Articles

Early Growing Season Flooding Influence on Seedlings of Three Common Bottomland Hardwood Species in Western Tennessee

Jonathan R. McCurry, Matthew J. Gray,* David C. Mercker

J.R. McCurry, M.J. Gray
University of Tennessee Wetlands Program, Department of Forestry, Wildlife and Fisheries, 274 Ellington Plant Sciences Building, Knoxville, 37996

D.C. Mercker
University of Tennessee, West Tennessee Research and Education Center, 605 Airways Boulevard, Jackson, 38301

Abstract

Understanding relative flood tolerance of hardwood bottomland seedlings is fundamental to restoring floodplain ecosystems. Thus, we quantified the effects of three early growing season flood duration (0, 15, and 30 d) treatments on survival and growth of overcup *Quercus lyrata*, Nuttall *Q. nuttallii*, and willow *Q. phellos* oak seedlings. Seedlings (n = 5,003) were planted January–March 2004 in a randomized design among six impoundments in a western Tennessee bottomland. We flooded four impoundments (two 15-d and two 30-d treatments) after seedling bud break initiated in April 2005 and 2006 to simulate overbank flooding of a river. Overall seedling survival measured in July and October 2005 and July 2006 was 96, 89, and 84% overcup, Nuttall, and willow, respectively. Survival of Nuttall and willow was greatest in unflooded control impoundments. All species exhibited the least growth in the 30-d treatment. Growth of Nuttall and willow were generally greater in the 15-d treatment than in the control treatment. We ranked relative seedling flood tolerance as decreasing from overcup to Nuttall to willow, which corresponds with previous greenhouse studies. We recommend that natural resource practitioners plant overcup at low elevations in bottomlands that flood frequently, plant Nuttall at mid-range elevations, and plant willow exclusively at higher elevations that flood infrequently to increase the likelihood of restoration success.

Keywords: bottomlands; restoration; wetlands; oak; forestry; flooding

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* Corresponding author: mgray11@utk.edu

Introduction

Hardwood bottomland ecosystems are forested wetlands adjacent to riverine systems that are important sites for timber production, floodwater storage, and nutrient cycling (Mitsch and Gosselink 2000). These wetlands also provide habitat for various fish and wildlife species (Langdon et al. 1981; Wharton et al. 1981). Most of the hardwood bottomlands in the southeastern United States have been drained or deforested (Turner et al. 1981). Tennessee has lost almost 60% of its wetlands, most of which were hardwood bottomlands (Turner et al. 1981; Johnson 2007). Drainage of forested wetlands was encouraged from the late 1800s through the 1970s for agriculture and other human land-use developments (MacDonald et al. 1979).

The Clean Water Act of 1975 authorized protection of floodplain wetlands. In the mid-1980s and early 1990s, successive legislation entitled the ''Farm Bills'' created several conservation programs (e.g., Conservation Reserve Program; Wetland Reserve Program) that provided funds to landowners to restore wetlands that were previously farmed (Stanturf et al. 2001). In Tennessee, most wetland restoration efforts have focused on hardwood bottomlands (Johnson 2007). Often these areas are replanted with oak seedlings but very little information is available on which oak species should be planted in Tennessee given the hydrology at a restoration site. Some oak species are more flood-tolerant; thus, these species may be more ideal to plant at a site if flooding during the growing season is common (King et al. 1998).

Greenhouse and uncontrolled field studies in forested wetlands indicate that flood tolerance differs among bottomland

