LONGLEAF PINE ADAPTATION TO FIRE: IS EARLY HEIGHT GROWTH PATTERN CRITICAL TO FIRE SURVIVAL?

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Abstract—Longleaf pine (*Pinus palustris* Mill.) forests are fire-dependent ecosystems because frequent surface fires prevent other species from being recruited into the canopy. The successful recruitment of longleaf pine has been attributed mainly to its unique fire adaptation – the grass stage. It is commonly believed that, while in the grass stage, longleaf pine seedlings build carbon reserves in the taproot, and this reserve is then mobilized to support fast height growth so that the apical meristem can quickly elevate above flame height. Based on this perception, we hypothesize that when longleaf pine emerges out of grass stage, (H1) height growth is a sudden process so that a critical threshold height can be reached quickly, and (H2) longleaf pine has faster height growth than its fire-susceptible co-genera, loblolly pine (*P. taeda* L.). To test H1, we examined early height growth patterns of planted longleaf pine seedlings. We found that height growth was a gradual rather than a "sudden" process, and there is no evidence for reaching a critical threshold value. To test H2, we conducted stem analysis for young longleaf and loblolly pine trees growing on the same sites. We found that longleaf pine, despite years in grass stage, did not grow any faster than loblolly pines when young. Our results suggest that the pattern and rate of height growth may not give longleaf pine any advantage for fire survival.

INTRODUCTION

Longleaf pine (*Pinus palustris* Mill.) historically dominated the southeastern United States, occurring on site types that included xeric sandhills, coastal plain flatwoods, and mountainous portions of Georgia and Alabama (Peet 2006). Its distribution range coincides with a frequent surface fire regime, with a historic return interval of 0-10 years (Brown and Smith 2000). This frequent surface fire regime maintained longleaf pine dominance throughout its range by preventing other tree species from being recruited into the canopy. For example, loblolly pine (*P. taeda* L.) was commonly restricted to wetter sites that experienced relatively infrequent fires (Schultz 1999), while upland oaks (e.g., *Quercus laevis*), despite their fire tolerance, were mostly restricted as a part of the understory vegetation in longleaf pine ecosystems (Wenk and others. 2011).

There is no doubt that the frequent surface fire regime has given longleaf pine a distinctive advantage over other tree species (Mattoon 1922, Wahlenberg 1946, Croker and Boyer 1975, Boyer 1990). As a large sapling or an adult tree, longleaf pine is very resistant to surface fire. Its apical meristems are well-protected because they are high up in the canopy and mostly out of the reach of surface fires. Additional protection to meristems is provided by insulation from needles and bud scales. Although the lower portion of the stem is exposed to fire, thick bark provides protection to the cambium. However, it is a long way to go from a tiny germinant to a fire-resistant large sapling or adult tree, and longleaf pine regeneration has to survive many repeated surface fires during this process. As a result, longleaf pine has evolved a unique adaptation to fire called the grass stage, a distinctive period of 2-20 years when seedlings remain stemless (Mattoon 1922, Wahlenberg 1946, Croker and Boyer 1975, Boyer 1990). It is believed that grass stage longleaf pine seedlings survive fire because the root collar is kept at the soil surface and the apical meristem is insulated by needles and bud scales. While in the grass stage, longleaf pine seedlings build carbon reserves in the taproot, and, once emerging out of the grass stage, this reserve is mobilized to support rapid height growth to elevate the apical meristem above flame heights (Boyer 1990).

However, our field observations suggest that rapid height growth may not be very important to the fire survival of longleaf pine regeneration. Prescribed fires often scorch the entire canopy of longleaf pine saplings, but most saplings survive nevertheless. Although some saplings may die due to fire, the mortality appears to be unrelated to height, which suggests that getting taller may not be critical to fire survival. In fact, young longleaf

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pine saplings retain dead needles on the stem (fig. 1). During burning, these dead needles likely act as a fuel ladder and spread fire to the upper part of the sapling, which could negate any advantage of growing tall. These circumstantial evidences present a compelling case to question the common wisdom, which believes that grass stage seedlings build carbon reserves in the taproot to support rapid initial height growth to quickly elevate the apical meristem above the flame of surface fires.

