THE RESPONSE OF SWEETGUM AFTER TOP-KILL IN DIFFERENT SEASONS OF BURN

by

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(Under the Direction of Doug P. Aubrey)

ABSTRACT

In the southeastern United States, the function and stability of pine ecosystems depends on frequent low intensity fires. Critically, fire suppresses hardwood competition by killing aboveground stems. Previous long-term studies correlated early growing season burns with higher understory mortality when compared to dormant season burns. Seasonal differences in mortality from insufficient carbon reserves in roots after leaf flush were posited as the mechanism; however, this has not been explicitly tested. In this experiment, two-year-old pot-grown sweetgums (*Liquidambar styraciflua*) were burned in the dormant season (February), and growing season (May), or left unburned. By the end of the first post-burn growing season, mortality was significantly higher after the dormant season burn than the growing season burn and unburned trees had nearly twice the mass of either the burned treatments. Starch concentrations were similar across treatments. Our results indicate the top-kill of dormant plants can be more damaging than growing season top-kill.

INDEX WORDS: Sweetgum, fire, growing, dormant, *Liquidambar*, starch, mortality, biomass

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BS, State University of New York at Geneseo, 2015

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2018

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August 2018

ACKNOWLEDGEMENTS

This experiment and thesis would not have been completed if it was not for the consistent help and support that I received during my time at the University of Georgia. First and foremost, I would like to thank Joe O'Brien for his initial faith in me as an intern nearly five years ago, and the continual reassurance that he has given me in the years since then. Doug Aubrey has also been an incredible mentor and has done a tremendous job teaching me in the ways of science especially considering that he was located two hours away in SREL. I would like to thank my parents and family for their support and instilling in me curiosity in the world. The community of the SRS Forest Service, Warnell, Aubrey Lab, frisbee and trivia squad have all been very warm and welcoming to me. I would also like to thank the Roberts lab for their help and advice on completing the nonstructural carbohydrate analysis. I like to thank Old Castle Shady Dale for their donation of the soil that was used in this project. Last but not least, I would like to thank my third committee member Nina Wurzburger who did a great job editing and honing my thesis.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

FIRE HAS SHAPED THE GEORGIA PIEDMONT

Georgia piedmont forests once covered the area between the Appalachians in North Georgia and the coastal plain. Similar to longleaf pine ecosystems in the Georgia coastal plain, Piedmont forests experienced frequent, low intensity surface fires (Guyette *et al.*, 2012). These low intensity frequent fires favored the regeneration of fire-tolerant plants and maintained the dominance of pine in the overstory. In the piedmont the typical fire return interval was between 2-6 years and ignitions were most often caused by lightning and Native Americans (Delcourt and Delcourt, 1997; Frost, 1998; Guyette *et al.*, 2012). If the interval between fires is long enough, fire-intolerant hardwoods become large enough that they escape top-kill (trees attain 7.5 cm dbh, Chen et al., 1975). Once fire-intolerant broadleaves become resistant to top-kill they can ascend into the canopy and replace fire-adapted trees. Fuels would then become patchy and the continuous fuel bed critical to maintaining fire-dependent ecosystems is interrupted creating a feedback that further releases the fire sensitive species (Mitchell et al., 2009). Fire exclusion in the early 20th century has radically altered the landscape thereby changing forest composition and function (Cowell, 1998; Knapp *et al.*, 2009). The transformation of large tracts of land to agriculture and poor agricultural practices led to substantial loss of topsoil (Magilligan and Stamp, 1997; Trimble, 2008). As fields were abandoned, forests reclaimed the land and new ecosystems developed. Where the canopies were once dominated by fire associated species, such as pines and oaks, the forests shifted towards maples, sweetgums and tulip-poplars (Nowacki and

Abrams, 2008). Changes in species composition and ecosystem function in the Georgia piedmont following fire suppression and widespread land change have created novel ecosystems (Hobbs *et al.*, 2006). Examples can be seen throughout the Appalachian Mountains where xeric ecosystems are transforming into mesic ecosystems (Nowacki and Abrams, 2008). The duff layer created through decomposition of xeric litter enhances the potential for damaging effects from reintroduced fire so that not even the fire tolerant species are resistant (Varner *et al.*, 2005). Because of the aforementioned changes and the loss of foundation species, such as chestnut, the current landscape is in a no-analogue state; one in which management objectives should be aimed at "achievable future conditions," instead of an unobtainable goal of restoration to some point in the past (Golladay *et al.*, 2016).

Forest managers currently use prescribed fire to restore, conserve and manage these ecosystems because the long history of low-intensity fires in the region make them especially effective. Prescribed fires are widely employed because they are the most ecologically appropriate and cost-effective method of obtaining many forest management objectives. Vegetation control, one of these major objectives, creates open stand structure with many other indirect effects by top-killing above-ground biomass (Cleaves *et al.*, 2000). Vegetation control was rated as highly and moderately important to forest managers in state or private forests and national forests respectively (Haines *et al.*, 2001). The presence of unwanted mid-story trees decreases a forest's habitability by endangered animals such as the Red-cockaded woodpecker (Sparks *et al.*, 1999; Cox and Widener, 2008). Complete kill of understory vegetation can lead to a 50% increase in growth of the overstory pines (Martin and Shiver, 2002). Reforestation and maintenance of threatened and endangered species are rated as either highly or moderately important to forest managers. Without fire, tree densities can increase to levels associated with vulnerabilities to insects and disease (Lafon *et al.*, 2007).

SWEETGUM

Sweetgum (*Liquidambar styraciflua*), an abundant root sprouting broadleaf tree is a pioneer species in Georgia piedmont and coastal ecosystems. The strong ability of sweetgum to colonize disturbed areas, as well as its vigorous sprouting after a disturbance, makes it particularly successful in the southeastern U.S. The deforestation and erosion associated with agriculture in Georgia during the European settlement favored the dispersal and proliferation of fast growing taxa such as sweetgum. Kormanik (1990) found that sweetgum trees start producing seeds at maturity (around 20-30 years old) and these wind dispersed seeds typically travel up 61 m. Sweetgum increased its relative abundance from pre-settlement in the Georgia piedmont by 365% to 1600% (Cowell, 1998). Sweetgum, like many pioneer species, tend to be shade intolerant, yet the consistent application of fire on the landscape and the open pine canopy ensures that sufficient light reaches the forest floor. Sweetgum prefers a soil with a high clay percentage so the highly eroded red clay soils of Georgia's piedmont are ideal (Kormanik, 1990). Indeed, most of the forests in this area are secondary forests, so sweetgum would have been very competitive in this region as a wind pollinated and dispersed pioneer during the reforestation process.

One characteristic that has enabled sweetgum to persist in fire-dependent ecosystems is its capacity to root sprout prolifically. It has been estimated that on bottomland sites up to 70% of the sweetgum sprouts are connected to one another through roots (Kormanik, 1990). Sprouting in sweetgum appears to be stimulated by disturbance. For example as many as 40 or more stems from seedling to sapling size can sprout from the root system of a single medium sized tree (Kormanik and Brown, 1967). Sweetgum mobilizes carbon reserves from the roots to subsidize the cost of resprouting (Wenger, 1953; Chapin *et al.*, 1990; Pausas *et al.*, 2016). The large carbon reserves allows for a competitive advantage against obligate seeders immediately after a disturbance (Pausas and Keeley, 2014). Over time this resprouting can create clonal colonies of sweetgum, often situated around one large sweetgum tree that has escaped the damaging effects of fire. In this way, even if the understory sweetgums were losing carbon through recurrent fire, the larger sweetgum could subsidize its sprouts. The sprouts in turn could help inhibit pine regeneration eventually lowering flammable fuel accumulation.

Sweetgum is a primary source of concern for both private and public land managers in the southeast. As mentioned above, a dense sweetgum midstory can be a hindrance to game and endangered wildlife. Shelterwood systems can promote oak regeneration; however, intense competition from sweetgum usually causes failures in the Piedmont (Brose *et al.*, 1999). In plantations too, sweetgum has become an issue because it competes with loblolly pine for water resources. Until the point of near death, sweetgum will continue to photosynthesize (Bormann, 1953). Bormann (1953) showed that when soil moisture was at 6%, sweetgum was at 50% of maximum photosynthesis, by 4% soil moisture, photosynthesis stops and at 3% sweetgum wilts. In comparison, loblolly pine stops all photosynthesis at 6% soil moisture. If water was a limitation in a plantation stand then the large amounts of water sweetgum uses could slow loblolly growth. Blight, *Botryosphaeria ribis*, is known to cause diebacks in sweetgum if soil moisture levels get too low (below 40% of field capacity), although at that point many of the other trees in the forest would also be drought stressed (Kormanik, 1990).

SEASON OF BURN

The timing of the application of fire is a continuing source of controversy in forest management. There have been mixed results so far in determining the best season for prescribed burning. Fires set by Native Americans occurred throughout the year and especially in autumn (Cowell, 1995). However, more recently, prescribed burns have been carried out during the dormant season (December to early March, after leaf senescence but before leaf flush), because fires are easier to control and smoke has less of an effect on air quality (Stanturf, 2002). In addition, concerns have been raised regarding the effect of growing season burns on the habitat of economically and ecologically important birds (Sisson and Speake, 1994). Short-term studies found that summer burns significantly decreased shrub and understory tree densities compared to dormant season burns (Waldrop *et al.*, 1992; Glitzenstein *et al.*, 1995; Sparks *et al.*, 1999), but a 30 year study found no significant differences in the number or diameter of sprouts between the two seasons of burn (Barlow *et al.*, 2015). It has also been suggested that a variable season of burn would be best for some understory plants, such as legumes (Hiers *et al.*, 2000).

The Santee Experimental Forest in Berkeley County, SC was established to test the effects of season of burn with plots burned annually in the dormant and growing season (Lewis and Harshbarger, 1976; Waldrop *et al.*, 1987; White *et al.*, 1990; Waldrop *et al.*, 1992). After 40 years of treatments, growing season burns drastically reduced the density of stems less than 1.5 m tall. Dormant season plots had over 400,000 stems ha^{-1}; whereas growing season plots had around 10,000 stems ha^{-1}. However, due to confounding variables the differences may not be as large as they first appear. Waldrop *et al.* (1992) collected density measurements during July, seven months post dormant season burn, but only one month post growing season burn. It is likely the differences in density could be because the plants in the annual summer treatment have not had the time to resprout. In addition, it was noted that in the methods of the 20 year vegetation study from the same plots (Lewis and Harshbarger, 1976) that “backfires were generally used in winter treatments and head fires in summer treatments”. Head fires in the summer were required because live vegetation during growing season burns can significantly decrease the fire intensity (Sparks *et al.*, 2002); thus, the effects they observed were confounded with different fire behavior in the treatments.

Season of burn can have differential effects on mortality (Glitzenstein *et al.*, 1995). The first hypothesized mechanism responsible for this higher mortality is extrinsic to the organism; that fire intensities are higher in growing season burns because of higher ambient temperatures during the summer. Temperatures above 60°C can induce mortality in plant cells, and if fires are more intense it is more likely that above-ground tissues will reach this temperature threshold. Fires with low residence time, like those present in the southeastern US, do not tend to damage below-ground tissues (Varner *et al.*, 2005). The other mechanism relates to plant physiology, where patterns of plant resource acquisition and allocation can affect vulnerability to fire damage. The proposed mechanism is that the nonstructural carbohydrate (NSC) reserves that subsidize resprouting are lowest in the growing season (Waldrop *et al.*, 1987); however, the evidence is mixed on whether carbon is the limiting factor in resprouting (Wenger, 1953). Glitzenstein *et al* (1995) found that higher top-kill occurred in the early growing season (partially due to higher fire intensities); however, mortality of these shrubs either exhibited no relation or a similar relation to time of burn. Even though their results indicated that top-kill may be higher in early growing season burns, relative mortality was not.

