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Effects of flood duration on seedling survival and growth of potential replacement species in black ash (*Fraxinus nigra* Marshall) forests threatened by emerald ash borer

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ABSTRACT

Within black ash (*Fraxinus nigra* Marshall) wetlands, black ash acts as a foundational species, resulting in high vulnerability to the invasive emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae). One mitigation strategy being considered is the planting of alternative tree species to increase compositional diversity, however, there is limited understanding of how replacement tree species tolerate flooding. A greenhouse experiment was used to explore early survival and growth of eighteen tree species in response to five flooding durations (3, 6, 9, 12, or 15 weeks). Seedlings were assigned to flood tolerance groups according to their responses to the various flooding duration treatments. *Taxodium distichum* (L.) Rich., *Ulmus americana* L., and *Betula nigra* L. were able to survive and grow with flooding durations of up to 15 weeks. *Thuja occidentalis* L., *Acer rubrum* L., *Larix laricina* (Du Roi) K. Koch, *Quercus bicolor* Willd., and *Betula alleghaniensis* Britton had high survival and growth rates with flooding durations up to 6 weeks in length. Finally, *Juglans nigra* L. and *Acer saccharum* Marshall responded poorly to flooding of any duration. These results can assist managers in matching potential black ash replacement species to the hydrology of their local black ash wetlands.

Introduction

Black ash (*Fraxinus nigra* Marshall) wetlands in the Lake States region, USA are uniquely threatened by the wood-boring beetle, emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) (Youngquist et al., 2017; Granger et al., 2020; Olson et al., 2021). Within its native range in Asia, EAB is considered a secondary pest, however, outside of that range, EAB is considered invasive and causes high levels of mortality of ash species found in North America (*Fraxinus* spp.) (Baranchikov et al., 2008). The arrival of this invasive insect in black ash wetlands is particularly concerning given that black ash acts as a foundational species (*sensu* Ellison et al., 2005), influencing hydrologic regime, wildlife habitat, and nutrient cycling (Slesak et al., 2014; Kolka et al., 2018; Grinde et al., 2022). Further, these wetlands are extensive throughout the western Great Lakes region, encompassing roughly 1.2 million ha of wetland forests (Grinde et al., 2022).

Facing the loss of black ash and its foundational role in local ecosystem function, researchers and managers are investigating methods to mitigate the impact of EAB on black ash wetlands via diversification of stand composition (Looney et al., 2015; Costanza et al., 2017). Diversification efforts may require planting in black ash wetlands where natural regeneration of non-ash species is limited post-EAB (Windmuller-Campione et al., 2020; Palik et al., 2021a). Establishment of replacement overstory species by planting could help maintain several of the foundational functions of black ash within the swamp hardwood forested ecosystems (Montoya et al., 2012).

Black ash wetlands in the western Great Lakes states are generally characterized by poorly drained peaty and/or mineral soils and typically form in depressional wetlands, wetland complexes, and riparian corridors (D'Amato et al., 2018). Due to the seasonal flooding of black ash wetlands and uncertainty of climate change, careful thought and investigation should be devoted to choosing replacement species. Tree

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species selected for planting within black ash wetlands will have to survive some period of flooding and the dramatic seasonal temperature fluctuations of the upper Great Lakes region. Flooding stresses woody plants in a variety of ways. First, the plant's ability to photosynthesize is limited in part due to reduction in stomatal conductance, a common plant response to flooding (Landhäusser et al., 2003). Energy shortages resulting from the limitation of photosynthesis then lead to reductions in root, shoot, and diameter growth as well as nutrient uptake (Bailey--Serres and Voesenek 2008). Several woody plant species have evolved morphological traits to tolerate flooding stress. Tamarack (*Larix laricina* (Du Roi) K. Koch), for example, is able to offset flood-induced root damage by growing adventitious roots (Islam and Macdonald 2004). Some flood tolerant species also develop aerenchyma tissue in their stems and roots which allows for better oxygen transport within the plant (Kozlowski 1997). Individual species will have to be matched to the type of black ash wetland that exhibits the flooding regime they are best adapted to.

Given the long-lived nature of trees, natural resource managers must consider both immediate and long-term conditions when determining which species to plant. For example, in addition to flooding, many North American tree species are expected to experience a northward expansion in climatically suitable habitat by midcentury due to climate change (Iverson et al., 2008). While some tree species may expand their ranges independently (Boisvert-Marsh et al., 2014; Fei et al., 2017), others may warrant assisted migration from more southerly latitudes (Pedlar et al., 2012; Schwartz et al., 2013). There is an urgent need to test the suitability of species for assisted migration to ensure that managers have information to guide species selection for planting in response to ecosystem threats such as EAB.

Several studies have already been initiated to evaluate potential replacement species in black ash wetlands, including potential future climate-adapted species. Eight years after planting, Palik et al. (2021b) found lower overall seedling survival in a clearcut treatment versus an uncut control was likely due to water tables existing at or above the soil surface for longer periods of time in a precipitation-fed, mid--productivity site in Minnesota. In the same study, American elm (*Ulmus americana* L.) and swamp white oak (*Quercus bicolor* Willd.) had the highest survival rates across a range of overstory treatments. In depressional and riparian black ash wetlands in northern Michigan, Bolton et al. (2018) found that American elm was able to tolerate long periods of soil inundation. While these studies and others have made important headway in exploring replacement species for black ash, controlled studies investigating and comparing specific factors that impact performance and the corresponding plant responses in candidate replacement tree species are lacking.

This study used a controlled greenhouse experiment to investigate the tolerance of 18 potential black ash replacement species to five flooding duration treatments: 3, 6, 9, 12, and 15 weeks flooded to the soil surface. These flooding durations were selected to reflect the full range of flooding durations likely during the growing season in the northern Great Lakes region (D'Amato et al., 2018). The specific objective was to determine the effect of flooding duration on the survival and growth of potential replacement species to inform the development of planting strategies to mitigate EAB impacts. The overarching goal is to provide information to forest managers in selecting trees species to mitigate the loss of critical ecosystem functions, such as hydrological control, that black ash contributes to the wetlands in which it dominates.

Materials and methods

Study design

This study was conducted in a greenhouse at the US Forest Service Northern Research Station in Rhinelander, WI, USA. Temperature in the greenhouse was maintained at 25 °C for the duration of the growing season. Inside the greenhouse, maximum photosynthetically active radiation was 556 μmol m^{-2} s^{-1}. Eighteen potential replacement species (Table 1) were evaluated; species were selected based on input from silviculturists at the Wisconsin Department of Natural Resources (DNR) as well as results from previous studies on black ash wetlands (Table 3; Looney et al., 2015, Iverson et al., 2016, Bolton et al., 2018). In the spring of 2020, bald cypress (*Taxodium distichum* (L.) Rich.) and sycamore (*Platanus occidentalis* L.) seedlings were obtained from state nurseries in Illinois and Iowa, respectively. Seedlings of each of the other species were obtained from the Wisconsin state nursery in Boscobel, Wisconsin. The age of the seedlings ranged from one to three years old (Table 1).

