

**PHOTOSYNTHESIS, WATER USE, AND BIOMASS ALLOCATION OF PRINCESS
TREE (*PAULOWNIA TOMENTOSA*) AND TULIP POPLAR (*LIRIODENDRON
TULIPIFERA*) FIRST YEAR SEEDLINGS ACROSS LIGHT AND PRESCRIBED FIRE
CONDITIONS**

A thesis presented to the faculty of the Graduate School of
Western Carolina University in partial fulfillment of the requirements
for the degree of Master of Science in Biology

By

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April 2021

ACKNOWLEDGEMENTS

I would like to thank my committee members and director for their assistance, encouragement, and resources. Especially Dr. Collins's flexibility, guidance, and tireless editing. I also extend my appreciation to the following people, without whom the completion of my thesis would have been impossible: my family, for providing me with a greenhouse and my study plot on our property; Joel Scott and Cindi Brown, for training me and allowing me to use the equipment at the Coweta's Hydrologic Lab; Dr. Thomas Martin for his endless patience and aid with statistics and experimental design; and Dr. Collins for allowing me to have access to the equipment needed to complete my research during the COVID-19 pandemic. I also would like to express my appreciation to Chelcy Miniati for all her dedication and advice throughout my thesis, and the resources and insight she was able to provide.

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LIST OF ABBREVIATIONS

PATO - <i>Paulownia tomentosa</i> (PATO, Princess tree).....	vii
LITU - <i>Liriodendron tulipifera</i> (LITU, Tulip poplar)	vii
N - Nitrogen	vii
P - Phosphorus	vii
K - Potassium.....	vii
WUE - Water Use Efficiency	viii
SLA - Specific Leaf Area	viii
A_{net} - Net photosynthesis	3
E - Transpiration rate	4
RH - Relative Humidity	14
T_{air} - Air Temperature.....	14
VWC - Volumetric Water Content	14
TDR - Time Domain Reflectometry.....	14
g_s - Stomatal conductance.....	15
PPFD - Photosynthetic Photon Flux Density.....	15
C - Carbon.....	16
C:N - Carbon to Nitrogen	16
QA - Quality Assurance.....	17
QC - Quality Control	17
VPD - Vapor Pressure Deficit.....	17
E _a - Actual vapor pressure.....	17
E _s – Saturation vapor pressure.....	17
kPa – Kilopascals.....	17
ANOVA - Mixed-model analysis of variance	18
FS - Full Sun	19
PS - Partial Sun	19
SH - Shade	19
BN - Burn.....	19
UN - Unburn	19
ppm– Parts per million.....	23

ABSTRACT

PHOTOSYNTHESIS, WATER USE, AND BIOMASS ALLOCATION OF PRINCESS TREE (*PAULOWNIA TOMENTOSA*) AND TULIP POPLAR (*LIRIODENDRON TULIPIFERA*) FIRST YEAR SEEDLINGS ACROSS LIGHT AND PRESCRIBED FIRE CONDITIONS

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Forest communities experience disturbances, such as fire and canopy removal, which create light gradients and microclimates that affect establishment, carbon gain, and height of native and invasive pioneer tree species that flourish in open or full sun areas. To test the hypothesis that the invasive tree *Paulownia tomentosa* (henceforth PATO, princess tree) has a stronger positive response to post-disturbance microclimates than native *Liriodendron tulipifera* (henceforth LITU, tulip poplar), I compared photosynthesis, biomass, and allometry of first-year seedlings of both species in a field experiment. The field study had a split-plot experimental design with plots distributed in two rows across forest light treatments (open, edge, canopy) and either burned or unburned treatments. Environmental variables (relative humidity, temperature, soil temperature, soil moisture), soil nutrients (nitrogen, phosphorus, and potassium (N, P, K)), gas exchange (transpiration, photosynthesis, and stomatal conductance), and allometry (number of branches, plant height, number of leaves, plant width, and stem width) measurements were made. Additional allometric measurements (leaf mass, average internode length per plant, root collar diameter, total plant biomass, average root length, number of lateral roots), along with tissue carbon: nitrogen ratios, were taken at the end of the growing season. Air temperature, soil moisture content, and soil temperature varied among light treatments. The interaction between

row and light treatments also differed in microclimates in the field study. The only significant difference detected for photosynthetic rates and stomatal conductance occurred between rows A and B; net photosynthesis and stomatal conductance of both species were higher in row B. Neither species differed in water use efficiency (WUE) between burned or unburned treatments or among light treatments. Neither mean leaf area, specific leaf area (SLA), nor root length differed among treatments. All other allometric measurements differed significantly between the species and among light treatments. PATO was larger in size across all allometric measurements. Overall, the allometric results suggest PATO had greater growth and was larger across all microclimates of burned and unburned soil conditions and light treatments compared to LITU. The C:N ratios revealed that PATO had more carbon in their roots compared to LITU, while LITU invested more carbon into their leaves than PATO. LITU had more nitrogen in its roots, leaves, and stems than PATO. Future research should be conducted to compare PATO with other native species such as yellow birch (*Betula alleghaniensis*), red maple and sugar maple (*Acer rubrum* and *Acer saccharum*), and American beech (*Fagus americana*). In addition to comparing PATO's photosynthetic rates, biomass accumulation, and success of establishment across different microclimates among different ecosystem communities, PATO's ability to obtain nutrients and association with arbuscular mycorrhizal fungi, which are the fungi that benefits plants by obtaining nutrients needed for growth and development, should be investigated due to the nutrient change found within the nutrient soil samples. Overall, PATO's ability to gain rapid height growth and leaf mass, and allocate its resources, especially in full sun, to growth and establishment suggest that PATO will continue to increase on the landscape in Southeastern forests, perhaps at the expense of LITU.

CHAPTER ONE: INTRODUCTION AND BACKGROUND

Timber harvest frequency in the U.S. has increased since the 1970s, predominantly in the hardwood regions, demonstrating the need for forest products found in mature second growth forests (Adams et al., 2000; Fajvan et al., 1998). The increase of timber harvest in mature forests has led to an increase in understory light availability and soil disturbance, which has historically allowed ‘shade intolerant’ species such as *Liriodendron tulipifera* (tulip poplar; hereafter, LITU) to regenerate and colonize these open disturbed areas (Busing, 1995; Mou et al., 1993). Recently, non-native invasive tree species such as *Paulownia tomentosa* (princess tree; hereafter, PATO) have begun to establish and are becoming more abundant following harvests or natural disturbances in eastern forests (Kuppinger, 2008). My research investigated first-year LITU and PATO seedlings’ photosynthetic responses, allometric growth and biomass, across different microclimates and natural light gradients and between prescribed fire, burned and unburned soil treatments, to determine whether PATO could continue to increase and possibly replace LITU in Southeastern forests.

Disturbance and Biodiversity

Forest biodiversity depends on species’ abilities to regenerate after human disturbances, such as timber harvests, or natural disturbances such as drought, fire, or severe storms (Westerling et al., 2006; Emanuel, 2005; Breshears et al., 2005; IPCC, 2001; Knutson et al., 1998; Overpeck et al., 1990). Disturbance frequency, predictability, size, severity, and intensity can determine which species colonize the area, impacting forest development (Busing, 1995; Denslow & Spies, 1990; Prentice & Leemans, 1990; Platt & Strong, 1989; Whittaker 1956).

Forest response and development after a disturbance occur along disturbance-generated environmental gradients; species traits such as shade tolerance, water and nutrient use efficiency, biomass allocation patterns, and height growth rates determine how species sort along these gradients (Dietze & Clark, 2008; Kota, 2007; George & Bazzaz, 1999a, b; Denslow et al., 1998; Fahey et al., 1998; Berkowitz et al., 1995; Facelli, 1994; Lorimer et al., 1994; Harmon & Franklin, 1989; Veblen, 1989; Harper, 1977; Korstian & Coile, 1938).

The spread of invasive plants, such as PATO, threatens native biodiversity, structure and function of ecosystems, and productivity of agricultural and natural resource industries (Mack et al., 2000; Hobbs & Mooney, 1998; Walker & Vitousek, 1991). Characteristics common to invasive plants are high allocation to reproductive tissues, rapid vegetative growth rates, and high acclimation potential (Rejmanek, 1996; Bazzaz, 1986). Other traits enabling invasive species to be more successful in their invaded environments than native species are their prolific seed production and dispersal, longer flowering periods, higher rates of seedling recruitment, more efficient leaf arrangement, faster growth rates, better recovery from leaf loss, or greater phenotypic plasticity (Durand & Goldstein, 2001; Ehrenfeld, 1999; Fogarty & Facelli, 1999; Lavergne et al., 1999; Martin, 1999; Williams et al., 1995).

One way to identify mechanisms of invasive plant species success is to compare native and non-native species that overlap in range, share morphological traits, and have a common life-history (Mack, 1996; Schierenbeck & Marshall, 1993). As described below, LITU and PATO are examples of such species, and investigating their early seedling growth can reveal differences in allometry, photosynthetic rates, and biomass allocation that might influence whether PATO, LITU, or both continue to increase in Southeastern forests.

Plant Ecophysiology and Allocation

Environmental conditions, including light, soil and air temperatures, carbon dioxide concentrations, and rainfall can influence the rate at which a plant assimilates carbon and loses water through its leaves (Chapin, 1991). Photosynthetic rates and active photosynthesis depend, in part, on how long the stomata remain open during the day. Plants in high light conditions and under water stress can have a rapid reduction in leaf net photosynthesis (A_{net}) and are more likely to be predisposed to photoinhibition than shaded plants (Abrams et al., 1992; Gamon & Pearcy, 1990; Gauh, 1979; Kolb et al., 1990; Ögren & Öquist, 1985; Björkman & Powles, 1984; Ludlow & Björkman, 1984). High light levels can lead to increased air and leaf temperatures, resulting in an increase in vapor pressure deficit and transpiration, which can trigger stomates to close when water uptake cannot meet demand (Chen et al., 1995; Larcher, 1980; Geiger, 1965).

Plant response to variation in light intensity and water availability is characterized by the trade-off between shade and drought tolerance. Different tolerances over environmental gradients such as light, nutrients, and water result in different optimal growth points among species and species shifts over gradients (Griscom & Griscom, 2012; Bigelow & Canham, 2002; Kobe et al., 1995; Huston & Huston, 1994; Kitajima, 1994; Pacala et al., 1994; Ellison et al., 1993; Latham, 1992; Smith & Huston, 1990; Keddy, 1990; Huston & Smith, 1987; Chapin, 1980; Mooney et al., 1978; Grime & Hunt, 1975; Whittaker, 1975). Typically, open-adapted plants have high rates of net photosynthesis (A_{net}) (Durand & Goldstein, 2001; Baruch & Goldstein, 1999; Wullschleger, 1993). Plants with high photosynthetic capacity exhibit high rates of biomass accumulation and growth, enabling them to outcompete and rapidly colonize areas compared to species that assimilate carbon at lower rates (Lambers & Poorter, 1992; Grime &

Hunt, 1975). Such plants may show a trade-off with water use. In general, carbon gain is increased by stomatal opening, high temperatures, carbon dioxide and light availability which results in greater water loss by transpiration (E). The ratio between rates of photosynthesis and transpiration provides an instantaneous measure of water use efficiency (WUE). Low water use efficiency due to high transpiration rates can limit plant growth in high light or dry air conditions.

Another mechanism for plant success is the minimization of carbon costs associated with photosynthesis, which leaves more carbon available for growth and reproduction. Leaf area per unit of leaf mass (specific leaf area, SLA) is a measure of the photosynthetic surface area per unit of investment in leaf tissue, and is positively associated with rapid growth rates (Walck et al., 1999; Reich et al., 1998; Lambers & Poorter, 1992). Invasive species tend to have higher maximum rates of photosynthesis and higher SLA than native species (Walck et al., 1999; Reich et al., 1998; Lambers & Poorter, 1992). This enables invasive species to be more efficient at capturing and utilizing light resources, especially in high light environments associated with disturbance, which serve as the entry point for many invasive species (Petryna et al., 2002; Hobbs, 1989). When non-native and native species have similar photosynthetic rates, invasive species can often be more successful, partly due to thinner leaves which cost less carbon per unit of photosynthetic area for leaf construction (Nagel & Griffin, 2001; Baruch & Goldstein, 1999; Pammenter et al., 1986). In general, plants with high photosynthetic rates and lower carbon cost in leaf production may allocate 'surplus' carbon to above- or belowground growth.

Allometry, or architecture, impacts plant photosynthetic and bioaccumulation rates. Shifts in biomass allocation can maximize carbon gain over environmental gradients (Chapin, 1991). Species-specific patterns of seedling growth, especially height, enable seedlings to exploit

available space, forage for higher light microsites, and possibly overtop surrounding vegetation (Givnish, 1995; King, 1994; Küppers, 1994; Caldwell, 1987). Understory tree characteristics vary with tree size (Claveau et al., 2002; Naumburg et al., 2001; Sterck & Bongers, 2001; Bond, 2000; King, 1986). Immature seedlings of tall-growing tree species in forested understories are resource limited, and high light interception and rapid height growth may be required for seedlings to establish themselves in the canopy (Oldeman & van Dijk, 1990; King, 1981; Horn, 1971). Species respond differently to environmental gradients through leaf-level physiological and morphological acclimation, plant-level acclimation, changes in biomass allocation, and crown architecture (Walters & Reich, 1999; Canham et al., 1999; Gardiner & Hodges, 1998; Beaudet & Messier, 1998; Kitajima, 1994; Sipe & Bazzaz, 1994).

