EXPLORING THE LINKAGE BETWEEN PHYSIOLOGY AND SHADE-RELATED MORTALITY IN LOBLOLLY PINE BRANCHES

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ABSTRACT

The importance of crown size in forest management is well recognized, with crown length influencing tree growth and survival. Crown length can serve as a proxy for available photosynthetic area and potential tree growth which makes it an important component of process-based forest models. However, predicting the height to crown base and, hence, crown length, accurately remains challenging due to limited understanding of mechanisms of branch mortality. We conducted an experiment to elucidate the conditions that lead to the death of lower branches under shade conditions in loblolly pine (*Pinus taeda*). To do this, we explored the relationship between parameters of photosynthetic light response curves and branch mortality using point biserial correlation. Light saturated net assimilation rate (A_{max}), dark respiration rate (R_d), light compensation point (LCP), and light saturation point (LSP) showed the strongest relationship with branch mortality (r_{bs} >0.64). We concluded that shade-induced mortality in branches is associated with several physiological changes which include a decline in $A_{max,}$ $R_{d,}$ LCP, and LSP. Results from this study will help us predict crown size more accurately and improved prediction of crown size will ultimately lead to improved process-based models predicting stem growth and mortality.

INTRODUCTION

The importance of crown size has been widely recognized in forest management. It is a commonly used variable in various forest models, including growth, stem taper and volume, biomass, and mortality models (Gonzalez-Benecke and others 2014, Jucker and others 2016). The quantity of foliage on a tree is a key factor in determining its growth and survival, with longer crowns typically carrying more foliage than shorter ones (Antos and others 2010, Macfarlane and others 2007). Mortality in trees has been a topic of extensive research over the years; however, most of these studies have primarily focused on drought-induced mortality of whole trees (Anderegg and others 2015, McDowell and others 2008, Sperry and Love 2015, Venturas and others 2018) while branch mortality has received little attention. Light availability plays a crucial role in tree growth and crown development (Niinemets 2010) and light is a critical resource for the growth and survival of individual branches (Lone and Khan 2007). Photosynthesis, which is fundamental to branch growth and survival, is modulated by the amount of light available in the environment the branch is growing (Givnish 1988). For example, increased light intensity on foliage usually results in a corresponding increase in photosynthetic carbon assimilation per unit of leaf tissue but at very high light levels, photosynthetic rates may decrease as the excess light damages the leaf tissues (Ögren 1993).

The survival of a branch depends on its ability to extend horizontally and expose the terminal bud and leaves to light. However, in older (lower) branches, the cost of horizontal extension is high, and the productivity of the branches is low. Furthermore, under low light conditions there is insufficient production of energy (reduced photosynthetic activity), often resulting in reduced branch growth (Shao and others 2014)

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and limited carbon assimilation (Samuelson and Stokes 2012). Studies on *Pinus radiata* (Warrington and others 1989), *P. taeda* (Teskey and Shrestha 1985), and *Betula pendula* and *Populus tremula* (Tsel'niker 1979) have all shown that assimilation rates decrease with decreasing light intensities. Inadequate light can also affect the chlorophyll content in leaves, impairing the ability of a branch to efficiently convert light energy into chemical energy (Tang and others 2019).

Trees in closed-canopy forests often experience branch mortality and crown recession because of light limitation, which significantly affects their growth and development (Tinkham and others 2016). The length of the crown is a function of the height to the base of live crown (HCB) and total height of the tree. HCB is calculated as the distance from the base of the live crown to the tip of the highest live branch on the tree and can be a proxy of available photosynthetic area and potential tree growth. The base of the live crown is the point on the stem where the live branches and foliage begin and is typically measured as the distance from the ground to the first live branches on the tree. While easy to conceptualize, the measurement of HCB is a time-consuming process. As a result, several studies have concentrated on the development of predictive models that employ more readily available stand variables to estimate the HCB of trees (Macfarlane and others 2007). Most of these models are based on static measurements using total height, diameter at breast height, stand basal area, crown competition factor, and dominant height or site index as predictor variables (Sharma and others 2017); however, changes in HCB are dynamic. For example, the lowermost branch in the canopy typically dies from shading by the upper branches, thereby increasing HCB as the crown recedes.

