo, Associate Professor, College of Agricultural, Consumer and Environmental Sciences, Department of Natural Resources and Environmental Sciences, University of Illinois, W-423 Turner Hall, 1102 S. Goodwin Ave, Urbana, IL 61801; Email: jmf@illinois.edu

Student Investigator:

Tyler Refsland, Graduate Research Assistant, Program in Ecology, Evolution and Conservation Biology, University of Illinois, Turner Hall, 1102 S. Goodwin Ave, Urbana, IL 61801; Email: refsland2@illinois.edu

This research was supported in part by the Joint Fire Science Program. For more information go to www.firescience.com



FIRESCIENCE.GOV
Research Supporting Sound Decisions

I. Abstract

Shifts in rainfall patterns due to climate change are expected to increase drought-induced stress and mortality in forests, with widespread, negative consequences for forest productivity. Additionally, the extent, frequency and severity of natural and anthropogenic fires are rapidly changing, highlighting the need to understand the interactive effects of fire and drought on forest productivity and recruitment. Given that fire disturbance often reduces tree density and improves the water relations of resprouting trees, fire tolerant tree species may have higher drought resilience in forests stands that experience periodic fires. Our objective was to investigate the consequences of prescribed fire on drought vulnerability of tree seedlings, the life history stage most vulnerable to drought and a bottleneck for overstory recruitment. Using rainout shelters deployed in the forest understory, we imposed summer drought on in situ and planted populations of *Quercus alba* seedlings located in periodically burned (three fires since 2002) and unburned sites in Shawnee National Forest, IL, USA. We monitored leaf gas exchange, leaf water potential (Ψ_{pd}) and relative growth rate (RGR) of seedlings for two years.

Burned sites had approximately twice the light availability ($P = 0.05$) and seedlings showed 33% higher transpiration rates than those in unburned sites ($P = 0.02$). The drought treatment reduced 2014 – 2015 mean soil water content (0 - 45cm depth) by 28% ($\pm 9\%$) relative to controls ($P < 0.001$). Regardless of burn treatment, drought significantly reduced Ψ_{pd} of in situ *Q. alba* seedlings ($P = 0.003$), but only post-fire *Q. alba* resprouts experienced drought-induced declines in max photosynthetic rates (-10%, $P = 0.37$) and stomatal conductance (-18%, $P = 0.16$). We observed similar patterns for ex situ *Q. alba* seedlings, with only those planted in burned sites experiencing drought-induced declines in max photosynthetic rates (-33%, $P = 0.28$) and stomatal conductance (-35%, $P = 0.26$). Burned sites had 10-13% greater drought-induced declines in RGR for both in situ ($P = 0.58$) and ex situ *Q. alba* seedlings ($P = 0.43$). These findings indicate that higher light availability and transpiration rates after fire can predispose shallow-rooted seedlings to increased water stress under drought. Forest management under future scenarios of hydroclimate variability should therefore consider the implications of fire on seedling drought tolerance.

II. Background and Purpose

Shifts in rainfall patterns due to climate change are expected to increase drought-induced stress and mortality in forests, with widespread, negative consequences for forest productivity (Zhao & Running 2010). Adapting management practices to mitigate such changes will require an understanding of drought response in trees, especially woody seedlings, the life history stage often most vulnerable to drought and a bottleneck for overstory recruitment (Kozlowski & Kramer 1991). Management plans must also consider how commonly used tools, such as prescribed fire, may mediate drought effects (Reichstein *et al.* 2013). Prescribed fire is used on over 7.9 million acres of forest per year in the United States (Melvin 2012) and has well-established effects on tree physiology and water relations (Johnson, Shifley & Rogers 2009). No studies to date, however, have examined *in situ* the consequences of these effects for drought resistance in woody seedlings. This study addresses this gap by experimentally inducing drought on white oak (*Quercus alba*) seedlings under active and suppressed fire regimes.

While the consequences of increased drought for forest fire behavior have been recently addressed (Loudermilk *et al.* 2013), there is a critical need to investigate the converse – how fire exposure may mediate the impacts of increased drought on forests. By understanding this direction of causality, especially in terms of the impact of fire on woody seedling survivorship

across large spatial extents (Clark *et al.* 1999), we will be able to better constrain vital rate estimates for matrix population models and thus improve predictions of recruitment limitation. This work lends important insight on how fire-based management may mitigate climate change effects on future forest stand structure and productivity.

Fire exposure directly impacts tree physiology by killing shoot tissue and thus increasing root to shoot ratios (Johnson *et al.* 2009). This positively affects tree water relations by reducing losses to transpiration (Reich *et al.* 1990). Additionally, fire may indirectly impact tree physiology through its legacy effects on the environment. The consumption of standing vegetation and leaf litter by fire increases light availability, soil surface temperatures, evaporation and run-off, promoting a more xeric microclimate at the soil surface (DeBano, Neary & Ffolliott 1998). For establishing seedlings still dependent on surface moisture, this xerification may negatively impact tree water relations and result in greater drought vulnerability. These direct and indirect effects of fire on tree physiology may have substantial consequences for the drought performance and survivorship of seedlings (Abrams 1996). In order to assess the impact of fire on the drought vulnerability of woody seedlings, I propose to test two hypotheses:

H1) If resprouts have improved water relations relative to unburned seedlings, then burned *in situ* *Quercus alba* seedlings will have higher fitness and survivorship under drought than unburned seedlings

H2) If fire promotes a more moisture-limited microclimate that exacerbates drought stress, then *ex situ* seedlings planted in burned stands will have lower fitness under drought than those planted unburned stands

Our main objective is to investigate the effect of fire management on the survival of seedlings experiencing drought in order to improve predictions of recruitment limitation under climate change. To accomplish our objective, we 1) conducted a field experiment imposing a realistic drought on seedling populations located in fire-managed and suppressed areas across multiple stands, and 2) quantified drought vulnerability through the physiological and growth response of seedlings.

III. Study Description and Location

Location:

This study was conducted in the eastern portion of the Lesser Shawnee Hills Ecoregion of the Shawnee National Forest (SNF), located in southern Illinois, USA (37°44' N, 88°67' W). The Shawnee region is characterized by a humid subtropical climate with a mean annual temperature of 15 °C and mean annual precipitation of 1250 mm distributed evenly throughout the year. The average length of the growing season is 185 days (ISWS).

