

Influences on growth and survival of seedlings planted in black ash stands of Northern Michigan and Wisconsin

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ABSTRACT

The invasive emerald ash borer (*Agrilus planipennis*) is a threat to all North American ash (genus *Fraxinus*) trees, but wetland ecosystems dominated by black ash (*F. nigra*) are of particular concern to land managers. The rapid and extensive death of black ash on the landscape causes unprecedented ecological and hydrological impacts to cascade through the ecosystem. A strategy to combat such impacts and maintain these wetlands as forested is to underplant these stands with seedlings of alternative species that are capable of maturing into canopy trees. This study planted seedlings of seven non-ash tree species in black ash wetlands across northern Michigan and Wisconsin and assessed the factors that have the greatest effect on seedling survival and growth. First year survival across all species was 54 %, and by two years after planting total survival was 47 % with a mean relative growth rate of 5.47 cm/yr. The best-performing species in terms of both survival and growth rates were river birch (*Betula nigra*), silver maple (*Acer saccharinum*), and swamp white oak (*Quercus bicolor*). Bur oak (*Q. macrocarpa*) and red maple (*A. rubrum*) also exhibited high rates of survival despite having below average growth rates. The main factors influencing seedling performance were hydrology and microtopography, with greatly increased survival for seedlings planted on higher microsites further from the water table. Insufficient natural regeneration of canopy species observed in the understory of all stands warrants planting within these systems to avoid the vegetative community shift to dominance of herbaceous or shrub species.

1. Introduction

Ash (genus *Fraxinus*) are one of the most widely distributed genera of trees in the north-central and the eastern United States, with substantial presence in both natural forest and urban settings (MacFarlane and Meyer, 2005). There are an estimated 8.7 billion ash trees in the United States covering over 9.8 million hectares (U.S. Department of Agriculture, Forest Service (USDA FS), 2023). Six of the 16 species of ash that naturally occur in the United States are considered commercially important (Stewart and Krajicek, 1973). One of these species, black ash (*F. nigra*) or *baapaagimaak* in Ojibwe is a cultural keystone species for many Tribal Nations across North America that holds high spiritual significance and great economic value in its harvest for basket making (Costanza et al., 2017; Siegert et al., 2023). Black ash also fills an important ecological niche in forested wetlands throughout its range and is often an integral part of the overstory (Wright and Rauscher,

1990). In the upper Great Lakes region of Michigan, Minnesota, and Wisconsin, black ash occurs in almost pure to completely pure stands (Erdmann, 1987) commonly on poorly drained organic or muck soils (Minnesota Department of Natural Resources, 2018). Black ash is also capable of growing in mineral soil habitats such as swamps, depressions with poor drainage, and the edges of streams (Erdmann, 1987). In the upper Great Lakes region alone, there are over 1.7 billion black ash trees across more than 974,000 ha of forest land (U.S. Department of Agriculture, Forest Service (USDA FS), 2023).

The emerald ash borer (*Agrilus planipennis*; EAB) is an insect native to Asia that was first detected in North America in 2002 near Detroit, Michigan (Herms and McCullough, 2014), and as of March 2025 has invaded 37 US states and six Canadian provinces (EAB Information Network, 2025). EAB is a wood-boring beetle whose larvae feed in galleries through the cambium and phloem of ash trees, effectively girdling them and killing the trees (Cappaert et al., 2005). Within three

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years of invading a stand, EAB can cause more than 99 % mortality of ash, which ultimately depletes the local ash seedbank and prevents natural regeneration in these stands (Kashian and Witter, 2011; Klooster et al., 2014). However, white ash (*F. americana*) has displayed considerable natural regeneration in post-EAB forests of southern Michigan despite high mortality of ash in the canopy (Wilson et al., 2025). As of 2025, hundreds of millions of ash trees have been killed by EAB in both urban and forested settings (EAB Information Network, 2025). The damage to black ash populations is of particular concern to land managers, especially in areas where black ash is dominant (Kashian and Witter, 2011), as its widespread and rapid death on the landscape generates cascading ecosystem impacts that leave a grim and uncertain future for these forested wetlands (Kolka et al., 2018).

