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Seed spacing and seedling biomass: Effect on root growth potential of loblolly pine (*Pinus taeda*)

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Application. Spacing loblolly pine seed further apart in the nursery did not increase seedling height but did increase both seedling biomass and root-growth potential. Since seedling biomass can affect root-growth potential, it may be desirable to analyze the results using diameter or foliage weight as covariates.

Abstract. Results from three studies conducted in bare-root nurseries indicate a positive linear relationship between seed spacing and root growth potential of *Pinus taeda* L. seedlings. However, root growth potential was also correlated with several morphological variables, including seedling weight, root collar diameter, root weight, root volume, foliage weight and stem weight. Because seedlings grown at wider spacings were larger in diameter and biomass, covariate analyses (using either root collar diameter or foliage ovendry weight) were also conducted. These analyses indicate that differences in root growth potential between seed spacings can be accounted for by differences in seedling size.

Introduction

Several studies conducted throughout the southern United States have demonstrated higher outplanting survival for loblolly pine (*Pinus taeda* L.) seedlings grown at low seedbed densities than for seedlings grown at higher densities (Shoulders 1961; Nebgen and Meyer 1986; Rowan 1986). In general, survival differences among seedbed densities increase as average outplanting survival decreases. For one study, survival of seedlings grown at an average spacing of 3.1 cm within the drill (215/m^2) was 55%,

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while seedlings grown at an average spacing of 2.1 cm (323/m^2) achieved only 45% survival (Rowan 1986). However, when average survival is greater than 96%, seedling spacing does not significantly affect seedling survival (Shipman 1964; Dierauf and Garner 1980; Rowan 1986).

There are several biological explanations why survival under adverse conditions is usually better for seedlings grown at wider spacings. It is possible that the explanation could simply be related to differences in seedling morphology. Better survival would be expected from the widely spaced seedlings since they usually exhibit lower shoot/root ratios (May 1933; Harms and Langdon 1977; Rowan 1986; Nebgen and Meyer 1986; Boyer and South 1988). However, Rowan (1986) speculated that seedlings grown at a density of 215/m^2 might possess a "physiological advantage." It is possible this advantage might be due to a difference in root growth potential (RGP). RGP may be important since initial survival on some sites depends in part on the ability of seedlings to produce new roots and thereby re-establish intimate contact with the soil (Ritchie and Dunlap 1980). Therefore, three studies were conducted to determine if RGP of loblolly pine could be increased by sowing seed at wide spacings in the nursery.

Methods

Studies were established in 1983 and 1985 at the Hammermill Paper Company Nursery near Selma, Alabama (32°22′ N, 86°55′ W, altitude 39 m), and in 1986 at the Morgan Nursery of the Georgia Forestry Commission near Byron, Georgia (latitude 32°38′ N, 83°42′ W, altitude 143 m). The climate for these areas is warm and humid with a mean annual precipitation of 1290 and 1280 mm, respectively. Density was controlled in each study by varying seed spacing within the drills.

1983 Study

On May 10, open-pollinated seeds from the Hammermill seed orchard were sown with a vacuum drum sower with 8 drills spaced 12.5 cm apart. Plots were installed in a randomized complete block design with 5 replications on two adjacent beds. Each treatment plot was 9.14 meters long.

Target spacings within a drill were 1.9, 2.8, 4.0, 5.0, and 6.0 cm. However, since seed were covered with soil during the sowing operation, actual seeding rates were not verified. An incorrect sprocket was used for the widest spacing, which resulted in a nominal spacing of 13.1 cm.

Fertilizer recommendations were made based on tests from soil samples collected in October of 1982. As a result, seedbeds were operationally fertilized prior to sowing with 67 kg/ha of N (from ammonium sulfate and diammonium phosphate), 30 kg/ha of P and 56 kg/ha of K. Seedlings were top-dressed with an additional 147 kg/ha of N (from a urea-ammonium nitrate suspension) during the growing season. Routine cultural practices were followed during the growing season except that seedlings were not top-pruned.

