UNDERSTANDING CARBON SINK-SOURCE RELATIONSHIPS IN SEED ORCHARD LOBLOLLY PINE RAMETS

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Abstract—Attributes of shoots and their female reproductive organs from six ramets of a single loblolly pine clone were assessed in 2015 and 2016 at a Louisiana seed orchard. Seasonal developmental patterns were similar between years. Female strobilus buds were visible in December of year 1, and female strobili were pollinated in early March of year 2. Conelets (pollinated female strobili) stopped increasing in length from June of year 2 until March of year 3 when rapid expansion occurred over the next 4 months. In March and April of 2016, 61 percent of female strobili and conelets of the 2017 crop were aborted whereas a few conelets of the 2016 crop were lost. Competition for carbohydrate among various actively growing sinks in the spring may play a critical role in the abortion of female strobili and conelets. Balancing the carbon sink-source relationships among vegetative and reproductive organs should be considered when the goal is to enhance the production and retention of female reproductive organs.

INTRODUCTION

Loblolly pine (*Pinus taeda* L.) is an economically important pine in the Southeast United States due to extensive natural range and intensive tree improvement efforts resulting in faster growth and improved disease resistance. Productivity in plantations of genetically improved loblolly pine has increased 7–12 and 13–21 percent over unimproved seedlots for the first and second generations of tree improvement programs, respectively (Li and others 1999). During the last 2 decades, the third generation of genetically improved seedlings has been deployed, and the estimated plantation productivity increase is even greater, especially when combined with intensive silvicultural practices (McKeand and Bridgewater 1998, McKeand and others 2006). Increasing the formation and retention of female strobili and seed efficiency per cone in clonal seed orchard ramets is a critical part of the tree improvement process.

Correlations exist between the environment and cone and seed production. Dewers and Moehring (1970) showed that loblolly pine trees subjected to April–June irrigation followed by July–September drought increased the number of conelets per tree in a Texas seed orchard. Wenger (1957) reported a correlation between May to July rainfall and cone crop size 2 years later. Soil fertilization at critical periods throughout the female reproductive cycle is also important (Schmidtling 1983, Wenger 1953). Several studies on shoot and foliage phenology as affected by silvicultural treatments, such as nitrogen fertilization and throughfall control, were conducted on plantation loblolly pine trees (Sword and others 1996, Tang and others 1999, Zhang and others 1997). There is little information, however, on the simultaneous phenology of vegetative shoots and their female reproductive organs in loblolly pine trees grown in plantations or seed orchards. To address this knowledge gap, a study was implemented on clonal loblolly pine in a Louisiana seed orchard in 2015 to evaluate developmental patterns in loblolly pine from the perspective of carbon sink-source relations. Our explicit objectives were: 1) to establish the temporal developmental patterns of vegetative and reproductive organs, and 2) to evaluate silvicultural treatments (soil fertilization and irrigation) for their impact on the production and retention of cones and on seed efficiency.

MATERIALS AND METHODS

Study Area and Experimental Design

The study was conducted at the International Forest Company's (IFCO) clonal seed orchard near Evans, LA. The experimental area is dominated by Hainesville

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fine sand having a 0–2 percent slope that is somewhat excessively drained (NCSS 2016). In January 2015, an experiment with a randomized complete block 2 x 3 factorial design with five blocks was imposed on 30 ramets of loblolly pine clone LSG-62. Blocking was based on competition index. For a given experimental unit (that is, a ramet), its competition index was calculated using equation 1.

