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RESEARCH ARTICLE

Seedling survival and growth of four forest tree species: the role of resource gradients in bottomland forests

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The survival and growth of bottomland tree species in floodplain ecosystems are largely driven by species-specific resource conditions. To assess the performance of native tree species along resource gradients, we planted seedlings of four native species, including Baldcypress (*Taxodium distichum*), Loblolly pine (*Pinus taeda*), Water oak (*Quercus nigra*), and Water tupelo (*Nyssa aquatica*), in southeastern Texas, United States, in 2019. Seedling survival and height were repeatedly monitored over 30 months following planting. The effects of soil texture, water table depth, soil pH, litter mass, light availability (both direct and diffuse), and leaf area index (LAI) on seedling survival and height were analyzed. Baldcypress exhibited the highest survival rate 30 months after planting (41.2 ± 2.7%, mean ± standard error). Baldcypress mortality was reduced with higher sand proportion ($r = -0.412$, negative coefficients indicate reduced mortality risk), higher soil pH ($r = -0.304$), higher diffuse ($r = -0.395$), and direct ($r = -0.406$) light proportion, and higher LAI ($r = -0.402$). Water oak mortality was decreased by decreased direct light proportion ($r = 0.358$). Water tupelo mortality was lower with decreased sand proportion ($r = 0.408$), lower soil pH ($r = 0.367$), lower direct light ($r = 0.627$), and decreased LAI ($r = 0.311$). The median survival times for Baldcypress, Loblolly pine, Water oak, and Water tupelo were 30, 4, 4, and 7 months, respectively. Diffuse and direct light availability, along with LAI, were key factors influencing height growth. In conclusion, species-specific responses to soil texture, pH, and light availability can guide species selection for bottomland forest restoration. Understanding canopy structure and light availability helps optimize site preparation and resource allocation, reducing replanting risks and management costs.

Key words: bottomland forests, flooding, light condition, seeding height, seedling survival, soil condition

Implications for Practice

- Baldcypress is a robust candidate for floodplain restoration in areas with prolonged flooding. It can tolerate soil with sand content up to 70.2%.
- Water tupelo restoration requires low belowground competition and sufficient light availability; the first 6 months post-planting are critical for seedling establishment.
- Loblolly pine and Water oak should be planted in areas with better drainage, avoiding sites that remain inundated for more than 3 months.

Introduction

Bottomland forests are one of the most rapidly diminishing wetland ecosystems in the southeastern United States (Allen et al. 2001). About two-thirds (4.8 million hectares) have been lost due to land conversion to agriculture, the construction of surface water impoundments, or being replaced by plantations (Williams et al. 2002). Both public and private landowners, as well as the federal government, are involved in restoration endeavors (Allen et al. 2001; Stanturf et al. 2004). Goals often encompass restoring wildlife habitat, improving water quality, and mitigating flood risks (Allen et al. 2001). Therefore, developing effective protocols is crucial for bottomland forest restoration.

Within the bottomland forest, wetland mitigation banks provide restored, created, or enhanced wetlands that offset bottomland forest habitat losses elsewhere. These banks are distributed nationwide across the United States, with higher concentrations in the southeastern region. They streamline the implementation of flood-damage reduction projects, enhance floodplain storage and habitat connectivity, and reduce the temporal loss of wetland functions and ecological value.

However, restoring bottomland forests has become more challenging with the increasing frequency and intensity of

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intense precipitation events over the recent few decades (Skeeter et al. 2018). These hydrological shifts have introduced greater uncertainty in seedling survival and growth, as the timing and duration of hydroperiods have become less predictable. Site-specific resource conditions are recognized as critical factors in determining the success of species-specific restoration in these ecosystems (Allen 1997; Stanturf et al. 2001; Simmons et al. 2011). Consequently, species selection for planting needs to be refined and expanded to improve the adaptability of seedlings to diverse site conditions.

Due to hypoxic or anoxic soil conditions caused by periodic flooding, belowground conditions are essential for the successful establishment of bottomland tree species (Baker & Broadfoot 1979; Hodges 1997). The diverse hydraulic site conditions distinguish the distribution of different flood-tolerant species (Allen et al. 2001). In bottomland areas, occasional flooding causes water levels to rise near rivers and streams, with water velocity varying by distance from the river during flood periods. This variation in water velocity affects deposition rates across the alluvial stream valley, leading to differences in sediment composition based on proximity to the river or stream (Hodges 1997). This means that, among various soil properties, soil texture is crucial to tree species suitability as it determines hydroperiod, soil drainage, and aeration (Stanturf et al. 2001). It affects seedling survival and growth in the establishment phase (Renninger et al. 2019), determines species composition (van Breemen et al. 1997), and on longer time scales, shapes the successional trajectory (Hodges 1997). Increasing soil moisture, which is also largely regulated by soil texture, has been shown to enhance the survival of species commonly planted for restoring wildlife habitat, such as Loblolly pine (*Pinus taeda* L.), Shortleaf pine (*P. echinata* Mill.), Sweetgum (*Liquidambar styraciflua* L.), and Cottonwood (*Populus deltoides* W. Bartram ex Marshall; Allen et al. 2001; Bhattacharjee et al. 2008). In addition to soil texture, soil pH, a key chemical property, influences nutrient availability that can determine seedling survival (Stanturf et al. 2001). For example, a soil pH above eight can lead to iron deficiency, resulting in increasing mortality of Nuttall oak (*Quercus texana* Buckley), Cherrybark oak (*Q. pagoda* Raf.), and Water oaks (*Q. nigra* L.; Stanturf et al. 2004). Therefore, both the physical and chemical properties of soil are fundamental considerations in the selection of species for successful bottomland forest restoration.

Aboveground resource conditions, such as canopy structure, regulate light availability and litterfall, both of which directly influence seedling recruitment and growth potential. Competition for light generally reduces seedling survival and initial growth, though these effects can vary based on species-specific biological characteristics and local light availability. For example, the survival and productivity of both Loblolly pine and Shortleaf pine increased with higher percentages of full sunlight (Ferrill 1953). Similarly, bottomland oak species exhibited shoot dieback in the absence of adequate light (Gardiner 2001). Additionally, dense overstory coverage can create habitat for small rodents and other animals that consume planted seeds or seedlings, impacting recruitment rates (Allen et al. 2001). Conversely, maintaining an optimal canopy cover can inhibit the growth of competing herbaceous ground plants, enhancing the establishment and growth of target tree seedlings (Dulohery et al. 2000). Therefore, understanding canopy cover light conditions is critical for balancing light availability and reducing competition, both of which are essential factors for successful seedling establishment.