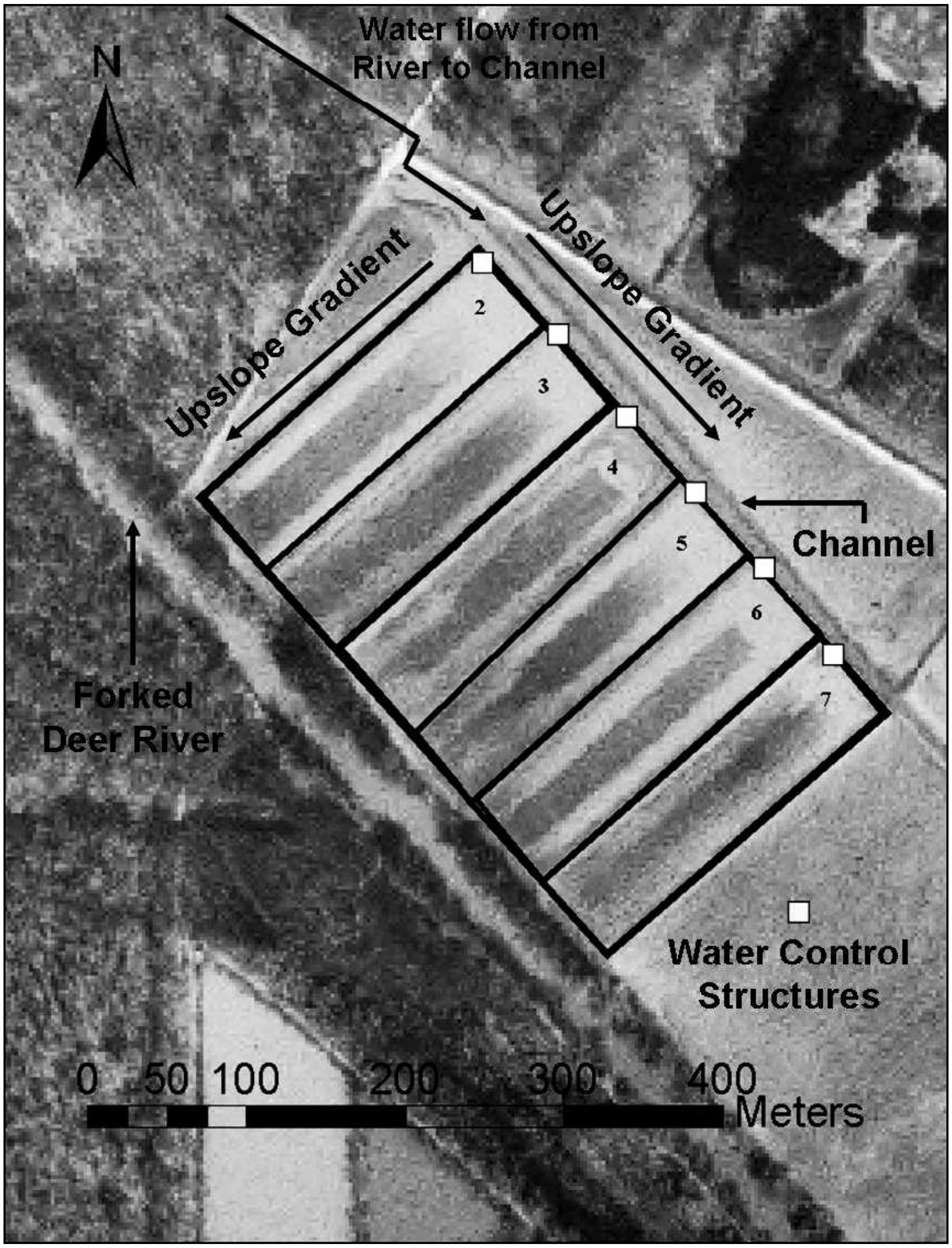

Figure 1. Impoundments 2–7 at the West Tennessee Research and Education Center, Jackson, Tennessee.

oak seedlings (Broadfoot and Williston 1973; Hook 1984; Gray and Kaminski 2005; McCurry et al. 2006). Willow *Quercus phellos*, Nuttall *Q. nuttallii*, and overcup *Q. lyrata* oak seedlings are commonly planted in hardwood bottomlands in the southeastern United States. However, no controlled field studies have been performed examining the relative flood tolerance for seedlings of these species. Thus, our objective was to test for differences in survival and growth of willow, Nuttall, and overcup oak seedlings exposed in the field to different growing season flood treatments. Based on lab studies, we hypothesized that seedling flood tolerance would decrease in the order of overcup oak, Nuttall oak, and willow oak.

Study Site

We conducted our study in a 6-ha bottomland at the University of Tennessee West Tennessee Research and Education Center (WTREC) located in Jackson, Tennessee (35°37′37″N, 88°51′36″W, 120 m mean elevation). The WTREC bottomland contained six 1-ha impoundments (numbered 2–7) with 1-m–high levees that contained drop-board water control structures at their lower end, which connected to a drainage channel (Figure 1). The impoundments differed predictably in elevation, with the gradient sloping upward from 2 to 7 and northeast to southwest (Figure 1; McCurry et al. [2006]). Existing surface and groundwater hydrology was a consequence of localized rainfall, runoff, and water levels in the adjacent channelized South Fork of the Forked Deer River. At high water levels, the river backed into the drainage channel that extended into the bottomland, and flowed through the water control structures into the impoundments (Figure 1). Water flow into and out of the bottomland could be stopped by placing gates in the water control structures or by closing screw gates in the channel. The predominant soil type was Waverly silt loam (Sease and Springer 1957). Prior to the study, the site was used for row-crop agriculture for over 40 y.