If carbon starvation is a driver of post-fire mortality, it requires acute and chronic carbon deficits to be considered separately and in detail. For example, there is an acute deficit in NSC concentrations in deciduous trees in the spring (Martínez-Vilalta *et al.*, 2016) because leaf flush drains carbon stores until the leaves are self-sustaining. NSC rarely show a large decrease in times of high C demand (Körner, 2003); however, other studies have shown otherwise (Cruz and Moreno, 2001; Martínez-Vilalta *et al.*, 2016). Regardless, research has indicated that leaves on trees were net exporters of sugar by the time the leaves are 10-50% expanded (Keel and Schädel, 2010). Once carbon-positive, the leaves then support new growth and storage for the next leaf flush. The mechanism of acute carbon deficit mortality is hypothesized to occur in growing season burns immediately after leaf flush when carbon reserves in hardwoods would already be low and trees would not have the reserves to support a second leaf flush. While superficially logical, resprouting trees adapted to disturbance have large carbon reserves (Pausas and Keeley, 2014) and low NSC reserves do not strongly effect the mortality and regrowth of resprouting plants (Richards and Caldwell, 1985; Cruz *et al.*, 2003). Mortality from a chronic carbon deficit could occur over multiple iterations of annual growing season burns. This mechanism is hypothesized to occur because trees do not have a full growing season to recuperate and therefore end the year before replenishing carbon reserves. Over the course of many annual burns, carbon reserves in the plants would continue to decrease until the plant could no longer resprout. Many of the previous studies of hardwood resprouting following different seasons of burn have used biomass and mortality as proxies of NSCs without measuring reserves directly (Lotti, 1956; Waldrop *et al.*, 1992; Glitzenstein *et al.*, 1995; Robertson and Hmielowski, 2014). Thus a study that follows both NSC reserves, mortality and biomass is critical to understanding the underlying mechanisms of mortality during resprouting.

CHAPTER 2

SWEETGUM RESPONSES FOLLOWING DIFFERENT SEASONS OF BURN[1]

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[1] Ruswick, S. K., J.J. O'Brien, and D.P. Aubrey. 2018. To be submitted to *Forest Ecology and Management*

ABSTRACT

In the southeastern United States, the function and stability of pine ecosystems depends on frequent low intensity fires. One of the critical impacts of fire is the suppression of hardwood competition by killing aboveground stems. Previous long-term studies correlated early growing season burns with higher understory mortality when compared to dormant season burns. Seasonal differences in mortality from insufficient carbon reserves in roots after leaf flush were posited as the mechanism; however, this has not been explicitly tested. In this experiment, two-year-old pot-grown sweetgums (*Liquidambar styraciflua*) were burned in the dormant season (February), and growing season (May), or left unburned. By the end of the first post-burn growing season, mortality was higher after the dormant season burn than the growing season and unburned trees had nearly twice the mass of either the burned treatments. Starch concentrations were similar across treatments. Our results indicate that the physiological impact of the top-kill of dormant plants can be more damaging than growing season top-kill. Considering the importance of top-kill to the maintenance of these forests, fires should be prescribed in the dormant season when possible and in the growing season when conditions can carry fire through clumps of sweetgum saplings.

INTRODUCTION

Pine forests are fundamental to the economic and ecologic landscape of the Southeastern United States. Within this region landownership is highly variable; land managers may be private citizens, corporate or representatives of local, state or federal agencies and their management goals can be just as diverse: timber, game production, endangered animals, or multiple uses. Fire has been an intrinsic element in both the evolutionary history and contemporary management of loblolly-shortleaf pine timberlands in the south and southeast (Delcourt and Delcourt, 1997). Frequent fires create an open and light-filled understory (Pecot *et al.*, 2005; Ryan *et al.*, 2013). These forests contain around 1.5 billion board feet of wood, one-sixth of the total softwood on timberlands in the nation (Oswalt, 2017). The frequently burned forest structure promotes pine reproduction, wildlife and game production, pollinator diversity (Hanula *et al.*, 2016) and is needed for the nesting of Red-cockaded woodpeckers (Sparks *et al.*, 1999; Haines *et al.*, 2001). The largest challenge that land managers face in maintaining these southern pine forests is eliminating understory hardwoods that rapidly overtake the understory and make the forest fire-resistant (Chen *et al.*, 1975; Haines *et al.*, 2001).

The light-filled understory necessary for the benefits of the southern pine ecosystem also creates the perfect growing conditions for fire sensitive shade-intolerant species, which, in the absence of fire, can cause a transition to an alternate stable state dominated by fire sensitive species (Grady and Hoffmann, 2012). Prescribed fire is the most widely used management tool in the southeast to maintain these areas because it is the most ecologically appropriate, cost-effective method to reduce competitors, promote fire-dependent species and pine regeneration (Lotti *et al.*, 1960). Resprouting is an adaption to aboveground disturbances where dormant root buds form new shoots and utilize carbon reserves to quickly grow and outcompete other plants

(Bond and Midgley, 2001; Pausas and Keeley, 2014). Hardwoods that resprout are particularly difficult to control because they are aggressive competitors, not only for light in the understory, but also for water in the soil (Mitchell *et al.*, 1993; Martin and Shiver, 2002). Sweetgum that escape fire damage and reach a diameter at breast height (dbh) of ~7.5 cm can become resistant to damage from low intensity fires and eventually they will mature (Chen *et al.*, 1975). Mature fire-intolerant hardwoods shade the forest floor (Messier, 1996), inhibit the growth of the next generation of pine seedlings, disrupt the fuel bed and enable the transformation from a fire dependent ecosystem to one unlikely to burn with the concomitant loss of ecosystem function brought by fire (O'Brien *et al.*, 2008).

Sweetgum, *Liquidambar styraciflua*, is one of the most abundant root-sprouters in the Southeast. Sweetgum is shade-intolerant and sprouts profusely from roots and stumps and, based on land surveys, it has increased in abundance by 360-1600% since European settlement (Cowell, 1998). Because of its tendency to root sprout, disturbed sweetgum often form thickets. In fact, in some bottomwoods, up to 70% of the sweetgum are linked by roots (Kormanik, 1990). Sweetgum is also known for its high water use, sweetgum plantations transpire 53% more water than loblolly plantations of the same age (Caldwell *et al*, in review), moreover, sweetgum maintains photosynthesis at lower soil moisture contents than loblolly pine (Bormann, 1953). Complete kill of hardwoods in the understory can result in a 53% growth increase of surrounding loblolly pine (Bacon and Zedaker, 1987). It is not surprising that a primary management objective is the elimination of sweetgum from forest understories (Lotti *et al.*, 1960; Brender and Cooper, 1968; Haines *et al.*, 2001).

Previous field experiments demonstrated that hardwoods decrease in abundance following repeated growing season burns (Brender and Cooper, 1968; Waldrop *et al.*, 1992;

Glitzenstein *et al.*, 1995). There are several hypotheses that have been cited for the increase in mortality following growing season burns (Chaiken, 1952; Glitzenstein *et al.*, 1995), but one of the most logical is the starvation of trees due to the acute drop in starch reserves. The acute impact is related to the drawdown of starch reserves in roots of hardwoods following leaf flush (Martínez-Vilalta *et al.*, 2016). If plants were unable to replenish depleted starch reserves before a growing season burn then there would be insufficient carbon capital to repair fire damaged tissues and plants would exhibit higher mortality than plants burned in the dormant season (Waldrop *et al.*, 1987). However, studies have also shown mixed results of the success of growing season burns (Wenger, 1953; Robertson and Hmielowski, 2014; Reilly *et al.*, 2017) and the definition of growing season is loosely defined (Waldrop *et al.*, 1992; Glitzenstein *et al.*, 1995). Since sweetgums are often connected by root sprouts, mortality in field studies may be confounded by nearby large fire resistant sweetgums. Because treatments are applied in different seasons, the dates of measurement can either occur at the same time of year, or the same time since burn, but not both. Unfortunately, due to the inherent nature of confounding variables present when applying treatments in different seasons and conducting measurements in the field, the mechanisms behind differential hardwood mortality remain unclear.

The acute carbon starvation of growing season burned trees is often studied by proxy of density and mortality measurements in the field; this study explicitly tests starch concentrations to assess the validity of this mechanism. Here we compared starch concentrations in the roots of burned sweetgum saplings throughout the year to evaluate this hypothesized mechanism in explaining differences in mortality and physiological performance driven by timing of burns. Due to the large number of confounding variables in field studies we designed this experiment to control these factors. In this experiment we not only measure biomass at the end of the year, but also growth rate to determine if sprout vitality differed. Differences in fire intensity has been postulated as a mechanism of the differential mortality, here we apply similar fire treatments to control for this effect. Typically, high resolution fire characteristics are difficult to measure over large areas, so our small burn plots allow for high quality fire data. Since sweetgum trees can form a connected network of trees, we grew the saplings in pots to observe individualistic responses. We hypothesized that growing season burned trees would have the lowest starch concentrations after burn and that this would correspond to higher mortality. Furthermore, we expected growth rates of dormant season and growing season burned trees to be similar but for biomasses at the end of the year to be different due to the differential length of post-burn growing seasons.

METHODS

STUDY SITE

The study site for this project was a plot in the University of Georgia's Whitehall Forest in Athens, GA (33°53'37.07 N, 83°21'32.96 W). The site is located in the Piedmont region of Georgia where there is an annual average of 1,175 mm of precipitation, and a daily temperature high of 23.1°C and low of 10.8°C.

We planted 240 one-year-old bare root sweetgum (*Liquidambar styraciflua*) seedlings in 26.5 L pots and grew them for one year. We initially planted two seedlings in each pot to ensure adequate sample sizes and after approximately two months of growth, one stem was severed at the base. Many of these redundant stems continued resprouting throughout the experiment and if present were cut in July and November 2016 and then at each harvest in 2017. The trees were spaced one meter away from one another in a grid, with a surrounding edge of extra potted sweetgum trees as a buffer for edge effects. Plants were initially potted in 3.8 L pots on 4/2/2016, they were repotted 6/5/2016 into 26.5 L pots filled with 18.9 L gallons of Proline 44N soil and fertilized on 7/1/2016 with 100 g of time release fertilizer (23-4-8, 12-14 month Everris Nursery Mix).

At the beginning of 2017 trees were randomly assigned to one of three treatments: unburned, dormant and growing season burns. Unburned trees remained unburned throughout the experiment, dormant trees were burned prior to leaf flush (2/15/2017) and growing season trees were burned approximately two months after bud break with fully expanded leaves (5/16/2017). Throughout the study trees were grown in a completely randomized design and irrigated overhead 3-4 times a week for 2-4 hours each except during periods of rainfall. Between 2016 and 2017, midday maximum photosynthetic active radiation (PAR) averaged around 1600 mmol m^{-2} of light between mid-April and mid-September with a low in late December around 1000 mmol m^{-2} of light. Meteorological data was collected 100 m away at a weather station instrumented for solar radiation (LI190R, LI200S, LiCor Biosciences Inc. Lincoln, NE), temperature/humidity (HC2S3, Campbell Scientific Inc., Logan, UT) and wind speed/direction (05103, Campbell Scientific Inc., Logan, UT). On 3/16/2017 there was a hard frost with a minimum temperature of -4.5°C, otherwise temperatures were warm throughout the early spring (Supplemental Figure 1). On 7/17/17 and 9/11/17 unburned trees suffered leaf loss due to high temperatures and a mistiming of watering, whereas trees in the other treatments did not lose leaves possibly due to their lower leaf area requiring less water. Leaf area of affected trees was reduced by approximately one third during each of the two dry periods. Herbivory across all treatments was not apparent and likely negligible.