Samples (0.3 m by 1.2 m) from each plot were obtained on December 15 for morphological measurements and to test for root growth potential. Seedlings were packed on ice and transported to cool storage (2 °C ± 1 °C) at Auburn, Alabama. On December 16, the seedlings were removed from cool storage and graded according to Wakeley's standard grades (Wakeley 1954). After removal of obviously diseased, bruised or broken seedlings, 8 plantable seedlings (Wakeley's grades 1 and 2) were randomly chosen from each plot for testing RGP. Root collar diameter and height of each seedling were measured and the root trimmed to a maximum length of 18 cm. All white root tips were removed from each seedling. Seedlings were potted in coarse sand in 2-liter containers with drainage holes. The 200 containers were placed on a rooting bed in a greenhouse according to a completely randomized design.

Bed temperature during the 28-day test period was maintained at approximately 25 °C and air temperatures ranged between 16 and 28 °C. Natural photoperiod was extended to 16 hours with incandescent lighting. Watering was done manually and all containers were kept adequately watered. No supplementary nutrients were provided. After removal from the rooting beds, the following measurements were obtained for each seedling: root collar diameter, stem length, number and oven-dry (70 °C) weight of all new roots ($\geqslant$ 0.5 cm), dry weights of the old root, stem and foliage.

1985 Study

The general plan of the 1983 study was followed with a few modifications. Seed source was the same, but in order to ensure that correct seed densities were obtained, seeds were sown with the aid of a hand-held vacuum seeder (White and Brendemuehl 1982). Seeds were sown at 1, 2, 3, 4, 5, and 6 cm spacings within the drill and 15 cm between drills. Soil tests indicated this area of the nursery had adequate levels of soil potassium and organic matter. Therefore, the area was operationally fertilized with 34 kg/ha of P just prior to sowing. Sowing was conducted on April 27, 1985 on 1.3 m plots. During the growing season seedlings received a total of 141 kg/ha of N (from ammonium sulfate).

Seedlings from each plot were lifted on January 15, 1986 and placed in cool storage (2 °C ± 1 °C). On January 16, the seedlings were transported to Auburn and were graded according to Wakeley's grades. The following day, 8 plantable seedings from each plot were randomly selected for testing RGP. Preparation of the seedlings, testing procedure and measurements obtained were identical to those in the 1983 study, except that an additional morphological measurement, root volume by displacement (Burdett 1979), was obtained.

1986 Study

Sowing was conducted on April 18, using seeds from Livingston Parish, Louisiana. Plots were 0.63 m long and were sown by hand, placing the seeds in the holes of a pre-drilled board to establish the correct spacings. Five replications were sown in a randomized complete block design. Seeds were sown at 1, 2, 4, and 6 cm spacings within the drill and 15 cm between drills. According to normal fertilization practices at this nursery, the soil was fertilized prior to sowing with 45 kg/ha of N (from ammonium sulfate and diammonium phosphate), 20 kg/ha of P, and 37 kg/ha of K. An additional 122 kg/ha of N (from ammonium sulfate) was applied as top-dressings during the year.

All seedlings from each plot were lifted on December 9, transported to Auburn and placed in cool storage (2 °C ± 1 °C). On Decemer 14, 8 plantable seedlings were randomly selected from each plot and used for testing RGP. Testing for RGP was the same as in the two previous studies.

Statistical analyses

The RGP tests were analyzed according to the experimental design in the nurserybeds (a randomized complete block design). The General Linear Model (GLM) procedure of the Statistical Analysis System (SAS Institute Inc. 1982) was used to test for linear and quadratic relationships. Correlation and regression analyses were used to examine the potential relationships between seedling morphology and RGP. In addition, covariate analyses were used in an effort to throw light on the nature of treatment effects (Snedecor and Cochran 1967). This method of analysis was used to determine if treatment differences in RGP could be accounted for by differences in root collar diameter or foliage dry weight.

For the 1986 study, the average diameter of 8 seedlings in one plot (replication one; 6 cm spacing) was 1.3 mm greater than for any other sample. These seedlings were not only large in diameter, but on the average, they produced more than 220 new roots per seedling. This one data point greatly influenced the analyses. A test of the leverage of this point (HAT DIAG H statistic of Proc REG; Freund and Littell 1986) indicated the influence was 5 times that expected. Therefore, this data point was deleted from use in all analyses.

