VARIATION IN FLOOD TOLERANCE OF CONTAINER-GROWN SEEDLINGS OF SWAMP WHITE OAK, BUR OAK, AND WHITE OAK

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Abstract.—How much variation in flood tolerance exists among seedlings within oak species, given the flood frequency of sites from which acorns are collected, has been largely unexplored. Our studies examined initial growth and flood tolerance for seedlings of swamp white oak (*Quercus bicolor* Willd.), bur oak (*Q. macrocarpa* L.), and white oak (*Q. alba* L.) grown from acorns collected from both upland and bottomland sites. Two-flush seedlings grown in a soil-less potting mix were subjected to partial inundation for 0, 4, and 8 weeks with stagnant water in a shade house covered with 50 percent shade fabric. Only 40, 20, and 13 percent of the seedlings for swamp white, bur, and white oak, respectively, produced a new growth flush following partial inundation flooding. Seedlings of all three species produced hypertrophied lenticels in response to partial inundation. Swamp white oak seedlings that flushed averaged 17 cm of new height growth across all flood treatments in contrast to bur and white oak seedlings, where net height growth decreased with increasing flood duration. Bur and swamp white oak seedlings from bottomland seed sources showed greater basal diameter growth than seedlings from upland sources before and after flooding. The reverse was true for white oak seedlings. Highly significant differences in seedling growth and flood tolerance both for topographic position within species and among half-sib family within position indicate adequate variation exists within native populations of all three species to identify seed sources for improved planting stock for bottomland plantings.

INTRODUCTION

Flood tolerance is defined as the physiological adaptation of plant roots to anoxic conditions, toxic substances, and other associated changes in soil properties induced by flooding (Gardiner and others 1993, Kabrick and others 2007, Unger and others 2007). Flood tolerance ratings for the major hardwood species in the Central Hardwood Region have been reported by several research groups (Hook 1984, Kabrick and Dey 2001, Allen and others 2001). The assignment of oaks (*Quercus* spp.) to flood tolerance classes ranging from intolerant to tolerant is based largely on case-studies following natural flooding events and a few greenhouse studies (Hosner and Leaf 1962, Bell and Johnson 1974, Whitlow and Harris 1979, Hook 1984, Loucks 1987).

Flood facility and greenhouse studies have confirmed the assignment of oaks to classes ranging from intolerant, that is, withstanding only short-duration flooding, to tolerant, that is, the capacity to withstanding partial inundation for up to one growing season (Gardiner and others 1993, Kabrick and others 2007). When constructed on bottomland sites, field flood facilities can mimic natural flooding events with some control of the timing, duration, and depth of flooding and allow for testing of large numbers of seedlings (Lockhart and others 2006, Coggeshall and others 2007, Kabrick and others 2007, Van Sambeek and others 2007). Greenhouse-type studies that offer greater control of the flood

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environment are still needed to provide more detailed information on the physiological, morphological, and genetic responses of individual seedlings to flooding (Tang and Kozlowski 1982, Gardiner and others 1993, Ponton and others 2002, Kaelke and Dawson 2003).

Battaglia and others (2004) suggest that many oak species have the capacity to grow on both upland and bottomland sites. Within the Central Hardwood Region, bur (*Q. macrocarpa* L.) and swamp white (*Q. bicolor* Willd.) are two oak species that can be found in natural stands ranging from droughty upland to frequently flooded bottomlands (Kurz 2003). Several studies on other hardwoods indicate the need to carefully consider the seed source for production of seedlings for bottomland plantings. Keeley (1979) reported that seedlings of black gum (*Nyssa sylvatica* Marsh.) from bottomland seed sources had better survival and greater biomass than seedlings from upland sources. Later, Anella and Whitlow (1999) found that flooding red maple (*Acer rubrum* L.) for 28 days decreased net photosynthesis and growth of seedlings from upland seed sources more than from bottomland seed sources. Subsequently, Baurele and others (2003) showed that red maple has distinct ecotypes based on their response to flooding.