FIRE TREATMENTS

We conducted the dormant season burn on February 15th and the growing season burn on May 16th 2017, with 5 burn repetitions conducted each day. For each repetition up to 14 plants were placed in holes cut into an 8'x 8' piece of plywood such that pot rims were flush with the surface of the plywood. Each burn consisted of an average of 4.6 kg dry weight of loblolly pine needle litter evenly spread on the test bed, the equivalent of 18.3 Mg/ha (~6 tons/acre). These fuel loads would be typical of those found in the Georgia piedmont following approximately 3-4 years without fire. The fuel moistures of the bales at the time of burn averaged 15.01% and 9.26% for the dormant and summer burns, respectively. The test beds were ignited as a ring fire, with the fire converging on the center. All plants in both treatments were watered to field capacity the day before the burn to ensure similar soil moisture. Weather at the time of the dormant and summer burns, respectively, was: 16°C and 30°C air temperature, 30% and 40% relative humidity, 3.3 and 1.5 m/s wind speed. Radiative heat was measured by an infrared thermal imager (A655, FLIR Systems, Wilsonville, OR) positioned for a nadir view 6 m above (Hiers *et al.*, 2009).

After flaming phase combustion was complete and the majority of the fuel consumed, the board and pots were sprayed with water to extinguish residual combustion. The burns did not consume any tree biomass except for some leaves during the growing season burns. We analyzed fire energy release over a consistent two minute interval because of nuisance variation in patches of smoldering fuels. The energy released by these patches would occur in the asymptote of the fire energy release integral. The two-minute interval captured the peak energy fluxes from each treatment and some denouement time.

The infrared images were analyzed using a combination of ResearchIR (FLIR Systems, Wilsonville, OR), python and R. ResearchIR was used to crop the image sequence from the beginning to the end of combustion. The images were post-processed to reflect the influence of air temperature and relative humidity during the burns. The lower temperature threshold of the imagery was 200°C. Each image was exported as a matrix of text values and cropped to the size of the burn bed using Python programming code (O'Brien *et al.*, 2016). Pixel temperatures were extracted from these images and transformed into energy released using the Stefan Boltzmann Law (O'Brien *et al.*, 2016) and subsequently analyzed. Pixels were also aggregated by pots, and joules released by each pot were analyzed. Since the thermal imaging system is an optical sensor, leaves obscured some of the burning fuel in the growing season burn. To estimate the heat release in pot-sized areas of growing season burns, radiation was measured in unobscured burning fuels.

HARVESTS

At each harvest period, 10 trees were randomly chosen from each treatment. Harvests occurred six times during the study: (1) 2/15/2017, (2) 4/5/2017, (3) 5/15/2017, (4) 7/18/2017, (5) 8/29/2017, and (6) 12/8/2018 (Table 2.1). Harvest 1 occurred immediately before the dormant burn and harvest 3 directly preceded the growing season burn treatment.

Mortality was determined when the remaining 50 plants in each treatment were harvested, or at the end of the year for unharvested plants. Mortality was the lack of living root tissue at the time of harvest, or the lack of resprouts if the plants were not harvested. We measured height and basal stem diameter of the tallest stem and the number of sprouts remaining. Basal stem diameter was measured 5 cm from the soil air interface to avoid any influence of buttressing. Stems were separate if they were not connected above the soil surface. These measurements were also recorded for any resprouts from the redundant initial planting.

To gather aboveground biomass, trees were cut at the soil-air interface. Since each tree took a substantial amount of time to run through the leaf area meter, trees were harvested randomly over multiple days (within a week). To measure leaf area of the plants, all leaves larger than 20 mm in width were severed halfway through the petiole. Leaves that were more than 50% brown and senesced were not included. Leaf area was determined using a leaf area meter (3100C, LiCor Inc, Lincoln, NE, USA). In addition to total leaf area, the number of leaves was recorded. The leaves and remaining stem biomass were dried to a constant mass at 65°C and weighed.

Root biomass was collected by spraying the root mass with a hose and removing as much soil as possible. Roots were air dried for five days and then placed in the oven at 65°C. The root mass removed for starch analysis was added to the total.

GAS EXCHANGE

Using an infrared gas analyzer (6400 XT, LiCor Inc, Lincoln, NE, USA), gas exchange measurements were conducted on the leaves and soils of five trees from each treatment chosen for the following harvest. Three fully expanded leaves from each plant were measured; one apical terminal leaf, one lateral terminal leaf and one lateral interior leaf. Light was maintained at current environmental levels within the chamber (6400-02B, LiCor Inc, Lincoln, NE, USA). The reference CO_2 concentration was maintained at 400ppm and stability was defined when photosynthetic rates remained within 0.3 umol m^{-2} s^{-1} for at least 15 seconds. For Harvest 3, measurements were taken around midday. For harvests 4 and 5 leaf gas exchange was measured diurnally at times of 0600, 0900, 1200, 1500, 1800, and 2200. Soil CO_2 efflux (6400-09, LiCor Inc, Lincoln, NE, USA) was measured at 1200 during harvest 3 and 4 and diurnally at harvest 5;

areas of measurement were moved to ensure no soil disturbance for at least 9 hours prior to data collection.

TISSUE CHEMISTRY

Root samples were collected from each of the thirty plants harvested. Soil was removed from the plants up until the first axillary coarse root at least 1 cm in diameter. A 2.5 cm segment was taken from this root and the stem of each of these plants. The root segments were put in plastic bags and placed on ice in a cooler until they could be frozen at -85°C at the end of the day. The samples were left in the freezer on average 3 days until they were removed and placed in a freezer operating at -20°C until they were dried (Pelletier *et al.*, 2010).

Once dried, tissue samples were ground in a ball mill (8000-D mixer/mill, Spex Sample Prep, Metuchen, NJ, USA) until they were a talc like powder (8 minutes). Samples for carbon and nitrogen (C/N) concentrations were taken from the powder of several dried leaves, root, and stem tissues. Stem tissues were collected and carbon/nitrogen samples were analyzed at the Stable Isotope Ecology Laboratory (SIEL) at the University of Georgia.

Root starch concentrations were analyzed using an enzymatic glucose assay test (Zhao *et al.*, 2010; Luedtke, 2013). Soluble sugars were extracted three times using 80% ethanol at 80°C for 15 minutes and decanted following centrifuge. Insoluble starch in the remaining pellet was solubilized and broken into glucose with α-amaylase (Sigma-Aldrich A3403) at 85°C for 30 minutes followed by amyloglucosidase (Sigma-Aldrich 10113) at 55°C for an hour. The NADH produced due to enzymatic reactions from a glucose enzyme reagent assay kit (Sigma Aldrich G3293) was measured on well plates (96 Costar clear, Corning NY, USA) at 340 nm in a microplate reader (Flexstation 3, Molecular Devices, San Jose, CA) after incubation at 30°C. Starch reserves in the roots were estimated by multiplying the starch concentration in the coarse roots with the total root biomass and the estimated fraction (0.516) of stump and coarse roots to the total mass in irrigated and fertilized sweetgum (Coyle *et al.*, 2008; Coyle *et al.*, 2016).

STATISTICS

A multinomial logistic regression was used to compare the probability of survival among the three treatments. Other fire metrics were analyzed using t-tests. We tested the effects of season of burn (n=3: unburned, dormant season burned trees, growing season burned trees), time of harvest (n=6: harvests 1-6) and their interaction on starch and biomass using ANOVA. Mean comparisons were analyzed using Tukeys HSD. The impact of the redundant stems was analyzed using Fishers Exact test. Mid-day photosynthetic rates for each treatment (n=3: unburned, dormant season burned trees, growing season burned trees) at different times in the season (n=3: May, July, August) were analyzed using an ANOVA, and mean comparisons were analyzed with Tukeys HSD. Diurnal measurements (n = 6; 6 am, 9 am, noon, 3pm, 6 pm, 10 pm) of leaf photosynthetic rates for each treatment (n=3: unburned, dormant season burned trees, growing season burned trees) were analyzed using repeated measures with a nested design and mean comparisons were analyzed with a Tukeys HSD. The effects of time of harvest treatment on nitrogen concentrations for stems (n=3: unburned, dormant season burned trees, growing season burned trees, n=2: harvest 1 and 6), roots (same as stems) and leaves (n=3: unburned, dormant season burned trees, growing season burned trees, n=3: harvests 3, 4, 5) were analyzed with ANOVAs. Slopes of post burn biomass growth were analyzed using an ANCOVA and a comparison of simple slopes. A type-I error rate of $\alpha = 0.05$ was used for all ANOVA and Tukey tests. All variances reported are standard error.

RESULTS

Fuel moisture in the summer burn (9.26 ± 0.16%) was significantly lower than in the dormant burn (15.4 ± 0.31%) ($p < 0.0001$). There was no significant difference between the fire radiative energy captured by the FLIR between the two treatments of burns. Averaged across treatments, mean total radiative energy release was 4.76 ± 0.312 MJ. Radiative energy release measured within a 0.05 m^2 leafless area was similar in dormant (80 ± 3.6 kJ) and growing season burns (90 ± 11 kJ). Although leaves would have affected the convective heat present and the radiative energy collected by the FLIR, combusting fuel under the canopy likely released similar energy values to those in the leafless areas. All trees in the burned treatments were top-killed.

THE BURN RESPONSE

Mortality was significantly higher in dormant season burned trees (DBTs) (24%) than in unburned trees (2%) and growing season burned trees (GBTs) (2%) ($p = 0.0001$) (Figure 2.1, Supplemental figure 1). Mortality was evenly distributed across dormant burn repetitions. Largely, trees that died showed no evidence of resprouting after the burn; however, three dormant sprouts that exhibited mortality later in the year, were noted as showing signs of resprouting in May or June. Up until the final harvest, some plants were harvested that exhibited no evidence of resprouting but still had live roots. Most of these plants were considered alive and in the process of resprouting, but two dormant plants and one growing season plant collected in July and August respectively (>3 months post-burn) had very diminished root mass and were considered dead. Mortality inducing areas of dormant fires did not release a significantly larger amount of energy (77.7 ± 5.7 kJ) than areas of those burns that did not cause mortality (79.9 ± 4.2 kJ). There also was no significant difference in the energy released by the pots of trees that died (68.2 ± 26.5 kJ), and the trees that survived (69.8 ± 48.8 kJ).

STARCH CONCENTRATIONS

Coarse root starch concentrations were influenced by the burn treatment, but time of harvest affected that result (treatment × harvest interaction $p<0.0001$) (Supplemental table 2). Starch concentrations in roots by the end of the year (Unburned: 9.59 ± 0.30%, DBTs: 9.74 ± 0.41%, GBTs: 10.1 ± 0.13%) were not significantly different from one another and not different than those collected at the beginning of the year. Starch concentrations in unburned and growing season burned trees appeared to regain pre-leaf flush levels by mid-May and stabilized at around 10% of dry mass by early September (Figure 2.2). Concentrations for the rest of the year appear to follow root biomass dynamics. When root mass decreased, there was a corresponding drop in starch concentrations and as roots regained mass, starch was replenished. Variance across the unburned and growing season burned trees appear to be relatively similar, dormant season burned trees had the greatest variance in mid-season starch concentrations and this is reflective of the variance in biomass and development that the trees exhibited throughout the year. Starch concentrations in dormant season burned trees were statistically higher than the other two treatments following leaf flush (Figure 2.2: harvest 2). Dormant season burned trees and growing season burned trees lowest recorded starch concentrations (DBTs: 4.27 ± 0.97%, GBTs: 1.64 ± 0.38%) occurred in May and July respectively.