Our ability to accurately predict HCB is further hampered by a limited understanding of the mechanisms underlying branch mortality in the lower crown. The main objective of this study was to measure and assess the effects of varying levels of light intensity on the photosynthetic properties of loblolly pine (*Pinus taeda*) branches. Specifically, in this study, we present an exploratory analysis of the relationships between mortality and parameters derived from light response curves of branch foliage developed under different shading conditions.

MATERIALS AND METHODS

Study Area

This study was carried out at Lee Memorial Forest in Washington Parish, southeast Louisiana (32.8°N, 90.0°W). The primary soil type in this forest was the Ruston series (well-drained, fine loamy, siliceous, thermic typic Paleudult). The forest was characterized by an average daily low and high temperatures of 12.0 °C and 25.6 °C, respectively, and mean annual rainfall of 1,600 mm (Dicus and Dean 2008).

Study Design

There was a south-to-north fertility gradient on this site. The southern part had a better site quality which decreased to the northern side. To account for this variation in soil fertility and separate its effects from the treatments being studied, two plots were established, one on the southern and the other on the northern side of the site.

Loblolly pine trees were planted in 2015 in field plots measuring 27 m by 27 m and with initial spacing of 3 m by 3 m. Nine trees per plot of similar height, at the edge of the plots (sun-exposed) and of desirable characteristics such as good form, vigor, and free of disease or insect damage, were selected for this study. Within each plot, one branch on each of three trees received one treatment of either no shade (0 percent), 30 percent shade, or 60 percent shade. Branch whorls were numbered on each tree from the top and an individual branch on the fifth whorl was selected as the target branch.

Shading Technique

Prior to bud burst in the spring, shade structures were installed on the 18 target branches on January 13, 2022 (fig. 1). Shade structures were constructed from concrete reinforcing wire, which was used to support the shading materials.

Figure 1—Shade structure with 30 percent Agfabric sunblock shade cloth on a target branch. (Photo courtesy of Adelodun Majekobaje)

Shading materials used were 30 and 60 percent Agfabric sunblock shade cloth. One shade covered one branch and was adjusted as the tree grew.

Gas Exchange Measurement

Monthly gas exchange measurements were carried out from August to November 2022. These were conducted on sunny days between 0930 and 1330 Central Daylight Time using the default light response program in a portable photosynthesis system (LI-6400xt, Li-Cor, Inc., Lincoln, NE). Attached to the system was a 6-cm^2 cuvette and a blue-red LED light source. For each measurement, two fully expanded fascicles from the first flush were selected. After each measurement, the diameter of the needles and the number of needles per fascicle were measured for data adjustment because the needle fascicles did not fill up the cuvette. The light response curve auto-program within the LI-6400xt system uses photosynthetic photon flux density (PPFD) levels of 1500, 1200, 1000, 800, 600, 400, 200, 100, 80, 60, 40, 20, and 0 μmol m^{-2} s^{-1}. Measurements were also carried out at PPFD level of 2000 μmol m^{-2} s^{-1} which was manually set to simulate full sunlight. In addition to the light-response parameters, stomatal conductance at light saturation point was also used in this study.

Prior to data analysis, gas exchange measurements were standardized with the leaf area per fascicle following the equation from Blazier and others (2018):

$$A = (N + \pi)\, 2LR \quad (1)$$

where

A = Area of needle fascicle (cm^2)

N = Number of needles per fascicle

L = Needle length (which is 3 because a 3-cm by 2-cm light source was used)

R = Radius of fascicle (cm)

Data Analysis

The study was a randomized complete block design with two blocks, three shade levels, and three replications. Eighteen branches were repeatedly measured in August and September while 17 and 13 were measured in October and November, respectively, due to mortality. In total, 66 measurements were carried out during the course of this study.

Statistical analysis on the data was performed in R (R Core Team 2023). A nonrectangular hyperbolic equation was fitted to individual light response curves using a least-square regression following the method of Marshall and Biscoe (1980) and light-response parameters were estimated (fig. 2). Relationships between branch mortality and parameters of light response curve were determined using point biserial correlation.

