

UNDERSTANDING THE FERTILIZATION AND IRRIGATION RESPONSE OF SEED ORCHARD LOBLOLLY PINE

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Abstract—A study of loblolly pine (*Pinus taeda* L.) reproduction began in January 2015 at the International Forest Company seed orchard near Evans, LA. Three levels of fertilization and two levels of irrigation were planned to favor reproduction. Fertilization levels were August broadcast application of (1) 112 kg ha⁻¹ nitrogen plus boron (1N), (2) 1N plus August application of 28 kg ha⁻¹ phosphorus (1N1P), or (3) 1N1P plus September application of 112 kg ha⁻¹ nitrogen (2N1P). Irrigation treatments were no irrigation or drip irrigation of 1090 l ramet⁻¹ day⁻¹ between mid-July and late September. Foliar nutrition and vegetative and reproductive growth were not affected by fertilization or irrigation in summer of 2015. This may be attributed to ramet adaptation to edaphic conditions since establishment. Correlation between reproductive carbohydrate demand and photosynthate supply validates the importance of available carbohydrate to new vegetative and reproductive organs. Ramet environment and shoot order are likely to affect these relationships.

INTRODUCTION

Genetic selection has produced commercial sources of loblolly pine (*Pinus taeda* L.) with superior growth and wood quality, providing land managers an opportunity to plant improved seedlings originating from open pollinated (OP) or controlled mass pollinated (CMP) seeds. Relative to woods-run seed sources, OP and CMP seed sources are expensive because of costs incurred during genetic improvement and seed production as well as the year to year variability on seed crops among ramets of a single clone. Operational treatments that increase female strobili emergence and retention have the potential to increase OP and CMP seed production and reduce the cost of genetically improved seedlings.

A 4-year study is underway in the International Forest Company seed orchard near Evans, LA to assess fertilization and irrigation effects on female reproductive processes among ramets of a single clone. Our objectives are twofold. First, we are evaluating operational irrigation and fertilization for their effects on female strobili emergence and retention, cone production, and seed efficiency. Second, in response to these treatments, we are also conducting measurements of vegetative and reproductive phenology, leaf area, and

nutrition dynamics. Together, these data allow a better understanding of the effects on loblolly pine reproduction from interactions among mature foliage as a source of carbohydrate, the carbohydrate and nutritional demands of immature vegetative and reproductive organs, available soil resources, and climate.

Our present purposes are to document soil and climatic characteristics, quarterly stemwood growth, and seasonal foliar nutrition among 30 ramets of a single clone; among a subset of these ramets, we are characterizing early spring relationships between variables representative of carbohydrate supply and both vegetative and reproductive organs. We hypothesize that irrigation and fertilization will favor fascicle and female strobili primordia differentiation in late summer, with corresponding increases in the growth of vegetative and reproductive organs the following spring.

The large-scale longleaf pine restoration effort outlined in the Range-wide Conservation Plan for Longleaf Pine (America's Longleaf 2009) requires a sustained supply of seed. Crane and Barbour (2009) estimated an annual longleaf pine seed demand of 27,500 pounds to meet this need, but reported a range-wide inventory of viable seed at 7,500 pounds. Longleaf pine seed

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supply problems stem, in part, from the infrequency of good or better cone crops. Therefore, a long-range goal of this study is to provide a foundation from which a better understanding of longleaf pine reproduction can be pursued.

MATERIALS AND METHODS

Study Site and Experimental Design

The International Forest Company seed orchard near Evans, LA is located on the flood plain of the Sabine River. The dominant soil series is Hainesville fine sand. The orchard consists of open-grown loblolly pine ramets with a ground cover of frequently mowed warm season grasses and forbs. In December 2014, we permanently identified 30 ramets of loblolly pine clone LSG-62 at age 25 years in orchard 216. We established a randomized complete block, two by three factorial experimental design with five blocks in January 2015. Blocking was based on the presence or absence of neighboring ramets.

Two levels of irrigation treatment were ambient rainfall or ambient rainfall plus drip irrigation under ramet crowns of 1090 l ramet⁻¹ day⁻¹ between July 10 and September 21, 2015. Three levels of planned fertilization treatment were (1) broadcast application of 112 kg ha⁻¹ nitrogen (N) as ammonium nitrate (AN) plus 1.1 kg ha⁻¹ boron (B) as Solubor® in mid-July (1N), (2) 1N plus 28 kg ha⁻¹ ramet⁻¹ of phosphorus (P) as triple super phosphate applied in mid-July (1N1P), and (3) 1N1P plus 112 kg ha⁻¹ ramet⁻¹ N as AN in mid-August (2N1P). The absence of precipitation in July through early August 2015 caused a delay in the application of 1N (applied on August 11, 2015) and the mid-August application of 2N1P (applied on September 9, 2015).