OBJECTIVES

The objectives of this study were to determine if collecting acorns from bottomland and upland stands affects seedling growth before, during, and following flooding and to determine the extent of seedling variation that exists among half-sib families of swamp white, bur, and white oak (*Q. alba* L.). Primarily, we wanted to determine if acorns collected from upland stands produce seedlings that are maladapted for planting on bottomland sites subject to flooding and if sufficient variation for flood tolerance exists within native populations to initiate breeding programs to produce improved oak planting stock for restoration of bottomland forests.

MATERIALS AND METHODS

From 15 September through 31 October 2005, acorns were collected from 10 swamp white oak, eight bur oak, and six white oak trees in central Missouri (Table 1). Each mother tree was assigned to either an upland or bottomland topographic position based on landscape position, soil series, drainage class, and flood frequency from information available at http://cares.missouri.edu website. Upland collection sites were typically on shoulder to summit slope positions that had not experienced any known flooding. Bottomland collection sites had experienced flooding either as short-duration flash-flooding or long-duration flooding such as in the Midwest floods of 1993 and 1995. Acorns from individual tree collections were stored in a walk-in cooler at 4 ^{o}C in 4-L plastic zipper bags punched with holes for air exchange.

On 28 November 2005, germinating acorns of each half-sib white oak family were placed on separate 40 x 40 x 13-cm deep polypropylene propagation flats with open lattice bottoms (Anderson Die and Manufacturing Co., Portland, OR). Trays were filled with a soil-less horticultural potting mix (10:4:4:1:1 by volume of pine bark, peat moss, vermiculite, perlite, and sand, respectively, amended with 0.5 L m^{-3} slow-release NH_4NO_3, urea, and micronutrients). Emerging radicals were placed into the potting medium and acorns covered. Flats were enclosed in polyethylene bags and set in the walk-in cooler at 4 ^{o}C until 16 February 2006.

On 13 February 2006, acorns of bur and swamp white oak were removed from cold storage, soaked in cold tap-water for 48 hours, and then float-tested. Twenty-five acorns of each half-sib family that did not float were measured for length and width to determine acorn volume (Rink and Coggeshall 1995). Remaining acorns were placed by families on separate propagation flats filled with the above potting mix.

Table 1.—Site characteristics, mother tree d.b.h., and mean acorn volume for the 24 half-sib families of the three oak species evaluated for initial seedling growth and flood tolerance

Species[1]	Topo-graphic position	Family name[2]	DBH (cm)	Acorn vol. (cm^3)	Slope position	Soil series[3]	Drain class[4]	Flooding frequency[5]
WHO	Upland	BN12W	79	----	Summit	Keswick SL	MWD	None
WHO	Upland	BN21W	61	----	Shoulder	Jamerson SL	WD	None
WHO	Upland	BN23W	122	----	Summit	Armstrong L	SPD	None
WHO	Upland	OS12W	46	----	Summit	Gravois L	MWD	None
WHO	Bottom	CO11W	102	----	Floodplain	Moniteau SL	VPD	Occasional*
WHO	Bottom	CO12W	114	----	Floodplain	Moniteau SL	VPD	Occasional*
BRO	Upland	AD11B	76	8.4	Shoulder	Gara L	MWD	None
BRO	Upland	BN11B	36	11.2	Shoulder	Weller SL	WD	None
BRO	Upland	BN12B	66	12.4	Shoulder	Weller SL	WD	None
BRO	Upland	SH11B	69	13.2	Foot slope	Viration GSL	WD	None
BRO	Bottom	BN21B	234	13.8	Floodplain	Darwin SCL	VPD	Occasional*
BRO	Bottom	BN31B	165	16.2	Floodplain	Haymond SL	MWD	Frequently
BRO	Bottom	CA11B	102	12.1	Floodplain	Belknap SL	SPD	Frequently
BRO	Bottom	HW11B	152	14.4	Floodplain	Hayne SL	SPD	Occasional*
SWO	Upland	AD12S	56	3.9	Shoulder	Gara L	MWD	None
SWO	Upland	AD14S	58	3.5	Shoulder	Gara L	MWD	None
SWO	Upland	BN22S	43	4.9	Summit	Weller SL	MWD	None
SWO	Upland	CA21S	76	3.5	Summit	Mexico SL	SPD	None
SWO	Upland	CA22S	81	4.4	Summit	Mexico SL	SPD	None
SWO	Bottom	BN12S	91	5.0	Floodplain	Perche L	VPD	Frequently
SWO	Bottom	BN13S	81	5.3	Floodplain	Perche L	VPD	Frequently
SWO	Bottom	CO11S	137	5.5	Floodplain	Moniteau SL	VPD	Occasional*
SWO	Bottom	PK11S	122	3.9	Terrace	Okaw SL	VPD	Rarely*
SWO	Bottom	PK21S	53	4.6	Floodplain	Twomile SL	VPD	Occasional*