BIOMASS

Biomass (total, stem, root, leaf) was influenced by burn treatment, but that effect depended on the time of harvest (treatment × harvest interaction $p<0.0001$) (Supplemental table 3, 4, 5, 7). Season of burn did not influence stem or root biomass at the end of the growing season, but unburned trees exhibited nearly twice the biomass as burned treatments (Figure 2.3). Leaves were the consistently the initial resprouting structures followed by stems. Despite the death of all-above ground biomass, burned trees ended the growing season with more total biomass than when they started, with no significant difference between treatments (Figure 1). Other than the September harvest, variances within treatments appear to be relatively small and similar. Biomass decreased slightly for dormant season burned trees and unburned trees between the last two harvests, this is due to leaf senescence. Growing season burned trees continued to increase in biomass after the September harvest indicating that perhaps growing season burned trees had higher growth rates in the last period or lost less leaf mass than the other treatments. Unburned trees gained 220 g more biomass than burned trees. There was no significant difference between the growth rates of dormant and growing season burned trees (p = 0.4311, data not presented).

Leaf and stem biomass increased before root biomass, but biomass of all three organs increased concurrently during the middle of the summer (Figure 2.4, 2.7). There was a slight decrease in biomass in the final harvest that was likely a legacy of leaf harvesting technique, because half of the petioles remained on the stem during growing season harvests. By the end of the year, stem biomass of burned treatments were not significantly different from one another (Figure 2.4). In contrast, unburned trees nearly quadrupled the above-ground biomass of the burned treatments (202.1 ± 6.0 g) by the end of the growing season. There was no significant difference between the growth form of the two burned treatments. The height (DBTs: 0.67 ± 0.03 m, GBTs: 0.71 ± 0.02 m) and stem diameter (DBTs: 1.21 ± 0.05 cm, GBTs: 1.10 ± 0.06 cm) of the tallest sprout and number of sprouts (DBTs: 3.53 ± 0.58, GBTs: 4.55 ± 0.58) in each pot were relatively similar.

By the end of the growing season, root biomass was similar in burned treatments (DBTs: 189.1 ± 21.4 g, GBTs: 197.5 ± 11.6 g) and were significantly greater than the beginning of the year (DBTs: 97.0 ± 7.0 g, GBTs: 96.1 ± 10.1 g). At the end of the experiment unburned trees had significantly more root biomass than either of the burned treatments (273.3 ± 7.8 g). In fact, it appears that dormant season burned trees and growing season burned trees had almost exactly the same pattern in regrowth (Figure 2.5). There was no significant decline in root biomass in any treatments coinciding with the flush of new leaves and stem growth (Figure 2.5). The rates of greatest root accumulation appear to occur just after the July harvest. Root biomass did not differ from the initial biomass until September for unburned trees and December for burned trees. Estimated root starch reserves (the product of coarse root biomass and starch concentrations) were affected by the burn treatment but these results depended on the time of harvest (treatment × harvest interaction $p < 0.0001$) (Supplemental table 6). At the end of the growing season starch reserves were double those at the beginning of the year (Figure 2.6). Unburned, dormant season burned and growing season burned trees exhibited their lowest recorded starch reserves in April (1.06 ± 0.43 g), May (1.42 ± 0.34 g) and July (0.64 ± 0.19 g), respectively.

By September there was no significant difference in the amount of leaf mass between growing season burned trees and dormant season burned trees (Figure 2.7). Unburned trees lost some leaves in July but as noted in the methods, these trees suffered two instances of low soil moisture that led to large leaf senescence. At least one unburned tree exhibited a leaf flush after a low water event. By September, growing season burned trees had leaves with significantly higher specific leaf area (SLA) (174.1 ± 3.5 cm^2g^{-1}) than the other two treatments (Unburned: 124.5 ± 3.3 cm^2 g^{-1}, DBTs: 130.5 ± 4.4 cm^2 g^{-1}) ($p<0.0001$). New leaves tend to have higher SLA than older leaves (Dillenburg *et al.*, 1995). Since growing season burned trees had on average more than 40 cm^2 g^{-1}than the other treatments, large surface area could come at a smaller carbon cost. Leaves started to flush at the end of March and beginning of April for all unburned plants, and some of the dormant season burned trees. Leaf area was collected for the second harvest on April 7th 2017, at this time leaves had an average of (10.2 ± 0.66 cm^2) leaf area. The final average of estimated individual leaf area was 21.8 ± 1.3 cm^2 in September. Coinciding with this, leaf mass reached its peak in July for unburned trees and in late summer for burned treatments (Figure 2.7).

The redundant stems that persisted did not affect the experiment. There was no difference between the number of dormant season burned trees and growing season burned trees that contained other stems when tested at both the July and December harvests. The presence of these stems did not cause a significant difference in the mortality of plants or the harvested biomass of the trees. Although these redundant stems did not influence the sweetgums of interest, they did provide interesting results on their own. Redundant stems only suffered ~20% morality at each clipping (Table 2.2).

GAS EXCHANGE

Net photosynthesis was influenced by treatment, but the treatment effect depended on the time of day (treatment ×time of day interaction $p<0.0001$) (Supplemental figure 8). Photosynthetic rates were highest during in the morning, as PAR values were sufficiently high, but temperatures were lower (Figure 2.8). Mid-day photosynthetic rates were influenced by treatment, but treatment effects depended on the date of measurement (treatment × date interaction $p=0.0062$) (Figure 2.9, Supplemental figure 9). Photosynthetic differences between treatments present during mid-day were present throughout most of the day (Figure 2.8). In May, the photosynthetic activity of the growing season burned trees was quantified on trees that had not yet been burned and there was no difference between these trees and the unburned trees; however, dormant burned trees exhibited higher net photosynthetic rates. In July, growing season burned trees exhibited the highest photosynthetic rates while unburned and dormant season burned trees were similar. In August, net photosynthetic rates were similar among treatments. Soil CO_2 efflux was not significantly affected by root biomass, or treatment and only by temperature (Temperature f = 17.8857, $p<0.0001$; Treatment f = 1.64, p = 0.2418, Root biomass f = 0.4063, p = 0.5388).

CARBON/NITROGEN

The Carbon/Nitrogen ratio for leaves, stems and roots increased throughout the year. Nitrogen levels of dormant season burned trees throughout tissues and time exhibited a large amount of variance. Leaves had a significantly lower mean C/N for all treatments by harvest 5 (32.6 ± 1.75) than during harvest 3 (21.3 ± 1.58). C/N ratios were lower for the new leaves created post-burn. During harvest 3, growing season burned trees (24.7 ± 1.2) and unburned trees (25.0 ± 0.9) had higher C/N ratios than dormant season burned trees (14.2 ± 2.3). During harvest 4, unburned trees (29.5 ± 0.4) were not significantly different than growing season burned trees (23.0 ± 0.4) but were higher than dormant season burned trees (21.9 ± 2.7). By harvest 5 there was no significant difference between the C/N ratios of the leaves. Stem and root nitrogen concentrations were significantly lower at the end of the year (0.45 ± 0.15%, 0.41 ± 0.13% respectively) than at the beginning (1.20 ± 0.11%, 1.32 ± 0.14% respectively) ($p < 0.0001$ for both). There was no significant differences between the treatments of stem and root nitrogen concentrations at the last harvest.

DISCUSSION

We observed no evidence to support the hypothesis that acute damage to stored reserves associated with growing season burns resulted in increased mortality. In fact, mortality following growing season burns was non-existent. Although starch concentrations decreased after top-killing growing season burned trees, they recovered relatively quickly (~45 days) to concentrations similar to unburned trees.

For growing season burns to impact starch reserves, the burn must occur within a narrow temporal period immediately after leaf flush when reserves are low, but before the new leaves begin repaying the debt. Starch concentrations decreased after growing season burns both after leaf flush and during resprouting; however, there was little mortality in this treatment. This finding suggests that newly expanded leaves quickly recoup carbon capitol expended by their construction, and starch depleted by leaf flush was replenished by at least May 15th. Not only did growing season burned trees survive the mid-May burn, but by the end of the growing season, starch concentrations among burn treatments were similar and root biomass was higher than pre-treatment. Starch concentrations in roots are notoriously variable among procedures and between laboratories, but relative concentrations within one laboratory and procedure appear to be fairly accurate (Quentin *et al.*, 2015). Depending on the type and size of tree, starch depletion during times of carbon demand is highly variable. We extracted starch from first lateral roots, and it is possible that starch mobility may be affected by the order of the roots, though starch can be mobilized throughout the root system (Aubrey *et al.*, 2012b; Aubrey and Teskey, 2018). Concentrations of starch in sweetgum declined during leaf flush and resprouting (Figure 2.2), though starch levels quickly returned to near pre-leaf flush levels by mid-May (at the latest by 45 days post leaf flush). This indicated that the non-resource-limiting environments of our study, sweetgum did not experience the hypothesized acute carbon deficit driven by leaf building. Leaves start exporting carbohydrates as soon they are 10-50% expanded (Keel and Schädel, 2010). This suggests that sweetgum trees not yet burned had starting exporting sugars by April 7th. It is likely that after this point the demand on stored root starch diminished and by the next harvest starch reserves in unburned trees were replenished. When sweetgum resprouted after top-kill, the first tissue replaced was a single leaf. Therefore, sweetgum only requires enough stored starch to supply the stem growth to the soil surface plus half of one leaf.

The higher mortality observed in the dormant season burns is at odds with previous hypotheses. While our experimental design did not capture the full effects of a prescribed fire in the field, fire radiative energy release did not differ between treatments and higher radiative release was not associated with higher mortality. A possible explanation for the dormant season burn mortality could be the hard frost that trees experienced in late March, to which resprouting plants are particularly vulnerable (Wolken *et al.*, 2009). Although we did observe some leaf damage, frost is unlikely the sole mortality agent as several dormant burned trees exhibited some resprouting in May and June and then experienced total dieback. Although we cannot be certain of the cause of mortality in the dormant burned trees it is appears very unlikely that lack of carbon reserves is principally responsible.

Fire intensity is a major driver in the amount of hardwood top-kill (Glitzenstein *et al.*, 1995). We top-killed all plants and it is unlikely that fire intensity is the reason for our differential mortality. As expected, energy release was not different between the two treatments in the leafless areas. While ambient temperatures theoretically increase growing season burn temperatures (Wagner, 1973; Wade and Johansen, 1986), the high water content of live fuels can dampen and cool these burns (Sparks *et al.*, 2002). However, fire energy release was sufficient to cause 100% top-kill in our study. Furthermore, any variation in fire energy release within the burns did not explain mortality. Also, the heat from low intensity burns generally does not impact roots (Varner *et al.*, 2005). While fire intensity is critical as a driver of top-kill in wildland fires, it is unlikely that heat alone was the mechanism of mortality in this experiment.

