New Forests (2012) 43:695–710
DOI 10.1007/s11056-012-9331-y

Quantifying flooding effects on hardwood seedling survival and growth for bottomland restoration

John M. Kabrick · Daniel C. Dey · J. W. Van Sambeek · Mark V. Coggeshall · Douglass F. Jacobs

Received: 20 December 2011 / Accepted: 9 April 2012 / Published online: 24 April 2012

Abstract Growing interest worldwide in bottomland hardwood restoration necessitates improved ecological understanding of flooding effects on forest tree seedlings using methodology that accurately reflects field conditions. We examined hardwood seedling survival and growth in an outdoor laboratory where the timing, depth, duration, and flow rate of flood water can be carefully controlled while simulating natural soil conditions occurring in floodplains. Flooding treatments were initiated in mid-May and included partial inundation (15–20 cm) during the growing season for 5-week flowing, 5-week standing, 3-week flowing, and control. We monitored the vigor, survival, and growth (changes in basal diameter and stem length) of six hardwood species representing a wide range in expected flood tolerance including eastern cottonwood (*Populus deltoides* Bartr. Ex Marsh.), pin oak (*Quercus palustris* Muenchh.), swamp white oak (*Q. bicolor* Willd.), bur oak (*Q. macrocarpa* Michx.), black walnut (*Juglans nigra* L.), and pecan [*Carya illinoensis* (Wangenh.) K. Koch]. All stock was 1-0 bareroot except that cuttings were used for eastern cottonwood. Five species—eastern cottonwood, bur oak, swamp white oak, pin oak, and pecan—exhibited high survival probabilities (>0.62 for cottonwood; >0.77 for the others) regardless of flood treatment. But of the survivors, only eastern cottonwood and swamp white oak maintained positive growth and healthy green foliage. Despite high survival, bur oak and pin oak suffered stem growth losses and exhibited chlorotic foliage in flood treatments suggesting greater vulnerability to other abiotic or biotic stresses if out-planted on flood-prone sites. Pecan also suffered stem dieback in controls suggesting vulnerability to competition and browsing when outplanted despite high survival after

J. M. Kabrick (✉) · D. C. Dey · J. W. Van Sambeek
USDA Forest Service, Northern Research Station, University of Missouri,
202 Natural Resources Building, Columbia, MO 65211, USA
e-mail: jkabrick@fs.fed.us

M. V. Coggeshall
Center for Agroforestry, University of Missouri, 203 Natural Resources Building, Columbia,
MO 65211, USA

D. F. Jacobs
Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907-2061,
USA

flooding. Our quantitative data helps to confirm and/or refine previously published qualitative flood tolerance ratings for these species, and describes operation of an in situ outdoor flood experiment laboratory that may prove effective in guiding future flood tolerance research.

Keywords Flood tolerance · Restoration · Bottomland hardwoods · Seedling growth · Seedling survival

Introduction

There is increasing worldwide interest in planting deciduous hardwood seedlings as part of forest restoration efforts to conserve soil, protect against extreme flooding, provide timber and wildlife habitat, or to reestablish native hardwoods on land formerly used for agriculture (Glenz et al. 2006; Dey et al. 2010; Maltoni et al. 2010; Jacobs et al. 2012). Survival of planted hardwood seedlings is often poor (Jacobs et al. 2004; Stanturf et al. 2004; Dey et al. 2010) and numerous authors have indicated that successful hardwood restoration requires carefully matching the ecological requirements and tolerance of species to environmental conditions of the planting site (Stanturf et al. 2001, 2004; Allen et al. 2004; Gardiner et al. 2009). Because periodic flooding occurs in bottomlands, it is particularly important that seedlings are adapted to the seasonality, depth, and duration of flood events of a site; Stanturf et al. (2004) suggests that lack of detailed knowledge of a species' flood tolerance is a major cause of regeneration failures in flood-prone areas.

Several factors influence the ability of trees to tolerate flooding. In addition to adaptive differences among species, the size and age of the trees, the timing and duration of flooding, and the oxygen content of the flood water are important variables (Kozlowski and Pallardy 1997). Trees are more likely to survive partial rather than complete inundation (Hosner 1960). Consequently, seedlings may be more vulnerable to minor floods than are mature trees because they are more likely to be completely inundated. Crown size and vigor, however, are other important determinants of flood tolerance (Hook 1984) and these attributes are generally sub-optimum in newly establishing seedlings. Floods during the growing season are more damaging than those during dormant periods because they restrict oxygen to roots when both root and shoot growth are most active. Standing flood water is more damaging to plants because it contains less oxygen than flowing water (Kozlowski and Pallardy 1997).

Published flood tolerance ratings can be used to guide species selection for restorations in flood-prone areas. However, the concept of flood tolerance remains difficult to define quantitatively. Consequently, flood tolerance ratings are expressed with vaguely-defined terms, such as "moderately tolerant" or "somewhat tolerant" (Allen et al. 2004). Even when explicitly defined, flood tolerance often has been determined observationally, based on case histories rather than experimentally from controlled studies where confounding influences were reduced or eliminated (Hosner 1960; Hook 1984; Loucks 1987; Allen et al. 2004). Where experimentation has been used to examine flood tolerance, most studies have been conducted with seedlings planted in pots or containers that are subsequently inundated (Catlin and Olsson 1986; Smith and Bourne 1989; Pezeshki et al. 1999; Kaelke and Dawson 2003), resulting in conditions that poorly emulate those of natural floodplains.

The interest in bottomland afforestation throughout North America (Stanturf et al. 2004, 2009; Dey et al. 2010) and Europe (Frye and Grosse 1992; Weber 2005; Glenz et al. 2006) has prompted us to more carefully examine seedling survival and growth when planted where they are subjected to flooding. Here we report on a series of experiments conducted on a wide variety of tree species native to North American bottomlands in a unique outdoor laboratory where the timing, depth, duration, and flow rate of flooding can be controlled on natural soils where conditions more closely emulate those occurring on natural floodplains. Our objectives were to compare the vigor, survival, and growth after flooding of hardwood seedlings having a range of published flood tolerance ratings and to examine the utility of these metrics for guiding species selection for bottomland hardwood plantings.