$$CI = (CR \times 1.0) + (DR \times 0.7) \tag{1}$$

where

CI = the calculated competition index

CR = the number of adjacent ramets located in four cardinal directions

DR = the number of adjacent ramets located in four diagonals

Treatments were two levels of irrigation (ambient rainfall or ambient rainfall plus drip irrigation at 1090 L per ramet per day between July 10 and September 21, 2015) and three levels of soil fertilization [operational annual broadcast fertilizer application (OFA) in mid-July, OFA plus 28 Kg/ha of phosphorus (P) as triple super phosphate (mid-August), or OFA plus 28 Kg/ha of P as triple super phosphate (mid-August) and 112 Kg/ha of nitrogen (N) as ammonium nitrate (mid-September)]. The 2015 OFA included 115 Kg/ha of N as ammonium nitrate and 1.1 Kg/ha of boron (B) as Solubor®. Fertilizer treatments other than OFA were applied based on the ground area within the dripline of each ramet. The original study was revised in 2016 because no or minimal treatment differences were observed in 2015. The revised experiment is a randomized complete block design with four location-based blocks, three treatments, and two replications. Six of the 30 ramets in the 2015 study were omitted in the new design. Results from these six trees are reported here.

Shoot Selection, Measurements, and Cone Assessment

In January 2015, two first-order branches receiving full sunlight in the southwest quadrant of the upper one-third of the crown of each ramet were identified. Ten main and lateral shoots formed in 2014 were permanently tagged with numbered zip ties for shoot morphology and female reproduction measurements. The phenology of vegetative and reproductive organs was followed at a 4-week interval between February and October. Before needle fascicles emerged, flush length was measured from the base to the tip of the flush, and once needle fascicles began to emerge from their sheaths, only the foliated portion of a flush was measured. Lengths of needles were measured from the fascicle base to the tip. These measurements were repeated for second and third flushes. Day of assessment was expressed as Julian day (JD) starting in 2015 and continuing through 2016.

One year before the start of this study, shoots in the upper crown of each ramet were bagged in early February 2014 for controlled mass pollination. These ramets were open-pollinated in 2015 and 2016. The number of female strobili on the main shoot and shoots lateral to the main shoot were recorded separately. At each measurement, one randomly selected female strobulus on the main shoot was measured for length. Mature cones were harvested at the end of September in 2015 and 2016. Cone morphological traits and number and dry weight of filled and partially filled seeds were obtained from all harvested cones. Each ovuliferous scale of a female strobilus bears two ovules which may eventually develop into seeds. Scales at the bottom of a female strobilus, although bearing wings, remain closed during pollination. The percent seed efficiency followed those of Bramlett and others (1977) with minor modifications as in equation 2.

$$SE = \frac{\left(\frac{FS}{2}\right) x100}{(TS - BUS)} \tag{2}$$

where

SE = the percent seed efficiency

FS = the number of filled seeds

TS = the total number of scales per cone

BUS = the number of base unopened scales

The potential seed efficiency was calculated in equation 3.

$$PSE = \frac{\left(\frac{FS + PFS}{2}\right) x100}{(TS - BUS)} \tag{3}$$

where

PSE = the percent potential seed efficiency

FS = the number of filled seeds

PFS = the number of partially filled seeds

TS = the total number of scales per cone

BUS = the number of base unopened scales

Most seeds were gently shaken from the open scales of the oven-dried cones. Some seeds were pried out from unopened scales sealed by resin from insect wounds or from neighboring injured cones.

Statistical Analysis

Results reported here were collected from the six ramets that were excluded from the revised study. Therefore, the 2015 treatment effects cannot be tested. Differences in flush length, flush number per year, and needle length were compared among years using a one-way analysis of variance (ANOVA) with the independent variable year as a class variable. Differences in flush length were compared among groups of shoots bearing different numbers of 2015 flushes using one-way ANOVA, also with year as the independent variable. Means were compared using Duncan's multiple range test at a significance level of 0.05 (SAS 2004). A paired t-test was used to compare the number of cones before and after apparent changes in cone number throughout cone development. Because there were multiple comparisons done on each trend line, a Bonferroni approach was used to maintain the experimentwise error rate for each line by using $p = 0.05/n$ where n was the number of comparisons done on each line.

