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Heritability of first-order lateral root number in *Quercus*: implication for artificial regeneration of stands

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Key words: first-order lateral roots, heritability estimates, *Quercus*, shade tolerance

Abstract

Natural regeneration of oak (*Quercus*) species in the USA has been easy to obtain on the lower quality xeric sites (site index $\leq$20 m at age 50) by developing advanced oak reproduction before stands are harvested. This approach has not been successful with *Q. rubra, Q. pagoda*, or *Q. alba* growing on highly productive river bottom, cove or other mesic sites (site index $\geq$23 m at age 50) because developing seedlings are overtopped by initially faster-growing and more shade-tolerant competitor species common on these sites. Artificial regeneration to increase percentages of these three valuable multiple-use species in specific stands has not been satisfactory because of limitations imposed by planting stock quality and by the traditional technology used to manage newly established stands. After the number of first-order lateral roots (FOLR) produced by an individual seedling was shown to be a highly heritable trait, artificial regeneration trials were started by the USDA Forest Service's Institute of Tree/Root Biology. A nursery fertility protocol was developed that could reliably and consistently produce seedlings of specific sizes. Thereafter, a seedling evaluation system was developed utilizing the parameters of FOLR, root collar diameter (RCD), and height (HT) for selecting seedling for outplanting. On mesic sites, survival and early growth for *Q. rubra* has been very good, with height growth of 4–5 m in 3–8 years. Trials are now being conducted with *Q. pagoda* and *Q. alba*. Methods for developing evaluation systems for oak species grown in nurseries under conditions different than the ones used in this study are discussed.

Abbreviations: FOLR – first-order lateral roots; RCD – root collar diameter; HT – height; NRO – northern red oak; WO – white oak; ITRB – Institute Tree/Root Biology; CBO – cherrybark oak; PAR – photosynthetic active radiation

Introduction

Members of the oak genus (*Quercus* spp) represent an important component of many forests in the eastern half of the United States as well as in many European countries. Oak species provide important forest lumber products and are of major importance for other uses such as mast production for numerous birds and wildlife species. Oaks also have other recreational values, and are of aesthetic importance in both urban and rural forests. They occupy a range of sites in the USA from the very fertile and productive river bottoms and mesic sites to the more xeric and less productive upland sites. Maintaining a significant oak component in new stands depends on having advanced oak regeneration when the current stand is harvested. Advanced oak regeneration on the lower quality upland sites (site index $\leq$ 20 m at age 50) is not difficult to obtain because competitive species are absent or techniques for obtaining advance regeneration have been developed (Sander, 1972; Sander et al., 1976; Sander and Clark, 1971). Obtaining oak reproduction on the higher quality sites has been difficult because of the competition from faster growing shade tolerant species that are released or that develop when the stand is thinned to encourage advanced oak regeneration (Lorimer, 1993). Clark (1993) reports that many foresters fear that the oak forests of Eastern United States may be experiencing radical changes in structure and composition and may be unstable on all but the more xeric sites because of competition from more shade tolerant species.

Some oak species like northern red oak (NRO) and white oak (WO) (*Quercus rubra* and *Q. alba*, respectively) have been more difficult to regenerate than others. Unless technology is developed for their retention in future stands, many believe that NRO may eventually disappear from the most productive mesic sites in the eastern hardwood forests (Kellision, 1993). Many have advocated the selection or shelterwood regeneration systems for obtaining advanced regeneration on these mesic sites such as been so effective on the lower quality upland sites (Loftis, 1983a,b). However, after almost 50 years of various modifications of these regeneration systems, very few new stands have been obtained on the higher quality sites (site index $\geq$ 23 m at age 50) even though some early partial regeneration successes have been reported. These poor regeneration results can usually be attributed to overestimating the shade tolerance of oak and their slow response to release compared to the rapid growth of competing shade tolerant species that quickly occupy the site (Loftis, 1990a; Nowacki et al., 1990). Unfortunately, even if one is successful in obtaining advanced oak regeneration, success is still not assured because when the final canopy is removed, the well-established, more shade tolerant species will generally occupy the site (Hodges and Gardiner, 1993).