Due to staffing problems resulting from the COVID-19 pandemic, the seedlings were lifted later than the optimal time; some had already begun to break bud. Upon arrival at the US Forest Service's Northern

Table 1
List of tree species used in the study. Stock type represents the age of the seedlings. Wetland indicator status taken from USDA PLANTS database. Fac. = Facultative, Ob. = Obligate. Standard error (SE) is shown in parenthesis.

Species	Common Name	Stock Type	Wetland Indicator Status	Initial Mean Height (cm)	Initial Mean Diameter (mm)
Acer rubrum L.	red maple	2–0	Fac.	18.1 (0.69)	5.6 (0.26)
Acer saccharinum L.	silver maple	2–0	Fac./Fac. Wetland	35.5 (0.83)	6.8 (0.36)
Acer saccharum Marshall	sugar maple	2–0	Fac. Upland/ Ob. Upland	32.6 (1.67)	7.1 (0.24)
Betula nigra L.	river birch	1–0	Fac. Wetland	26.4 (0.66)	2.9 (0.11)
Betula alleghaniensis Britton	yellow birch	2–0	Fac./Fac. Upland	29.6 (0.99)	4.8 (0.37)
Carya cordiformis (Wangenh.) K. Koch	bitternut hickory	2–0	Fac./Fac. Upland	29.5 (1.44)	7.3 (0.33)
Juglans nigra L.	black walnut	1–0	Fac. Upland/ Ob. Upland	33.2 (0.67)	7.3 (0.26)
Larix laricina (Du Roi) K. Koch	tamarack	2–0	Fac. Wetland	55.9 (2.23)	5.9 (0.39)
Picea glauca (Moench) Voss	white spruce	3–0	Fac./Fac. Upland	31.7 (1.47)	4.5 (0.25)
Picea mariana (Mill.) Britton, Sterns & Poggenb.	black spruce	3–0	Fac. Wetland	43.1 (1.41)	5.4 (0.24)
Pinus resinosa Aiton	red pine	2–0	Fac. Upland	13.5 (0.54)	4.1 (0.16)
Pinus strobus L.	eastern white pine	3–0	Fac. Upland	30.8 (1.25)	4.5 (0.21)
Platanus occidentalis L.	sycamore	1–0	Fac./Fac. Wetland	29.0 (0.72)	2.8 (0.10)
Quercus alba L.	white oak	1–0	Fac. Upland	19.1 (1.13)	4.7 (0.17)
Quercus bicolor Willd.	swamp white oak	1–0	Fac. Wetland	31.1 (1.15)	5.7 (0.25)
Taxodium distichum (L.) Rich.	bald cypress	1–0	Ob. Wetland	61.9 (2.44)	5.2 (0.32)
Thuja occidentalis L.	northern white cedar	3–0	Fac. Wetland	45.5 (1.60)	6.6 (0.47)
Ulmus americana L.	American elm	1–0	Fac./Fac. Wetland	32.9 (0.77)	5.4 (0.24)

Research Station in Rhinelander, Wisconsin, seedlings were placed in a walk-in cooler, and maintained at 4 °C. Four days later, in mid-May, they were potted into plastic containers (10 cm x 10 cm x 30 cm) with a soil mixture of sphagnum peat moss (60–70%), bark, and perlite (Berger BM7 Bark Mix).

The study was designed as a split plot randomized complete block design where treatments included flooding durations of 3, 6, 9, 12, and 15 weeks; each species-treatment combination was replicated eight times. A single seedling of each species was placed in 40 stock tanks (dimensions of 132 cm x 79 cm x 36 cm) which were then randomly assigned to a flooding treatment within each block. Within each tank, seedlings were randomly assigned to one of 18 positions according to a spacing pattern that maximized the distance between each individual within a given tank. For reference, we also subjected each of the 18 species to a no flood treatment where seedlings were grown ($n = 8$) in stock tanks with the water table maintained at a depth of 27 cm below the surface. Results from this reference cohort are presented in the results; however, they were not included in any statistical analysis (Figs. 1 and 2).

Basal diameter and height of each seedling was measured (using digital calipers with a precision of 0.1 mm, and a meter stick with a precision of 0.1 cm, respectively) immediately prior to treatment initiation. Height was measured from the soil surface to the tip of the uppermost living tissue and basal diameter was measured one cm above the root collar. Flooding treatments were applied by filling the tanks with tap water until water levels equilibrated at the soil surface. At the end of their respective flooding periods, stock tanks in a treatment were drained and the cohort was then kept at field capacity for the duration of the growing season by maintaining the water table 27 cm below the soil surface. At the end of the growing season, survival, height, and basal diameter were measured. Negative height values resulted from stem dieback and negative basal diameter values resulted from stem shrinkage in response to water stress (Kramer and Kozlowski, 1979). Dead seedlings were defined as those exhibiting no visible green tissue.

Both percent decrease and absolute change in height and basal diameter are presented in the results. Percent decreases were rounded to the nearest integer divisible by five and listed as an average to account for the variability in the value. Absolute change values represent the difference in initial and final measurements for each individual seedling, which were then averaged for each species. Ranges of absolute change