The objective of our study is to examine the role of early height growth patterns in fire survival. Based on the perceived importance of rapid height growth when longleaf pine emerges out of grass stage, we hypothesize that: (H1) height growth is a sudden process so that a critical threshold height can be reached quickly, and (H2) longleaf pine has faster height growth than loblolly pine, its fire-susceptible co-genera. To test H1, we used data obtained from longleaf pine seedlings planted for a longleaf pine restoration project conducted at Fort Benning, GA. To test H2, we used data obtained from naturally regenerated longleaf and loblolly pine saplings sampled at Brosnan Forest in Dorchester County SC.

METHODS

Two sets of data were used in the study. Dataset 1 was obtained from measurements of planted longleaf pine seedlings at Fort Benning GA, and dataset 2 came from conducting stem analysis of naturally regenerated longleaf and loblolly pines at Brosnan Forest, SC.

Dataset 1: This dataset was from a large project, in which longleaf pine seedlings were planted during winter 2007/2008 in clearcuts, loblolly pine stands thinned to residual basal areas ranging from 5-9 m^2/ha, and gaps (0.12-0.50 ha) created in loblolly pine stands. A detailed description of the project is given in Knapp and others (2013). We randomly selected and monitored 396 seedlings that had emerged out of the grass stage during the second (2009) or third (2010) growing seasons after planting, and we monitored those seedlings for five growing seasons. Height and diameter growth of each seedling were measured after the 2009, 2010, and 2012 growing seasons. We use 15 cm height (from the root collar to the terminal bud) as the threshold to classify a seedling as either in the grass stage or the height growth stage. Based on our 2009 measurements, seedlings were divided into those still in the grass stage and those in the height growth

Figure 1—Photos to illustrate the retention of dead needles on the stem of a young longleaf pine sapling (A and B). Photo B is a close-up photo of the lower stem portion of a longleaf pine sapling.

stage for one growing season. Similarly, we used the 2010 measurements to divide seedlings into those in the height growth stage for one growing season and those for two growing seasons. For our 2012 measurements, seedlings were divided into those in height growth for three growing seasons and those in height growth for four growing seasons.

Dataset 2: We sampled four stands with both naturally regenerated longleaf and loblolly pine saplings at Brosnan Forest. Between 5 and 10 dominant stems were destructively sampled for each species in each stand. A total of 29 stems were sampled for each species. For each destructively sampled stem, total height was measured in the field. Each stem sampled was marked at 0, 0.3, 0.6, 1.4, 2.4, and in 1 m intervals thereafter. A stem disk was taken from each marked position along the stem. Stem disks were taken to the laboratory, sanded using progressively finer sand paper, and the number of rings was counted on each disk. Based on the position of each disk and the number of rings counted, a series of height and age data were derived for each stem. We used Carmean's (1972) method of interpolation to derive the true height for the corresponding age recorded on each disk due to hidden tips between successive stem disks. For longleaf pine stems, the ranges of height, diameter at breast height, and age were 5-14 m, 4-9 cm, and 9-24 years, respectively. For loblolly pine stems, the ranges of height, diameter at breast height, and age were 5-15 m, 4-12 cm, and 5-25 years, respectively.

Data analyses: For dataset 1, we displayed height prior to the height growth stage (year 0) and height after one to four growing seasons using box plots. We also calculated frequency of seedlings in each of five height classes (< 30, 31-60, 61-90, 91-120, and >120 cm) after one to four growing seasons. For dataset 2, we plotted height over age, based on which we fitted the height-age relationship for each species using the Chapman-Richards model. The Chapman-Richards model has been commonly used to describe growth-age relationships (e.g., Pienaar and Turnbull 1973, Wang and others. 1994). The two resulting equations were then graphically compared to show differences in early height growth between longleaf and loblolly pine. Statistical analyses were conducted using SYSTAT 13 (Systat Software, Inc. 2009).