Methods

We planted seedlings of Nuttall, overcup, and willow oaks in monospecific plots with 3 × 3 m spacing in six 36 × 36 m elevation blocks per impoundment (Figure 2). We experimentally divided impoundments into low and high ends to randomly assign species to elevation blocks. Within each impoundment and end, we randomly assigned seedling species to each elevation block without replacement, thereby ensuring that a species was not clustered at low or high elevations. We planted approximately 144 seedlings per elevation block, although portions of some blocks in impoundments 5, 6, and 7 could not be planted because of a natural gas pipeline. Also, water oak *Q. nigra* was planted instead of overcup oak in impoundments 6 and 7; thus, overcup oak was replicated in only two of the flooding treatments (discussed below). We did not include water oak in the analyses because it was replicated in the control treatment only.

We acquired all seedlings (1–0 stock) from the Tennessee Division of Forestry State Nursery, and stored them at 4°C in a walk-in cooler at WTREC until planted. To standardize planting conditions, 1-m–width rows were subsoiled at 36-cm depth along planting locations. We planted seedlings during January–March 2004 using a Whitfield® Tree Planter (R. A. Whitfield Manufacturing, Mableton, GA), which is designed specifically for planting hardwood seedlings. At the time of planting, all seedlings within species appeared in similar physical condition, and individuals of each species were planted randomly within elevation blocks. Due to this designed randomization, we assumed that all seedling response variables were not correlated with elevation and no differences existed in these variables among impoundments (i.e., treatments) at the time of planting. We individually marked all seedlings ($n = 5{,}003$) with numbered metal tags in October 2004.

Pairs of impoundments were assigned the following early growing season flood treatments: control (0-d), 15-d, and 30-d. These treatments corresponded to flood duration in controlled greenhouse experiments (e.g., Hosner and Boyce 1962). Impoundments 2 and 3 = 30 d, 4 and 5 = 15 d, and 6 and 7 = 0 d. Flooding consisted of the presence of surface water and not the complete inundation of seedlings. We flooded impoundments starting 18 April 2005 and 17 April 2006 after seedlings initiated bud break. Water was pumped from the adjacent channel into impoundments 2–5 using a Gator® pump (Gator Pump Inc., Brownwood, TX). We maintained water depth in impoundments by placing gates in the water control structures for the treatment duration. We did not flood or place gates in the water control structures for impoundments 6 and 7, because they served as experimental controls. After 15 and 30 d of flooding, we removed gates from impoundments 4–5 and 2–3, respectively. Impoundments drained in <3 d. After impoundments were drained, we did not replace boards (and screw gates in the channel remained open), to allow all impoundments to experience unrestricted hydrology. To measure surface and groundwater hydrology in impoundments during natural and prescribed flooding, we installed PVC wells and water-level recorders (Infinities USA Inc., Port Orange, FL) in the center of the 12 elevation blocks (Figure 2), and programmed them to measure water depths twice daily. To characterize hydrology in the WTREC bottomland during our study, we calculated flooding frequency, depth and duration by averaging readings from the four wells in each treatment.

We determined seedling survival in July and October 2005 and July 2006. A seedling was considered dead if leaves were not present and its cambium was not green (determined by scraping a small section of the bark). We measured seedling height and diameter in October 2004, 2005, and 2006, and calculated second- and third-year growth as the difference between October 2004–2005 and 2005–2006 measurements, respectively. Seedling height was measured to the nearest 0.5 cm from the ground to the terminal bud using a meter stick. Root-collar diameter was measured to the nearest 0.5 mm at ground level using calipers.

We designated seedlings as experimental units for analyses. Given that seedlings were planted within impoundments, they may be considered pseudoreplicates of flooding treatments (Hurlbert 1984). Pseudoreplication in bottomland studies that involve large-scale flooding treatments is common (e.g., Gray and Kaminski 2005). Thus, we caution readers that our results may be limited to the WTREC bottomland.