Restoration challenges in bottomland forests, such as extremely low natural regeneration and poor seedling survival due to prolonged inundation, herbivory, and competition, are well-documented (Stanturf et al. 2004). Seedling planting is one of the most reliable artificial regeneration methods to enhance forest restoration in bottomland forests (Allen et al. 2001; Stanturf et al. 2009). Tree species selection is thus a demanding task. However, there are more than 50 commercial species available for restoration, and they have varying resource needs for establishment, survival, and growth (Kellison & Young 1997). Meanwhile, sites must achieve at least 54–63% of the species' maximum productivity level to fulfill the effective restoration requirement (Baker & Broadfoot 1979). Such challenges and demands call for a deeper ecological understanding of how seedlings adapt to both aboveground and belowground resource gradients to enhance restoration success in areas such as wetland mitigation banks, which helps prevent unavoidable impact from development or agriculture.

The objective of this study was to examine how aboveground and belowground resource gradients influence the establishment and growth of selected typical bottomland tree species over the first 3 years of growth at the Green Bayou Wetland Mitigation Bank (GBWMB) in Harris County, Texas, United States. We investigated the effects of soil texture, soil pH, soil water depth, light availability (direct and diffuse), leaf area index (LAI), and litter mass on seedling monthly survival and height growth.

Methods

Study Site

Our study area is located within the Green Bayou Wetlands Mitigation Bank, situated along the floodplains of Garners and Greens Bayou in Harris County, Texas, United States (29.93° N, 95.22° W). The GBWMB covers 389 ha and is comprised primarily of open ponds, marshes, grassland prairies, and wetlands (Fig. 1). Garners and Greens Bayou define the western boundary, while the Texas 8 Beltway forms the northern boundary. The elevation is generally below 45 m above sea level, with minor topographic variations (15–18 m). The growing season lasts approximately 250 days (mid-March to late November). The area experiences hot, humid summers and mild winters, with an average annual temperature of 21.9°C and annual mean precipitation of 1339.6 mm from 1990 to 2021 (NOAA 2021). Specifically, the annual precipitation during our study period was 1403 mm in 2019, 1413 mm in 2020, and 1392 mm in 2021. The wetter months are May, June, and September, while the drier months are February, March, July, and August. The overstory was dominated by Loblolly pine (41% of basal area), Water oak (18%), willow oak (*Q. phellos* L.; 11%), and Sweetgum (9%),



Figure 1. Plots located in Greens Bayou Wetland Mitigation Bank (GBWMB). Twenty plots were installed for a field study identifying the main factors contributing to seedling survival and growth at different sections of GBWMB at Harris County, Texas, 2019–2021.

according to a previous field survey conducted in 2015 and 2016 (unpublished data).

Field Layout and Planting

In January 2019, 1-year-old bare-root planting stock (1–0) of four typical bottomland tree species, including two evergreen gymnosperms, Baldcypress (*Taxodium distichum* [L.] Rich.) and Loblolly pine, and two deciduous angiosperms, Water oak and Water tupelo (*Nyssa aquatica* L.), was obtained from Arbor-Gen Inc. (SC, U.S.A.). The purpose of using such stock type was to be operational, as it was the company's conventional practice. Provenance information was unavailable, although western Gulf Coastal Plain sources were requested. Bare-root seedlings can be expected to survive and grow well if planted during the dormant season (December to mid-March), when the site is not too dry and soil conditions are otherwise favorable in southern bottomland forests (Allen et al. 2001).

The four species were selected for their ecological functions within the region, diverse growth dynamics, roles in successional stages under different site conditions, and distinct adaptations to flooding (Kellison & Young 1997). Baldcypress and Water tupelo are swamp species, which are the most flood-tolerant species in bottomland ecosystems, especially during the seedling stage (McKnight et al. 1980; Burns & Honkala 1990a, 1990b). These species dominate the mid-successional stage in poorly drained major and minor bottomlands, respectively (Hodges 1997). In contrast, Loblolly pine is the most extensively planted commercial pine species in the southern United States, where commercial timber accounts for 60% of the nation's timber production (Fox et al. 2007), while Water oak is a leading species in

bottomland hardwood restoration with its high value in timber and wildlife habitat (Olson 1974) but is less tolerant to flooding (Conner et al. 1998).

In February 2019, twenty 220 × 220 cm plots were established, with 13 to 21 seedlings per species planted at 30 × 30 cm spacing and tagged. Photos of the seedling planting are presented in Figure S1. Altogether, 1340 seedlings were planted. Light availability, annual saturation, and soil conditions were considered to stratify locations across the GBWMB. Plot locations were then randomly selected within these strata to encompass the widest possible range of light, flooding, and soil conditions, from open areas receiving more than 90% full sunlight to shaded microhabitats with less than 10% full sunlight beneath the canopy of trees and shrubs (Fig. 1).

Characterization of the Resource Gradients

The aboveground (direct and diffuse light proportion and LAI) and belowground (soil texture and pH) environments were characterized for each plot. Canopy cover, direct light, and diffuse light transmitted through the canopy were estimated using hemispherical canopy photography (Evans & Coombe 1959; Rich 1990). Photographs were taken at the center of each plot using a SIGMA SD15 digital camera equipped with a 4.5 mm 1:2.8 fisheye lens (SIGMA Japan). The camera was mounted on a tripod 1.3 m aboveground, with the lens leveled and focused on the zenith and oriented toward magnetic north. Photographs were taken between June and July 2020, with a second set taken in August 2021. All images were captured either predawn, post-dusk, or on overcast days to avoid direct sunlight interference in image interpretation.

We analyzed the images and determined pixel classification thresholds using SideLook version 1.1 (Nobis & Hunziker 2005), a software program used to assess vegetation structure from digital images. Each pixel was classified as either sky or canopy based on these determined thresholds. Using these classifications, we estimated both the direct and diffuse light proportion transmitted through the canopy under clear sky conditions, as well as the LAI for each plot, utilizing Hemiview canopy analysis software (Delta-T Devices, Cambridge, U.K.).

For belowground analysis, three soil samples were randomly collected from each plot prior to seedling planting, using either a shovel or auger, from a depth of 0–20 cm. Soil texture (percentages of sand, clay, and silt) and soil pH were analyzed at the Soil, Plant, and Water Analysis Laboratory at Stephen F. Austin State University, following standard physiochemical testing protocols (Bouyoucos hydrometer method; Bouyoucos 1962).