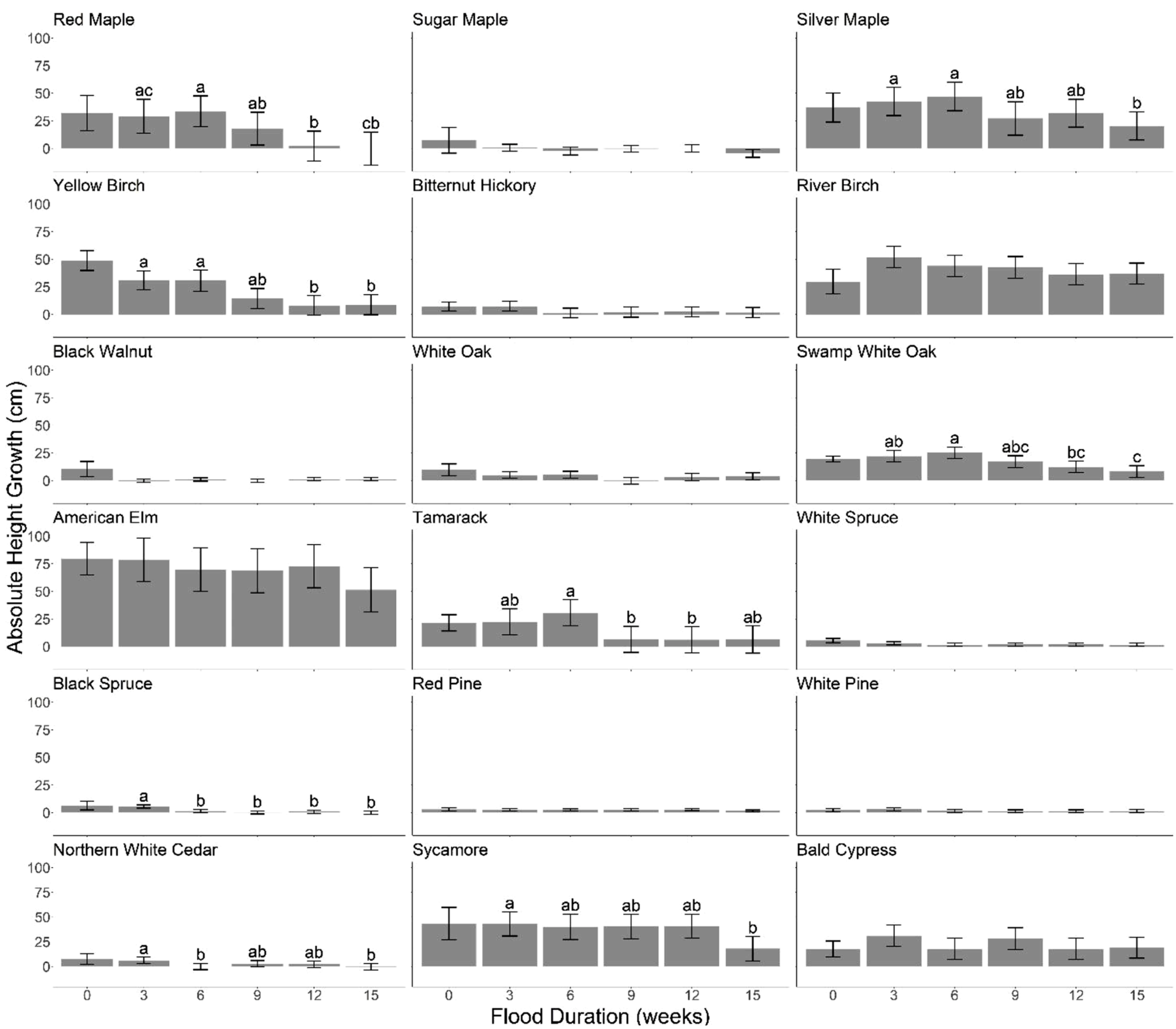

Fig. 1. Absolute seedling height growth at the end of the growing season by flooding duration treatment for all 18 species. Values from the reference cohort of seedlings not subjected to flooding are presented in the “0 weeks” flood duration position. Lowercase letters indicate significant differences between flooding duration treatments in panels with significant treatment effects ($p < 0.05$). Error bars represent 95% confidence intervals.

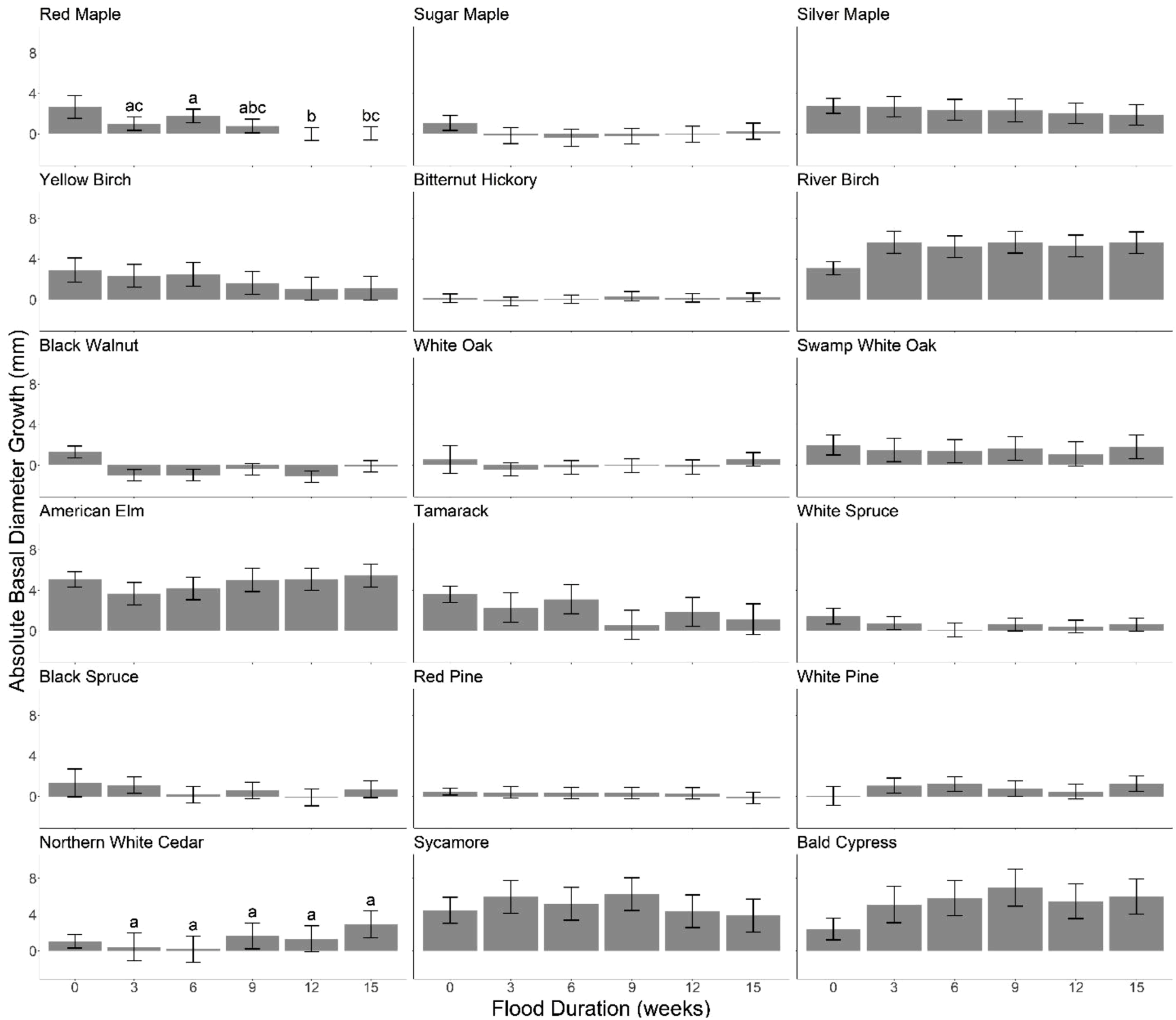

Fig. 2. Absolute seedling basal diameter growth at the end of the growing season by flooding duration treatment for all 18 species. Values from the reference cohort of seedlings not subjected to flooding are presented in the "0 weeks" flood duration position. Lowercase letters indicate significant differences between flooding duration treatments in panels with significant treatment effects ($p < 0.05$). Error bars represent 95% confidence intervals.

represent the maximum and minimum values for the group of species listed.

