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FLUSH DEVELOPMENT DYNAMICS IN FIRST-YEAR NURSERY-GROWN SEEDLINGS OF EIGHT OAK SPECIES

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Abstract—Two experiments were conducted to follow flush development dynamics exhibited by various oak species. In experiment I, southern red oak acorns were sown in mid-March 2001 at Whitehall Nursery (Athens, GA). In experiment II, acorns of black oak, cherrybark oak, Nuttall oak, Shumard oak, southern red oak, swamp chestnut oak, white oak, and willow oak were sown in December 2001 at the same nursery. Compared to the 2001-grown southern red oak seedlings, the 2002-grown southern red oak seedlings had higher germination percent and one more flush. In both years, randomly selected seedlings from each species were monitored daily for flush development. The flush elongation period (FEP), the rest period (RP), and the bud-to-bud development period (BBP) were recorded for each selected seedling. For a given flush order, RPs varied among species but FEPs did not. Consequently, BBPs varied among species. Cherrybark oak and willow oak had shorter RPs and BBPs and developed more flushes than the other oaks. A strong correlation (r = 0.94) existed between individual flush length and the maximum elongation rate in the FEPs for all eight species.

INTRODUCTION

On clearcut mesic sites, successful artificial regeneration of some oak (*Quercus*) species requires planting high-quality 1-0 nursery stocks and keeping the sites weed free for the first 2 or 3 years (Kormanik and others 1997, 1998, 2000). The species tested in such efforts included northern red oak (*Q. rubra* L.), white oak (*Q. alba* L.), southern red oak (*Q. falcata* L.), swamp chestnut oak (*Q. michauxii* Nutt.), and cherrybark oak (*Q. pagoda* Raf.). After lifting from nursery beds, 1-0 oak seedlings are graded by their height, root-collar diameter, and number of first-order lateral roots that are > 1 mm in diameter. The specified regeneration protocol utilizes only the top 50 percent of all graded seedlings (Kormanik and others 1994).

Increasing cases of oak disease and decline in the Southern United States have made restoration of oak in hardwood stands critical. Growing different oak species using this nursery protocol and understanding basic biology of individual oak species are essential in providing high-quality oak seedlings for restoration efforts. Here, we analyzed eight oak species for their germination and first-year flush development dynamics.

MATERIALS AND METHOD

Experiment I

Open-pollinated southern red oak acorns were collected from 12 mother trees in Savannah River Site forest stands (New Ellenton, SC) in the fall of 2000. These acorns were floated in water for half an hour, and those that floated were discarded. Acorns that sank were stored in plastic bags at 4 °C. In mid-March 2001 acorns were sown at a density of 54 to 57/m^2 at the Whitehall Experimental Forest Nursery (Athens, GA). The 12 half-sib families were planted by family in a randomized block design with 2 replications. One hundred and thirty acorns per family were planted in each replication. Seedlings were grown using the hardwood nursery protocol of Kormanik and others (1994). Germination was assessed on May 1 and May 18, 2001.

A seed was considered to have germinated when its epicotyl emerged. In early June, 10 seedlings were randomly tagged from each family in each of the 2 replications to record daily flush elongation beginning with the second flush. The flush elongation period (FEP) began with a bud visible to unaided eyes and ended when flush length remained unchanged for 3 days. The rest period (RP) was the period between the completion of elongation and the appearance of buds beginning the next flush. The bud-to-bud development period (BBP) was the sum of the FEP and the RP.

Flush length was modeled on an individual seedling basis with the logistic equation defined as:

$$FLUSH = a / \left(1 + e^{b + cDAY}\right)$$

where

FLUSH = flush length (cm)

DAY = days since the first observation of a visible bud

a, b, c = parameters of the logistic function.

Nonlinear regression was used to estimate the parameters using PROC NLIN (SAS Institute, Inc. 1989). The instantaneous rate of flush growth on a given day was obtained by determining the slope of the specific logistic equation evaluated then. This was found by differentiation with respect to *DAY*, yielding $SLOPE = \left(-ace^{b+cDAY}\right) / \left(1 + e^{b+cDay}\right)^2$ and then substituting the appropriate day in this equation. The inflection point was where the instantaneous rate of flush growth reached its maximum and began to slow down. It was found by setting the second derivative equal to zero and solving for *DAY*, which yielded inflection point day = -b / a.