In each plot, all aboveground vegetation components were collected from four randomly selected quadrants, each measuring 25 × 25 cm. This included litter and the living material of herbaceous species and tree seedlings, excluding the planted seedlings. There were no invasive species included since GBWMB has controlled the invasive Chinese tallow (*Triadica sebifera* L.) and other invasives for years using herbicides. The collected components were stored in plastic bags and transported to the Soil, Plant, and Water Analysis Laboratory at Stephen F. Austin State University, where they were dried at 60°C for 96 hours to a constant mass and then weighed to calculate litter mass. Litter mass (g) per quadrant was converted to litter mass per square meter for each plot (g/m^2).

In summary, the average soil sand proportion across the plots was 70.6% (±13.0), with values ranging from 47.8 to 92.4%. Soil clay proportion averaged 11.6% (±7.5), ranging from 1.3 to 25.3%. Soil silt proportion averaged 17.8% (±6.5), ranging from 5.6 to 28.8%. Soil pH averaged 5.6 (±0.9), ranging from 4.2 to 7.5. Water table depth averaged 51.5 cm (±22.2), ranging from 31.0 to 80.0 cm. Direct light proportion averaged 0.300 (±0.093), ranging from 0.140 to 0.460. Diffuse light proportion averaged 0.318 (±0.084), ranging from 0.185 to 0.496. LAI averaged 1.485 (±0.289), ranging from 0.950 to 2.054. Litter mass averaged 48.92 g/m^2 (±19.48), ranging from 8.13 to 91.05 g/m^2. Plot-level values for all variables are detailed in Table S1.

Seedling Monitoring

Each seedling within the plot was tagged and monitored; its survival and height were tracked monthly until December 2019 (10 months after outplanting) and then quarterly until August 2021 (30 months after outplanting). Seedling status was determined through visual inspection: seedlings were considered dead if there was no aboveground green tissue or leaves with the root still there. Missing stems, or stems pulled from the ground with the rootstock consumed, or if the seedling could not be located, were presumed to have been eaten by feral hogs (*Sus scrofa*), which are known to chew and consume plant rootstocks and the lower portions of stems and disrupt soil structure in eastern Texas (Mayer et al. 2000; Mahaffey & Evans 2016; Jacques et al. 2022). These included 25 seedlings in total: 12 Baldcypress, four Loblolly pine, four Water oak, and five Water tupelo seedlings. These seedlings were not included in the analysis. Seedling survival was calculated at 2, 4, 5, 6, 7, 8, 9, 10, 12, 16, 20, and 30 months post-planting, while seedling height was measured at 2, 4, 5, 6, 7, 8, 9, 10, and 30 months post-planting.

Statistical Analysis

To estimate survival probabilities over time, we first used Kaplan–Meier survival curves to estimate the monthly survival probability for each species. The Kaplan–Meier curves were used to visually summarize and display the probability of seedling mortality occurring over time of each species (Kalbfleisch & Prentice 2002). Differences in survival between species were assessed using log-rank tests, and a Bonferroni correction was applied to adjust p values for multiple pairwise comparisons.

A mixed effects Cox proportional hazards model was then developed to evaluate the influence of resource variables on seedling survival duration for each species. Soil texture variables (proportions of clay, sand, and silt), water table depth derived from Web Soil Survey (Soil Survey Staff 2020), soil pH, light (both direct and diffuse), LAI, and litter mass (including litter and ground plant) were included as predictors. The species were treated as a categorical variable, with Baldcypress

selected as the reference species due to its consistently highest survival rate up to 30 months after outplanting. Multicollinearity was checked using variance inflation factors (VIF). A variable with a VIF value above five would be removed. This led to the removal of silt proportion from the model. Continuous variables were standardized by subtracting their means and dividing by their standard deviation to ensure each variable contributes equally to the analysis. Plot was set as a category variable and included as a random effect to account for spatial variability. The initial hazard model considered all species and resource variables and the second-order interactions between species and resource variables. Then, we reduced variables to optimize the final model by selecting the model with the lowest corrected Akaike Information Criterion (AIC; Akaike 1974) using bidirectional elimination. Residual plots for mixed effects Cox models are presented in Figure S2.

Subsequently, to simulate how survival probability changes with different resource conditions over time, we set the minimum, mean, and maximum values of each environmental variable that significantly affected each species' survival in the final Cox proportional hazards models. In these predictions, all other variables in the model were held constant at their median values to isolate the effects of each significant predictor.

For height increment, we first conducted an analysis of variance (ANOVA) to compare the height of each species at each monthly measurement. Tukey's test was used for post hoc pairwise comparisons. The summaries of ANOVAs and post hoc analyses are in Tables S2 and S3.

Subsequently, we applied a generalized linear mixed model (GLMM) to assess the effects of soil texture, water table depth, soil pH, direct and diffuse light, LAI, and litter mass on monthly seedling height increments for Baldcypress as the reference species and to compare the remaining three species with it. Following the survival analysis protocol, silt proportion was excluded due to multicollinearity, and plot was incorporated as a random effect. Given the high mortality 1 year after outplanting, we focused on monthly height increments measured between 2 and 10 months post-planting in 2019 and only considered the seedlings that had been continuously recorded in 2019. For the height increment between April and June, we averaged the height increments in April and June because of the missing data in May to represent the monthly height increment during these 3 months. The GLMM included resource variables as fixed effects and incorporated months as a fixed factor. Monthly increments were treated as categorical due to the likelihood of non-continuous growth, influenced by flooding and herbivory damage. The average height increment between April and June was set as the reference level. Initial height was also included as a covariate. An initial full GLMM fitted all variables and the interactions between species and all resource variables, and we selected the final model with the lowest AIC through bidirectional elimination. Residual plots for GLMM are presented in Figure S3. An α level of 0.05 was used to distinguish statistical significance from non-significance.

All analyses and visualizations were performed in R v4.4.1 (R Core Team 2024). Kaplan–Meier survival analysis was conducted using the *survival* package (Therneau & Grambsch 2000); mixed effects Cox proportional hazards models were fit with the *coxme* package (Therneau 2024), GLMMs were fit using the *lme4* package (Bates et al. 2015), and model selection via AIC was performed with the *MuMIn* package (Bartoń 2023).

Results

Seedling Survival and Height Increment Over Time

The seedling survival rate of the four species decreased significantly within 30 months after planting (Fig. 2). At the end of the first growing season (November 2019; 10 months post-planting), the mean (±SE among plots) survival rates for Baldcypress, Loblolly pine, Water oak, and Water tupelo were 88.7% (±1.7), 20.5% (±2.2), 19.0% (±2.2), and 26.7% (±2.4), respectively. By August 2021 (30 months post-planting), survival rates had dropped to 41.2% (±2.7), 5.5% (±1.3), 1.2% (±0.6), and 1.2% (±0.6), respectively.

