DEVELOPMENTAL DYNAMICS OF LONGLEAF PINE SEEDLING FLUSHES AND NEEDLES

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Abstract—Longleaf pine (*Pinus palustris* Mill.) seedlings were grown for 27 weeks in containers of three cavity sizes and two cavity types (with and without copper coating) and then outplanted in central Louisiana in November 2004. Three seedlings from each plot were assessed repeatedly for shoot flush and needle development in 2007 and 2008. Cavity type had no effect on seedling size or number of flushes. Cavity size did not affect number of flushes or needle length. However, seedlings grown in large cavities were taller than seedlings from medium and small cavities. Within each cavity size class, the first flush formed was the longest, and flushes formed thereafter were of similar lengths. Needles from flushes formed later in the year were shorter than those from the earlier flushes. Except for the first flush, it took needles twofold to threefold more time to complete elongation than the flushes.

INTRODUCTION

Disappearance of about 96 percent of the pre-European settlement longleaf pine (*Pinus palustris* Mill.) ecosystems in the South has been caused by extensive harvest of longleaf pine for timber and naval store products between late 1800s and early 1900s, conversion of lands supporting longleaf pine to agriculture farms or other fast-growing pine species, and exclusion of fire from the landscape (Brockway and Outcalt 1998, Landers and others 1995, Outcalt 2000). For the last two decades, many public, industrial, and private land managers and owners have been actively restoring longleaf ecosystems in the Southern United States (Barnett 2002, Boyer 1989, Landers and others 1995). In most artificial longleaf regeneration efforts, container-grown seedlings usually have had a higher survival rate than bare-root stock (South and others 2005 and references cited therein). However, one noted drawback of using container-grown stock for planting is that the established trees have experienced windthrow during strong wind events (South and others 2001). One of the attempted improvements in the morphological quality of container stock root systems was to coat the inside of the cavity with copper (Cu). Slow release of low concentration Cu stops seedling lateral roots from elongating once they reach the cavity wall (Ruehle 1985). In a root growth potential test, longleaf pine seedlings grown in Cu-coated cavities produced more new roots than those grown in non-Cu containers or bare-root seedlings (South and others 2005). Lodgepole pine (*P. contorta* Douglas ex. Louden) grown in Cu-coated cavities had fewer leaning seedlings 3 years after planting than those from cavities without a Cu coating (Krasowski 2003).

A study comparing the short- and long-term effects of different container cavity sizes and types on longleaf pine seedling growth, field performance, and tree stability was implemented in 2004 in central Louisiana. This report will focus on the effects of container cavity size and type on the seasonal developmental dynamics of individual flushes and their needles in 2007 and 2008 from that study.

MATERIALS AND METHODS

Seedling Culture and Stand Establishment

Seedlings were from a long-term study where the effects of container cavity size and cavity coating type on longleaf pine seedling growth, physiology, and root system architecture during greenhouse culture and subsequent field planting were being investigated. Details of the seedling culture and the plantation establishment were presented by Sung and others (2010). Briefly, longleaf pine seeds from a Florida seed orchard were sown in containers in April 2004. There were six container treatments—three cavity sizes and two cavity coating types. Cavity volume for the small (S), medium (M) and large (L) cavity sizes were 54, 93, and 170 ml, respectively. Styroblock® and Copperblock® containers (Beaver Plastics Ltd, Edmonton, Alberta, Canada) of the above mentioned cavity sizes were used for no coating (R) and Cu coating treatments, respectively. Cu oxychloride was the active ingredient in the coating. Protocols for growing longleaf pine by Barnett and McGilvray (2000) were adapted for this study with some modifications (Sung and others, 2010).