RESULTS AND DISCUSSION

Vegetative Phenology

The lengths of the first flushes were similar in all years; however, lengths of the 2016 second, third, and all flushes combined were significantly shorter than those of the 2015 flushes (table 1). Needle lengths were similar among years. Needles of the third flush were shorter compared to those formed earlier in the year which can be attributed to cooler temperatures in the fall. These needles did not resume extension during the subsequent spring (data not shown). Compared to results from a loblolly pine plantation in central Louisiana (Tang and others 1999), the seed orchard ramets had longer needles but similar foliated flushes lengths.

Shoots grew more flushes per year in 2014 and 2015 than in 2016 (table 1). Thirty, 23, and 5 percent of shoots grew three flushes in 2014, 2015, and 2016, respectively. Conversely, 2, 5, and 20 percent of shoots had only one flush in 2014, 2015, and 2016, respectively. Decreased flush growth in 2016 can be partially attributed to the many cloudy or rainy days in March and also to the competition from the developing conelets of the 2016 cone crop which was substantial.

During the growing season, vegetative buds either developed into the subsequent flushes or remained dormant through the remainder of the season. These buds overwintered. The 2015 overwinter buds appeared in shoots with one, two, and three flushes in late March, mid-April, and late June of 2015, respectively (fig.1). The lengths of these overwinter buds continued to increase slightly for the rest of 2015, and they did not differ in lengths until after JD 421 (February 25, 2016). This temporal development is similar to the observations made by Greenwood (1980) on loblolly pine ramets at a North Carolina seed orchard. The appearance of overwinter buds occurred between early June and early July, and the development of vegetative and reproductive primordia continued through the summer at that seed orchard. Lengths of the overwinter resting buds did not differ before spring of 2016 (fig. 1). Once the overwinter buds start elongating as the first flushes in spring of 2016, the final lengths of the first flushes seem to be closely associated with previous year's flush numbers. Shoots with one 2015 flush had shorter 2016 first flushes than those from shoots with two or three 2015 flushes (fig. 1). Total flush lengths in 2015 for shoots with one, two, or three flushes were, 10.4, 23.6, and 49.3 cm, respectively. Fascicles formed in

Table 1—Morphological parameters of vegetative shoots in six loblolly pine ramets in a Louisiana seed orchard

	2014	2015	2016
		per year	
Number of flushes	2.3a	2.2a	1.9b
		length (cm)	
First foliated flush	17.7a	18.3a	14.6a
Second foliated flush	6.8ab	8.6a	4.5b
Third foliated flush	1.9a	2.1a	0.3b
Total foliated flush	26.4a	29.0a	19.4b
First flush needle	18.8b	19.9a	19.1ab
Second flush needle	18.0ab	19.1a	17.9a
Third flush needle	15.3b	17.9a	17.0ab

Means followed by the same letter within a row are not significantly different at the 0.05 level.

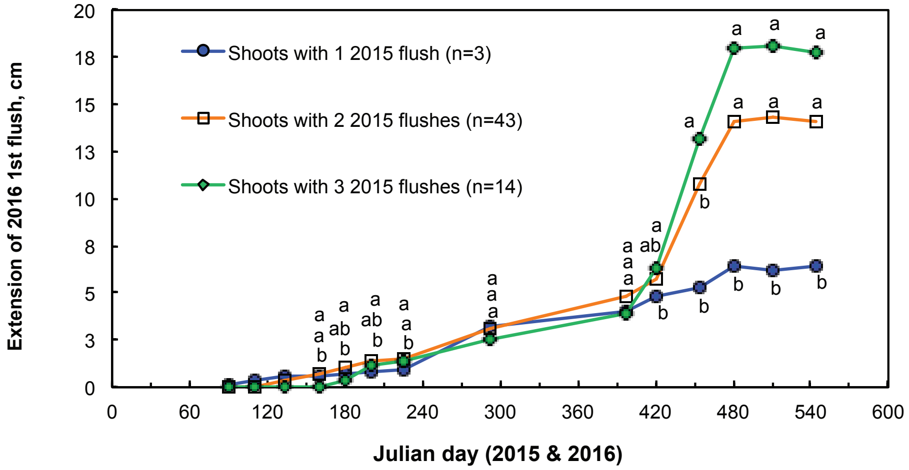

Figure 1—Extension of 2016 first flushes from 2015 overwinter resting buds on shoots with various numbers of 2015 flushes. Ten shoots from each of the six ramets of a single loblolly pine clone were tagged in early 2015 and monitored over time. Means with the same letter within a measurement date were not significantly different at the 0.05 level.