A weather station (Vantage Pro2, Davis Instruments, Vernon Hills, IL) located at the seed orchard office began continuous operation in April 2015. Data between March 29, 2016 and May 25, 2016 were not recorded due to a power outage caused by an unprecedented flood event, but comparable weather station data for these dates were obtained from the National Oceanic and Atmospheric Administration's Lake Charles, LA Regional Airport weather station (National Oceanic and Atmospheric Administration 2017). Measurement variables included air temperature (°C, degrees Celsius) recorded by a 5-minute interval and daily total rainfall (cm). We calculated daily average air temperature, summed total rainfall by month, and estimated monthly water surplus and deficit by the Thornthwaite water balance model (McCabe and Markstrom 2007). We determined values of plant-available water holding

capacity (PAWHC) using a rooting depth of 1.0 m or 2.5 m [PAWHC: 4.7 cm (1.0 m), 11.5 cm (2.5 m)].

In January 2015, we sampled mineral soil by a soil probe to a 15-cm depth at 10 random locations around the crown drip line of each ramet and pooled by ramet. We quantified soil water content at field capacity (-0.03 megapascal, MPa) and permanent wilting point (-1.5 MPa) and estimated PAWHC among experimental ramets by the pressure plate method (Klute 1986). Through services at Waters Agricultural Laboratories in Camilla, GA, we also evaluated soil samples for available P, exchangeable potassium (K), magnesium (Mg), and calcium (Ca); hydrogen soil pH; and concentrations of sulfate-sulfur (S), B, zinc (Zn), manganese (Mn), iron (Fe), and copper (Cu).

Twice, we also sampled soil at a 0–15-cm depth within the study area (two locations in February 2015 and three locations in May 2016) as part of an operational assessment of soil fertility across the seed orchard. Commercial soil fertility analyses at Waters Agricultural Laboratories in Camilla, GA used standard methods but differed by extraction solution. A Mehlich I extract was used for the January 2015 samples across orchard 216, and a Mehlich III extract was used for the February 2015 and May 2016 samples (Mehlich 1984).

Ramet Stem Growth

We measured diameters at breast height (dbh, 1.37 m above the soil surface) of each experimental ramet by diameter tape in December 2014. In January 2015, we fitted experimental ramets with diameter bands at dbh (Keeland and Young 2014). After a 3-week equilibration period, we measured ramet diameters quarterly in February, May, August, and November. In February 2016, it was apparent that the diameter bands did not contain enough leader to measure dbh through 2018. As a result, in February 2016, we measured dbh by both diameter band and diameter tape and then removed the bands. Thereafter, we measured dbh by diameter tape and calculated quarterly dbh growth and daily dbh growth by quarter for each ramet.

Experimental Shoot Leaf Area and Phenology

For each ramet, we identified two or three first or second order branches receiving full sunlight in the upper third of the southwest side of the crown in January 2015. Among these, we permanently identified 10 main or lateral shoots by numbered zip ties. We determined the order of experimental shoots with 1M shoots designated as the terminal bud of a first order branch, 2M shoots designated as the terminal bud of a second order branch, and 2L shoots designated as a lateral bud of a

second order branch. In January 2015, we measured foliated internode and mean fascicle lengths by flush produced in 2014 among experimental shoots. In 3- to 4-week intervals between February 2015 and May 2016, we monitored foliated length by flush of the main shoots, median fascicle length by flush, numbers of female strobili and conelets by main and lateral shoots, median main shoot conelet and cone lengths, and number of lateral shoots with female strobili.

In November 2015, we excised one sample shoot from the north side of the upper third of ramet crowns. For each sample shoot, we assessed main and lateral shoots for flush number, foliated internode length, number of fascicles, and average fascicle all-sided surface area by the water displacement method (Johnson 1984). We estimated leaf area by flush as the product of fascicle number and average fascicle leaf area. By the method of Murthy and Dougherty (1997), we conducted regression analyses by shoot order and flush to establish regression coefficients for estimating flush leaf area by a combination of both foliated flush length and fascicle density. Subsequently, we made predictions of leaf areas by shoot order and flush produced in 2014 and 2015. Estimates of experimental shoot leaf area produced in 2014 utilized fascicle densities of sample shoot foliage produced in 2015. We used the sum of leaf areas produced in 2014 and 2015 to estimate the 2015 peak leaf area of experimental shoots.

In May 2016, due to a change in the experimental design, we excluded six of the 30 experimental ramets from the study. Among excluded ramets, we calculated mean values by shoot order (i.e., 1M, 2M, 2L) and ramet between January 2015 and May 2016 for the following variables: foliated length of the first flush produced in 2016 by late June (Julian date 180), bud length of the second flush produced by late June 2016, foliated length of the total shoot produced in 2015, estimated leaf areas produced in 2014 and 2015, peak leaf area of experimental shoots in 2015, number of second-year conelets in January 2016, number of female strobili emerged from main and lateral shoot buds in February 2016 (Julian date 56), number of first-year conelets (i.e., formerly female strobili in February 2016) remaining in April 2016 (Julian date 116), and numbers of main and lateral shoot female strobili or first-year conelets lost between February and April 2016.

