FREQUENCY DISTRIBUTIONS OF SEEDLINGS BY FIRST ORDER LATERAL ROOTS: A PHENOTYPIC OR GENOTYPIC EXPRESSION

Paul P. Kormanik, John L. Ruehle and H. David Muse[1]

Abstract.--Presented are frequency distributions of numbers of strong, first-order lateral roots (FOLR) in half-sib progeny of forest tree nursery seedlings. Seedling size at lifting time and first-year survival after outplanting are influenced by FOLR. Data from nursery studies with sweetgum and loblolly pine suggest that FOLR development may help identify potentially competitive seedlings. This information may eventually be used in grading systems for bare-root tree seedlings.

Additional keywords: Heritability, seed orchards, root morphology.

One of the major technological advances in forestry in the United States since World War II has been forest tree improvement. In the Southern and Southeastern United States tree improvement efforts have been concentrated on southern pine species. Improved seed orchards and highly mechanized nurseries are part of a plantation technology that now accounts for more than half of the pine regeneration in the South. Most pine seedlings outplanted there now come from improved seed orchards.

Since tree improvement began in the South, one of the major benefits expected from it was the development of uniform, high-quality planting stock. It was known that large seedlings performed better than small ones after outplanting, and one improvement objective was to increase the percentage of large seedlings being produced (Wakeley 1954). Genetically improved seeds did not consistently produce larger seedlings, however, seedling size was increased significantly through improved nursery technology.

By the late 1950s and mid 1960s, before genetically improved seeds were generally available, some seedlings often were too large for typical planting operations. In addition, the largest seedlings tended to inhibit the growth of adjacent seedlings in nursery beds. Thus, the objective of growing seedlings with a larger average size often resulted in an unacceptable range in seedling sizes. Nursery practices, such as additional fertilization, controlled seedbed density, mowing tops, and improving irrigation were employed to increase size and uniformity of seedlings with little attention was given to seedling root development.

[1] Silviculturist and Plant Pathologist, Institute for Mycorrhizal Research and Development, Southeastern Forest Experiment Station, USDA Forest Service, Athens, Ga., and Professor, Department of Mathematics, University of North Alabama, Florence, Ala. This research was funded in part by the U.S. Department of Energy Interagency Agreement No. DE-AI09-76SR-00870 and Georgia Forestry Commission Collection Agreement 29-303.

Many nursery operators assumed that increase and uniformity in size implied higher and uniform quality, shippable seedling became synonymous with a plantable one. All plantable seedlings were assumed to be potentially competitive because of their certified parentage. Now, after 25 years of tree improvement and related technology, it is apparent that early expectations of the program are not being fully realized. We still need to develop suitable criteria for identifying seedling quality.

Recent reports show that numbers of first-order lateral roots (FOLR) are positively correlated with growth and development of seedlings of several tree species (Kormanik 1986a, Kormanik and Muse 1986, Ruehle and Kormanik 1986). FOLR morphological characteristics may be better predictors of a seedling's competitive potential after outplanting than are commonly used aboveground attributes such as root collar diameter (RCD) and seedling height (Kormanik 1986b).

Current research at the Institute for Mycorrhizal Research and Development project at the USDA Forest Service Forestry Sciences Laboratory in Athens, Georgia, demonstrates that, even among superior mother trees, a significant proportion of progeny develop few FOLR in nursery beds. Increasing fertility during the growing season usually increases size, but rarely affects FOLR development, which appears to be fairly constant for a given mother tree. Extensive nursery and field research will be required to determine the appropriate combination of stem and root characteristics for each selected tree species. We suggest, however, that lateral root morphology may provide a biological basis for assessing a seedling's quality. Morphological stem characteristics, which are currently used to assess seedling quality, are too easily altered by nursery cultural practices, they often vary considerably from year to year, and among nurseries. By using FOLR counts, we might eventually be able to examine progeny and recognize those with a good genotype. Thus, FOLR counts on tree seedlings, a morphological characteristic less influenced by edaphic factors and having strong genetic control, might be used to advantage in a protocol for assessing seedling quality.

In this paper we report FOLR frequency distributions of bare-root seedlings of several important forest species derived from data on progeny from selected mother trees. We also suggest how FOLR might be used to help define quality and probable field performance of planting stock.