Black ash plays an important and unique role in regulating the water table and evapotranspiration (ET) rates within forested wetlands where it occurs (Slesak et al., 2014). Black ash stands that experienced high levels of ash mortality displayed significantly reduced ET and water table drawdown rates, ultimately leading to higher inundation throughout the growing season in both depressional wetlands (Van Grinsven et al., 2017; Shannon et al., 2022) and riparian systems (Krzemien et al., 2024). Black ash is a foundational species with a significant role in nitrogen cycling (Youngquist et al., 2017). Leaf litter from black ash is nutrient rich and has a nitrogen concentration higher than that of co-occurring non-ash species within forested wetlands (Davis et al., 2019). In addition to fundamentally altering nitrogen cycling in these systems (Youngquist et al., 2017; Davis et al., 2019), EAB-induced black ash mortality reduces dissolved oxygen concentrations and macroinvertebrate diversity in the surface water of riparian habitats (Larson et al., 2023).

These changes in hydrology and nutrient cycling have pronounced effects on the floral and faunal communities of EAB-infested wetlands. Black ash mortality at the canopy level is positively correlated with mortality at the seedling level, indicating that there is not a sufficient pool of healthy seedlings to naturally regenerate the overstory of these stands (Palik et al., 2012, 2021b). Following overstory mortality, herbaceous vegetation greatly increases in species richness, diversity, and height, and can increase in overall percent cover (Davis et al., 2017; Looney et al., 2017b). Further, in stands where shrubs such as speckled alder (*Alnus incana*) or mountain maple (*Acer spicatum*) are present in the understory there is an increase in stem size and density for these species (Palik et al., 2012; Looney et al., 2017b). The transition to dominance of herbaceous or shrub species after EAB invasion has the potential to inhibit tree seedling establishment in these stands (Royo and Carson, 2006; Young and Pepper, 2010), partially through increased competition for sunlight from the canopy where seedlings receiving less light exhibit stunted height growth and diminished crown development (Bartlett and Remphrey, 1998). Browsing pressure on woody species from herbivores in forest understories can further shift the vegetative community from forested to herbaceous-dominant (Boucher et al., 2004; Stockton et al., 2005; Rooney, 2009). In addition to increases in native herbaceous and shrub species, the loss of natural ash regeneration in the understory promotes the colonization and heightened growth rates of invasive plant species, further threatening ash-dominated ecosystems (Klooster et al., 2018; Hoven et al., 2020, 2022).

The invasive EAB is considered to be the most ecologically destructive and the most economically devastating forest pest to invade the United States (Aukema et al., 2011; McCullough, 2020), with costs for removal, replacement, or treatment of ash trees numbering in the billions of dollars (Hermes and McCullough, 2014; McCullough, 2020). Early attempts at eradicating and containing EAB close to the epicenter of invasion were very expensive and unsuccessful at preventing its spread (Poland and McCullough, 2006; Hermes and McCullough, 2014). Inaction would save on costs in the short-term, but in the long-term it is projected to cause great financial burden from the loss of timber revenue, hazard tree removal in residential areas, and potential replanting of other species post-mortality (Liu, 2018). Chemical control through

pesticide trunk injection, soil application, and aerial spraying varies in cost and effectiveness (Hermes et al., 2014) and is more feasible for individual ash trees than forested stands (Liu, 2018). Large-scale biological control using parasitoid insects from the Order Hymenoptera have limited effects, as the overall rates of parasitism on EAB larvae are considered to be low (Duan et al., 2009, 2012, 2013).

Due to the ecological consequences of EAB-induced ash mortality and the challenges presented by other mitigation strategies, forest managers are engaging in proactive silvicultural strategies to replace black ash on the landscape, rather than preserve it, while still maintaining the same ecosystem functions this species provides within forested wetlands. Underplanting ash wetlands with seedlings of non-ash species before EAB invasion, which can substitute the ash in the canopy once it dies, has growing interest (D'Amato et al., 2018; Kolka et al., 2018; Markowski-Lindsay et al., 2023). When selecting species for planting in these systems, it is paramount to consider their natural co-occurrence with black ash, tolerance of wetland conditions, and adaptability to future climate change projections in the region (Iverson et al., 2016). Planting some species from more southern climate zones, a form of range expansion or assisted migration, could positively contribute to climate change resilience of these systems in the future (Iverson et al., 2016). Additionally, planting seedlings on elevated microsites has been shown to greatly increase survival and growth rates (Bolton et al., 2018). Once planted, seedlings are vulnerable to browsing pressure from herbivores such as white-tailed deer (*Odocoileus virginianus*) (Horsley et al., 2003; Côté et al., 2004) and snowshoe hare (*Lepus americanus*), which share dietary selections with deer and preferentially feed on more species (Telfer, 1972). The limited number of studies that have tested seedling plantings in wetland forests have either been focused on boreal species (Looney et al., 2015; Palik et al., 2021a), used seedling stock that differed in age-related initial height (Bolton et al., 2018), or have occurred under simulated hydrologic conditions, lacking the biological complexity of in situ plantings (Keller et al., 2023, 2024). This study aimed to assess the growth and survival of seven ash replacement tree species planted in black ash stands across northern Michigan and Wisconsin. Our study examined the effects of microtopography, water table depth, light availability, vegetation competition, and herbivory on seedling outcomes for the first and second years after planting. The first two years of seedling survivorship after planting are an important indicator of future survival and growth (Bolton et al., 2018; Keller et al., 2023). We hypothesized that 1) higher elevation microsites (i.e., hummocks and flats) that experience shorter periods of seasonal inundation will have higher rates of survival; 2) increasing cover and height of vegetative competition around planted seedlings will have negative effects on both the survival and growth rates across species; and 3) the presence of browse and increased browsing intensity on individual seedlings from white-tailed deer and snowshoe hare will reduce survival and growth rates.