The region is a western extension of the unglaciated Interior Low Plateau with a bedrock of Pennsylvanian and Mississippian sandstone and some interbedded limestone. The bedrock is topped with a shallow to deep layer of loess on south and north-facing slopes, respectively. Soils are moderately well-drained silt loams classified as Oxyaquic fraguidalfs or Ultic hapludalfs. The differences in soil depth and moisture availability with landscape position and elevation drive tree species distribution in the Shawnee region (Fralish 1988).

Historically, low elevation and north-facing sites were dominated by closed forests while higher elevation, south-facing sites were dominated by open forests and savanna (Jones and Anderson 2011). Natural vegetation in this region is broadly classified as oak-hickory forest with the two most dominant species being white oak (*Quercus alba*) and black oak (*Q. velutina*). Mesic, north-facing slopes contain *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Quercus alba*, *Q. rubra* and *Carya cordiformis* as dominant canopy species, whereas xeric, south-facing slopes are dominated by *Q. alba*, *Q. marilandica*, *Q. rubra*, *Q. stellata*, *Carya glabra*, *C. laciniosa*, *C. ovata* and *Juniperus virginiana*. High abundance of oak and hickory species and relatively low tree densities and basal areas throughout the Shawnee Hills, especially in upland sites, suggest that periodic fires were commonplace in this region (Jones and Anderson 2011).

SNF was chosen for this project because of the observed susceptibility of the greater Ozark region to drought, the increasing use of fire management in the region, and the high abundance of oak species⁴ Recent drought stress has led to large oak defoliation and mortality events in the Ozarks, substantially impacting carbon stocks.¹³ Additionally, central North America was found to be one of the most vulnerable regions to climate extremes such as drought, with observed gross primary productivity varying dramatically over the past three decades.¹⁴ Furthermore, the shallow soils on south-facing slopes in SNF provide a natural means to restrict deep-rooting species (e.g. *Quercus*) from reaching the water table and therefore assists in imposing experimental drought conditions. We chose to study *Q. alba* because its response to drought and fire is representative of many tree species native to the region⁵ and it is one of the most abundant and economically important tree species in North America, underscoring its importance in extrapolating the results of this study across large spatial extents. We targeted seedlings specifically because juveniles are among the most drought-vulnerable life stage and often a demographic bottleneck for *Quercus*.¹⁷

We selected two mature, upland forest sites within SNF that contained both burned and unburned stands and were at least 12 km apart. Burned stands were approximately 167 and 263 ha each and experienced three to four prescribed fires between 2002 – 2013, with the most recent being a spring 2013 burn. Unburned stands had no visual evidence of recent burns nor any record of fire activity in the past three decades, according to United States Forest Service records dating back to 1980 (Scott Crist, pers. comm.). Both sites had similar elevations (170 – 200 m), slopes (10 - 25%), and mature (70-100 yr) hardwood canopies consisting primarily of *Quercus* and *Carya* species.

Study Description:

Experimental design

Within each site, we established nine paired plots on south-facing slopes in burned and nearby (< 1 km) unburned stands. We chose plots locations that had at least three in situ *Quercus alba* seedlings (< 1.4 m tall) but few nearby *Q. alba* adults in order to minimize the presence of adult stump sprouts. Plots within each pair were 16 m² and < 4 m apart so as to minimize environmental differences. Each was randomly assigned to an ambient or drought treatment. Drought plots (n = 18) were covered with a 16 m² rainout shelter, constructed of clear 4mil greenhouse fabric and suspended 2 m above the ground (Fig. 1). Rainout shelters were in place during the growing season (May – October 2014 and March – October 2015) and taken down for the winter to allow for unobstructed litterfall. Because rainout shelters excluded approximately

100% of growing season rainfall (approx. 675mm from April - August), we decided not to trench around each plot in order to allow some moisture to permeate into drought plots. To account for the artifact of a 5-10% reduction in light caused by the rain shelters, we placed shade cloth made of deer netting over ambient plots, as employed by previous researchers.¹⁹

In 2014, we identified and tagged all *in situ* *Quercus alba* individuals. Only those within the center 4m² of each plot were monitored to account for edge effects. Additionally, in late March 2015, we planted twelve *Q. alba* seedlings in each plot (n = 432), hereafter referred to as *ex situ* seedlings. *Ex situ* seedlings were one year old, bareroot stock sourced from Hensler Nursery, Hamlet, IN. *Ex situ* seedlings were equally spaced in the center 4 m² subplot, tagged and left for two weeks to establish. In April 2015, we randomly assigned half of the *ex situ* seedlings in each plot to a coppicing or control treatment. Prior to leaf out, those seedlings assigned to coppicing were cut approximately 2 cm above the ground to simulate top-kill and subsequent resprouting, as occurs with fire disturbance.

Seedling relative growth rate and drought vulnerability

To investigate the effect of prescribed fire on *Q. alba* water relations and drought vulnerability (**H1**), we compared the survival, relative growth rates (RGR), maximum photosynthetic rate (A_{\max}), leaf stomatal conductance (g_{\max}) and predawn leaf water potential (Ψ_{pd}) of *in situ* seedlings in ambient versus drought treatments across burned and unburned stands. Ψ_{pd} is an indicator of leaf water status, where the more negative the value, the more dehydrated the leaf. We used an infrared gas analyzer (LI-COR 6400) to quantify leaf gas exchange rates and a pressure chamber (PMS 1000) to measure leaf water potential. A_{\max} and g_{\max} were the observed rates of gas exchange when the chamber conditions were set to 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, 400 ppm [CO₂] and ambient temperature. We measured leaf gas exchange between 9:00-11:30am and 1:00 – 4:00PM to minimize daily fluctuations due to dawn and dusk. We measured Ψ_{pd} approximately 1-2 hr prior to dawn on freshly clipped stems containing several mature, undamaged leaves. Physiological measurements of *in situ* seedlings were taken in July and August of 2014 – 2015. We quantified growth rates by recording seedling height, basal diameter, and number of leaves per individual in May and August 2014, and May and August 2015. We estimated aboveground oak biomass (AGB) over the course of the study using an allometric relationship that we derived from field measurements and aboveground dry mass of nearby, harvested *Q. alba* seedlings [AGB (in grams) = $-0.837 + (0.112 \times \text{height in mm}) + (0.281 \times \text{leaves})$], $r^2 = 0.835$, $P < 2.2\text{e-}16$, $n = 100$]. Relative growth rate was quantified as $(\ln(\text{AGB}_{\text{May, 2015}}) - \ln(\text{AGB}_{\text{May, 2014}})) / \text{time interval}$.