Foliar Nutrition

We evaluated the foliar nutrition of experimental ramets six times between March 2015 and May 2016. Each sample consisted of 25 randomly chosen, healthy fascicles having three needles without lesions

from the first or second flush of 2014 or 2015 in the upper crown excluding the fascicles of experimental shoots. We oven-dried fascicle samples to equilibrium at 70 °C and shipped them to Waters Agricultural Laboratories (Camilla, GA) for macronutrient and micronutrient analyses.

Statistical Analyses

We subjected daily dbh increment by quarter and periodic foliar mineral nutrient concentrations to analyses of variance by a two by three factorial, randomized complete block experimental design with five blocks based on the proximity of neighboring ramets. Main effects were two levels of irrigation and three levels of fertilization. We compared means by the Least Significant Difference test and considered them to be significantly different at an alpha level of 0.05.

Among the six experimental ramets that were excluded from the study in May 2016, we conducted source-sink correlation assessments and determined Pearson correlation coefficients for variables representing the carbohydrate demand of reproductive and vegetative organs (number of second-year conelets per experimental shoot in January 2016, numbers of female strobili or first-year conelets per experimental shoot by main and lateral buds on Julian dates 56 and 116 of 2016, numbers of female strobili or first-year conelets lost from main and lateral buds between Julian dates 56 and 116 of 2016, first flush foliated length by late June 2016, and second flush bud length by late June 2016), and the potential supply of carbohydrate by foliage (2015 foliated shoot length, leaf area of shoots produced in 2015, and peak leaf area in 2015). We considered the F statistics and coefficients of determination to be significant at $p \leq 0.05$.

RESULTS

Climate and Soil

Climate measurements were variable by month and year. During the 16-month period between January 2014 and April 2015, month-to-month differences in water surplus were large (fig. 1A). A 3-month period of water deficit occurred between July and September 2015 with a magnitude that decreased as the root zone increased from 1.0 m to 2.5 m (fig. 1B). Mean daily air temperature was greatest in the summer months of June through August 2015 but was less variable at this time compared to fall and winter (data not shown).

Soil physical properties at the 0- to 15-cm depth showed low water holding capacity of Hainesville sand (table 1). Soil water contents at field capacity (SWC_{fc} , -0.03 MPa),

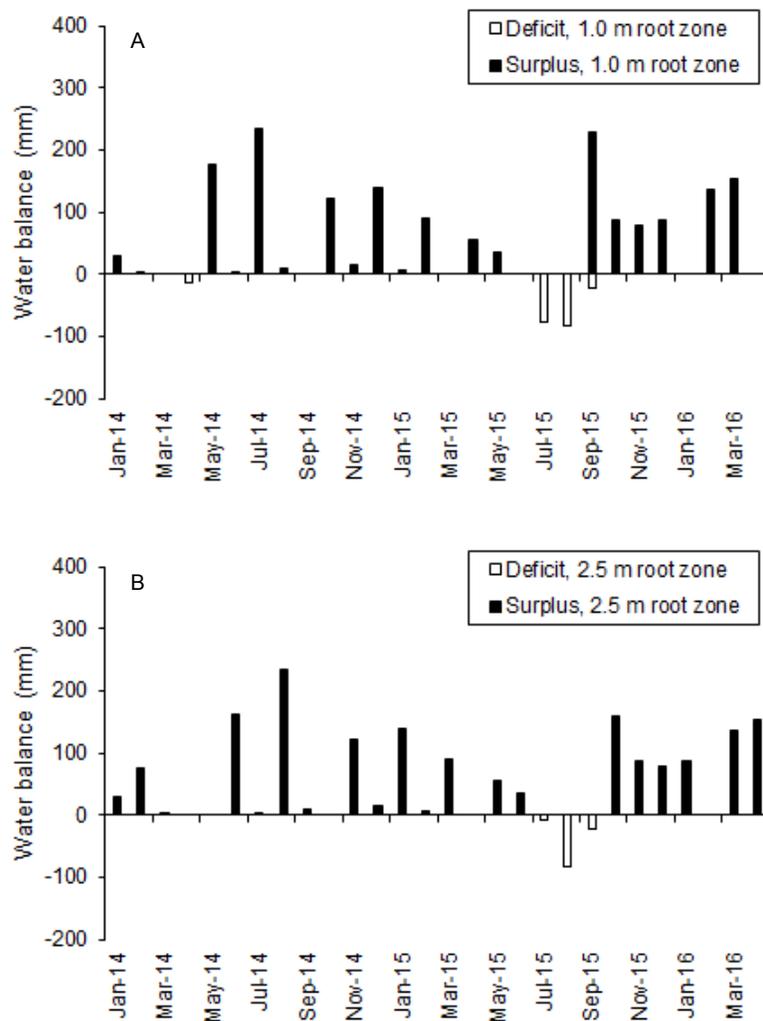


Figure 1—Monthly water surplus and deficit predicted by the Thornthwaite water balance model (McCabe and Markstrom 2007) for the International Forest Company seed orchard near Evans, LA between January 2014 and April 2016 using a root depth of (A) 1 m and (B) 2.5 m.