Another proposed mechanism explaining mortality, referred to as chronic starch depletion, is that after growing season burns, plants do not have time to replenish carbon reserves before then end of the year and after multiple years of annual growing season burns, plants fail to resprout (Waldrop *et al.*, 1992). We found that by the end of this experiment, the burned trees not only had coarse root starch concentrations similar to pre-flush levels (Figure 2.2), but final estimated starch root reserves had also surpassed pre-harvest levels suggesting complete recovery (Figure 2.6). Since this was not a multiple year study we were not able to directly address this mechanism; however, results indicate that chronic carbon depletion is not the mechanism for sweetgum mortality. While clipping hardwood sprouts may be less damaging than burning, because enough sustained heat can damage dormant root buds (de Groot and Wein, 2004), redundant stems experienced only ~20% mortality when clipped at each harvest (Table 2.2), contrary to the increasing mortality percentage that would be expected with chronic starch depletion. Even if plants burned in the growing season were unable to replenish their reserves in resource-limiting conditions, annual burning may not be a useful technique as one-year fuel accumulation is often insufficient to top-kill hardwoods (Glitzenstein *et al.*, 1995). By the end of the experiment, starch reserves were twice as large as at the beginning (Figure 2.6). These results indicate that in optimal growing conditions (i.e. high light, sufficient water and nutrients), annual prescribed burns are unlikely to deplete sweetgum starch reserves.

Plants burned in the dormant season did not capitalize on the three extra months they had to grow above-ground biomass compared to the growing season treatment. By early December following the burns, unburned trees had nearly 100% more total biomass, 300% more above-ground biomass and 50% more root biomass, than both burned treatments. Although dormant season burned trees had an additional 90 post-burn growing days, unfavorable growing conditions and low metabolic rates in cool seasons are likely reasons why the first 45 days post-burn yielded little growth. By early April, root starch reserves in the unburned treatments had declined, whereas average starch remained largely unchanged in dormant season burned trees because of the high variability in initiation of resprouting. Growing season burned trees also tended to establish terminal buds later in the year than either unburned or dormant season burned trees. Although previous studies found that trees burned in the dormant season had more sprouts, growth forms among burned treatments in our experiment were relatively similar.

Photosynthetic rates among burned treatments were similar, although mid-day rates peaked at different times of the year among the treatments (Figure 9). Newer leaves on plants typically have higher photosynthetic rates than older leaves (Taiz and Zeiger, 2002). Differential photosynthetic rates likely did not substantially affect the growth rates of burned treatments because dormant season burned tree's and growing season burned tree's periods of peak photosynthesis from young leaves were similarly far from the summer solstice. Thus, the high rates of photosynthesis in new leaves on unburned trees likely contributed to the plants ability to replenish starch reserves and add above-ground biomass between the second and third harvest. Water stress in unburned trees, led to low photosynthetic rates and in extreme cases drought induced leaf senescence, resulting in a decreased amount of accumulated carbon.

There are many environmental factors that exist in forests that were not replicated in this experimental study that may be responsible for similar biomass of burned treatments at the end of the growing season despite difference in length of the post-burn growing season. The unburned plants became pot-bound, restrained from typical root growth. Maintaining adequate water was also a consistent problem in the pots of unburned trees because unburned trees transpired large amounts of water and their canopies diverted the overhead irrigation off of the pots. Without the constraints of the water shortages and being root bound, unburned trees likely would have gained even more biomass. The plants used in our study were not connected to each other via rooting networks. Despite the lack of evidence for carbon starvation being the cause of mortality, root connections could be fundamental for saplings ability to fight disease. Growing season burned trees growing in suboptimal conditions in forests may not be able to recover as quickly after growing season burns. While trees were initially grown in fertilized conditions, leaf nitrogen levels were similar to those found in the field (Norby and Iversen, 2006). In addition, final nitrogen concentrations in coarse roots were similar to those in other hardwoods (Hendrick and Pregitzer, 1993; Aubrey *et al.*, 2012a; Akburak *et al.*, 2013; Terzaghi *et al.*, 2013). Since there was no significant difference between final nitrogen concentrations it is unlikely that nitrogen would have been more limiting of growth in dormant season burned or unburned trees. However, it is possible that over the course of years, lack of nitrogen could limit the resprouting of sweetgums. While there could be some other unaccounted environmental variables, we have found no evidence of the physiological impacts proposed as driving higher growing season burn mortality.

Drawing conclusions about the effects of season of burn are difficult because contradictory results (Glitzenstein *et al.*, 1995; Drewa *et al.*, 2002; Sparks *et al.*, 2002; Robertson and Hmielowski, 2014; Reilly *et al.*, 2017). It is likely that much of this variability across studies could be explained by environmental conditions on the day the burn, including fuel characteristics and the amount of live vegetation within the burn. For example, studies have either found little to no difference between tree densities and mortalities (Robertson and Hmielowski, 2014; Barlow *et al.*, 2015), some differences (Glitzenstein *et al.*, 1995) or large differences. While Waldrop *et al.* (1992) is considered a foundational study of the effects of season of burn and first proposed starch concentrations as the mortality mechanism, it has serious methodological issues due to the timing of the post-burn measurements. Summer annual burns were measured 1-month post-burn, whereas winter annual plots were measured 7 months post-burn. In another long term study, trends of top-kill across season are similar to those of mortality (Glitzenstein *et al.*, 1995). This lack of difference between top-kill and mortality indicates that either fire burned hotter in their early growing season plots, or trees were more sensitive to girdling at that time of year, but not that starch concentrations caused higher mortality in top-killed trees. The results of the research reported here, in Cruz *et al.* (2003) and in Robertson and Hmielowski (2014) on season of burn provide little to no evidence that reduced starch concentrations after different seasons of burn induce mortality in resprouting hardwoods.

Based on the results of our study, we find that growing season burns do not cause higher mortality than dormant season burns if fire intensities are similar. Given the mixed results in the past and the importance of top-kill in maintaining this ecosystem, we suggest that managers prioritize burning more acreage over waiting for a particular season. While our treatment was designed to ensure top-kill, prescribed fires in the growing season can be patchy and low intensity due to high live fuel moisture and vegetation impeding wind and air flow in fires. Sweetgum can grow in large clusters connected by roots which could amplify both the fire dampening effect and provide for greater stored carbon reserves building resiliency to growing season burns (Glitzenstein *et al.*, 1995). Our findings suggest that decreased starch concentrations from leaf flush occur at most about 45 days but likely much less, in optimal growing conditions. In addition, there was no evidence in this experiment that low starch concentrations caused mortality during resprouting. For fire managers looking to decrease sweetgum abundance, it is advisable to burn whenever the conditions are most optimal for the fuel to carry fires. While the mortality we detected occurred in an experiment setting, and needs to be pursued in a field setting, the results were both compelling and counter to the established paradigm. Since the application of prescribed fire is already constrained by many variables outside the control of a manager, the addition of a further seasonal constraint to control sweetgum is not supported by available evidence.

While we did not find support for our hypothesis that available carbon in the form of starch was the mechanisms driving patterns of mortality, the question of what drove the high dormant season mortality remains. We argue that continued research should focus on the root tissues of plants that suffered mortality. We showed that the mechanisms behind tree mortality from different seasons of burn are more nuanced than depletion of carbohydrate reserves and it was difficult to observe when plants that are top-killed finally suffer mortality, doing so is critical to understanding the underlying mechanisms of mortality. An experiment designed around testing the tissues of recently deceased top-killed trees for carbon, nutrients and possibly hormones could provide insight into the mechanism driving mortality. While this study focused on sweetgum, further research studying the response of other resprouting hardwoods such as oaks is also required and important in other fire dependent systems where sweetgum is less prevalent.

CONCLUSION

Season of burn experiments are inherently hard to carry out due the temporal separation of the application of fire and the variability of fire. Comparing the growth of trees following a disturbance is difficult because not only can the timing of the disturbance be different, but the environmental conditions in which the plants resprout will also be different. Confounding just one or two of the myriad of variables may have led to the conclusion of differences between dormant and growing season burns. The purpose of this study was to carefully control what we thought were the most important variables to explicitly explore the mechanisms causing mortality.

The most significant finding from this experiment was that the only significant mortality occurred after the dormant season burn. While we are cautious in applying these results out of context, this result certainly deserves deeper investigation as it is completely counter to the majority of research published on season of burn. This is partially because we chose an experimental setting and many other studies reported on field manipulations. It is interesting that many trees failed to resprout with considerable NSC reserves suggesting some other physiological mechanism. A relatively conservative interpretation of our results is that if sweetgum control is a management objective, top-killing stems regardless of season is critical.

A second significant result was that, in spite of a total loss of aboveground biomass, burned plants gained biomass over the course of the study. By the end of the study, unburned trees had almost twice the biomass as the burned treatments. It is likely that if the trees weren't root-bound that their year-end biomass would have been significantly higher. Due to the root constriction unburned trees also suffered moisture stress that caused premature leaf senescence in July and August. This is also evidence of higher water use by the unburned trees than the burned trees.

Previous papers repeatedly cite the decreasing density of woody stems to be the reason that managers should burn in the growing season (Waldrop *et al.*, 1992; Glitzenstein *et al.*, 1995). The presence of the higher stem densities does not necessarily mean that the above-ground biomass for dormant season burned trees is higher, as was seen in this experiment. Indeed even if the sprouts in the different seasons of burn do have different biomasses, this may not be reflective of the individual’s vitality (Grady and Hoffmann, 2012). Due to the confounding variables in some of the previous studies, and the results of this study, it seems likely that the benefits of growing season burns in decreasing the amount of above-ground biomass for shrubs has been overstated.

CHAPTER 3

CONCLUSIONS

Sweetgum (*Liquidambar styraciflua*) resprouts are a hindrance to the productivity and stability of southern pine ecosystems (Martin and Shiver, 2002). Fire is an efficient and cost effective method to maintain these ecosystems and control hardwood resprouts. Although recurrent fires every one to two years can decrease the abundance of these hardwoods in pine stands (Reilly *et al.*, 2017), burning in different seasons has produced mixed effects in decreasing hardwood abundance. In this study we grew sweetgum in optimal conditions and controlled for top-kill in dormant season (February) and growing season (May) burns. Contrary to hypothesized mechanisms for sweetgum mortality, dormant season burned trees had the lowest survival, and starch reserves can be replenished within 45 days of leaf flush or top-kill. Despite fewer post burn growing days, growing season burned trees ended the year with similar biomass and starch concentrations as dormant season burned trees. Although both burned treatments ended the year with more biomass than initial measurements, they still only had half of the biomass of unburned trees. These results indicate that sweetgum grown in a high resource environment can persist even if forests burn annually, and regardless of season of burn.

Though we saw significantly higher mortality in the dormant season burned plants, we still lack field studies to verify these results. We have strong support for the influence of top-killing (Wenger, 1953; Lotti, 1956; Waldrop *et al.*, 1992; Glitzenstein *et al.*, 1995; Robertson and Hmielowski, 2014), it is advisable that land managers should aim to control rather than eradicate sweetgums. Top-kill of sweetgums is therefore essential. We observed that sweetgum that does not become top-killed will have around 4 times the above-ground biomass of top-killed sweetgum by the end of the growing season. Likely this above-ground biomass will transpire more water resulting in higher competition with desirable pine. If these trees grow a large enough dbh (7.5cm) (Chen *et al.*, 1975) then not only do they become resistant to fire, they begin succession to a hardwood forest and can support tens to hundreds of sweetgum root sprouts (Kormanik, 1990). Growing season prescriptions are known to burn in a mosaic fashion throughout the forest, likely due to the large impact live fuel moisture can have on a fire (Sparks *et al.*, 2002). Fire should be applied to areas with these large clusters only when the fuel and conditions are appropriate to top-kill all of the sweetgum in the group. Since biomass at the end of the year was equal between season of burn treatments, managers should burn at their own discretion on all available days that will top-kill all sweetgum rather than focus on one season. Annual burning has been shown to be effective at reducing the density of hardwood stems in an area (Reilly *et al.*, 2017), but our study shows that persistence may still occur if growing conditions are optimal. Indeed, fuel loading on annually burned plots often is not high enough to ensure top-kill in these areas (Glitzenstein *et al.*, 1995), so these burns should be considered only if fuels are adequate to top-kill sweetgum. Due to the large variety of southern pine ecosystems and the elusiveness of eradication, land managers looking to control sweetgum should use their own discretion and knowledge of their plots to burn when they can ensure top-kill.