2. Methods

2.1. Study areas and planting

Four black ash-dominated stands were selected for the study with two located in the Chequamegon-Nicolet National Forest (CN1 and CN2) in northern Wisconsin and two in the Ottawa National Forest (OT1 and OT2) in the western Upper Peninsula of Michigan. Stands for this study were selected based on having a minimum of 21 m²/ha basal area of black ash, ranging in total canopy cover from 32 to 51 m²/ha. A total distance of 182 km separates the northernmost Ottawa National Forest site from the southernmost Chequamegon-Nicolet National Forest site (Fig. 1). Averaged across the four sites, cumulative 30 year daily normal precipitation was 837.3 mm per year, with the highest temperature being 25.9°C and the lowest temperature being −16.3°C (PRISM Climate Group, 2025). Over the course of the study, the lowest measured temperature across the four sites was −33.7°C while the maximum

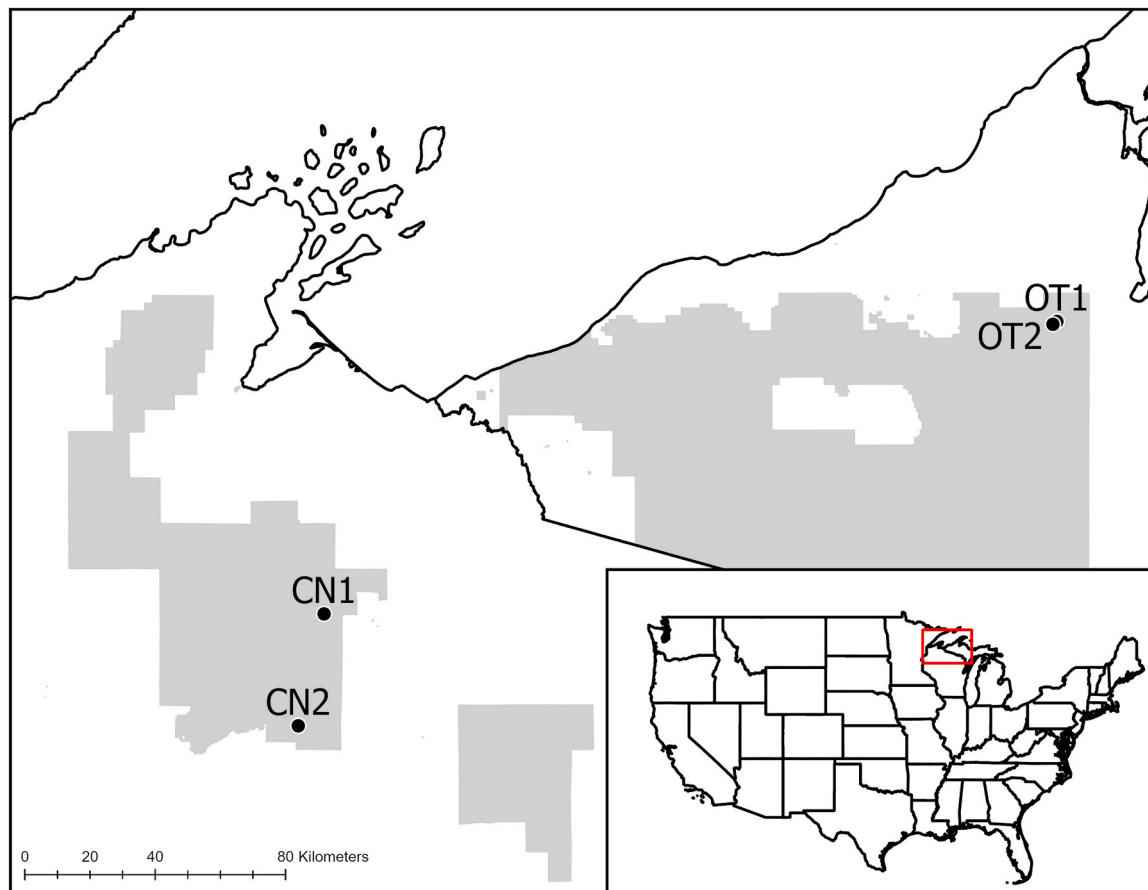


Fig. 1. Stands 1 and 2 in the Chequamegon-Nicolet National Forest (CN1 and CN2) and stands 1 and 2 in the Ottawa National Forest (OT1 and OT2). National Forest boundaries marked in grey. General study location in relation to the United States indicated by the red rectangle in the lower-right insert.

measured temperature was 36.3°C. Average monthly growing season temperature across the four sites was 16.3°C during the study. All three years of the study were wetter than average. Mean annual precipitation across the four sites was 939.2 mm the year of planting (2022), 853.2 mm in year 1 (2023) after planting, and 884.2 mm in year 2 (2024) after planting. Within each black ash stand, an 800 m² area representative of the stand was selected and a planting grid was marked using PVC corner posts and 100 cm fiberglass posts for each seedling location.

Seven tree species were selected for testing. These species were selected based on their performance in the water table manipulation study of Keller et al. (2023), (2024) and use in previous planting studies in the region (Looney et al., 2017a; Bolton et al., 2018). Additionally, the native range of each species occurs within 483 km of all planting sites and all seven species were readily available to regional managers from Wisconsin and Michigan DNR tree nurseries. Planted tree species were river birch (*Betula nigra*), black spruce (*Picea mariana*), bur oak (*Quercus macrocarpa*), red maple (*A. rubrum*), silver maple (*A. saccharinum*), swamp white oak (*Q. bicolor*), and tamarack (*Larix laricina*). A total of 50 individuals per species were planted per site, with 1400 total planted seedlings across all four sites. Seedlings were planted in rows 2 m apart, with two of each species per row across 25 rows, with at least 1 m spacing between seedlings. Species location was pre-selected in systematic grid design to avoid any species randomly occurring disproportionately in either the middle or edges of the planting grid. Planting of the four sites occurred in June of 2022, which is when the standing water from snowmelt had drained enough to allow trees to be planted into soil, with only minimal standing water. Seedlings were not treated during any point of the study to enhance their resilience against winter weather.