Results and discussion

Seedling morphology

Plantable seedling diameter, component weights and root volume were increased by wider spacing (Tables 1—3). However, average seedling height was not affected by spacing. Shoot/root ratio was decreased by wider spacing in two of the studies. These findings are in agreement with a number of other density studies conducted with southern pines (Shoulders 1961; Switzer and Nelson 1963; Shipman 1964; Burns and Brendemuehl 1971; Harms and Langdon 1977; Dierauf and Garner 1980; Carlson 1986; Nebgen and Meyer 1986; Brissette and Carlson 1987; Boyer and South 1987; Boyer and South 1988; Marx and Cordell 1989). However, one researcher reported a positive correlation between seedling spacing and height of loblolly pine seedlings (Rowan 1986).

Root growth potential

Typically, bare-root loblolly pine seedlings in the southern United States usually exhibit mean values of less than 60 new roots per seedling (21 to 28-day test) when lifted during December and January (Rhea 1977; Larsen and Boyer 1986; Carlson 1986; Barden 1987; Brissette 1987; DeWald and Feret 1987). However, RGP was high in all three density studies with each treatment averaging more than 85 new roots/seedling. Even at these high levels, RGP tended to increase at the wider seed spacings. Seedlings grown at a spacing $\geqslant$ 5 cm exhibited more new roots and greater new root weight than seedlings grown at a spacing $\leqslant$ 3 cm. Most of the variation (59 to 79%) in RGP among plots could be accounted for by an ANOVA model that included only replication and spacing (Table 4). This indicates that at some nurseries, RGP of seedlings can be increased by lowering the seedbed density.

However, the increase in the number of new roots appears minimal for spacings of less than 3 cm (Tables 1—3). Although a 1 cm increase in average spacing between nursery seedlings can, in some cases, increase outplanting survival of from 4 to 10 percentage points (Shoulders 1961; Nebgen and Meyer 1986; Rowan 1986), it appears doubtful that increas-

Table 1. Treatment means and significance levels for the linear, quadratic, and lack of fit terms for the Hammermill Nursery density study in 1983.

Characteristics of plantable seedlings	Seed spacing (cm)					Probability of a greater F value		
Variable	1.9	2.8	4.0	5.0	13.1	Linear	Quadratic	Lack of fit
Root collar diameter (mm)	4.9	5.0	5.4	5.6	6.3	0.0002	0.1257	0.8323
Stem height (cm)	21.7	20.5	23.4	22.1	20.7	0.5506	0.3294	0.4078
Stem weight (g)	1.0	1.03	1.31	1.39	1.57	0.0203	0.2306	0.7642
Foliage weight (g)	1.67	1.70	2.10	2.30	2.86	0.0012	0.2613	0.8404
Original root weight (g)	1.07	1.10	1.26	1.45	1.71	0.0008	0.1847	0.7675
Shoot/root ratio	2.53	2.50	2.76	2.55	2.67	0.5763	0.6877	0.5538
RGP — number	97	88	112	115	135	0.0009	0.2774	0.2882
RGP — weight (g)	0.29	0.31	0.36	0.32	0.41	0.0002	0.5252	0.1670

Table 2. Treatment means and significance levels for the linear, quadratic, and lack of fit terms for the Hammermill Nursery density study in 1985.

Characteristics of plantable seedlings	Seed spacing (cm)						Probability of a greater F value		
Variable	1	2	3	4	5	6	Linear	Quadratic	Lack of fit
Root collar diameter (mm)	4.3	5.3	5.7	6.3	6.9	7.3	0.0001	0.2616	0.8469
Stem height (cm)	28.0	31.2	29.3	29.2	29.9	29.1	0.9359	0.4065	0.3971
Stem weight (g)	1.24	1.91	2.09	2.42	2.90	3.04	0.0001	0.5192	0.8521
Foliage weight (g)	1.59	2.60	2.84	3.57	4.06	4.49	0.0001	0.4934	0.8137
Original root weight (g)	0.74	1.14	1.34	1.60	1.96	2.15	0.0001	0.7242	0.8775
Shoot/root ratio	3.95	4.04	3.69	3.73	3.51	3.47	0.0025	0.9278	0.5558
Root volume (cc)	2.23	3.49	4.12	4.97	6.35	6.59	0.0001	0.6062	0.7239
RGP — number	88	118	119	148	169	180	0.0001	0.8223	0.6311
RGP — weight (g)	0.21	0.24	0.24	0.29	0.38	0.37	0.0001	0.3935	0.2748

Table 3. Treatment means and significance levels for the linear, quadratic, and lack of fit terms for the Morgan Nursery density study in 1986.