Table 2.1: The dates and contexts of the harvests

Harvest	**Date**	**Context**
1	2/15/2017	Pre-dormant season burn harvest
2	4/05/2017	Leaf flush harvest
3	5/16/2017	Pre-growing season burn harvest
4	7/18/2017	Mid-Summer Harvest
5	8/29/2017	Late Summer Harvest
6	12/08/2017	End of Year Harvest

Table 2.2: Information on the redundant stems present in the experiment. Redundant stems were clipped twice in 2016 (July, December). They were then clipped again in May, June, July, August and September of 2017, after their presence was recorded.

Date	**Total Pots**	**Pots with stems**	**Total number of stems**	**Stems/ pot**	**Times cut**	**% of Pots**	**% Decrease**
May-17	180	94	508	5.40425531	2	0.522222	
Jun-17	150	62	314	5.06451612	3	0.413333	0.208511
Jul-17	150	63	226	3.58730158	4	0.42	-0.01613
Aug-17	120	37	117	3.16216216	5	0.308333	0.265873
Dec-17	75	18	68	3.77777777	6	0.24	0.221622

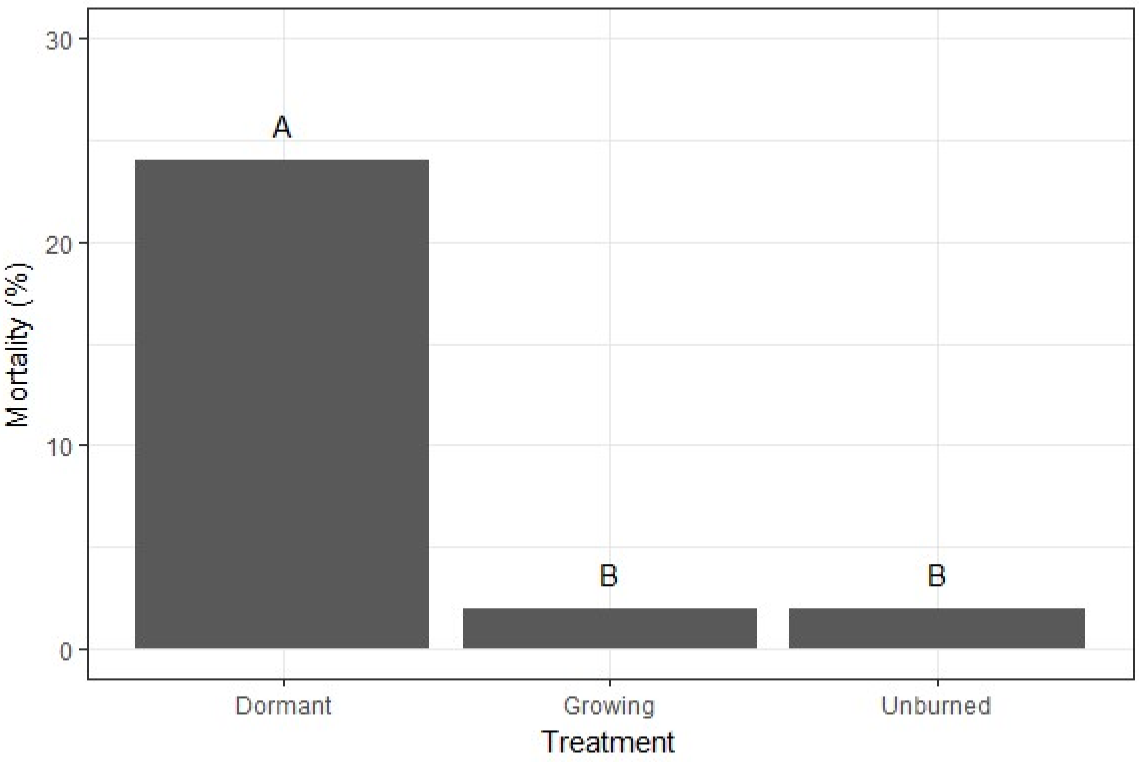

Figure 2.1: Mortality of trees in each treatment. Mortality was determined by examining the roots at the time of harvest. For trees not harvested by the end of the year, trees were considered dead if there was no above-ground biomass.

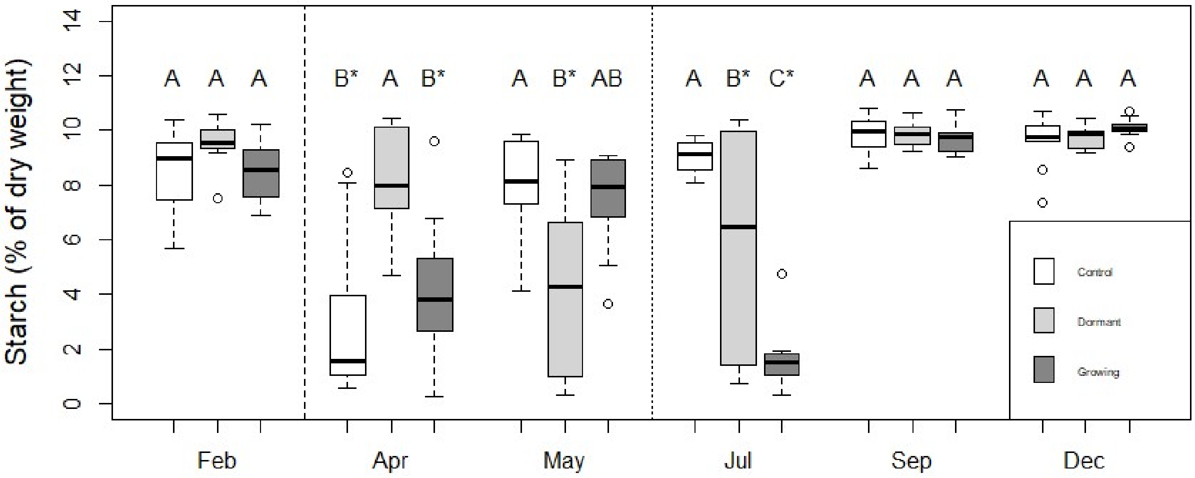

Figure 2.2: Starch concentrations (% dry weight). Boxplot displays median, upper and lower quartiles of the population. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05). Asterisks represents significant difference from initial biomass.

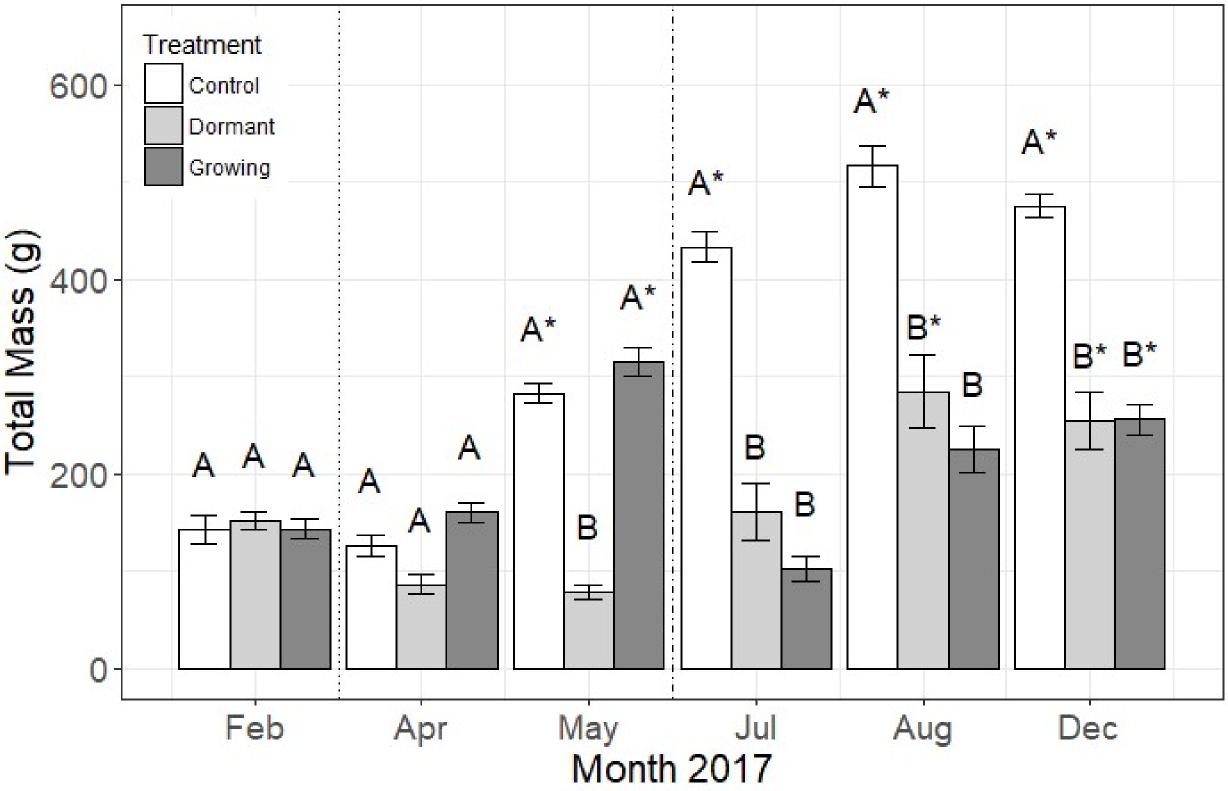

Figure 2.3: Average biomass in grams of the whole plant masses in the different treatments. The first dotted line indicates the application of the dormant burns and the second vertical line is the application of the growing season burns. Error bars represent the standard error. Asterisks represent significant difference from initial biomass. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05)

