Trees (2023) 37:1121–1136
https://doi.org/10.1007/s00468-023-02411-7

ORIGINAL ARTICLE

Resiliency of Nuttall oak but not Shumard oak to winter and spring flood: dormancy alone does not confer flood tolerance

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Received: 5 December 2022 / Accepted: 14 April 2023 / Published online: 9 May 2023

Abstract

Key message **Whereas Shumard oak seedlings are intolerant of dormant season flood, Nuttall oak seedlings are tolerant. Flooding more than 1–2 months beyond budbreak may have persistent negative impacts on Nuttall oaks.**

Abstract Since flooding in winter and spring is an integral part of bottomland hardwood ecosystems in the southeastern United States, moderately flood-tolerant oaks, like Nuttall oak (*Quercus texana*), should be well adapted to flooding during these seasons. To quantify the potential for injury from different lengths of winter flooding, we flooded seedlings of Nuttall oak and moderately flood intolerant Shumard oak (*Q. shumardii*) for 0, 1, 2, and 3 months, with the first month of flooding occurring during the dormant season. Flooding during dormancy had no effect on Nuttall oak, but Shumard oak seedlings had reduced growth in the spring. Flooding that extended beyond budbreak resulted in reduced leaf area and root biomass accumulation in spring for both species, while Shumard oaks also experienced high mortality. At the end of the growing season, Nuttall oaks that had been flooded accumulated tissue biomasses similar to non-flooded seedlings, except taproot biomass, which was reduced 40% by 3 months of flooding. It appears that Nuttall oak delayed fully investing in spring growth until after flooding subsided, and then was largely able to compensate following flooding that extended one month beyond budbreak. However, flooded Shumard oaks did not show similar signs of recovery. Thus, sites that flood at any time of year would not be suitable for Shumard oak. Our results suggest that natural or human-imposed flooding can extend several weeks beyond budbreak without harming Nuttall oaks, but inundation prolonged several months beyond budbreak could weaken the ability to respond to subsequent stresses.

Keywords Flood tolerance · Winter dormancy · Bottomland hardwood forests · *Quercus* seedlings · Greentree reservoirs · Lower Mississippi Alluvial Valley

Introduction

Bottomland hardwood forests are valuable, both ecologically and economically. As wetlands, they provide many ecological services such as natural flood water control, nutrient and sediment filtration, wildlife habitat, and net sequestration of 3.2–18.5 tons CO_2 equivalents per hectare annually (Jenkins et al. 2010). However, as flood control improved at the turn of the twentieth century, much of the bottomland hardwood forest in the southeastern United States was converted to agricultural land. For example, in the Lower Mississippi Alluvial Valley (LMAV), bottomland hardwood forests were reduced from 10 million hectares to only 2.8 million hectares in 1980 (Dabbert and Martin 2000). This deforestation resulted in habitat loss and fragmentation, as well as losses of the other ecosystem services bottomland forests provide. Over the past 30 years, efforts have focused on restoring

Communicated by M. Heydari.

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and conserving the dwindling bottomland hardwood forests in the South Eastern United States through incentive programs, such as the Wetland Reserve Program, and creating greentree reservoirs (Cowan 2008; Jenkins et al. 2010; King and Fredrickson 1998). Greentree reservoirs are sections of forested wetlands that are deliberately impounded to attract ducks, and to recreate other bottomland ecosystem functions (Dabbert and Martin 2000).

The specific hydroperiod impacts patterns of regeneration and long-term sustainability of bottomland hardwood forests. Flooding also shapes the tree species composition and distribution within bottomlands by preventing flood intolerant species from inhabiting low lying frequently flooded areas, while flood tolerant species survive in flood zones due to various physiological adaptations (Gardiner 2001; Hodges 1997; Lockhart et al. 2005; Simmons et al. 2011; Tanner 1986). Thus, within bottomland hardwood forests species with a range of flood tolerance exist, as flood tolerant species inhabit areas that are frequently flooded, while moderately flood intolerant species inhabit ridges that are not flooded as frequently or are flooded less intensely. Nuttall oak and Shumard oak (*Quercus texana* and *Q. shumardii*, respectively) are common in bottomland hardwood forests of the southeastern United States, especially in the LMAV, and are desirable from both wildlife and timber production perspectives. Both Nuttall and Shumard oaks can withstand a brief flood, but the effects of longer duration flooding are more severe (Anderson and Pezeshki 2000; Hosner and Boyce 1962; King and Fredrickson 1998; Pezeshki and Anderson 1997). Nuttall oak, a moderately flood tolerant species, responds to flooding by slowing overall root and shoot growth, and producing adventitious roots and hypertrophied lenticels, allowing individuals to survive inundation, albeit with reduced leaf, stem and root biomass (Anderson and Pezeshki 2001; Jacques et al. 2021; Pezeshki and Anderson 1997; Pezeshki et al. 1999). In Shumard Oak, a moderately flood intolerant species, flooding inhibits root growth and within two months leads to lateral root mortality, and substantial shoot mortality (Hosner and Boyce 1962).

One of the major stresses imposed by flooding is hypoxia, because molecular oxygen diffuses much more slowly through water than air, which reduces the oxygen availability to roots (Sauter 2013). This can interrupt sucrolysis and aerobic respiration, which impacts the production of ATP (adenosine triphosphate), the energy currency of the cell (Kogawara et al. 2014; Sloan et al. 2016). Low oxygen supply forces roots to produce ATP by anaerobic respiration, which is very inefficient, producing only 5.5–11% the amount of ATP per unit of glucose compared to oxidative phosphorylation (Parent et al. 2008; Sauter 2013; Voesenek and Bailey-Serres 2013). Reliance on anaerobic respiration may also constrain the capacity to perform cellular maintenance functions and other energetic processes, and may be a contributing factor in the reduction of root growth observed in oaks during periods of flooding (Colin-Belgrand et al. 1991; Gardiner and Hodges 1996; Pezeshki 1991). Under prolonged inundation, the inefficiency of anaerobic respiration could quickly deplete carbohydrate stores (Angelov et al. 1996; Gérard et al. 2009; Gravatt and Kirby 1998), which may limit the length of time roots can survive flooding (Fujita et al. 2020; Repo et al. 2020). Barriers reducing radial oxygen loss from roots may be an adaptation that increases oxygen retention in roots thereby increasing oxygen use efficiency (Colmer et al. 2019; Ejiri and Shiono 2019; Pedersen et al. 2021b; Watanabe et al. 2017). The flood-tolerant oak *Quercus robur* is able to retain and use oxygen more efficiently than the less flood tolerant *Quercus petraea*, and perhaps maintain some aerobic respiration in roots (Bourgeade et al. 2018). Additionally, stress and damage may be incurred due to oxidative stress during reoxygenation when flooding subsides, and rapid induction of antioxidant pathways may be another important aspect of flood tolerance (Yuan et al. 2017). Therefore, it is possible that flood tolerant species are not only able to tolerate flooding, but may be better able to cope with reoxygenation stress compared to less flood tolerant species.

Flooding may affect aboveground functions, such as transpiration and photosynthesis, as well (Gardiner and Hodges 1996; McLeod et al. 1999; Rasheed-Depardieu et al. 2015; Repo et al. 2017). Reduced sink demand as indicated by reduced translocation of carbon to roots precedes, and therefore may trigger downregulation of photosynthesis (Sloan et al. 2016; Sloan and Jacobs 2008). Nuttall oak leaves decreased photosynthetic gas exchange and stomatal conductance when flooded during the growing season, which led to a reduction in total biomass and leaf area (Anderson and Pezeshki 2000). However, species such as Nuttall oak, that can quickly recover photosynthesis after a short-term flood (Anderson and Pezeshki 2000; Pezeshki and Anderson 1997), are at an advantage over those that are slower to recover (Gong et al. 2007; Pezeshki et al. 1996; Renninger et al. 2020). The physiological effects of flooding on Shumard oak have been less well studied, but Shumard oak is expected to have decreased height growth and decreased survival when flooded during the growing season compared with Nuttall oak (Hook 1984; Jacques et al. 2021). If seedlings are allowed the chance to recover once a flood subsides, the chance of survival increases (Bratkovich et al. 1994). To recover, the plant must repair the damage from the flood by replacing dead roots, restoring stressed roots to full functionality, and replenishing leaf area. Therefore, it is possible that flood tolerant species, such as Nuttall oak, are better able to recover after flooding compared to species more susceptible to flooding, such as Shumard oak.