Water oak experienced the earliest and most rapid mortality, with nearly half of the seedlings dead only 2 months after planting, resulting in a survival rate of 52.6% (±2.7). Loblolly pine exhibited a pronounced decline in survival 4 months post-planting (June 2019), with survival decreasing sharply to 44.5% (±2.8). Water tupelo showed a marked reduction in survival between 5 and 7 months after planting (July to September 2019), as the survival rate dropped from 78.9% (±2.2) to 30.0% (±2.5). In contrast, Baldcypress did not exhibit any significant sharp decline but only a gradual decline in survival throughout the study period.

The median survival time (the time at which the survival probability first dropped below 50%) varied significantly among the four species (Table S2; Fig. 3; $\chi^2 = 545$, degrees of freedom [*df*] = 3, p 0.001). The median survival time for Baldcypress was the longest (30 months), and that for Loblolly pine and Water oak was the lowest (4 months), while that was also low (7 months) for Water tupelo.

Height over 30 months varied by species. Baldcypress increased from 59.1 cm (±0.8) at 2 months to 61.0 cm (±1.2) at 30 months. Loblolly pine grew from 23.4 cm (±0.2) to 36.6 cm (±1.2). Water oak decreased in final height from 45.6 cm (±0.2) to 37.6 cm (±1.3), indicating frequent dieback

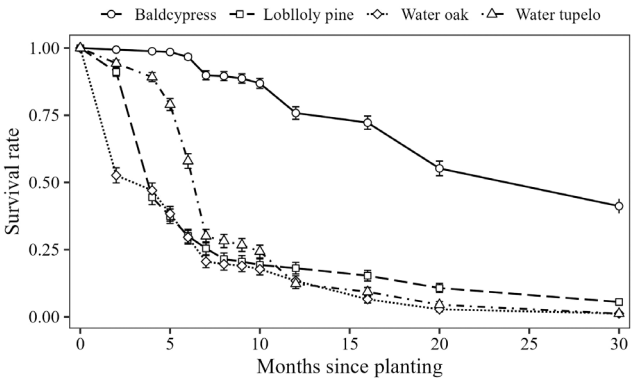


Figure 2. Seedling survival over time. Planting was done in February 2019.

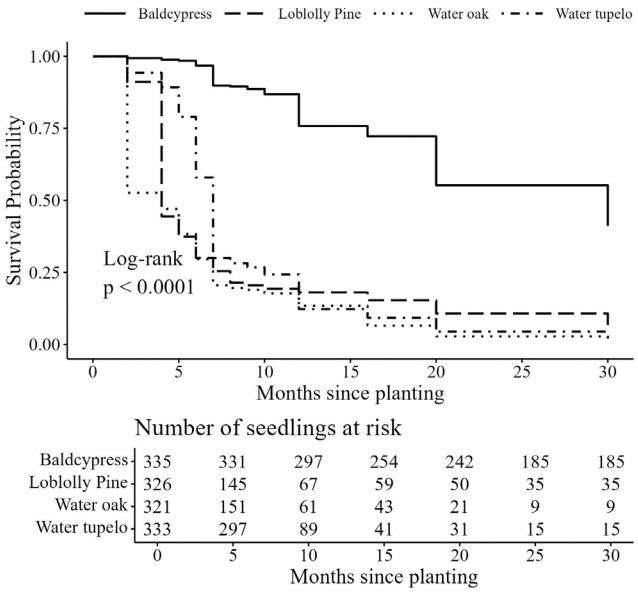


Figure 3. Survival probability and number of seedlings at risk of four species. Survival functions were estimated using the Kaplan–Meier method.

from flooding. Water tupelo showed the greatest growth, increasing from 43.1 cm (±0.6) to 70.9 cm (±1.8).

During the first growing season, height differed significantly among species (Tables S3 & S4; Fig. 4). Baldcypress consistently was the tallest, followed by Loblolly pine, Water tupelo, and Water oak. However, at 30 months post-planting, differences between Baldcypress and Water tupelo, and between Loblolly pine and Water oak, were no longer statistically significant.

Resource Variables Influencing Seedling Survival

According to mixed effects Cox hazard analysis (Table 1), soil sand proportion, soil pH, direct light proportion, diffuse light proportion, and LAI were identified as the most influential resource variables determining seedling survival rates. For Baldcypress, increasing sand proportion, soil pH, direct and diffuse light proportion, and LAI were associated with reduced mortality (Table 1; Fig. 5). The significance of these resource variables for the other three species was assessed in comparison to Baldcypress. For Loblolly pine, none of the resource variables demonstrated a significant impact on seedling survival, although the model with soil sand proportion, soil pH, direct light proportion, and LAI was the most parsimonious. For Water oak, increasing the direct light proportion increased the risk of mortality. In contrast, for Water tupelo, increasing soil sand proportion and LAI decreased mortality, whereas higher soil pH and direct light proportion were linked to increased mortality.

The median survival time varied significantly with changes in resource gradients for each species (Fig. 6). For Baldcypress, median survival time increased from 16 to 30 months as sand proportion rose from 47.8 to 70.2%. It also improved stepwise from 16 to 20 to 30 months as the proportion of diffuse light increased from 0.184 to 0.320 to 0.496 and LAI rose from 0.949 to 1.477 to 2.054. The median survival time also increased from 20 to 30 months as soil pH rose from 4.2 to 5.7. In contrast, changes in direct light (0.140–0.460) had no effect. For Water tupelo, increasing sand proportion from 70.2 to 92.4%, LAI from 1.491 to 2.053, direct light from 0.297 to 0.460, and soil pH from 5.6 to 7.5 shortened the median survival time from 7 to 6 months. For Water oak, the median survival time remained constant at 4 months across the range of direct light proportions. For Loblolly pine, no resource variable significantly influenced survival time, and therefore no comparisons were made (Table 1).

Resource Variables Influencing Seedling Height Growth

Seedling height increments varied significantly across the first growing season (Table 2; $R^2_{\text{marginal}} = 0.021$, $R^2_{\text{conditional}} = 0.021$, $p < 0.001$). The monthly height increment between April and June 2019 was significantly higher than during other periods in 2019. Both direct and diffuse light, as well as LAI, were retained in the final models of height increment based on AIC selection, suggesting their relative importance in explaining variability in growth across species. However, none of these factors demonstrated statistical significance ($p < 0.05$).