Experiment II

In fall 2001, open-pollinated southern red oak acorns were collected from 19 mother trees in Savannah River Site

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forest stands. Six of these half-sib families were from the same mother trees used for Experiment I. Black oak (*Q. velutina* Lam.) acorns were collected from one mother tree in South Carolina. White oak acorns were collected from individuals in Virginia and North Carolina and from the Georgia State Forest Commission's Arrowhead Seed Orchards. There were 28, 22, and 14 half-sib white oak families from Virginia, North Carolina, and Georgia, respectively. Cherrybark oak was collected from one mother tree in Georgia. Mixed seedlots were collected from Texas for cherrybark, Nuttall, Shumard, swamp chestnut, and willow oaks.

In December 2001 only acorns that sank were sown by family at the same density and in the same nursery as in experiment I. Southern red oak acorns were sown in a randomized block design with two replications. Each replication had 19 families with 104 acorns per family. White oak families were randomly planted in two replications, with 26 to 52 acorns per family per replication. All Texas oaks, Georgia cherrybark oak, and black oak acorns were planted in 1 block with 182 acorns per species. All seedlings were grown with the same hardwood nursery protocol used in experiment I. Germination was scored on April 17 and May 13, 2002.

In mid-May, 24 randomly selected seedlings were tagged for each of the black, Georgia cherrybark, Texas cherrybark, Nuttall, Shumard, swamp chestnut, and willow oak species. Also, two white oak seedlings per family and six families from each of the three States were selected from each of the two replications. The 24 tagged southern red oak seedlings consisted of 2 seedlings per family and 6 families per replication. These tagged seedlings were measured daily for flush development. The logistic equation used in experiment I was used to analyze flush development dynamics.

RESULTS AND DISCUSSION

Germination

By mid-May, mean germination for southern red oak acorns was 67 percent in experiment I and 86 percent in experiment II (table 1). The six southern red oak families tested in both years had mean germination of 58 percent and 86 percent for experiments I and II, respectively. Poor germination by families 614 and 617 in 2001 was not observed in 2002. Such year-to-year variation in germination was not observed in the other four families.

By mid-May 2002, germination of black oak, Georgia cherrybark oak, and white oak from all three States was < 75 percent, while germination of the other species was ≥ 80 percent (table 2). Germination increased by > 10 percent between mid-April and mid-May for Nuttall, southern red, Virginia white, and willow oaks. In the Virginia white oak collection, most acorns seemed dry and light. Even though only the sunk acorns were sown, Virginia white oak still had low germination percent as well as a prolonged period of emergence. The negative effects of desiccation on acorn germination have been reported in different oak species (Farmer 1975, Gosling 1989, Schroeder and Walker 1987). To avoid prolonged desiccation after acorn drop, it is essential to collect acorns over short time intervals. Because of their radical protrude before sowing, white oak acorns are especially susceptible to pre- and postcollection desiccation.

Table 1—Germination of southern red oak acorns collected in 2000 and 2001 and sown in March and December of 2001, respectively, in Athens, GA

Family	05-1-01	05-18-01	04-17-02	05-13-02
	- - - - - - - - - Germination percent - - - - - - - -			
520	70	78	65	83
612	72	76	76	95
614	14	14	80	90
617	39	51	85	95
618	60	74	62	88
619	55	57	56	66
543	61	62	—	—
610	64	66	—	—
611	63	67	—	—
613	85	90	—	—
615	80	85	—	—
616	76	82	—	—
517	—	—	65	86
620	—	—	74	89
621	—	—	48	60
622	—	—	77	90
623	—	—	71	83
624	—	—	62	81
625	—	—	86	93
626	—	—	65	79
627	—	—	74	88
629	—	—	79	89
630	—	—	84	93
632	—	—	87	92
633	—	—	77	87

Table 2—Germination of oak acorns collected from five States and sown at Whitehall Nursery (Athens, GA) in December 2001

Oak species; State	04-17-2002	05-13-2002
	- - - Germination percent - - -	
White; VA	46	63
White; NC	58	65
White; GA	70	73
Black; SC	59	60
Southern red; SC	72	86
Shumard; TX	83	86
Nuttall; TX	67	80
Swamp chestnut; TX	73	81
Willow; TX	68	80
Cherrybark; TX	91	92
Cherrybark; GA	53	54