Historically, bottomland hardwood forests with natural hydrology in the mid-south and southeastern United States experienced flood primarily during winter and spring, when inputs from both precipitation and snowmelt runoff are greatest. Flooding most often occurred in pulses of short duration (weeks), but occasionally some winters had flooding of longer duration (months). Presently many bottomlands are commonly flooded for longer durations, often well into the spring, due to a combination of human influence on hydrology and changing weather patterns. Dormant season flooding is assumed to be tolerable for bottomland red oaks (King and Fredrickson 1998). However, studies of birch (*Betula* species) suggest that flooding can impact subsequent growth, even when flooding occurs during winter dormancy (Domisch et al. 2018; Repo et al. 2021; Wang et al. 2015, 2017). Presumably the more flood-adapted Nuttall oak is less stressed than Shumard oak when flooding extends beyond the dormant season. However, it is unclear how long flooding would need to continue before growth reductions and root damage would have persistent effects.

Our study sought to determine how well Nuttall oak and Shumard oak seedlings can tolerate flooding that occurs only during the dormant season, and when flooding extends beyond dormancy into the growing season. To address this, we flooded potted seedlings of both species for different durations, beginning in the dormant season, to test for effects on survival over winter and spring growth. Additionally, we tested whether any winter or spring flood effects were merely delays in growth, or if they persist beyond the initial spring growth period if flooding is removed for the rest of the growing season. Since taproot biomass accumulation appeared to be the most sensitive persistent flood effect, we developed a regression model of the relationship between flood duration and the magnitude of end-of-season taproot biomass for both species that could be used to predict the possible consequences of different flooding scenarios.

Materials and methods

Plant materials and growth

One-year-old bare root Nuttall and Shumard oak seedlings were provided by the Arkansas Forestry Commission. Seed was an open-pollinated genetic mix from the Arkansas Forestry Commission seed orchard, and were all grown under the same conditions at Baucum Nursery (North Little Rock, AR, USA). In late January and early February of 2018, we planted 132 seedlings per species in individual 9600 cm^3 pots containing top soil with low organic matter for growth outdoors on the University of Arkansas at Monticello Campus (33°35′29.66″N, 91°48′54.33″W). Once planted, eleven seedlings of each species were selected randomly for placement in each of the twelve 0.42 m^3 tubs, which were fitted with drain holes and plugs to implement and remove the flood treatment. Within tubs, seedlings were interspersed so seedlings of the same species did not neighbor each other. Seedlings that were not destructively harvested at the end of the flooding treatment were watered to field capacity conditions every 3–4 days until the end of the growing season.

Flooding treatment

Soil flooding was imposed by plugging drain holes and filling the tubs, which brought water to 2.5 cm above the soil line (Fig. 1). We included four flooding treatments of different duration, a control that was not flooded, 1 month of flooding, for which the entirety of the flood was during the dormant season, two months of flooding with one month during the dormant season and one month during the growing season, and 3 months of flooding with 1 month in the dormant season and two months in the growing season. The flood treatments were all initiated on 18 February 2018 and ended on 18 March 2018 for the one month flood, 18 April 2018 for the two month flood, and 18 May 2018 for the three month flood. Once all flooding treatments were complete, half of the plants were sampled for measurements as described below.

Sampling for non-destructive measurements

We measured leaf chlorophyll content, new branch growth, seedling height, and basal diameter to evaluate flooding effects on spring growth. In addition to a spring measurement on 18 May 2018, we measured chlorophyll three more times in mid-summer, including 4 July 2018, 16 July 2018, and 7 August 2018. Chlorophyll content was determined by fluorescence (CCM-300, Opti-Sciences, Hudson, New Hampshire), from the linear relationship between the ratio

Fig. 1 Nuttall and Shumard oak seedlings in tubs. To impose the flood treatment, the drainage holes of the treated tubs were plugged, and the tubs filled to the top with water. River stones were placed at the bottom of tubs prior to placing pots to adjust pots to the desired flood depth

of fluorescence at 735 nm/700 nm and total leaf chlorophyll content (Gitelson et al. 1999).

New branch growth was taken on 27 June 2018, and again near the end of the growing season on 10 October 2018, when no further branch growth was expected (Sample and Babst 2019). We used bud scars to identify and measure the prior year branch lengths, and the lengths of the first, second, and third flushes of new growth for each branch. From those measurements, the total number of branches on each seedling was tallied, and total branch length of each seedling were determined as the sum of all branch lengths.

We measured heights to the tallest live shoot tip and basal diameters using a meter stick and calipers, to the nearest 0.1 cm and 0.1 mm, respectively. Heights and basal diameters were measured at the beginning of the experiment (18 February 2018) to obtain baseline levels before growth, after all flood treatments concluded (18 May 2018), and at the end of the growing season just before harvest (9 October 2018). Height relative growth rate (height RGR) was calculated as: $\frac{\text{height}-\text{height}_{\text{initial}}}{\text{height}_{\text{average}}\times\text{days}}$ where *height* is the height at the time of consideration, the $height_{initial}$ is the height at the beginning of the experiment, $\text{height}_{\text{average}}$ is the average of initial and final heights, and *days* is the number of days between the two height measurements. Diameter relative growth rate (diameter RGR) was calculated using the same formula, but substituting diameters for height measurements.

Biomass and leaf area determination

We conducted a spring and a fall harvest to assess differences in seedling growth between the flooding treatments. The spring harvest was immediately after the longest flooding treatment ended (18 May 2018) and the fall harvest was at the end of the growing season (18 October 2018). Total leaf area for each plant was measured as soon as the leaves were removed from each seedling during the harvest using a LI-3100C (LiCor, Lincoln, Nebraska, USA). Each sampled seedling was separated into 6 different tissues: main stem, branches, leaves, taproot, fine roots, and new roots. We defined fine roots as any lateral root growing from the taproot; we defined new roots as any white fleshy roots either growing from the taproot or from the end of a brown fine root. The number of seedlings sampled for the three month long flooding treatment was very low due to high mortality (Table 1). All samples were oven dried at 60 °C until dry and then weighed to obtain dry biomass for each tissue.

Statistical analysis

SAS ver. 9.4 was used for all statistical analysis. The data for each species and sampling period were analyzed using a general linear model (GLM) to determine flood duration effects on the dependent variables: leaf mass, stem mass, branch mass, fine root mass, new root mass, taproot mass, height RGR, diameter RGR, leaf area, chlorophyll concentration, and new branch growth. Where GLM indicated a significant treatment effect, a post hoc Tukey–Kramer multiple comparison analysis was used to test for differences between flooding treatments. Mortality was analyzed by the Logistic procedure, using the contrast statement to test for pairwise differences between flood treatments. Assumptions for all tests were checked visually, and $\alpha = 0.05$.