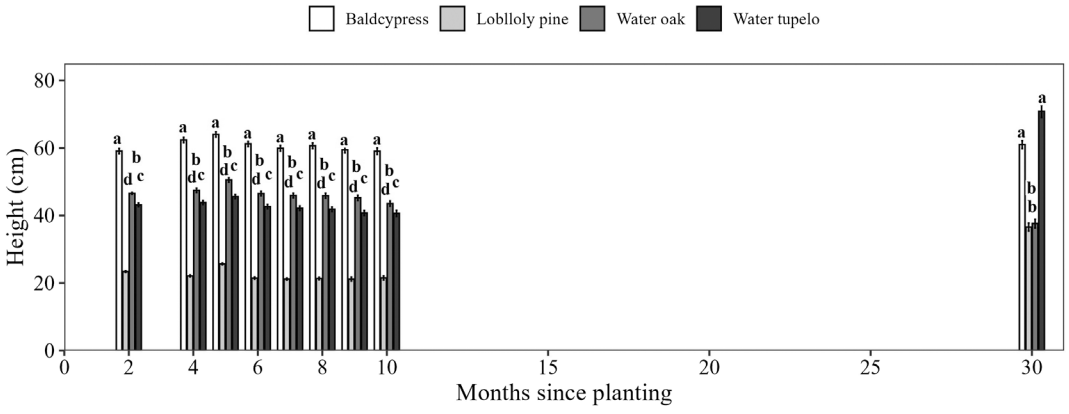


Figure 4. Seedling height at specific month. Planting was done in February 2019. The small letter of each species in each month indicates the statistical significance between species according to Turkey's post hoc analysis.

Table 1. Summary of mixed effects Cox hazard analysis. The estimates and hazard ratio of Loblolly pine, Water oak, and Water tupelo were compared to Baldcypress as the baseline. The variance of the random intercept for plot is $\sigma^2 = 0.0319$. The estimate coefficients, hazard ratios, and p values of Loblolly pine, Water oak, and Water tupelo are relative to Baldcypress.

Species	*Resource variables*	*Estimate*	*Hazard ratio*	p *Value*
Baldcypress	Sand proportion	−0.412	0.662 ± 0.147	0.005
	Direct light	−0.406	0.666 ± 0.137	0.003
	Diffuse light	−0.395	0.673 ± 0.111	<0.001
	LAI	−0.402	0.669 ± 0.145	0.006
	Soil pH	−0.304	0.738 ± 0.155	0.050
Loblolly pine	Sand proportion	−0.040	0.961 ± 0.166	0.809
	Direct light	0.296	1.345 ± 0.152	0.051
	LAI	0.129	1.137 ± 0.133	0.333
	Soil pH	−0.097	0.907 ± 0.18	0.589
Water oak	Sand proportion	−0.016	0.984 ± 0.153	0.915
	Direct light	0.358	1.43 ± 0.158	0.023
	LAI	0.033	1.033 ± 0.134	0.808
	Soil pH	0.150	1.162 ± 0.167	0.366
Water tupelo	Sand proportion	0.408	1.504 ± 0.155	0.009
	Direct light	0.627	1.872 ± 0.149	<0.001
	LAI	0.311	1.365 ± 0.133	0.019
	Soil pH	0.367	1.443 ± 0.166	0.027

Discussion

Successful restoration in bottomland forests requires careful consideration of various factors, including flooding, herbivory, seedling type, species adaptation, and site conditions. While many of these factors are beyond managers' control, selecting species that are well-suited to specific site conditions is one of the fundamental silvicultural practices to improve restoration outcomes. In this study, we aimed to evaluate the initial field performance of four ecologically and economically important bottomland species, including Baldcypress, Loblolly pine,

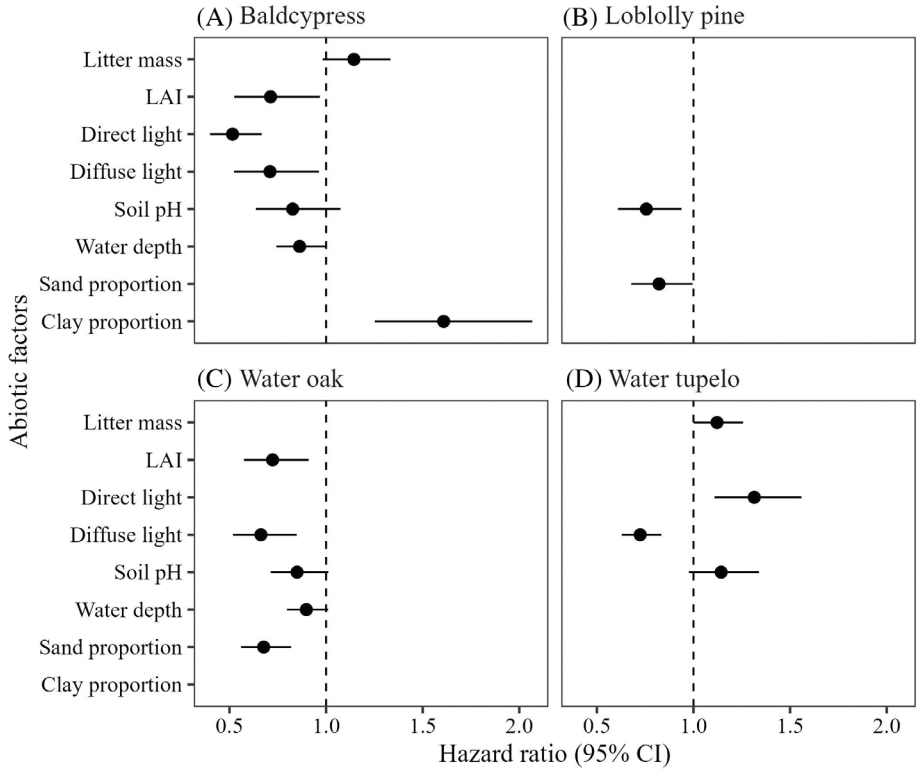


Figure 5. Hazard ratio of resource variables on Baldcypress, Loblolly pine, Water oak, and Water tupelo. A value less than one indicates that increasing one unit of the variable reduces 1% of mortality, while a value greater than one indicates that increasing one unit of the variable increases 1% of mortality.