permanent wilting point (SWC_{wp} , -1.5 MPa), and PAWHC averaged 7.1, 2.7, and 3.4 percent, respectively. In January 2015, surface mineral soil levels of P, K, Mg, and Ca were within or greater than the recommended range for loblolly pine management (Moorhead and Dickens 2002) (table 2). Comparisons among Mehlich III estimated or actual values of soil P, K, Mg, and Ca in January 2015, February 2015, and May 2016 suggested that soil fertility was adequate for loblolly pine but soil P availability was variable.

Ramet Stem Growth and Foliar Nutrition

Mean daily increment of ramet diameter growth was not significantly affected by irrigation or fertilization in the two 3-month quarters of 2015 after the treatments

started or the first 3-month quarter of 2016 (fig. 2). Foliar macro- and micronutrient concentrations by flush, production year, and foliage condition (green or brown/senescent) were not significantly affected by fertilization or irrigation treatments between July 2015 and May 2016. Dormant season K, N, P, Mg, Ca, and S concentrations of green first flush foliage produced in 2014 and 2015 maintained levels at or above the threshold between sufficiency and deficiency for loblolly pine (Albaugh and others 2010) (fig. 3). Dormant season micronutrient concentrations were variable but consistently at or above sufficient levels [B: 7–34 parts per million (ppm), Zn: 21–77 ppm, Mn: 129–541 ppm, Fe: 43–105 ppm, Cu: 2.6–8.8 ppm] (Albaugh and others 2010).

Table 1—Mean mineral soil physical properties of the 0- to 15-cm depth among four spatial blocks of seed orchard 216

Variable ^a	Orchard block ^b			
	2	3	7	8
n	9	7	5	9
Bulk density (g cm ⁻³)	1.37 (0.03)	1.36 (0.02)	1.34 (0.02)	1.31 (0.02)
SWC _{fc} (% g g ⁻¹)	6.9 (0.9)	7.8 (2.0)	6.8 (0.6)	6.9 (0.4)
SWC _{wp} (% g g ⁻¹)	2.4 (0.3)	2.5 (0.3)	3.0 (0.4)	2.9 (0.2)
PAWHC (% g g ⁻¹)	3.6 (1.2)	4.4 (1.9)	2.7 (1.0)	3.0 (0.4)

^a n = number of samples; SWC_{fc} = soil water content at field capacity (-0.03 MPa); SWC_{wp} = soil water content at wilting point (-1.5 MPa); PAWHC = plant-available water holding capacity.

^b Values in parentheses are the standard deviation of the mean.

Table 2—Mineral soil chemical properties of the 0- to 15-cm depth among experimental ramets in orchard 216 in January 2015, and among soil sampled from orchard 216 in February 2015 and May 2016 as part of annual soil fertility assessments

Soil variable ^a	January 2015 mean		Critical value		February 2015 mean	May 2016 mean
	n ^b =30		-		n = 2	n = 3
	Mehlich I value	Mehlich III estimate ^d	Mehlich I value	Mehlich III estimate ^d	Mehlich III value	Mehlich III value
	<i>kg ha⁻¹</i>					
P	13 (38) ^c	61	9–13 ^e	27–62	45	48
K	43 (14)	47	21–33 ^e	25–37	57	63
Mg	102 (19)	112	22–37 ^e	45–57	100	124
Ca	772 (25)	740	78–126 ^e	289–319	684	767
S	44 (17)	-	- ^f	-	19	19
B	0.2 (36)	0.8	-	-	0.2	1.0
Zn	6.1 (45)	8.7	-	-	7.1	7.6
Mn	46 (19)	103	-	-	202	323
Fe	35 (28)	-	-	-	277	327
Cu	2.7 (49)	5.3	-	-	4.9	7.1
pH _w	5.5 (4)	-	-	-	6.5	6.2

^a Soil variables are available phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), sulphur (S), boron (B), zinc (Zn), manganese (Mn), iron (Fe), and copper (Cu); pH_w is soil pH using water as an extract.

^b Number of samples.

^c Values in parentheses are coefficients of variation.

^d The extraction method changed from Mehlich I to Mehlich III between January and February 2015. For comparison among dates, application of available equations that express Mehlich III values by Mehlich I values were applied (Mylavarapu and others 2002) to express means on the basis of a Mehlich III extraction.

^e Critical values delineating insufficiency by Moorhead and Dickens (2002).

Dashes indicate that elements were not evaluated.