Flush Development

Experiment I—Southern red oak seedlings began their second flush around June 20, 2001. Flush elongation periods increased by 4 and 2 days over previous FEPs, for the third and the fourth flush, respectively (fig. 1). Bud-to-bud development periods for the last flush was 5 days

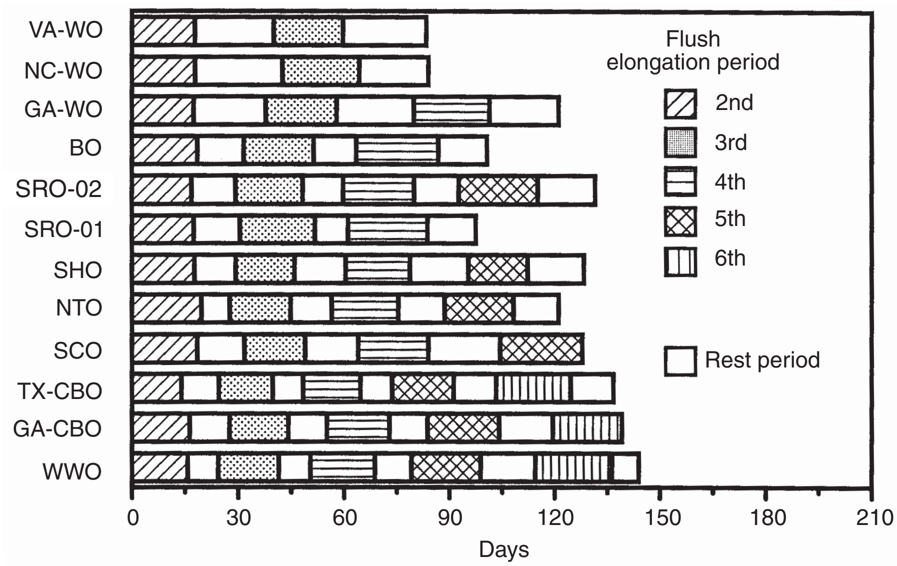

Figure 1—Duration of flush elongation period (filled blocks) and duration of the rest period (open blocks) in first-year oak seedlings from acorns collected in five States and grown in Georgia in 2002. The species included white oak (WO) from Virginia, North Carolina, and Georgia; black oak (BO); southern red oak (SRO) grown in 2001 and 2002; Shumard oak (SHO); Nuttall oak (NTO); swamp chestnut oak (SCO); cherrybark oak (CBO) from Texas and Georgia; and willow oak (WWO).

longer than for the second and the third flush. These spring-sown southern red oak grew one fewer flush than those that were winter-sown (fig. 1). Two lines of evidence support the fact that spring-sown southern red oak seedlings had a shorter growing season than the winter-sown: (1) spring-sown seedlings emerged later (table 1), and (2) spring-sown seedlings began a second flush about 3 weeks later than winter-sown seedlings. Of course, the differences in growth between winter- and spring-sown seedlings would be clearer if seedlings were evaluated in the same growing season.

Experiment II—Seedlings of Georgia and Texas cherrybark oak and willow oak began a second flush development in late May, whereas those of North Carolina and Virginia white oak did not start their second flush until the second week of June 2002. The rest of the oaks began their second flush near June 1. Within the same order of flush, little variation in FEPs was observed among species. Elongation periods for the second flushes in all species were about 17 days (fig. 1). With every next flush order, the periods increased 1 to 2 days. About 21 days were recorded for the sixth flushes in cherrybark oak and willow oak (fig. 1). The third and the fourth FEPs for the 2001-grown southern red oak seedlings took 2 more days than for the 2002-grown seedlings.

At the completion of flush elongation, most of the flush leaves were immature. Some of the top one to three leaves on each flush had not fully matured when the bud for the next flush was visible. Thus the RP had more to do with the completion of flush length growth than with leaf expansion or maturation. Our RP definition was equivalent to the sum of the linear leaf expansion stage and the lag phase in the morphological index system developed by Hanson and others (1986) for northern red oak. In contrast to the FEPs, the RPs for a given flush order varied greatly among species (fig. 1). Variation in the RPs was evident with the appearance of different flush orders at any given time after mid-July. For example, by mid-August white oak from North Carolina and Virginia had finished their third flush, which was the final flush for most of them. In the meantime, Georgia cherrybark oak and willow oak were already in the elongating phase of the fifth flush, and Nuttall, Shumard, southern red, and swamp chestnut oaks had finished the fourth flush elongation. With the exception of those occurring before the season's final flush, RPs remained constant among different flush orders of individual species (fig. 1). For year-to-year production of oak seedlings at the same nursery, duration of RPs proves to be a useful tool for early assessment of stock quality. A longer than average RP may indicate fewer flushes and less height growth, thus poor seedling quality.