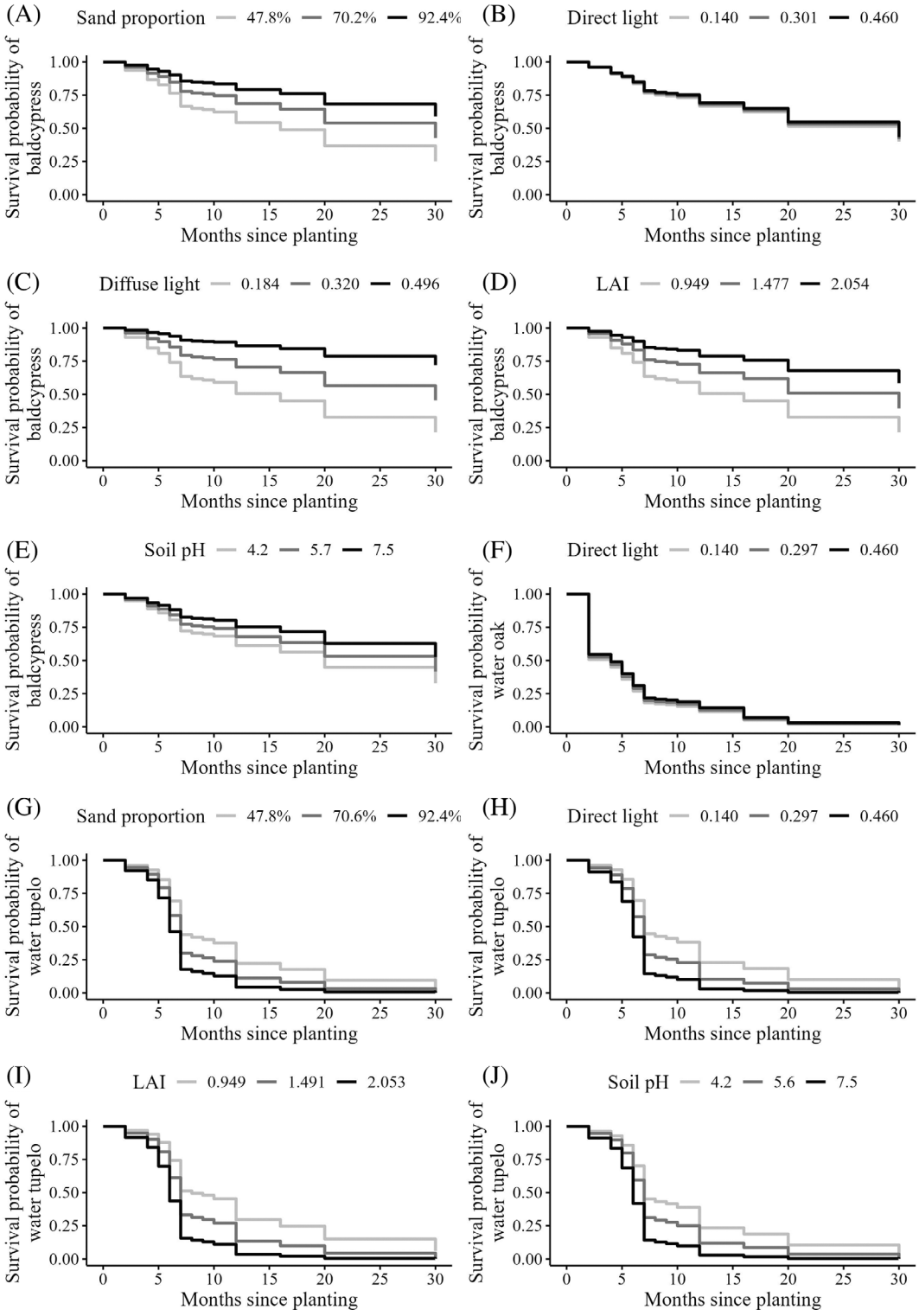


Figure 6. Survival probability since planting of Baldcypress (A–E), Water oak (F), and Water tupelo (G–J) under minimum, mean, and maximum level of each significant resource variable within the study site from Cox hazard analysis.

Water oak, and Water tupelo, within a wetland mitigation bank. We found Baldcypress consistently had the highest survival rate, with over 40% survival at 30 months after planting. However, the survival of Loblolly pine, Water oak, and Water tupelo had already dropped sharply within 7 months after planting. These findings align with previous regional studies, which

Table 2. Statistical summary from GLMM for seedling monthly height increment. The height increment was set as the mean height increment between April and June as the reference level. The estimates of Loblolly pine, Water oak, and Water tupelo were referred to as Baldcypress. The estimates, SE, and *p* values of April height, JUN-JUL increment, JUL-AUG increment, AUG-SEP increment, SEP-OCT increment, OCT-NOV increment, and NOV-DEC increment for Loblolly pine, Water oak, and Water tupelo are the same as Baldcypress, while the intercepts among them are different.

Species	*Predictors*	*Estimate*	*SE*	p *Value*
Baldcypress	(Intercept)	2.451	4.462	0.583
	April height	−0.045	0.012	<0.001
	JUN-JUL increment	0.281	0.620	0.651
	JUL-AUG increment	−3.444	0.620	< 0.001
	AUG-SEP increment	−2.007	0.620	0.001
	SEP-OCT increment	−0.819	0.620	0.187
	OCT-NOV increment	−2.652	0.620	<0.001
	NOV-DEC increment	−2.045	0.620	0.001
	Loblolly pine	1.894	7.960	0.812
	Water oak	6.026	9.879	0.542
	Water tupelo	1.154	6.882	0.867
	Direct light	−0.024	3.795	0.995
	Diffuse light	3.728	5.859	0.525
	LAI	0.251	1.723	0.884
Loblolly pine	Direct light	−0.290	8.562	0.973
	Diffuse light	−7.419	12.742	0.560
	LAI	−0.963	3.179	0.762
Water oak	Direct light	−1.857	10.322	0.857
	Diffuse light	−8.481	17.159	0.621
	LAI	−2.445	3.634	0.501
Water tupelo	Direct light	0.521	6.409	0.935
	Diffuse light	−3.611	9.433	0.702
	LAI	−0.803	2.721	0.768

have documented high early mortality in similar systems. For instance, 90% of Wetlands Reserve Program sites failed to meet the target density of 247 stems per hectare within 3 years following planting or direct seeding (Stanturf et al. 2004). Soil sand proportion and pH were crucial for seedling survival. Baldcypress survival increased as soil sand proportion rose from 47.8 to 70.2% and soil pH increased from 4.2 to 5.7, whereas Water tupelo showed an inverse trend. Increasing understory light availability enhanced the survival of Baldcypress and Water oak while decreasing it for Water tupelo. Light availability was the most relevant factor influencing seedling height increment.