Methods

Experimental site

The outdoor Flood Tolerance Laboratory (FTL) is located at the University of Missouri Horticulture and Agroforestry Research Center in New Franklin, Missouri, USA (39.0098892° Latitude, −92.7706931° Longitude). At the time of this study, the facility comprised twelve, 6-m-wide × 180-m-long channels constructed on the floodplain of a perennial stream that flows into the Missouri River (Fig. 1). Soils underlying the FTL are a mix of moderately well-drained Nodaway silt loam (fine-silty, mixed, nonacid, mesic, Mollic Udifluvents) and poorly-drained Carlow silty clay (fine, montmorillonitic, mesic, Vertic Endoaqualls) (Grogger and Landtiser 1978). Soil excavated for a retention pond on the down-slope end of the FTL was used to build parallel, 2-m-high berms to form the twelve channels; care was taken during construction to not alter the soil within the channels. The drop within each channel averages < 15 cm from inlet to outlet. Two

Fig. 1 Aerial photograph of the Flood Tolerance Laboratory at the Horticulture and Agroforestry Research Center in New Franklin, MO, USA. Flood treatments were applied in three blocks comprising four adjacent channels. Block I comprises the four channels nearest the gravel road, block II comprises the middle four channels, and block III comprises the four channels on the *left side* of the photograph. Three channels (one per block) remained unflooded (control treatment)

1,600 L h^{-1} electric pumps move water from the retention pond to adjustable butterfly valves located at the inlet end of each channel. Adjustable flood leveling gates at the outlet end control the depth of water between 0 and 0.3 m for flowing water flood treatments. Flow rates within channels can be adjusted to exchange the water up to once each day (120 L min^{-1}). Adjustable float valves were installed on the inlet end to control flooding depth for standing water flood treatments. Excess water in all channels flows back into the retention pond through outlet pipes installed 15 cm lower than the surface of each channel. A 6-m × 5-m depression approximately 20 cm deep was excavated at the outlet end of each channel to collect post-flooding water and allow the use of self priming water pumps (930 L min^{-1}) to rapidly drain each channel when flooding treatments are terminated. There also is a supplemental drain pipe across all channels beneath the outlet depressions and 20-cm-deep ditches along both sides of each channel to increase post-flooding flow of water from the channel and to intercept water seeping under berms into the control channels. Detailed information about the soil conditions at the FTL is given in Van Sambeek et al. (2006).

Species

We evaluated flood responses of pin oak (*Quercus palustris* Muenchh.), swamp white oak (*Q. bicolor* Willd.), bur oak (*Q. macrocarpa* Michx.), black walnut (*Juglans nigra* L.), eastern cottonwood (*Populus deltoides* Bartr. Ex Marsh.), and pecan [*Carya illinoensis* (Wangenh.) K. Koch], which commonly are used in bottomland restoration plantings of the central USA. We used 30-cm-long cuttings for cottonwood and 1-0 bareroot stock for the other species. All stock was produced at the George O. White State Forest Nursery located near Licking, MO, USA.

Experimental design and treatments

The design was a randomized complete block with treatments replicated in space (three blocks) and time (the experiment was repeated in two different years). This was done by grouping four adjacent channels in three blocks. Within blocks, a single treatment was randomly assigned to each of the four channels: control, 3-week flowing, 5-week flowing, or 5-week standing. Soil properties of the three blocks are provided in Table 1 and Fig. 2. Prior to planting all channels were cultivated to a depth of 10 cm with a tractor-mounted, 1.5-m-wide rotary tiller. Within each channel, 25 seedlings or cuttings (cottonwood) of each species was planted on a 0.75-m × 0.75-m spacing (25 seedlings or cuttings per species per channel, 75 seedlings per species per treatment, and 1800 seedlings total). During the first experiment, flood treatments were initiated on May 15, 2004, approximately 1 month after seedling planting. In flooded channels, the water depth was maintained at 20–25 cm. The timing and depth of the flood treatments were selected to simulate late spring floods common in the central USA. When not flooded the herbaceous plants and other competing vegetation was controlled by mowing and by applying glyphosate (0.5 % solution) one time in the rows in between established seedlings in late June or early July when competing ground vegetation was approximately 15 to 20 cm tall.

The second experiment was conducted in 2005 using the same approximate time schedule (e.g., flooding initiated on May 23, 2005, approximately 1 month after seedling planting), treatments, and flood depth. Prior to initiating the second experiment, seedlings from the previous experiment were removed and the channels were cultivated in preparation for planting. Treatments within blocks were re-randomized as were the species

Table 1 Soil properties within the top 20–25 cm across three replications of four channels each within the outdoor Flood Tolerance Laboratory

Variable	Block I	Block II	Block III
Dominant USDA soil series	Carlow and Nodaway	Nodaway and Carlow	Nodaway
Soil texture			
Silt content	58	63	68
Clay content	34	28	23
Available water holding capacity (cm)	4.5	5.1	5.6
Soil pH			
Post flooding in 2003	7.4	6.9	6.5
During flooding in 2005	6.9	6.8	6.6
Post flooding 2005	6.6	6.6	6.5
Soil redox potential (mV)			
Post flood 2005 recovery	357	394	422
Soil nutrients, pre-flooding (kg ha^{-1})			
Ca	6,520	5,280	4,950
Mg	821	808	765
K	512	518	529
P	98	83	77

Data adapted from Van Sambeek et al. (2006). See Fig. 1 for arrangement of blocks

within channels. As with the first experiment, we planted the same six species and stock. For both experiments combined, this yielded six complete blocks (reps) comprising 600 individual trees each of six species (3,600 individual trees total).

Measurements

Immediately after planting, we recorded stem length (soil surface to the tip of the main stem) and basal diameter (1 cm above soil surface measured twice in orthogonal directions) (Table 2). At the termination of each experiment in September, stem length and basal diameter were re-measured. We also recorded presence or absence of stem dieback and rated foliage appearance (green and healthy or chlorotic).