Variations in BBP resulted mostly from variations in the RPs, because in any given order of flushes, the FEPs remained constant among species. Alternatively, BBP can be used to assess oak stock quality. Without measuring the length, it is impossible to note with any certainty when elongation ends. However, it is easy to observe bud appearance. Bud-to-bud periods lasted an average of 27 to 30 days for all flushes of Georgia and Texas cherrybark oak, Nuttall oak, and willow oak (fig. 1). For black oak, southern red oak from both years, and Shumard oak, BBPs were about 33 to 35 days for all flushes. Periods of 40 and 42 days were recorded for most of the white oak seedlings. The BBPs for second and third flushes of white oak from all three States were similar, although Georgia white oak had one additional flush. Therefore, it appeared that the residual effects of desiccation might affect the numbers of flushes but not the BBPs.

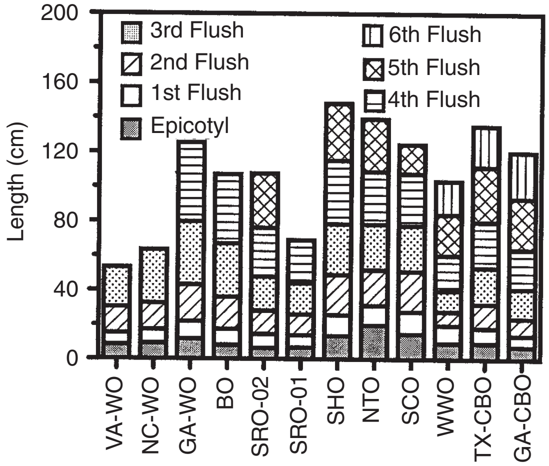

Figure 2—Individual flush lengths of first-year oak seedlings from acorns collected in five States and grown in Georgia in 2002. Species abbreviations are the same as in figure 1.

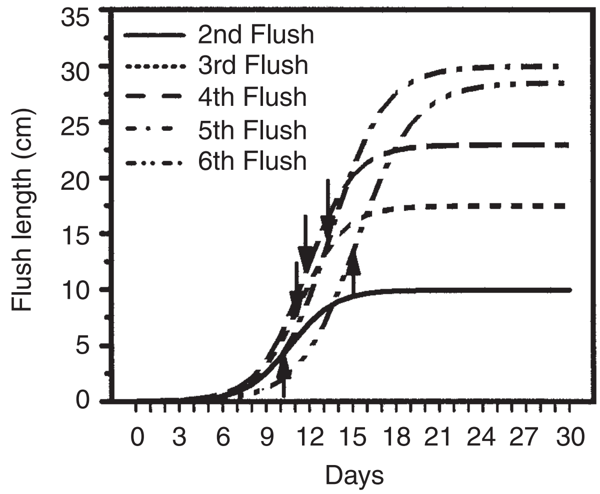

Figure 3—Logistic curves for flush length growth of the second, third, fourth, fifth, and sixth flushes of first-year cherrybark oak seedlings from Georgia. Arrows indicate inflection point day.

Generally, each flush was longer than the one before it for all oak seedlings (fig. 2). However, most last flushes occurring after mid-September were shorter than earlier flushes. For example, the fifth flush of swamp chestnut oak was much shorter than the fourth flush, and the sixth flush of willow oak was shorter than its fifth. These last flushes grew when days were shorter and day and night temperatures were lower than conditions for growth of earlier flushes. In contrast, the last flushes of white oak were the longest because they developed in summer (fig. 2). Of all species grown, Nuttall, Shumard, and swamp chestnut oaks had the longest epicotyl and first flushes. An earlier study reported correlations between first flush length and final seedling height in white oak (Sung and others 2002). Similar correlations may be established with the other oak species in future seedling growth studies. Because not all continuously monitored seedlings produced equal numbers of flushes, mean height for these seedlings were generally shorter than the sum of all individual flush lengths in figure 2. Mean height for Shumard and Nuttall oak seedlings was about 125 cm. The height of swamp chestnut, Georgia cherrybark oak, and Georgia white oak was about 110 cm. The height for black oak, Texas cherrybark oak, and willow oak was about 100 cm, and the height of North Carolina and Virginia white oak were 54 and 35 cm, respectively. Heights for the spring-sown and winter-sown southern red oak were 67 cm and 98 cm, respectively.