To investigate how fire-driven changes to the environment affect seedling drought vulnerability (**H2**), we compared the survival, RGR, A_{\max} , g_{\max} and Ψ_{pd} of uncoppiced *ex situ* seedlings planted in burned and unburned stands and subjected to ambient versus drought treatments. We used identical methods as described above, except measurements were taken only in 2015.

Environmental covariates

In order to assess the effectiveness of the drought treatment, we quantified soil moisture conditions across treatments throughout 2014-2015. We determined gravimetric soil moisture (105°C, $\text{g H}_2\text{O g soil}^{-1}$) in all plots from soil samples collected at depths of 0-45 cm in June and August. We also logged continuous soil moisture content (15 and 30 cm depths) and air temperature (May – October) at a subset of plots using Onset HOB0 Micro Station Data

Loggers. We installed the temperature probes on wooden tent stakes 20 cm above the ground surface and covered with white plastic cups, which allowed us to accurately measure temperature while reflecting direct sunlight.

We quantified inorganic nitrogen and phosphorus availability in each plot using ion-exchange resin membranes. A pair of activated anion and cation membranes (6.0 x 2.5 cm) were installed at 0-6-cm depth in each subplot and left *in situ* for 30 days (July – August 2014, 2015). After removal, membranes were cleaned with DDI water and refrigerated until extraction in 2 mol/L KCl. KCl extracts of ion-exchange membranes were filtered through 0.7- μm Whatman filter paper and frozen (-20°C) until analysis. Extracts were analyzed for NH_4^+ -N using the phenolate method, NO_3^- plus NO_2^- -N (hereafter referred to as NO_3^-) using a cadmium column reduction, and PO_4^{3-} using the ammonium molybdate method, all on a Lachat QuickChem 8500 (Hach Company, Loveland, Colorado, USA). Following correction for laboratory and field blanks, nutrient availability is presented as $\mu\text{g N or P cm}^{-2} \text{ month}^{-1}$.

We estimated light availability in each plot using a LI-COR 191 Line Quantum Light Sensor. On cloudless days, we quantified photosynthetically active radiation (PAR) in canopy gaps and took twelve replicate measurements at ground-level that spanned the area of each plot. Light availability was quantified as the plot-level PAR reading divided by the PAR reading of the canopy gap (%). Due to time-dependent nature of sunflecks in the forest understory, we measured PAR in the morning and afternoon and averaged the readings.

Finally, in order to account for differences in competitor density across plots, we quantified the percent cover of understory vascular plant species by functional group in each plot: trees, shrubs, graminoids and forbs.

Data analysis

We analyzed the effect of prescribed fire on the drought vulnerability of *in situ* and *ex situ* seedlings using analysis of variance (ANOVA). Fire, drought and their interaction were treated as categorical predictor variables while the responses of leaf gas exchange rates, leaf water potential and RGR were all treated as continuous responses. Because of the large degree of variation in size of *in situ* seedlings, we divided the population by the median initial height (32 cm) to assess the effects of fire and drought on small (< 32 cm) and large (≥ 32 cm) seedlings separately. Finally, we also analyzed the effect of fire and drought on the environmental factors of soil moisture, light and N-availability and understory plant cover. Data were averaged across individuals in each plot and across years in the case of *in situ* seedlings (2014, 2015) to account for lack of independence within plots and across multiple years. All statistical analyses were conducted with R version 3.2.3 (R Core Team 2016).

IV. Key Findings

Effects of Fire and Drought on Environmental Conditions

The drought treatment had significant effects on soil moisture and nitrogen availability, as well as understory plant cover. Rainout shelters reduced mean gravimetric soil moisture (0 – 45 cm) by 28% through 2014 – 2015 ($P < 0.001$) (Fig. 2). The effectiveness of the shelters varied significantly with year (*drought x year* $P < 0.001$) and soil depth (*drought x depth*: $P = 0.007$). The drought-induced reduction in soil moisture was 2.8 times greater in 2015 than 2014 (10% reduction in 2014, 29% reduction in 2015). Drought treatment resulted in a 12 - 36% reduction in

mean soil moisture at deep (30 – 45cm) and shallow (10 – 15cm) depths, respectively. Drought severity did not vary with fire (*drought x fire* $P = 0.14$).

Light availability under the rainout shelters did not differ significantly from control plots ($P = 0.61$). Burned plots had two-fold greater light availability than unburned plots (burned $l_{\text{mean}} = 13.7\%$, unburned $l_{\text{mean}} = 6.8\%$, $P = 0.059$).

Drought treatment significantly reduced nitrate (NO_3) availability ($P = 0.01$), resulting in a mean reduction of 64% when averaging across burn treatment. Ammonium (NH_4) availability was not strongly influenced by drought treatment. Instead, NH_4 availability was influenced by time, increasing over three-fold from June to August ($P < 0.001$). We did not observe any difference in inorganic N availability with burn treatment ($P = 0.56$).

Burned plots had 24.4% greater total understory cover on average than unburned plots ($P < 0.0001$), made up primarily of *Quercus* and *Carya* tree species, graminoids and forbs. Drought decreased total cover 4.9% and 10.1% in burned and unburned plots, respectively ($P = 0.31$, $P = 0.07$). In general, drought reduced understory cover by decreasing the prevalence of shrub and vine species (e.g. *Symphoricarpos orbiculatus*, *Lonicera japonica*, *Parthenocissus quinquefolia*)

Drought vulnerability of burned v. unburned seedlings

Drought significantly reduced leaf water potential of *in situ* seedlings ($P = 0.004$) and as predicted, burned *in situ* seedlings experienced less severe drought-induced declines in Ψ_{pd} than unburned seedlings (*fire x drought*: $P = 0.22$) (Fig. 3). Counter to predictions, however, burned seedlings had greater drought-induced declines in photosynthesis rates (A_{max}) and stomatal conductance (g_{max}) than unburned individuals (*fire x drought*: $P = 0.37$). As a result, burned seedlings experienced greater drought-induced declines in RGR than unburned individuals (*fire x drought*: $P = 0.43$) (Fig. 3). Mortality was low among all treatments, with drought-induced mortality of 1% and 3% for unburned and burned stands, respectively.

The effects of fire on drought vulnerability were highly dependent on seedling size. Although drought-induced declines in growth rate were greater for burned than unburned seedlings when averaging across size classes (Fig. 3), this pattern is not consistent across small and large size classes. For small seedlings (initial height < 32 cm), drought caused a greater reduction in RGR for unburned rather than burned seedlings, whereas for large seedlings (initial height ≥ 32 cm) the trend was opposite, with drought-induced declines in the growth rate of burned seedlings but a drought-induced *increase* in growth rates of unburned seedlings (*drought x initial height class*: $P < 0.01$; *fire x drought*: $P = 0.09$) (Fig. 4).