McCurry et al. (2006) ranked the elevation of each 36 × 36 m block where seedlings were planted (Figure 2), and reported that elevation influenced first-year growth of oak seedlings in the WTREC bottomland due to differences in flood duration and depth. Groundwater also was correlated with elevation, and ranged 0–1 m belowground for >75% of the annual cycle (McCurry 2006). Thus, we used ranked elevation for each block according to Figure 2 as a covariate in all statistical analyses. We used logistic regression to test for differences ($\alpha = 0.05$) in survival among flood treatments and species (Stokes et al. 2000). When the main-effect chi-square tests associated with logistic regressions were significant, we used large-sample *Z*-tests for two proportions that were Bonferroni-corrected ($\alpha = 0.017$) for pair-wise comparison of percent survival between treatments (Milton and Arnold 1995). We used an analysis of variance (ANOVA) to test for differences ($\alpha = 0.05$) in height and diameter growth among treatments and species. In all cases, species and treatment effects interacted; thus, analyses were performed by species. Ryan's-Q multiple-comparison test was used for pair-wise treatment comparisons when the overall ANOVA was significant (Westfall et al. 1999). We used the SAS® system v.9.1 and Minitab® v.14 for all analyses.

Results

Flooding in impoundments was a consequence of natural and prescribed flooding, and was related with elevation. Flooding in the 30-d treatment impoundments occurred on average 12.75 times from 17 April 2005 to 9 July 2006 for 103.3 d at a mean depth of 28.21 cm (Table 1). In the 15-d impoundments, flooding occurred on average 12.5 times during the same dates for 77.4 d at a mean depth of 31.04 cm. Flooding occurred only 6.5 times on average for 23.5 d at a mean depth of 23.05 cm in the control impoundments (Table 1).

Across all flood treatments and sample periods, survival was 96, 89, and 84% for overcup *Q. lyrata*, Nuttall *Q. nuttallii*, and willow *Q. phellos*, respectively. In July 2005, survival of willow *Q. phellos* was 8–9% greater in the control than in the 15-d and 30-d treatments ($\chi^2_2 = 21.2$, $P < 0.001$; Table 2). Survival of Nuttall *Q. nuttallii* in July 2005 was 4% greater in the control than in the

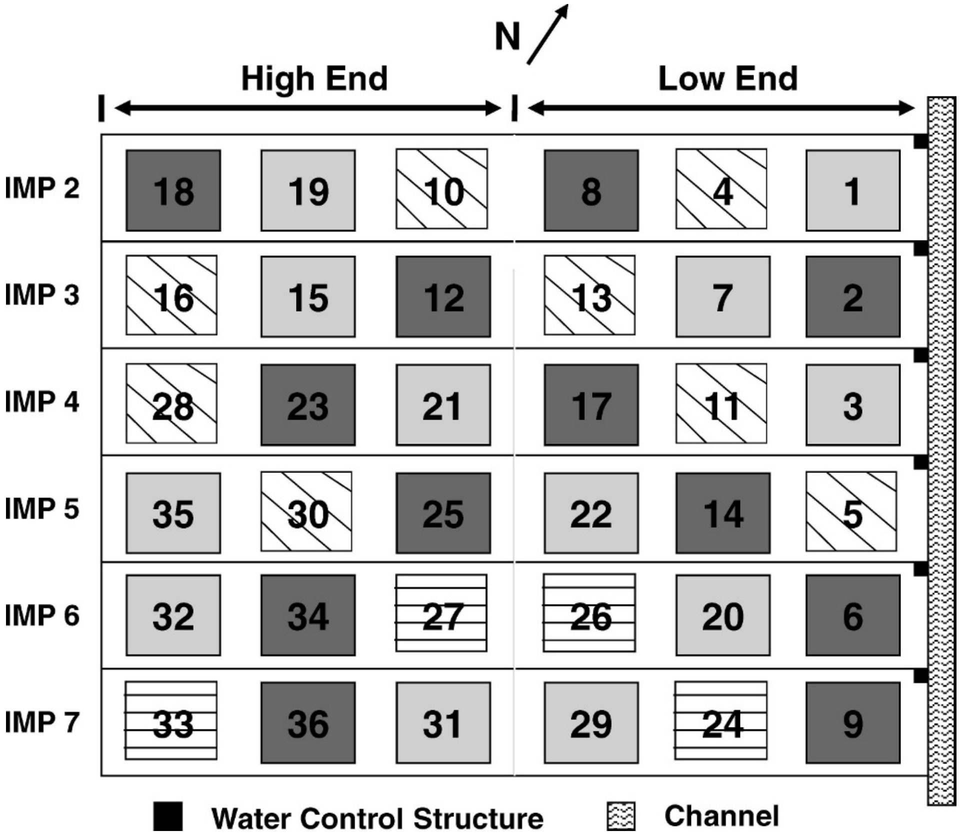

Figure 2. Planting and elevation schematic of hardwood bottomland seedlings in six impoundments (IMP 2–7) in a western Tennessee bottomland. Elevation increased according to ordinal ranking of blocks (McCurry et al. 2006). Willow oak *Quercus phellos* = dark gray, Nuttall oak *Q. nuttallii* = light gray, overcup oak *Q. lyrata* = diagonal hatching, and water oak *Q. nigra* = horizontal hatching. Blocks 4, 7, 11, 14, 15, 19, 20, 23, 24, 30, 34, and 36 contained water-level meters.