GENERAL

We have been conducting FOLR research for the past 10 years. The initial studies were on sweetgum (*Liquidambar styraciflua* L.) (Kormanik 1986b). Then investigations were extended to other hardwoods and several southern pine species (Kormanik and Muse 1986). After these trials, Kormanik (1986a) proposed "that regardless of the phenotypic characteristics of a mother tree, associated progeny will exhibit a range in seedling development related to distribution of strong first-order lateral roots and that seedlings with fewer lateral roots will be the least competitive in a forest environment."

Research results over the past 5 years indicate that FOLR development is under significant genetic control, can be predicted for a given species and is stable for a given mother tree. Results on sweetgum seedlings also suggest that FOLR development at lifting can be used to predict the future competitive potential of these seedlings after outplanting.

Production of seedlings.--FOLR frequency distributions for seedlings from individual mother trees have been calculated for progeny grown at the Whitehall Experimental Forest maintained in cooperation with the School of Forest Resources, University of Georgia, Athens. The seedlings described here were grown in 10 concrete block nursery beds (1.22 m x 18.29 m). Beds had a 25 cm gravel base covered by a 6 mil black polyethylene barrier. Above the barrier were 50 cm of a soil mixture (1:1:1) of loamy forest topsoil, sand, and finely ground pine bark. For all hardwood species, seedbed density was maintained at $65m^2$. Loblolly pine (*Pinus taeda* L.) seedlings were maintained at approximately $275/m^2$.

Bed fertility varied somewhat from year to year, but available soil P (Bray II) and K were adjusted each year to 50 to 75 ppm P and 80 to 100 ppm K. Calcium was maintained in the range of 390 to 504 kg/ha.— For hardwood species, we applied total N at rates equivalent to 450 to 560 kg/ha as NH4NO3 in 8 to 10 equal increments. For loblolly pine, 112 to 168 kg/ha of N were applied in four or five small increments with the final application scheduled for mid-July. Water was applied as needed, but once seedlings were well established they received 2.5 to 3.0 cm of water per week from rain and supplemental watering.

The beds were fumigated with methyl bromide under clear polyethylene plastic at 1 kg/18 m^2 of soil surface area. We fumigated when mycorrhizal inoculum was added to the soil, when tree species were changed, and before or after cover crop rotations. Thus some beds were fumigated annually while others were not fumigated for 2 or 3 years.

Hardwood seeds were obtained from mother trees in Georgia, Virginia, and North and South Carolina. Each mother tree's seeds and progeny were handled separately, but mixed seedlots were sometimes included for comparisons. Loblolly pine seeds were collected from individual ramets in the Georgia Forestry Commission's Arrowhead and Baldwin seed orchards or from selected ramets in orchards operated by industrial cooperators.

Seedlings were lifted during the dormant winter season, and diseased seedlings or those damaged during lifting (usually only 1 percent of the seedlings lifted) were eliminated. We normally collected data from the first 100 seedlings lifted from each treatment per replicate. Height and RCD were measured and number of FOLR are recorded for each seedling.

Seedling FOLR distribution data.--We obtained FOLR frequency distributions for six species: sweetgum, loblolly pine, northern red oak (Quercus *rubra* L.), white oak (*Q. alba* L.), black walnut (*Juglans* nigra L.), and green ash (*Fraxinus pennsylvanica* Marsh.) (Figure 1). Our largest data bases were developed for sweetgum and loblolly pine. Although their distributions appear similar, the sweetgum data can be approximated using a Gamma distribution, while the loblolly data are best described as a truncated normal distribution. Both red and white oak have distributions similar to loblolly pine, and black walnut and green ash tend to follow an exponential distribution but the data bases for these species were too small to properly define their appropriate distribution pattern.

Our initial results indicate that, at similar seedbed densities, nursery fertility practices can significantly affect a species seedling stem sizes, but that they usually have only a minimal influence on numbers of strong FOLR. Under our nursery protocols, we count only lateral roots that are >1 mm at the proximal end (at the taproot) and have developed a mature suberized periderm. We used the same standards for rating FOLR of all species reported here, but realize that the 1 mm diameter minimum may not be appropriate for all species. It is possible that 1 mm may be too low for walnut and oak, and may not be low enough for some southern pines.