Environmental-mediated effects of fire on seedling drought vulnerability

As predicted, *ex situ* seedlings planted in burned plots experienced greater drought-induced declines in Ψ_{pd} (*fire x drought*: $P = 0.51$), A_{max} and g_{max} (*fire x drought* $P > 0.20$), and RGR (*fire x drought*: $P = 0.69$) than those individuals planted in unburned plots (Fig. 5). Drought reduced A_{max} of seedlings in burned stands by 33.1% while increasing rates 2.3% for those planted in unburned stands. Drought reduced g_{max} of burned seedlings by 35.1% while increasing it 9.8% for unburned seedlings. Drought reduced the RGR of seedling in burned plots by 32.2% while reducing growth rates 27.3% for unburned seedlings.

V. Management Implications

Importance of seedling size

We found the effects of fire on tree drought vulnerability to be highly dependent on seedling size. Because of their shallower root systems, small seedlings are expected to be more sensitive to drought than larger, more established seedlings. No studies we are aware of, however, have shown that repeated prescribed fire can increase the drought vulnerability of small seedlings relative to unburned stands. By promoting a more open canopy, fire increases sunlight penetration, soil temperature and evapotranspiration rates. Although greater light availability generally improves recruitment of shade-intolerant *Quercus spp*, it can also promote a drier microclimate and intensify drought-induced stress. Results from *in situ* and *ex situ* experiments provide support for the later, that by creating a drier microclimate, prescribed fire may negatively impact the fitness of smaller seedlings under drought.

In contrast, we found the larger, *in situ* seedlings to be larger resilient to the drought treatment and, in the case of many unburned individuals, drought even increased their growth rate relative to those under ambient conditions. Like most oak species, *Q. alba* develop deep tap roots as they mature, allowing individuals to access groundwater rather than depend on inconsistent sources on the surface. Our experimental drought was likely not severe enough to stress these deeply-rooted individuals. That being said, it is remarkable that many large seedlings in unburned stands performed better under drought than ambient treatment. As we observed primarily in unburned stands, drought reduced competition between *Q. alba* seedlings and neighboring species, especially shrub cover, and in turn likely increasing light or nitrogen availability for the seedlings and promoting faster growth.

Compared to microclimate effects, we found less evidence that changes in root:shoot ratio with fire improves the drought fitness of *Q. alba* seedlings. We found drought-induced declines in Ψ_{pd} (Fig. 3) and the RGR of small seedlings was less severe for burned than unburned seedlings (Fig. 4). Given the microclimate of burned stands negatively affected *ex situ* seedlings fitness, our observation that small, burned *in situ* seedlings performed better than unburned seedlings suggests changes in root:shoot with fire may provide increased drought resistance despite drier conditions in burned stands.

Importance of fire frequency

Although beyond the scope of our study, it is important to consider how different fire frequencies affect the age structure of oak forests and the consequences this may have for drought performance. Our stands were periodically burned since 2002, experiencing approximately one prescribed fire every 4 years. In our sites, this periodic burn schedule promotes high densities of *Q. alba* seedlings, especially on south-facing slopes, but it also slows or prevents the transition of many seedlings into the sapling size class. It would likely be ill-advised for managers to adopt a more frequent burn schedule, because such frequent burns would likely reduce *Quercus* survival over time and most certainly prevent recruitment into larger height classes, regardless of rainfall. In addition, the drier microclimate produced by annual burning may only exacerbate drought conditions when they occur. While fire suppression helps retain high shade that can ameliorate drought stress conditions, it also results in greater light limitation for seedlings and allows fire-intolerant competitors to establish, slowing the annual growth rate of *Quercus* seedlings across all size classes. If the management goal is to increase oak recruitment as well as overall drought resilience of oak forests, then a low

frequency, periodic burning schedule (i.e. 5-10 yr return interval) likely achieves the best balance between increasing resource availability for recruits while also providing a large enough window for seedlings to grow into larger size classes with deep, drought-resilient root systems.

VI. Relationship to Other Work

No other studies, to our knowledge, have examined the effect of prescribed fire on tree drought vulnerability. Past work has studied how fire alters the microclimate and competitor density, as well as how resprouting may influence drought vulnerability. Iverson and Hutchinson (2002) found that after a single prescribed fire in mixed-oak forests in Ohio, soil temperature increased 3-6°C on south-facing slopes for over 100 days post-fire and soil moisture was lower on burned sites for the early part of the growing season. Several studies have found that higher soil moisture conditions under closed canopies can facilitate the survival of vulnerable tree seedlings, especially under abiotic stress (Callaway 1995; Mueller *et al.* 2005). This is consistent with our results, where seedlings planted in unburned stands, with greater canopy cover, performed better under drought than those planted in burned stands.

In terms of competition, Lorimer *et al.* (1994) found that artificial removal of competing tree species lead to greater survival and growth of oak seedlings, suggesting that fire can release oaks from intense competition by top-killing fire-intolerant tree species. However, other studies have found fire to promote colonization and vigorous growth of herbaceous species (Peterson & Reich 2001; Knapp, Stephan & Hubbart 2015), which have been shown, especially under water-limiting conditions, to compete with tree seedlings for water (Davis, Wrage & Reich 1998; Kambatuku, Cramer & Ward 2012). Therefore, while it is well-established that fire changes the competitor composition, it is highly context-dependent whether oak seedlings experience a net increase or decrease in competition for resources such as water.

The consensus is also mixed when it comes to the effects of post-fire resprouting on tree water relations. Researchers have found resprouting ability in chaparral shrub communities to aid in maintaining deep root systems (DeSouza, Silka & Davis 1986) higher leaf water potentials (Saruwatari & Davis 1989) and higher leaf gas exchange rates under drought (Clemente, Rego & Correia 2005). Other studies, however, have observed resprouters may be more vulnerable to drought-induced mortality than their unburned counterparts due to the depletion of carbohydrate reserves by resprouting (Pratt *et al.* 2013). Unfortunately, few studies exist on managed temperate forests and the importance of resprouting in these ecosystems, making comparisons difficult. Of the studies that exist, our results are more in agreement with those that have found resprouting to have neutral or positive effects on plant water relations.