Data analysis

Effect of flood duration on seedling survival was assessed using generalized linear mixed models with a binomial distribution. Flood duration was included as a fixed effect and seedling position within the tank was included as a random effect to account for shading of seedlings towards the center of the tank. Models were run for each species individually. Random effects had to be removed and generalized linear models run for some species due to convergence problems. A cumulative log-log link was added to the model for black walnut (*Juglans nigra* L.) due to the dominance of zeroes in the data (high mortality). Mixed model regressions were applied using the glmmTMB function in the 'glmmTMB' package (Hupperts et al., 2020) in R 4.0.3 software (R Core Development Team, 2018) and fitted by the Type II Wald chi-square test.

Effect of flood duration on absolute height and basal diameter growth was analyzed using linear mixed effects models with a normal distribution. Flood duration was included as a fixed effect and seedling position within the tank was included as a random effect. Pre-treatment height and basal diameter were included as covariates. Models were run for each species individually. Mixed models were applied using the lme function in the 'nlme' package (Looney et al., 2017) in R 4.0.3 software (R Core Development Team, 2018). Post-hoc pairwise multiple comparisons of mean absolute height and basal diameter growth across flooding duration treatment levels were conducted with the 'emmeans' package (Lenth et al., 2018) using Tukey's HSD adjustment. In all models, an alpha level of 0.05 was used.

To facilitate interpretation, species were grouped according to five flood tolerance categories (Fig. 3). Categories were created using a qualitative approach that took survival, height and basal diameter growth into consideration. One additional category was created for species for which results were inconclusive. While the categories are presented as discrete groups in this paper to aid in discussion, the flood tolerances of these species in the field will be more nuanced and based on factors specific to individual seedlings (e.g. stock type, seed zone, genetics etc.) and the environment in which the seedlings are planted.

Results

Survival

At the end of the growing season, the survival rate across species was 73%. Survival by species was: American elm (100%), silver maple (*Acer saccharinum* L.) (100%), sycamore (100%), bald cypress (100%), river birch (*Betula nigra* L.) (98%), swamp white oak (95%), red maple (*Acer rubrum* L.) (87%), bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) (87%), eastern white pine (*Pinus strobus* L.) (80%), northern white cedar (*Thuja occidentalis* L.) (78%), yellow birch (*Betula alleghaniensis* Britton) (75%), white oak (*Quercus alba* L.) (73%), red pine (*Pinus resinosa* Aiton) (70%), tamarack (69%), white spruce (*Picea glauca* (Moench) Voss) (48%), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) (43%), sugar maple (*Acer saccharum* Marshall) (16%), black walnut (5%). Flood duration did not have a significant effect on the survival of any of our study species (Table S1, Table S2).

Absolute height growth

Height growth was variable among species and flood duration (Fig. 1). Very low height growth (−4 – 8 cm) regardless of flood duration treatment, was exhibited by black walnut, sugar maple, white spruce, white oak, eastern white pine, red pine, and bitternut hickory (Fig. 1). Northern white cedar and black spruce also exhibited very low height

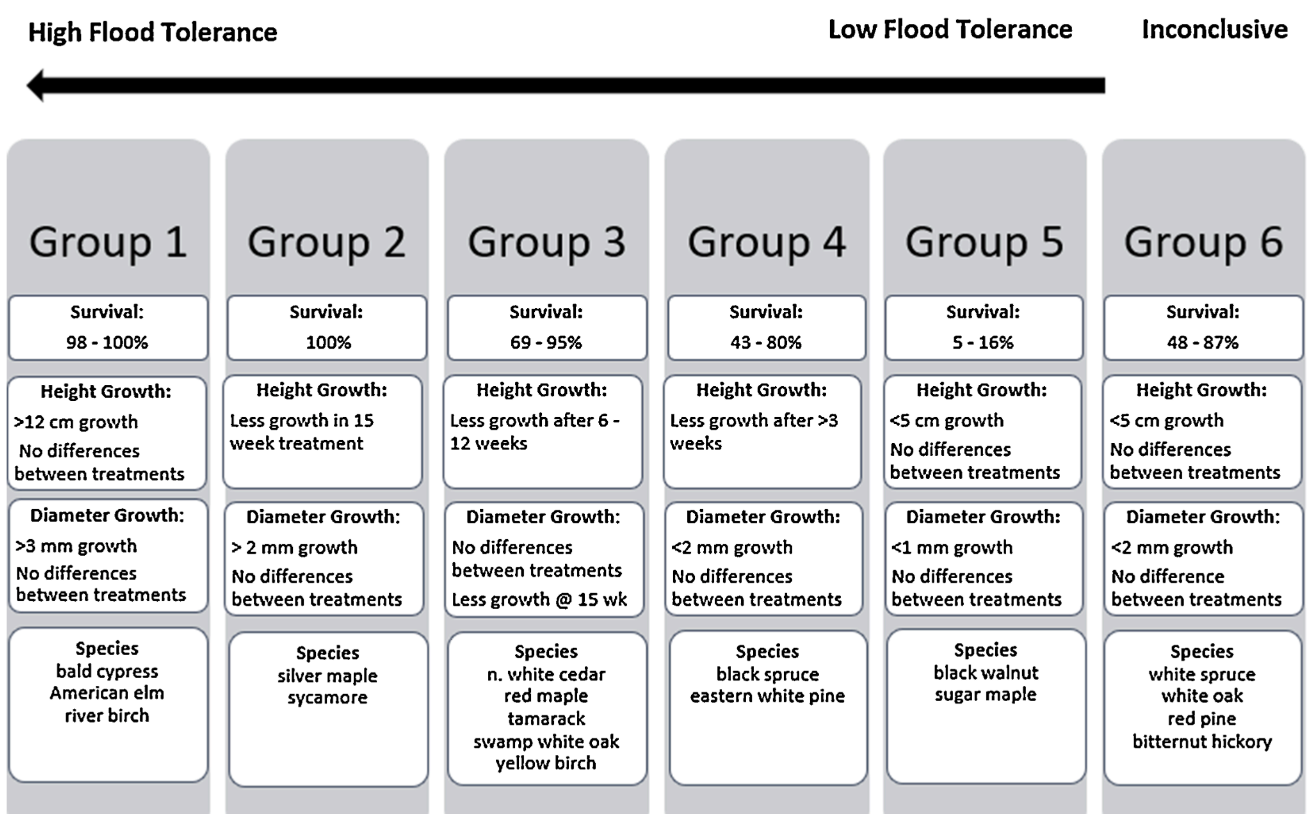

Fig. 3. Description of criteria delineating flood tolerance groupings presented in the discussion and the species associated with each group. Flooding tolerance is greatest is Group 1 and decreases to Group 5. Group 6 includes species for which the data was inconclusive.