RESULTS AND DISCUSSION

Before entering the height growth stage, longleaf pine seedlings averaged 8.5 cm tall, which demonstrated a gradual, rather than sudden, increase in height when emerging from the grass stage (fig. 2). Seedlings

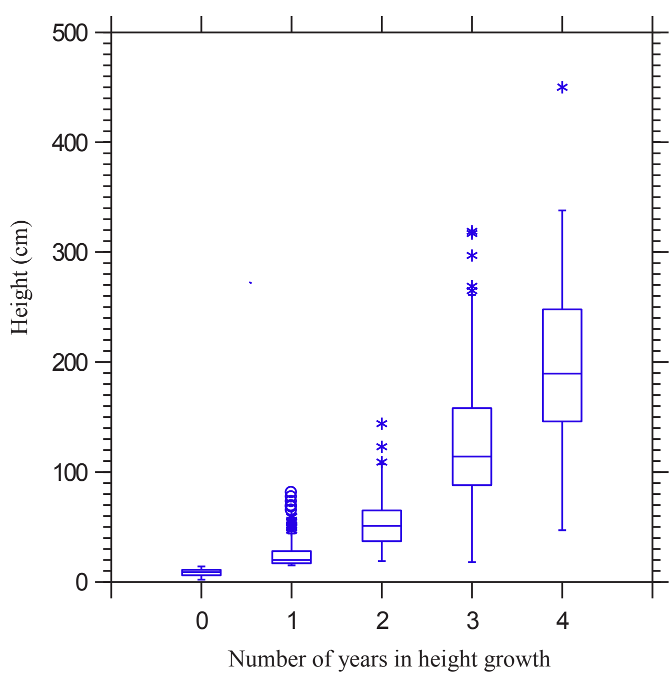

Figure 2—Boxplots showing the height of longleaf pine seedlings after different numbers of years in height growth. For each year, the height data are divided into four quartiles. The first and third quartiles from bottom to top form the box, which includes 50% of the data and divided evenly by the median in the center of box. One quartile of data each is above and below the box, illustrated by the two vertical lines (also called whiskers). The asterisks are called outside values. The dots are called far outside values.

averaged 24.2, 55.0, 124.9 and 193.2 cm tall, respectively, after their 1st, 2nd, 3rd and 4th years in height growth (fig. 2). The height growth rate accelerated over the first four years, and it averaged 16, 31, 70 and 68 cm per year during the 1st, 2nd, 3rd and 4th growing season, respectively, after emerging out of grass stage. Croker and Boyer (1975) suggested a critical height threshold of three feet (about 90 cm) for fire resistance during the height growth stage. We found that most seedlings did not reach this critical height after the first two growing seasons (table 1). After one growing season, none of the seedlings reached 90 cm tall. After two growing seasons, only 9.2 percent seedlings were 90 cm or taller. More than half of the seedlings (58.6 percent) were taller than 90 cm after three growing seasons. Most seedlings (close to 90 percent) were taller than 90 cm after four growing season (table 1).

Longleaf pine did not grow faster than loblolly pine, despite many years spent in the grass stage before initiating height growth (fig. 3). In fact, longleaf pine had slightly slower height growth than loblolly pine (fig. 3). Our results suggest that growing tall alone is not a viable strategy for fire survival. Indeed, we question the usefulness of using height to predict fire survival, but more studies are needed to fully understand the mechanisms of fire survival for juvenile longleaf pine.