Seedlings with small leaves require longer branches, than those with larger leaves, in order to support an equal area of leaves (Givnish, 1984). Small, simple leaves favor plants that form wide crowns (Oldeman & van Dijk, 1990; Kohyama, 1987; Givnish, 1984; Ashton, 1978). Crown morphological characteristics determine the pattern of light interception by leaves in the canopy (Givnish, 1995; King, 1994; Küppers, 1989, 1994; Canham, 1990, 1988; Kohyama, 1987). A species' first branching height of a young tree is thought to be related to leaf-size (Cao, 1995; King, 1994; White, 1983). Positive relationships between the ratio of height growth to lateral growth and light has been observed (Chen et al., 1996; Parent & Messier, 1995; Klinka et al., 1992). Crown or trunk biomass ratio significantly influences a tree's stability and height growth (King 1981, 1986). Branching morphology and leaf size are correlated with sapling crown and trunk allometries (Karizumi, 1979). Corner's rule predicts the thicker the plant's axis, the larger the plant's appendage(s) (Kohyama & Hotta, 1990; Kohyama, 1987; Givnish, 1984; White, 1983; Halle' et al., 1978).

Tree root biomass can also be affected by light conditions. A large allocation of biomass to roots is a beneficial adaptation for surviving in shade and increasing establishment (Cannell & Dewar, 1994; Rogers et al., 1993). Trees in areas with shade and partial sun may invest more in roots than in open areas with open or in full sun (Cannell & Dewar, 1994). Over time, immature trees can decrease root allocation and invest more in aboveground biomass, altering their root - to-shoot ratio (Cannell & Dewar, 1994; Kitajima, 1994; Rogers et al., 1993). Similar alterations also occur with water stress. Smith and Huston (1990) proposed plants in drier conditions would allocate more biomass to roots than to aboveground structures. Root architecture affects a tree's mechanical stability and its ability to acquire water and nutrients. Deeply rooted seedlings may be better able to resist drought and may occur more frequently within plant communities (Becker & Castillo, 1990). A tree's rooting depth is genus- or species-specific (Deans et al., 1996). Species that experience senescence, stem, or leaf die-back, have an increase in root-to-shoot ratios. The ratio of roots decreases as height increases for saplings (Walters & Reich, 1996; Shukla & Ramakrishnan, 1984; Kira & Shidei, 1967). Root biomass allocation in seedlings increases a plant's fitness by storing its resources in the roots until the desired conditions are presented for those resources to be allocated to shoot growth. Species with this adaptation can become more prevalent in ecosystems, which can aid invasive species by increasing their establishment and success within Southeastern forests.

Princess tree (*Paulownia tomentosa*)

PATO is a rapidly growing, highly invasive, non-native, deciduous tree species that occurs in the southeastern United States in frequently disturbed sites. PATO is a species in the Scrophulariaceae family. Mature PATO trees have opposite, heart-shaped leaves that are pubescent on the abaxial and adaxial surfaces (Brown & Leopold, 2007). In early spring, large,

purple, pubescent flowers bloom, then form persistent pecan-shaped capsules in terminal clusters (Brown & Leopold, 2007). PATO trees also have hollow pith and lateral buds located above the axillary bud on stems, and notched leaf scars (Brown & Leopold, 2007). Juvenile PATO have a different appearance with large, cordate serrated leaf margins.

PATO was introduced to North America from Asia for multiple uses, such as phytoremediation and timber production (Kumar et al., 1999; Bergmann, 1998). It can increase biomass rapidly and reach maturity in 8–10 years in the wild or 3–4 years in plantations (Tenter et al., 2018; Beckjord & McIntosh, 1983). It has been naturalized in the Southeast for about 150 years, but the rate of spread has increased since 2000 (Kuppinger, 2008, Tang et al., 1980). Mature trees are estimated to produce 20 million small, oval, winged seeds per year that are wind dispersed. Plants can also regrow quickly from stump sprouts or root suckers when aboveground tissues are damaged (Vujičić et al., 1993). This species is known to have rapid growth rates and mature early (Longbrake, 2001; Carpenter et al., 1983; Hu, 1961). Seedlings grow best in open sun but can be found in shaded areas (Lovenshimer & Madritch, 2017). Shaded trees can be outcompeted by native canopy species (Kuppinger et al., 2010); thus, the majority of PATO occurs on exposed areas where there is high light availability and few to no trees to compete with (Kuppinger et al., 2010; Kuppinger, 2008).

PATO is dimorphic; adult trees have smaller leaves, while immature trees have broad, larger leaves (personal observation, Dinkins). Combined with high photosynthetic rates, this leaf dimorphism could confer an advantage when exposed to low light levels (Venekiaas & Poorter, 1999) and allocation to large leaves can shade out competing native plants (Lovenshimer & Madritch, 2017). Although adults have smaller leaves, as trees gain height, the crown shades an

increasingly larger area. Thus, impacts made by PATO on native plant communities can depend on the time since they have invaded (Dostál et al., 2013; Strayer et al., 2006).

Princess Trees and Ecological Disturbance

Disturbances create favorable conditions for PATO to invade (Manel & Holderegger, 2013; Todorović et al., 2010). Patterns of invasion over a landscape depend on variables such as elevation and vegetation cover, which influence seed dispersal patterns (Manel & Holderegger, 2013; Todorović et al., 2010;). PATO seeds tend to grow and germinate in recently disturbed areas (Brose et al., 2013; Kuppinger et al., 2010; Kuppinger, 2008; Keeley, 2006; Longbrake, 2001; Langdon & Johnson, 1994; Carpenter et al., 1983). Seeds can remain viable in seedbanks for 2–15 years until exposed to a minimum light requirement for germination, facilitating seedling establishment after disturbances (Todorović et al., 2010; Longbrake, 2001;). Once established, trees can survive fire and other disturbances by adventitious root or stump shoots (Hu, 1961).

PATO allometry has been shown to differ with light conditions. Longbrake and McCarthy (2001), found that seedlings and transplanted cuttings grown over light gradients allocate resources to belowground growth in the first few weeks, then shifted allocation to aboveground growth. Shaded plants had lower growth rates but larger leaf areas than full sun plants. Further, the ability to re-sprout was determined by the amount of belowground biomass, which was reduced in low light conditions (Longbrake & McCarthy, 2001). In general, immature trees had larger leaves than adults, which increased carbon gain in low light conditions (Longbrake & McCarthy, 2001). In the wild, such variation in allocation to leaf and shoot biomass may allow young trees to maximize growth in the complex conditions following a canopy or fire disturbance.

Tulip poplar (*Liriodendron tulipifera*)

LITU is a deciduous tree, native to the Southeastern United States, tending to have bright yellow fall foliage. LITU is a tree species in the family Magnoliaceae. The leaves are simple, alternate, and “dog face” shaped (Brown & Leopold, 2007). LITU does not have different growth patterns between adult and immature trees. Leaf scars are large and tend to be almost circular. LITU have light- to dark—gray, smooth bark that tends to have black “v” shaped marks below branches. The tulip-shaped flowers have green-yellow petals with orange blotched spots near the center. The fruits of LITU flowers are cone-like, brown, winged samaras (Brown & Leopold, 2007).

LITU is a prolific, early successional, hardwood species known for its extensive height. It grows rapidly and can live up to 300 years. It is used commercially for construction and furniture, and as a food source for wildlife and pollinators, especially bees (Beck, 1990). Its wide geographic distribution reflects its tolerance to a wide variety of conditions. A single tree can produce 741,000 seeds, of which 5–90 percent will germinate depending upon conditions. The wind dispersed seeds tend to travel 600 feet from the parent tree and can remain viable in seedbanks for extensive periods, and sprout after disturbance (Kota et al., 2007; Beck, 1990; Clark & Boyce, 1964). Cut trees can stump sprout above or below the soil (Wendel, 1975).

Tulip poplar and Ecological Disturbance

Historically, LITU has responded to ecological disturbances where light availability increases (Busing, 1995; Mou et al., 1993). Timber harvests within mature forests have increased the amount of light availability to the understory. LITU seeds can be viable within the seedbank for many years, without germinating, due to the light requirement needed to grow (Beck, 1990). Timber harvests also cause soil disturbance, which has historically allowed ‘shade intolerant’

species such as LITU to regenerate. The combination of soil disturbance and light availability in the understory creates favorable conditions for LITU to germinate and colonize these areas (Busing, 1995; Mou et al., 1993).

CHAPTER TWO: METHODS

PATO seeds were collected fall, 2019, by harvesting ripe seed pods from four trees located in Yadkin and Haywood Counties, NC, USA. Once the pods were collected, the seeds were extracted by cracking the pods open and scraping out the seeds with forceps. LITU seeds were purchased online from Sheffield's Seed Company Inc. in fall 2019. Both species' seeds have a light requirement for germination, but also need to be exposed to cold, or stratified, for 60 to 90 days to break dormancy. However, LITU seeds have a 5-90 percent germination rate, while PATO almost has a 100 percent germination rate when exposed to light (Kota et al., 2007; Zhen, 1999; Beck, 1990; Clark & Boyce, 1964). Once all the seeds were harvested or had arrived, they were placed into plastic bags containing peat and a small amount of water. Bags were sealed and placed into the refrigerator over winter, 2019/2020. The seeds were stratified for 92 days at the maximum temperature of 5.5 °C. Once the outdoor temperature dropped below 0 °C at night and the daily high was below 5.5 °C, seeds were placed outside for four days to be exposed to natural temperature variation.

Germination Methods

During germination, in March 2020, I tested the germination rates between the two species in burned and unburned soil. I planted 100 seeds from each species in 7 x 14 gridded cell trays, each cell was 5.1 cm x 2.54 cm. Unburned trays contained soil that was burned in 2017 from a prescribed fire, to allow me to isolate the effect of burning. Unburned trays contained the same soil, but from unburned areas. The top two inches of the soil were removed from the top of a sloping hill, the burned and unburned soil was gathered from the same hill and location. The collected soil was not manually inoculated by a mature tree from either species. Each cell contained two seeds from the same species within the tray, but both species were present in the

same tray and exposed to the same environmental conditions within a greenhouse. A total of 50 cells were planted in each tray: 25 cells contained LITU seeds, while the other 25 cells had PATO. Seeds were not immersed into the soil but laid on the surface of the soil to resemble natural dispersal, as a light requirement is needed, and trays were watered daily.

Field Experiment Methods

A field experiment was conducted to examine first-year growth of LITU and PATO. Newly germinated seedlings of PATO (described above) and field collected newly germinated seedlings of LITU were grown under shade, partial sun, and full sun conditions, and between burned and unburned soil conditions over the summer growing season of 2020. Each light treatment had two rows of replication. Half of each set of plots within each light treatment were burned, and the other half was left unburned, creating a blocked, nested, split-plot design with six blocks (Figure 1). To generate seedlings, seeds from each species were placed in open trays filled with fertilized potting soil and inoculated soil from around the roots of mature trees from each species and placed within their separate respective trays. The trays were watered daily. However, since no LITU seedlings germinated, the seedlings needed for this study were collected from the wild and placed into open flats and watered daily. After germination, seedlings were planted in the field design (Figure 2).

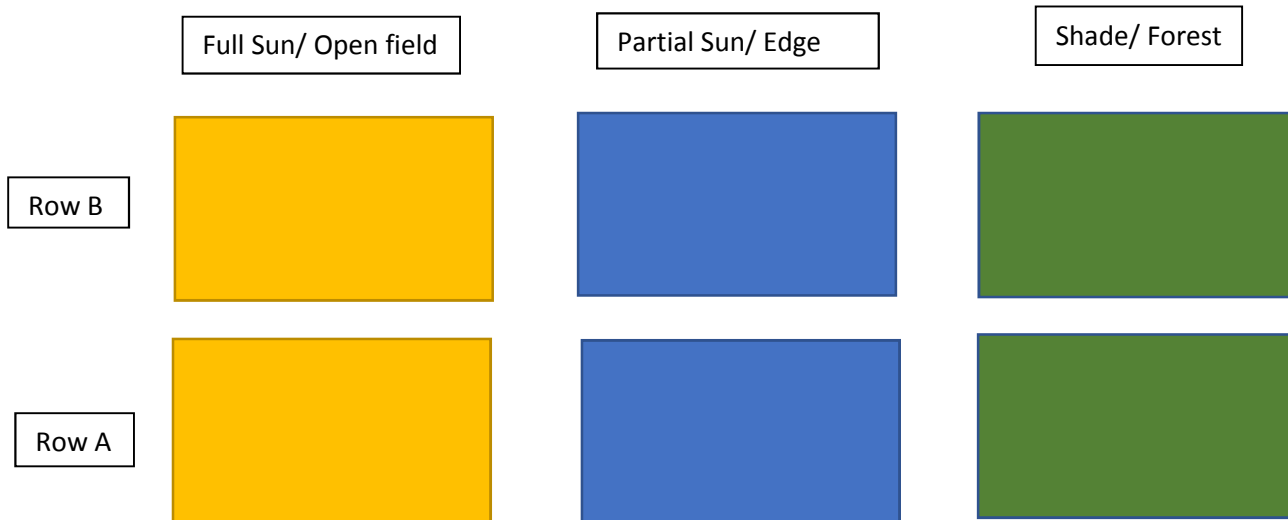


Figure 1. The arrangement of all six schematic blocks of this experimental design, which contain two replicate blocks in each light treatment of open, edge, forest. The rows A and B were located 15.24 m apart and the full sun, partial sun, and full shade blocks in each row were 9.25 m apart.