Table 1 Mortality of Nuttall and Shumard oak seedlings across three different flood durations, and an unflooded control

	Flood duration (months)			
	0	1	2	3
Nuttall oak	6%	3%	9%	9%
Shumard oak*	3%^{a}	9%^{a}	52%^{b}	94%^{c}

Mortality at the day of the second harvest (18 October 2018) is shown as a percent of the total number of seedlings planted. Seedlings that were alive and were taken for the first harvest (18 May 2018) were included as live seedlings. * indicates statistical significance of the logistic model. Different subscript letters indicate values that are significantly different

Results

There were no significant flood effects on Nuttall oak mortality, but Shumard oak mortality was significantly increased by 2 and 3 months of flooding (Table 1). After the conclusion of the longest flood treatment on 18 May 2018, among Nuttall oak, only the seedlings exposed to 3 months of flooding had significantly reduced total biomass, to 47% of the unflooded control seedling biomass (Fig. 2). Biomasses of surviving Shumard oak seedlings were significantly reduced by 43% even with only 1 month of flooding during the dormant season, and by 58% for the 2-month flood treatment compared to unflooded controls (Fig. 2). In the three-month long treatment, all of the Shumard oak seedlings appeared to be dead, and so were not sampled in the spring. However, two of the Shumard oak seedlings from the three month flood treatment eventually re-sprouted later in the summer.

Tissue specific effects of flooding during dormancy and beyond bud break on spring growth

Nuttall oak aboveground biomass on 18 May 2018 (i.e., “Spring”) was largely unaffected by exposure to one month of flooding that was limited to the dormant season. However, there were 60–90% reductions in leaf area, leaf mass, and branch mass for the two or more month flooding treatments that overlapped with the early growing season (Fig. 3).

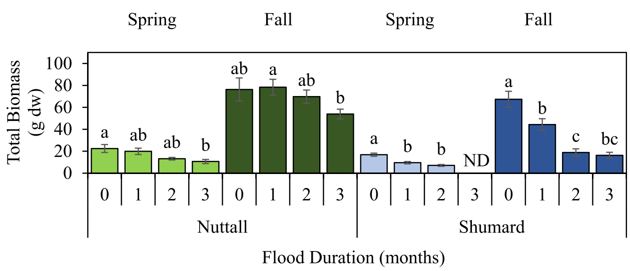

Fig. 2 Nuttall and Shumard oak total plant biomass from two harvests, one in the spring (18 May 2018) and one in the fall (18 October 2018), across four levels of flood treatment duration. Flooding of all durations, except the unflooded control, was initiated 18 February 2018. Flood duration levels include (0) unflooded controls, (1) 1 month flooding treatment which occurred during the last month of winter dormancy, and (2 and 3) 2 and 3 month flooding treatments, respectively, where flooding extended into the growing season. Where ANOVA indicated statistically significant differences between flood treatments, different letters above error bars represent significant differences between flooding lengths according to a Tukey–Kramer analysis. Error bars are standard error. In Nuttall oaks $n=15$ except for the three month long flood treatment in the spring harvest ($n=9$), and in the controls and three month flood treatment in the fall harvest ($n=13$ and 19, respectively). In Shumard oaks $n\geq 12$ except for the two month long flood treatment in the spring harvest ($n=5$) and the two and three month long flood treatment in the fall ($n=9$ and 2, respectively). ND indicates where no data was available due to high mortality

Conversely, Shumard oak leaf area, leaf mass, and branch mass were negatively impacted even by dormant season flooding (reduced by 49%, 55%, 70%, respectively). Flooding that extended into the growing season led to more severe reductions in Shumard oak aboveground biomass and leaf area (Fig. 3). Also, we observed a tendency for some Shumard oak seedlings that were still inundated during budbreak to initiate new shoots that would wilt and dry out before reaching 1–2 cm in length. There were no significant flood effects on main stem biomasses for either species.

On 27 June 2018 (i.e., "Summer"), 6 weeks after the removal of the longest flood treatment, many seedlings were growing a second or third flush of leaves. The more flood-tolerant Nuttall oaks had no significant losses in new branch growth when flooding was limited to the dormant season (Fig. 4). Growth of new branches was reduced in Nuttall oaks only as a result of the longest flood duration, differing from Shumard oaks, where new branch growth was reduced by all flooding treatments (Fig. 4). Only the Nuttall oak seedlings that had been exposed to 3 months of flooding had significantly reduced first flush length and total length of new branches summed for the whole plant, which were both reduced by about 66% compared to unflooded controls (Fig. 4). In contrast, at the same time point, all flood durations significantly reduced first flush length and total new branch length of Shumard oaks, including a 54–58% reduction where flooding was terminated before bud break. Average branch length followed a similar trend as total branch length for all treatments in both species. There was a significant reduction in the average number of branches only for the Shumard oak seedlings that were flooded for 2 months (Fig. 4).

For seedlings harvested in spring, new root growth was decreased by flooding in both species. Nuttall oak fine roots, new roots, and taproots were not significantly affected by dormant season flooding, but flooding that extended into the growing season significantly reduced new root mass (Fig. 3). Nuttall oak fine root and taproot masses were not significantly affected by flooding. Shumard oak roots were impacted by even one month of flooding in the dormant season. Exposure of Shumard oaks to only one month of flooding during the dormant season caused a significant 78% reduction in new root mass compared to controls, and the reduction was more severe for seedlings exposed to longer flooding that extended into the growing season (Fig. 3). The overall model indicated significant flood effects on Shumard oak fine root biomass ($P=0.04$), but the Tukey's post hoc test did not detect any significant pairwise effects between flood treatments. There was no significant flood effect on Shumard oak taproot mass in spring (Fig. 3). Whole seedling morphology was not affected in Nuttall oak but was in Shumard oak. Two months of flooding significantly increased the root:shoot biomass ratio of Shumard oak seedlings (Table 2).

Recovery or persistence of flood effects through the growing season

By the end of the growing season (sampled 18 October 2018; i.e., "Fall"), whole seedling biomass of Nuttall oaks that were exposed to only dormant season flooding remained similar to unflooded control seedlings at the end of the growing season, indicating no delayed effects of dormant season flooding (Fig. 2). Shumard oaks that were flooded only during the dormant season, however, still had 34% less total biomass than unflooded controls by the end of the growing season (Fig. 2). Flooding that extended one month beyond budbreak (i.e., 2 months total flooding) did not affect whole seedling biomass of Nuttall oak, but flooding two months beyond budbreak significantly reduced total biomass by 29%. Growing season flood was much more stressful for the Shumard oak seedlings, and with 72–76% lower total biomass than control seedlings, they showed little sign of recovery from flooding by the end of the growing season (Fig. 2).

Above-ground growth of flooded Nuttall oak had mostly recovered to similar levels as non-flooded controls across all flooding treatments (Fig. 3, 4). There was a significant overall flood effect on Nuttall oak main stem biomass ($P=0.047$), but no pairwise differences were detected