[1]WHO=white oak, BRO = bur oak, SWO = swamp white oak.
[2]Family names indicate county, stand, tree number within stand, and species where AD = Adair, BN = Boone, CA = Callaway, CO = Cole, HW = Howard, OS = Osage, PK = Pike, and SH = Shannon County.
[3]Soil abbreviations: L = loam, S = silt, C= clay, and G = gravelly
[4]Drainage classes: VPD = very poorly drained, SPD = somewhat poorly drained, MWD = moderately well drained, and WD = well drained.
[5]An asterisk indicates the tree was partially inundated in 1993 and/or 1995.

On 16 February 2006, all propagation flats were placed on wire-mesh benches in a heated greenhouse maintained at 23 °C transmitting 50 to 60 percent of full sunlight without supplemental lighting. On 20 March 2006, one-flush air-root pruned seedlings were transplanted into individual 24-cm tall, 1.65-L slotted bottom treepots (Stuewe and Sons, Inc., Corvallis, OR) filled with the above potting mix and allowed to grow a second flush. On 10 May 2006, seedlings were moved to a large shade house covered with 50 percent shade cloth to acclimate to ambient summer temperatures and natural light.

Beginning on 29 May 2006, seedlings were flooded for 0, 4, or 8 weeks. Three individually tagged seedlings of each half-sib family had been placed in one of twelve 1,126-L galvanized stock tanks housed in the above shade house. Seedlings of each species were kept together, with the white oak seedlings located at either end of the tank to reduce shading by the taller bur and swamp white oak seedlings. The three seedlings for each family were randomly placed within a species block regardless of topographic acorn origin. Flooded seedlings were partially inundated to a depth of 5 cm above the potting mix.

Flood water was replenished twice a week using water under pressure pumped from an on-site catchment pond. During post-flood recovery, water was drained from the stock tank and seedlings watered as needed until harvested using the same source of water. No attempt was made to control water temperature; however, the study was done under black polyethylene shade cloth to reduce heating of the flood water. We used 50 percent shade cloth assuming a light compensation point of less than 50 percent of full sunlight for seedlings of all three oak species based on previous research with other oak species (Kozlowski 1949, Ponton and others 2002).

Data on survival, number of flushes, height above the soil line, basal diameter at 2.5 cm above the soil line, and occurrence of hypertrophied lenticels were determined at the initiation of flooding treatments (29 May 2006), termination of the 4-week flood (26 June 2006), termination of the 8-week flood (24 July 2006), and post-flood recovery (21 August 2006). At the end of the growing season (2 October 2006), seedlings were destructively sampled to determine number and area (LI-3000, Li-Cor Inc., Lincoln, NE) of leaves by flush, leaf and stem weight by flush, and root dry weight in addition to previous measurements. Five seedlings of each half-sib family were also destructively sampled on 29 May 2006 for pre-flood measurements.