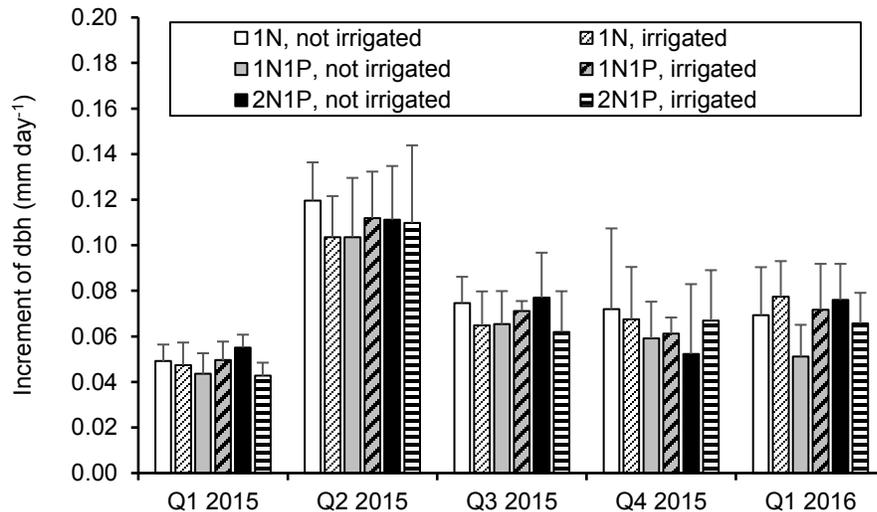


Figure 2—Mean daily increment of ramet diameter growth at breast height (dbh, 1.37 m) of loblolly pine clone LSG-62 estimated by annual quarter in response to two levels of irrigation and three levels of fertilization. The first, second, third, and fourth quarters of 2015 and first quarter of 2016 correspond to December 2014–April 2015, May–July 2015, August–October 2015, November 2015–January 2016, and February–April 2016, respectively. The first and second quarter of 2015 are pretreatment values. Error bars represent one standard error of the mean.

Source-Sink Correlation Assessments

Among the 1M, 2M, and 2L shoot orders of the six experimental ramets excluded from the study in May 2016, we observed significant, positive correlations between mean shoot numbers of main and lateral bud female strobili on Julian date 56 and first-year conelets on Julian date 116 and all shoot means of variables representing carbohydrate supply (2015 foliated shoot length, leaf area of shoots produced in 2015, and peak leaf area in 2015) (table 3). We also observed similar significant, positive relationships for the 2016 first flush foliated length and second flush bud length by late June when correlated with mean shoot foliated length in 2015, mean shoot leaf area produced in 2015, and mean shoot peak leaf area in 2015. Compared to the 2M and 2L shoot orders, the 1M shoot order had greater mean values of 2016 first flush foliated length, 2016 second flush bud length, and 2015 foliated shoot length (fig. 4) as well as 2015 leaf area and 2015 peak leaf area (data not shown). The 1M shoot order also had greater mean shoot numbers of main and lateral bud female strobili on Julian date 56 and first-year conelets on Julian date 116 compared to the 2M and 2L shoot orders (fig. 5). The loss of female strobili or first-year conelets between Julian dates 56 and 116 from the 1M (main: 3.5 shoot⁻¹; lateral: 8.2 shoot⁻¹) and 2M (main: 5.8 shoot⁻¹; lateral: 1.1 shoot⁻¹) shoot orders was larger than those from the 2L (main: 1.1 shoot⁻¹; lateral: 0.5 shoot⁻¹) shoot order.

Percentages of loss for 1M, 2M, and 2L shoots, however, were similar for main (49 ± 6 percent) and lateral buds (73 ± 4 percent). We did not detect significant correlations between second-year conelet number in January 2015 and variables representing carbohydrate supply in 2015.

DISCUSSION

Southern pines are well adapted to sandy soil. Belowground attributes such as a taproot or sinker roots and the horizontal elongation of first order lateral roots form a large network of fine roots and ectomycorrhizae in the upper horizons of the soil profile (Eissenstat and others 1994, Harrington and others 1989). Comparison of the relative areas of foliage and absorbing roots on sites characterized by high and low levels of soil resource supply has demonstrated the plasticity of southern pine root system architecture (Addington and others 2006, Hacke and others 2000). Hacke and others (2000), for example, compared two loblolly pine stands of similar stand densities growing on sand or clay loam soils. They found more than a fivefold greater ratio of root-to-leaf surface area on the sand compared to the clay loam. We anticipated that loblolly pine ramets growing on Hainesville sand exhibited a similar root system architecture and would be effective foragers of irrigation water and nutritional amendments applied to the soil surface.