Seedling Survival and Its Influencing Resource Variables

Despite anaerobic conditions in wetlands being generally considered stressful, in floodplain environments where higher stream flows occur during flooding, these conditions can nonetheless provide increased soil moisture, reduced competition, and an influx of nutrients that are beneficial to certain bottomland species (Young et al. 1995). However, current changes to natural hydrologic regimes of wetlands in the United States due to urbanization and the construction of levees, roads, and reservoirs are altering these site conditions and disrupting species adaptation (Mahaffey & Evans 2016). These modifications impact the frequency, depth, and duration of floods, consequently changing soil moisture availability, competition levels, and nutrient influxes for bottomland species. A lack of attention to the adaptation of species to specific site conditions remains the primary cause of restoration failures in bottomland forests (Stanturf et al. 2009).

The greater survival rates of Baldcypress confirm that it can grow under a wide range of soil and light levels (Neufeld 1983; Burns & Honkala 1990a). Baldcypress is a dominant canopy tree species of the deep-water swamps and bottomland forests of the southeastern United States (Young et al. 1995). It can grow in soil conditions ranging from anaerobic to saturated-aerated (Neufeld 1983). In anaerobic conditions, Baldcypress exhibits greater radial growth by maintaining its actively growing root systems with nutrient uptake, root growth, and shoot growth (Young et al. 1995) and may show a dormancy period if submerged in water for 60 days (Burns & Honkala 1990a). These morphological and physiological adaptations enhance Baldcypress survival in various resource conditions.

The sharp decline in survival rates of Loblolly pine, Water oak, and Water tupelo during the first 7 months after planting aligns with common patterns observed in bottomland reforestation, where the period immediately following establishment often experiences the highest mortality (Ferrill 1953; Stanturf et al. 2004). This elevated mortality is likely driven by intense competition with understory herbaceous vascular plants, which can limit resources such as light, nutrients, and water (Williams et al. 2002). Additionally, competition may reduce seedling vigor, making them more susceptible to herbivory and further compounding mortality rates (Jacques et al. 2022).

Loblolly pine is predominantly found in upland forests within river floodplains (Allen et al. 2001), reflecting its limited

tolerance to flooding. Consequently, high mortality rates, up to 100%, can be observed when this species is planted under flooded conditions for 6 months (Conner et al. 1998; Poulter et al. 2008). The rooting habitat is strongly influenced by soil properties, with longer taproots developing in deep, sandy, or loamy soils, and shorter, stouter taproots forming in heavier clay soils (Burns & Honkala 1990a). While smaller seedlings have been shown to exhibit higher survival rates under limited resource conditions, the shoot-to-root ratio remains a critical determinant of bare-root Loblolly pine survival (Conner et al. 1998; Grossnickle 2012). Although soil sand proportion, soil pH, direct light proportion, and LAI were identified as key factors influencing seedling survival in this study, no significant effects of these variables were detected for Loblolly pine. Nevertheless, the overstory was dominated by planted Loblolly pine, suggesting that this species can establish successfully in wetland mitigation banks despite its relatively low flood tolerance. This outcome implies that other resource conditions, such as seedling age at planting, planting timing, and interannual variability in hydrology and climate, may play a critical role in its survival and long-term establishment.

Water oak exhibited the lowest survival rate in our study, with a steep decline in survival as early as 2 months after planting. This is possibly due to the inability of bottomland oaks to develop aerenchyma cells or utilize anaerobic root respiration, which are critical adaptations for surviving hypoxic conditions. Seedlings of oak species are particularly less tolerant to such conditions compared to mature trees (Gardiner 2001). Our findings align with previous studies that showed over 35% mortality of Water oak seedlings within 3 months under flooding conditions (Conner et al. 1998). These results indicate that Water oak seedlings are highly sensitive to anaerobic soil environments. Moreover, Water oak is considered a slow-growing species during the establishment phase and may experience higher rates of dieback compared to faster-growing species such as Baldcypress (Williams et al. 2002). Therefore, the combination of slow growth and low flood tolerance likely contributed to the high mortality observed in our study.

Although Water tupelo is considered a swamp species, we observed a very low survival rate, with only 30% surviving 7 months after planting. Previous studies have also reported much lower survival rates for Water tupelo (15, 24%) compared to Baldcypress (99, 98%) 3 years after planting in lower corridor and delta regions, respectively (Kolka et al. 1998), and less than 20% for Water tupelo compared to over 50% for Baldcypress 4 years after planting in the Upper Coastal Plain (Dulohery et al. 2000). These findings imply that flooding tolerance cannot solely predict species performance in bottomland forest restoration.

In our study, a higher soil sand proportion decreased the survival of Water tupelo but increased the survival of Baldcypress. This contrast may be attributed to the influence of sand on soil water dynamics. Higher sand content is associated with faster water percolation, which reduces water availability to seedling roots (Hooker et al. 2021). The larger particle size of sand creates larger pores within the soil, which in turn decreases its water-holding capacity. As a result, sandy soils drain quickly, allowing more air into the soil but leaving less moisture available for plant roots to absorb (Weil & Brady 2008). Baldcypress prefers well-drained fine sandy loams with enough soil moisture (Mills 1994); a higher soil sand proportion thus appears to be more favorable for Baldcypress but less suitable for Water tupelo.

A higher soil pH increased the survival of Baldcypress but decreased the survival of Water tupelo. This is because Baldcypress is more tolerant of a wide range of soil conditions. Higher soil pH may favor its survival by improving nutrient availability for essential elements like calcium and magnesium, while Water tupelo is more suitable in acidic wetland soils or is less competitive than other species when planted in higher pH soils (Pezeshki et al. 1999; Allen et al. 2001).

Baldcypress is shade-intolerant, while Water oak and Water tupelo exhibit intermediate tolerance to shade at the early stage (McKnight et al. 1980; Self et al. 2020). In our study, increased understory light conditions facilitated the survival of Baldcypress but decreased the survival of Water oak and Water tupelo. The positive correlation between light availability (direct and diffuse solar radiation) and the survival of Baldcypress suggests that this species benefits from the higher light levels associated with open canopies (Burns & Honkala 1990a, 1990b; Keller et al. 2024). Previous studies have reported that removal of 50% overstory enhanced the emergence and growth of Baldcypress (Kellison & Young 1997; Kolka et al. 1998). Conversely, the negative correlation between light availability and Water tupelo survival indicates that increased light could exacerbate competition with herbaceous plants (Kolka et al. 1998). This competition may be detrimental to Water tupelo seedlings, as their initial height was significantly lower than that of Baldcypress and Water oak during the first year. Therefore, our findings align with existing literature on floodplain forests, where predictions of regeneration success and successional trajectories are strongly influenced by light availability and competition (Battaglia et al. 2001).