2.2. Field data collection

Shallow water table monitoring wells were installed to measure water table depth. Wells consisted of slotted PVC 5 cm in diameter and were installed to a minimum depth of 1 m below soil surface in the middle of each planting area. Belowground depth and remaining aboveground height of each well was recorded. A HOBO U20L-04 sensor (Onset Computer Corp., Bourne, MA) was used to record hourly water table level inside the well and one HOBO U20L-04 sensor was used to measure barometric pressure per National Forest since the two sites at each forest were within 25 km of each other. Water table depth was measured in all stands from June to November 2022. Well sensors were reinstalled at each site except CN2 in August 2023 and collected in May 2024, before being redeployed to each well from May to October 2024. All water level measurements were adjusted for barometric pressure. Two additional wells were installed per site in 2024 to gather more data on water table depth dynamics, located approximately 40 m apart from one another within the planting area, with one installed in a depressed microsite and the other on an elevated microsite. Manual water table depth measurements were taken in June, July, August, and October 2024.

Photosynthetic photon flux density (PPFD, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) available to the planted seedlings was measured at each site using an Apogee Instruments SQ-521 (Logan, UT) connected to a METER ZL6 data logger (Pullman, WA). The PPFD sensor was mounted 1.3 m above the soil surface and data was recorded every 30 min. PPFD measurements were conducted for a total of one week per site from August to September 2024, with the sensor being moved from one site to the next at the end of each one week period.

Planted tree seedling heights were measured at the time of the initial

planting in June of 2022, then in August of 2023, and again in June and July of 2024. The height of the planted seedlings was recorded by measuring the distance between soil surface and the top of the apical meristem. All heights were recorded to the nearest centimeter. During these measurements, any dead seedlings were noted as part of the survival checks. Dead individuals were defined as any seedling with less than two nodes of green growth. Herbivore browsing by white-tailed deer and/or snowshoe hare was recorded on all seedlings as being present or not present. Additionally, browsing intensity on individual seedlings was assessed by dividing the total count of browsed woody stems (i.e., twigs or modules *sensu* Pastor and Danell, 2003) by the total count of available woody stems on each seedling and converting this value to a percentage.