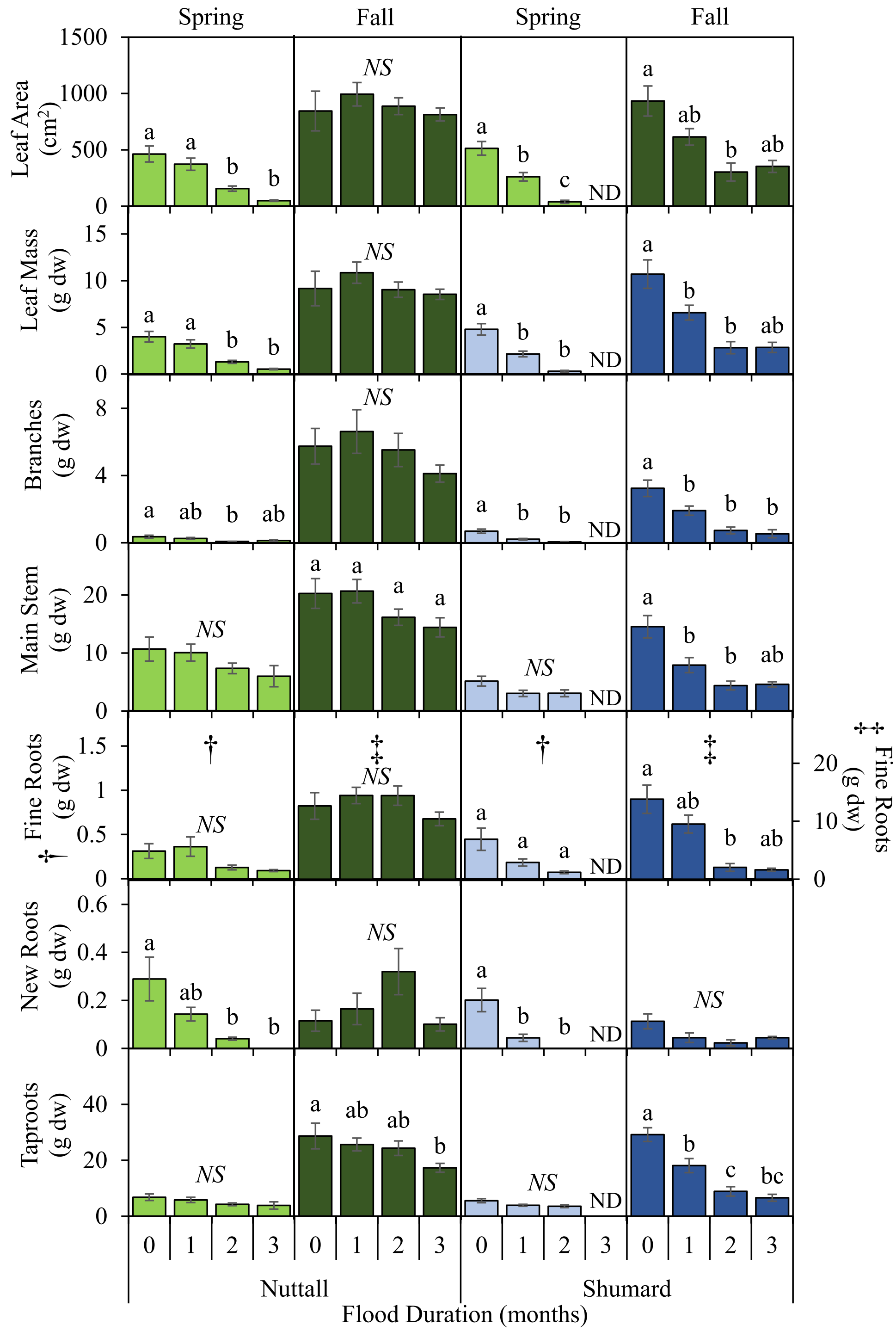

Fig. 3 Flood duration effects on Nuttall oak and Shumard oak tissue biomass from two harvests, one in the spring (18 May 2018) and one in the fall (18 October 2018). Flood treatments of 0, 1, 2, and 3 months duration are as described in Fig. 2 caption. Where the ANOVA comparing flood duration effects was significant, different letters above error bars represent significant differences between flooding duration levels according to a Tukey–Kramer analysis. *NS* indicates where the ANOVA was not significant. Error bars are standard error. ND represents no data available to due to high mortality. For all Nuttall oaks tissues in the spring harvest $n=15$ except for the three month long flood treatment where $n=9$. In the fall harvest of Nuttall oaks $n \geq 13$ for all tissues. For the spring harvest of Shumard oaks $n=12$ for all treatments and tissues except for the 2 and 3-month long flood where $n=5$ and 0, respectively. For the fall harvest of Shumard oaks $n=14$, 15, 9, and 2 for the 0–3 month treatments, respectively. † indicates where fine root biomass is scaled to the left Y axis. ‡ indicates where fine root biomass is scaled to the right Y axis

between flood treatments. However, for flooded Shumard oak, growth of most above-ground tissues was still 34–76% lower than unflooded controls, especially seedlings for which flooding extended into the growing season (Fig. 3, 4).

Flood treatments had no impact on number of branches, individual flush lengths, total branch growth, or height RGR of Nuttall oak seedlings by the end of the growing season, but diameter RGR was significantly reduced (Fig. 4, 5). However, Shumard oaks flooded for even one month still had significantly reduced branch elongation (Fig. 4). Those Shumard oaks exposed to longer duration flooding that overlapped the growing season had significantly reduced total branch length, height RGR, and diameter RGR compared to unflooded controls, except for the 3 month flood treatment, which had a limited sample size ($n=2$ surviving seedlings; Fig. 4, 5). In fact, diameter RGR was near zero for Shumard

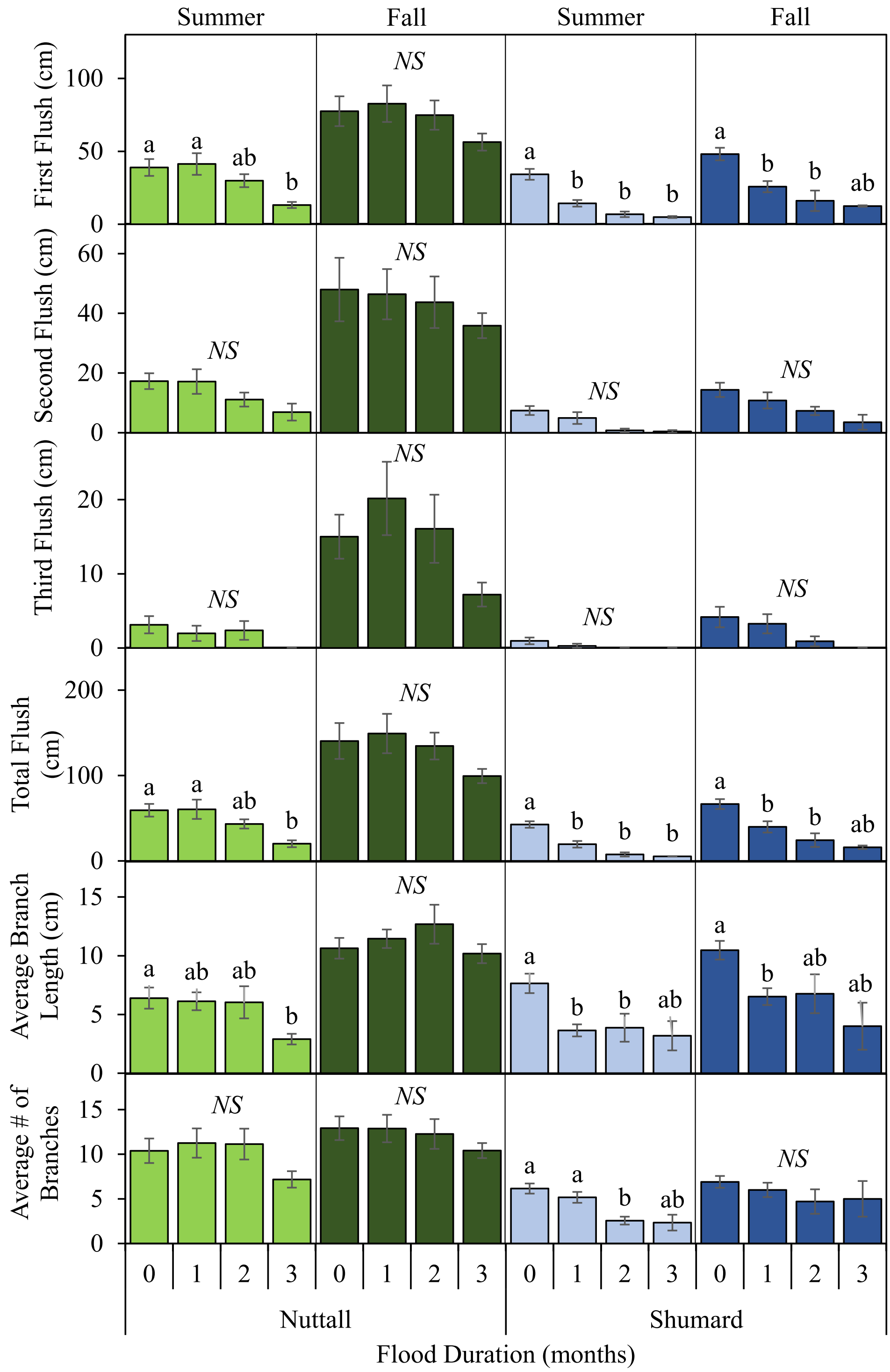

Fig. 4 Patterns of new growth of Nuttall and Shumard oak seedlings across four levels of flood duration. Measurements were taken in the early summer (27 June 2018) and in the fall (10 October 2018), and include average length of first flush of growth (Flush 1), average second flush length (Flush 2), average third flush length (Flush 3), total new branch length per seedling (sum of all flush lengths), average new length per branch, and average number of branches per seedling. ANOVA was used to test for differences between flooding lengths for each new growth measurement in either early summer or fall for each species. Different letters above error bars represent significant differences according to a Tukey–Kramer analysis. Error bars are standard error. Sample sizes for the controls, one month, two month, and three month long flood treatments, respectively: Summer Nuttall oak $n = 13$, 16, 15, 17; Fall Nuttall oak $n = 12$, 16, 15, and 22; Summer Shumard oak $n = 20$, 18, 9, and 3; Fall Shumard oak $n = 20$, 17, 10, 2