The field study site is located on the Palustris Experimental Forest within the Kisatchie National Forest in Rapides Parish of central Louisiana (31°11' N, 92°41' W). The soil is a moderately well-drained, gently sloping Beauregard silt loam (fine silty, siliceous, superactive, thermic, Plinthaquic Paleudults). Mima mounds of Malbis fine sandy loam (fine loamy, siliceous, subactive, thermic, Plinthic Paleudults) are scattered across the study area. The field study is a randomized complete block factorial design with four replications. Blocking was by soil drainage. Twenty-four treatment plots of 0.0576 ha (24 by 24 m) each were established. Seedlings grown in the six cavity treatments (R-S, Cu-S, R-M, Cu-M, R-L, and Cu-L) were randomly assigned to a plot in each block. In early November 2004, 27-week-old container-grown longleaf pine seedlings were lifted and planted on the same day. Seedlings were planted at 2- by 2-m spacing. Treatment plots are 12 rows of 12 trees. All

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plots were prescribed burned in February 2006 (15 months postplanting) as part of the routine management of the site.

Field Measurements

In July 2006 (20 months postplanting), 3 seedlings from each of the 24 plots were randomly selected and tagged for repeated measurements. Flush development in these 72 seedlings was monitored in 2007 and 2008. The bud for the first flush of any given year was formed during the previous year. The starting day for the first flush was the same for all seedlings and was set at March 8 and February 8 when the field measurements began for 2007 and 2008, respectively. Flush length was measured periodically from mid-March through mid-December. In 2007, needle elongation was measured on needles within 5 cm above the nonneedle growing region at flush base. In 2008, specific needles were marked with lightweight paper clips so that the same needles were measured each time. Periodically, lengths of needles near the marked needles were measured to verify that the weight of the paper clip did not interfere with needle elongation. Needle development began with the protrusion of needles from their white fascicle sheaths.

Statistical Analysis

The randomized complete block analysis was used for all study variables that were associated with the entire seedling such as tree heights and number of flushes per seedling. The study was extended to a split-plot design by considering flush order (1 to 6) within each seedling as the split-plot factor. Analyses on variables associated with flushes or needles were analyzed according to this split-plot design. PROC MIXED (SAS Institute Inc. 2004) was used for all analyses and pairwise comparisons were performed using least squares means with a Bonferroni adjusted experimentwise significance level of 0.05. The logistic function was used to model the developmental pattern of flush length and needle length on an individual seedling basis (Sung and others 2004). Because of the less frequent monitoring of the shoot flush and needle development in 2007 than in 2008, only the 2008 shoot flush and needle lengths were modeled. The logistic equation was defined as:

$$\text{Length} = a / (1 + e^{b+c\text{Day}})$$

where

Length = flush or needle length (cm)

Day = days since the observation of a new bud or since the protrusion of needles from the fascicle sheath

a, b, c = parameters of the logistic function

Nonlinear regression was used to estimate the parameters using PROC NLIN (SAS Institute Inc. 2004). The instantaneous rate of flush or needle elongation at a given day was obtained by determining the slope of the specific logistic equation evaluated at that day:

$$\text{Slope} = (-ace^{b+c\text{Day}}) / (1 + e^{b+c\text{Day}})^2$$

The inflection point was where the instantaneous rate of flush or needle elongation reached its maximum and began to slow down:

$$\text{Inflection point day} = -b/c$$

RESULTS AND DISCUSSION

The flush development sequence of longleaf pine seedlings observed in this study can be classified into the following seven stages. Stage 1 is when a bud becomes visible to the unaided eye and still has tight scales (cataphylls) either white or light brown in color. At stage 2, the bud scales become loose. At stage 3, the lower portions of some bud scales turn green. At stage 4, intact white fascicle sheaths are visible. These fascicle sheaths usually start appearing at the lower portion of a flush. In some flushes, however, the fascicle sheaths appear from other portions of a developing flush, and their appearance is not necessarily synchronized around the circumference of a flush. At stage 5, green needle tips protrude out of the fascicle sheaths. At stage 6, the flush axis which has been elongating since stage 2 completes elongation when the flush elongation rate slows down to <0.5 cm over a 2-week period. At stage 7, needles complete elongation (that is, <1-cm increases over a 2-week period), and thus the entire flush development is considered complete for the purposes of this study.