2015 are the main carbohydrate source for the growth of first flushes and their needles and developing female reproductive organs during spring of 2016.

Reproductive Phenology

It takes loblolly pine more than 2 years to complete its life cycle: from the formation of the female strobilus primordia to cone maturation and seed release (Bramlett and O'Gwynn 1980, Bramlett and others 1977, Greenwood 1980, Williams 2009). Male and female strobilus primordia form in early and late summer of year 1 (primordia year), respectively (Greenwood 1980). For clone LSG-62 at the IFCO seed orchard, some male and female strobilus buds were visible in October and November of year 1 (primordia year), respectively. Male and female strobilus buds break in January and February of year 2 (pollination year), respectively. Pollination of female strobili usually occurs in early March for this clone, and the pollinated female strobili become conelets. Fertilization of eggs in the archegonia of conelets does not take place until early June of year 3 (fertilization year) (Williams 2008, 2009). Fertilized conelets of LSG-62 usually mature in late September at the IFCO seed orchard.

Cones that matured in the fall of 2015, 2016, or 2017 were used to represent each crop (fig. 2). No significant loss in 2015 main or lateral cones occurred throughout year 3 (fig. 2). Number of 2016 main cones was sixfold greater than those on the shoots lateral to the main shoots. It was noted that some of the female strobilus buds did not emerge on the lateral shoots until mid-April of 2015, indicating the delayed development of female strobili on the lateral shoots. Overall loss of the 2016 cone crop from JD 90 (March 31, 2015; year 2) to JD 602 (August 24, 2016; year 3) was 16 and 21 percent for main and lateral shoot cones, respectively (fig. 2). An 80-percent retention of the conelets over 2 years can be attributed to the intensive insect control management. Insect damage can cause substantial loss of conelets and cones. In a clonal seed orchard in central Louisiana, a loss of 25–35 percent of female strobili and conelets during March and April of each of the 4 years monitored was attributed to insect damage by McLemore (1977). No apparent insect damage was observed in March and April of 2016 (year 3) at the IFCO seed orchard. The 2016 main cones numbered more than threefold those in 2015 whereas lateral cone numbers were similar in both years (fig. 2).

Maximum numbers of the 2017 main and lateral cones were reached by JD 421 (February 25, 2016; year 2) (fig. 2). However, the number of 2017 main cones decreased 27 and 23 percent in March and April of 2016, respectively. Loss of the 2017 cones from lateral shoots was even greater with 50- and 23-percent loss occurring in March and April of 2016, respectively. In contrast to the 2016 cone crop, the lateral shoots had as large a 2017 cone crop as the main shoots before the March abortion. By JD 602 (August 24, 2016; year 2), the number of 2017 lateral cones was similar to that of 2016 lateral cones, whereas the 2017 main cones were fewer than 50 percent of the 2016 main cones. As stated previously, heavy competition for current photosynthate occurs in March and April among developing flushes and their needles, female strobili, and conelets of previous and current years. Almost no loss in conelets of the 2016 cone crop during March and April of 2016 indicated that they are the stronger sinks of reproductive female organs. Compared to the 2015 season, shorter final lengths of the 2016 first flushes (table 1) implies that suboptimal weather for photosynthesis in March of 2016 caused more severe carbohydrate competition between reproductive and vegetative organs than in other years.