Finally, past research has found fire frequency and timing to have critical effects on *Quercus* recruitment and important implications for drought vulnerability. In a study of oak savannas in Minnesota, Peterson and Reich (2001) conclude that a fire frequency of four or more fires per decade will likely result in reduced oak recruitment, whereas fire at decadal scales may suppress shrub competitors and promote grass and forb cover instead. Pratt *et al.* (2013) found that the timing of fires can have severe consequences for the drought fitness of resprouting species; early growing season fires (April – June) can negatively affect carbohydrate stores of seedlings to such a degree that it predisposes individuals to severe carbon limited during summer droughts and possibly increased drought-induced mortality.

VII. Future Work Needed

There is a strong need for studies on the effects of various land management practices on the resilience of forests to changing climate conditions. Of particular importance are prescribed fire and thinning because of their prevalence in oak forest and savanna conservation. Several recent studies have concluded that the combination of fire and thinning treatments are important for maximizing oak recruitment (Albrecht & McCarthy 2006; Iverson *et al.* 2008), but research is now needed on the resilience of these managed ecosystems to changing precipitation regimes. Unlike prescribed fire, thinning quickly reduces stem density and stand basal area. Such a reduction in competitor density may have important consequences not only for seedling drought fitness, but sapling and adult trees as well. Indeed, in a study of red pine (*Pinus resinosa*) plantations under different thinning intensities, D'Amato *et al.* (2013) found recently thinned stands to be more resilient to drought stress. Additionally, researchers of other oak ecosystem types, such as oak barrens or savannas, should consider the impact of forest practices relevant to their particular study system (e.g. grazing).

Climate predictions for the Central Hardwoods Region highlight the need not only for studies on forest drought response, but also how forests respond to increased precipitation (Brandt *et al.* 2014). Although recent projections carry a great deal of uncertainty when it comes to future precipitation, there is growing consensus that climate change will promote more extreme rainfall patterns, characterized by heavier rainfall events and longer drought intervals (Brandt *et al.* 2014). Similar to past studies at Oak Ridge National Laboratory (Hanson, Todd & Amthor 2001), experiments that manipulate precipitation quantity and frequency are invaluable for understanding on how eastern deciduous forests will respond to a range of potential future climate conditions. Innovative studies on the effects of altered rainfall patterns (e.g. many small rainfall events v. few large events) are ongoing in grassland ecosystems (Wilcox *et al.* 2014), but similar studies are needed for forests. Although prohibitively costly to impose on adult trees, such studies are possible if the scope is limited to tree seedling and understory response.

Finally, little research thus far has examined how the indirect effects of fire, such as changes in vegetation, affect tree recruitment and forest functioning. For example, its well-known that repeated prescribed fires change plant community composition, promoting fire-tolerant tree species as well as herbaceous plant cover (Glasgow & Matlack 2007). It is less known, however, how this vegetation change alters other components of the forest community, such as the mycorrhizal fungi community that forms mutualistic relationships with most plants (Johnson *et al.* 1991; Hart *et al.* 2005). Because mycorrhizal fungi colonize tree root tissue and exchange nutrients (and possibly water) for carbon fixed by the plant, fire-induced changes in the fungi community could have important consequences for tree drought fitness. Additionally, mycorrhizae can link the root systems of multiple trees, both among and between species, forming common mycorrhizal networks that facilitate the absorption and transfer of water and nutrients among individuals (Teste *et al.* 2009). In order to draw generalities on the effect of plant-fungal interactions on tree drought vulnerability, especially as a result of fire-driven changes to forest ecosystems, there is a strong need to investigate how prescribed fire impacts mycorrhizal communities and, in turn, tree drought performance.

VIII. Crosswalk Table

Deliverable Type	Description	Delivery Dates
Workshop	Discussed with managers the results and implications for management under drought scenarios	Illinois Prescribed Fire Council 2016 Symposium February 10, 2016
Computer model	Life table analysis projecting impact of seedling mortality on overstory recruitment	In progress, to be submitted August 2016
Dataset	Documented field and geospatial data with USFS for inclusion in the Climate Change Response Framework	In progress, to be submitted August 2016
Presentations	Central Hardwoods Forest Conference, Midwest Ecology and Evolution Conference, Ecological Society of America Annual Meeting	March 20, 2016 / March 29, 2016 / August 2016
Webinar	Oak Woodlands & Forests Fire Consortium: Potential for prescribed fire to promote drought resistance of <i>Quercus alba</i> seedlings in a changing climate: https://vimeo.com/161613188	March 29, 2016
Peer-reviewed publication	One publication (effects of fire on seedling drought response)	In progress, to be submitted for peer review in Fall 2016
Ph.D. Dissertation	Three chapters (effects of fire on SOC stocks, effects of fire on seedling drought response, effects of fire on adult drought response)	In progress, tentative defense date December 2017
Final Report	JFSP Final Report, Electronic Version	May 2016

IX. Literature Cited

- Abrams, M.D. (1996) Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *53*, 487–512.
- Albrecht, M.A. & McCarthy, B.C. (2006) Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *226*, 88–103.
- Brandt, L., He, H., Iverson, L., Thompson, F.R. & Butler, P. (2014) *Central Hardwoods Ecosystem Vulnerability Assessment and Synthesis*. USDA Forest Service, Newtown Square, PA.
- Callaway, R.M. (1995) Positive interactions among plants. *The Botanical Review*, **61**, 306–349.
- Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J. & Wyckoff, P. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany*, **86**, 1–16.
- Clemente, A.S., Rego, F.C. & Correia, O.A. (2005) Growth, water relations and photosynthesis of seedlings and resprouts after fire. *Acta Oecologica*, **27**, 233–243.
- D'Amato, A.W., Bradford, J.B. & Fraver, S. (2013) Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological ...*, **23**, 1735–1742.
- Davis, M.A., Wrage, K.J. & Reich, P.B. (1998) Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology*, **86**, 652–661.
- DeBano, L.F., Neary, D.G. & Ffolliott, P.F. (1998) *Fire Effects on Ecosystems*.
- DeSouza, J., Silka, P.A. & Davis, S.D. (1986) Comparative Physiology of Burned and Unburned Rhus-Laurina After Chaparral Wildfire. *Oecologia*, **71**, 63–68.
- Fralish, J.S. (1988) Predicting potential stand composition from site characteristics in the Shawnee Hills forest of Illinois. *American Midland Naturalist*, 79–101.
- Glasgow, L.S. & Matlack, G.R. (2007) The effects of prescribed burning and canopy openness on establishment of two non-native plant species in a deciduous forest, southeast Ohio, USA. *Forest Ecology and Management*, **238**, 319–329.
- Hanson, P.J., Todd, D.E. & Amthor, J.S. (2001) A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. *Tree Physiology*, **21**, 345–358.
- Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D. & Boyle, S.I. (2005) Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *220*, 166–184.