Stage 1 was recorded as the beginning of a new flush except for the first flush. Buds that developed into the first flushes for any given year were formed in the previous year, staying dormant until the following spring. In most cases, stage 1 of the subsequent flush proceeded shortly before the end of stage 6 of the currently elongating flush. At the latter part of stage 6, the tip of the elongating flush became a tight bud which was recorded as the beginning (stage 1) for the subsequent flush. There was a narrow region below this newly formed bud that did not have needles. This bare region would later extend to 0.5 to 2.5 cm in length. Thus, it was easy to count how many flushes a longleaf pine seedling produces within a year. In recent yet fully extended needles, however, the chlorophyll contents and photosynthetic rates have yet to reach the highest levels.[2] Thus, these needles are not yet physiologically mature at the end of stage 7. In first-year northern red oak (*Quercus rubra* L.) seedlings, the fully expanded median leaf in the third flush did not photosynthesize as much as the fully expanded median leaves in the first two flushes at the end of flush development (Hanson and others 1986). These authors attributed it to the fact that physiological and anatomical development of oak leaves do not proceed at the same rate in all flushes.

Number of flushes in 2007 and 2008 were not affected by cavity type or size (data not shown). All seedlings grew at least three flushes in 2007 and 2008. In 2007, 92, 71, and 25 percent of seedlings grew at least four, five, and six flushes, respectively. In 2008, 97, 79, and 32 percent of seedlings grew at least four, five, and six flushes, respectively. Since less

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than one-third of seedlings assessed in this study produced six flushes, longleaf pine, like *Quercus* spp. (Hanson and others 1986), displays a semideterminate, recurrently flushing pattern of shoot growth. Sheffield and others (2003) reported that mature longleaf pine trees in south Georgia exhibited a determinant pattern (one flush per year) of shoot flush and needle growth in some years and an indeterminate pattern (multiple flushes per year) in other years.

In 2008, cavity type did not affect flush length, needle length, flush elongation duration, needle elongation duration, flush inflection point day and its slope, and needle inflection point day and its slope (table 1). Nor did cavity type affect flush length in 2007 (data not shown). Cavity size affected flush length and inflection day slope significantly in 2008 (table 1). Flush order had the most significant effects on the assessed parameters in 2007 (data not shown) and 2008 (table 1). Cavity size had significant effects on seedling heights in the first 4 years after planting. Four years after planting, the L seedlings were 29 and 55 percent taller than the M and the S seedlings (fig. 1). There were no height differences between the M and the S seedlings.

When lengths of individual flushes were analyzed, L seedlings always had longer flushes than those from the S seedlings for each of the first four flushes formed in 2007 (table 2). Within each cavity size class, the first flush of 2007 was always the longest among all the flushes formed. Flushes formed after the first one were similar in length. In 2008, there were no interactions between flush and cavity size effects on flush lengths. Mean flush lengths for the L seedlings were significantly greater than that of the S seedlings (table 2). The first flush of 2008 was the longest among all flushes (table 2, fig. 2). The fifth and sixth flushes which were formed later in the year were the shortest. This is quite different from the flush size reported for oaks. In the first-year seedlings of several oak species, all flushes except for the last flush of the season were longer than their proceeding flushes (Sung and others 2004).

Needle lengths were affected by cavity type and size in 2008 through their significant interaction. Needles from the earlier formed flushes in a year, such as the first three flushes, were significantly longer than those from the later flushes, such as the fifth and the sixth flushes (table 3, fig. 2). When needles of the fifth and sixth flushes started developing, it was late in the growing season (see below) and these needles did not have as many days for elongation before the short day length and cool temperatures stopped them from elongating. These shorter needles did not resume elongation the following spring. Cavity type affected needle lengths in 2007, and there were three- way interactions among type, size, and flush (data