LAI primarily reflects the structure and functioning of the overstory plant communities, besides its role in modulating light availability to the understory plants (Parker 2020). In this study, a higher LAI enhanced the survival of Baldcypress but suppressed the survival of Water tupelo. These contrasting responses confirmed species-specific strategies for resource use and competitive ability, which may in turn influence shifts in species composition during forest succession (Stanturf et al. 2009). Stands with higher LAI are typically characterized by higher air and soil moisture levels and less understory herbaceous plant cover (von Arx et al. 2013). Such conditions likely promote the survival of Baldcypress, which prefers moist to saturated soil environments and benefits from reduced competition with herbaceous plants (Dulohery et al. 2000). In contrast, the suppressed survival of the Water tupelo under these conditions may result from either intensified competition in more open stands or prolonged soil saturation in denser canopies (Bhattacharjee et al. 2008). This interpretation is consistent with the observed low survival rates of Water tupelo and its negative association with increasing soil sand proportion, indicating that prolonged soil saturation may reduce its survival. Previous

studies also reported that Water tupelo exhibited reduced height growth under saturated conditions (Tracy et al. 2024), lower survival in wetter areas (Kolka et al. 1998), and decreased survival under closed overstory canopies (Dulohery et al. 2000).

In addition to site-specific resource conditions influencing seedling survival, broader hydrological events, such as the timing and intensity of flooding, can significantly affect the rate and type of woody species establishment (Allen 1997). Notably, Tropical Storm Imelda, which impacted southeastern Texas from 17 to 21 September 2019, brought substantial rainfall during the first year of study. Meanwhile, the above-average precipitation recorded in Harris County between 2019 and 2021 probably led to very low seedling survival at the end of our study period. Such intensified precipitation during 2019 and 2020 likely resulted in prolonged inundation lasting several months. Similar studies have indicated that those flood-intolerant bottomland species died when they were under inundation for over 3 months (Oliver et al. 2018), and Water tupelo's performance was better at drier sites (Kolka et al. 1998). The interannual hydrological variation during the study period led to the survival of Loblolly pine, Water oak, and Water tupelo under 6% at the end of our study period.

Seedling Height Growth and Its Influencing Resource Variables

The height of seedlings was closely correlated with frequent dieback and re-sprouting events throughout the study period, which made analyzing height growth over time challenging. Compared to the initial monthly height increments between April and June, the monthly height increments from July to September were significantly lower. This decline in growth can largely be attributed to the late summer drought during this period (Lawal et al. 2024). The lower height increments observed from October to December were primarily due to the conclusion of the growing season (Tracy et al. 2024).

Seedling height of all four species was primarily determined by direct and diffuse light and LAI. These results align with findings for Baldcypress, Loblolly pine, and several oak species in the southern United States, which require full sunlight for optimal growth (Mills 1994). Light conditions influence both the availability of resources for photosynthesis and the competitive dynamics with understory vegetation. This highlights the close relationship between overstory composition and structure and understory seedling growth, as LAI can vary with overstory tree species (Stanturf et al. 2009). Furthermore, overstory tree height plays a crucial role in determining light availability, as it influences the proportion of direct and diffuse light reaching the understory, although it was not directly measured in this study (Bhattacharjee et al. 2008). This suggests that overstory structure may explain part of the variation in seedling height growth. Future studies incorporating both light conditions and canopy structure may provide a more comprehensive understanding of resource gradients and their effects on bottomland seedling development dynamics.

Other Variables Influencing Seedling Survival and Height Growth

Although soil texture influences water drainage rates and water table depth may indirectly reflect the duration of inundation, hydrological conditions, including the depth of inundation, duration of the hydroperiod, and its seasonal timing, may also critically affect seedling survival and growth, particularly in areas subjected to frequent hurricanes (Kroschel et al. 2025). However, these variables were not included in our study because they are largely driven by interannual variability in precipitation and temperature, making it difficult to standardize through measurements. In contrast, soil properties and aboveground light conditions remained relatively stable throughout the study period.

Together with seedling survival and growth response to resource gradients, we found that Baldcypress is a robust candidate for restoration in areas similar to this wetland mitigation bank. Its ability to tolerate prolonged flooding and thrive in soils with sand proportions as high as 70% suggests strong adaptive potential for hydrologically dynamic environments. Baldcypress benefits from overstory canopy cover for reducing competition from herbaceous plants, while adequate direct light in the understory remains essential for optimal performance (Dulohery et al. 2000). For Water tupelo, prolonged inundation during the early seedling stage, particularly within the first 6 months after planting, appears to limit survival, indicating that flood tolerance may develop later as seedlings grow larger. Adjusting the timing of planting or selecting sites with shorter flood durations thus could enhance early seedling performance of Water tupelo. It can tolerate shaded conditions better than Baldcypress, but height growth is slow in the first growing season; careful management of understory competition may be necessary to support its establishment. For Water oak, a key species for hardwood forest restoration, site hydrology is critical. Survival is more likely in areas that experience seasonal flooding during winter rather than year-round inundation, like the case in our study (Baker & Broadfoot 1979). Aboveground growth is typically slow during the early stages, and the species exhibits a relatively high light demand (Renninger et al. 2019). Effective control of understory competition is strongly recommended to promote establishment and growth (Oliver et al. 2018; Renninger et al. 2019). For Loblolly pine, a commercially important species often planted in bottomland forests, early survival is significantly reduced in areas subject to frequent flooding. Its height growth is relatively slow during the initial stages. Successful establishment may require planting on better-drained sites (Burns & Honkala 1990b). Resource variables beyond soil texture, soil pH, and light availability, such as nutrient status, should be considered when selecting appropriate sites.

The restoration environments for bottomland species vary widely. Our study highlights the significant influence of resource conditions such as soil texture, soil pH, and light availability on seedling survival and growth of four typical bottomland tree species. Species-specific responses to these resource gradients emphasize the importance of selecting tree species that are well-suited to the site conditions, particularly in flood-prone areas. Our findings also underscore the role of overstory

composition in shaping understory survival growth. More interactions between resource gradients and seedling performance need to be examined to enhance the restoration of bottomland forests.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Photos of the seedling planting.
Figure S2. Residuals plot of mixed effects Cox hazard model for seedling survival.
Figure S3. Residuals plot of linear mixed effects model for seedling monthly height increment.
Table S1. Values of each resource at each plot.
Table S2. Pairwise comparisons of survival probabilities among the four species were conducted using the log-rank test, with p values adjusted for multiple comparisons using the Bonferroni correction method.
Table S3. Summary of ANOVA for monthly height increment for Baldcypress, Loblolly pine, Water oak, and Water tupelo.
Table S4. Summary of Turkey's post hoc analysis for monthly height increment for Baldcypress, Loblolly pine, Water oak, and Water tupelo.

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