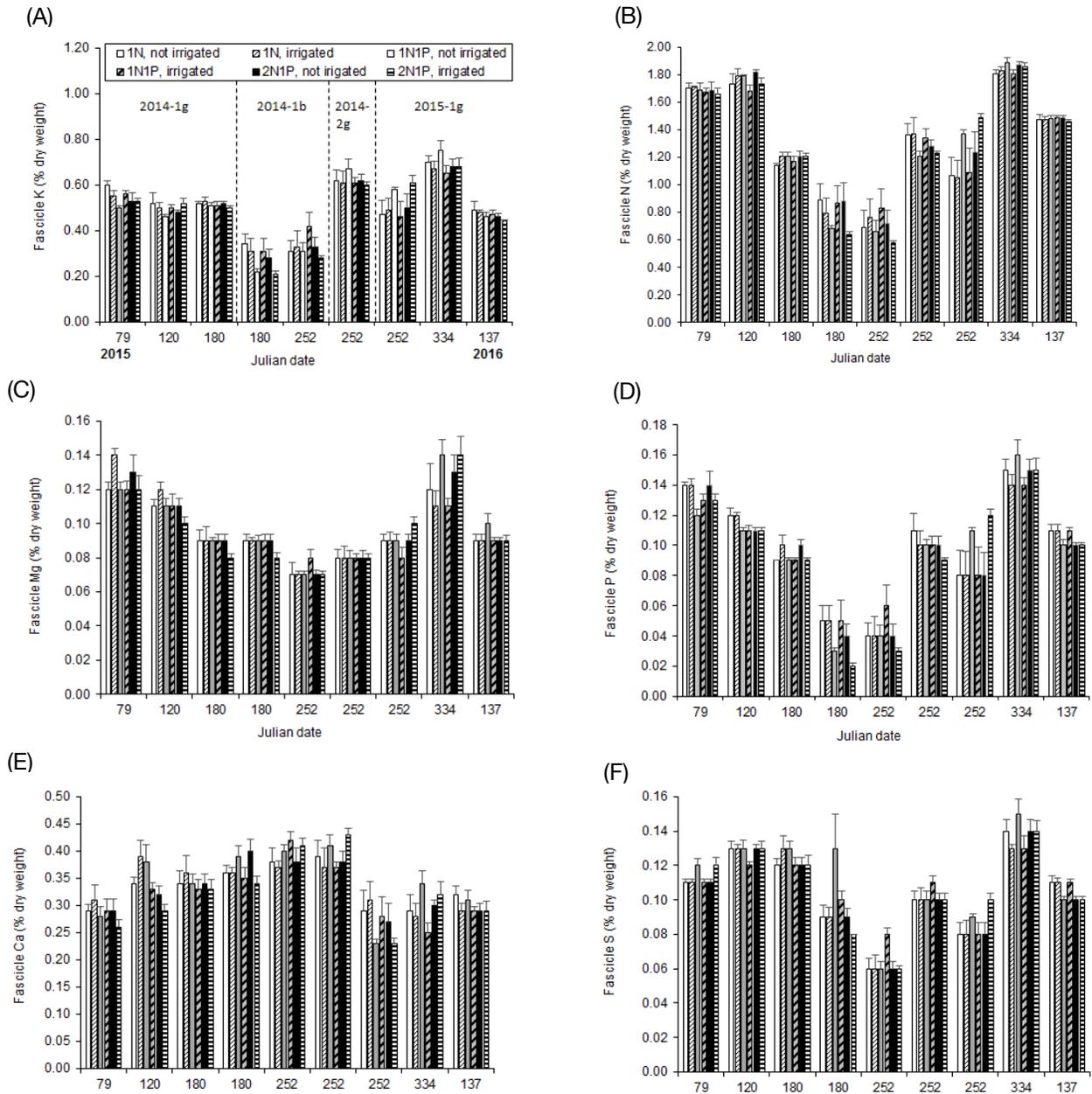


Figure 3—Mean mineral nutrient concentrations of foliage types in response to six combinations of irrigation and summer fertilization treatments. Foliage types include green first and second flush foliage produced in 2014 (2014-1g and 2014-2g, respectively), green first flush foliage produced in 2015 (2015-1g), and brown senescent first flush foliage produced in 2014 (2014-1b) between Julian date 79 of 2015 and Julian date 137 of 2016. For all panels, the dashed lines and abbreviations for foliage type in panel (A) delineate changes in foliage type among all panels. Panels represent information about (A) potassium (K), (B) nitrogen (N), (C) magnesium (Mg), (D) phosphorus (P), (E) calcium (Ca), and (F) sulphur (S). Error bars represent one standard error of the mean.