Ten to 15 years ago the USDA Forest Services' Institute of Tree/Root Biology (ITRB) began a series of investigations to determine the feasibility of developing advanced regeneration of NRO in forest tree nurseries as 1-0 seedlings. These seedlings were to be used for modifying traditional artificial regeneration technology, or to enrich existing stands, or to develop entirely new stands with highly competitive individual seedlings. This extensive research effort now encompasses several broad scientific disciplines which include determining heritability values for various seedling root characteristics, basic seedling physiology, development of nursery protocols to produce seedlings, and developing systems for evaluating seedling competitive potential as well as soil modification procedures to maximize early oak seedling development. While 15 oak species have been studied in the nursery, NRO, WO and cherrybark oak (CBO) (*Q. pagoda*) have received the greatest effort in evaluating nursery seedlings in conjunction with field testing.

The discovery of the importance of first-order lateral root (FOLR) number to the competitive ability exhibited by loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) seedlings was the catalyst for continued research with oak species (Kormanik, 1986; Kormanik et al., 1990). Kormanik and Muse (1986) reported on early nursery and field trials with these species and they concluded that "regardless of phenotypic characteristics of mother trees, their progeny can be stratified by number of first-order-lateral roots (FOLR), and that seedlings with fewest lateral roots will be least competitive in the nursery and after outplanting in a forest environment". This report stimulated interest in potential widespread application of artificial regeneration for oak species in various sections of the United States through more thorough scrutiny of oak seedlings' root systems (Kormanik, 1989; Schultz, 1988; Schultz and Thompson, 1990). However, before valid heritability estimates could be obtained or a biologically sound seedling evaluation system developed, a nursery protocol was needed to permit consistency in seedling production so valid statistical comparisons could be made among families and different nursery locations for different years.

Materials and methods

Nursery protocol

Fifteen oak species have been used during development of a nursery protocol that would reliably produce seedlings of specific sizes in southeastern US nurseries (Kormanik et al., 1994a). Although many oak species are being evaluated for this nursery research protocol, only open pollinated half-sib progeny from specific NRO, CBO, and WO mother trees have been tested in sufficient quantities to obtain reliable, but albeit tentative heritability estimates for FOLR. These species will be addressed here. It is quite likely that modification of the protocol will be required when oak, or even other hardwoods, are produced in regions with significantly different environmental and edaphic conditions than exist in the southeastern United States (Kormanik et al., 1994a,b, 1995).

Briefly, the nursery fertility protocol that we developed appears to be effective, if not optimal, for most hardwood species (Kormanik et al., 1994a). The soil fertility levels for this nursery protocol are adjusted annually before acorns are fall sown. The levels of Ca, K, P, Mg, Cu, Zn and B are set at 500, 130, 100, 50, 0.3–3, 3–8, and 0.4–1.2 ppm, respectively, based on soil test results from standard Mehlich extraction. The desired seedling bed density is between 54–57/m^2. Eight to 12 N applications (as NH_4NO_3) are required during the growing season depending upon species and seedling size desired. The first two N applications are 17 kg/ha, the third at 56 kg/ha and subsequent ones at 168 kg/ha. Nitrogen applications start in mid-May and continue at 10-day intervals until mid-September. Stopping N top dressing at this time permits 60–90 days for seedling to harden off before first frost is anticipated at our nursery location. Irrigation is provided as needed until seedlings are well established in mid-June and thereafter when moisture tensiometers register 30–40 centibars at 15–20 cm depth. When seedlings approach the desired height, i.e., 1.0–1.2 m for NRO and CBO or 0.60–0.70 m for WO, either top dressing of N, irrigation frequency, or both can be altered to reduce stem elongation in favor of RCD and root expansion. It is important to maintain consistency in nursery practices if valid annual comparisons among progeny from various mother trees are to be undertaken. For example, a significant change in seedling bed density affects development of lateral roots and can significantly affect FOLR numbers and RCD without materially affecting seedling height. This results in a spindly seedling that may not survive or compete satisfactorily for several years.