Analysis of variance using PROC GLM (SAS Institute, Inc., Cary, NC) was used to determine if differences existed due to flooding, species, position within species, family within position, and their interactions. The experimental design was a randomized complete block for a split, split-plot design with four replications of three flood treatments as main plots, three species as sub-plots, and two to five half-sib families within the two topographic positions as sub-sub-plots. Family means were calculated from three seedlings for each combination of block and flood treatment before testing for normality using PROC UNIVARIATE. Duncan's new multiple range test was used for mean separations of main effects with statistical differences at alpha = 0.05 percent. Fisher's unprotected least significant difference was calculated from appropriate error mean squares and t-values to evaluate interaction with statistical differences for alpha = 0.01 percent. When family means for count or percentage data were not normally distributed, a Chi-square analysis was used to test for differences.

RESULTS

Seedling survival was high for all three species with no mortality in the non-flooded control. Approximately 1 percent (11 of 864) of the seedlings partially inundated for 4 weeks died. Less than 1 percent of bur and swamp white oak seedlings (5 of 648) and 11 percent of the white oak seedlings (24 of 216) died when flooded for 8 weeks. Survival of white oak from bottomland seed sources was greater than survival from upland seed sources, with the highest mortality in upland families OS12W and BN21W ($X^2 = 44.57$, $p < 0.001$).

Differences existed among species and position within species for stem length before flooding (Fig. 1). The two-flush swamp white and bur oak seedlings grown from the bottomland seed families produced longer flushes than seedlings from the upland families ($p < 0.001$). In contrast, the white oak seedlings from the four upland families produced longer second flushes than did seedlings from the two bottomland families. Differences ($p < 0.001$) existed among families within all positions within species except for the five families within the swamp white oak upland sources (Walsh 2007).