growth that varied by flood duration treatment (Fig. 1 and Table 2). These species grew significantly more in the 3-week flooding treatment than in the longer flooding treatments (100% decrease between 3-week and 15-week treatment, on average). The main effect of flood duration treatment was also significant for tamarack, swamp white oak, red maple, silver maple, and yellow birch (Table 2). These species grew the most in the 3-week and 6-week flood duration treatments and steadily decreased in growth with increasing flooding duration (70% decrease, on average, between 6-week and 15-week treatments). Sycamore, while also demonstrating decreasing height growth with increasing flood duration (60% decrease between 3-week and 15-week treatments), still exhibited relatively high growth in the 15-week treatment (18 – 20 cm). Bald cypress did not have particularly high (31.1 cm, maximum) relative height growth values, but it exhibited no significant difference across flooding duration treatment levels. A large amount of height growth (65 cm, on average), with no significant difference across flood duration treatments, was exhibited by American elm and river birch (Fig. 1 and Table S3).

Absolute basal diameter growth

Flood duration treatment had very little effect, overall, on basal diameter growth (Table 2). Very low basal diameter growth (−0.5 – 0.6 mm) regardless of flood duration treatment, was exhibited by black walnut, white oak, bitternut hickory, sugar maple, red pine, white spruce, and black spruce (Fig. 2). Red maple was the only species to exhibit a significant decrease in basal diameter growth in response to flood duration treatment (Table 2 and Fig. 2). This species grew the most in the 3-week and 6-week flood duration treatments and steadily decreased in growth with increasing flooding duration (95% decrease, on average, between 6-week and 15-week treatments). Five species exhibited an intermediate level of basal diameter growth (0.2 - 3.2 mm) regardless of flood duration; those species include eastern white pine, yellow birch, swamp white oak, northern white cedar, and tamarack (Fig. 2). Finally, five species exhibited high basal diameter growth (2 – 7 mm) with no significant difference across flood duration treatments; those species include silver maple, American elm, sycamore, river birch, and bald cypress (Fig. 2).

Discussion

The expansion of emerald ash borer (EAB) across the Great Lakes region threatens the ecological functioning of black ash wetlands which are extensive throughout the region (Youngquist et al., 2017). For this reason, managers and scientists alike are investigating ways to maintain ecosystem services after the elimination of black ash by EAB (D'Amato et al., 2018; Windmuller-Campione et al., 2020). Utilizing a controlled experiment, this study determined how one season of different flooding durations influenced the growth of 18 potential replacement species. Species generally had variable responses to the different flooding durations, requiring managers to match species selected for planting to local site conditions.

The group of species that exhibited the highest flood tolerance includes bald cypress, American elm, and river birch (Group 1, Fig. 3). These species had very high growth and survival rates overall. This finding is consistent with Frye and Grosse (1992) who reported that, of 22 species studied, bald cypress maintained the most robust growth rates in fully flooded conditions for 120 days in a controlled outdoor study. Additionally, American elm is a dominant species in floodplains in the Midwest and river birch is commonly found in forested wetlands (Barnes and Wagner, 1981; Guyon and Battaglia, 2018). In a depressional black ash wetland in northern Michigan, Bolton et al. (2018) also found that American elm had high survival rates especially if planted on hummocks (Table 3).

Despite their high flood tolerance, this group has several limitations in being utilized as replacement species. The greatest limitation of planting American elm as a replacement species for black ash is the presence of Dutch elm disease (DED, *Ophiostoma novo-ulmi* Brasier) in North America which kills mature elms (Brasier, 1991). There is, however, active research exploring disease resistant varieties of American elm (Martín et al., 2021; Townsend et al., 2005), and planting elm may also be effective at maintaining ecosystem functions for decades before it typically succumbs to DED. Bald cypress, on the other hand, could be limited by its cold hardiness: the northern limit of its range currently extends to southern Illinois (Burns and Honkala, 1990). The Great Lakes region currently experiences long, cold winters (−5 °C, average high temperature in January in Rhinelander, WI, US Climate Data), short growing seasons, and an average annual precipitation of 78 to 97 cm (Environment and Climate Change Canada and the U.S. 2021). This climate is greatly influenced by the Great Lakes, with areas closer to these bodies of water experiencing warmer and snowier winters and cooler summers. Climate change, however, is expected to increase growing season length and the intensity of extreme heat and rainfall events (GLISA, 2014). As a result, bald cypress may become successfully established in the region in the future, especially with the aid of assisted migration (Pedlar et al., 2012), an option that should be carefully considered in consultation with local indigenous nations (Schwartz et al., 2013; Pelai et al., 2021).

The group of species that grew significantly less in the 15-week flooding treatment but still had substantial growth overall, and 100% survival in all treatments, includes silver maple and sycamore (Group 2, Fig. 3). These species are dominant in floodplains and bottomlands in the Midwest, so it is not surprising to find them moderately flood tolerant (Tang and Kozlowski, 1982; Peterson and Bazzaz, 1984). Bolton et al. (2018) also found that 4-year old silver maple seedlings had high survival rates when planted in depressional black ash wetlands in Michigan's upper peninsula (Table 3). Additionally, it has been suggested that climate change will greatly expand the habitat of silver maple in Minnesota (Kozlowski, 1997). While sycamore may show excellent potential as a replacement for black ash in terms of its flood tolerance, it is limited by winter hardiness. Currently, sycamore reaches its northern limit in southern Wisconsin (McAlpine, 1973); however, its range could be expanded with assisted migration in anticipation of climate change.

The group of species that is somewhat flood tolerant grew the most in the 3-week and 6-week flooding treatments and includes northern white cedar, red maple, tamarack, swamp white oak, and yellow birch (Group 3, Fig. 3). These species had intermediate survival rates (69–95%). These results are corroborated by several studies investigating replacement species in black ash wetlands specifically. Eight years after planting, Palik et al. (2021b) found that red maple and swamp white oak were

Table 2
F-statistic probabilities for fixed treatment effects of flood duration on height and basal diameter growth. P-values ≤ 0.05 are bolded.