15-d treatment ($\chi^2_2 = 6.3$, $P = 0.04$). No differences among treatments were detected for willow *Q. phellos* or Nuttall *Q. nuttallii* during other sample periods or for overcup *Q. lyrata* during all sample periods ($\chi^2_2 < 0.6$, $P > 0.19$; Table 2). The covariate (bottomland elevation) explained significant variation in percent survival of Nuttall *Q. nuttallii* and willow *Q. phellos* in October 2005 and overcup *Q. lyrata* and Nuttall *Q. nuttallii* in July 2005 ($\chi^2_1 > 4.1$, $P < 0.04$).

Overcup oak survival was 7–12% greater than Nuttall *Q. nuttallii* and willow *Q. phellos* in the 15-d and 30-d treatments in July 2005 ($\chi^2_2 > 42.4$, $P < 0.001$; Table 2). Survival of overcup *Q. lyrata* was about 3% greater than Nuttall *Q. nuttallii* and willow *Q. phellos* in the 30-d treatment in October 2005 ($\chi^2_2 = 13.8$, $P = 0.001$). In July 2006, survival of overcup *Q. lyrata* and Nuttall *Q. nuttallii* was 2.1% greater than willow *Q. phellos* in the 15-d treatment, and Nuttall *Q. nuttallii* was 1.3% greater than willow *Q. phellos* in the control ($\chi^2_1 > 4.5$, $P < 0.03$; Table 2). No other differences in survival among species were detected. Bottomland elevation explained significant variation in percent survival in the 15-d treatment during all sample periods and in the 30-d treatment in October and July 2005 ($\chi^2_1 > 6.2$, $P < 0.01$).

Differences in mean height growth during the second and third growing seasons existed among treatments for nearly all species ($F_{2,1246} > 26.4$, $P < 0.001$; Table 3). Height growth was lowest for all species in the 30-d treatment in 2005 and 2006, greatest in the 15-d for all species in 2006, and greatest in the control for willow *Q. phellos* in 2005. Differences also existed in mean diameter growth among treatments ($F_{1,1235} > 39.8$, $P < 0.001$; Table 3). Diameter growth was lowest in the 30-d treatment for all species in 2005 and 2006 and greatest for Nuttall *Q. nuttallii* in the 15-d treatment in 2006; no other differences among treatments were detected. Bottomland elevation explained significant variation in height growth for Nuttall *Q. nuttallii* and willow *Q. phellos* and diameter growth for all species in 2005 ($F_{1,1259} > 3.2$, $P < 0.02$). In 2006, bottomland elevation explained significant variation in height and diameter growth across all species ($F_{3,1246} > 3.7$, $P < 0.01$).

Discussion

Overall survival was 96, 89, and 84% for overcup *Q. lyrata*, Nuttall *Q. nuttallii*, and willow *Q. phellos*, respectively. Early growing season flooding for 30 d negatively affected the survival of Nuttall *Q. nuttallii* in 2005 and willow *Q. phellos* both years. Overcup oak survival was not influenced by flooding treatments. Also, Nuttall *Q. nuttallii* and overcup *Q. lyrata* survival usually was greater than willow *Q. phellos* for all treatments. Our survival results support findings from previous field studies. Gray and Kaminski (2005) found that overcup *Q. lyrata* seedlings had 10% greater survival than willow *Q. phellos* seedlings in a Mississippi hardwood bottomland that was continuously flooded during winter. Day et al. (1998) reported that spring flooding significantly decreased the survival of Nuttall *Q. nuttallii* and willow *Q. phellos* seedlings in the Mississippi Delta, and Nuttall *Q. nuttallii* survival was greater than willow *Q. phellos*. Further, McLeod et al. (2000) found that

Table 1. Flooding duration, frequency, and depth in a replanted western Tennessee bottomland, 2005 and 2006.