Table 3—Pearson correlation coefficients between vegetative and reproductive carbohydrate sinks and variables representative of carbohydrate supply^a

Carbohydrate sink variable	Carbohydrate supply variables		
	2015 foliated length (cm)	2015 leaf area (cm ²)	2015 peak leaf area (cm ²)
June 2016 foliated flush length (cm)	0.8241 ^b	0.7770	0.7551
June 2016 second flush bud length (cm)	0.7863	0.7626	0.7813
January 2016 second-year conelets in (#)	0.3633	0.4078	0.3845
February 2016 main bud female strobili (#)	0.9175	0.9101	0.8923
April 2016 main shoot first-year conelets (#)	0.7618	0.7957	0.7225
February 2016 lateral bud female strobili (#)	0.8857	0.9000	0.9033
April 2016 lateral shoot first-year conelets (#)	0.7229	0.7512	0.7209
2016 main bud female strobili or first-year conelet loss (#)	0.8790	-0.8864	-0.9015
2016 lateral bud female strobili or first-year conelet loss (#)	0.8387	-0.8030	-0.8287

^a Data are means by three shoot orders and ramet between January 2015 and May 2016 among six LSG-62 loblolly pine ramets.

^b The F statistics and coefficients of determination were significant at p < 0.05 level for all relationships except those between second-year conelets in January 2016 and the three carbohydrate supply variables.

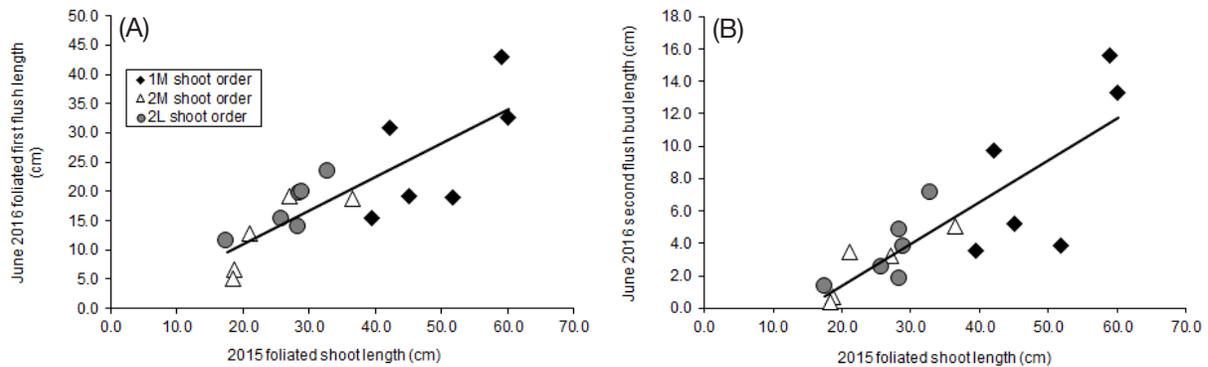


Figure 4—Vegetative carbohydrate sinks evaluated by (A) June 2016 foliated first flush length and (B) June 2016 second flush bud length in relation to final length of the foliated shoot produced in 2015. Values represent means by shoot order and ramet among six ramets evaluated between January 2015 and June 2016.

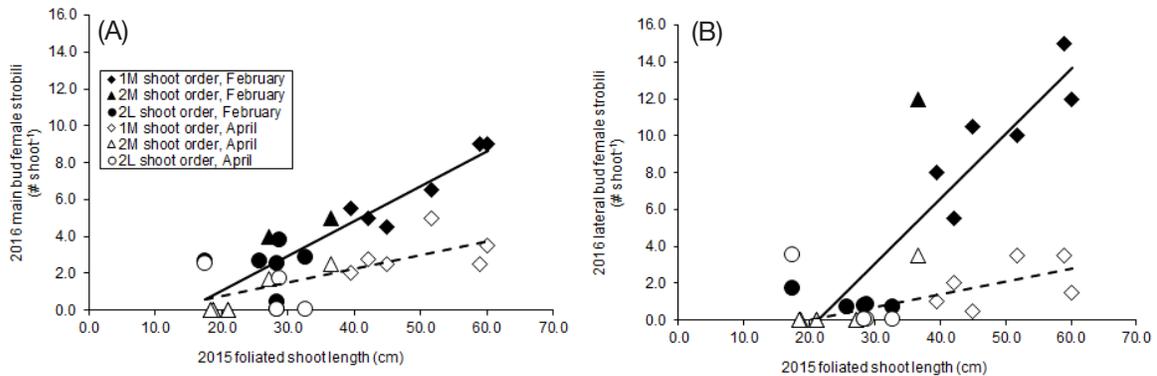


Figure 5—Numbers of female strobili and first-year conelets recorded in February and April 2016, respectively, among (A) main and (B) lateral buds in relation to 2015 final length of the foliated shoot. Values represent means by shoot order and ramet among six ramets evaluated between January 2015 and June 2016.

Pine root system architecture is initiated at germination and continues after planting (Fitter 1996). Past research has shown that vertical and horizontal root system expansion contributes to strong loblolly pine growth on sandy soils (Albaugh and others 2004, Butnor and others 2003, Hacke and others 2000, King and others 1999). Albaugh and others (1998) demonstrated this on a Wakula sand with 94, 84, and 95 percent increases in foliage, stem plus branch, and root system biomass, respectively, in response to annual fertilization between ages 7 and 10 years.