Cones and Seeds

Except for seed efficiency, parameters assessed for cones and seeds were similar between years (table 2). The open-pollinated cones of 2016 had greater seed efficiency and potential seed efficiency compared to the controlled mass pollination cones of 2015. It is generally acknowledged that the controlled mass-pollination cones have a lower seed efficiency than open-pollinated cones (Snyder and Squillace 1966). One way to increase seed efficiency is to increase carbohydrate allocation to partially filled seeds. An increase of 8 percent in seed efficiency would be realized if all partially filled seeds were fully filled (table 2).

Carbon Source and Sink Relationships

The temporal dynamics of loblolly pine carbohydrate sources and sinks were estimated non-destructively using organ length measurements as a surrogate for sink strength. Conventional measures of sink strength, such as net accumulation of dry matter, the synthesis rate of carbon reserves, the import rate of assimilate, or sucrose metabolizing enzyme activities, all require destructive sampling (Ho 1988, Sung and others 1989). Figure 3 presents the development patterns of sink strength in various carbohydrate sinks from JD 40 (February 9, 2015) to JD 544 (June 27, 2016). For clarity, 2015 third flushes and their fascicles were not included

Table 2—Parameters of the controlled mass pollination cone crop of 2015 and the open-pollinated cone crop of 2016 harvested from six loblolly pine ramets in a Louisiana seed orchard

Parameters	2015 crop	2016 crop
Cone (#/10 shoots/ramet)	15.2 (63.8)	33.8 (9.2)
Cone length (cm)	9.8 (7.1)	9.4 (3.2)
Cone dry weight (g)	22.1 (11.3)	20.8 (10.1)
Filled seed (#/cone)	93.7 (19.7)	102.3 (19.4)
Filled seed dry weight (mg/seed)	25.8 (8.1)	24.1 (7.1)
Filled seed dry weight allocation (%)	10.9 (22.9)	11.7 (14.5)
Partially filled seed (#/cone)	24.3 (28.3)	12.8 (71.1)
Partially filled seed dry weight (mg/seed)	3.2 (21.9)	4.4 (11.4)
Seed efficiency (%)	46.0 (8.7)	61.3 (9.6)
Potential seed efficiency (%)	57.6 (7.3)	69.2 (5.0)

Note: values in parentheses are coefficients of variation.

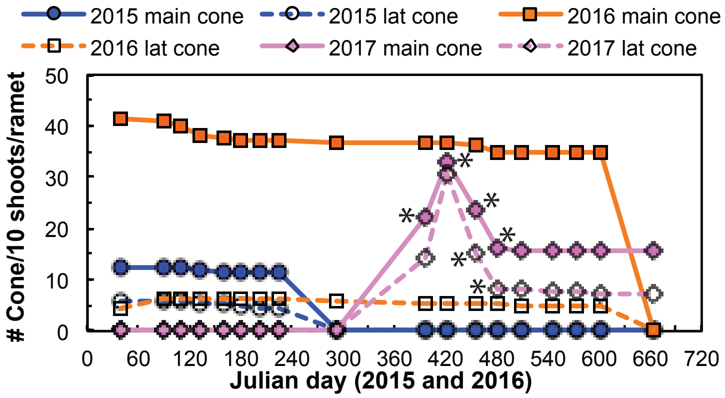

Figure 2—Temporal dynamics in mean numbers of 2015, 2016, and 2017 cone crops from main or lateral shoots in each of the six ramets of a single loblolly pine clone. The same 10 shoots from each ramet were monitored over time. Means with a * were significantly different from their previous data point in time using the Bonferonni paired t-test.