Characteristics of plantable seedlings	Seed spacing (cm)				Probability of greater F value		
Variable	1	2	4	6	Linear	Quadratic	Lack of fit
Root collar diameter (mm)	3.7	3.8	4.4	4.7	0.0004	0.8923	0.4275
Stem height (cm)	17.1	14.6	15.7	15.1	0.2261	0.3515	0.0549
Stem weight (g)	0.56	0.53	0.72	0.86	0.0006	0.4986	0.3183
Foliage weight (g)	0.98	1.01	1.33	1.65	0.0002	0.5344	0.6461
Original root weight (g)	0.52	0.57	0.74	0.93	0.0001	0.6040	0.8379
Shoot/root ratio	2.58	2.19	2.23	2.16	0.0017	0.0287	0.0132
Root volume (cc)	1.45	1.47	2.10	2.83	0.0001	0.1739	0.4672
RGP — number	98	104	97	135	0.0122	0.0513	0.2089
RGP — weight (g)	0.10	0.12	0.14	0.18	0.0023	0.9785	0.4768

Table 4. Comparison between ANOVA and Analysis of Covariance on the effect of seed spacing on number of new roots (RGP) of plantable loblolly pine seedlings.

ANOVA					Analysis of covariance				
Source	df	F value	$P > F$	R^2	Source	df	F value	$P > F$	R^2
				1983					
				0.59	Diameter	1	35.6	0.0001	0.79
Block	4	0.7	0.5872		Block	4	2.1	0.1157	
Spacing	4	5.1	0.0074		Spacing	4	1.1	0.3754	
Error	16				Error	15			
					Foliage	1	40.8	0.0001	0.78
					Block	4	2.0	0.1541	
					Spacing	4	1.0	0.4238	
					Error	15			
				1985					
				0.79	Diameter	1	78.1	0.0001	0.87
Block	4	4.2	0.0128		Block	4	4.2	0.1471	
Spacing	5	11.5	0.0001		Spacing	5	0.3	0.8868	
Error	20				Error	19			
					Foliage	1	113.9	0.0001	0.88
					Block	4	5.1	0.0057	
					Spacing	5	0.6	0.6765	
					Error	19			
				1986					
				0.72	Diameter	1	24.1	0.0006	0.85
Block	4	3.2	0.0547		Block	4	3.2	0.0621	
Spacing	3	5.2	0.0180		Spacing	3	7.4	0.0069	
Error	11				Error	10			
					Foliage	1	16.7	0.0022	0.78
					Block	4	1.9	0.1916	
					Spacing	3	2.9	0.0869	
					Error	10			

ing seedling spacing from 2.1 cm (323 seedlings/m^2) to 3.1 cm within the drill (215/m^2) would increase RGP enough to account for the increase in survival.

Mean seedling RGP was positively correlated with seedling size. Basal area, diameter, root weight, root volume and total weight were all positively correlated with RGP (Table 5). Mean seedling height, however, was not related to RGP. In some cases, seedling height can be negatively correlated to RGP (Larsen and Boyer 1986). This may partially explain why root collar diameter is often positively correlated with survival (South et al. 1985) while seedling height is not. In fact, there are several instances

Table 5. Simple linear correlations of selected morphological characteristics with RGP of plantable loblolly pine seedlings.