Basal area of the overstory trees at all four stands was measured in the summer of 2024. Three variable radius plots using a basal area factor of 10 were conducted per stand. All trees counted in the plot were recorded for live or dead, their diameter at breast height, their species, and on ash trees whether presence of EAB was noticeable. Visible signs of EAB infestation include crown dieback, increased woodpecker activity, characteristic D-shaped exit holes, and epicormic branching on the main trunk (Wilson and Rebek, 2005). In addition to overstory trees, the understory natural regeneration was also recorded. Seedling surveys were conducted using four circular 2.52 m diameter plots per stand, which totaled 80 m² of area, 10 % of the total planting area. Plots were systematically spaced throughout the planting, occurring between the same rows at each of the four stands to fully represent the planted area. Woody stems < 2.54 cm diameter, including shrubs, were tallied and totaled across the four plots per stand.

Vegetation competition to the planted seedlings was assessed by using a 1 m² quadrat placed around each of the planted seedlings (all 1400 seedlings for the entire study), with the seedling being in the middle of the quadrat. These measurements were conducted to understand what vegetation was present near the planted seedling and whether it impacted seedling growth or survival. Vegetation was grouped into functional groups (ferns and forbs, graminoids, woody shrubs and natural regeneration seedlings, bryophytes), as well as standing water and bare ground at all four sites. Within the quadrat, competition to the planted seedling was given a categorical rating between 0 and 6 (Hanley, 1978), with 0 representing no competition is present and 6 representing vegetation competition is extremely high. The height of the tallest vegetation for each functional group was recorded, as well as maximum depth of any standing water.

Microtopographic position of each individual seedling was categorized at the time of planting as either a flat, hollow, or hummock. Additionally, the relative elevation of each seedling compared to known-elevation control points was recorded using a Trimble S7 robotic total station (Trimble Inc., Westminster, CO). Control points for the elevation measurements were collected with a handheld Garmin GPSMAP 64x (Olathe, KS) with $\pm$ 3–5 m vertical error (Garmin Ltd., 2025). Relative elevation was measured directly adjacent to each individual seedling at the soil surface in which they were planted and is accurate to the mm level (Trimble Inc., 2015). The relative elevation at the soil surface of each well that contained sensors was also recorded using the total station.

2.3. Data analysis

Seedling relative growth rate (RGR, cm/yr) was calculated as the seedling height in 2024 minus the height in 2022 divided by two. Negative values reflect stem dieback and/or herbivore browse. Light data was averaged for each day using only the non-zero values recorded by the quantum sensor. Daily average PPFD and maximum PPFD were calculated for each of the four sites. Climate data was summarized by site as the maximum and minimum temperatures experienced in the 2022–2023 and 2023–2024 measurement periods, as well as the total amount of daily precipitation in millimeters in the 2022–2023 and

2023–2024 measurement periods.

To account for the vertical error of the known-elevation measurements in the field, US Geological Survey digital elevation models (DEMs) at 1 m resolution (U.S. Geological Survey, 2024a, 2024b, 2024c) were used to find the true elevation of the control points established in the field using ArcGIS Pro software (Esri, Redlands, CA). The relative elevation values of the planted seedlings, along with the water table monitoring wells, were added to the true elevation values calculated from the DEMs to determine the precise elevation of each individual seedling and well across all sites.

Hydrology variables were created by synthesizing data from the well sensors and Trimble total station. Mean daily water levels in each well were converted from cm to m and added to the elevation of the well at the soil surface. These values were then subtracted from the elevation of every seedling at the soil surface within a stand to count the number of days water was above the soil surface (DWASS), as well as the number of days the soil was saturated within 10 cm below the soil surface (DSS). Additionally, the mean water table elevation from 2022 to 2024 was calculated for all stands separately and subtracted from each seedling's elevation to produce the distance from mean water table (DFMWT). To account for differences in measurement periods, DWASS and DSS were converted to percentages. Rather than being broken down by calendar year, these variables span the time during the 2022–2023 and 2023–2024 measurement periods where data was available. Data was available from June to November 2022 for all stands (DWASS22 and DSS22); August 2023 to May 2024 for all stands except CN2 (DWASS23 and DSS23); and May to July 2024 for all stands (added to DWASS23 and DSS23).