- Iverson, L.R. & Hutchinson, T.F. (2002) Soil temperature and moisture fluctuations during and after prescribed fire in mixed-oak forests, USA.
- Iverson, L.R., Hutchinson, T.F., Prasad, A.M. & Peters, M.P. (2008) Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *Forest Ecology and Management*, **255**, 3035–3050.
- Johnson, N.C., Zak, D.R., Tilman, D. & Pfleger, F.L. (1991) Dynamics of Vesicular-Arbuscular Mycorrhizae During Old Field Succession. *Oecologia*, **86**, 349–358.
- Johnson, P.S., Shifley, S.R. & Rogers, R. (2009) *The Ecology and Silviculture of Oaks*.
- Kambatuku, J.R., Cramer, M.D. & Ward, D. (2012) Overlap in soil water sources of savanna woody seedlings and grasses. *Ecohydrology*, **6**, 464–473.
- Knapp, B.O., Stephan, K. & Hubbart, J.A. (2015) Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. *Forest Ecology and Management*, **344**, 95–109.
- Kozłowski, T.T. & Kramer, P.J. (1991) *The Physiological Ecology of Woody Plants*. Tree Physiology.
- Lorimer, C.G., Chapman, J.W. & Lambert, W.D. (1994) Tall Understorey Vegetation as a Factor in the Poor Development of Oak Seedlings Beneath Mature Stands. *Journal of Ecology*, **82**, 227–237.
- Loudermilk, E.L., Scheller, R.M., Weisberg, P.J., Yang, J., Dilts, T.E., Karam, S.L. & Skinner, C. (2013) Carbon dynamics in the future forest: the importance of long-term successional legacy and climate-fire interactions. *Global Change Biology*.
- Melvin, M. (2012) *National Prescribed Fire Use Survey Report*. Coalition of Prescribed Fire Councils Inc.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., III, Gehring, C.A. & Whitham, T.G. (2005) Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology*, **93**, 1085–1093.
- Peterson, D.W. & Reich, P.B. (2001) Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. *Ecological Applications*, **11**, 914–927.
- Pratt, R.B., Jacobsen, A.L., Ramirez, A.R., Helms, A.M., Traugh, C.A., Tobin, M.F., Heffner, M.S. & Davis, S.D. (2013) Mortality of resprouting chaparral shrubs after a fire and during a record drought: physiological mechanisms and demographic consequences. *Global Change Biology*, **20**, 893–907.
- Reich, P.B., Abrams, M.D., Ellsworth, D.S., Kruger, E.L. & Tabone, T.J. (1990) Fire Affects Ecophysiology and Community Dynamics of Central Wisconsin Oak Forest Regeneration. *Ecology*, **71**, 2179–2190.

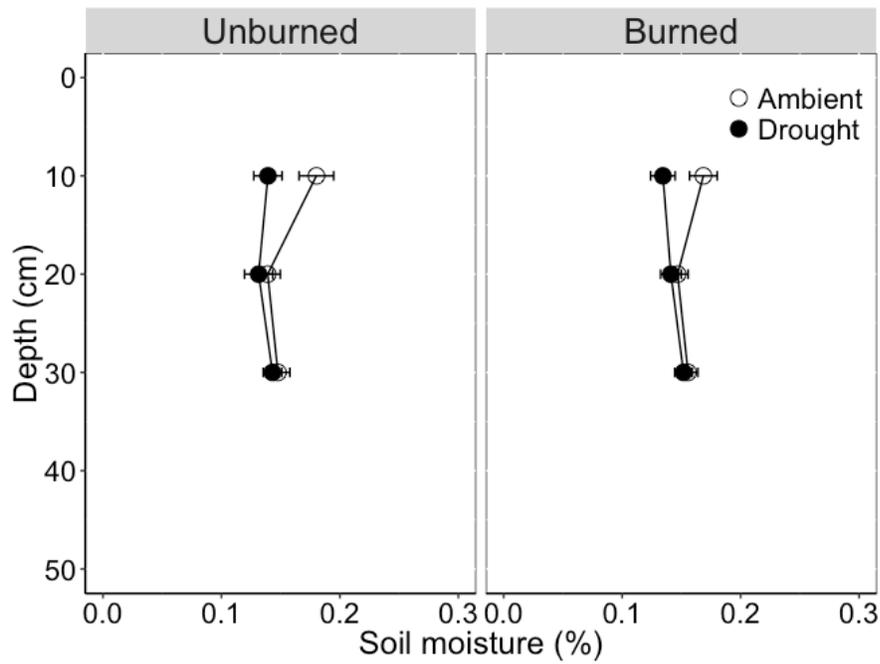
- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A. & Wattenbach, M. (2013) Climate extremes and the carbon cycle. *Nature*, **500**, 287–295.
- Saruwatari, M.W. & Davis, S.D. (1989) Tissue water relations of three chaparral shrub species after wildfire. *Oecologia*, **80**, 303–308.
- Teste, F.P., Simard, S.W., Durall, D.M., Guy, R.D., Jones, M.D. & Schoonmaker, A.L. (2009) Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. *Ecology*, **90**, 2808–2822.
- Wilcox, K.R., Fischer, von, J.C., Muscha, J.M., Petersen, M.K. & Knapp, A.K. (2014) Contrasting above- and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. *Global Change Biology*, **21**, 335–344.
- Zhao, M. & Running, S.W. (2010) Drought-Induced Reduction in Global Terrestrial Net Primary Production from 2000 Through 2009. *Science*, **329**, 940–943.

X. Figures



Figure 1. Example of the 4 x 4m (16 m²) drought rainout shelter used to experimentally reduce soil moisture content in burned and unburned stands in Shawnee National Forest. Within 2 m is the paired control plot (not pictured) of the same dimensions (16 m²) but constructed out of deer netting to replicate the 5-10% shading artifact produced by the rainout shelters.

A.



B.