Species	Absolute Height	Absolute Basal Diameter
red maple	**0.001**	**0.001**
sugar maple	0.078	0.400
silver maple	**0.003**	0.691
yellow birch	**0.001**	0.179
bitternut hickory	0.275	0.536
river birch	0.284	0.914
black walnut	0.317	0.095
white oak	0.280	0.220
swamp white oak	**0.001**	0.902
American elm	0.438	0.114
tamarack	**0.012**	0.112
white spruce	0.559	0.344
black spruce	**0.001**	0.072
red pine	0.189	0.590
white pine	0.230	0.453
northern white cedar	**0.027**	**0.004**
sycamore	**0.027**	0.259
bald cypress	0.209	0.669

Table 3
Overview of survival and height growth results from in-situ black ash studies as compared to the present study. Growth categorizations were determined by comparing each species to the performance of its peers within each study. Growth categorizations for the present study were estimated from the water table depth treatment responses. Values from Bolton et al., 2018 are taken from seedlings planted on natural and/or artificial hummocks. Looney et al., 2015, Looney et al., 2017, and Palik et al. (2021b) all used results from the same study, but report at different time periods of response.

	Looney et al., 2015 & 2017				Bolton et al., 2018				Palik et al., 2021b				Present Study	
	Control		Clearcut		Ottawa National Forest		Superior Munic. Forest		Control		Clearcut			
Species	Survival (%)	Growth	Survival (%)	Growth	Survival (%)	Growth	Survival (%)	Growth	Survival (%)	Growth	Survival (%)	Growth	Survival (%)	Growth
Fraxinus mandshurica Rupr.	74	low	57	low					21	low	30	low		
Populus balsamifera L.	29	high	39	high					4	low	33	high		
Populus deltoides W. Bartram ex Marshall	5	medium	12	high					0	low	0	low		
Celtis occidentalis L.	77	medium	17	low			66	low	62	low	5	low		
Populus tremuloides Michx.	0	low	8	low					0	low	0	low		
Abies balsamea (L.) Mill.					7	low								
Quercus macrocarpa Michx.					38	low								
Tilia americana L.					64	medium								
Acer rubrum L.	33	medium	15	medium	11	low	68	high	42	medium	16	medium	87	medium
Acer saccharinum L.					76	high							100	high
Ulmus americana L.	93	low	32	medium	68	high			82	low	56	medium	100	high
Betula alleghaniensis Britton	4	low	0	low	8	low			0	low	0	low	75	medium
Picea mariana (Mill.) Britton, Sterns & Poggenb.	17	medium	11	low	13	medium			7	low	21	low	43	low
Thuja occidentalis L.	16	medium	4	medium	39	medium	39	low	0	low	0	low	97	low
Larix laricina (Du Roi) K. Koch	8	high	8	high	0	low			10	low	32	low	69	medium
Quercus bicolor Willd.	83	medium	68	medium					80	low	50	medium	95	medium
Acer saccharum Marshall													16	low
Betula nigra L.													98	high
Carya cordiformis (Wangenh.) K. Koch													87	low
Juglans nigra L.													5	low
Picea glauca (Moench) Voss													48	low
Pinus resinosa Aiton													70	low
Pinus strobus L.													80	low
Platanus occidentalis L.													100	high
Quercus alba L.													73	low
Taxodium distichum (L.) Rich.													100	high

particularly successful when planted in a group selection cut in a precipitation-fed, mid-productivity site in Minnesota (Table 3). Bolton et al. (2018) also found that red maple and northern white cedar showed promising growth and survival rates, especially when planted on hummocks in depressional and riparian black ash wetlands in northern Michigan (Table 3). Finally, Iverson et al. (2016) suggested red maple and swamp white oak as replacement options for black ash due to the fact that they are predicted to do well under expected climate change scenarios which include extreme precipitation events as well as drought (Niu et al., 2014).

Due to the fact that the species' ranges in the somewhat tolerant category cover a large geographic area that includes the Great Lakes region, managers should have reliable access to seedlings of these species at local nurseries. While these species may currently be well-adapted to the local climate, however, some of them may not respond well to climate change. For example, the ranges of northern white cedar, tamarack, and yellow birch are not expected to include the Great Lakes region under future climate change scenarios (Iverson et al., 2016). For these species, the movement of populations from the southern portion of their ranges to areas further north may be warranted (Tepe and Meretsky, 2011; Aitken and Bemmels, 2016). Managers can evaluate the suitability of seed sources for assisted population migration using recently developed tools such as the Seedlot Selection Tool (St. Clair et al., 2022).

The group of species with low tolerance for flooding grew the most in the 3-week flooding treatment and include black spruce and eastern white pine (Group 4, Fig. 3). The placement of black spruce in this category, while justified based on the results of the present study, is unexpected given the silvics of the species. Black spruce is commonly found in frequently inundated peatlands, and thus would be expected to tolerate flooding well (Lieffers and Rothwell, 1986). Despite the fact that black spruce is typically a slow-growing species in comparison to its more common competitors (Heinselman, 1957), the exceptionally low amount of growth and survival it exhibited in this study may be due to damage sustained from late nursery lifting resulting from the COVID-19 pandemic. In contrast, the placement of eastern white pine in this category is less remarkable. This species is generally limited to drier hummock microsites when it is found in poorly drained soils (Wilson and McQuilkin, 1963).

Lastly, the flood intolerant group exhibited the lowest growth and survival in response to all flooding durations as compared to the reference condition and includes black walnut and sugar maple (Group 5, Fig. 3). The low survival rate of black walnut matches the results of Coggeshall et al. (2007) who found that, in a controlled experiment in Missouri, black walnut had a survival rate of 12.5% after being exposed to 5 weeks of 15 cm deep flowing or stagnant water. The determination of sugar maple as generally unsuitable for planting in wetlands aligns well with the USDA PLANTS database classification of this species, which ranges from facultative to obligate upland status. While these species have been known to establish in lowlands, they are likely inhabiting drier microsites (Burns and Honkala, 1990).

It is difficult to draw reliable conclusions from this study about the flooding tolerance of white spruce, white oak, red pine, and bitternut hickory, therefore they were assigned to Group 6, the inconclusive category (Fig. 3). These species did not grow well in either the reference condition or the flooded conditions and survival models did not reveal a significant effect of flooding treatment. It is possible that these species were damaged by late nursery lifting which resulted in poor growth and, in the case of white spruce, poor survival. Consequently, results for these species should be considered with caution.

Our study quantifies the response of seedlings to flooding duration, providing critical information to assess the suitability of replacement species for black ash, however, there are some limitations. For example, this study was conducted over the course of a single growing season. Consequently, it is difficult to conclude whether or not the species suggested for planting in black ash wetlands will remain suitable with continued annual flooding. Despite this, it has been noted that survival in the seedling's first year is an important indicator of future performance (Bolton et al., 2018). Another limitation of this study is that it does not take flooding intensity into account. The depth of water table below the soil surface is variable both spatially (in terms of microtopography) and temporally in black ash wetlands (Slesak et al., 2014; Diamond et al., 2020; Cianciolo et al., 2021). Thus, while this study will be helpful in matching species to the temporal aspect of a site's hydrology, further studies are needed to quantify the depth of water table each of these species is able to tolerate. This study also does not explicitly consider seedling age at planting, which has been shown to have a positive relationship with survival in flooded environments (Horsley et al., 2003). Finally, this study does not take the impact of browse on seedlings in the field into account. Given the abundance of whitetail deer (*Odocoileus virginianus* Zimm.) in the Great Lakes region, this will be a critical aspect to consider when choosing replacement species for black ash (Horsley et al., 2003; Patton et al., 2021).