oaks treated with two and three months of flooding. There was a negative height RGR in Shumard oaks exposed to growing season flood, which was due to top dieback that reduced the height of those seedlings (Fig. 5).

At the end of the growing season, Nuttall oak belowground biomass mostly did not differ from controls. The exception, taproot mass was significantly reduced by 40% in the longest duration flood treatment. In contrast to Nuttall oaks, by the same time, both fine root and taproot biomasses of Shumard oak seedlings were significantly affected by flooding. In fact, Shumard oak seedlings that had experienced flooding only during the dormant season still had 38% less taproot biomass than unflooded controls (Fig. 3). Longer than one month of flooding reduced end of growing season

Table 2 Root:shoot biomass ratios of Nuttall oak and Shumard oak seedlings across three different flood durations, and an unflooded control in spring (18 May 2018) and fall (18 October 2018)

	Flood duration (months)			
	0	1	2	3
Nuttall oak				
Spring	0.52 ± 0.07	0.49 ± 0.04	0.58 ± 0.09	0.97 ± 0.44
Fall	1.16 ± 0.10	1.10 ± 0.06	1.29 ± 0.14	1.08 ± 0.06
Shumard oak				
Spring	0.62 ± 0.08[a]	0.83 ± 0.06[ab]	1.22 ± 0.23[b]	ND
Fall	1.63 ± 0.13	1.76 ± 0.19	1.81 ± 0.61	1.03 ± 0.03

Mean ± SEM of root:shoot ratios (g dry wt/g dry wt) are shown. Flood effects were significant only for spring sampling of Shumard oak (Shumard oak spring $P = 0.003$; Shumard oak fall $P = 0.8$; Nuttall oak spring $P = 0.2$; Nuttall oak fall $P = 0.4$). Different subscript letters indicate values that are significantly different. In Nuttall oaks $n = 15$ except for the three month long flood treatment in the spring harvest ($n = 9$) and in the controls in the fall harvest ($n = 13$). In Shumard oaks $n \geq 12$ except for the two month long flood treatment in the spring harvest ($n = 5$) and the two ($n = 9$) and three month long flood treatment ($n = 2$) in the fall. ND indicates where no data was available due to high mortality

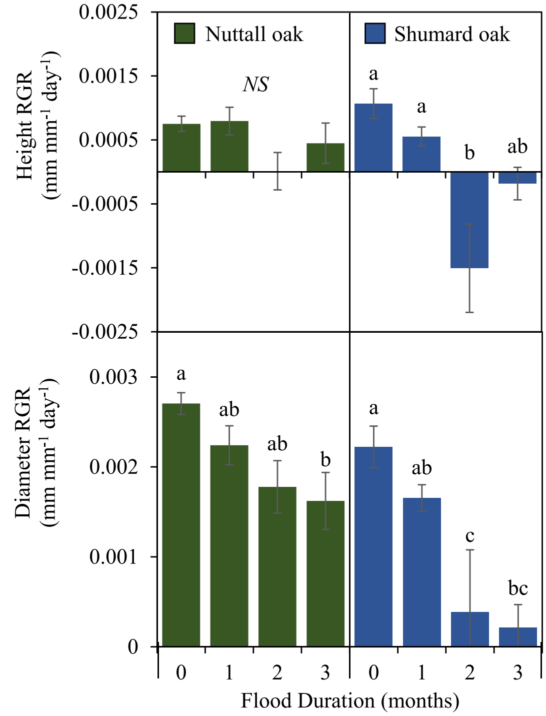

Fig. 5 Flood duration effects on Nuttall and Shumard height and diameter relative growth rates or RGR [RGR = (height$_{final}$–height$_{initial}$)/(mean height × days)]. Measurements are from planting (18 February 2018) to the end of the growing season (9 October 2018). ANOVA was used to test for differences between flood duration levels. Where ANOVA indicated a significant difference, different letters above error bars represent significant differences between flooding lengths according to a Tukey–Kramer analysis. *NS* indicates where the model was not significant. Top die-back resulted in some height growth measurements that were negative. Error bars are standard error. For Nuttall oaks, $n = 13$, 15, 15, and 22 for control, 1, 2, and 3 month flood durations, respectively. For Shumard oaks, $n = 20$, 17, 10, and 2 for the controls, 1, 2, and 3 month long flood treatments, respectively

root biomasses by ~ 75–80% in Shumard oak (Fig. 3). By the fall, whole seedling morphology (i.e., root:shoot biomass ratio) was not affected by flood in either Nuttall oak or Shumard oak seedlings (Table 2). Since reduced main stem and taproot masses were the only persistent effect of flooding on Nuttall oak, we generated a model using linear regression to predict the magnitude of the end-of-season main stem and taproot biomass reductions from the number of days exposed to flooding (Fig. 6). The relationships were significant for both species, with a stronger relationship for taproot (TR) than main stem (MS), and for Shumard oak ($R^2_{TR} = 0.49$; $P_{TR} < 0.0001$; $R^2_{MS} = 0.33$; $P_{MS} < 0.0001$) than Nuttall oak ($R^2_{TR} = 0.14$; $P_{TR} = 0.003$; $R^2_{MS} = 0.11$; $P_{MS} = 0.008$). The intercept for the taproot-flood duration regression was similar for both species (~ 29 g), consistent with similar end-of-season taproot masses for unflooded control seedlings of both species. However, there was a steeper slope for Shumard oak (− 0.31 g of taproot per day of flooding) than for Nuttall oak (− 0.12 g of taproot per day of flooding), reflecting the greater persistent flood effects on taproot growth in Shumard oak (Fig. 6). For the main stem, the intercept was higher for Nuttall oak (21 g) than Shumard oak (14 g), and there was a steeper slope for Shumard oak (− 0.15 g of main stem per day of flooding) than for Nuttall oak (− 0.08 g of main stem per day of flooding) (Fig. 6).

Flood-stressed seedlings tended to have delayed accumulation of chlorophyll in leaves. Flooding had limited impact on chlorophyll content in Nuttall oak, but there were some stronger trends in Shumard oak leaves in early spring that dissipated later in the growing season. In the spring, Nuttall oaks in the three month flood treatment had slightly lower (19%) leaf chlorophyll content than controls, but in Shumard oaks the 2-month flood treatment reduced chlorophyll content by 64% (Fig. 7). Nuttall oak seedlings that experienced the longest flooding increased their leaf chlorophyll content during the post-flood recovery period, to final chlorophyll contents 30% higher than unflooded controls (Fig. 7). Late in the recovery period, in August, leaf chlorophyll concentrations of Shumard oak seedlings flooded during the growing season became similar to those in non-flooded control seedlings (Fig. 7).