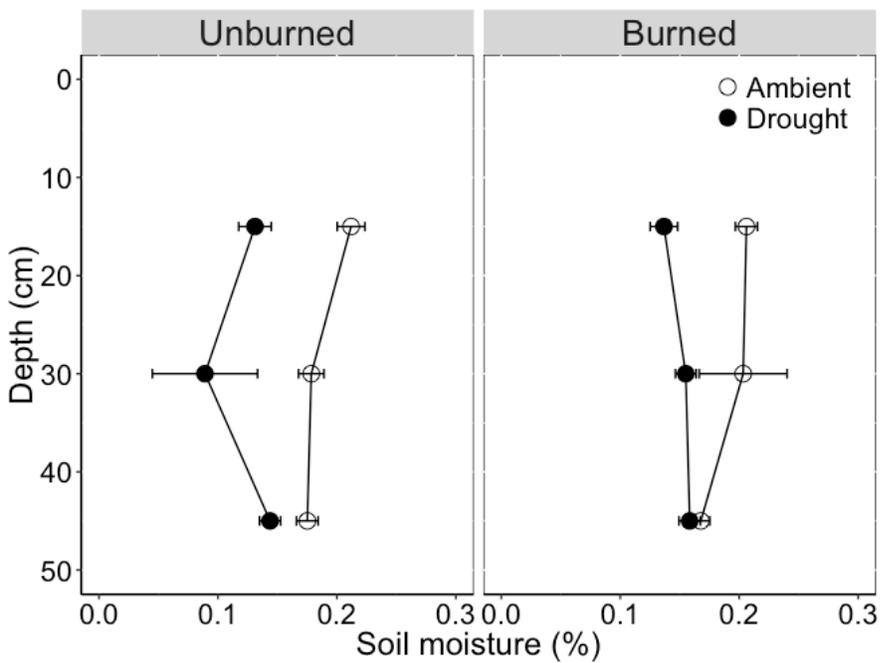


Figure 2. Gravimetric soil moisture (mean \pm SE) with depth (0–45 cm) in ambient (white) and drought (black) plots within unburned and burned stands in Shawnee National Forest. Data are presented as averages of June and August observations for (A) 2014 and (B) 2015 study years.

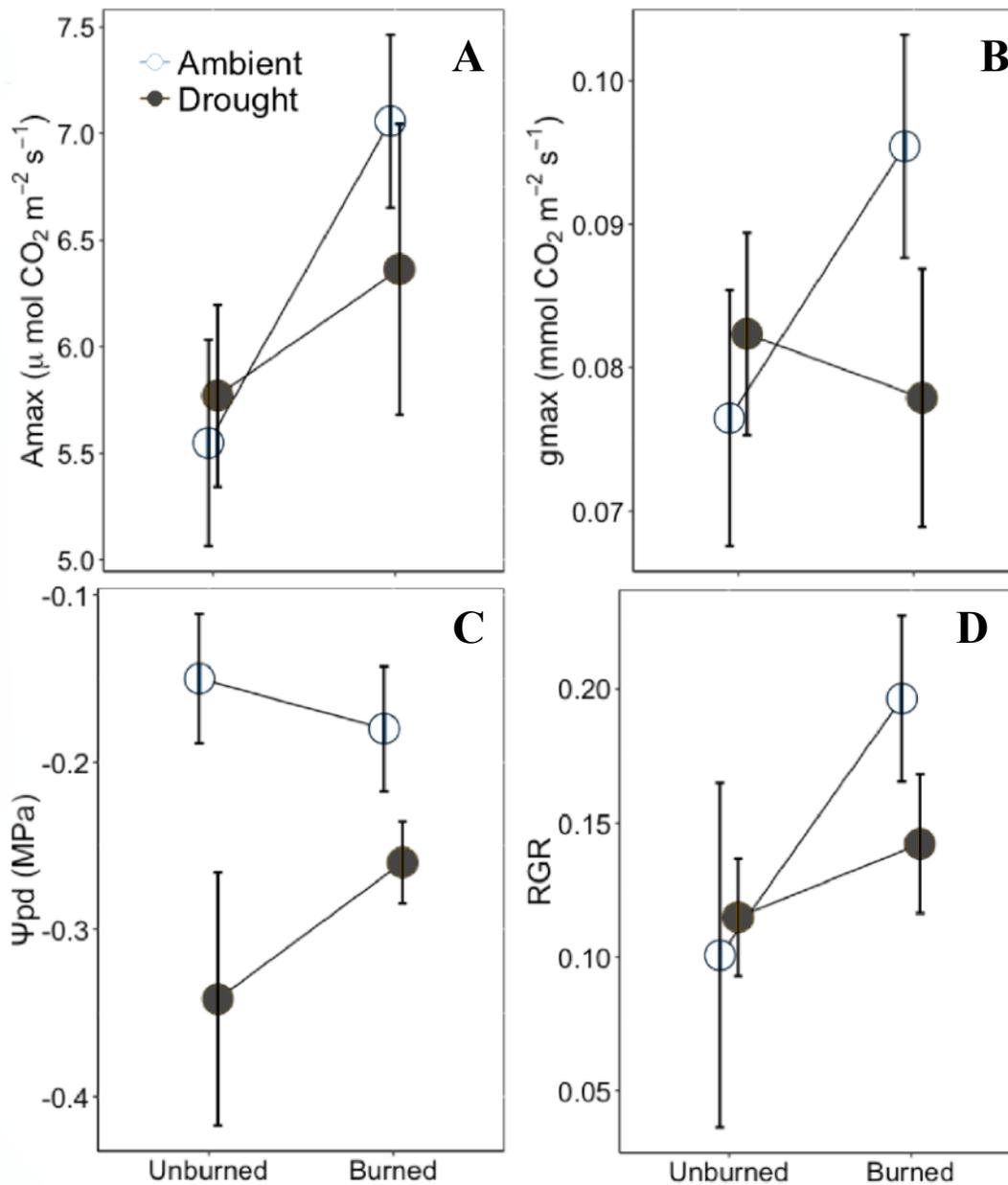


Figure 3. Fitness of *in situ* seedlings growing in unburned and burned stands and subjected to ambient (white) or drought (black) treatment. Mean (\pm SE) (A) maximum photosynthetic rate (A_{max}), (B) maximum stomatal conductance (g_{max}), (C) predawn leaf water potential (Ψ_{pd}) and (D) relative growth rate (RGR) from May, 2014 to August, 2015. Physiological data are averages from 2014 and 2015 observations.