Deleterious effects of flooding on tree seedling survival and growth may not be fully observed during the same growing season that flood treatments are implemented (Frye and Grosse 1992). This may be particularly applicable to species such as oaks, black walnut, and pecan in which terminal shoot growth during a flush may be strongly influenced by seedling vigor while buds are being set. In our experiments, the growth that occurred likely was influenced by both pre- and post-flood conditions. Thus, we allowed the seedlings to remain in the ground over winter without additional flooding after the termination of the second experiment in 2005. In June 2006, near the termination of the first shoot flush in the oaks, black walnut, and pecan, we recorded the number of living seedlings and re-measured stem length of all seedlings.

Analysis

We compared treatments using the mixed linear models procedure (PROC MIXED) in SAS statistical software (SAS version 9.1, SAS Institute, Cary, NC, USA). We compared

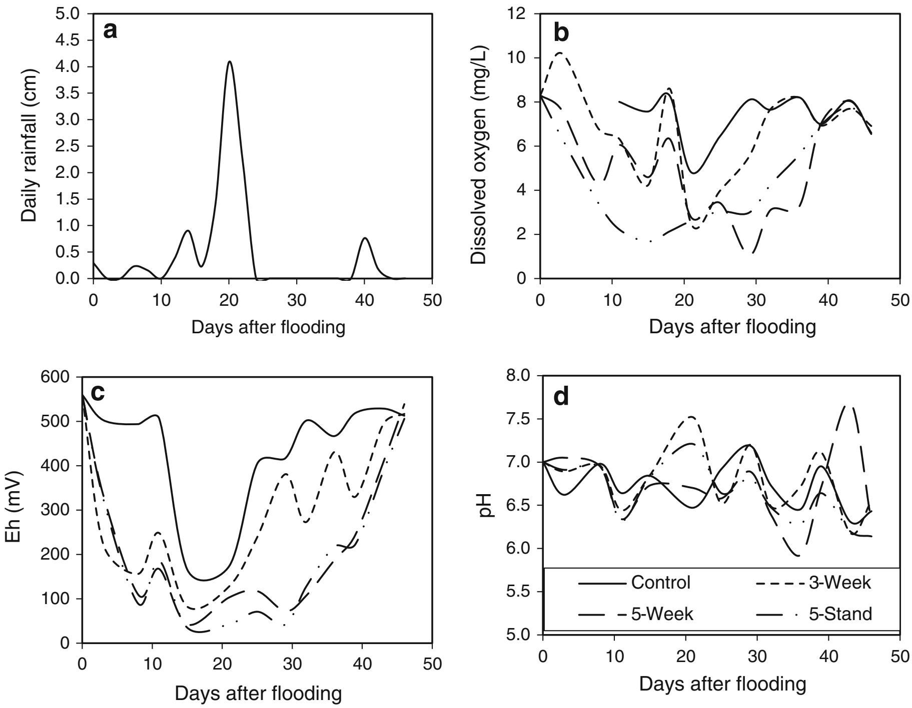

Fig. 2 Daily rainfall (**a**), dissolved oxygen (**b**), redox potential (**c**), and pH (**d**) after flooding treatments. Flood treatments were initiated on May 23, 2005 (Day 0) and terminated on day 21 for 3-week flowing (3-week) and day 35 for 5-week flowing (5-week) and standing (5-stand) treatments. Data adapted from Van Sambeek et al. (2006)

the fixed effects of treatment and the species × treatment interaction and the random effects of block × treatment and block × treatment × species, respectively, as the error. For the survival assessment, we modeled the binary response (live or dead) with a logistic function and transformed it into survival probabilities. We evaluated the effects of treatments on foliar health by analyzing as the response variable the proportion of healthy seedlings (no dieback and healthy, green foliage). For assessing flood treatment effects on growth, we calculated the change in stem length and basal diameter that occurred during the growing season (the initial stem length or basal diameter was subtracted from those determined at the end of the growing season or after overwintering). When significant effects were detected in the ANOVA ($\alpha = 0.05$), we compared individual means using Fisher's least significant difference test ($\alpha = 0.05$).

Results

Flooding effects

Compared to the control, flood treatments significantly decreased survival ($P < 0.01$), stem growth ($P = 0.05$), and basal diameter growth ($P = 0.02$) when examined without regard to species (Table 3; Fig. 3). Generally, survival and growth nominally decreased with

Table 2 Mean pretreatment seedling basal diameter and stem length by species and treatment type for both experiments

Species	Treatment			
	Control	3-Week flood, flowing	5-Week flood, flowing	5-Week flood, standing
Basal diameter (mm)				
Black walnut	5.4	5.6	5.4	5.5
Pecan	4.0	4.2	4.3	4.2
Bur oak	4.2	5.0	5.0	4.5
Pin oak	5.0	4.9	4.9	4.6
Swamp white oak	4.9	5.5	5.3	5.3
Cottonwood	–	–	–	–
Stem length (cm)				
Black walnut	51	54	54	56
Pecan	21	22	21	21
Bur oak	30	32	34	33
Pin oak	40	38	40	36
Swamp white oak	32	33	32	32
Cottonwood	–	–	–	–

Table 3 Probability of (a) seedling survival and (b) the percentage of healthy seedlings (i.e., having no indication of stem dieback or leaf chlorosis) at the end of the growing season

Species	Treatment				
	Control	3-Week flood, flowing	5-Week flood, flowing	5-Week flood, standing	All
(a) Survival (probability)					
Black walnut	0.55 A a	0.12 AB a	0.05 B a	0.03 C a	0.11 a
Pecan	0.81 A a	0.93 A b	0.62 A b	0.64 A b	0.78 c
Bur oak	0.94 A a	0.75 A b	0.68 A b	0.56 A b	0.77 c
Pin oak	0.96 A b	0.93 A b	0.88 A b	0.87 A b	0.91 c
Swamp white oak	0.95 A b	0.90 A b	0.80 A b	0.80 A b	0.88 c
Cottonwood	0.78 A b	0.67 A b	0.47 A b	0.52 A b	0.62 b
All	0.88 A	0.76 AB	0.56 BC	0.53 C	
(b) Healthy seedlings (%)					
Black walnut	34 A a	13 A a	2 A a	2 A a	13 a
Pecan	61 A a	79 A b	47 A b	51 A b	60 bc
Bur oak	60 A a	50 A b	43 A b	41 A b	48 b
Pin oak	81 A b	77 A b	54 A b	65 A b	69 c
Swamp white oak	77 A a	73 A b	63 A b	66 A b	70 c
Cottonwood	73 A a	62 A b	47 A b	52 A b	58 bc
All	64 A	59 A	43 B	46 B	