FOLR: heritability

All heritability trials were conducted at the ITRB Experimental Nursery located approximately 7 km from the US Forest Service Laboratory in Athens, Georgia. The soil fertility protocol described earlier was followed and nursery layout was uniform for all heritability trials regardless of oak species being evaluated. The experimental nursery beds have been described in detail elsewhere (Kormanik, 1986), are 1.2×18.2 m, and have 120 rows with approximately 0.15 m between rows. There are 10–12 contiguous rows per mother tree per replication depending on whether 10 or 12 progeny groups are being evaluated. Thirteen sowing spots are included in each row and there are two replications per trial.

Family mean heritability (h^2) estimates, on a plot mean basis, are computed for FOLR number according to Kormanik et al. (1990) as:

$$h^2 = \frac{MS_F - MS_{RF}}{MS_F}$$

where MS_F is mean square for family, and MS_{RF} is mean square for the replication×family interaction, which are obtained from analysis of variance for the randomized block design. An estimate of the standard error of h^2 is computed as:

$$\text{S.E.}(h^2) = \left[\frac{2d^2(d+n-2)}{n(d-2)^2(d-4)} \cdot \frac{MS_{RF}^2}{MS_F^2}\right]^{0.5}$$

where d is degrees of freedom for family, and n is degrees of freedom for the replication×family interaction.

Table 1. First-order lateral roots (FOLR) family means broad sense heritability estimates for three *Quercus* species in several studies[a]

Study	Heritability[2]	Standard Error[3]
Q. rubra (NRO)		
1	0.898	0.153
2	0.870	0.114
3	0.843	0.235
Q. pagoda (CBO)		
1	0.904	0.104
2	0.783	0.271
3	0.558	0.428
Q. alba (WO)		
1	0.843	0.138
2	0.918	0.073

[a] 12 families were used in each test except for *Q. pagoda*, test 1, which had nine families. There were always two replications in each test.

Table 1 contains heritability estimates for northern red, white and cherrybark oaks from different experiments conducted over the past 8 years. Where multiple studies values are shown, the mother trees and years are different. Except for cherrybark oak, which represents acorn collections primarily from coastal plain of South Carolina, the original mother trees of NRO and WO were from scattered areas in the states of Georgia, North Carolina, Virginia, Tennessee and Kentucky. Heritability estimates for NRO families in this test number 3 (Table 1) were also obtained from seedlings produced in Tennessee by a different nursery protocol. The seedlings grown in Tennessee were significantly

Table 2. Morphological and growth characteristics of 1-0 northern red oak (*Quercus rubra*) seedling from which seedling evaluations are made[a]

Family	FOLR#		% Seedling with FOLR#	RCD (mm)		HT (cm)	
	$x_{,}$	Range	$\leq x_{,}$	$x_{,}$	Range	$x_{,}$	Range
1-14-915	6.4	0–26	58	9.8	3.9-18.7	125	22-233
2-10-540	5.6	0–23	54	8.4	3.7-15.8	135	40-262
2-19-630	4.6	0–25	57	9.0	2.9-17.1	131	43-238
4-14-2459	5.9	0–20	52	10.5	3.4-18.9	125	22-253
2-29-565	5.2	0–24	58	9.8	3.2-19.2	134	18-260
2-6-735	4.0	0–16	63	9.1	3.4-17.6	117	28-211
3-3-526	4.9	0–19	54	9.1	3.3-15.7	114	33-243
4-2-902	3.6	0–15	62	8.4	3.6-15.2	124	46-223
4-14-200	5.0	0–20	58	8.6	3.0-15.9	120	41-232
4-27-100	4.2	0–19	56	9.3	2.9-17.9	141	33-246
4-4-882	4.0	0–19	57	8.8	3.9-16.4	126	47-243
2-23-850	2.3	0–25	72	6.2	1.0-16.9	73	8-207