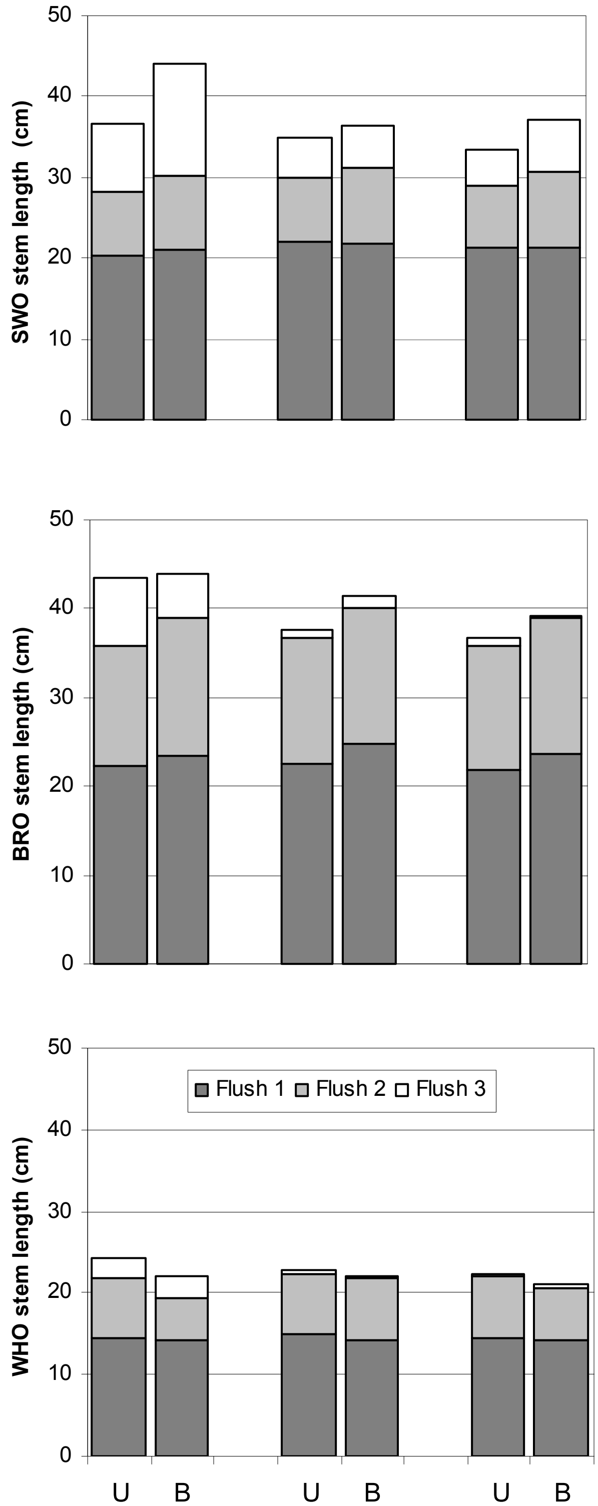

Figure 1.—Preflood stem length (flush 1 + 2) and post-flood new shoot growth (flush 3) for white oak (WHO), bur oak (BRO), and swamp white oak (SWO) seedlings produced from upland (U) and bottomland (B) natural stands subjected to mid-season flooding for 0, 4, and 8 weeks.

Following initiation of flooding and during post-flood recovery, new shoot growth, shown as stem length for the third flush in Figure 1, declined for all three oak species with increasing duration of flooding. Data for length of the third flush were calculated as the mean for all seedlings without deleting those that failed to initiate a third flush. Following initiation of the mid-season flooding treatment, only 13, 20, and 43 percent of the white, bur, and swamp white oak seedlings, respectively, flushed or increased in height (table 2). The percentage of seedlings with new shoot growth following initiation of flood treatments was

Table 2.—Percentage of seedlings producing new shoot growth following initiation of flood treatments that originated from upland and bottomland seed sources of white, bur, and swamp white oak

Oak species	Topographic position	Flood duration			Pos. mean
		0-wk	4-wk	8-wk	
White oak	Upland	21	13	12	15
	Bottomland	21	4	8	11
Bur oak	Upland	50	8	21	26
	Bottomland	25	10	8	14
Swamp white	Upland	55	32	28	38
	Bottomland	68	28	48	48
Weighted means		43	18	23	

greater within the control treatment than in both the 4-week and 8-week flood treatments (43, 18, and 23 percent, respectively). A higher percentage of swamp white oak seedlings from bottomland seed sources flushed versus upland seed sources (48 verses 38 percent, $X^2 = 47.41$, $p < 0.001$). In contrast, a higher percentage of bur oak seedlings from upland seed sources flushed compared to bottomland seed sources (17 versus 14 percent, $X^2 = 21.13$, $p < 0.001$). The lack of a third flush and no new height growth on most seedlings following initiation of flood treatments precluded analyses for differences among families within position within species.

Before initiation of the flood treatments, the two-flush seedlings from bottomland seed sources of both bur and swamp white oak had greater stem basal diameter ($p < 0.001$) than seedlings from upland seed sources (shown as 0 DAT [0 days after initiation of flood treatments] in Fig. 2). In contrast, seedlings of white oak from upland sources had greater stem diameter than seedlings from bottomland sources. Differences ($p < 0.001$) existed in basal stem diameter of two-flush seedlings among families within all positions within species except for the five families within the swamp white oak upland sources (Walsh 2007).

During the 28 days after the flooding treatments were initiated, the basal diameter growth for flooded seedlings of white oak from both upland and bottomland sources slowed by more than 50 percent compared to the non-flooded controls (28 DAT in Fig. 2). Post-flood diameter growth rates for white oak seedlings flooded for 4 weeks appeared to recover while growth rates of seedlings flooded for 8 weeks did not, especially for seedlings from the two bottomland seed sources.