Treatment[a]	Flooding period[b]	Duration (d) $\bar{x}$	Duration (d) SE	Frequency $\bar{x}$	Frequency SE	Depth (cm) $\bar{x}$	Depth (cm) SE
Control	Treatment 2005	0	0	0	0	0	0
	Treatment 2006	0	0	0	0	0	0
	Nontreatment	22.63	1.71	6.00	0.71	23.58	1.07
	Total	23.50	1.74	6.50	0.65	23.05	1.05
15-d	Treatment 2005	14.9	0.13	1.00	0.00	21.74	0.59
	Treatment 2006	15.0	0.35	1.00	0.00	21.62	0.79
	Nontreatment	47.63	3.21	10.50	0.50	36.84	1.28
	Total	77.38	3.49	12.50	0.50	31.04	0.86
30-d	Treatment 2005	26.3	2.37	1.00	0.00	22.09	0.79
	Treatment 2006	23.13	4.51	1.00	0.00	20.13	0.77
	Nontreatment	54.0	9.35	10.75	0.63	34.60	1.22
	Total	103.3	14.56	12.75	0.63	28.21	0.73

[a] Flooding treatments constituted soil inundation for 0 (control), 15 (15-d), and 30 (30-d) days.
[b] Flooding periods when treatments were applied were 18 April–20 May 2005 (Treatment 2005) and 17 April–19 May 2006 (Treatment 2006), when treatments were not applied were 21 May 2005–18 April 2006 and 20 May–9 July 2006 (Nontreatment), and for the entire study period was 17 April 2005–9 July 2006 (Total).

overcup *Q. lyrata* seedlings had greater survival than Nuttall *Q. nuttallii* and willow *Q. phellos* over a 3-y period in South Carolina bottomlands that periodically flooded during the growing season and winter.

Extended early growing season flooding may have negatively influenced survival of Nuttall *Q. nuttallii* and willow *Q. phellos* by creating anoxic conditions in the soil and negatively affecting seedling physiology. When soils are flooded, available oxygen in the soil is quickly used by respiring roots and microorganisms (Kozlowski 1984). Reduction of oxygen in the soil decreases aerobic metabolism, ultimately decreasing photosynthetic rates, carbohydrate synthesis, and ion absorption, which can negatively affect survival of seedlings (Kozlowski and Pallardy 1984).

Table 2. Survival of overcup *Quercus lyrata* (OCO), Nuttall *Q. nuttallii* (NTO), and willow *Q. phellos* (WIO) oak seedlings exposed to three early growing season flood treatments in a replanted western Tennessee bottomland, 2005 and 2006.

Date	Species	Control[a] n	Control[a] $\hat{S}$[b]	15-d n	15-d $\hat{S}$	30-d n	30-d $\hat{S}$
Jul 2005	OCO		NA	661	0.969 Aa	677	0.972 Aa
	NTO	671	0.929 Aa	688	0.891 Bb	492	0.898 ABb
	WIO	507	0.941 Aa	663	0.854 Bb	448	0.857 Bb
Oct 2005	OCO		NA	646	0.991 Aa	659	0.988 Aa
	NTO	628	0.986 Aa	626	0.991 Aa	444	0.962 Ab
	WIO	481	0.975 Aa	566	0.990 Aa	382	0.953 Ab
Jul 2006	OCO		NA	640	0.997 Aa	651	0.997 Aa
	NTO	618	0.998 Aa	609	0.997 Aa	427	0.998 Aa
	WIO	469	0.985 Ab	545	0.976 Ab	365	0.984 Aa

Treatments[c]

[a] Overcup oak seedlings were not available (NA) for sampling in the control treatment.
[b] Survival estimates in rows followed by unlike uppercase letters are different ($P \leq 0.04$); estimates for species within columns and dates followed by unlike lowercase letters are different ($P \leq 0.03$) by pair-wise Bonferroni-corrected chi-square tests.
[c] Flooding treatments were applied 18 April–20 May 2005 and 17 April–19 May 2006, and constituted soil inundation for 0 (control), 15 (15-d), and 30 (30-d) days.

Another possibility for the observed trends is that flooding may have negatively influenced seedling survival through accumulation of toxic chemicals. Flooding causes transformation of chemicals in the soil from an oxidized to a reduced state (Kozlowski 1997). For example, nitrogen, manganese, iron, and sulfur are quickly reduced (<2 wk) in flooded soils (Mitsch and Gosselink 2000). When these chemicals accumulate (e.g., $Fe^{2+} >$ 750 μM), they are toxic to seedlings (Jackson and Drew 1984; Laan et al. 1991). Extended flooding can also produce hydrocarbons, alcohols, phenolic acids, and volatile sulfur in the soil, which can inhibit seedling physiological processes (Kozlowski 2002). We surmise that Nuttall *Q. nuttallii* and willow *Q. phellos* have fewer physiological adaptations to cope with flooding compared to overcup *Q. lyrata*.