Study Site and Field Design

The field study site used for this research was a sloping hill comprised of meadow, ecotone, and forest near an abandoned homestead in East Bend, Yadkin County, North Carolina, USA. A total of 144 seedlings, 72 from each species, were planted in the field experiment. The six plots were divided between rows A and row B, with each of three light treatments in each row (Figure 1). Rows A and B were located 15.24 m apart. The full sun, partial sun, and full shade plots in each row were located 9.25 m apart. Each of the six plots contained 12 seedlings, six from each species (Figure 2). Half of each plot was treated with prescribed fire 26 days before seedlings were planted, creating twelve 2 m x 3 m subplots. Prescribed fire was performed by removing the debris from the outer edges of the burned areas to create a fire break. Once the fire break had been created gasoline was poured on the furthest edge that went the direction the wind was blowing to create a backfire. The other half of the six replications had

current vegetation or forest understory removed by raking or weed-eating the current vegetation down to less than 1 cm in height. Each meter contained two individuals of the same species. Seedlings were arranged randomly in two rows of six, containing the two species (Figure 2).

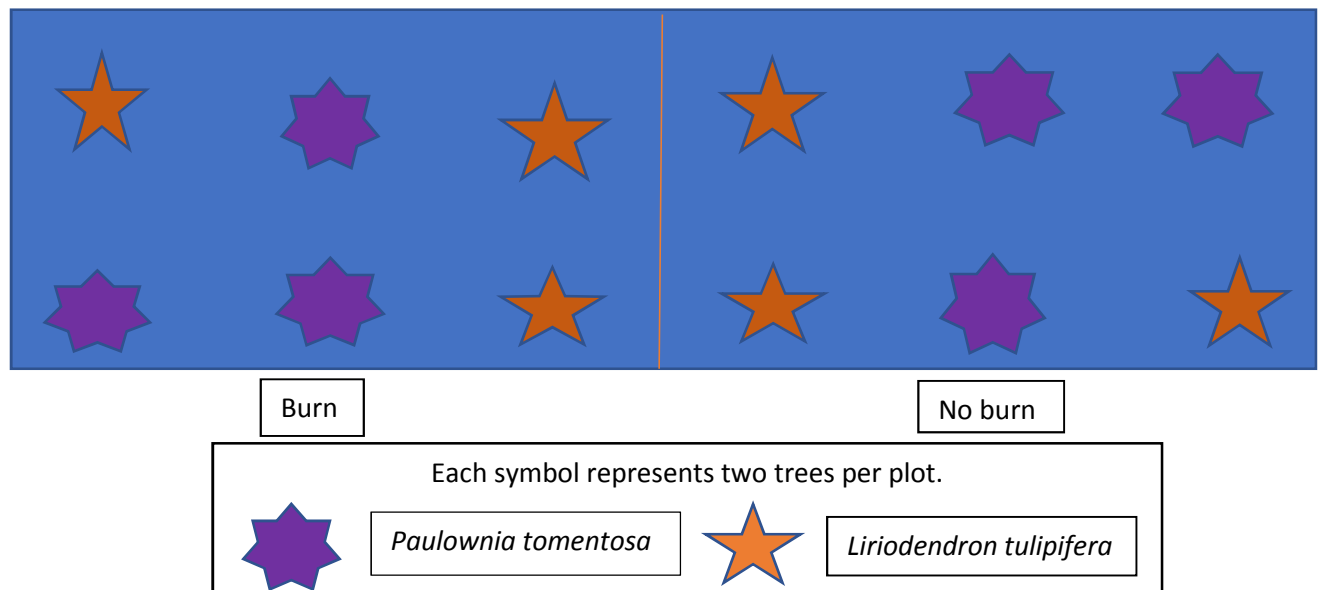


Figure 2. One of the six schematic experimental plantings to test photosynthesis, water use efficiency, and biomass allocation in PATO and LITU first-year seedlings across a light treatment (open, edge, forest) and burned vs. unburned soil/litter conditions.

Environmental Measurements

The following measurements were taken daily in burned and unburned sections of each of the six plots: soil temperature ($^{\circ}\text{C}$) and volumetric water content (VWC, %) (Time Domain Reflectometry, Spectrum TDR). Daily values were averaged seasonally. In each of the six plots I also measured air temperature (T_{air} , $^{\circ}\text{C}$) and relative humidity (RH, %) (ibuttonTM) every 10 min

at 20 cm above ground height during the growing season. One day before planting the seedlings in their respective plots, 12 soil samples were taken for soil nutrient analysis (N, P, K). Samples were analyzed by Waypoint Analytical Virginia, Inc., using their basic standard testing procedures for soil analysis and fertility. Each soil sample was taken within each light treatment and among subplots that had been burned or unburned. After the trees had been planted for 115 days, at the end of the growing season, another 12 soil samples were taken the day plants were harvested in each light treatment among burned and unburned subplots and analyzed as described above.

Photosynthetic Measurements

Net photosynthesis rates (A_{net} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf area s}^{-1}$) were collected during the summer for each tree. Photosynthetic measurements were taken around mid-day (11 am -3 pm) when net photosynthesis was at its daily peak; a daily total of 24 specimens were measured on a rolling weekly basis. Photosynthetic measures of photosynthesis (A_{net}), stomatal conductance (g_s), and transpiration rates (E) were measured by using an open system and clamping the (Li-6400, Licor Inc.) chamber onto the leaf and measuring gas exchange under reference CO_2 at 400 ppm and at a photosynthetic photon flux density (PPFD) of $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ conditions (Li-6400, Li-Cor).

Allometric, Biomass, and Carbon and Nitrogen Measurements

Seedlings grew until October 3rd (summer/early fall). The biomass accumulation and allometric measurements were taken at the end of the growing season. End-of-season allometric measurements were taken in the field when plants were being harvested. Some other measurements were taken in the lab, after the plants had been harvested, such as total biomass.

End-of-season allometry measurements and ratios included leaf area (cm^2), leaf mass (g), ratio of leaf mass to area (SLA, $\text{g}:\text{cm}^2$), number of leaves, number of branches, average internode length per plant (mm), total height and width (cm), root collar diameter (mm), average root length (cm), number of lateral roots, ratio of aboveground (cm) to belowground root length (cm), ratio of aboveground height (cm) to total plant biomass (g), and ratio of root length (cm) to total plant biomass (g) (Pisek et al., 2011; Westoby et al., 2002; Holmgren, 2000). Some allometric measures were made in the field, such as aboveground height (cm), width of the plant (cm), average internode length (mm), number of leaves, and number of branches. Stem diameter (mm) and root collar diameter (mm) was measured in the field with calipers, and the total height was measured from the soil to the top of the plant (Holmgren, 2000). The width of the plant was measured at the widest part of the plant with a meter stick, and the length of roots was also measured with a meter stick from the tip of the root to the root collar. Leaf area was determined digitally by using the Leafscan iPhone application; a picture was made of the leaf on a 10cm^2 grid and the app calculated leaf area (Construction Landing Page, 2021). Leaf area was measured on both species across all light treatments and burned and unburned soil conditions. Leaves larger than 10 cm^2 were measured with a meter stick at the widest part of the leaf and at the leaf's tallest point. These measurements were digitally calculated using the geometric shape formula for the area of a heart. Samples of each species were weighed before they were dried to obtain wet mass (Holmgren, 2000). The entire plant for each species was dried in an oven at $60\text{--}70\text{ C}^\circ$ and weighed to the nearest 0.01 g , until the plants weight stabilized (Mettler Toledo scale) (Brantley et al., 2016).

Dried plant mass was sorted into foliage, stem, or roots biomass categories. In each category I determined percent of carbon (C, $\text{g/g}\%$), percentage of nitrogen (N, $\text{g/g}\%$), and C:N

ratio (Peñuelas & Estiarte, 1996). Larger specimens were ground to pass through a 5 mm mesh (Wiley mill), while smaller samples were ground to a finer powder in a ball mill (dual ball mixer mill). Ground samples from both tree species were placed and folded into packets to be analyzed on an elemental analyzer (Flash EA 1112 NC analyzer, CE Elantech, Lakewood, NJ) with standard configurations to determine percentage of carbon, percentage of nitrogen, and carbon to nitrogen ratios (C:N ratios, ppm) of each plant part for each specimen (Peñuelas & Estiarte, 1996). The quality assurance and quality control (QA and QC) errors were accounted for by running triplicates of a sample every 10th sample to determine user error. Standard error and variation for the machine and packaging was also accounted for by using standards of tomato (*Solanum* spp.) and apple (*Malus* spp.) leaf samples.

Data Analysis

Instantaneous water use efficiency (WUE, A_{net} to E , $\text{kg ha}^{-1} \text{mm}^{-1}$) at the leaf level was calculated as the ratio of photosynthetic rates to transpiration rate. Air temperature and relative humidity were used to calculate vapor pressure deficit (VPD, kPa) (Saturation vapor pressure (E_s) = $0.6108^{(17.27 * \text{Average Temperature} / (\text{Average Temperature} + 237.3))}$, Actual vapor pressure (E_a) = $\text{Average RH} / 100 + E_s$, $\text{VPD} = E_a - E_s$). Data were assessed for quality in the following way: all negative photosynthetic values were converted to 0; all missing values were deleted; all photosynthetic values had 100 added to the photosynthetic measurements for analysis to account for variation. The same procedures were performed for transpiration data.

No analysis was conducted on the germination experiment due to germination success; instead, germination ratios of germinates to seeds, were determined to see if the difference in germination rates between species and burned or unburned treatments. A mixed-model analysis of variance (ANOVA) was conducted by using the lmerTest package in the R statistical program

to test for differences among daily average photosynthetic rates, WUE, allometric measurements, total plant biomass, C:N ratio, and carbon and nitrogen percentages for all tissues (R Core Team, 2019; Kuznetsova et al., 2017). The end of growing season allometric measurements were analyzed with an ANOVA using the same lmerTest package to test for differences among the light treatments (fixed effect), fire (fixed effect) and row (random effect) for the following areas of allometry: average leaf area (cm^2), average leaf mass to area (SLA $\text{g}:\text{cm}^2$), average number of leaves, average number of branches, average internode length per plant (mm), average total height and width (cm), average root collar diameter (mm), average root length (cm), average number of lateral roots, average ratio of aboveground (cm) to belowground root length (cm), average ratio of aboveground height (cm) to total plant biomass (g), and average ratio of root length (cm) to total plant biomass (g). The differences between the environmental factors within the different subplots were tested using an ANOVA with the same package to determine if there was a difference between light treatments and burned or unburned soil treatments; these factors were soil temperature ($^{\circ}\text{C}$), volumetric water content (VWC), air temperature (T_{air}), and vapor pressure deficit (VPD). A Tukey's post-hoc test was performed on VWC and soil temperatures in R Studio. A paired t-test was used to compare the nutrient levels of phosphorus (P) and potassium (K), before and after the seedlings were planted. All analyses were performed using the statistical analysis software R Studio (R Core Team, 2019).

CHAPTER THREE: RESULTS

Results

Results are broken down into four sections: germination trial, environmental effects, ecophysiology, and allometric measurements. The light treatments are abbreviated or indicated in graphs and figures as full sun (FS), partial sun (PS), and full shade (SH). The different rows within the experimental design are designated by A or B. Fire treatments are designated as burned (BN) and unburned (UN). Where not shown in the text, ANOVA tables are in the Appendix.

Germination Trial

Germination rates between burned and unburned soil conditions were too low for statistical analysis. Only five of 50 PATO seeds germinated after 26 days in burned soil. One PATO seed germinated in unburned soil after the same number of days. No LITU seeds germinated in burned or unburned soil (Table 1).

Table 1. The number of germinates of PATO and LITU in burned and unburned soil conditions.