At least two conditions contribute to positive growth responses to fertilization on sandy soils. First, nutritional limitations to growth must be alleviated by fertilization which requires growth to be nutritionally constrained before fertilization. Second, contact between loblolly pine absorbing roots plus mycorrhizae and soil amendments must occur. Absence of these conditions in the present study may have precluded observation of a year 1 fertilization effect on ramet vegetative and reproductive variables. Specifically, in March 2015, the mineral nutrition of first flush fascicles produced in 2014 exceeded dormant season deficiency thresholds (Albaugh and others 2010). Therefore, we did not anticipate a rapid growth response to summer fertilization caused by alleviation of a nutritional deficiency or imbalance. Because the accumulation of leaf area under high light interception controls loblolly pine growth (Fox and others 2006, Vose and Allen 1988), we predicted that summer fertilization would stimulate fascicle development in the overwinter bud leading to an increase in foliage production in spring and summer of the next year, and subsequently, greater annual ramet stemwood growth.

A rogueing operation removed unwanted clones and stumps in orchard 216 in July 2015. We characterized the architecture of these rogued ramet root systems by vertically-oriented lateral roots that accessed water at a depth of 2.5 m. Further observation indicated that rogued root systems did not have an expansive network of lateral roots and mycorrhizae in the upper soil horizons. Rather, first order lateral roots were vertically oriented and had few second or higher order lateral roots emerging from them. Clearly since planting, the rogued ramets had adapted to prolonged periods of dry soil. It is likely that the experimental ramets in the present study have adapted similarly. Therefore, the effect of drip irrigation and fertilization on ramet nutrition and growth may have been limited.

Past research has established the positive relationship between pine reproduction and both crown size and foliage mass (Shoulders 1967, Shoulders 1968). Gains in reproductive potential attributed to foliage production are also demonstrated in our study with significant, positive correlations between female strobili numbers

and variables representative of carbohydrate supply at the time of female strobili primordia differentiation and emergence. It is apparent that carbohydrate imported from mature foliage produced in 2015 also supported first and second flush growth by May 2016. These results emphasize the importance of maximizing the amount of foliage per reproductive shoot in seed orchard ramets. With maturation of the first and second flush of 2016, female strobili primordia differentiation in 2016 and emergence in 2017 are likely to benefit from a greater amount of foliage per shoot.

It became apparent in year 1 that an array of factors had the potential to interfere with the positive relationship between reproductive organ success and carbohydrate supplied by mature foliage. There were, for example, 3 consecutive months of water deficit between July and September 2015. Loblolly pine experiences foliage senescence under prolonged water deficit (Pallardy and others 1995, Tang and others 2004). Because late summer drought and possible acceleration of foliage senescence coincided with normal periods of seed fill and female strobili primordia differentiation (Williams 2008), early foliage senescence may have impacted the carbohydrate available for these reproductive processes. Tang and others (1999) reported a decline in the net photosynthesis of loblolly pine in central Louisiana when air temperatures exceeded 93 °F (34 °C). Therefore, it is also possible that prolonged periods of elevated air temperature in summer reduced the supply of carbohydrate to reproductive sinks such as seeds and female strobili primordia undergoing differentiation. Alternatively, the unique root system architecture of experimental ramets may have accessed deep water and allowed some level of gas exchange to continue in late summer. Under the growth-differentiation-balance hypothesis (Loomis 1932), this scenario would have allowed photosynthate to be allocated to an array of non-growth metabolites.

Distinct differences in amounts of foliage and female strobili by shoot order suggest that shoot size and position in the crown also affect carbohydrate source-sink relationships in reproductive shoots. As such, attention to genetic control of branch number, angle, and distribution in ramet crowns as well as pruning activities that favor fewer but larger reproductive shoots may be warranted. We observed more mature foliage and female strobili and a greater loss of female strobili or first-year conelets between February and April for the 1M shoots compared to 2M and 2L shoots. One factor that may have contributed to these observations is a lower potential for shading of 1M shoots compared to 2M and 2L shoots. This, together with a higher frequency of three flushes among the 1M shoots compared to the 2M and 2L shoots suggests that 1M shoots were better able to support reproductive organs compared to 2M and 2L shoots.

We have compiled environmental information and stemwood growth and foliar nutrition trends among 30 experimental ramets of clone LSG-62 between March 2015 and May 2016. This information provides new knowledge for understanding whole-ramet physiological function at the Evans, LA seed orchard. We have also evaluated a snapshot of the relationships between carbohydrate demand by reproductive organs and the carbohydrate supply by mature foliage among three shoot orders. These observations are providing insight for understanding the importance of current photosynthate and mineral nutrients to female reproductive organs within a single loblolly pine shoot.

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