Parameters of Light Response Curve

Figure 2 shows a fitted light response curve and the derived parameters estimated from the curve. Light-saturated net assimilation rate (A_{max}) is the maximum photosynthetic capacity of a plant under high light intensity. Light saturation point (LSP) describes the point at which the photosynthetic rate reaches a plateau and does not increase commensurately with further increase in light intensity. Light compensation point (LCP) represents the equilibrium between energy production (photosynthesis) and consumption (respiration) in plants. It is the light intensity where the net assimilation rate becomes zero. Rate of respiration or dark respiration (R_d) is the

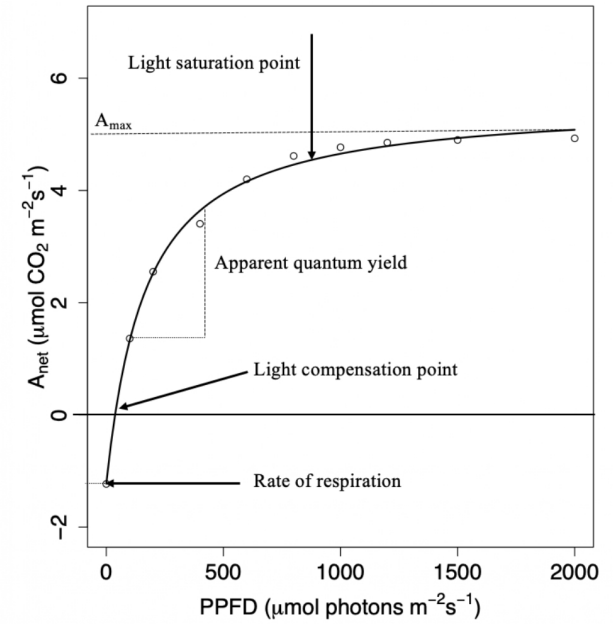

Figure 2—Fitted light response curve and the derived parameters. A_{max} = assimilation at light saturation, PPFD = photosynthetic photon flux density, A_{net} = net assimilation rate.

assimilation rate in the absence of light (i.e., when PPFD was zero).

RESULTS AND DISCUSSION

Observed Branch Mortality

At the end of the 2022 growing season, 11 branches had survived and 7 had died. Greatest mortality was observed in branches under the deepest shade (60 percent) where two of three branches died on both plots while branches under full light (0 percent) performed best with one death recorded on the northern plot. This is consistent with similar studies on whole-tree mortality that found improved growth and survivorship under high light intensity (Kunstler and others 2005, Lin and others 2002).

Relationship Between Branch Mortality and Parameters of Light Response Curve

Figure 3 shows the relationships between mortality and the derived parameters of light