Soil Conditions	Species	Number
Burned	PATO	5
Unburned	PATO	1
Burned	LITU	0
Unburned	LITU	0

Environmental Variation among Treatments

Seasonal Air Temperature and Vapor Pressure Deficit

Average daily temperatures between September and October differed among light treatments ($p = 0.037$), but not rows ($p = 0.69$), and there was a significance between light treatment by row interaction ($p = 0.006$; Appendix, Table A). Average daily air temperatures were higher in FS and PS locations than in SH by 1.33 °C (Figure 3, Table 2). The significant interaction reflects that row A had higher temperatures in FS and PS, but lower temperatures in SH. Maximum daily temperatures also differed among light treatments ($p = 0.002$) but did not differ between rows ($p = 0.23$), and there was a significant light treatment by row interaction ($p = 0.026$; Appendix, Table A). FS and PS locations had significantly higher maximum daily air temperatures than SH by 5.34 °C (Figure 3, Table 2). The significant interaction reflects higher daily maximum temperatures in row A in FS, but lower daily maximum temperatures in row A compared to row B in PS and SH. Minimum daily temperatures did not differ among light treatments ($p = 0.84$) or rows ($p = 0.57$), but there were significant light treatment by row interaction ($p = 0.05$; Appendix, Table A). Average daily VPD (kPa) between September and October did not differ significantly among light treatments ($p = 0.54$) or between rows ($p = 0.99$) (Figure 4; Appendix, Table B).

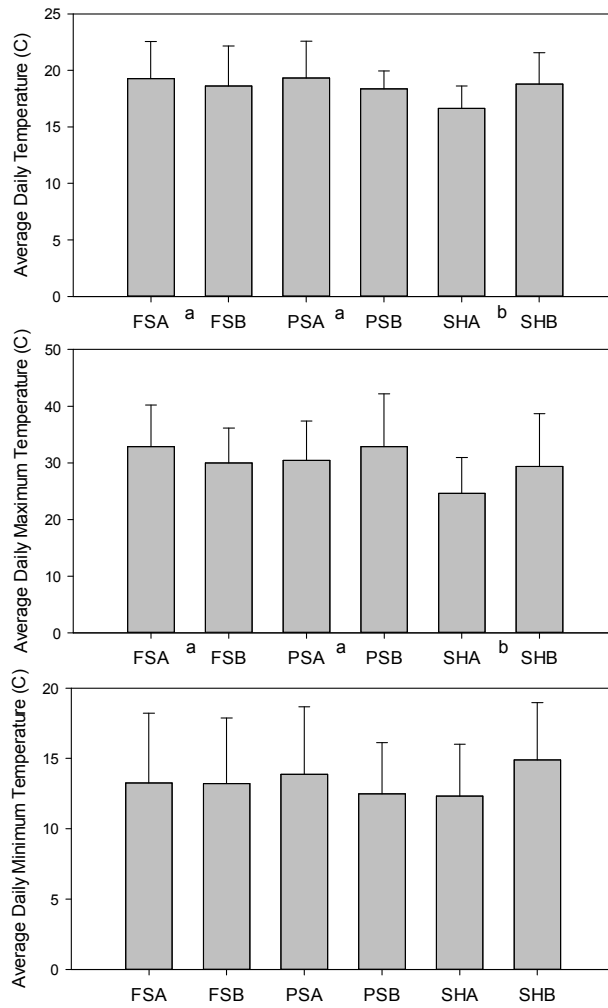


Figure 3. Seasonal Average, maximum, and minimum daily air temperatures (°C) (\pm standard error) in two rows (A, B) within each light treatment (FS, PS, SH). For each measure, different letters indicate significant differences among canopy locations.

Table 2. Seasonal Average and standard error of the mean, maximum, and minimum daily air temperatures (°C) by rows (A, B) and for each light treatment (FS, PS, SH).

	Light Treatments			Row	
	FS	PS	SH	A	B
AVG	18.64 ± 3.15	18.84 ± 2.39	17.31 ± 2.29	18.42 ± 2.82	18.10 ± 2.40
MAX	30.75 ± 6.56	31.22 ± 8.24	25.41 ± 6.93	29.26 ± 6.84	29.0 ± 7.65
MIN	13.07 ± 4.65	13.27 ± 4.19	13.14 ± 3.85	13.18 ± 4.46	13.14 ± 4.00

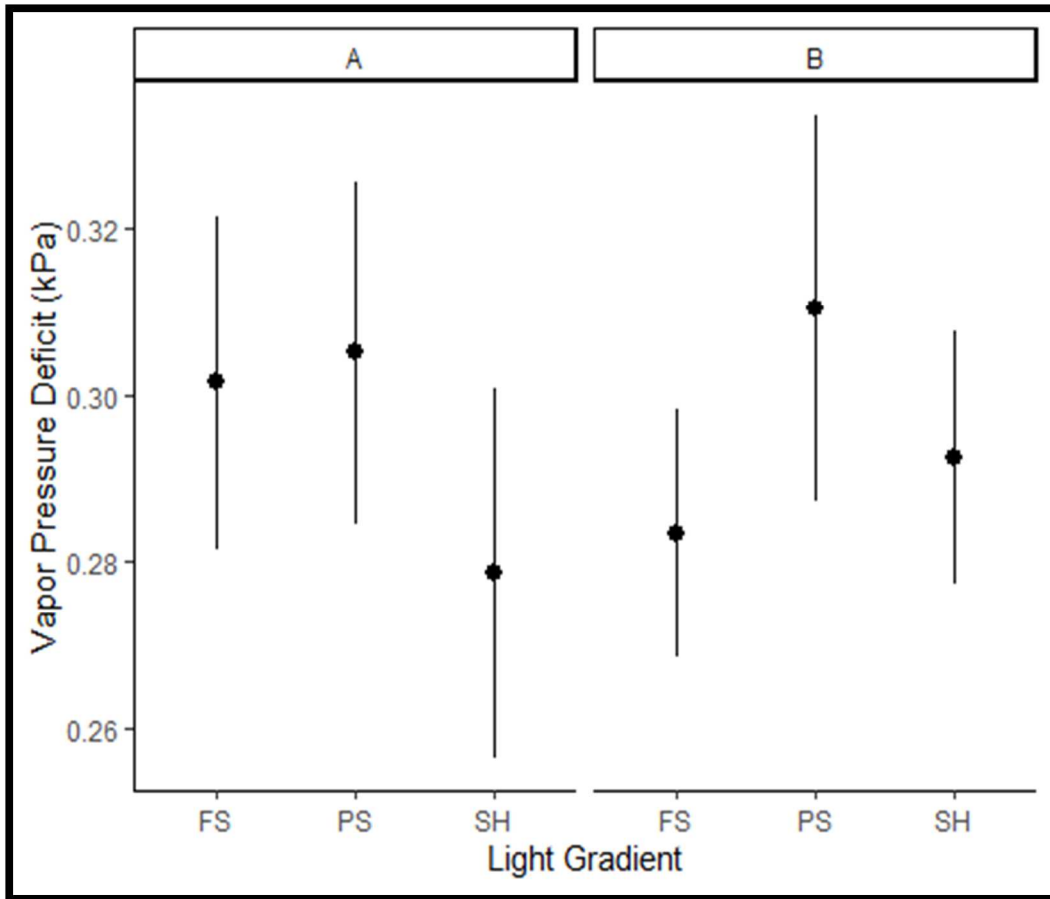


Figure 4. Seasonal average (\pm standard error) VPD (kPa) in the two rows (A, B) within each light treatment of FS, PS, and SH.

Before and after soil nutrient levels

The comparison of soil nutrient values before and after trees were planted shows an increase in mean soil phosphorus (P, ppm) and potassium (K, ppm) after the seedlings were planted for 115 days (Table 3). No statistics were conducted for nitrogen (N), since there was no variation between the before and after measures.

Table 3. Comparison of average N, P, and K soil content one day before trees were planted and 115 days after the trees were planted in their plots. ** indicates a significance less than 0.05, *** indicates a significance of less than 0.001.

Nutrients	Df	T	P	Mean Before (ppm)	Mean After (ppm)
Nitrogen	11	N/A	N/A	3	3
Phosphorus	11	3.3166	0.006***	3.63	4.13
Potassium	11	2.862	0.015**	5.08	5.63

Seasonal Soil Measurements

Average soil volumetric water content (VWC, %) from June 15 to July 25 differed across light treatments ($p = 0.04$) but did not differ between burned and unburned treatments ($p = 0.57$), or between rows ($p = 0.13$), and there were no significant interactions (Appendix; Table C). The light treatments FS and SH had the greatest difference in soil VWC (Figure 5, Table 4). Average

soil temperature from June 15 to July 25 differed among light treatments ($p = 0.00$) but did not differ between burned and unburned treatments ($p = 0.65$) or between rows ($p = 0.80$), and there were no significant interactions (Appendix, Table C). The highest soil temperatures occurred in the SH light treatments, while PS and SH light treatments had similar temperatures between row A and B (Figure 6, Table 4). Light treatments between FS and SH were different, in addition to there being a difference between PS and FS (Figure 6, Table 4).

Table 4. Post hoc test results for a Tukey’s test for VWC and Soil Temperature. ** indicates a significance less than 0.05, *** indicates a significance of less than 0.001

Comparisons	VWC Percent (%)	Soil Temperature °C
PS-FS	0.18	0.04**
SH-FS	0.09*	0.008***
SH-PS	0.84	0.31

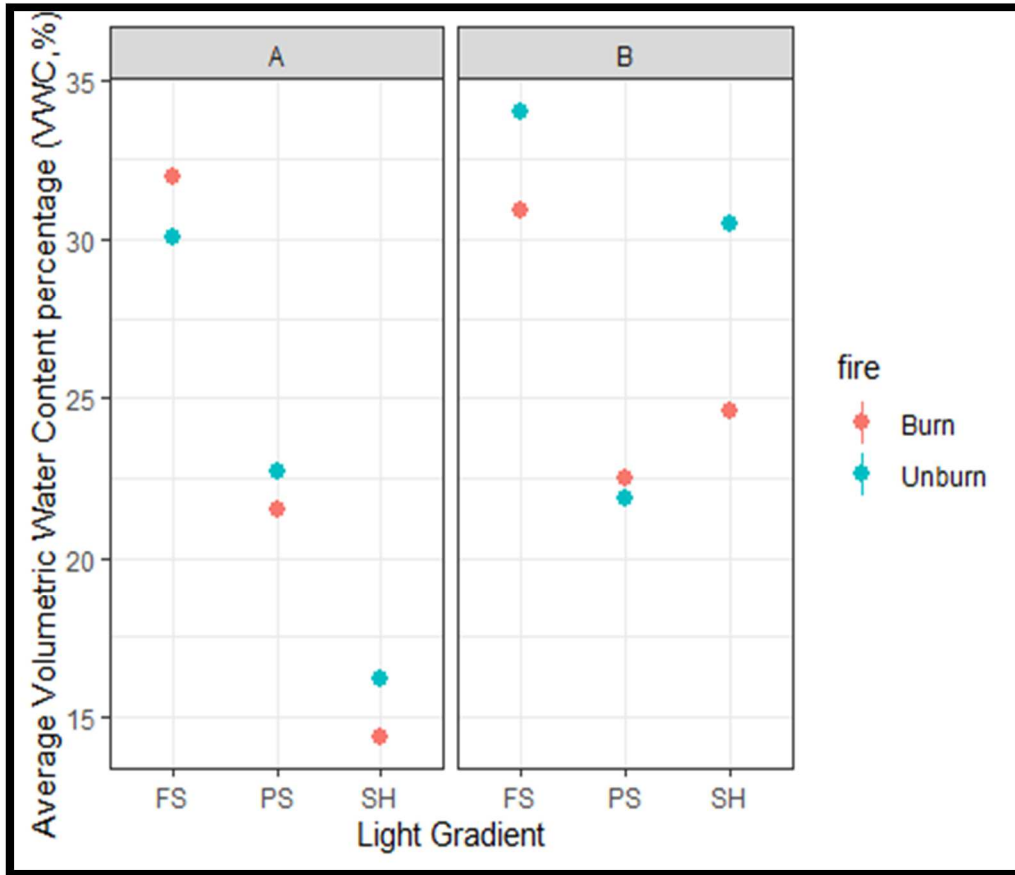


Figure 5. Average (\pm standard error) seasonal soil volumetric water content (VWC, %) in rows, light treatments, and burn treatments.