Seedlings of both bur and swamp white oak had greater basal diameter growth while flooded ($p < 0.001$) than did the seedlings in the non-flooded control (28 DAT in figure 2). Although 75 percent of the surviving flooded white oak seedlings produced hypertrophied lenticels, these seedlings did not show greater diameter growth than the non-flooded control seedlings, which was in contrast to what was observed with bur and swamp white oak seedlings ($p = 0.006$). At the end of the growing season, basal diameter of bur and swamp white oak seedlings from the bottomland seed sources were larger than seedling basal diameters for upland seed sources ($p < 0.001$). The interaction for flood treatment x family within position within species ($p = 0.008$) is largely explained by one bottomland bur oak family (HW11B) that put on greater than 3 mm of new diameter growth on more than 75 percent of its seedlings that were flooded. At the end of the study, differences ($p < 0.001$) existed in seedling basal stem diameters among families within all positions within species (Walsh 2007).

At the end of the growing season, seedling root and stem dry weight, but not leaf dry weight, had a highly significant flood x species interaction ($p = 0.012$, <0.001, and $= 0.692$, respectively). Root and stem dry weights of swamp white seedlings were less affected by duration of flooding than were root and shoot dry weight of white oak and bur seedlings, both of which showed marked declines with increasing duration of flooding (Fig. 3). Mean root dry weight of white oak seedlings inundated for 8 weeks was less than that for the seedlings destructively sampled when flood treatments were initiated (3.6 versus 5.0 g, respectively). Tang and Kozlowski (1982) also found partial inundation of 4-week-old bur oak seedlings for 4 weeks reduced plant dry weight, especially root dry weight.

A flood x position within species effect was not found for root, stem, or leaf biomass ($p = 0.177$, 0.276, and 0.224, respectively); however, a position within species was found for these variables ($p <0.001$, <0.001, and $= 0.009$, respectively). As was found with the variables described earlier, root biomass and stem biomass of white oak seedlings from upland seed sources were larger than those of seedlings from bottomland sources (Fig. 3). For bur oak, the position within species effect was most evident for root biomass, where seedlings from bottomland seed sources had larger root biomass compared to seedlings from upland seed sources. With swamp white oak, there was no pronounced position within species effect for root, stem, or leaf biomass.

DISCUSSION AND CONCLUSIONS

Percent seedling survival was high for all three oak species treated with 0, 4, and 8 weeks of partial inundation of container-grown seedlings in a well drained soil-less potting mix. Based on previous results with bare-root white oak seedlings in riparian soils (Kabrick and others 2007), we expected few if any white oak seedlings would survive 8 weeks in water-saturated soils. In this study, we did not measure dissolved oxygen within the stagnant flood water or redox potential of the soil-less potting mix; however, in a separate laboratory study, the redox potential after 1 week of flooding was higher in the soil-less potting mix than in the riparian topsoil taken from the Flood Tolerance Laboratory (150 to 200 versus 50 to 100 mV, respectively). Likewise, dissolved oxygen measured near the surface of the soil-less potting medium averaged 60 to 80 percent, compared to less than 5 percent in riparian topsoil. Several factors besides the potting mix may have contributed to a higher than expected dissolved oxygen content. The frequent replenishing of stagnant flood waters using water under pressure may have also helped replenish dissolved oxygen. Because studies were done in a shade house, flooded tanks were also exposed to rain events, which have also been shown to replenish dissolved oxygen (Broadfoot 1967, Van Sambeek and others 2007). Finally, the shade cloth covering the shade house kept flood waters cooler than had been found with exposed stock tanks and may have reduced oxygen demand for root respiration.