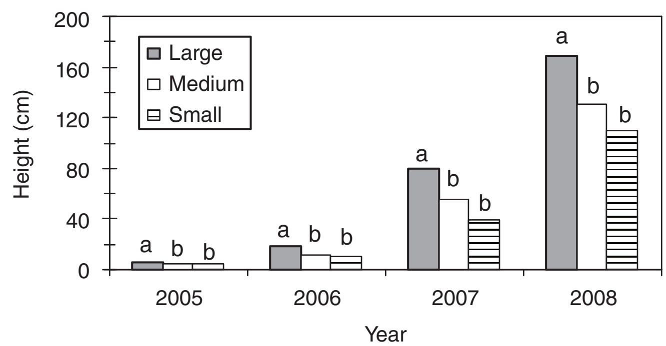

Figure 1—Effects of container cavity size on longleaf pine seedling height growth in the field. Seedlings were grown in containers for 27 weeks in a greenhouse and planted in central Louisiana in November 2004. Least square means with the same letter for each year were not significantly different at the Bonferroni adjusted 0.05 level.

Table 1—Probabilities of a greater *F*-value for the fourth-year longleaf pine seedling flush length, flush elongation duration, flush logistics inflection day, flush slope at inflection, needle length, needle elongation duration, needle logistics inflection day, and needle slope at inflection in response to container cavity size (small, medium, and large), coating type (with and without copper), and flush order in 2008

Source of variation	FL	FED	FI	FIS	NL	NED	NI	NIS
Type	0.6218	0.6674	0.6435	0.4250	0.3553	0.9012	0.3420	0.9051
Size	0.0196	0.3226	0.9303	0.0246	0.4219	0.9261	0.6288	0.0814
T × S	0.2062	0.7281	0.5324	0.0629	0.2039	0.2223	0.0748	0.0577
Flush	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
T × F	0.9370	0.9681	0.7522	0.8657	0.5355	0.9866	0.6352	0.7441
S × F	0.1370	0.1908	0.8796	0.2773	0.0329	0.4490	0.1280	0.4993
T × S × F	0.8709	0.3888	0.0129	0.5601	0.5696	0.9445	0.6760	0.5048

FL = flush length; FED = flush elongation duration; FI = flush logistics inflection day; FIS = flush slope at inflection; NL = needle length; NED = needle elongation duration; NI = needle logistics inflection day; NIS = needle slope at inflection.

Table 2—Lengths of the third-year (2007) and the fourth-year (2008) longleaf pine seedling flushes. The third year had a significant size x flush interaction while the fourth year did not.

Container size	First	Second	Third	Fourth	Fifth	Sixth
	2007 individual flush length (*cm*)					
Large	23.8[a] a A	9.2 a B	10.0 a B	8.8 a B	8.3 a B	6.7 a B
Medium	15.1 b A	6.6 ab B	7.2 ab B	6.6 ab B	5.5 a B	5.3 a B
Small	10.4 c A	4.1 b B	4.6 b B	5.1 b B	4.5 a B	3.4 a B
	2008 all flush length (*cm*)					
Large	15.7 a					
Medium	13.7 ab					
Small	12.6 b					
	2008 individual flush length (*cm*)					
All sizes	34.0 A	13.4 B	13.0 B	10.8 B	7.4 C	5.3 C

[a] Least square means followed by the same letter within a column (lower case) or a row (upper case) were not significantly different at the Bonferroni adjusted 0.05 level.