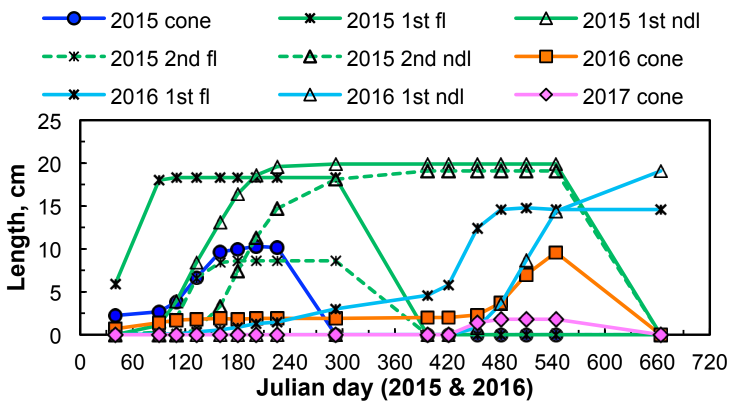

Figure 3—Temporal development patterns of sink strength in various carbohydrate sinks from loblolly pine ramets during 2015 and 2016. Lengths of individual organs were used as a surrogate for sink strength.

in this figure and neither were lateral shoots of the 2016 main shoots. By JD 160 (June 9, 2015), 2015 first flush fascicles reached 65 percent of their final length (fig. 3), became autotrophic, and no longer imported current photosynthate from 1-year-old fascicles (Dickson 1991). Based on the works of Chung and Barnes (1980) in North Carolina, we also predict that loblolly pine decreases the contribution of photosynthate from 1-year-old foliage to expansion of current-year second flushes and their fascicles by mid-August. In this study, second flush fascicles reached 62, 81, and 100 percent of final lengths by JD 201 (July 20, 2015), JD 225 (August 13, 2015), and JD 292 (October 19, 2015), respectively (fig. 3), which, when adjusted for location, is consistent with previous measures of second flush fascicle growth in central Louisiana (Sword and others 1996). In this study at the IFCO seed orchard in southwest Louisiana, ramets displayed more active and faster vegetative growth compared to loblolly pine in cooler areas (Chung and Barnes 1980) or in plantations (Sword and others 1996, Tang and others 1999).

Between February and mid-May of each year (JD 40 to JD 133 in 2015 and JD 397 to JD 510 in 2016), current photosynthate produced by 1-year-old foliage is allocated to all the developing carbohydrate sinks including current-year first flushes and fascicles originated from main and lateral overwinter buds, current-year second flushes, male strobili, female strobili, current-year conelets, and 1-year-old conelets. The abnormally wet and cloudy weather in March of 2016 may have contributed to the heavy abortion of female strobili in March and April for three reasons. First, reduced photosynthate production by the previous year's needles during this period of time may have resulted in strong competition among developing sinks. Second, 1-year-old conelets still rapidly expanded at this time, and their mortality was minor. This suggests a hierarchy in carbon allocation among sinks. In addition to the aborted 2016 female strobili, the shorter 2016 first flushes may also lose in competition with 1-year-old conelet development. Third, the unusually wet weather in March may have resulted in poor pollination. Compared to other pine species, loblolly pine female strobili can tolerate less than optimal pollination and still be retained by the tree and develop (Williams 2009). In lodgepole pine (*P. contorta* var. *latifolia*), female strobilus drop occurred when less than 80 percent of ovules in a female strobilus were pollinated (Owens and others 2005). The very scarce pollen available to female strobili has resulted in the extensive abortion of female strobili in March 2016. Continued abortion of female strobili in April may have been a direct result of photosynthate allocation to other stronger reproductive and vegetative sinks.

The current-year first flush needles only become a carbohydrate source after June when most of the weaker sinks, female strobili and conelets, had already been aborted. Furthermore, it takes 16 to 17 weeks for loblolly pine seeds to become mature from the fertilization of eggs in early June (Kapik and others 1995, Williams 2009). In other words, the immature cones almost reach their final length before egg fertilization takes place (fig. 3). Therefore, from June to December, needles from current-year first and second flushes are carbon sources for the developing seeds in the immature cones (current-year cone crop) and formation of the female strobilus primordia in overwinter buds (cone crop to be mature 2 years later). During the subsequent spring, these 1-year-old needles are the major contributor for growth of both vegetative and male and female reproductive organs. Thus, the dynamics of source and sink allocations by loblolly pine spans 2 years. This complicates the implementation of efficient silvicultural treatments, such as soil fertilization, to enhance cone production and retention.

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