[a]Within a half-sibling group, individuals whose development exceeds the mean values for FOLR number, RCD and HT should be acceptable for artificial regeneration.

smaller in root collar diameter (RCD) and height (HT) and the FOLR were smaller in diameter and not as well developed as those grown at our experimental nursery, but the h^2 estimates were comparable.[1] The h^2 estimates for FOLR reported here for oak (Table 1) are comparable to those reported for loblolly pine (*Pinus taeda*) which were obtained from seedlings produced under different nursery protocols (Kormanik and Ruehle, 1989; Kormanik et al., 1990). This suggests that genetic control of root morphological traits may be quite significant and need to be considered when evaluating seedlings of other species.

Seedling evaluation

Major emphasis for evaluating competitive potential of oak seedlings in the United States has emphasized seedlings' RCD and heights, but both of these parameters have varied considerably depending on nursery protocol and geographical location of nurseries. Established quality standards for oak seedlings have not been developed in the United States or elsewhere in the world and may be reflected in the absence of wide acceptance of artificial regeneration of oak species. Tentatively we have begun to set standards for outplanting stock of the three oak species reported here which involves a combination of FOLR numbers, RCD, and HT. We select NRO, CBO and WO seedlings with FOLR numbers ≥5 and RCD ≥7 mm. Heights for NRO and CBO should be ≥1 m, but WO are acceptable at heights of ≥0.60 m. However, final determination of these standards must await both more nursery and field trials under different environmental and edaphic conditions to verify their utility. A single standard for evaluating all oak species may be unlikely but a procedure to develop a standard for any species appears feasible using these three variables in conjunction with a consistently applied nursery protocol adapted to individual locations.

Our oak seedling evaluation concept began by periodically excavating seedlings in the nursery and under forest conditions. In the forest stands, oak seedling decline became obvious after they were overtopped by faster growing competitors or when canopy closure occurred. WO seedlings survived better than NRO or CBO in the forest due to their early fall germination because it prevents the acorn desiccation that is so injurious to the recalcitrant oak acorns. NRO and CBO however, may remain on the forest floor for several months without germinating and viability can be significantly reduced through desiccation as has been reported by others (Bonner and Vozzo, 1987). Normally, however, the advantage of WO fall germination is shortlived, and if not released they pass out of the stand in 2–3 years. All surviving seedlings beginning to decline in vigor in forest stands were found to have few, if any, FOLR. Observing root morphology of individual seedlings in the forest involved

[1] Data on file at Scott Schlarbaum, Department of Forestry, Knoxville, Tennessee.

Table 3. Morphological and growth characteristics of 1-0 cherrybark oak (*Quercus pagoda*) seedling from which seedling evaluations are made[a]

Family	FOLR#		% Seedling with FOLR#	RCD (mm)		HT (cm)	
	x_t	Range	$\leq x_t$	x_t	Range	x_t	Range
Combic 1	4.9	0–18	52	7.3	2.1-12.1	102	33-160
Combic Int	4.8	0–22	56	7.6	3.2-12.5	103	23-161
Combic 2	4.7	0–15	59	7.7	2.0-13.1	105	23-174
Gillin 20	3.1	0–14	64	6.1	2.6-10.8	94	24-160
Kirby 17	4.4	0–15	56	6.8	2.9-10.8	104	37-156
Mahan 18	3.4	0–16	56	6.2	2.4-11.1	103	40-172
Moraux 19	4.4	0–17	56	6.4	1.9-10.6	95	26-165
Museum	4.9	0–17	47	6.6	2.1-12.4	105	31-189
Orchard	4.4	0–16	57	6.8	2.4-13.6	102	24-172