Several observations confirm that the flood treatments were effective. Although less than half of the seedlings grew a third flush after flood treatments were initiated, flooding did decrease numbers of seedlings that flushed when flooded or during post-flood recovery. Flooded seedlings of bur and swamp white oak produced greater basal diameter growth than the control seedlings. Gardiner and others (1993) also reported greater basal diameter growth on two of four southern oak species when partially inundated. No studies were done to determine if the increased basal diameter growth for flooded bur and swamp white oak seedlings was due to increased production of xylem, hypertrophied lenticels, or aerenchyma; however, Gardiner (2001) indicated southern bottomland oaks, including white oak, do not appear to be equipped to develop aerenchyma tissue. Although no seedlings produced adventitious roots, flooded seedlings of all three species produced hypertrophied lenticels. Tang and Kozlowski (1982) reported both hypertrophied

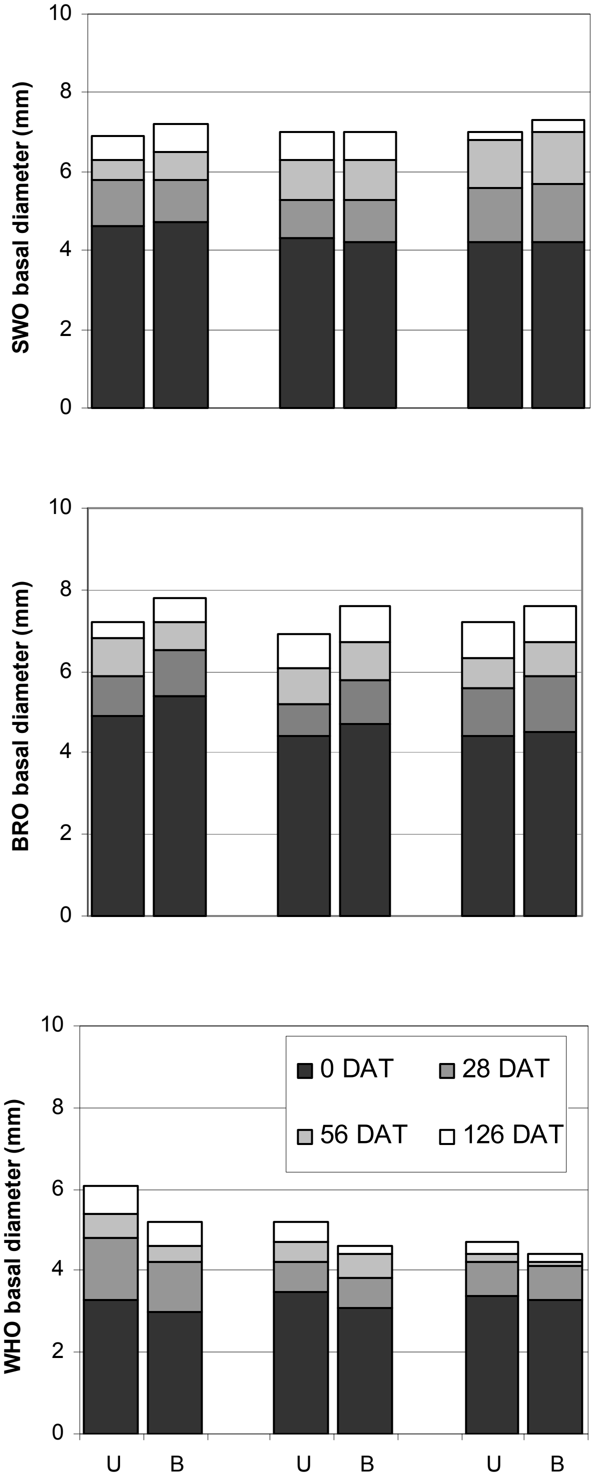

Figure 2.—Seedling basal diameter for white (WHO), bur (BRO), and swamp white oak (SWO) produced from upland (U) and bottomland (B) acorn sources 0, 28, 56, and 126 days after initiation of flooding (DAT) for 0, 4, and 8 weeks.