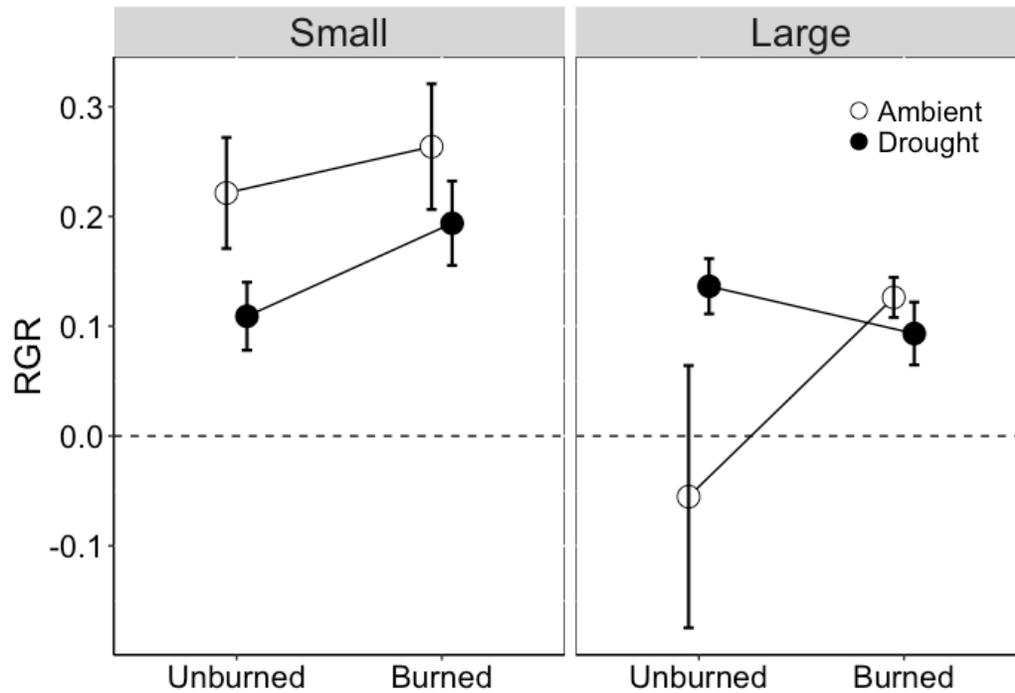


Figure 4. Mean (\pm SE) relative growth rate (RGR) of ‘small’ (initial height < 32 cm) and ‘large’ (initial height \geq 32 cm) *in situ* seedlings growing in unburned and burned stands and subjected to ambient (white) and drought (black) treatments. RGR is calculated as the change in growth from May, 2014 to August, 2015.

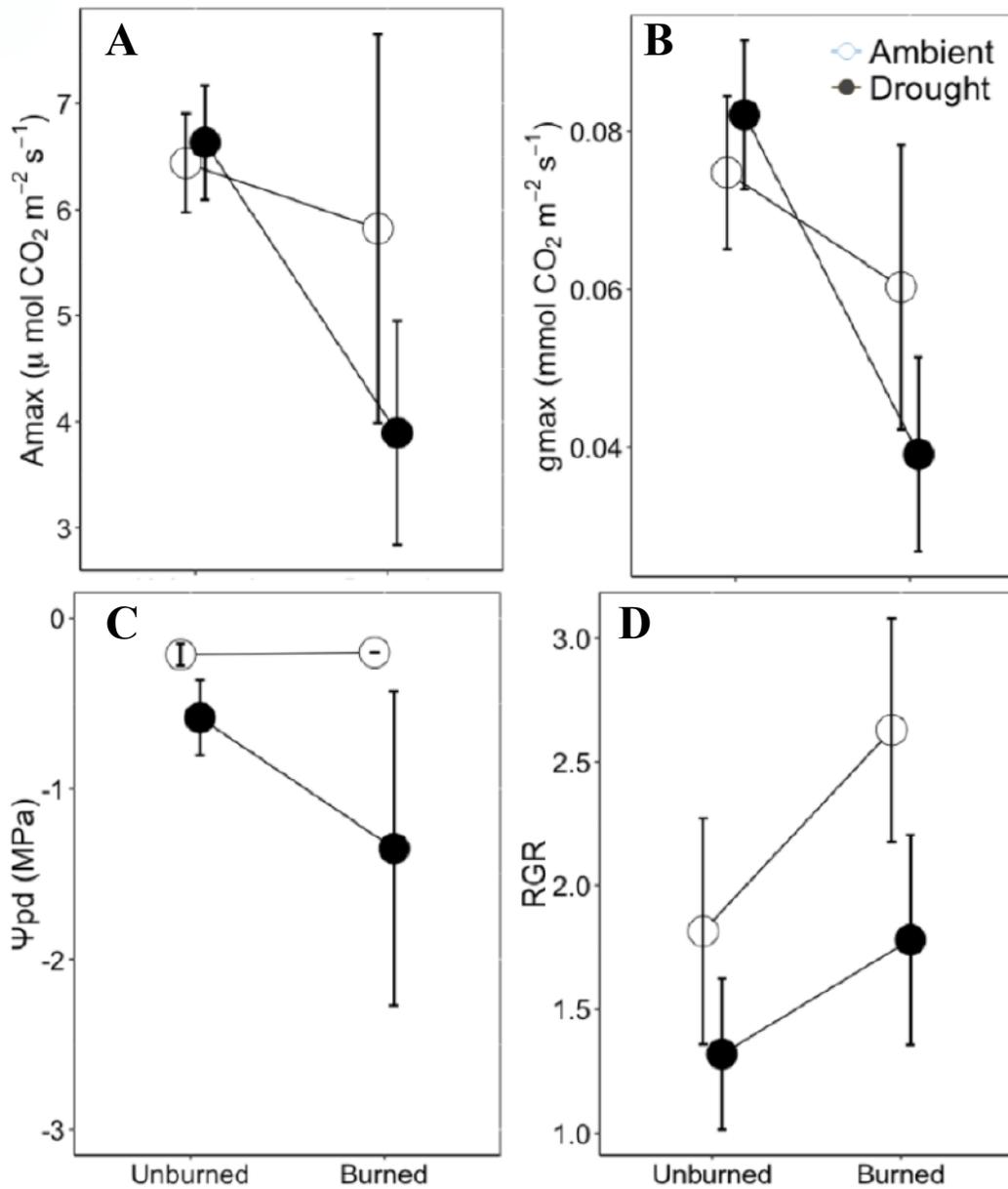


Figure 5. Fitness of *ex situ* seedlings growing in unburned and burned stands and subjected to ambient (white) or drought (black) treatment. Mean (\pm SE) (A) maximum photosynthetic rate (A_{max}), (B) maximum stomatal conductance (g_{max}), (C) predawn leaf water potential (Ψ_{pd}) and (D) relative growth rate (RGR) from May, 2015 to August, 2015. Physiological data are from 2015 observations.