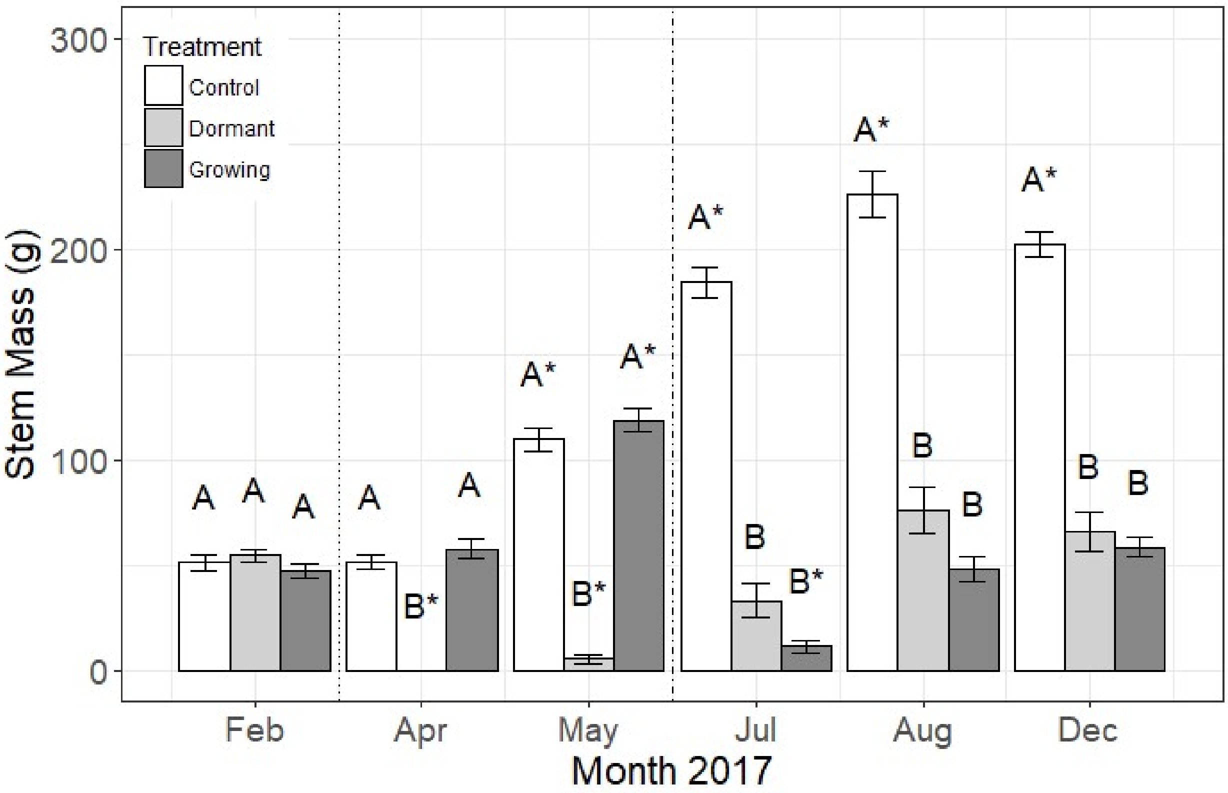

Figure 2.4: Average stem biomass in grams of the plants in the different treatments. The first dotted line indicates the application of the dormant burns and the second vertical line is the application of the growing season burns. Error bars represent the standard error. Asterisks represent significant difference from initial biomass. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05)

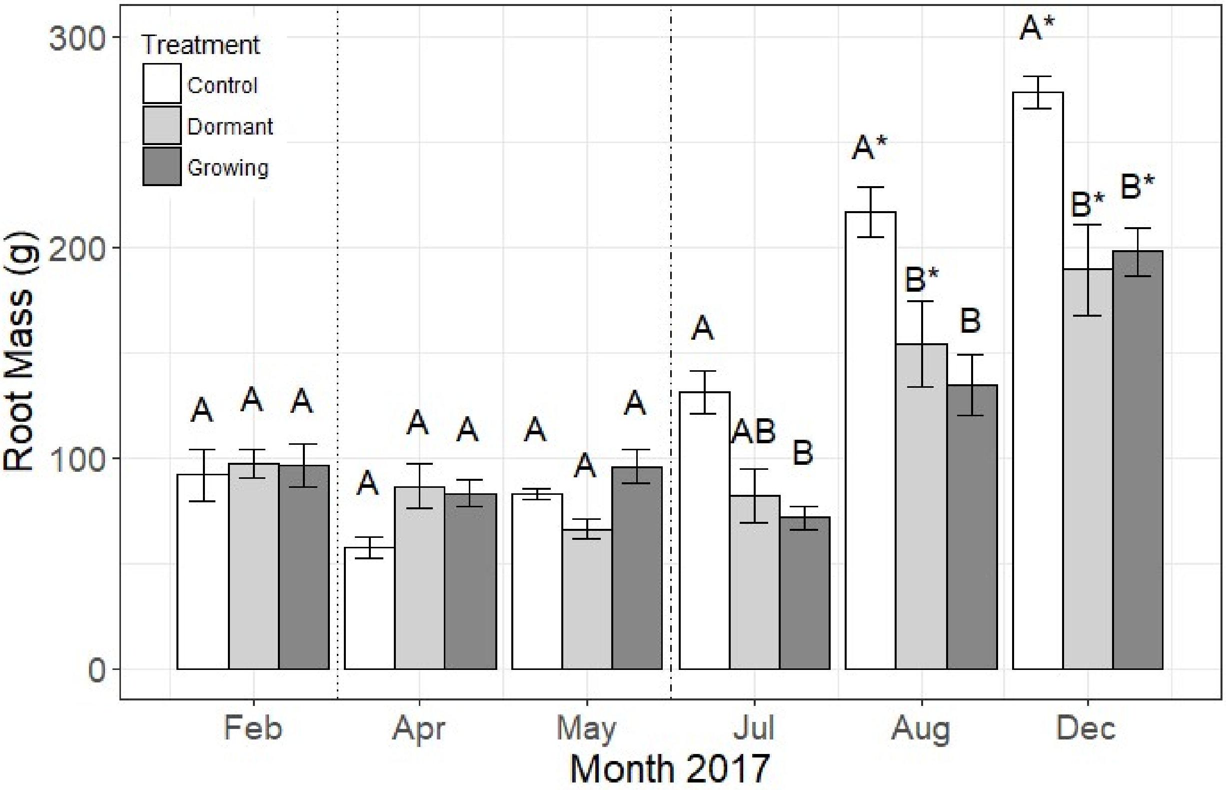

Figure 2.5: Average root biomass in grams of the plants in the different treatments. The first dotted line indicates the application of the dormant burns and the second vertical line is the application of the growing season burns. Error bars represent the standard error. Asterisks represent significant difference from initial biomass. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05)

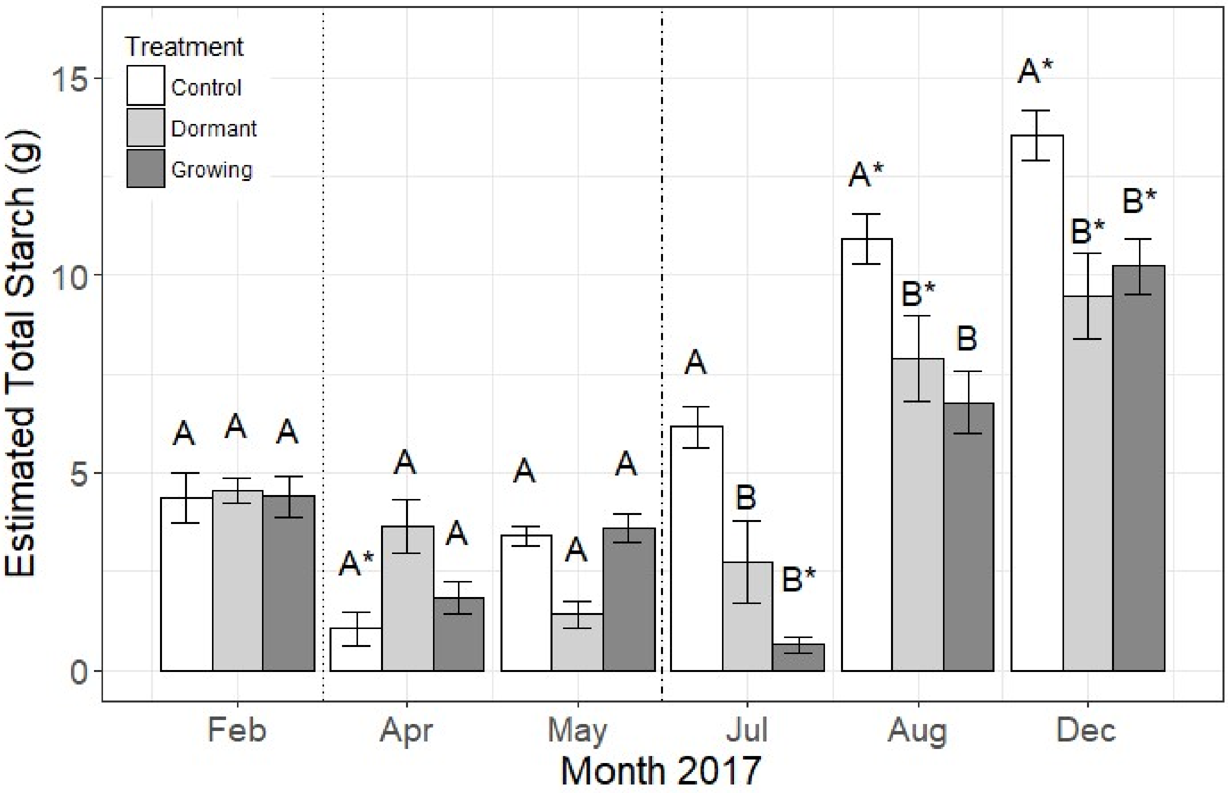

Figure 2.6: Average estimated starch mass in grams of the plants in the different treatments. Starch is estimated by multiplying the starch concentration by the root mass by the estimated fraction of the root that are coarse roots. The first dotted line indicates the application of the dormant burns and the second vertical line is the application of the growing season burns. Error bars represent the standard error. Asterisks represent significant difference from initial biomass. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05)

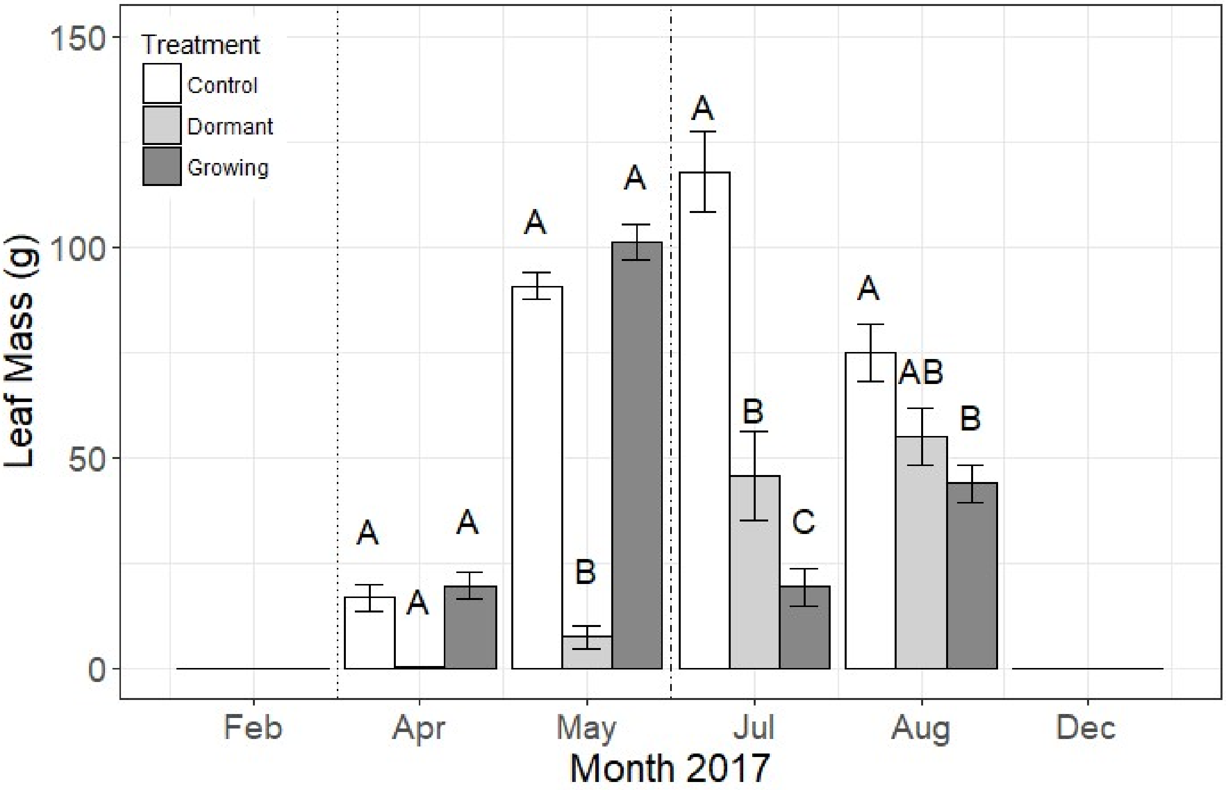

Figure 2.7: Average leaf biomass in grams of the plants in the different treatments. The first dotted line indicates the application of the dormant burns and the second vertical line is the application of the growing season burns. Error bars represent the standard error. Asterisks represent significant difference from initial biomass. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05)