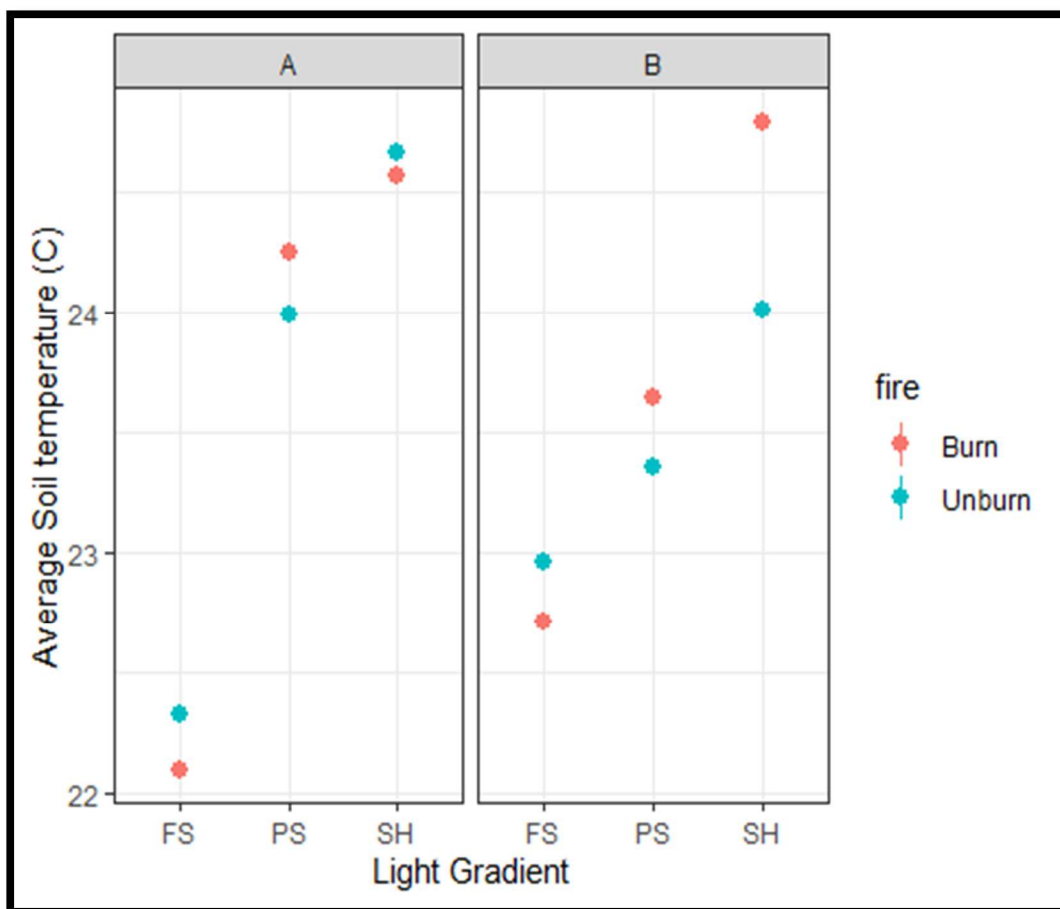


Figure 6. Average (\pm standard error) seasonal soil temperature ($^{\circ}$ C) in rows, light treatments, and burn treatments.

Photosynthesis, Stomatal Conductance, and WUE

Average net photosynthesis, measured at photosynthetically active photon flux density (PPFD) = $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, did not differ among light treatments ($p = 0.29$), burned and unburned treatments ($p = 0.22$), or species ($p = 0.61$), and there were no significant interactions (Appendix, Table D). However, there was a significant difference between rows ($p = 0.02$). Net photosynthetic rates were higher in row B than in row A (Figure 7). Average stomatal conductance measured at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD did not differ between species ($p = 0.61$), light treatments ($p = 0.28$), or burned and unburned treatments ($p = 0.22$), and there were no significant interactions (Appendix, Table D). A significant difference was detected between rows ($p = 0.02$) for stomatal conductance. Stomatal conductance was lower in row A compared to row B, with the most pronounced difference between rows occurring in the FS light treatment (Figure 8). For WUE there were no significant differences among row ($p = 0.11$), light treatments ($p = 0.96$), burned or unburned treatments ($p = 0.20$), species ($p = 0.75$), or their interactions (Figure 9, Appendix, Table D).

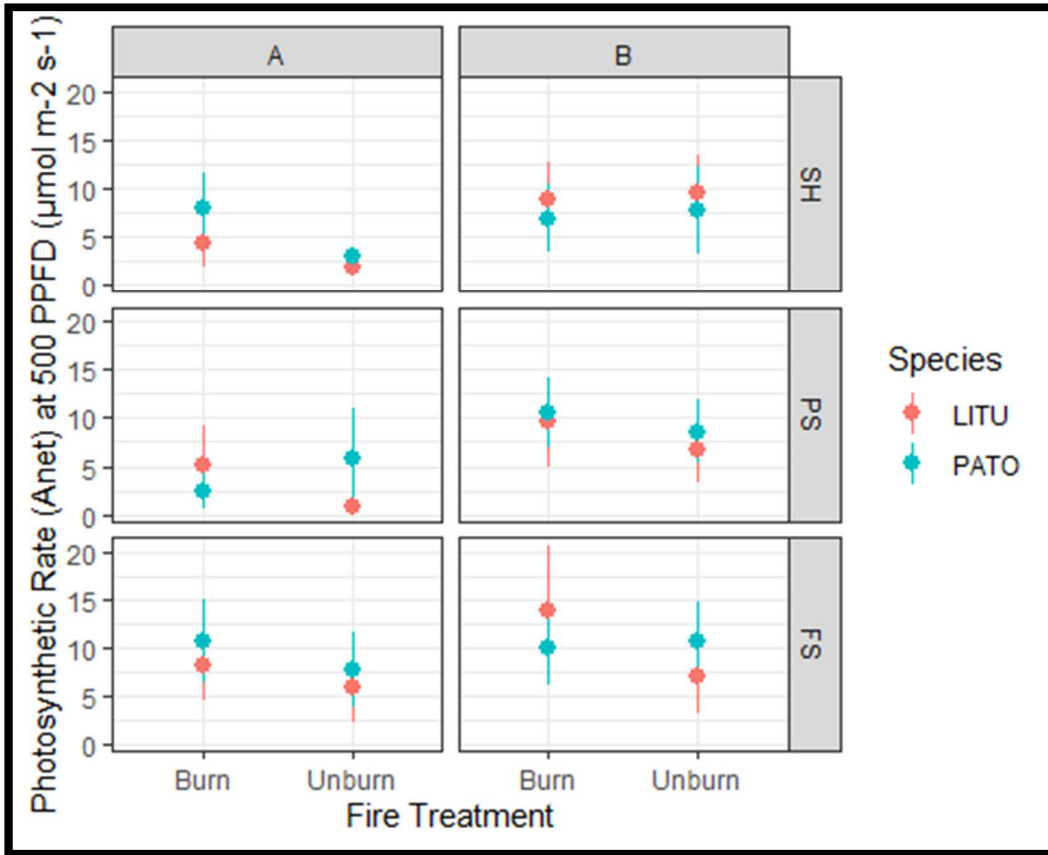


Figure 7. Daily average (\pm standard error) net photosynthetic rate (A_{net}) PPFD = 500 ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for each species in rows, burned or unburned plots, and light treatment canopy locations.

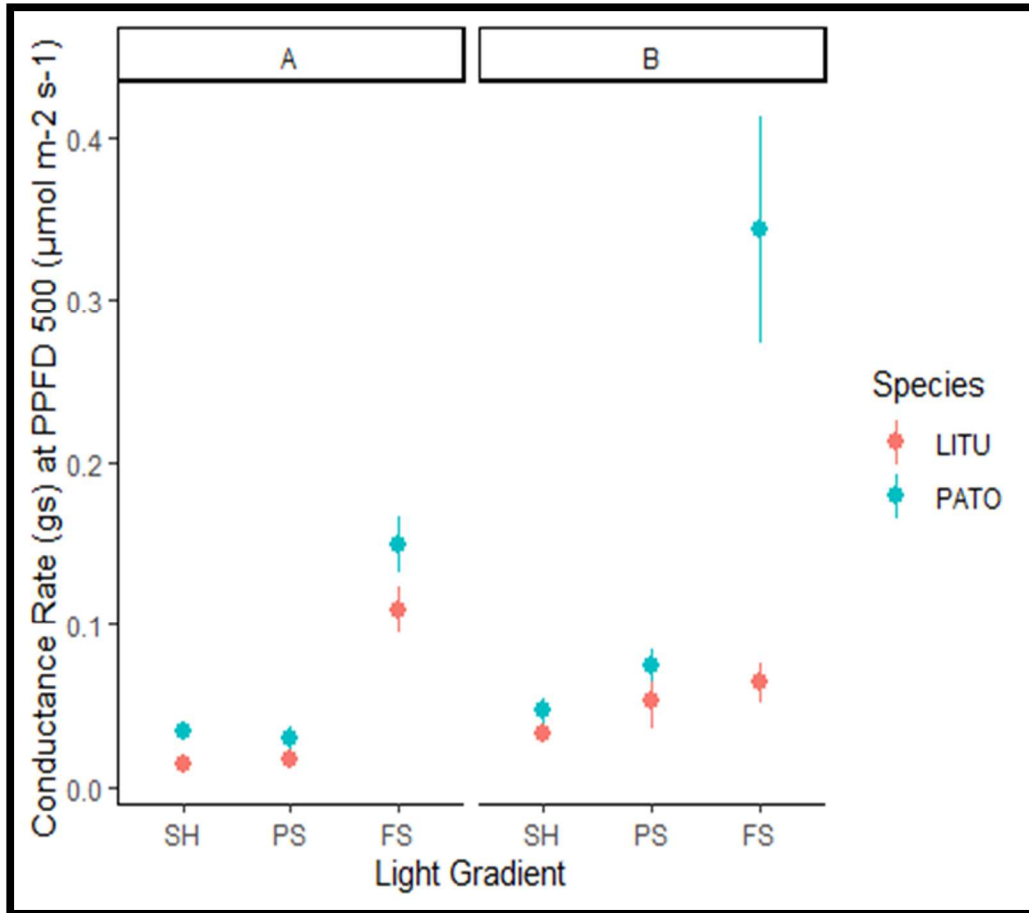


Figure 8. Daily average (\pm standard error) stomatal conductance (g_s) at PPFD = 500 ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for PATO and LITU seedlings in light treatment rows, canopy treatments, and burn treatments.

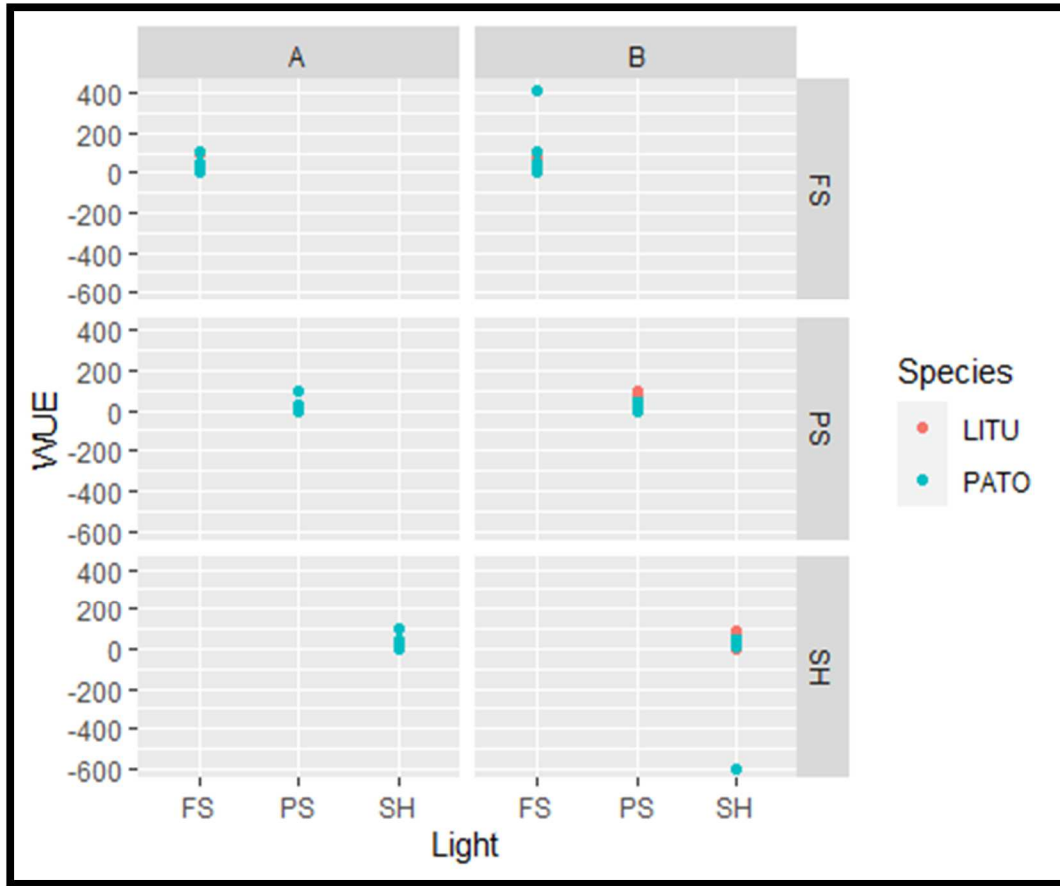


Figure 9. Daily average (\pm standard error) WUE ($kg\ ha^{-1}\ mm^{-1}$ at PPFD = 500 ($\mu mol\ m^{-2}\ s^{-1}$) for PATO and LITU seedlings in light treatment rows, canopy treatments, and burn treatments.