Differences within columns are indicated with lowercase letters and differences within rows are indicated with uppercase letters ($P < 0.05$)

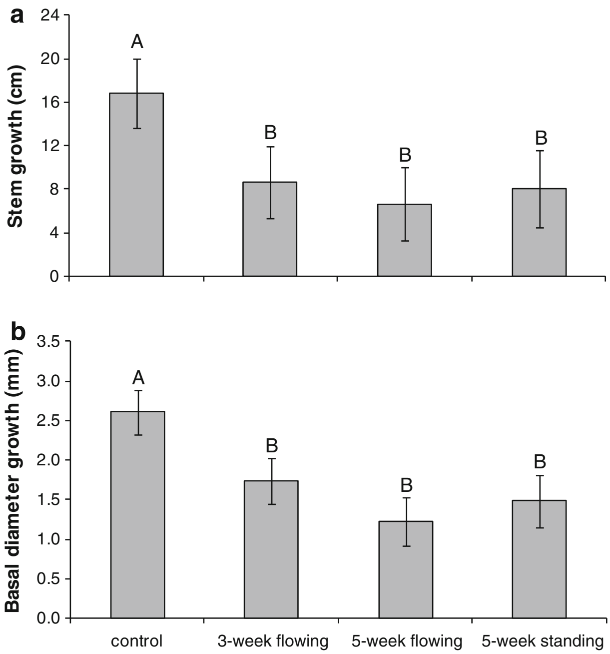

Fig. 3 Stem growth (**a**) and basal diameter growth (**b**) by flood treatment for all six species combined as determined at the end of each growing season in 2004 and 2005. Flood treatments were initiated in May, 1 month after planting during two different experiments. Error bars are ± one SE. Means followed by a *different letter* indicate significant treatment differences ($\alpha = 0.05$)

increasing flooding duration; however our analyses indicated few significant differences among the three flood treatments. We also observed that the proportion of seedlings exhibiting dark green foliage and no evidence of shoot dieback also decreased significantly ($P < 0.01$) with increased flood duration concomitantly with the survival probabilities (Table 3). We anticipated that seedlings would suffer more dieback or greater mortality in the 5-week standing water treatment because of the anoxic soil conditions. Despite evidence verifying that the soil in the five-week standing treatment had a lower Eh and a lower dissolved oxygen concentration than did the five-week flowing treatment during flooding (Fig. 2), the overall stem growth and basal diameter growth between these treatments were statistically similar.

Species by treatment interactions

There was considerable variation among species. Black walnut suffered the greatest mortality and stem and basal diameter growth reductions in flooded channels (Table 3; Figs. 4, 5). We also found that black walnut in controls maintained a relatively low survival probability compared to other species and the foliage of a large proportion of individual seedlings exhibited chlorosis. This most likely occurred because the soils of the control channels became nearly saturated after rain events (Fig. 2) and also because of seepage from adjacent channels (Van Sambeek et al. 2006). Pecan had very high survival, but also had substantial stem dieback in all treatments (Table 3; Figs. 4, 5). Most of the stems that died back also resprouted, producing stems shorter in length and smaller in basal

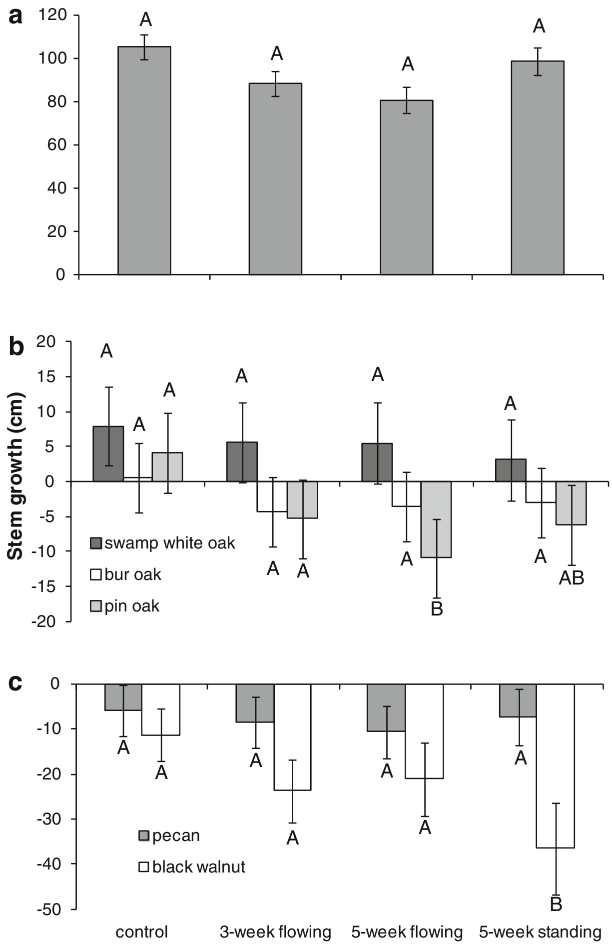

Fig. 4 Stem growth of cottonwood (**a**), oaks (**b**), and walnut and pecan (**c**) by flood treatment determined at the end of each growing season in each of 2004 and 2005. Flood treatments were initiated in May, 1 month after planting during two different experiments. Species were arranged by growth increment. Error bars are ± one SE. Means followed by a *different letter* indicate significant differences ($\alpha = 0.05$)

diameter. This may not have been caused by flooding because the seedlings in the control treatment also suffered as much dieback as those in the flooded treatments.

Eastern cottonwood maintained moderate survival and rapid growth (Table 3; Figs. 4, 5). There were nominal but non-significant reductions in stem and basal diameter growth in the three-week flowing and five-week flowing treatments that were not as evident in the five-week standing water treatment. Although we cannot explain why this occurred, we observed that this species suffered little dieback and maintained dark green foliage in all treatments, suggesting that there were few other negative impacts of flooding on surviving plants.