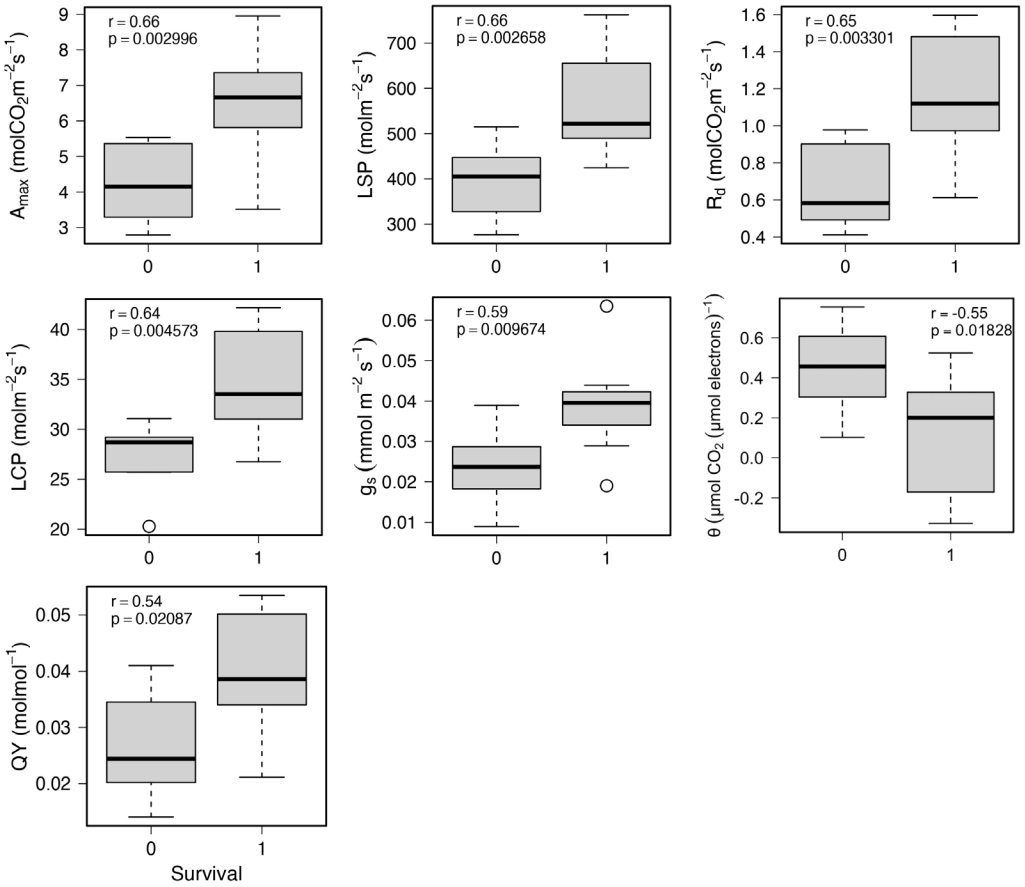

Figure 3—Biserial correlation between branch mortality and parameters of light response curve. 1 = branch alive (n = 11), 0 = branch died (n = 7). A_{max} = assimilation at light saturation, LSP = light saturation point, R_d = rate of respiration, LCP = light compensation point, g_s = stomatal conductance, θ = the convexity of the curve, QY = quantum yield.

response curves as well as stomatal conductance (g_s). Generally, A_{max}, LSP, LCP, and R_d are higher in plants grown under high light intensity (Bond and others 1999, Lewis and others 2000). Quantum yield (QY), which is the initial slope of the light response curve, describes the efficiency with which plants convert absorbed photons into fixed carbon through photosynthesis. Higher QY means more effective conversion of light energy to chemical energy while lower QY indicates lower photosynthetic efficiency (Genty and others 1989). Theta (θ) defines the convexity of the curve and how efficiently photosynthesis responds to changes in light intensity. When the convexity of light response curve is high, photosynthesis in the intermediate range is most effective (Ögren 1993).

In our study of planted loblolly pine, A_{max}, LSP, LCP, and R_d showed the strongest relationships with branch mortality while g_s, θ, and QY showed moderate correlation. In a drought response study, Mitchell and others (2013) found a strong relationship between A_{max}, and R_d and mortality in *Eucalyptus globulus*, *Eucalyptus smithii*, and *Pinus radiata* where they observed death in the three species 40, 50, and 115 days, respectively, after A_{max} reached 0 μmol m^{-2} s^{-1}. A similar trend of higher mean values in surviving branches was observed for all parameters except the convexity term (θ) where the opposite was the case. A similar pattern was observed in Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), where convexity increased between the sun and shade needles, suggesting that photosynthetic efficiency at low light was higher (Lewis and others 2000). High θ values observed in the branches that died (which were mostly shade branches) suggests that these branches rapidly increased their photosynthetic rate with low light intensity, ensuring efficient light capture and utilization in limited light conditions (Ögren 1993).

CONCLUSION

Our study investigated the relationship between parameters of photosynthetic light response curves and mortality in loblolly pine branches grown under contrasting light conditions. The results revealed that branches under deepest shade experienced highest mortality rates while those under full sunlight showed lowest mortality. Among the derived parameters, A_{max}, LSP, LCP, and R_d exhibited the strongest correlation with branch mortality highlighting their significance in promoting growth and survival. Branches undergoing mortality exhibited decline in all these parameters. Shade reduces the chlorophyll content in leaves, which limits the branch's capacity to efficiently convert light energy to chemical energy and thus lead to a decline in A_{max}. Reduction in chlorophyll content also lowers the light absorption capacity of leaves and decreases the light compensation and saturation points. With declining A_{max}, energy (ATP) production is reduced and because dark respiration is dependent on the availability of ATP for cellular processes, dark respiration rate declined in dead branches. Our research contributes to a better understanding of the mechanism of branch mortality in trees by offering insightful information about the physiological responses of branches to shade conditions. It has the potential to improve predictions of tree crown size, growth, and biomass allocation. These improvements can enhance process-based forest growth models, ultimately supporting better forest management practices.

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