Allometric and Biomass Measurements

End of Season Allometric Measurements

Averages of all allometric measures except root length, number of leaves, leaf area, and SLA differed between species and were larger for PATO. (Table 5; Appendix, Table E). The average number of leaves for both species was only significant among light treatments (Appendix, Table E). On average, PATO had twice as many branches and lateral roots, four times longer stem internodes, 1.5 times longer roots, was 3.5 times taller, and four times wider than the largest average for LITU. In addition, PATO had four times greater leaf area, three times larger root collar diameter, and 24.5 times the total plant mass of LITU (Figure 10, Figure

11). Allometric ratios were also larger for PATO. Specific leaf area was 1.5 times larger, plant height to biomass ratio was 8.5 times larger, root length to plant biomass ratio was 15.6 times larger, and plant height to belowground length ratio was 2.5 times larger for PATO than LITU (Table 5).

The greatest growth for both species tended to be higher in the FS light treatment and in row B, even though row was only significant for the number of lateral roots (Table 5; Appendix, Table E). The allometric average for the total number of leaves was only significant in light treatments (Appendix, Table E). Average number of lateral roots, number of leaves, and stem width differed among light treatments and were highest in FS for both PATO and LITU (Table 5; Appendix, Table E). Total plant biomass averages also differed among light treatments, but the species showed different trends as indicated by the significant light by species: PATO and LITU biomasses were highest in FS (Table 5; Appendix, Table E). LITU produced larger allometric measures in burned conditions, while PATO had a greater average of allometric measures in unburned conditions than burned (Table 5). Plant height differed between burn treatments, and the species showed different trends as indicated by the significant interaction of fire (burn/unburned) and species: LITU was taller in burned plots while PATO heights were similar in burned and unburned plots (Table 5; Appendix, Table E). However, PATO had slightly larger averages for most measurements taken in unburned plots (Table 5). There were two significant two-way interactions for the average number of lateral roots, one interaction was between species and fire, while the other two-way interaction was between fire and light treatment (Appendix, Table E). The fire and light interaction show FS light treatment had a larger number of lateral roots, but the fire effect depended on species (Table 5; Appendix, Table E). The interaction between fire and species reflects a trend toward a greater number of PATO lateral

roots in unburned plots, while number of lateral roots for LITU was slightly greater in burned than unburned plots were similar (Table 5; Appendix, Table E). Number of lateral roots and plant biomass also differed between rows, primarily due to larger PATO, with more lateral roots in row B compared to row A (Table 5; Appendix, Table E).

Table 5. The average and standard error end of season allometric measurements by species (LITU= *Liriodendron tulipifera*; PATO = *Paulownia tomentosa*), light treatments (FS=full sun, PS=partial sun, SH=shade), burned (BN) or unburned (UN) fire treatment, and row.

LITU Average Allometric Measurements and Ratios							
Allometric Measures	Light Treatments			Fire		Row	
	FS	PS	SH	BN	UN	A	B
No. leaves	3.66 ±	0.75 ±	0.25 ±	2.61 ±	1.66 ±	1.33 ±	1.77 ±
	1.12	0.44	0.14	0.45	0.68	0.30	0.83
No. branches	3.83 ±	0.75 ±	0.25 ±	2.76 ±	1.63 ±	1.30 ±	1.91 ±
	1.20	0.44	0.14	0.56	0.63	0.28	0.90
Stem width (mm)	1.56 ±	0.33 ±	0.14 ±	1.53 ±	0.68 ±	0.59 ±	0.76 ±
	0.45	0.19	0.07	0.20	0.27	0.11	0.36
Plant height (cm)	10.82 ±	1.90 ±	0.63 ±	7.08 ±	4.25 ±	3.65 ±	5.25 ±
	3.33	1.12	0.34	1.57	1.63	0.72	2.48
Plant width (cm)	9.18 ±	1.93 ±	0.31 ±	6.02 ±	3.63 ±	2.89 ±	4.72 ±
	3.10	1.12	0.17	1.55	1.38	0.66	2.28
Internode length (mm)	4.44 ±	0.71 ±	0.18 ±	3.07 ±	1.75 ±	1.37 ±	2.18 ±
	1.52	0.45	0.10	0.64	0.74	0.25	1.13
No. lateral roots	14.70 ±	2.79 ±	1.5 ±	8.35 ±	7.83 ±	7.05 ±	6.43 ±
	4.83	2.07	0.55	2.45	2.52	1.18	3.79
Root length (cm)	10.47 ±	3.04 ±	1.21 ±	6.48 ±	5.29 ±	3.26 ±	6.56 ±
	3.46	1.77	0.69	1.83	2.12	0.76	3.19
Root collar diameter (mm)	2.46 ±	0.51 ±	0.20 ±	2.11 ±	1.05 ±	0.94 ±	1.18 ±
	0.82	0.29	0.10	0.30	0.51	0.26	0.55
Total plant biomass (g)	0.83 ±	0.39 ±	-0.02 ±	1.13 ±	0.34 ±	0.21 ±	0.58 ±
	0.20	0.44	0.01	0.24	0.30	0.15	0.31
Leaf Area (cm ²)	13.54 ±	3.54 ±	0.42 ±	8.99 ±	4.78 ±	3.58 ±	8.09 ±
	2.13	1.30	0.83	2.40	1.18	1.18	1.91
Specific leaf area (cm ² /g)	141.33 ±	131.95 ±	-1.07 ±	143.86 ±	71.83 ±	52.62 ±	128.85 ±
	184.49	204.35	2.03	387.08	47.51	275.63	103.24
Plant height (cm): Total Plant biomass (g)	54.55 ±	16.02 ±	-11.94 ±	36.37 ±	13.41 ±	29.14 ±	9.95 ±
	25.69	16.22	18.45	34.22	12.74	47.04	11.91
Root length (cm): Total Plant biomass (g)	57.51 ±	24.71 ±	-21.07 ±	35.79 ±	13.67 ±	30.44 ±	10.32 ±
	22.10	25.00	21.47	33.92	17.43	40.01	15.97
Aboveground height (cm): Belowground length (cm)	0.98 ±	0.31 ±	0.15 ±	1.16 ±	0.49 ±	0.35 ±	0.61 ±
	0.11	0.00	0.19	0.08	0.10	0.13	0.08

PATO Average Allometric Measurements and Ratios							
No. leaves	8.20 ± 1.79	2.20 ± 0.53	0.04 ± 0.04	3.80 ± 0.68	3.16 ± 0.89	2.05 ± 0.41	4.91 ± 0.97
No. branches	8.45 ± 1.73	2.54 ± 0.58	0.04 ± 0.04	3.97 ± 0.70	3.38 ± 0.87	2.11 ± 0.40	5.25 ± 1.17
Stem width (mm)	6.02 ± 0.83	1.29 ± 0.30	0.18 ± 0.20	2.47 ± 0.45	2.52 ± 0.44	1.21 ± 0.24	3.78 ± 0.65
Plant height (cm)	37.65 ± 5.80	6.79 ± 1.62	1.21 ± 1.33	15.34 ± 2.70	15.09 ± 3.14	6.49 ± 1.66	23.95 ± 4.17
Plant width (cm)	37.94 ± 7.76	6.05 ± 1.56	0.37 ± 0.41	15.26 ± 2.57	14.32 ± 3.92	7.40 ± 1.97	22.17 ± 4.52
Internode length (mm)	17.92 ± 3.81	2.09 ± 0.61	1.66 ± 1.82	7.16 ± 2.06	7.29 ± 2.10	2.64 ± 0.74	11.80 ± 3.42
No. lateral roots	29.29 ± 5.95	10.91 ± 2.92	1.58 ± 1.73	12.80 ± 2.86	15.05 ± 4.21	7.13 ± 1.83	20.72 ± 5.24
Root length (cm)	17.64 ± 2.44	4.97 ± 1.01	0.58 ± 0.63	7.70 ± 1.30	7.76 ± 1.43	3.31 ± 0.93	12.15 ± 1.79
Root collar diameter (mm)	7.62 ± 1.09	1.71 ± 0.36	0.25 ± 0.27	3.17 ± 0.57	3.21 ± 0.58	1.49 ± 0.33	4.89 ± 0.82
Total plant biomass (g)	20.40 ± 5.79	0.62 ± 0.38	0.09 ± NA	6.51 ± 3.63	7.56 ± 4.35	1.29 ± 1.77	12.78 ± 5.10
Leaf Area (cm ²)	55.67 ± 5.29	5.09 ± 1.65	1.09 ± NA	17.46 ± 3.90	23.77 ± 4.35	9.96 ± 1.77	31.27 ± 5.10
Specific leaf area (cm ² /g)	234.69 ± 195.64	58.09 ± 34.24	-7.76 ± NA	77.89 ± 110.41	87.61 ± 119.47	75.38 ± 195.64	90.62 ± 34.24
Plant height (cm): Total Plant biomass (g)	6.41 ± 1.92	8.52 ± 3.79	41.27 ± NA	22.11 ± 2.61	15.35 ± 2.47	3.35 ± 2.73	34.12 ± 2.45
Root length (cm): Total Plant biomass (g)	3.67 ± 1.49	6.35 ± 3.27	20.58 ± NA	13.08 ± 2.01	7.32 ± 2.16	1.96 ± 1.52	18.44 ± 1.98
Aboveground height (cm): Belowground length (cm)	2.15 ± 0.20	0.75 ± 0.21	1.11 ± NA	1.27 ± 0.21	1.40 ± 0.19	0.70 ± 0.24	1.97 ± 0.18

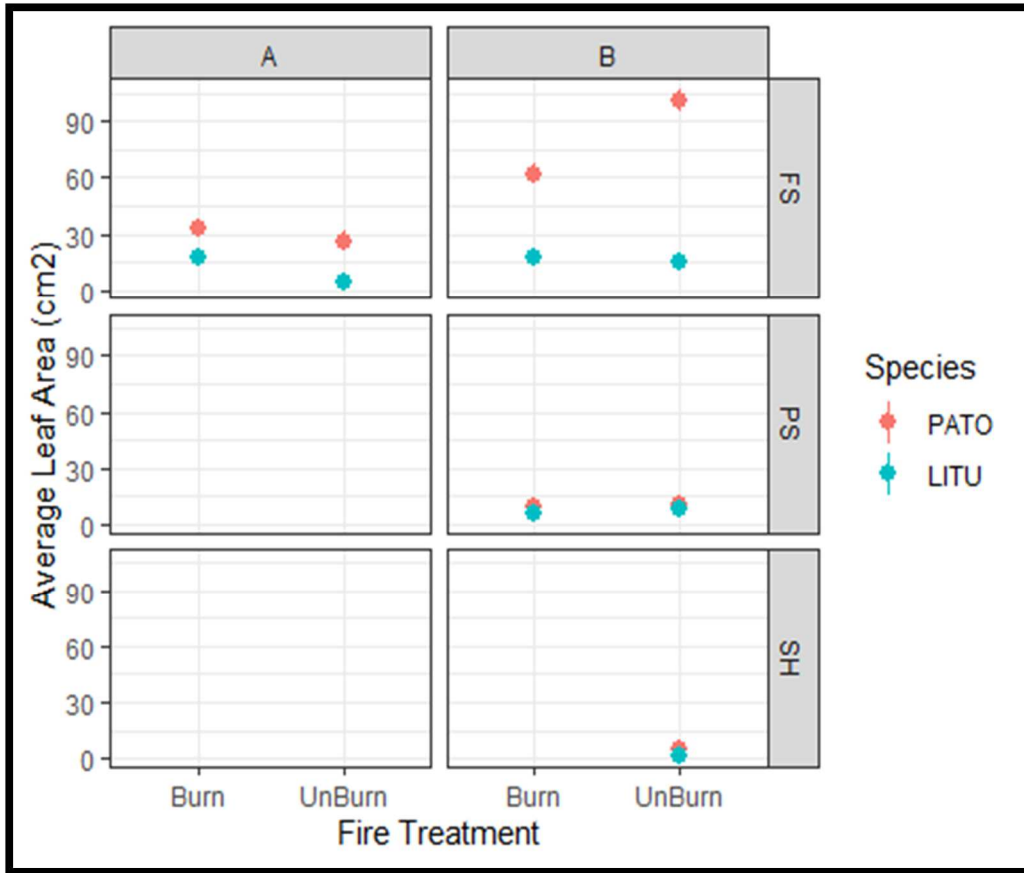


Figure 10. Average (\pm standard error) leaf area (cm^2) across light treatments, burned and unburned treatments, and between rows and species.