Swamp white oak and pin oak seedlings maintained greater survival probability than cottonwood, exceeding 0.80 regardless of treatment (Table 3). Moreover, swamp white oak maintained a high growth rate that was second only to cottonwood (Figs. 4, 5). Swamp white oak suffered very little dieback and maintained healthy and dark green foliage

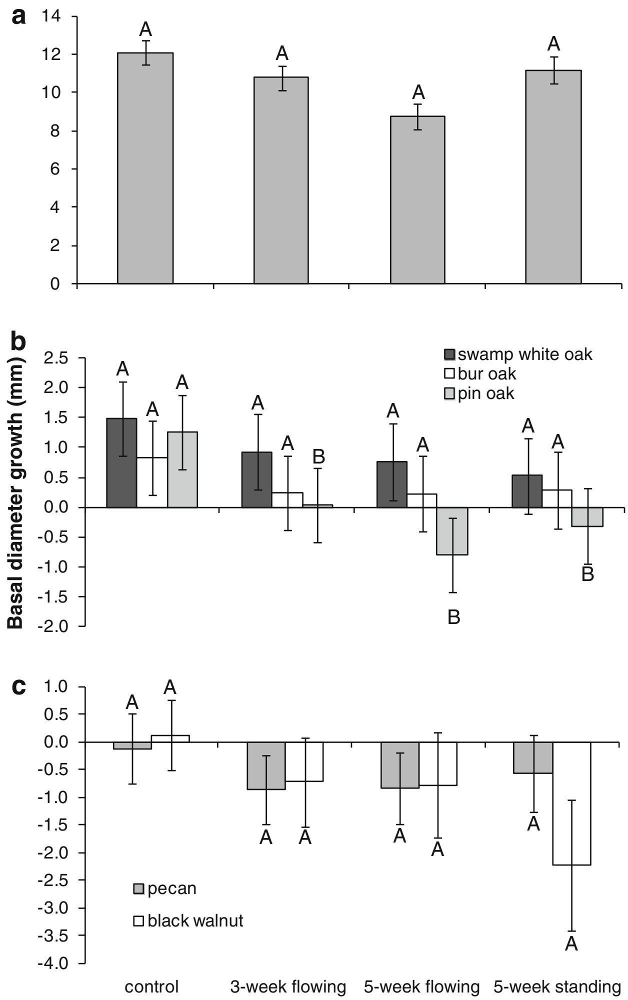

Fig. 5 Basal diameter growth of cottonwood (**a**), oaks (**b**), and walnut and pecan (**c**) by flood treatment determined at the end of each growing season in each of 2004 and 2005. Species were arranged by growth increment. Means followed by a *different letter* indicate significant differences ($\alpha = 0.05$)

regardless of treatment (Table 3). Despite a high survival probability, pin oak had substantial basal diameter and stem length reductions with increased flooding due to stems dying back and resprouting. Bur oak also appeared sensitive to flooding and had reductions in survival and shoot growth in all flood treatments (Figs. 4, 5). However, these reductions were not statistically significant and a positive basal diameter growth was maintained regardless of treatment.

Seedling survival and growth after overwintering

During the second experiment, we compared the survival probability and stem and basal diameter growth of each species assessed at the end of the growing season to those evaluated in June after the tree seedlings overwintered (Table 4) to determine if the

Table 4 Comparison of survival probability when determined in autumn during the same growing season of flood treatments versus when determined in the spring after overwintering following flooding

	Survival probability		Stem growth (cm)	
	September 2005	June 2006	September 2005	June 2006
Pin oak	0.77 A	0.76 A	−9.6 A	−4.8 A
Bur oak	0.67 AB	0.61 AB	−4.1 A	−3.0 A
Swamp white oak	0.61 ABC	0.55 AB	−2.9 B	0.4 B
Pecan	0.53 BC	0.55 AB	−13.7 C	−7.0 A
Cottonwood	0.38 C	0.35 B	96.6 D	97.4 C
Black walnut	0.12 D	0.08 C	−39.0 E	No estimate

Values within columns followed by a different letter are significantly different ($P < 0.05$)

ranking of species would differ depending on when observations were recorded. Although there was a slight increase observed in stem growth when determined in the spring, survival probabilities by species were roughly similar and the ranking of species by survival or growth did not change.

Discussion

Seedling survival and growth

Our findings show both consistencies and discrepancies in seedling survival and growth compared to published flood tolerance ratings (Table 5). There generally is good agreement in the literature that black walnut is flood intolerant (Teskey and Hinckley 1977; Whitlow and Harris 1979) and it was included in our study to serve as a sensitive indicator of flood-induced stress. Eastern cottonwood was included because it is considered tolerant (Whitlow and Harris 1979) to very tolerant of flooding (Teskey and Hinckley 1977), as our findings confirm. However, the published flood tolerances of the bottomland oaks that we examined ranged from intolerant to tolerant and no single species consistently rated as more tolerant than the others. Our findings strongly suggested that swamp white oak is much more tolerant to partial inundation than are the other oaks that we examined and it appeared to survive flood treatments better than did eastern cottonwood cuttings in the year of establishment. Other studies have shown that swamp white oak maintains high survival and growth after partial inundation (Walsh et al. 2008) or when planted as bareroot or container seedlings in bottomland restoration efforts on a range of soil textures and soil drainage classes in the central USA (Kabrick et al. 2005; Steele et al. 2008; Weigel et al. 2008).