Discussion

In dormancy, Nuttall oak was very tolerant of flooding, but Shumard oak was not. Most studies of flood effects on bottomland hardwood species have focused on the effects

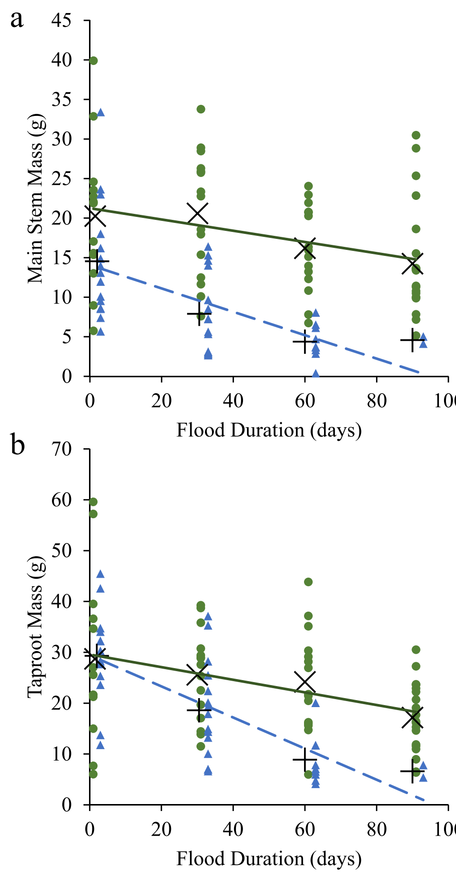

Fig. 6 End of season main stem mass **a** and taproot mass **b** as a function of flood duration in Nuttall oak and Shumard oak. Flood duration treatments were the same for both species, beginning during the dormant season as described in the Fig. 2 caption, but Shumard oak symbols (triangles) are slightly offset to the right in the graph to avoid overlap with Nuttall oak symbols (circles). Means within flood duration treatments are indicated by "×" for Nuttall oak, and "+" for Shumard oak. Linear regression lines are indicated by solid line for Nuttall oak (main stem: $P=0.008$, $R^2=0.11$, intercept = 21.3, slope = − 0.077; taproot: $P=0.003$, $R^2=0.14$, intercept = 29.4, slope = − 0.124), and dashed line for Shumard oak (main stem: $P<0.0001$, $R^2=0.33$, intercept = 13.6, slope = − 0.148; taproot: $P<0.0001$, $R^2=0.49$, intercept = 28.5, slope = − 0.306). For Nuttall oaks $n=62$, and for Shumard oaks $n=40$

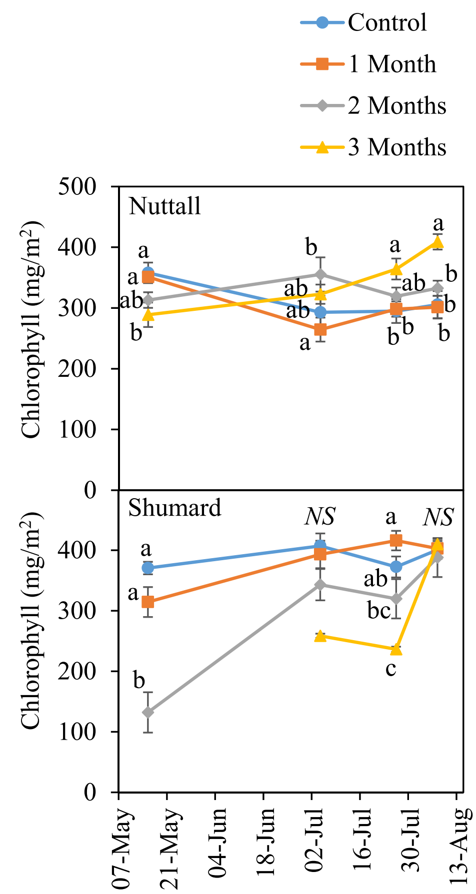

Fig. 7 Flood duration effects on leaf chlorophyll content of Nuttall oak and Shumard oak seedlings during spring (15 May 2018) and summer (4 July, 26 July, 7 August 2018). ANOVA was used to test for differences between flood duration levels within each date. Where ANOVA indicated a significant difference, different letters near markers represent significant differences according to a Tukey–Kramer analysis. *NS* indicates where there was not a significant flood effect. Error bars are standard error. For Nuttall oaks, $n\geq 13$ for all flood durations and time points, except on 15 May where $n=9$ for the 3-month long flooding treatment. For Shumard oaks $n\geq 12$ for 0–2 month flood durations and time points, except on 15 May where $n=5$ for 2 month flood. For the Shumard oak three month long flooding treatment, $n=2$ for all time points due to high mortality, except on 15 May, when $n=0$, because no leaves had emerged on Shumard oak seedlings that were flooded for 3 months immediately following flood due to high mortality and dieback

of flood during the growing season. However, flooding in many places, including the southeastern United States and especially the LMAV, is more common during the dormant season and early spring due to greater seasonal precipitation and runoff from snowmelt. Given that flooding inhibits growth in oaks (Fujita et al. 2020; Gérard et al. 2009; Jacques et al. 2021), the responses of oaks to flooding are most similar to the "low oxygen quiescence strategy" described by Bailey-Serres et al. (Bailey-Serres et al. 2012), which involves reducing metabolic activity and growth to conserve resources. Thus, it seems reasonable to suppose that dormancy, which is defined by quiescence, would result in flood tolerance even for tree species that are less tolerant of flooding during the growing season. In our study, soil flooding that was limited to the dormant season (i.e., 1 month flood treatment) caused no mortality and no signs of stress in Nuttall oak seedlings, which are considered moderately flood tolerant. On the contrary, winter flooding inhibited growth of Shumard oak, which is moderately flood intolerant, during the subsequent growing season, as evidenced by a 34% reduction in total biomass accumulation. The lower impact of flooding during dormancy on Nuttall oak than Shumard oak, suggests that dormancy alone does not confer complete tolerance of flooding. In birch grown in

Finland also, winter flooding had greater effects on the less flood tolerant *Betula pendula* than the more flood tolerant *B. pubescens* (Wang et al. 2015). Even so, winter flood effects on *B. pendula* were very limited including no effects on leaf production in the spring following flooding (Domisch et al. 2018; Repo et al. 2021), unlike the growth reduction we observed in Shumard oak. These trends of varying tolerance of dormant season flood in both oak and birch species suggest that mechanisms other than the reduced metabolic activity during dormancy are essential to protect trees from winter flood effects on subsequent spring growth.

Since roots were the only tissues directly exposed to flooding, all effects of dormant season flood on Shumard oaks in our study originated from root stress. Dormant season flooding impacted both branch elongation and root growth, resulting in reduced biomasses of most Shumard oak tissues, including leaves, branches, and new roots. Similarly in birch, dormant season flooding inhibited subsequent spring root growth more in *B. pendula* than in the flood tolerant *B. pubescens* (Wang et al. 2015). Inhibited lateral root initiation and elongation, and fine root mortality have also been observed as a consequence of flooding during the growing season in red oaks, regardless of flood tolerance ranking (Anderson and Pezeshki 2001; Bourgeade et al. 2018; Fujita et al. 2020; Pezeshki et al. 1999). Roots, especially fine roots, are important in the acquisition of soil nutrients and water to support new stem and leaf growth, and photosynthesis in the spring (Gazal and Kubiske 2004). Therefore, the aboveground growth losses were probably caused by a reduction in functional root tissues in Shumard oaks, but not in Nuttall oaks. Similar to Nuttall oak, although flooding during the growing season can harm *B. pubescens* roots, soil flooding during winter caused little damage to roots of *B. pubescens* (Repo et al. 2021). Freezing of flooded soils during dormancy reduced root growth and increased root mortality, and disrupted the allocation of carbohydrates between stem and roots of *B. pendula* (Domisch et al. 2018; Repo et al. 2021). However, combined flooding and freezing is not typically a factor for Nuttall oak and Shumard oak, because freezing temperatures below the soil surface are rare in the southeastern United States. Flood tolerant *Betula* also has the capacity for compensatory root growth in the spring following winter root damage (Repo et al. 2021). Thus, it is possible that the greater subsequent overall spring growth of Nuttall oak than Shumard oak seedlings that were flooded during dormancy may have been due to higher survival of fine roots in Nuttall oaks, as well as a greater ability to quickly resume growth of new fine roots.