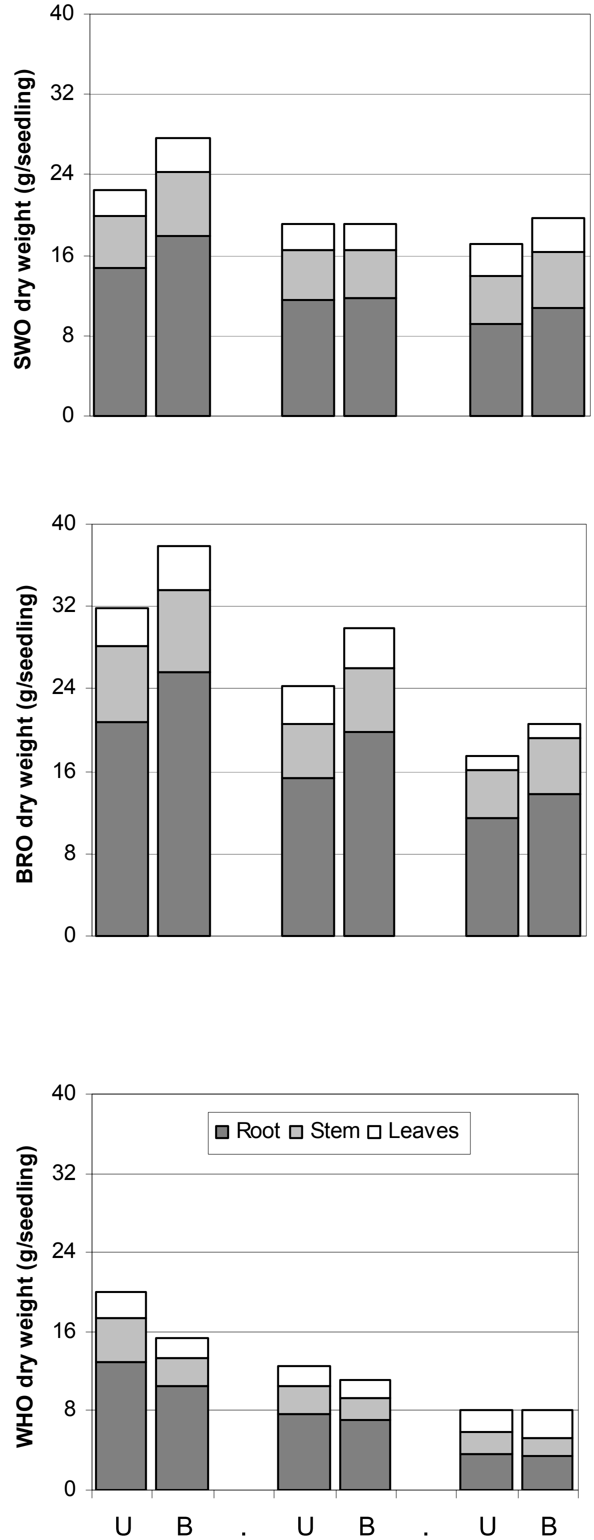

Figure 3.—Mean seedling root, stem, and leaf dry weight for white, bur, and swamp white oak grown from upland and bottomland acorn sources and flooded in mid-season for 0, 4, or 8 weeks.

lenticels and adventitious roots on bur oak seedlings flooded for 4 weeks. In addition, seedling root biomass at the end of the growing season for white oak flooded for 8 weeks was less than that for white oak seedlings when flood treatments were initiated.

Basal diameter growth and seedling biomass for white oak declined with increasing flood duration. In contrast, seedling growth and biomass of swamp white oak were largely unaffected by 4 or 8 weeks of partial inundation. For bur oak seedlings, basal diameter was largely unaffected; however, new shoot growth and biomass decreased with increasing flood duration. The relative rankings for flood tolerance of swamp white oak > bur oak > white oak in our study is similar to that reported by Kabrick and Dey (2001), but is not supported by the species rankings reported earlier by Bell and Johnson (1974), Whitlow and Harris (1979), or Allen and others (2001).

All three species had highly significant differences among families within position within species for most variables, suggesting excellent opportunities exist for selection and genetic improvement for flood tolerance. Results also suggest collection of acorns from bottomland stands of bur and swamp white oak are likely to produce better seedlings for bottomland restorations than seedlings from acorns collected from upland stands.

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