[a]Within a half-sibling group, individuals whose development exceeds the mean values for FOLR number, RCD and HT should be acceptable for artificial regeneration.

destructive sampling, and, thus, repeated observations on the same seedling were not possible. However, measurement of photosynthetic active radiation (PAR) indicated less than 10% of full sunlight was reaching most newly developing seedlings that were in declining vigor. This low light intensity at the forest floor has been reported by others and is not sufficient for long term development of oak seedlings (Hodges and Gardiner, 1993).

We began evaluating nursery seedlings as soon as most seedlings had completed their initial flush, and by mid-June a comparable absence of FOLR development was evident among the smaller and less competitive individuals. This was comparable to what was observed with low vigor seedlings in the forest. If oak seedlings were overtopped in the nursery by siblings by mid-July, they seldom were ever free to grow again. When seedlings bed density was reduced to alter competition among seedlings, the least competitive seedlings still produced few FOLR even though they had larger stem calipers. Oak seedlings that produced few FOLR represented at least 50% of the population from given half-sibling lots. These seedlings that were not competitive in the nursery also were not able to compete successfully after outplanting (Kormanik et al., 1998).

Seedling data collected earlier for obtaining heritability estimates were addressed again in light of the field responses that were being observed from the initial NRO plantings. This nursery data indicated for NRO, WO and CBO that the mean number of FOLR for open pollinated half-sib progeny generally averaged between 4 and 6 while the range in FOLR numbers varied widely among these three species from 0 to 40. It was evident that the FOLR mean values of seedlings were significantly affected by the skewed frequency distribution because seedlings with the fewest FOLR were occurring with the greatest frequency even under ideal nursery conditions. Examples of the skewness of seedlings' morphological characteristics are presented in Tables 2, 3 and 4 for NRO, CBO and WO respectively.[2] These species examples are for the first heritability values for each species shown in Table 1. All acorns used in these specific trials were from single tree selections. The NRO were from the USDA Forest Service's Watuga Seed Orchard located in western Tennessee, the CBO from the Coastal Plain of South Carolina and the WO from various locations on the Piedmont Plateau region of Georgia.

Each table contains the family means and ranges for FOLR, percentage of seedlings with FOLR numbers≤the mean FOLR, RCD and HT. These values are all important parameters for evaluating oak seedlings regardless of nursery production protocols used at a particular location. In many nursery trials involving these three species, as well as 12 other oak species, we have found that the individuals with FOLR numbers≥than the crops' mean FOLR values will represent the more competitive individuals of that species or sibling lot. The least competitive individuals usually have a single taproot with only fine, poorly developed, hair-like lateral roots that atrophy rapidly when seedlings are lifted from the nursery bed or after

[2] Data for other tests on file at ITRB, USDA Forest Service, Athens, GA 30602.

Table 4. Morphological and growth characteristics of 1-0 white oak (*Quercus alba*) seedling from which seedling evaluations are made[1]

Family	FOLR#		% Seedling with FOLR#	RCD (mm)		HT (cm)	
	$x_.$	Range	$\leq x_.$	$x_.$	Range	$x_.$	Range
KYWO 11	3.4	0–17	63	7.5	2.0-13.8	46	12-128
KYWO 31	3.0	0–19	66	8.4	3.0-15.3	35	8-104
NAWO-01	2.5	0–16	67	7.2	3.2-13.6	28	8-87
NAWO 23	4.1	0–22	62	8.2	2.9-15.2	48	8-142
SAWO 28	6.2	0–36	64	8.4	2.2-19.3	45	12-171
NAWO-24	3.8	0–21	60	7.9	2.8-15.0	39	14-147
NAWO-29	2.3	0–18	67	6.5	1.0-15.3	25	8-100
SAWO 12	2.8	0–16	58	7.4	2.4-13.0	36	11-112
NAWO-28	2.1	0–18	72	6.5	2.5-11.6	24	6-68
SAWO 14	4.6	0–32	64	8.6	2.7-18.4	46	12-151
SAWO 3	3.9	0–27	61	8.7	3.6-18.0	39	12-110
SAWO 7	3.6	0–23	61	9.0	2.7-17.4	48	12-134