Except for oaks, and perhaps walnut, the FOLR important to a seedling's early development appear to emerge from the taproot 20 to 25 cm below the root collar. After seedlings are undercut and lifted, the remaining taproot is approximately 20 to 25 cm long. The early rapid penetration of red oak and walnut taproots after seed germination results in FOLR development at depths upto 45 cm, but the greatest number occur on the first 30 cm of the taproot. For these two species, therefore, FOLR counts are made only on the top 30 cm of taproot.

Results with sweetgum seedlings from specific mother trees and different yearly seed collections indicate that the distribution curve of numbers of FOLR on seedlings from a mother tree is predictable since the numbers are relatively constant. The number of FOLR also is positively associated with seedling size in the nursery (Table 1). We have been accumulating data from several young sweetgum plantations that show how FOLR affects seedling performance after outplanting (Figure 2a & b). Various morphological traits of all seedlings were measured in the nursery and each seedling was tagged prior to outplanting. Seedlings were planted at random and their positions were mapped in the field. In this design individual traits acquired in the nursery by each seedling could be correlated to their field performance. The sweetgum survival data shown in figure 2 were obtained from outplantings for 2 consecutive years. Similar trends were reported in the original paper describing the effect of FOLR development on sweetgum seedling survival (Kormanik 1986b). Because of an extended severe drought approximately 60 percent of the seedlings died in the 2 years after planting, but 75 percent of those that died had less than four FOLR.

Heritability of FOLR.--Heritability, an expression of genetic control over some trait, is important in tree breeding (Zobel and Tolbert 1984). Narrow-sense heritability estimates (h^2) range from 0 to 1 with values near 1 indicating strongly inherited characteristics. Often, h^2 is limited in value because nursery cultural practices and environment influence phenotypic expression of morphological traits, resulting in error terms as large as their associated h^2 values.

Table 1.--Distribution frequency of sweetgum seedlings from 12 mother trees stratified by numbers of first-order lateral roots, heights, and root collar diameters

Number of laterals	Height	Root collar diameter	N	Cumulative percentage
	cm	mm		
0	88.43	5.66	80	3.14
1	96.33	6.43	128	8.18
2	100.12	7.17	224	16.98
3	101.81	7.90	265	27.40
4	104.15	8.67	281	38.44
5	105.17	9.24	280	49.45
6	105.18	10.06	258	59.59
7	106.31	10.61	250	69.42
8	105.44	11.15	196	77.12
9	105.84	11.57	136	82.47
10	103.64	11.94	116	87.03
11	106.16	12.54	96	90.80
$\geq$12	104.52	13.71	234	100.00

We had difficulty obtaining reliable h^2 estimates for FOLR of sweetgum. We only used four or six mother trees in these initial experiments and arbitrarily decided to stop counting FOLR at 10 on each seedling for practical reasons. When we designed these studies there was no plan to develop h^2 estimates. Later, attempts to develop h^2 estimates from the data suggested that 10 or more mother trees should have been used and all FOLR should have been counted

In the meantime we obtained h^2 estimates for FOLR in loblolly pine seedlings grown at the Whitehall nursery. Twelve open-pollinated mother-tree seedlots were tested in 1986, and an additional 25 mother-tree seedlots were tested in 1987. Although h^2 estimates are for seedlings grown in an ideal situation free of stress and field data is not yet available, we found some rather interesting trends.

The primary differences between years were an approximate 30 percent reduction in P and N fertility rates and the absence of a specific ectomycorrhizal treatment in 1987. The h^2 estimates and their standard errors for 1986 and 1987 were 0.77 ± 0.17 and 0.77 ± 0.11 with a combined estimate of 0.77 ± 0.09. These data suggest a rather strong genetic control over FOLR distribution within a population of seedlings.

Combining all 37 families into one mean value (Table 2) shows that approximately 40 percent of the seedlings had <3 FOLR. However, we see that stem characteristics of the seedlings in this inferior root category would readily fit into the desirable grade 2 class for loblolly pine (RCD ≥3.2 mm) and all exceed the height requirements. Most of the seedlings produced in these tests, therefore, would be considered high-quality seedlings. We used typical nursery cultural practices, which apparently tend to permit potentially inferior seedlings (based on FOLR counts) to become phenotypically acceptable. We eliminated pruning of seedling tops, a common practice used to obtain uniform height. The data in table 2 justify this decision, because when seedlings are separated by root morphological characteristics, we see increased number of FOLR associated with increased seedling height and larger RCD.