However, our results also indicate that short-duration flooding during the second growing season may positively influence survival of Nuttall *Q. nuttallii* and willow *Q. phellos* seedlings. Although significant differences were not detected, Nuttall *Q. nuttallii* and willow *Q. phellos* survival was greatest in the 15-d treatment in October 2005. Chamberlain and Leopold (2005) suggested that short-duration periodic flooding may increase survival of bottomland oak seedlings. Burkett et al. (2005) reported that natural flooding in a reforested wetland in Mississippi increased survival of Nuttall *Q. nuttallii* seedlings. We hypothesize that the mechanism driving this response is related to an ideal range of soil moisture for these species. We measured soil moisture in July 2005 and 2006, and it was greater in the 15-d treatment ($\bar{x}$ = 20.5%, SD = 0.52) than in the control ($\bar{x}$ = 18.2%, SD = 0.43; McCurry [2006]). Increased soil moisture can positively influence survival of bottomland oak species by reducing rodent herbivory, vegetation competition and drought stress (Burkett et al. 2005; Chamberlain and Leopold 2005). However, given that survival generally was lower in the 30-d treatment than in the 15-d and control treatments for Nuttall *Q. nuttallii* and willow *Q. phellos*, there must be a threshold for these species, where duration of flooding and increased soil moisture negatively affects seedlings. Our results suggest that this threshold is between 15 and

Table 3. Annual height (cm) and diameter (mm) growth of overcup *Quercus lyrata* (OCO), Nuttall *Q. nuttallii* (NTO), and willow *Q. phellos* (WIO) oak seedlings exposed to three early growing season flood treatments during the second (2005) and third (2006) growing seasons in a replanted western Tennessee bottomland.

			Treatments[c]								
			Control[a]			15-d			30-d		
Year	Variable	Species	*n*	$\bar{x}$ [b]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
2005	Height	OCO		NA		580	34.05 A	0.78	583	23.52 B	0.68
		NTO	579	42.65 A	0.90	580	46.88 B	1.05	393	31.40 C	1.01
		WIO	446	30.27 A	1.00	482	26.50 B	0.79	304	18.94 C	0.99
	Diameter	OCO		NA		635	10.65 A	0.19	635	8.14 B	0.18
		NTO	614	12.80 A	0.24	600	12.94 A	0.25	413	7.78 B	0.24
		WIO	467	8.79 A	0.19	537	9.16 A	0.23	346	4.70 B	0.16
2006	Height	OCO		NA		619	59.95 A	1.14	626	51.38 B	1.04
		NTO	591	62.10 A	1.11	568	66.73 B	1.45	406	37.60 C	1.22
		WIO	437	55.48 A	1.42	508	58.48 A	1.46	317	43.95 B	1.67
	Diameter	OCO		NA		601	12.48 A	0.23	627	10.52 B	0.20
		NTO	581	15.01 A	0.27	564	16.56 B	0.30	402	10.84 C	0.27
		WIO	428	12.15 A	0.29	493	11.65 A	0.27	319	8.76 B	0.29

[a] Overcup oak seedlings were not available (NA) for sampling in the control treatment.
[b] Means within rows followed by unlike letters are different ($P \leq 0.05$) by Ryan's-Q multiple-comparison test.
[c] Flooding treatments were applied 18 April–20 May 2005 and 17 April–19 May 2006, and constituted soil inundation for 0 (control), 15 (15-d), and 30 (30-d) days.

30 d of 100% soil moisture during the first month of the growing season.

Early growing season flooding for 30 d negatively impacted second- and third-year seedling growth for all species. Similar results have been found in other bottomland studies. Conner et al. (1998) reported that 17 wk of growing season flooding in a greenhouse significantly reduced first-year height and diameter growth of Nuttall *Q. nuttallii* and overcup *Q. lyrata* seedlings. Day et al. (1998) reported that flooding negatively influenced height growth of Nuttall *Q. nuttallii* seedlings in the Mississippi Delta. Several other studies also have documented reduced growth of *Nyssa aquatica*, *Nyssa sylvatica* var. biflora, *Acer rubrum*, and *Taxodium distichum*, in response to growing season flooding in bottomlands (Donovan et al. 1988; Keeland et al. 1997). Reduced growth of seedlings is a typical response to flooding, because anaerobic conditions in the soil diminish energy storage and metabolism (Kozlowski 1984). Flooding also induces stomatal closure in various woody plants, which can reduce photosynthetic activity and, thus, growth potential (Kozlowski and Pallardy 2002). Flooding can negatively affect active transport of essential nutrients into the roots due to the anoxic state, which can reduce growth (McKevlin et al. 1998; Kozlowski 2002). In addition, flooding can reduce growth by affecting the quantity and ratio of growth hormones in the plant (Kozlowski 2002).