When flooding is encountered during dormancy, it is possible that moderately flood tolerant trees, such as Nuttall oak, might further downregulate root activity, or that intolerant species such as Shumard oak may increase root activity as a maladapted stress response. Alternatively, Nuttall oak may have additional adaptations to flooding and hypoxia that Shumard oaks do not have. Studies of flooding during the growing season have suggested multiple adaptations of flood tolerant oak species, including hypertrophied lenticels that may provide water and/or oxygen to the stem (Anderson and Pezeshki 2001; Parelle et al. 2006; Pezeshki and Anderson 1997; Rosner and Morris 2022), adventitious roots that can access sufficient oxygen to supply water and nutrients to shoots (Anderson and Pezeshki 2001; Kreuzwieser and Rennenberg 2014; Le Provost et al. 2016; Parelle et al. 2007; Pezeshki and Anderson 1997; Shimamura et al. 2010), barriers to radial oxygen loss from roots for more efficient use of available oxygen (Bourgeade et al. 2018; Le Provost et al. 2016), adaptations to maintain metabolism anaerobically over the long-term, such as elevated alcohol dehydrogenase activity (Ferner et al. 2012; Parelle et al. 2006; Provost et al. 2012; but see also Pezeshki 1991; Pezeshki et al. 1996), greater carbohydrate reserves to maintain the inefficient anaerobic respiration for a longer period of time (Gérard et al. 2009), an unknown mechanism that allows continued phloem unloading during hypoxia to maintain soluble sugar supplies in roots (Ferner 2009), adaptations to efficiently metabolize or excrete the toxic byproducts of anaerobic respiration, such as ethanol and its downstream product acetaldehyde (Armstrong et al. 1994; Crawford 1982; Ferner et al. 2012; Schmull and Thomas 2000), and mechanisms that allow faster recovery of stomatal conductance (Renninger et al. 2020), which may include upregulation of aquaporins to recover water conductivity through the root system, and adaptations of the signal transduction pathways regulating response to hypoxia (Tan et al. 2018). Differences in stomata anatomy and function would have been irrelevant while the seedlings had no leaves during the dormant season. Similarly, adventitious roots may be less important during dormancy, when there is no need to maintain a transpiration stream. Also, one of the coping mechanisms to avoid ethanol/acetaldehyde toxicity is to transport ethanol from roots via the transpiration stream and metabolize the ethanol in leaves (Ferner et al. 2012; Kreuzwieser et al. 2004, 1999; MacDonald and Kimmerer 1993). With no transpiration stream to remove ethanol from roots during winter, metabolic means of minimizing ethanol/acetaldehyde buildup, as well as maintaining carbohydrate reserves, restricting radial oxygen loss, and maintaining the minimum required metabolism during winter might be of greater importance. The AtNIP2;1 channel for excretion of lactic acid, which increases early during hypoxia, was recently discovered, and appears to be an important adaptation for survival of flood (Beamer et al. 2021). In addition to limiting radial oxygen loss, the suberin-based barrier may restrict entry of phytotoxic compounds produced by soil microbes under hypoxia or elements mobilized from soil under reducing conditions (Colmer et al. 2019; Ejiri and Shiono 2019; Pedersen et al.

2021a, b; Watanabe et al. 2017). Switching to pathways that use ATP more efficiently and to noncyclic tricarboxylic acid pathways by inhibition of succinate dehydrogenase and upregulation of γ-aminobutyric acid and alanine biosynthesis has been demonstrated in annual crop species (António et al. 2015; Jorge et al. 2016). However, it is also possible that post-hypoxic damage is important, which may require mechanisms to cope with the potential for rapid ROS formation such as increased antioxidant biosynthesis (e.g., ascorbic acid and glutathione), and several biochemical consequences, including accelerated conversion of ethanol to acetaldehyde, oxidation of transition metals in enzyme catalytic sites (e.g., iron), and irreversible damage to membranes (Crawford 2003; Yuan et al. 2017).

When flooding was extended beyond the dormant season into the growing season, increased stress was observed in both Nuttall oaks and Shumard oaks compared to only dormant season flood, but again more so for Shumard oaks. For example, there was no increase in seedling mortality for Nuttall oak, while 52% and 94% of Shumard oak seedlings died due to two and three months of flooding, respectively. One additional month of flooding beyond bud break (2-month flood treatment) was sufficient to decrease leaf area production, and leaf, branch and new root biomass accumulation in both species during spring, relative to seedlings that experienced no flooding. Winter flooding that extended into spring also reduced shoot growth in *Populus deltoides* (Miao et al. 2017). A similar reduction in leaf area was observed previously in *B. pendula* and *B. pubescens* seedlings exposed to flood extending from the dormant season into the growing season, but reduced root biomass was apparent only in *B. pendula*, which is less flood tolerant (Wang et al. 2015). When flooding that extends into the growing season reduces new root mass, those direct impacts on roots likely then initiate a cascade of indirect effects due to the interdependence of shoot and root tissues. Shoot growth is dependent on water and nutrient uptake from the soil. Whether due to fine root mortality, reduced root growth or physiological reduction in root hydraulic conductivity (Islam and Macdonald 2004; Rasheed-Depardieu et al. 2015; Schmull and Thomas 2000; Tan et al. 2018), or due to impaired xylem development in flooded portions of the stem (Copini et al. 2016), the consequent reductions in water and nutrient fluxes to the stem and leaves decreases the amount of leaf area that can be formed. Reduced leaf area, in turn, decreases photosynthetic carbon (C) assimilation, which then decreases the amount of C available for root growth, completing a potential negative feedback loop. Carbon assimilation may be further reduced, because low soil oxygen inhibits photosynthesis and initiates stomatal closure in oaks, which limits both water uptake and CO_2 intake (Gardiner and Krauss 2001; Pezeshki and Anderson 1997; Sloan et al. 2016; Sloan and Jacobs 2008). Hence, the interactions between roots and shoots and the resulting limitation of C assimilation, and water and nutrient uptake may be the reason why the moderately flood tolerant Nuttall oak had reduced initial growth when flooding extended into the growing season. Greater magnitude C, nutrient and water limitations, and perhaps greater fine root mortality, presumably resulted in the large increases in mortality observed in Shumard oak seedlings exposed to flooding during the growing season. Autumn flooding reduced nutrient uptake in Nuttall oak seedlings, but this may have been a consequence of fine root mortality (Sample and Babst 2020). As dormant and early spring flooding caused no detectable fine root mortality, Nuttall oak roots may be more susceptible to flood in the autumn than spring. It is not clear whether the increased impact of flooding following budbreak compared to winter flooding was due to the direct effects of flooding on roots (e.g., due to higher activity tissues being more prone to damage), or due to the demands for water by developing leaves and the accompanying interactions between roots and shoots. Given the wilting of branches and the seedling mortality that occurred before the 3-month flood treatment was removed, it is clear that flood damage to Shumard oak is not dependent only on post-hypoxic mechanisms, but can occur during spring flooding.