[a]Within a half-sibling group, individuals whose development exceeds the mean values for FOLR number, RCD and HT should be acceptable for artificial regeneration.

seedlings are outplanted. When these least desirable seedlings are outplanted, they will become overtopped and die within 2–3 years. The poor performance often reported from artificial regeneration attempts with NRO on high quality mesic sites can often be related back to seedling size and poor vigor of the planting stock (McGee and Loftis, 1986). This combination of inferior seedling traits resulted in rapid seedling suppression by competing vegetation and such seedlings are eliminated from the forest soon after outplanting. This may simply be a function of the absence of lateral root development and the competitive potential of individuals with few FOLR. It is unlikely, however, that any single morphological trait will be able to realistically quantify a seedling's competitive potential.

These three oak species, like most oak species, are shade intolerant and during the first several years after outplanting allocate significant amounts of carbon production to root development. Unfortunately, without adequate sunlight, the root system appears to be a poor carbon sink, and lateral root development is significantly reduced and over a relatively short period begins to atrophy (Sung et al., 1998). Within a few years the seedlings lose their tenuous competitive position and die. This is also the sequence observed in the understory for naturally regenerated oak by others (Hodges and Gardiner, 1993; Lorimer, 1993).

Regeneration application

The oak seedlings selected for general outplanting should be chosen from the top 50% of the crop and should have FOLR numbers ≥ the mean FOLR number from the crop being evaluated. This selection criteria will assure the forester of obtaining the taller stems with the larger RCD. If, however, outplantings are to serve primarily as mast producing areas and be potential seed orchards, we recommend selecting only those seedlings in the top 25–30% of the crop. These seedlings will have the largest number of FOLR and be the tallest with the largest RCD. These are easily identified even before they are lifted. The largest NRO seedlings produced under these exacting nursery conditions typically develop quickly and may begin to produce acorns in 5–8 years under the proper field conditions. Under present seed orchards management conditions, NRO and CBO may attain RCD of from 10–15 cm and heights of 4–6 m during this 5–8 year period. In regenerated forest stands, without supplemental irrigation and fertilization, heights may be comparable but their RCD may be reduced by about 50 percent and the seedlings may need to be released from competition between year three and five (Kormanik et al., 1998). White oak have, in our limited tests, grown at about half the rate of the two red oaks but we have not observed early acorn production. Since acorn production is under considerable genetic control, it is risky to cull individuals from potential seed orchards until more definitive research on acorn production is obtained (Schlarbaum et al., 1994).

Seedlings produced in different environments due to geographic location may not develop as quickly as those in the southeastern United States. However, seedling evaluation for potential competition ability may still be readily accomplished. The parameters for FOLR, RCD and HT can be obtained by random sampling of 100–200 individual seedlings to obtain data for these mean values. In environmental conditions where seedlings may attain 1 year heights of only 25–35 cm, it is unrealistic to expect many FOLR to develop and seedlings with 2–3 FOLR may represent competitive seedlings under those conditions. However, we currently have serious reservations for growing the seedlings as 2-0 or 1-1 planting stock to improve seedlings' root and stem characteristics in eastern United States. With proper nursery management, oak seedlings of outstanding competitive potential can easily be produced in one growing season provided the acorns are fall sown. We find that much second year growth is directed to root development that is removed when the 2-year-old seedlings are lifted. The second year does not result in much improvement in root characteristics of seedlings if these seedlings were not competitive as 1-0 nursery stock.

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Alexia Stokes
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