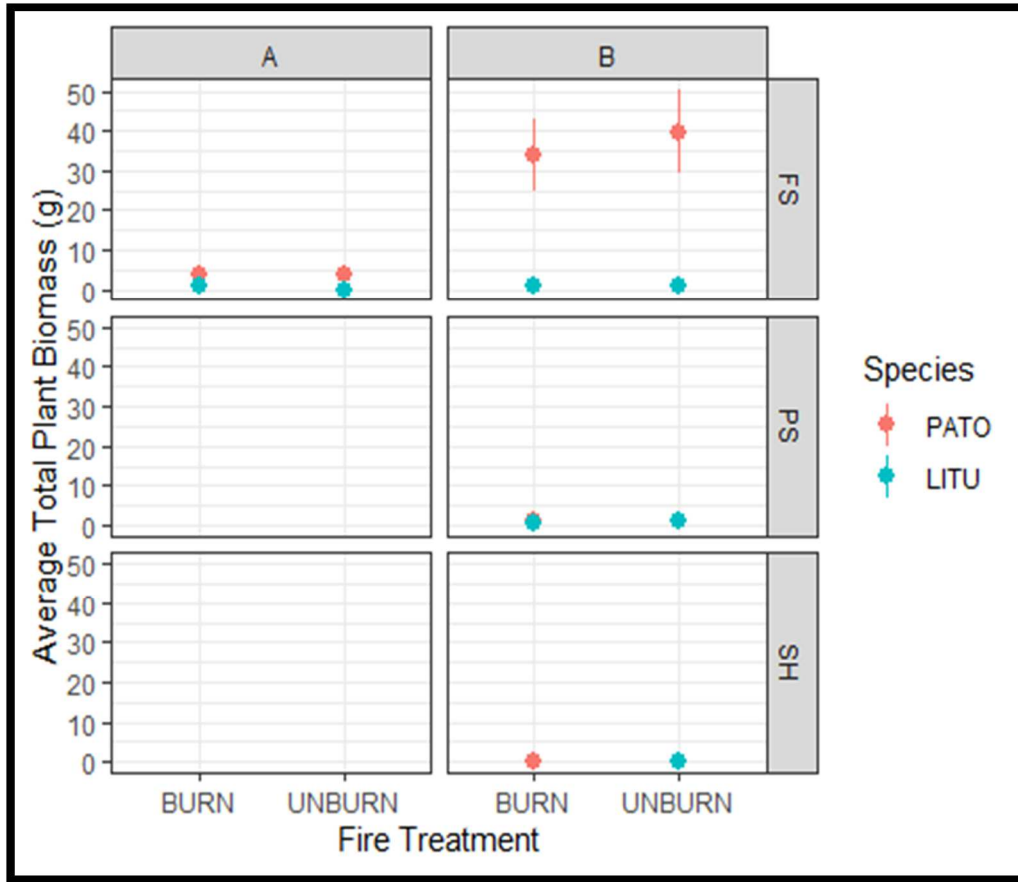


Figure 11. Average (\pm standard error) total plant biomass (g) across light treatments, burned and unburned treatments, between row and species.

Carbon (C) and Nitrogen (N) Analysis

ANOVA results for the percentage of carbon within plant parts showed three significant three-way interactions (Appendix, Table F). One of the three-way interactions was between light treatments, plant part, and species (Appendix, Table F). The percentage of carbon was higher for PATO leaves in PS and FS light treatments than LITU. The ANOVA results portrayed the percentage of nitrogen within plant parts to be significant in a three-way interaction between fire, part, and species (Figure 13, Appendix, Table F). The C:N analysis show that LITU had a higher percentage of nitrogen in leaves, roots, and stem than PATO. PATO had more carbon in their

roots compared to LITU; LITU had higher percentage of carbon in leaves than PATO (Figure 12). PATO had more carbon in stems compared to LITU. The ANOVA for the C:N ratio determined there was a significant difference in a three-way interaction of light treatments, fire, and species ($p = 0.08$) along with a significant difference in a two-way interaction between part and species ($p = 0.07$) (Figure 13; Appendix, Table F). PATO had a higher C:N ratio than LITU in across all parts and most light gradients (Figure 14; Appendix, Table F).

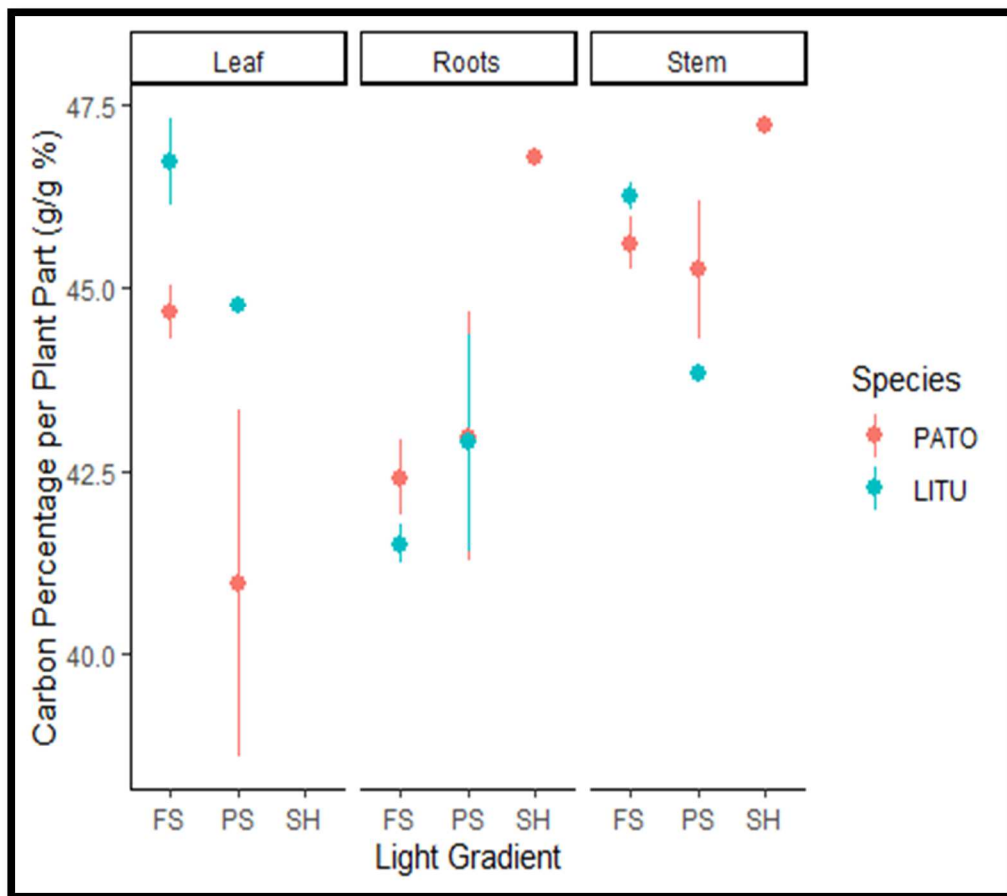


Figure 12. Average (\pm standard error) percentage of carbon found in different plant parts (roots, leaves, and stems) for PATO and LITU.

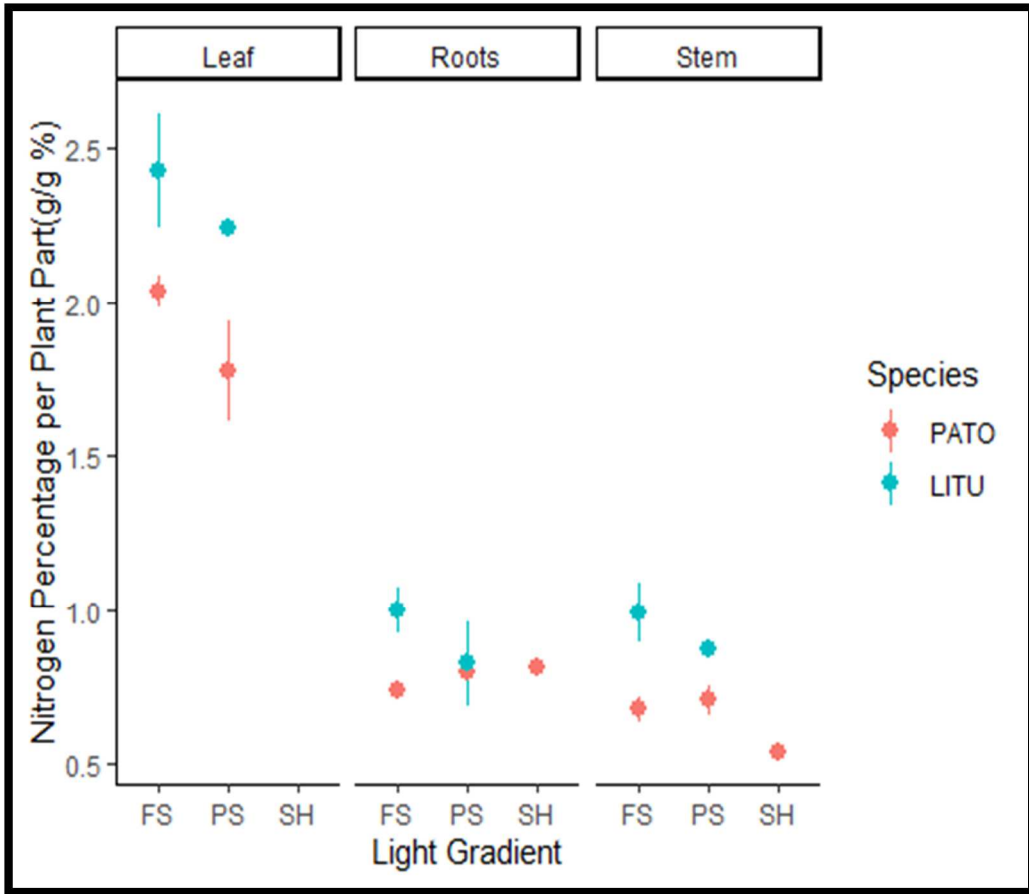


Figure 13. Average (\pm standard error) percentage of nitrogen found in different plant parts (roots, leaves, and stems) for PATO and LITU.

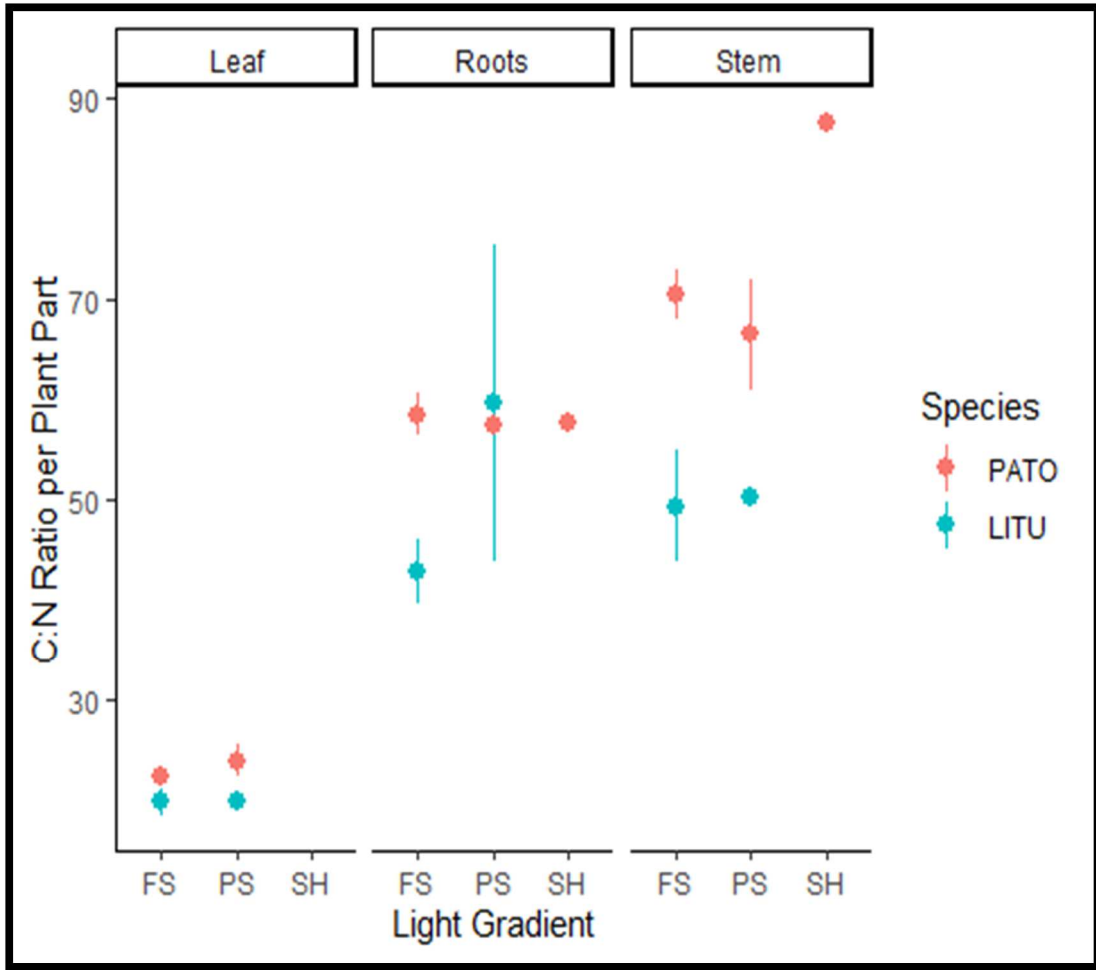


Figure 14. Average (\pm standard error) Carbon to Nitrogen ratio found in different plant parts (roots, leaves, and stems) for PATO and LITU.