After the conclusion of the flooding treatments, when given the rest of the growing season without flooding, Nuttall oak seedlings that had been flooded for 1 or 2 months grew to nearly the same size and mass as unflooded control seedlings, suggesting compensatory growth. On the contrary, Nuttall oaks flooded for 3 months and all flooded Shumard oaks continued to lag 34–76% behind unflooded seedlings. Several mechanisms may have contributed to the apparent compensatory growth of Nuttall oaks that were flooded for two months or less. First, previous studies of plant responses to herbivory suggest that compensatory growth could be due to elevated photosynthetic activity, developmental changes such as delayed senescence, and shifts in biomass allocation (Bassman and Zwier 1993; Gassmann 2004; Mabry and Wayne 1997; Nowak and Caldwell 1984; Ozaki et al. 2004). We measured end of season biomass before leaf senescence began, ruling out the potential for delayed senescence to be the underlying cause of compensatory growth measured in our study, and there was no change in root:shoot biomass allocation of Nuttall oak seedlings. In Nuttall oak, photosynthesis and stomatal conductance are not suppressed as much by flooding, and are quicker to recover compared to less flood tolerant oaks (Anderson and Pezeshki 2000; Pezeshki and Anderson 1997), which could have helped to minimize the long-term persistence of flood effects in Nuttall oak seedlings. It is possible physiological or anatomical features that have not yet been identified, such as those found in *B. pubescens* (Wang et al. 2017), may have aided the rapid recovery of Nuttall oak from flood stress.

A second possible explanation of compensatory growth may have been the combined effects of the quiescence response to flooding discussed above and the determinate growth pattern of oaks. In the presence of flooding, Nuttall oaks may have delayed development of the burst of growth that typically occurs immediately after budbreak in the absence of flooding. Downregulation of growth and metabolism during early growing season flooding would have maintained carbohydrate stores during the period of stress, as documented in *Q. robur* (Ferner et al. 2012), and perhaps winter nutrient reserves were maintained, as well. Downregulating spring stem growth during flooding might also protect the vascular cambium in submerged stem tissues. Although stems were not submerged in our study, xylem vessel development in oaks can be disrupted by flooding in early spring in stem tissues that are submerged, resulting in collapsed vessels and reduced conductivity (Copini et al. 2016). Once flooding subsided, the remaining storage reserves of carbohydrates and nutrients could have been mobilized and utilized for growth. Our data indicate that the compensatory growth of Nuttall oak seedlings that were flooded for two months or less was not due to additional flushes or new branches emerging after flooding was removed, but due to prolonged expansion of the three flushes of growth that had already been initiated. Although branch numbers and lengths were not significantly reduced by two months or less of flooding in Nuttall oak, leaf area, leaf mass and new root mass were reduced by the 2-month flooding treatment in the spring, suggesting that Nuttall oaks slowed leaf and new root development during flooding that extended into spring. Slowing growth and keeping root activity low while conditions were not ideal may have also reduced damage to roots from hypoxia. Simply keeping roots alive with minimal damage may have aided the recovery of Nuttall oak seedlings by allowing them to resume new root growth, and water and nutrient uptake quickly after flooding subsided.

During recovery from the 3 month long flooding treatment, Nuttall oak seedlings increased from one of the lowest chlorophyll concentrations to the highest by the end of the growing season. The increase could be due to a delay of full greening in leaves until flooding subsided, which may be caused by reduced nutrient uptake during flooding or a metabolic delay in the remobilization of stored nutrients. Shumard oak seedlings that experienced growing season flooding had a similar pattern of delayed full greening of leaves, with increasing chlorophyll concentrations during the growing season after flooding ended. Since most leaf and stem elongation growth in oaks occurs early in the growing season in the spring, oaks usually do not produce a new flush of growth at the time when the three month flood ended. As a result, it is possible that the nutrients that were being mobilized from storage reserves or taken up from the soil after flooding ended may have been partitioned to the existing leaf area, and that leaves were no longer expanding at that time, thereby resulting in elevated chlorophyll concentrations.

In flooded Nuttall oak seedlings, recovery of resource acquisition capabilities was favored over storage tissues, and this allocation pattern has potential longer-term consequences. Nuttall oak seedlings largely recovered leaf area and fine root biomass from 2- and 3-months flood treatments, which extended 1 and 2 months into the growing season, respectively. But taproots and main stems in the 3-month flood treatment grew substantially less than unflooded controls by the end of the growing season. In Shumard oak seedlings, which were clearly more stressed by the same flood treatments, reductions in biomass were distributed more uniformly across all tissues, indicating that both resource acquisition and storage tissues were decreased. A smaller taproot and main stem indicates that flooding similar to our three month flood treatment could have potentially persistent effects on Nuttall oak seedlings, and even 1 month of dormant season flooding could similarly impact Shumard oak seedlings. *Quercus* species are more susceptible to mortality and biomass reductions over winter and the following growing season, if storage reserves are insufficient (Angelov et al. 1996; Frye and Grosse 1992). Thus, persistently smaller taproots due to soil flooding that extended from the dormant season into the growing season in both Nuttall and Shumard oak seedlings could increase the risk of mortality over the next winter and subsequent growing season. The recovery that we observed in Nuttall oaks exposed to 2 months of flooding is likely crucial for both immediate and future survival.

The recovery of Nuttall oak seedlings in our study may have been facilitated by ideal moisture conditions and full sunlight for the remainder of the growing season after flood was removed. However, many bottomland hardwood forests experience both prolonged periods of flood in spring and then periods of drought during the summer or fall. It is possible that the initial lag in root growth due to spring flooding may leave Nuttall oaks susceptible to water stress if drought occurs before new root growth has progressed sufficiently. This risk might be mitigated somewhat by the prolonged dry-down period that would be expected of the clay soils where bottomland red oaks are typically found. Furthermore, given that most bottomland red oaks are moderately shade intolerant (Collins and Battaglia 2008; Johnson 1975), the low light conditions often found in the understory of bottomland forests (Cunningham and Volenec 1996; Jenkins and Chambers 1989) might impede the recovery of Nuttall oak seedlings that are flooded in the early spring, especially if flooding delays development of full photosynthetic capacity until after overstory leaf expansion. Hence, our results may represent a best-case scenario for recovery from flooding prior to the next winter, perhaps limiting Nuttall oak to locations where flood subsides early in spring. On the other hand, since mature oak trees may be less susceptible to flooding (Broadfoot 1967; Broadfoot and Williston 1973; Hosner 1960; Hosner and Boyce 1962), it is possible that Nuttall oak seedlings that are initiated during years with less flooding in locations where flooding would ordinarily remain slightly later in spring, might become established as saplings and persist as adult trees.

Conclusions

Timing of seasonal flooding will be an important determinant of whether valuable red oak species, such as Nuttall oak and Shumard oak, will persist in bottomland forests. Flooding during the dormant season does not harm Nuttall oaks, and regression analysis indicates that flooding can extend about 18 days beyond bud break before surpassing a 20% reduction in taproot mass, as well as a 6% reduction in main stem mass, at the end of the growing season. Therefore, afforestation, reforestation and rehabilitation operations that aim to re-establish Nuttall oak in natural bottomlands, should plant Nuttall oak seedlings where natural flooding typically subsides after early spring. Greentree reservoirs where Nuttall oaks are desired need to be drained in spring before damage can occur, at least during the seedling stage. In contrast, since Shumard oak seedlings were stressed even if flooding was limited to the dormant season, they will be limited to the higher elevations within bottomlands that rarely flood.

Author contribution statement All authors contributed to the study conception and design, material preparation, data collection and analysis. The first draft of the manuscript was written by JC, and BB and RS made major revisions to the manuscript. All authors read and approved the final manuscript.

Acknowledgements We would like to thank the Arkansas Department of Agriculture Division of Forestry for donating the *Quercus* seedlings used in this experiment, and for technical assistance, thanks to Alyssa Sanders, Zachary Reed, Jason Lam, Will Tietz, Roberto Bernal, Lesly Jean-Francois, Colby Mohler, Ethan Russell, Jacob Schwantz, Gabby Sherman, Richard Vaerewyck, Dalton Weatherly, and Stacy Wilson.

Funding This project was supported in part by the National Science Foundation's Research Infrastructure Improvement Award OIA-1457888 to the CASE project (Center for Advanced Surface Engineering) of the Arkansas EPSCoR Program, and by the United States Department of Agriculture, National Institute of Food and Agriculture, McIntire-Stennis project number 1009319.

Data availability All data generated or analyzed during this study are included in this published article.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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