Similar to survival, moderate-duration early growing season flooding positively influenced growth but depended on species and seedling age. Nuttall oak generally experienced the greatest height and diameter growth in the 15-d treatment during both years, while greatest height growth for willow *Q. phellos* in this treatment occurred during the third growing season. Greatest height growth for willow *Q. phellos* during the second growing season was in the control treatment; thus, it appears that the benefits of early growing season flooding for this species does not occur until the third growing season, which may be related to its lower flood tolerance compared to Nuttall *Q. nuttallii*. Interestingly, height and diameter growth were inversely related for willow *Q. phellos*, suggesting that there may be energetic trade-offs in growth. Considering that height growth of seedlings probably is most important initially in bottomlands because it decreases the likelihood of inundation, our results suggest there is a possible benefit of short duration (<15 d) early growing season flooding for Nuttall *Q. nuttallii* during the second and third growing seasons and for willow *Q. phellos* during the third growing season.

A basic understanding of species-specific flood tolerance is fundamental to restoration success (Kozlowski 2002). Hook (1984) classified flood tolerance of overcup *Q. lyrata*, Nuttall *Q. nuttallii*, and willow *Q. phellos* as very flood tolerant, moderate to very flood tolerant, and moderately flood tolerant, respectively. McKnight et al. (1981) ranked flood tolerance of overcup *Q. lyrata* and Nuttall *Q. nuttallii* as moderately flood tolerant and willow *Q. phellos* as weakly to moderately flood tolerant. Thus, our field study confirmed previous greenhouse results that flood-tolerance ranking for seedlings of these species decreases from overcup *Q. lyrata* to Nuttall *Q. nuttallii* to willow *Q. phellos*.

Management Implications

Our results indicate that natural resource practitioners should not replant hardwood bottomlands in a random species arrangement across elevation gradients. Seedlings of bottomland species differ in flood tolerance, and flood frequency and depth are typically correlated with elevation (McCurry et al. 2006). Overcup oak seedlings were the most flood tolerant among our species. Thus, managers should consider planting overcup *Q. lyrata* at sites with longer and more frequent flooding, and at lower elevations. Overcup oak is widely acknowledged as a desirable tree species to plant for wildlife due to its tendency to produce nest cavities and regular acorn crops. Overcup oaks produce large-diameter acorns that can be completely encapsulated with its cap. These characteristics may make it difficult for waterfowl to ingest or digest (Barras et al. 1996). Thus, biologists that manage bottomlands exclusively for waterfowl may consider managing low elevations that flood frequently as moist-soil wetlands. Moist-soil wetlands are highly productive (Gray et al. 1999), and they are important natural habitats for various species, including waterfowl and amphibians (Gray et al. 2004; Baldassarre and Bolen 2006).

We ranked Nuttall *Q. nuttallii* as moderately flood tolerant; thus, we recommend planting Nuttall *Q. nuttallii* in bottomlands that receive short (≤30 d) periodic flooding during the growing season. It appears that some flooding (e.g., 15 d) in the growing season benefits Nuttall *Q. nuttallii* survival and growth. Because flood duration is usually correlated with elevation (McCurry et al. 2006), we recommend planting Nuttall *Q. nuttallii* seedlings at mid-range elevations. In the WTREC bottomland, mid-range elevations were 0.5–0.75 m above the incipient point of overbank flow for the South Fork of the Forked Deer River. Nuttall oak also has moderate timber value and its acorns are generally smaller than overcup *Q. lyrata* (Young et al. 1995; Barras et al. 1996). Therefore, for waterfowl, we suggest Nuttall *Q. nuttallii* is a better species for bottomland restoration than overcup *Q. lyrata*.

Willow oak was the least flood tolerant among species given its lower survival rate and growth in the 30-d flood treatment. Thus, we recommend planting willow *Q. phellos* at higher elevations (e.g., >0.75 m above the incipient point of overbank flow). Despite its lower flood tolerance, willow *Q. phellos* is a good species to plant for bottomland restoration, because it has a moderate timber value and small acorns that are preferred by waterfowl (Young et al. 1995; Barras et al. 1996). Based on hydrology in the WTREC bottomland (Table 1), we would classify annual flood frequency at low, mid-range, and high elevation as >12, 8–12, and <8 times per year, respectively. Implementing this planting design, which is based on species-specific flood tolerance and flooding depth, duration, and timing in a western Tennessee bottomland, should increase the likelihood of restoration success.

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