CHAPTER FOUR: DISCUSSION AND MANAGEMENT IMPLICATIONS

Although germination was low (6 of 100 seeds) in PATO, five seeds germinated in burned soil and one seed germinated in unburned soil. These results support previous research by Todorović et al. (2010), who found that light and chemicals associated with fire (smoke, nitrogenous compounds) could stimulate PATO germination and partly explain its establishment after fires. The lack of LITU germination in this research also agrees with previous research by Kota et al. (2007), who found low rates of LITU germination in disturbed areas. Most tree species are limited by seedling recruitment (Hubbell et al., 1999; Clark et al., 1998). PATO's prolific seed production, minimal light requirement and sensitivity, and higher germination rate than LITU could lead to increasing abundance of the invasive compared to the native in southeastern forests (Todorović et al., 2010; Longbrake, 2001). Both PATO and LITU seedlings showed differences in photosynthesis and allometric growth patterns over light or microclimate gradients in this research.

Most strikingly, net photosynthesis for both species was higher in 'row B', which had lower seasonal temperature and lower VPD than 'row A'. Row A also had the highest average and maximum air temperature in the FS light treatment, and lower stomatal conductance rates than row B. The high average and maximum air temperatures in row A in the FS light treatment would account for the difference in photosynthetic rates and stomatal conductance between rows, as well as lower allometric measures for both species. Both rows A and B had the highest VWC in the FS light treatment which could be due to the lack of competition between other plants, or interception by mature trees in the SH light treatment. Having a high VWC in the FS light gradient would also contribute to increased photosynthetic rates and allocation to growth, due to water availability. Row A had a higher seasonal VPD and a higher air temperature in the FS light

treatment, which could have decreased stomatal opening and net photosynthesis over the season. In the field experiment row A was located near a younger forest that was bordered by an agricultural field. The young age of the forest and its aspect allowed row A to receive constant sun light all day without a shading effect from the younger forest. Row A received air flow from its surrounding environment, due it being near the “edge” of a mature forest, which could contribute to why it had lower temperatures. Row B was located closer to a larger mature forest which shaded the row. Row B’s aspect only allowed the plants to receive sunlight later, when it was not as intense, by being partially shaded during the early morning. Row B PS and SH light treatments were in the middle of a mature forest with little to no air flow which could have caused increased air temperatures. Perhaps resulting from these higher photosynthetic rates, both species, and especially PATO, had greater biomass and more lateral roots in row B. Canopy openness also affected growth of both species; seedlings in FS had more leaves and lateral roots, and wider stems, than seedlings in partial or full shade. Even though photosynthetic rates (A_{net}) were similar between species, PATO had more leaf area and leaves per seedling which created a greater plant biomass. PATO and LITU biomass also was greatest in FS. In contrast to the light gradient, the burn treatment had little effect on seedling ecophysiology or growth; but LITU’s had slightly greater allometric averages in burned treatments, especially height in burned plots. PATO tended to have similar allometric averages in burned or unburned conditions, but averages in unburned conditions seemed to be slightly lower.

Variations over microenvironments created by light, fire, and soil moisture gradients can filter regeneration among species (i.e., can defining a species' 'regeneration niche') (Coomes & Grubb, 2000; George & Bazzaz, 1999 a, b; Denslow et al., 1998; Fahey et al., 1998; Huston & Huston, 1994; Pacala & Tilman, 1994; Pacala & Roughgarden, 1982; Grubb, 1977). Across all

microenvironmental gradients, PATO had stronger responses than LITU. Over the first season, PATO grew taller and wider than LITU, with longer stem internodes, more branches, and larger leaf area. PATO also had longer roots and more lateral roots than LITU. In addition, the allometric ratios revealed PATO invested more than LITU in leaf area and both stem and root elongation relative to plant biomass. Collectively, these results indicate young PATO seedlings can outcompete LITU, especially under open canopy. When looking at C:N ratios and percentages, PATO and LITU have different above ground biomass allocation patterns. LITU tended to invest higher percentage of carbon and nitrogen into its leaves and stem than PATO. PATO allocated most of its above ground biomass to its leaves, which are lost every year when the plant senescence, while LITU structures remain demonstrating the species different biomass allocation patterns.

LITU's average height growth after two growing seasons can reach at least 0.3 m tall (Beck, 1990). In the FS canopy treatment PATO seedlings were able to reach an average height of 0.37 m in the first growing season. As early growth rates strongly determine success in reaching the canopy, especially in opportunistic or 'gap obligate' species, rapid initial growth could favor increasing abundance of the invasive PATO following forest disturbance (Landis & Peart, 2005; Knapp & Canham, 2000; Orwig & Abrams, 1994). LITU's allocation of carbon in their leaves coincides with their primary competition strategy of being the tallest competitor, which is similar to PATO's response in the shaded light gradients, by allocating more carbon into their stem to increase shoot growth in a response to competition. PATO was larger than LITU across all the allometric measurements including height. This faster growth could affect the existing composition of forested ecosystems in the southeast, in addition to altering forest

composition in the future, since these two species seem to be ecologically similar in their response to photosynthetic rates and WUE.

Forest understory resources and environmental conditions affect the growth and survival of seedlings, acting as filters among regenerating tree species (George & Bazzaz, 1999a, b; Berkowitz et al., 1995; Facelli, 1994; Lorimer et al., 1994; Harmon & Franklin, 1989; Veblen, 1989; Harper, 1977; Korstian & Coile, 1938). The similar photosynthetic and growth responses of PATO and LITU across the light gradients and microenvironments in this research suggest these species are similar in their disturbance-generated 'regeneration niche' (Grubb, 1977). PATO's higher germination rates, combined with its greater biomass gain and root and shoot extension over the first growing season, indicate that the invasive is the better initial competitor, and may be expected to increase more than the native following disturbance. Further research should be conducted to compare PATO to other rapidly growing hardwood species such as maple (*Acer* spp.) and birch (*Betula* spp.), which also tend to germinate quickly and are hardy species that establish within the different light gradients found in forested ecosystems. Yellow birch (*Betula alleghaniensis*) is well adapted to exploit temporarily high light levels under canopy openings. Birch species have a high growth rate for both sun and shade gradients ranging from 13 to 100 percent sunlight (Walters et al., 1993; Bellefleur & LaRocque, 1983; Logan, 1965). Yellow birch (*Betula alleghaniensis*) is generally classified as a mid-tolerant canopy light gradient species; it favors establishment in canopy openings and after soil disturbance (Erdmann, 1990; Baker 1949). Similarly, birch is more shade-tolerant and has an opportunistic pattern of height growth (Beaudet & Messier, 1998). However, LITU favors areas of disturbance with high nutrient levels similar to *Acer* species (Wilson & Shure, 1993). Sugar maple (*Acer saccharum*) is tolerant of shade and can survive for many years under closed canopies as advanced regeneration

in addition to sustaining multiple episodes of growth suppression (Kobe et al., 1995; Canham 1990, 1985; Baker, 1949).

The intriguing finding that soil phosphorus and potassium were higher at the end of the season compared to their levels before planting suggests another avenue of future research. Change in soil nutrient levels among different tree species, including PATO and LITU, and in different microclimates could be investigated. In addition, further research is needed to determine if a difference of arbuscular mycorrhizal fungi (AMF) presence is found within the roots between wild trees and those grown in greenhouse conditions, or if AMF differ across different microenvironments. AMF create symbiotic relationships with plants in the roots. This relationship benefits plants by obtaining nutrients such as N, P, and K for growth and development in exchange for photosynthate. Research should also be conducted to determine PATO's ability for nutrient uptake compared to nutrient availability, among different soil conditions and microclimates. Finally, field study of LITU and PATO over environmental gradients and within disturbed areas of differing ages can reveal if the initial patterns observed in this research persist as plants grow into the canopy.

CHAPTER FIVE: LITERATURE CITED

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CHAPTER SIX: APPENDIX

Seasonal Air Temperature and Vapor Pressure Deficit

Table A. The ANOVA results for the difference in the maximum, minimum and average Air temperature among light treatments and rows. * indicates a significance of 0.1, ** indicates significance at 0.05, *** indicate significance at 0.01 and **** indicates significance at 0.001.

Effects	Average Air Temperature (AT)	Average Maximum AT	Average Minimum AT
Light treatment	0.037**	0.002****	0.84
Row	0.69	0.23	0.57
Light treatment: Row	0.005****	0.026**	0.05**

Table B. The ANOVA results for the difference for the vapor pressure deficit (VPD) in for September and October between light treatments and rows among plots.

VPD	
Effects	P
Light treatments	0.54
Row	0.99

Seasonal Soil Measurements

Table C. The ANOVA results for the difference of the seasonal average volumetric water content (VWC) and seasonal average Soil temperature between row, light treatments, and fire between plots. ** indicates a significance of 0.05.

Effects	Temperature	VWC
	P	P
Row	0.8	0.14
Light treatments	0.004***	0.04**
Fire	0.65	0.57
Light treatments: Fire	0.63	0.83
Residuals	NA	NA

Ecophysiology Measurements of Photosynthetic rates across light treatments and WUE

Table D. ANOVA results of difference in Photosynthetic rates, Stomatal conductivity, and WUE in micromoles (μmol) at the light level 500 across the different light treatment ss, fire, species, and row taken during the growing season. **indicate significance level of less than 0.05.

Effects	WUE	Stomatal Conductivity	Photosynthetic Rates
	P	P	P
Species	0.75	0.61	0.61
Light treatments	0.96	0.28	0.29
Fire	0.2	0.22	0.22
Row	0.11	0.02**	0.02**
Species: Light treatment s	0.86	0.92	0.92
Species: Fire	0.85	0.62	0.62
Light treatments: Fire	0.84	0.92	0.92
Species: Light treatments: Fire	0.86	0.75	0.75

End of Season Allometric Measurements and Ratios

Table E. ANOVA results (P values) for end of growing season allometric measures: Stem width (mm), plant height (cm), plant width (cm), internode length(mm), no. lateral roots, length of roots (cm), root collar diameter (mm), no. leaves, leaf area (cm²) to mass(g) (SLA), leaf Area (cm²), aboveground height to belowground height ratios, natural log of aboveground height, natural log of total biomass, aboveground height to total plant mass ratios, and root length to total plant mass ratios to see if there was a difference among the treatments of fire, light treatment treatments, species, row and their interactions. * indicates a significance of 0.1, ** indicates significance at 0.05, *** indicate significance at 0.01 and **** indicates significance at 0.001.

Allometric Measurements P-values	Fire	Light treatments	Species	Row	Fire: Light Treatments	Fire: Species	Light treatments: Species	Fire: Light treatments: Species
No. leaves	0.73	0.05*	0.1	0.41	0.74	0.74	0.46	0.5
Stem Width (mm)	0.97	0.1*	0.04 **	0.17	0.99	0.78	0.42	0.74
Plant height (cm)	0.75	0.77	0.07*	0.67	0.99	0.72	0.48	0.88
Plant width (cm)	0.65	0.42	0.03**	0.5	0.86	0.72	0.17	0.83
Internode length (mm)	0.73	0.13	0.07*	0.11	0.71	0.72	0.45	0.98
No. lateral roots	0.4	0.01****	0.01**	0.01**	0.06**	0.06*	0.22	0.22
Root length (cm)	0.24	0.25	0.81	0.22	0.36	0.23	0.17	0.84
Total plant biomass (g)	0.71	0.21	0.08*	0.54	0.51	0.85	0.23	0.55
Leaf Area (cm ²)	0.82	0.14	0.13	0.18	0.93	0.59	0.38	0.68
Specific leaf area (cm ² /g)	0.97	0.65	0.86	0.81	0.84	0.45	0.68	0.57
Plant height(cm) : Total Plant	0.67	1	0.09*	1	0.93	0.61	0.18	0.94

biomass (g) Root length (cm): Total Plant biomass (g) Aboveground height(cm) : Belowground length (cm) ratio	0.88	1	0.02**	1	0.91	0.8	0.13	0.82
	0.27	0.13	0.0****	0.94	0.27	0.3	0.17	0.25

Carbon and Nitrogen Analysis

Table F. ANOVA results for the percentage of carbon (C), percentage of nitrogen (N), and the carbon to nitrogen ratio (C:N) found in different plant parts (roots, leaves, and stems) to determine if there was a difference between among the following treatments and their interaction. * indicates a significance of 0.1, ** indicates a significance of 0.05, *** indicated a significance of 0.01 and **** indicates a significance of 0.001.

	C	N	C:N
Effects	P	P	P
Light treatments	0.14	0.1	0.52
Fire	0.23	0***	0.005***
Part	<0.001****	<0.001****	<0.001****
Species	0.2	<0.001****	<0.001****
Light treatments: Fire	0.28	0.57	0.292
Light treatments: Part	0.05**	0.08	0.44
Fire: Part	0.26	0.46	0.22
Light treatments: Species	0.57	0.24	0.12
Fire: Species	0.93	0.86	0.07*
Part: Species	0.08*	0.41	0.08*
Light treatments: Fire: Part	<0.001****	0.77	0.73
Light treatments: Fire: Species	0.09*	0.47	0.082*
Light treatments: Part: Species	0.07*	0.9	0.23
Fire: Part: Species	0.93	0.07*	0.34
Light treatments: Fire: Part: Species	NA	NA	NA