Conclusions

Using findings from this controlled study to examine growth and survival response to flooding duration, we present five groups of species that are suitable for a range of flooding duration conditions in black ash wetlands. Managers can use these groupings to match potential replacement species with the black ash wetlands that exhibit the conditions to which they are best suited. Despite the fact that logistics become more complicated as number of species increases, managers should consider planting more than one replacement species in any given black ash wetland (Nyland, 2016). There is no single species that will act as a perfect replacement for black ash across the range of conditions found in black ash wetlands, and greater compositional diversity may impart greater resilience to future stressors (Montoya et al., 2012). As the EAB invasion continues, the findings of this study may prove useful to managers as they mitigate the impact of this destructive invasive pest in black ash wetlands.

Author contributions

RS and DB conceived and designed the experiment. GK, RS, DB, and MW developed the methodology and protocols; GK analyzed the data; GK wrote the paper with contributions from all coauthors. AM developed the figures. All authors reviewed the paper, provided editorial comment, and approved of the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

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References

Aitken, S.N., Bemmels, J.B., 2016. Time to get moving assisted gene flow of forest trees. Evol. Appl. 9 (1), 271–290.

Bailey-Serres, J., Voesenek, L.A.C.J., 2008. Flooding Stress acclimations and Genetic Diversity. Annu. Rev. Plant Biol. 59 (1), 313–339.

Baranchikov, Y., Mozolevskaya, E., Yurchenko, G., Kenis, M., 2008. Occurrence of the emerald ash borer, Agrilus planipennis in Russia and its potential impact on European forestry. Bull. OEPP 38 (2), 233–238.

Barnes, B., Wagner, W., 1981. Michigan Trees A Guide to the Trees of Michigan and the Great Lakes Region. University of Michigan Press, Ann Arbor, MI, USA, 1981.

Boisvert-Marsh, L., Périé, C., de Blois, S., 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere 5 (7), 1–33.

Bolton, N., Shannon, J., Davis, J., Grinsven, M.Van, Noh, N.J., Schooler, S., Kolka, R., Pypker, T., Wagenbrenner, J, 2018. Methods to improve survival and growth of planted alternative species seedlings in black ash ecosystems threatened by emerald ash borer. Forests 9 (3), 146.

Brasier, C.M., 1991. Ophiostoma novo-ulmi sp. nov., causative agent of current Dutch elm disease pandemics. Mycopathologia 115 (3), 151–161.

Burns, R., Honkala, B. 1990. Silvics of North America. United States Forest Service.

Cianciolo, T.R., Diamond, J.S., McLaughlin, D.L., Slesak, R.A., D\'Amato, A.W., Palik, B. J., 2021. Hydrologic variability in black ash wetlands implications for vulnerability to emerald ash borer. Hydrol. Process 35 (4), 1–13.

St Clair, J.B., Richardson, B.A., Stevenson-Molnar, N., Howe, G.T., Bower, A.D., Erickson, V.J., Ward, B., Bachelet, D., Kilkenny, F.F., Wang, T, 2022. Seedlot selection tool and climate-smart restoration tool web-based tools for sourcing seed adapted to future climates. Ecosphere 13 (5), e4089.

Coggeshall, M.V., Van Sambeek, J.W., Schlarbaum, S.E., 2007. Genotypic variation in flood tolerance of black walnut and three southern bottomland oaks. In: Buckley, David S., Clatterbuck, Wayne K. (Eds.), Proceedings, 15th central hardwood forest conference. e-Gen. Tech. Rep. SRS-101. U.S. Department of Agriculture, Forest Service, USA. Southern Research Station.

Costanza, K.K.L., Livingston, W.H., Kashian, D.M., Slesak, R.A., Tardif, J.C., Dech, J.P., Diamond, A.K., Daigle, J.J., Ranco, D.J., Neptune, J.S., Benedict, L., Fraver, S.R., Reinikainen, M., Siegert, N.W., 2017. The precarious state of a cultural keystone species tribal and biological assessments of the role and future of black ash. J. Forestry 115 (5), 435–446.

D\'Amato, A.W., Palik, B.J., Slesak, R.A., Edge, G., Matula, C., Bronson, D.R., 2018. Evaluating adaptive management options for black ash forests in the face of emerald ash borer invasion. Forests 9 (6), 348.

Diamond, J.S., McLaughlin, D.L., Slesak, R.A., Stovall, A., 2020. Microtopography is a fundamental organizing structure of vegetation and soil chemistry in black ash wetlands. Biogeosciences 17 (4), 901–915.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N. L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3 (9), 479–486.

Environment and Climate Change Canada and the U.S. National Oceanic and Atmospheric Administration (ECCC & US NOAA). 2021. 2020 Annual Climate Trends and Impacts Summary for the Great Lakes Basin.

Fei, S., Desprez, J.M., Potter, K.M., Jo, I., Knott, J.A., Oswalt, C.M., 2017. Divergence of species responses to climate change. Sci. Adv. 3 (5), e1603055.

Frye, J., Grosse, W., 1992. Growth responses to flooding and recovery of deciduous trees. J. Biosci. 47 (9), 683–689.

Granger, J.J., Zobel, J.M., Buckley, D.S., 2020. Differential impacts of emerald ash borer (agrilus planipennis fairmaire) on forest communities containing native ash (fraxinus spp.) species in Eastern North America. Forest Sci. 66 (1), 38–48.

Great Lakes Integrated Sciences and Assessments (GLISA). 2014. Synthesis of the Third National Climate Assessment for the Great Lakes Region.

Grinde, A., Youngquist, M., Slesak, R., Kolbe, S., Bednar, J., Palik, B., D\'Amato, A, 2022. Potential impacts of emerald ash borer and adaptation strategies on wildlife communities in black ash wetlands. Ecol. Appl. E2567.

Guyon, L., Battaglia, L., 2018. Ecological characteristics of floodplain forest reference sites in the upper Mississippi river system. For. Ecol. Manage. 427, 208–216.

Heinselman, M.L., 1957. Silvical Characteristics of Black Spruce (Picea mariana) (No. 45). Lake States Forest Experiment Station. US Department of Agriculture, Forest Service.

Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-Tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13 (1), 98–118.

Hupperts, S.F., Webster, C.R., Froese, R.E., Dickinson, Y.L., 2020. Seedling and sapling recruitment following novel silvicultural treatments in Great Lakes northern hardwoods. For. Ecol. Manage. 462, 117983.