Pin oak also exhibited high survival regardless of treatment. However, it suffered significant stem dieback with increasing flood duration. Reduced stem growth or dieback associated with flooding has also been linked to reduced root mass and lowered root-shoot ratios in other hardwood species, which was considered evidence of intolerance to flooding (Tang and Kozlowski 1982; Glenz et al. 2006). Growth reductions associated with flooding have also been attributed to reduced metabolism in the root systems because of soil anoxia (Kozlowski 1984; Glenz et al. 2006), along with stomatal closure (Pereira and Kozlowski 1977) that results in reduced photosynthetic activity (Pezeshki et al. 1996; Kozlowski 1997). Bur oak also suffered nominal reductions in stem length and diameter, suggesting

Table 5 Published flood tolerances for the tree species evaluated in this study, illustrating the variation among and within each species and variability in tolerance definitions among authors

Species	Flood tolerance		
	Teskey and Hinckley (1977)[a]	Whitlow and Harris (1979)[b]	Allen et al. (2004), Haynes et al. (1988)[c]
Black walnut	Intolerant	Intolerant	Weakly tolerant
Pecan	Intermediately tolerant	Tolerant to very tolerant	Weakly tolerant
Bur oak	Tolerant	Somewhat tolerant	Intolerant
Pin oak	Intermediately tolerant	Tolerant	Moderately tolerant
Swamp white oak	Tolerant	Somewhat tolerant	Moderately tolerant
Eastern cottonwood	Very tolerant	Tolerant	Weakly tolerant to moderately tolerant

[a] Very tolerant: withstands flooding for two or more growing seasons; tolerant: withstands flooding for most of one growing season; intermediately tolerant: survives flooding for 1–3 months during the growing season; intolerant: cannot withstand flooding during the growing season

[b] Very tolerant: survives prolonged flooding for more than 1 year; tolerant: survives flooding for one growing season; somewhat tolerant: survives flooding or saturated soil for 30 consecutive days during the growing season; intolerant: unable to survive more than a few days of flooding during the growing season

[c] Tolerant: survives saturated or flooded soil for long periods during the growing season; moderately tolerant: survives saturated or flooded soil for several months during the growing season; weakly tolerant: survives saturated or flooded soil for a few days or weeks during the growing season; intolerant: unable to survive short periods of saturated or flooded soil during the growing season

that this species was nearly as vulnerable to the deleterious effects of flooding as was pin oak. However, bur oak growth losses were smaller in magnitude and not statistically significant compared to the control.

Pecan is rated as weakly tolerant (Allen et al. 2004) to very tolerant (Whitlow and Harris 1979) to flooding. Our data indicated high survival but substantial reductions in both stem length and basal diameter; however, stem dieback and resprouting occurred in all treatments including the control, suggesting that this was not caused by flooding. Despite stem dieback, a large proportion of pecan seedlings generally appeared dark green and healthy in all treatments. In contrast to our findings, Pezeshki and DeLaune (1998) reported large reductions in biomass growth of pecan with increased duration of partially-inundated seedlings and concluded that this indicated a relative intolerance to flooding. However, in the study by Pezeshki and DeLaune (1998), seedlings were planted in containers and partially inundated for up to 63 days. This allowed the soil Eh to fall below −70 mV, well below that in our study with the native soils in the FTL (see Fig. 2). These lower Eh values measured by Pezeshki and DeLaune (1998) may have decreased nutrient uptake and transport and created greater plant stress than in our study. Gardiner et al. (2009) stated that very little information has been reported about the establishment of pecan in afforestation efforts so it is difficult to determine if our results were typical of operational responses. However, slow juvenile growth or stem dieback may be characteristic for this species as Krinard and Kennedy (1987), Stanturf et al. (1998), and Jacobs et al. (2012) all reported that pecan seedlings planted in the Lower Mississippi Alluvial Valley in the south-central USA grew more slowly in height than did other bottomland hardwood species such as sweetgum (*Liquidambar styraciflua* L.), green ash (*Fraxinus pennsylvanica* Marsh.), American sycamore (*Platanus occidentalis* L.), or eastern cottonwood.

We initially were concerned that the growth response to flooding of the recurrent-growth or determinant-growth species including the oaks, black walnut, and pecan would be fully expressed only in the growth flushes occurring after flood treatments or during the next growing season. For these species, the first growth flush was likely influenced greatly by practices in the nursery prior to planting in the FTL. However, the fact that we observed significant treatment effects compared to the control indicates that seedling responses were not simply carryover effects from the nursery. This was further supported by our comparison of survival and growth determined at the end of the same growing season and again during the following growing season where only minor differences were observed, which would not lead to different conclusions about species suitability for planting in flood-prone areas. For most species, survival probabilities after overwintering and flushing were slightly lower and the stem lengths were slightly greater. This suggests that studies where flood response was determined during the same growing season of flooding (e.g., Pezeshki and DeLaune 1998) or determined during the second growing season after flooding (e.g., Frye and Grosse 1992) yield comparable results.

Implications for bottomland forest restoration

Bottomland restoration efforts will greatly benefit from accurate information about the species suitability for the site hydrology (McCurry et al. 2010). Although much has been published about tree growth responses to flooding and flood tolerance of individual species, reported inconsistencies may in part be artifacts of the experimental methods used. A number of studies have been conducted by inundating tree seedlings planted in pots, large tanks, or in soil that is sealed to prevent seepage (Tang and Kozlowski 1982; Frye and Grosse 1992; Pezeshki et al. 1999; Walsh et al. 2008). However, inundation in pots or other containers reduces soil Eh and dissolved oxygen to lower levels and much more quickly than typically occurs in natural floodplains. For example, soil Eh derived from experiments conducted with seedlings planted in pots were reported to be −160 mV (Pezeshki and DeLaune 1998) or lower (Pezeshki and Chambers 1985) after only a few days of inundation. In natural soils in bottomlands, wetlands, or in poorly-drained uplands, the Eh typically remains above −100 mV or less for only a few days (Vepraskas and Faulkner 2001; Karathanasis et al. 2003; Verpraskas et al. 2004). Treatments causing more rapid onset of or more severe level of oxygen depletion in the soil are more likely to illicit flood stress symptoms in plants. The hypoxia limits the oxygen available to roots causing damage that can reduce nutrient uptake and leaf growth, and increase leaf chlorosis, leading to leaf senescence and abscission, and/or mortality (Kozlowski 1997; Glenz et al. 2006). Our data from the FTL presented here and in greater detail elsewhere (see Unger et al. 2008) demonstrated that dissolved oxygen was never completely consumed and that the average soil Eh remained above 0 mV during short-term (21- to 35-days), growing-season floods (Fig. 2). This suggests that the level of hypoxia created in the FTL more closely resembles that occurring in natural floodplains and the survival, growth rates, and dieback that we observed are more applicable to bottomland hardwood restoration efforts.