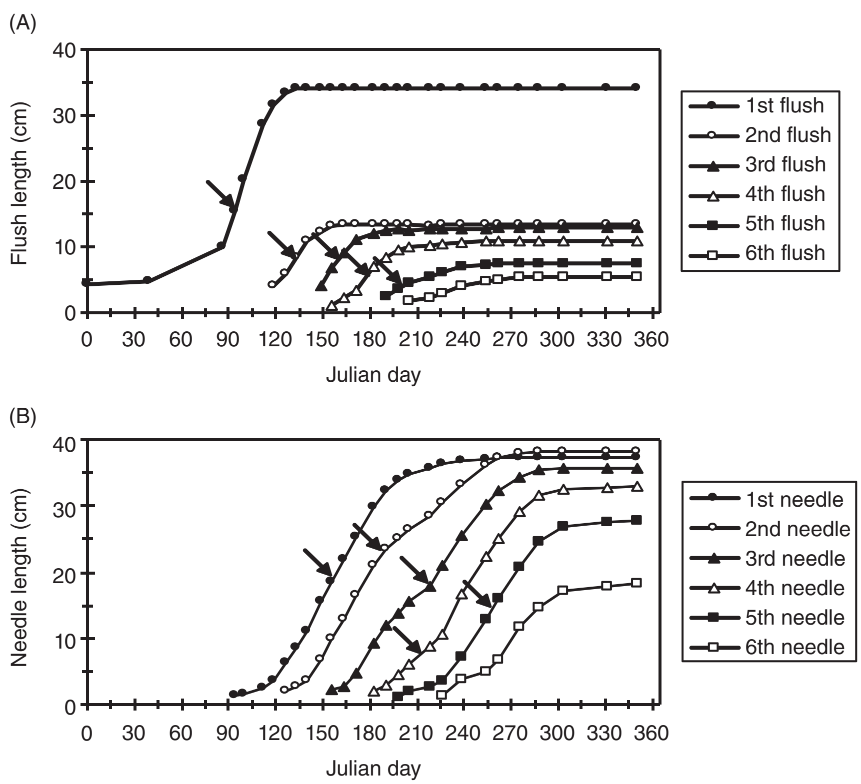

Figure 2—Temporal patterns of the fourth-year longleaf pine seedling (A) flush and (B) needle development in 2008. Arrows indicate the inflection point day for each curve.

Table 3—Lengths of needles from different flushes of the fourth-year longleaf pine seedlings in 2008

Container size	First	Second	Third	Fourth	Fifth	Sixth
	-------	-------	-------	*cm*	-------	-------
Large	37.3[a] A	38.8 A	36.4 AB	32.9 B	28.0 C	16.2 D
Medium	38.1 A	37.9 A	34.6 AB	32.0 BC	29.4 BC	22.9 D
Small	36.6 AB	38.0 A	36.2 AB	33.7 B	26.1 C	16.5 D

[a] Least square means within the same row followed by the same letter were not significantly different at the Bonferroni adjusted 0.05 level.

not shown). Nevertheless, as in 2008, needles from the sixth flush were shorter compared to needles from earlier flushes in 2007 (mean value of 25 cm for the sixth flush and mean value of 38 cm for the first five flushes).

Cavity type or size did not affect the starting date for all the flushes formed after the first flush in 2007 or 2008 (data not shown). Nor did the container type or size affect the duration of flush and its needle elongation for all six flushes in 2007 (data not shown) or 2008 (table 1). However, the order of flush had significant effects on the duration of shoot flush and needle extension in 2008 (table 4). Figure 2 presents the temporal patterns of shoot flush and needle development in 2008. When the first flush bud started to elongate in late February and early March, temperatures were still cool at night and at times during the day. When the second and third flush buds appeared in late April and May, respectively, temperature and soil water content at this site were favorable for plant growth. Therefore, duration of flush elongation was the shortest for these two flushes. Flushes that started between late June and July were affected by the drought and high temperatures in July and August in this area and thus had longer elongation duration than those formed in spring. Sword and others (1996) reported similar results of limited resource affecting flush elongation in loblolly pine (*P. taeda* L.) trees grown in this area. Although the flush elongation duration was long for the first flush, the instantaneous rate (cm per day) of flush elongation at the inflection point was still the highest for this flush (table 5). Except for the sixth flush, mean daily elongation rate for the first through the fifth flushes (flush length divided by flush duration, cm per day) were twofold to fourfold more than the reported values for shoot elongation in mature longleaf pine trees (Sheffield and others 2003). The duration of first flush elongation was greater than the values (20 to 69 days) reported for mature trees (Sheffield and others 2003).

During the development of the first flush, some of the current photosynthate produced by needles of the previous 1 or 2 years are used to grow the first flush stem and its needles. By the time the first flush needles finished elongation in mid-August, the seedlings had grown three or four more flushes.