Stand-level climate data was collected for each site using Oregon State PRISM software (PRISM Climate Group, 2025) at a resolution of 800 m². Data gathered from PRISM included daily maximum and minimum temperatures in °C, as well as the daily amount of precipitation in mm, between each measurement period. The first measurement period spanned from the day of planting at each site in 2022 (June 22nd for CN1 and CN2; June 29th for OT1 and OT2) to the day of remeasurement in 2023 (August 3rd for CN1 and CN2; August 2nd for OT1 and OT2). The second measurement period spanned from the day after remeasurement in 2023 to the day of remeasurement in 2024 (July 18th for CN1 and CN2; June 28th for OT1 and OT2). This process was conducted to mimic the hydrology variables that were broken down by the 2022–2023 and 2023–2024 measurement periods where data was available instead of by calendar year.

All data analysis was completed in R (R Core Team, 2022). Data exploration was carried out using the 'tidyverse' package (Wickham et al., 2019). The RGR and survival of seedlings by the end of the study period were response variables. The distribution of RGR across species and stands was checked for normality using the procedures outlined by Zuur et al. (2010). Outliers from growth were identified and included in all analyses. Explanatory variables were tested for both response variables separately. Predictors for RGR and survival were stand, species, microsite, herbivory, competition cover and height in 2024, hydrology during the 2022–2023 measurement period (DWASS22 and DSS22), hydrology during the 2023–2024 measurement period (DWASS23 and DSS23), distance from mean water table, light availability, and climate during the 2022–2023 and 2023–2024 measurement periods. Generalized linear models (GLMs) were constructed for both response variables, with the gaussian family used for RGR due to its normal distribution, and the binomial family used for survival. For broader categories describing multiple variables (i.e., herbivory, hydrology, competition cover and height, light availability, and climate), GLMs were created to test one explanatory variable at a time against each response within each separate category to determine which produced the lowest Akaike Information Criterion (AIC) score, as per Burnham and Anderson (1998), (2002). The variables within each broader category that produced the lowest AIC for RGR and survival were amalgamated into global models for final model selection. One insignificant variable was removed at a

time from the global models for both RGR and survival until the global models with the lowest AIC were identified, following Burnham and Anderson (1998, 2002). Models were visually checked for variance assumption by plotting the residual versus fitted values and by using the ‘check_model’ function from the ‘performance’ package in R (Lüdtke et al., 2021). Rather than comparing categorical variables to the first sublevel in alphabetical order as is the default in R, we assigned the worst-performing sublevels of each category (e.g., stand, species, microsite) for both RGR and survival as the comparison sublevel for easier interpretation.

By default, coefficients of predictors in binomial GLMs are reported as a change in the log-likelihood of success, equal to the natural logarithm of the probability of success divided by the probability of failure (UCLA Statistical Consulting Group, 2025). To make these values easier to interpret, coefficients from the final survival model were exponentiated to odds-ratios (ORs) using the ‘exp’ function in base R, effectively reversing the log transformation and providing the probability of success over failure for each variable. The ORs for predictors are reported as an increase or decrease chance of survival when all other variables are held constant in the model, where an OR above one indicates increased odds and an OR below one indicates decreased odds. The ORs for categorical predictors are reported as a factor while the ORs for numerical predictors are reported as a percentage.

Further analysis for the effect of distance from mean water table on each species was initiated using basic linear models and binomial GLMs for RGR and survival, respectively. Coefficients from the species-level survival models were exponentiated to ORs and reported as a percentage increase or decrease chance of survival for every one cm increase in distance from mean water table.

Analysis of variance (ANOVA) was conducted for several effects to test for significant differences between response and explanatory variables. The R package ‘agricolae’ (de Mendiburu, 2021) was used to identify and assign significant groups between the levels of these categorical variables. RGR was examined for significant differences between stand, species, microtopography, and browsed and unbrowsed seedlings. All hydrological variables were tested by stand and microtopography. Light and climate data were gathered at the stand level, excluding them from further investigation.

3. Results

3.1. Overstory and seedling surveys

All of the mature black ash within the Ottawa National Forest sites were likely infected before the experiment began and died during the course of our study (Table 1). Conversely, ash mortality was relatively low throughout the study period in the Chequamegon-Nicolet National Forest sites, with stand CN2 exhibiting 5 % and CN1 exhibiting 0 % black ash mortality in the canopy. Over 40 % of the total live and dead basal area was occupied by black ash across all four stands, and all of the

Table 1

The condition of planted stands in the Chequamegon-Nicolet National Forest (CN1 and CN2) and the Ottawa National Forest (OT1 and OT2) two years after planting. Total basal area (BA) in m²/ha, the percent of BA occupied by black ash (*Fraxinus nigra*; FN), the percent of BA occupied by dead FN, the percent of FN with signs of EAB, and the mean diameter at breast height (DBH) in cm of FN trees.