Our findings also illustrate that the survival and growth response to flooding is complex and a comprehensive assessment for identifying ideal species to plant in bottomland restoration efforts cannot be made by considering a single metric. For example, had survival been the only metric considered, we would have concluded that most of the species that we examined except black walnut were suitable for planting in floodplains where 3- to 5-week growing-season floods occur. However, the observed reductions in basal diameter and, in particular, stem length were also important for distinguishing among species and useful for assessing the likelihood of long-term survival in bottomland reforestation efforts. In bottomlands, planted seedlings not only have to survive flood events, but also must remain vigorous to compete with hardwoods and herbaceous vegetation (Frye and Grosse 1992) on rich floodplain soils where the supply of nutrients and water is seldom limiting (Dey et al. 2010). Species that survive a flood event but suffer dieback and have chlorotic foliage will be at a competitive disadvantage compared to those that retain vigorous growth and foliage development (Tang and Kozlowski 1982; Kozlowski 1997; Frye and Grosse 1992; Dey et al. 2004). Stem growth reductions or stem dieback induced by flooding are also associated with root growth reductions or root mortality (Kozlowski 1997). These stem and root growth impairments not only cause increased vulnerability to deleterious effects of competing vegetation, but also increased vulnerability to complete inundation by future flood events (Tang and Kozlowski 1982). This underscores the importance of evaluating seedling growth and vigor following flooding in addition to survival as metrics defining flood tolerance.

Conclusions

The FTL offers the opportunity to examine hardwood seedling flood response where the timing, depth, duration, and flow rate of flood water can be carefully controlled while simulating soil conditions that better mimics those occurring in natural flood plains. Experiments in the FTL indicated that published flood tolerance ratings were not particularly useful for identifying suitable species for floodplain reforestation efforts. Our findings suggested that survival following flooding may not be the best indicator of seedling suitability. For most species, stem and basal diameter growth were more indicative of a species' suitability for establishment in flood-prone areas. Stem growth was particularly useful for distinguishing among the oak species compared to the published flood tolerance ratings. Species that suffered stem dieback due to flooding are potentially more vulnerable to complete inundation during subsequent flood events and to competition-induced mortality by flood-tolerant competing vegetation during the establishment phase in bottomland restoration efforts. Survival probabilities and stem or basal diameter growth rankings did not change from the end of the first growing season to the beginning of the second growing season, indicating that conclusions about the short-term effects of flooding made at the end of the growing season will be similar to those made after overwintering.

Acknowledgments We thank John Thompson, and Ray Glendening (Univ. of Missouri Center for Agroforestry), Jonathon Motsinger (formerly with the Forestry Department, Univ. of Missouri) and all of the technicians with the flood facility at the Univ. of Missouri Horticulture and Agroforestry Research Center for assisting with the establishment, maintenance, or measurements of this study and Drs. Mike Gold and Gene Garrett (Univ. of Missouri) for supporting this project. Mark Ellersieck provided statistical guidance. We also thank the two anonymous reviewers and an Associate Editor for comments that greatly improved the final version of this paper. This research was funded by the USDA Forest Service, Northern Research Station and through the University of Missouri Center for Agroforestry under cooperative agreements AG-02100251 with the USDA ARS Dale Bumpers Small Farms Research Center, Booneville, AR, USA and C R 826704-01-0 with the US EPA.

References

Allen JA, Keeland BD, Stanturf JA, Clewell AF, Kennedy HE Jr (2004) A guide to bottomland hardwood restoration. US Geological Survey, Biological Resources Division Information and Technology Report USGS/BRD/ITR-2000-0011. Gen Tech Rep SRS-40. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, 132 pp

Catlin PB, Olsson EA (1986) Response of eastern black walnut and northern California black walnut seedlings to waterlogging. HortScience 21:1379–1380

Dey DC, Kabrick JM, Gold MA (2004) Tree establishment in floodplain agroforestry practices. In: Sharrow SH (ed) Proceedings of the 8th North American agroforestry conference. Oregon State University, Corvallis, pp 102–115

Dey DC, Gardner ES, Kabrick JM, Stanturf JA, Jacobs DF (2010) Innovations in afforestation of agricultural bottomlands to restore native forests in the eastern USA. Scand J For Res 25:31–42

Frye J, Grosse W (1992) Growth responses to flooding and recovery of deciduous trees. Z Naturforsch 47:683–689

Gardiner ES, Jacobs DF, Overton RP, Hernandez G (2009) Root-collar diameter and third-year survival of three bottomland hardwoods planted on former agricultural fields in the lower Mississippi Alluvial Valley. In: National Proceedings: Forest and conservation nursery associations-2008. Proceedings of RMRS-58. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, pp 85–89

Glenz C, Schlaepfer R, Iorgulescu I, Kienast F (2006) Flooding tolerance of Central European tree and shrub species. For Ecol Manag 235:1–13

Grogger HE, Landtiser GR (1978) Soil survey of Howard County, Missouri. US Department of Agriculture, Soil Conservation Service, Washington, p 94

Haynes RJ, Allen JA, Pendleton EC (1988) Reestablishment of bottomland hardwood forests on disturbed sites: an annotated bibliography. Biol Rep 88(42). US Department of the Interior, Fish and Wildlife Service, Washington, 104 pp

Hook DD (1984) Waterlogging tolerance of lowland tree species of the south. South J Appl For 8:136–148

Hosner JF (1960) Relative tolerance to complete inundation for 14 bottomland tree species. For Sci 6:246–251

Jacobs DF, Ross-Davis AL, Davis AS (2004) Establishment success of conservation tree plantations in relation to silvicultural practices in Indiana, USA. New For 28:23–36

Jacobs DF, Goodman RC, Gardiner ES, Salifu KF, Overton RP, Hernandez G (2012) Nursery stock quality as an indicator of bottomland hardwood forest restoration success in the Lower Mississippi River Alluvial Valley. Scand J For Res 27:255–269