Our results confirmed that longleaf pine seedlings could grow as much as 1.5 m in three years (Mattoon 1922). However, this growth rate was similar to or surpassed by a fire sensitive con-generic, loblolly pine, growing on the same sites. Other common competitors of longleaf pine, such as oaks, have the ability to sprout after fire, and it is likely their initial height growth is also comparable to longleaf pine. Given that longleaf pine, loblolly pine, and perhaps oak sprouts have comparable height growth rates, the success of longleaf pine and the failure of other species under a frequent surface fire regime must be attributed to other factors. Future studies should identify these factors and determine their role in the fire survival of small longleaf pine saplings (i.e., seedlings in early height growth stage).

CONCLUSIONS

Our results did not support our first hypothesis (H1), which height growth is a sudden process so that a critical height threshold can be reached during the first growing season. Longleaf pine seedlings did not emerge out of the grass stage suddenly. The annual height growth rate accelerated during the first four years after emerging from the grass stage, but it took 3-4 years for seedlings in the height growth stage to reach the perceived critical level (Croker and Boyer 1975).

Our results also failed to support the second hypothesis (H2), that longleaf pine has faster height growth than its fire-susceptible co-genera, loblolly pine. Despite many years in the grass stage, longleaf pine did not grow any faster in height than loblolly pine. In fact, loblolly pine grew consistently faster than longleaf pine during the first 20 years. Despite its faster height growth, however, loblolly pine regeneration fails completely in a frequent surface fire regime, with which longleaf pine copes extremely well.

Based on testing H1 and H2, we conclude that the early height growth pattern is not a critical factor responsible for fire survival of juvenile longleaf pine.

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Table 1—Percentage of longleaf pine seedlings in each height class after 1, 2, 3, and 4 years since initiating height growth

	Year 1	Year 2	Year 3	Year 4
Height < 30 cm	80.8	12.2	1	0
Height 30-60 cm	17.7	55.2	14.1	3.4
Height 60-90 cm	1.5	22.4	26.3	6.8
Height 90-120 cm	0	8.2	38.9	8.0
Height > 120 cm	0	1.0	19.7	81.8

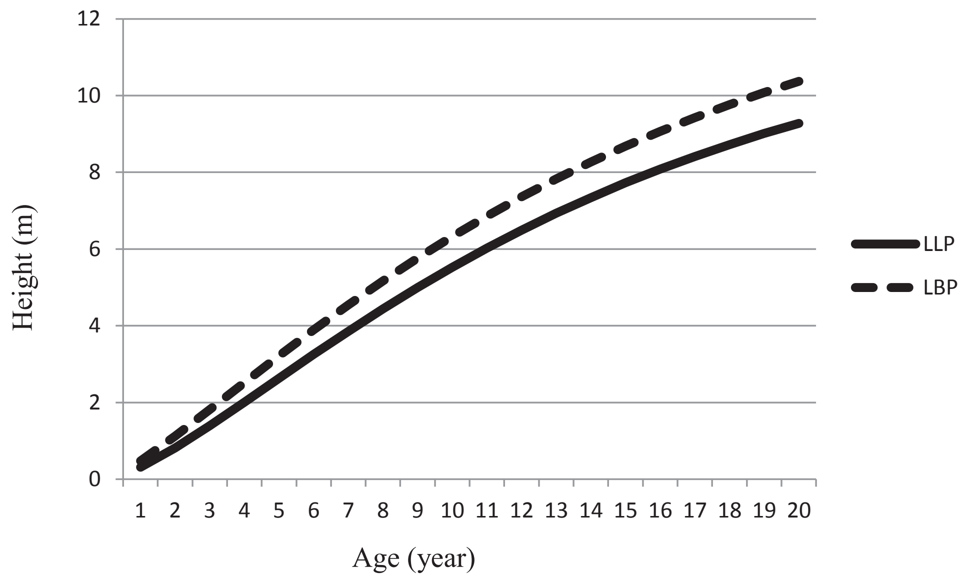

Figure 3—A comparison of height growth between longleaf (LLP) and loblolly (LBP) pine. Note that the age of longleaf pine is the number of years in height growth, while the age of loblolly is the true age since germination.

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