Table 2.--Relationship between number of first-order lateral roots and other morphological traits of 1-0 loblolly pine seedlings from 37 families[a]

Number of laterals	Height	Root collar dia.	D^2H	Average number lateral roots	Fresh weights top	Fresh weights root	Fresh weights total	Percent of total seedlings
	cm	mm	cm^3		- - - - g - - - -			
0-3	39.1	3.9	6.74	1.56	10.2	1.9	12.1	37
4-5	46.0	5.3	13.19	4.54	16.6	3.1	19.7	23
6-7	48.2	5.9	17.36	6.44	20.9	4.0	24.9	19
≥8	49.1	6.7	23.92	9.64	29.1	6.2	35.3	21

[a] Top weight, root weight, and total weight values were determined by measurement of representative subsamples; each subsample contained 100 seedlings.

These loblolly pine data indicate that FOLR development may be under significant genetic control, and is related to seedling vigor in the nursery. Field studies designed like the aforementioned sweetgum studies, have been established with representative seedlings of those 37 families. Data on field performance is not available at this time. Even in improved seedlots, a significant percentage of seedlings appear to be inferior. Using FOLR, we may be able to begin to unlock the secrets of a seedling quality. We also may be able to develop a satisfactory grading system to eliminate inferior individuals, regardless of aboveground size and appearance. If we can use the nursery bed as a testing ground for determining future competitive potential of seedlings before they are outplanted, we may be able to produce suitable guidelines for grading of second- and third-generation seed orchards.

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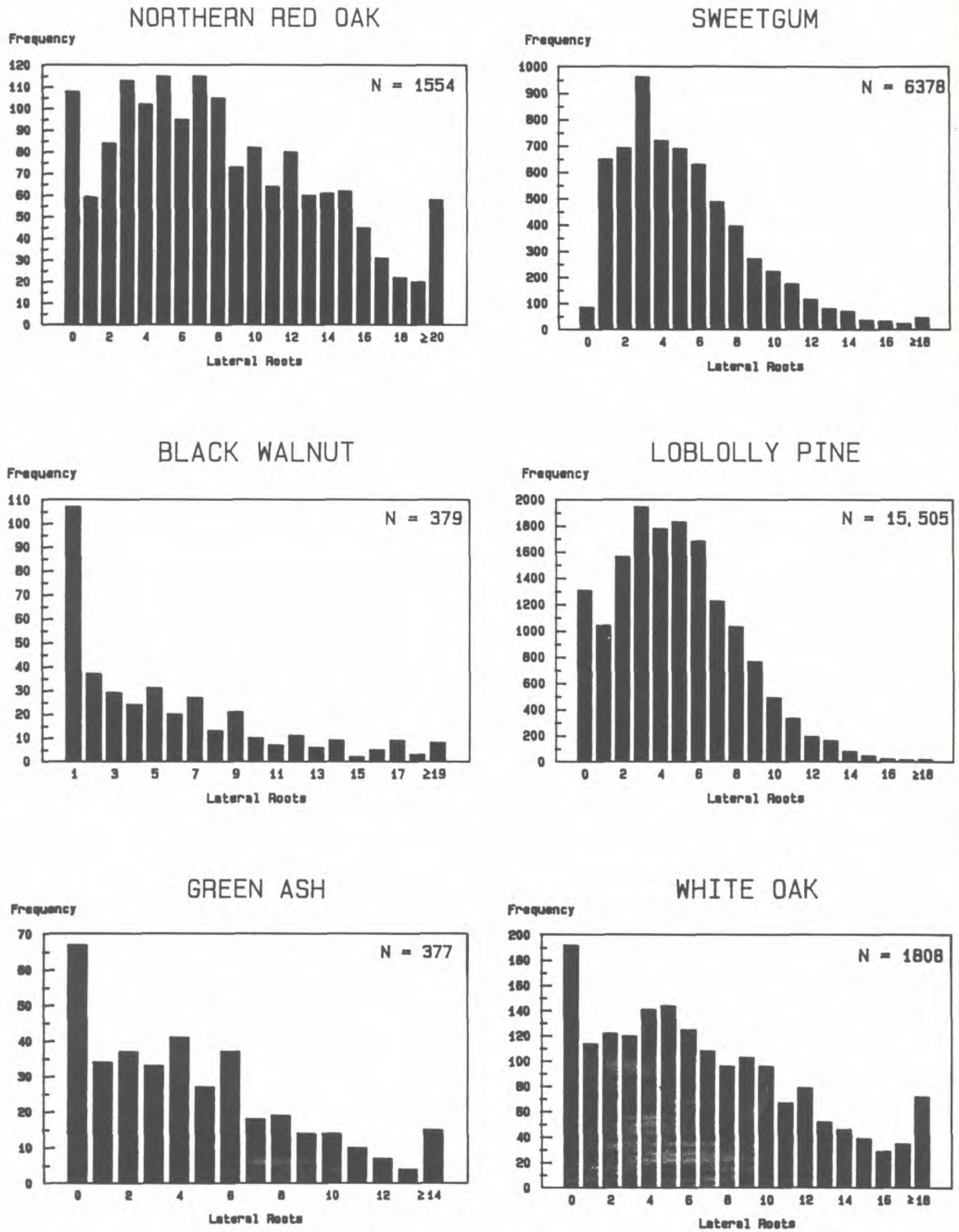