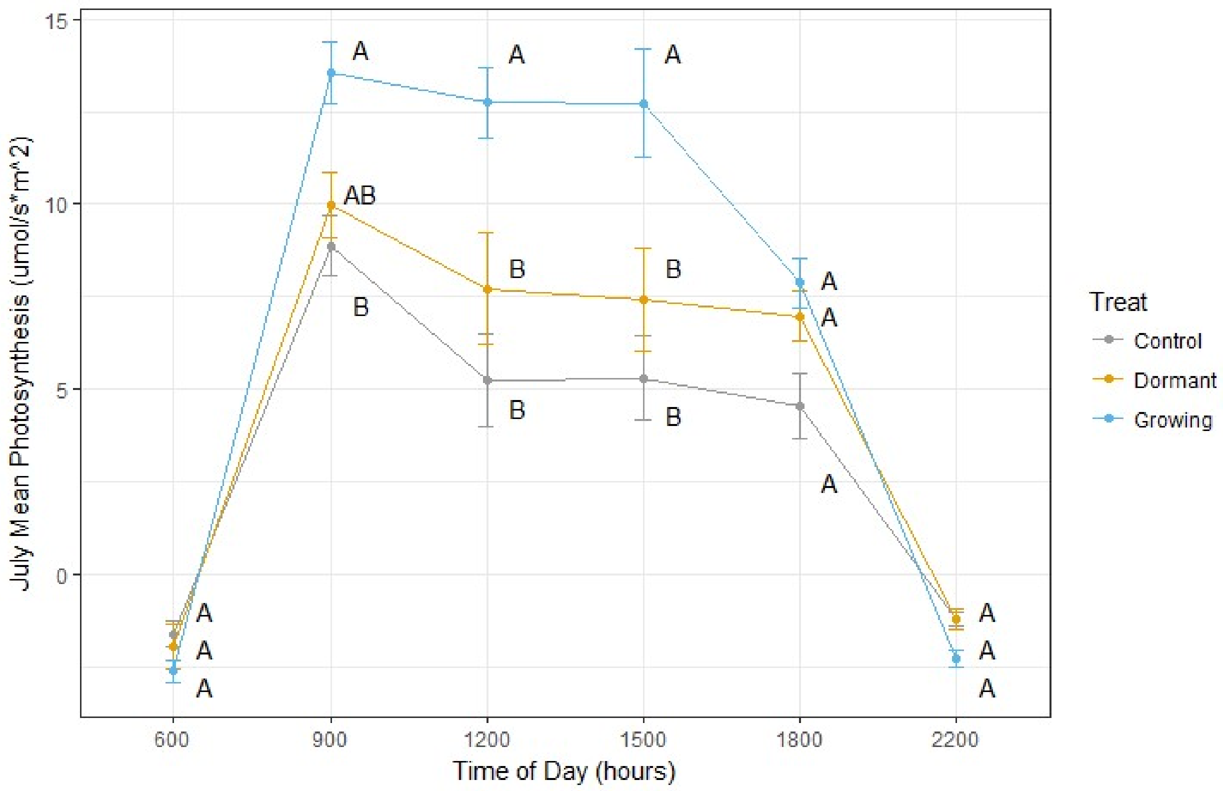

Figure 2.8: Diurnal Photosynthesis in July. Error bars represent the standard error for each treatment. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05)

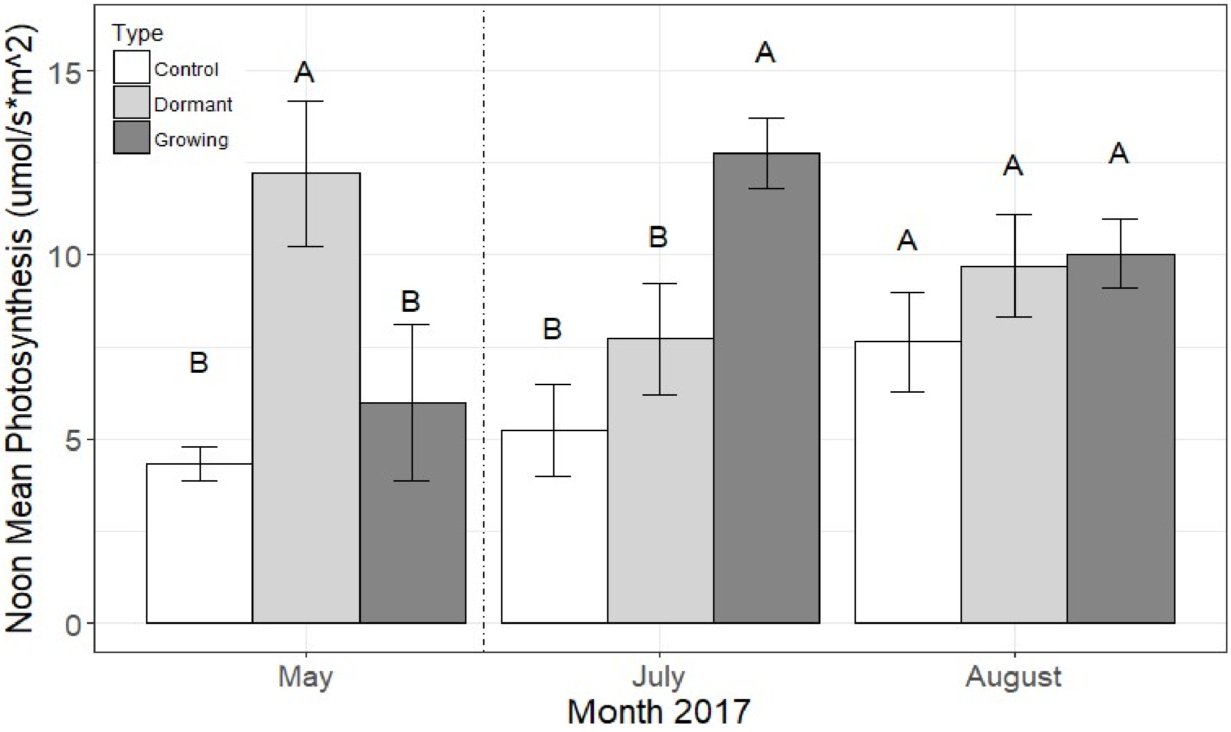

Figure 2.9: Photosynthesis at noon in different months, Error bars represent the standard error at each time point. Means sharing a letter within a given month are not significantly different (Tukeys HSD α = 0.05)

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APPENDIX A: SUPPLEMENTAL TABLES

Supplemental Table 1: Parameter Estimates of the Logistic regression of Mortality:

Term	*Estimate*	*Std Error*	*ChiSquare*	*Prob> Chisquare*
Intercept	-2.972	0.489	36.96	<.0001
Burn[Unburnedl]	-0.899	0.761	1.4	0.2374
Burn[Dormant]	1.819	0.525	12.01	0.0005

Supplemental Table 2: ANOVA table: Starch Concentrations ~ Harvest × Treatment with an adjusted r^2 of 0.661.

Source	*Partial SS*	*Df*	*MS*	*F*	*Prob>F*
Model	1157.20	17	68.07	20.0104	<.0001
Harvest	634.2	5	126.84	37.2921	<.0001
Treatment	38.65	2	19.33	5.6806	0.0042
*Treatment*Harvest*	458.87	10	45.89	13.4891	<.0001
Error	506.86	150	3.38		
Total	1664.06	167			

Supplemental Table 3: ANOVA table: Total Biomass ~ Harvest × Treatment with an adjusted r^2 of 0.856.

Source	*Partial SS*	*Df*	*MS*	*F*	*Prob>F*
Model	2897070.5	17	170416	61.1170	<.0001
Harvest	1170637.0	5	234127.4	83.9661	<.0001
Treatment	826803.8	2	413401.9	148.2601	<.0001
*Treatment*Harvest*	901291.7	10	90129.2	32.3234	<.0001
Error	432195.1	155	2788		
Total	3329265.7	172			

Supplemental Table 4: ANOVA table: Stem Biomass ~ Harvest × Treatment with an adjusted of r^2 0.926.

Source	*Partial SS*	*Df*	*MS*	*F*	*Prob>F*
Model	708529.31	17	41678.2	127.7529	<.0001
Harvest	140730.92	5	28146.2	86.2743	<.0001
Treatment	315158.57	2	157579.3	483.0153	<.0001
*Treatment*Harvest*	256584.61	10	25658.5	78.6488	<.0001
Error	50567.32	155	326.2		
Total	759096.63	172			

Supplemental Table 5: ANOVA table: Root biomass ~ Harvest × Treatment with an adjusted r^2 of 0.748.

Source	*Partial SS*	*Df*	*MS*	*F*	*Prob>F*
Model	603842.59	17	35520.2	28.6811	<.0001
Harvest	498356.69	5	99671.3	78.8867	<.0001
Treatment	33359.16	2	16679.58	15.463	<.0001
*Treatment*Harvest*	73906.83	10	7390.7	6.6217	<.0001
Error	177759.24	155	1146.8		
Total	781601.83	175			

Supplemental Table 6: ANOVA table: Starch Reserves ~ Harvest × Treatment with an adjusted r^2 of 0.788.

Source	*Partial SS*	*Df*	*MS*	*F*	*Prob>F*
Model	2256.82	17	132.8	37.2646	<.0001
Harvest	1839.76	5	368.0	103.2861	<.0001
Treatment	126.51	2	63.3	17.7565	<.0001
*Treatment*Harvest*	260.18	10	26.2	7.3033	<.0001
Error	530.81	149	3.56		
Total	2787.62	166			

Supplemental Table 7: ANOVA table: Leaf biomass ~ Harvest × Treatment with an adjusted r^2 of 0.899.

Source	*Partial SS*	*Df*	*MS*	*F*	*Prob>F*
Model	262084.95	17	15416.8	90.8570	<.0001
Harvest	1476823.51	5	29536.5	174.0701	<.0001
Treatment	29499.57	2	14749.8	86.9262	<.0001
*Treatment*Harvest*	80466.98	10	8046.7	47.4223	<.0001
Error	26300.66	155	169.7		
Total	288385.61	172			

Supplemental Table 8: ANOVA table: Photosynthesis ~ Date × Treatment with an adjusted r^2 of 0.341.

Source	*Partial SS*	*Df*	*MS*	*F*	*Prob>F*
Model	1085.72	8	135.715	9.62	<.0001
Date	61.7952	2	30.899	2.19	0.1161
Treatment	487.918	2	243.959	17.294	<.0001
*Treatment*Date*	509.203	4	127.3	9.02	<.0001
Error	1763.28	125	14.106		
Total	2849	133			

Supplemental Table 9: ANOVA table of repeated measures of photosynthesis in July with an adjusted r^2 of 0.800.

Source	*DF*	*F Ratio*	*Prob >F*
Type	2	15.267	0.0005
Time	5	173.9185	<.0001
*Type*Time*	10	8.3234	<.0001

APPENDIX B: SUPPLEMENTAL FIGURES

Supplemental Figure 1: Figure 2.10: Average daily temperatures (°C) during the experiment. Temperatures were recorded every fifteen minutes at a field station 100 m away from the plants. Maximum and minimum temperatures of the day are in grey, and the average temperature is in orange.