Islam, M.A., Macdonald, S.E., 2004. Ecophysiological adaptations of black spruce (Picea mariana) and tamarack (Larix laricina) seedlings to flooding. Trees - Structure Function 18 (1), 35–42.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manage. 254 (3), 390–406.

Iverson, L., Knight, K.S., Prasad, A., Herms, D.A., Matthews, S., Peters, M., Smith, A., Hartzler, D.M., Long, R., Almendinger, J., 2016. Potential species replacements for black ash (fraxinus nigra) at the confluence of two threats emerald ash borer and a changing climate. Ecosystems 19 (2), 248–270.

Kolka, R.K., D\'Amato, A.W., Wagenbrenner, J.W., Slesak, R.A., Pypker, T.G., Youngquist, M.B., Grinde, A.R., Palik, B.J, 2018. Review of ecosystem level impacts of emerald ash borer on black ash wetlands what does the future hold? Forests 9 (4), 1–15.

Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiol. 17 (7), 490. –490.

Kramer, P.J., Kozlowski, T.T., 1979. Physiology of Woody Plants. Academic Press, Orlando, FL, USA.

Landhäusser, S.M., Silins, U., Lieffers, V.J., Liu, W., 2003. Response of Populus tremuloides, Populus balsamifera, Betula papyrifera and Picea glauca seedlings to low soil temperature and water-logged soil conditions. Scand. J. For. Res. 18 (5), 391–400.

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. 2018. Emmeans estimated marginal means, aka least-squares means. R package version 1*(1)*, 3.

Lieffers, V., Rothwell, R., 1986. Effects of depth of water table and substrate temperature on root and top growth of Picea mariana and Larix laricina seedlings. Can. J. For. Res. 16 (6), 1201–1206.

Looney, C.E., D\'Amato, A.W., Palik, B.J., Slesak, R.A, 2015. Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened Fraxinus nigra forests in Minnesota, USA. Can. J. For. Res. 45 (12), 1728–1738.

Looney, C.E., D\'Amato, A.W., Palik, B.J., Slesak, R.A, 2017. Canopy treatment influences growth of replacement tree species in Fraxinus nigra forests threatened by the emerald ash borer in Minnesota, USA. Can. J. For. Res. 47 (2), 183–192.

Martín, J.A., Domínguez, J., Solla, A., Brasier, C.M., Webber, J.F., Santini, A., Martínez-Arias, C., Bernier, L., Gil, L., 2021. Complexities underlying the breeding and deployment of Dutch elm disease resistant elms. New For. 1–36.

McAlpine, R.G., 1973. American sycamore. US Department of Agriculture. Forest Service.

Montoya, D., Rogers, L., Memmott, J., 2012. Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends Ecol. Evol. 27 (12), 666–672.

Niu, S., Luo, Y., Li, D., Cao, S., Xia, J., Li, J., Smith, M.D., 2014. Plant growth and mortality under climatic extremes an overview. Environ. Exp. Bot. 98, 13–19.

Nyland, R.D., 2016. Silviculture Concepts and Applications. Waveland Press.

Olson, S.K., Smithwick, E.A.H., Lucash, M.S., Scheller, R.M., Nicholas, R.E., Ruckert, K. L., Caldwell, C.M., 2021. Landscape-scale forest reorganization following insect invasion and harvest under future climate change scenarios. Ecosystems 24 (7), 1756–1774.

Palik, B.J., D\'Amato, A.W., Slesak, R.A, 2021a. Wide-spread vulnerability of black ash (Fraxinus nigra Marsh.) wetlands in Minnesota USA to loss of tree dominance from invasive emerald ash borer. Forestry 94 (3), 455–463.

Palik, B.J., D\'Amato, A.W., Slesak, R.A., Kastendick, D., Looney, C., Kragthorpe, J, 2021b. Eighth-year survival and growth of planted replacement tree species in black ash (Fraxinus nigra) wetlands threatened by emerald ash borer in Minnesota, USA. For. Ecol. Manage. 484, 118958.

Patton, S.R., Russell, M.B., Windmuller-Campione, M.A., Frelich, L.E., 2021. White-tailed deer herbivory impacts on tree seedling and sapling abundance in the Lake States Region of the USA. Ann. For. Sci. 78 (4), 1–11.

Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O \'Neill, G.A., Winder, R.S., Ste-Marie, C., 2012. Placing forestry in the assisted migration debate. Bioscience 62 (9), 835–842.

Pelai, R., Hagerman, S.M., Kozak, R., 2021. Whose expertise counts? Assisted migration and the politics of knowledge in British Columbia\'s public forests. Land Use policy 103, 105296.

Peterson, D., Bazzaz, F., 1984. Photosynthetic and Growth Responses of Silver Maple (Acer saccharinum L.) Seedlings to Flooding. Am. Midl. Nat. 112 (2), 261–272.

Schwartz, M.W., Hellmann, J.J., McLachlan, J.M., Sax, D.F., Borevitz, J.O., Brennan, J., Camacho, A.E., Ceballos, G., Clark, J.R., Doremus, H., Early, R., Etterson, J.R., Fielder, D., Gill, J.L., Gonzalez, P., Green, N., Hannah, L., Jamieson, D.W., Javeline, D., Zellmer, S., 2013. Managed relocation integrating the scientific, regulatory, and ethical challenges. Bioscience 62 (8), 732–743.

Slesak, R.A., Lenhart, C.F., Brooks, K.N., D\'Amato, A.W., Palik, B.J, 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. 44 (8), 961–968.

Tang, Z.C., Kozlowski, T.T., 1982. Ethylene production and morphological adaptation of woody plants to flooding. Can. J. Bot. 62 (8), 1659–1664.

Tepe, T.L., Meretsky, V.J., 2011. Forward-looking forest restoration under climate change—are US nurseries ready? Restor Ecol. 19 (3), 295–298.

Townsend, A.M., Bentz, S.E., Douglass, L.W., 2005. Evaluation of 19 American elm clones for tolerance to Dutch elm disease. J. Environ. Hortic. 23 (1), 21–24.

Wilson, R.W., McQuilkin, W.E., 1963. Silvical characteristics of eastern white pine (Pinus strobus). In: Northeastern Forest Experiment Station, Forest Service, 13. US Department of Agriculture.
Windmuller-Campione, M.A., Russell, M.B., Slesak, R.A., Lochner, M., 2020. Regeneration responses in black ash (Fraxinus nigra) wetlands implications for forest diversification to address emerald ash borer (Agrilus planipennis). New For. 52 (4), 537–558.
Youngquist, M.B., Eggert, S.L., D\'Amato, A.W., Palik, B.J., Slesak, R.A, 2017. Potential effects of foundation species loss on wetland communities a case study of black ash wetlands threatened by emerald ash borer. Wetlands 37 (4), 787–799.