Figure 1.--Frequency distribution of seedlings stratified by FOLR for sweetgum, loblolly pine, northern red oak, white oak, black walnut, and green ash.

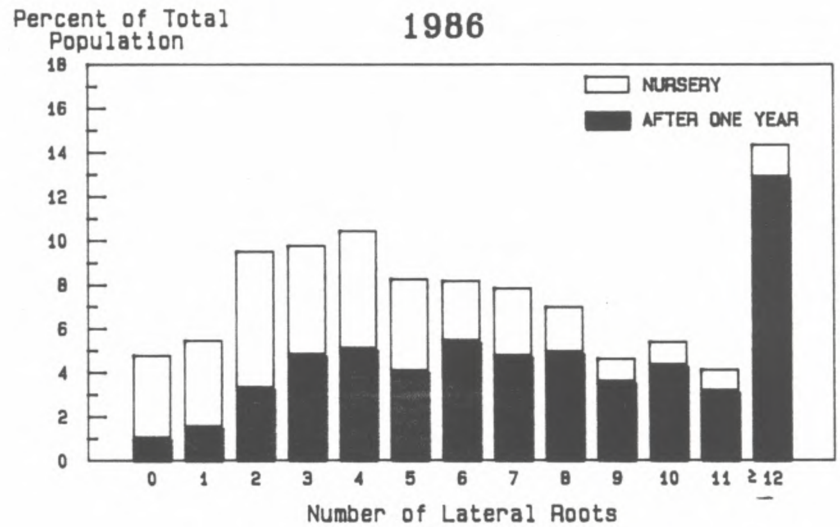

Figure 2a

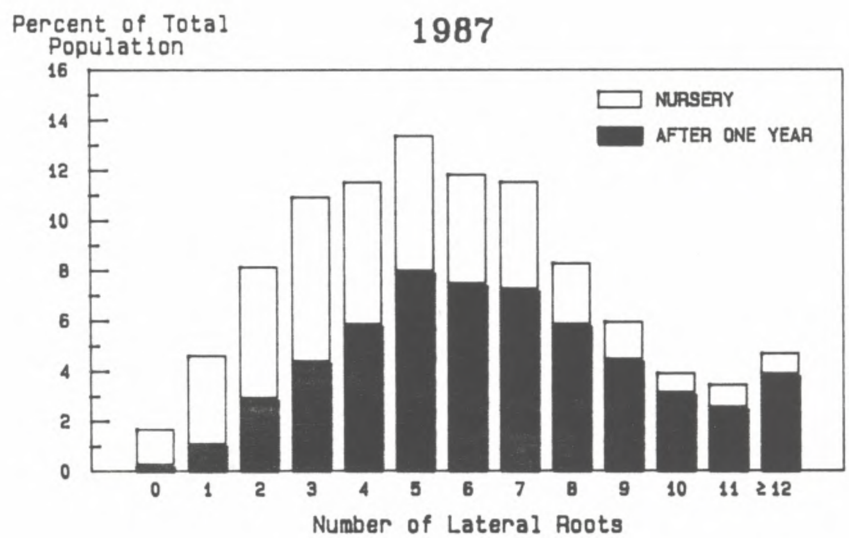

Figure 2b

Figure 2.--Frequency distribution of sweetgum seedlings stratified by FOLR when lifted from nursery bed (entire bar) and seedlings surviving after one growing season (darkened bar).