stand	total BA	% BA FN	% BA dead FN	% FN with EAB	mean FN DBH
CN1	49	42	0	100	22.1
CN2	32	81	5	100	32.6
OT1	42	58	58	100	27.0
OT2	51	41	41	100	33.1

Note: To see this data represented in English units, please see Table B1 in Appendix B.

black ash sampled across the four sites, living or dead, showed signs of EAB infestation. Woody plant regeneration in the understory also varied greatly between stands (Table 2). Stands with the greatest to least amount of black ash regeneration were CN1 (2500 stems/ha), OT2 (1125 stems/ha), OT1 (500 stems/ha), and CN2 (125 stems/ha). Shrubs from the genus *Rubus* were prevalent in stands CN1 and CN2, comprising nearly 50 % and 75 % of the total woody regeneration layer, respectively. Natural regeneration of all canopy species combined was low within all sites with CN1 (6625 stems/ha) exhibiting the greatest and CN2 (1250 stems/ha) exhibiting the lowest regeneration potential.

3.2. Hydrological differences by stand and microsite

Significant differences were detected for all hydrological variables examined between stands and microsites (Table 3). Results of ANOVA by stand ($p < 0.001$) indicated that OT2 possessed the greatest mean proportion of days during which water was above (DWASS) or within 10 cm below (DSS) the soil surface during the 2022–2023 measurement period. Stand OT2 also had the greatest average DWASS during the 2023–2024 measurement period. Stands CN1 and OT1 were consistently the driest sites with no significant differences between them except for mean DSS during the 2022–2023 measurement period, where OT1 displayed a significantly greater proportion of soil saturation than CN1. Additionally, the average distance from mean water table (DFMWT) in CN1 and OT1 was not significantly different from each other. Stand OT2 had the lowest average DFMWT compared to the other sites. Stand CN2 had a significantly higher average DFMWT than OT2 but was still significantly lower than CN1 and OT1. Results of ANOVA by microsite ($p < 0.001$) revealed that, as expected, hollows consistently displayed the greatest mean DWASS and DSS while hummocks consistently displayed the lowest mean DWASS and DSS during both the 2022–2023 and 2023–2024 measurement periods. Flat microsites did not have significantly different mean DWASS and DSS during the 2022–2023 measurement period than hollows. However, flat microsites had significantly lower DWASS and DSS than hollows and significantly greater DWASS and DSS than hummocks during the 2023–2024 measurement period. Hummocks displayed the greatest and hollows displayed the lowest average DFMWT. The average DFMWT of flat microsites was significantly greater than hollows and significantly lower than hummocks.

3.3. Survival and RGR

Overall first-year survival across all stands and species was 54 % (Table 4, $n = 759$). The best-surviving species in order from greatest to least were swamp white oak (81 %), bur oak (72 %), silver maple

Table 2

The amount of stems per hectare of woody seedlings less than 1 m in height and less than 2.54 cm diameter organized by stand. Canopy species marked with a *.

species	CN1	CN2	OT1	OT2
balsam fir (<i>Abies balsamea</i>)*	125	0	0	0
red maple (<i>A. rubrum</i>)*	2125	125	750	375
sugar maple (<i>A. saccharum</i>)*	0	125	0	500
yellow birch (<i>B. alleghaniensis</i>)*	1875	750	0	0
paper birch (<i>B. papyrifera</i>)*	0	0	250	0
musclewood (<i>Carpinus caroliniana</i>)	0	125	0	0
beaked hazelnut (<i>Corylus cornuta</i>)	250	250	0	0
black ash (<i>F. nigra</i>)*	2500	125	500	1125
winterberry holly (<i>Ilex verticillata</i>)	0	0	625	0
currants (<i>Ribes</i> spp.)	0	875	375	0
brambles (<i>Rubus</i> spp.)	6500	7375	0	250
American elm (<i>Ulmus americana</i>)*	0	125	0	125
Canopy species total	6625	1250	1500	2125
All species total	13,375	9875	2500	2375

Note: To see this data represented in English units, please see Table B2 in Appendix B.