Table 4—Elongation duration of flush and its needles in different flushes of fourth-year longleaf pine seedlings in 2008

Flush	Flush	Needle
	--------- *days*	---------
First	86[a] a	117 b
Second	32 d	125 a
Third	30 d	116 b
Fourth	40 c	104 c
Fifth	44 bc	99 c
Sixth	52 b	85 d

[a] Least square means within the same column followed by the same letter were not significantly different at the Bonferroni adjusted 0.05 level.

Table 5—Slopes of flush and needle elongation at the inflection point day in different flushes of the fourth-year longleaf pine seedlings in 2008

Flush	Flush	Needle
First	0.91[a] a	0.52 a
Second	0.44 bc	0.43 b
Third	0.51 b	0.42 b
Fourth	0.38 c	0.49 a
Fifth[b]	0.23 d	0.49 a

[a] Least square means within the same column followed by the same letter were not significantly different at the Bonferroni adjusted 0.05 level.

[b] No logistics were analyzed for the sixth flush or needles because less than one-third of seedlings grew the sixth flushes.

From May through August, longleaf pine seedlings and trees in the Southern United States are active in stem height and diameter growth, fine root elongation, and storing starch reserves (Sung and others 2004, Sword-Sayer and Haywood 2006). Therefore, competition for current photosynthate produced by previous years' needles and the first flush needles of the current year within a seedling or tree is heavy. This could explain why the slopes of the second and third flushes were about 50 percent of the first flush slope (table 5) even though the environment is better for them to elongate than for the first flush. There generally was no lag period between flush elongation completion and the appearance of the subsequent flush bud. This developmental pattern is different from those of oak species where a 10-day-to-2-week lag period was reported between flushes (Hanson and others 1986, Sung and others 2004).

Duration of needle elongation lasted more than 3 months for all flushes except for the last flush (table 4). Sheffield and others (2003) also reported this unique developmental pattern of unsynchronized elongation between flush and its needles in mature longleaf pine trees. In loblolly pine and slash pine (*P. elliottii* Engelm), elongation of flush and needle occur simultaneously (Dougherty and others 1994). However, shoot flush and needle development of young loblolly pine trees in central Louisiana was also unsynchronized (Tang and others 1999). Unlike the mature longleaf pine trees where there was a 30-day delay between flush elongation cessation and needle elongation (Sheffield and others 2003), needles of these young longleaf pine seedlings started elongation before flush elongation was almost complete (fig. 2). Needles from the first three flushes had longer elongation duration than that from the fourth and the fifth flushes. The short elongation duration for the sixth flush needle was caused by the onset of short day length and cold temperatures. Slopes for needle elongation were dissimilar for flushes one through five (table 5). Slopes for the first, fourth, and fifth flush needles were greater than those of the second and third flush needles. Mean daily elongation rate for needles from the first through the fifth flushes (flush length divided by needle duration, cm per day) were 30 percent more than the reported values for needle elongation in mature longleaf pine trees (Sheffield and others 2003). We found the duration of first flush needle elongation was similar to the reported values from mature trees (Sheffield and others 2003).

The developmental patterns of flush and needles are only affected by the order of the flush and not by container treatments. The delineated developmental dynamics of flush and needle in longleaf pine should offer researchers a way to use flushes and needles of similar morphological attributes to evaluate treatment effects on some of the physiological parameters such as photosynthetic rate, chlorophyll contents, and carbohydrate pools. For example, one should note that even when needles have fully extended, it does not mean that these needles have reached physiological maturity.

FURTHER RESEARCH QUESTIONS

In longleaf pine plantation management, prescribed burns are usually implemented every 2 to 3 years and alternated between dormant season and growing season. This study site is scheduled to be burned in spring (April or May) of 2009. Shoot flush and needle development will be monitored in 2009 to assess how prescribed fire affects the developmental dynamics of flushes and needles. If the previous years' needles and the current year first and second flush needles are scorched by the fire, one would speculate that growth of the third and fourth flushes and needles has to come from the stored reserves in stems and taproots, and thus probably would not be sizable. How will the dormant season burn impact the developmental pattern of the next year's first flush and needles? Can one use the shoot flush and needle developmental dynamics to justify burning in one season versus the other?

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