Kabrick JM, Dey DC, Van Sambeek JW, Wallendorf M, Gold MA (2005) Soil properties and growth of swamp white oak and pin oak on bedded soils in the lower Missouri River floodplain. For Ecol Manag 204:315–327

Kaelke CM, Dawson JO (2003) Late-season flooding regimes influence the accretion and partitioning of nitrogen and biomass in silver maple seedlings. In: Van Sambeek JW et al (eds) Proceedings of the 13th central hardwood forest conference. Gen Tech Rep NC-234. US Department of Agriculture, Forest Service, North Central Research Station, St. Paul, pp 167–176

Karathanasis AD, Thompson YL, Barton CD (2003) Long-term evaluations of seasonally saturated "wetlands" in Western Kentucky. Soil Sci Soc Am J 67:662–673

Kozlowski TT (1984) Responses of woody plants to flooding. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, Orlando, pp 129–164

Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiology monograph No 1. Heron Publishing, Victoria

Kozlowski TT, Pallardy SG (1997) Growth control in woody plants. Academic Press, New York

Krinard RM, Kennedy HE Jr (1987) Planted hardwood development on clay soil without weed control through 16 years. Res Note SO-343, 4 pp. US Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA

Loucks WL (1987) Flood-tolerant trees. J For 85:36–40

Maltoni A, Mariotti B, Tani A, Jacobs DF (2010) Relation of *Fraxinus excelsior* seedling morphological attributes to growth and root proliferation during field establishment. Scand J For Res 25:60–67

McCurry JR, Gray MJ, Mercker DC (2010) Early growing season flooding influence on seedlings of three common bottomland hardwood species in western Tennessee. J Fish Wildl Manag 1:11–18

Pereira JS, Kozlowski TT (1977) Variations among woody angiosperms in response to flooding. Physiol Plant 41:184–192

Pezeshki SR, Chambers JL (1985) Responses of cherrybark oak seedlings to short-term flooding. For Sci 31:760–771

Pezeshki SR, DeLaune RD (1998) Responses of seedlings of selected woody species to soil oxidation-reduction conditions. Environ Exp Bot 40:123–133

Pezeshki SR, Pardue JH, DeLaune RD (1996) Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions. Tree Physiol 16:453–458

Pezeshki SR, DeLaune RD, Anderson PH (1999) Effect of flooding on elemental uptake and biomass allocation in seedlings of three bottomland tree species. J Plant Nutr 22:1481–1494

Smith MW, Bourne RD (1989) Seasonal effects on flooding on greenhouse-grown seedling pecan trees. HortSci 24:81–83

Stanturf JA, Schweitzer CJ, Gardiner ES (1998) Afforestation of marginal agricultural land in the lower Mississippi River Alluvial Valley, USA. Silva Fenn 32:281–287

Stanturf JA, Schoenholtz SH, Schweitzer CJ, Shepard JP (2001) Achieving restoration success: myths in bottomland hardwood forests. Restor Ecol 9:189–200

Stanturf JA, Conner WH, Gardiner ES, Schweitzer CJ, Ezell AW (2004) Recognizing and overcoming difficult site conditions for afforestation of bottomland hardwoods. Ecol Restor 22:183–193

Stanturf JA, Gardiner ES, Shepard JP, Schweitzer CJ, Portwood CJ, Dorris LC Jr (2009) Restoration of bottomland hardwood forests across a treatment intensity gradient. For Ecol Manag 257:1803–1814

Steele KL, Kabrick JK, Jensen RG, Wallendorf MJ, Dey DC (2008) Analysis of riparian afforestation methods in the Missouri Ozarks. In: Jacobs DF, Michler CH (eds) Proceedings of the 16th central hardwood forest conference. Gen Tech Rep NRS-P-24. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, pp 80–90

Tang ZC, Kozlowski TT (1982) Physiological, morphological, and growth responses of *Platanus occidentalis* seedlings to flooding. Plant Soil 66:243–255

Teskey RO, Hinckley TM (1977) Impact of water level changes on woody riparian and wetland communities. Vol III: Central Forest Region. Biological Services Report. US Department of the Interior, Fish and Wildlife Service, Washington, 36 pp

Unger IM, Muzika RM, Motavalli PP, Kabrick J (2008) Evaluation of continuous *in situ* monitoring of soil changes with varying flooding regimes. Commun Soil Sci Plant Anal 39:1600–1619

Van Sambeek JW, McGraw RL, Kabrick JM, Coggeshall MV, Unger IM, Dey DC (2006) Developing a natural field facility for evaluating flood tolerance of hardwood seedlings and ground covers. In: Buckley DS, Clatterbuck WK (eds) Proceedings of 15th central hardwood forest conference. Gen Tech Rep SRS-101. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, pp 727–733

Vepraskas MJ, Faulkner SP (2001) Redox chemistry of hydric soils. In: Richardson JL, Vepraskas MJ (eds) Wetland soils: genesis, hydrology, landscapes, and classification. Lewis Publishers, Boca Raton

Verpraskas MJ, He X, Lindbo DL, Skaggs RW (2004) Calibrating hydric soil field indicators to long-term wetland hydrology. Soil Sci Soc Am J 68:1461–1469

Walsh MP, Van Sambeek JW, Coggeshall MV (2008) Variation in flood tolerance of container-grown seedlings of swamp white oak, bur oak, and white oak. In: Jacobs DF, Michler CF (eds) Proceedings of the 16th central hardwood forest conference. Gen Tech Rep NRS-P-24. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, pp 446–456

Weber N (2005) Afforestation in Europe: lessons learned, challenges remaining. In: Stanturf JA, Madsen P (eds) Restoration of boreal and temperate forests. CRC/Lewis, New York, pp 121–135

Weigel DR, Dey DC, Kabrick JM (2008) Evaluation of Root Force^{TM} container seedlings of four oak species for bottomland forest restoration in southern Indiana: 5-year results. In: Lockhart BR, Gardiner ES, Dey DC (eds) 10th workshop on seedling physiology and growth problems in oak plantings. Gen Tech Rep NRS-P-32. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, p 11

Whitlow TH, Harris RW (1979) Flood tolerance in plants: A state-of-the-art review. Technical Report E-79-2. US Army Corps of Engineers Washington, Washington, 161 pp