Logistic Equation Parameters of Flush Elongation

All flush elongations for the Georgia cherrybark oak seedlings were sigmoid curves (fig. 3) and similar to those reported earlier for white oak (Sung and others 2002). The other oak species, including southern red oak sown in spring 2001, had curves similar (data not shown) to those of Georgia cherrybark oak.

With some exceptions, inflection point days for all flushes occurred 10 to 14 days after flush bud appearance (table 3). In other words, once a flush bud began to grow, it followed a tightly controlled developmental program.

Table 3—Inflection Point Day and its slope from the logistic equation for flush length growth in first-year oak seedlings fromacorns collected in five States and grown in Athens (GA) in 2002 and from first-year southern red oak seedlings grown in 2001

	Flush number				
Oak species; State	2	3	4	5	6
	- - - - - - Inflection point day - - - - - -				
White; VA	13.4	13.6	—	—	—
White; NC	13.0	14.0	—	—	—
White; GA	12.2	13.2	12.0	—	—
Black; SC	12.4	13.6	15.8	—	—
Southern red; SC	12.6	14.0	14.4	15.9	—
2001-Southern red; SC	1.5	14.6	16.1	—	—
Shumard; TX	11.3	10.6	11.0	10.7	—
Nuttall; TX	11.6	10.9	11.1	13.0	—
Swamp chestnut; TX	1.1	11.0	12.6	15.1	—
Willow; TX	10.1	11.0	11.2	12.5	15.3
Cherrybark; TX	11.3	11.4	11.2	13.6	15.1
Cherrybark; GA	10.8	11.4	12.0	13.6	15.3
	- - Slope for inflection point day - -				
White; VA	2.5	3.4	—	—	—
White; NC	2.4	4.4	—	—	—
White; GA	3.0	4.3	5.6	—	—
Black; SC	2.7	4.4	5.0	—	—
Southern red; SC	2.2	3.2	4.4	3.9	—
2001-Southern red; SC	2.2	2.9	3.5	—	—
Shumard; TX	3.5	4.4	5.3	4.6	—
Nuttall; TX	2.4	3.9	3.9	3.5	—
Swamp chestnut; TX	3.3	4.1	3.9	2.1	—
Willow; TX	1.5	2.3	3.6	4.0	2.8
Cherrybark; TX	2.3	3.5	4.2	4.2	3.0
Cherrybark; GA	1.6	2.8	3.5	4.0	3.6

However, the inflection point slope (elongation rate) varied greatly among flushes and among species (table 3). With FEPs (fig. 1) and inflection point days (table 3) similar among species, variation in flush length (fig. 2) must have resulted from different elongation rates (table 3). The correlation coefficient between the inflection day elongation rate and flush length for all flushes of all species was 0.94. For southern red oak, the inflection point day and its slope and the flush length for the second, third, and fourth flushes were similar between two crops (table 3).

CONCLUSIONS

The lower percent acorn germination, fewer flushes, and shorter total height for the 2001-grown southern red oak as compared with the 2002 seedlings might be because the former was spring sown and the latter was winter sown. Except in some seedlings' last flushes, each oak flush had a greater maximum elongation rate and longer final length than the flush preceding it. Most species studied here had a similar FEP for a given flush order. However, the RP varied greatly among species. Except for those occurring before the last flush, the RPs remained constant among different flush orders within the same species. Cherrybark oak and willow oak, having shorter rest periods and thus shorter BBD, produced more flushes than other oaks. The less-than-satisfactory germination and growth of white oak from Virginia may have caused by excessive acorn desiccation before collection.

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Station ID: GTR-SRS-071

Description: Ninety-two papers and thirty-six poster summaries address a range of issues affecting southern forests. Papers are grouped in 15 sessions that include wildlife ecology; fire ecology; natural pine management; forest health; growth and yield; upland hardwoods - natural regeneration; hardwood intermediate treatments; longleaf pine; pine plantation silviculture; site amelioration and productivity; pine nutrition; pine planting, stocking, spacing; ecophysiology; bottomland hardwoods - natural regeneration; and bottomland hardwoods—artificial regeneration.