Variable	Number of new roots			Weight of new roots		
	1983	1985	1986	1983	1985	1986
	(n = 25)	(n = 30)	(n = 19)	(n = 25)	(n = 30)	(n = 19)
	(r values)					
Basal area	0.80	0.87	0.59	0.81	0.77	0.77
Diameter	0.78	0.86	0.59	0.80	0.76	0.76
Total weight	0.78	0.85	0.71	0.81	0.77	0.78
Root weight	0.73	0.84	0.68	0.77	0.77	0.85
Root volume		0.86	0.57		0.83	0.87
Foliage weight	0.78	0.85	0.62	0.79	0.76	0.76
Stem weight	0.74	0.85	0.72	0.76	0.76	0.67
Shoot height	0.34 NS	0.24 NS	0.43 NS	0.41	0.25 NS	−0.07 NS

[1] NS = Not significantly different at the 0.05 level of probability (coefficients greater than 0.57 are significant at the 0.01 level of probability).

where seedling height has been negatively correlated with survival (Tuttle et al. 1987; 1988).

Although several morphological measurements were correlated with RGP, root collar diameter was certainly the quickest to measure. However, neither the root collar nor the root is the source of carbohydrates needed for new root growth (Gilmore 1964). For several conifer species, new root growth depends on current photosynthesis (van den Driessche 1987). Therefore, the production of new loblolly pine roots depends on both the presence of foliage (Gilmore 1965) and the amount of foliage (Larsen et al. 1989a). Except at nurseries where frequent top-pruning is practiced, the amount of foliage on a seedling is usually correlated with the root collar diameter. This could partially explain why, in some cases, RGP can be correlated with root collar diameter (South et al. 1989).

The number of new roots also depends on the number of sites available for new root growth (Deans et al. 1990). Since the formation of new roots occurs primarily on lateral roots (Rhea 1977; DeWald and Feret 1987), seedlings with large diameters and more lateral roots will have more sites available for new root growth. For loblolly pine, RGP has been correlated with length of laterals (Rhea 1977), lateral root weight (Barden 1987), total root weight (Feret and Kreh 1986; Larsen and Boyer 1986; Barden 1987; Williams et al. 1988; Williams and South 1988; Larsen et al. 1989b) and root volume (Carlson 1986).

When nursery treatments result in differences in seedling size, RGP is likely to be correlated with root collar diameter since it is related to both the foliage and root system. However, it is not likely that RGP will be correlated with root collar diameter if the seedlings are desiccated (Feret et al. 1985), if roots have been stripped (South and Stumpff 1990), if too much foliage has been removed (Larsen et al. 1989a), if samples include a range of lifting dates (South et al. 1989), if there is minimal variation in seedling diameter among treatments, or if the test conditions result in a high coefficient of variation for RGP (Freyman and Feret 1987).

Because RGP of loblolly pine can be related to seedling size (Brissette and Roberts 1984; Carlson 1986; Barden 1987; Williams and South 1988; Williams et al. 1988; South et al. 1989), it is not known if the effect of wider spacing on RGP is due to an increase in seedling size or to a change in some "non visible characteristic of the seedling." In an attempt to answer this question, the data were subjected to linear covariance analysis. Use of covariance analysis has been recommended for analysis of studies involving RGP (Ritchie 1985; South et al. 1989).

For all three studies, covariance analysis accounted for 78 to 88% of the variation in RGP among plots (Table 4). When foliage weight was used as the covariate, the spacing treatment was no longer significant ($P > F \leqslant 0.05$) for any study. At the Hammermill Nursery, diameter as the covariate also reduced the significance of spacing. However, for the 1986 study at the Morgan Nursery, using diameter as the covariate reduced the significance of spacing ($P > F = 0.0685$) only when RGP was measured on a weight basis (analysis not shown).

The ability to account for variation in RGP by changes in morphology suggests that the increase in RGP associated with wider spacings could be attributable just to an increase in seedling size. These findings are in agreement with those of van den Driessche (1984) and Balneaves and Fredric (1983).

Conclusion

RGP of loblolly pine seedlings can be affected by spacing in the nursery; however, the effect is likely to be greatest for spacings wider than 3 cm within the drill. Although increasing average spacing from 2 cm between seedlings to 3 cm can increase loblolly pine survival on some planting chances by 4 to 10 percentage points (Shoulders 1961; Nebgen and Meyer 1986; Rowan 1986), the increase in RGP associated with this density change is likely to be minimal. The effect of increasing RGP by increasing seed spacing is likely due to improving seedling morphology rather than to greatly affecting the rate of some physiological process.

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