Table 3

The mean percentage of days water was above the soil surface (DWASS) and days the soil was saturated within 10 cm below the surface (DSS) of individual seedlings, organized by stand and microsite. The digits 22 and 23 indicate data gathered during the 2022–2023 and 2023–2024 measurement periods, respectively. Average distance from the mean water table (DFMWT) of seedlings planted is also reported in cm. Letters in parentheses denote groups where the means are significantly different from one another when no letters are shared between groups. Groups are unique to each column and do not apply across rows.

stand	mean DWASS22 (%)	mean DSS22 (%)	mean DWASS23 (%)	mean DSS23 (%)	mean DFMWT (cm)
CN1	0.05 (b)	3.79 (c)	0.01 (c)	1.91 (b)	38.94 (a)
CN2	0.51 (b)	3.74 (c)	11.07 (b)	49.33 (a)	23.92 (b)
OT1	4.07 (b)	13.67 (b)	0.39 (c)	3.95 (b)	39.80 (a)
OT2	32.89 (a)	52.87 (a)	25.76 (a)	43.87 (a)	13.01 (c)
microsite	mean DWASS22 (%)	mean DSS22 (%)	mean DWASS23 (%)	mean DSS23 (%)	mean DFMWT (cm)
hollow	10.91 (a)	21.11 (a)	14.22 (a)	40.44 (a)	23.70 (c)
flat	10.34 (a)	19.79 (a)	8.11 (b)	18.59 (b)	30.42 (b)
hummock	4.32 (b)	11.01 (b)	3.14 (c)	9.59 (c)	35.10 (a)

Table 4

Mean relative growth rate (RGR) and total first- and second-year survival rates by species ($n = \sim 200$ per species) across all sites. One standard deviation indicated in parentheses next to mean values. Grand total growth and survival rates of all planted seedlings across all sites ($n = 1394$) are included in the bottom row.

species	mean RGR (cm/ yr)	survival 2023 (%)	survival 2024 (%)
river birch	6.89 (12.04)	61.11	48.48
black spruce	1.64 (6.40)	17.5	13.5
bur oak	2.57 (6.82)	71.86	56.28
red maple	4.54 (11.58)	58	53.5
silver maple	6.14 (9.35)	69	62.5
swamp white oak	6.72 (8.56)	81.41	74.87
tamarack	8.75 (10.28)	22.22	18.18
Total	5.47 (9.75)	54.45	46.77

(69 %), river birch (61 %), red maple (58 %), tamarack (22 %), and

black spruce (17.5 %) (Fig. 2).

Total survival across all species and stands two years after planting was less than the first year at approximately 47 % (Table 4, $n = 652$), reflecting a 7 % drop in survival from the first year after planting. The best-surviving species in order from greatest to least were swamp white oak (75 %), silver maple (62.5 %), bur oak (56 %), red maple (53.5 %), river birch (48.5 %), tamarack (18 %), and black spruce (13.5 %) (Fig. 2).

Mean RGR across both years was a positive gain of 5.47 cm/yr (Table 4, $n = 652$). No species experienced negative RGR on average, indicating an overall increase in growth two years after planting by all seven species examined. The species that exhibited higher than average RGR from greatest to least were tamarack (8.75 cm/yr), river birch (6.89 cm/yr), swamp white oak (6.72 cm/yr), and silver maple (6.14 cm/yr). The remaining species that displayed below average RGR from greatest to least were red maple (4.54 cm/yr), bur oak (2.57 cm/yr), and black spruce (1.64 cm/yr).

3.4. Factors influencing growth and survival

Vegetative competition cover, browse presence and intensity, hydrology during the 2022–2023 and 2023–2024 measurement periods, light availability, and climate during the 2022–2023 and 2023–2024 measurement periods were all found to be insignificant to RGR and were not included in the final model. The factors remaining in the final model for RGR were stand, microsite, woody shrub and seedling height in 2024, standing water depth in 2024, and distance from mean water table (Table 5). Compared to stand OT2, stands CN1 (10.26 cm/yr,

Table 5

Final model predictors, coefficients, standard error, t-values, and p-values for relative growth rate (RGR). Group refers to categorical variables with multiple subcategories. Significant values are marked with a †.

group	variable	estimate	std. error	t-value	p-value	
	intercept	5.318	2.49	2.136	0.034	†
stand	CN1	10.26	2.342	4.381	< 0.001	†
stand	CN2	6.782	2.174	3.119	0.002	†
stand	OT1	4.919	2.33	2.111	0.036	†
microsite	flat	0.405	1.462	0.277	0.782	
microsite	hummock	-0.714	1.741	-0.41	0.682	
	SSheight24	< 0.001	0.0144	0.004	0.997	
	WTdepth24	-0.174	0.1212	-1.435	0.152	
	DFMWT	-0.132	0.04935	-2.67	0.008	†

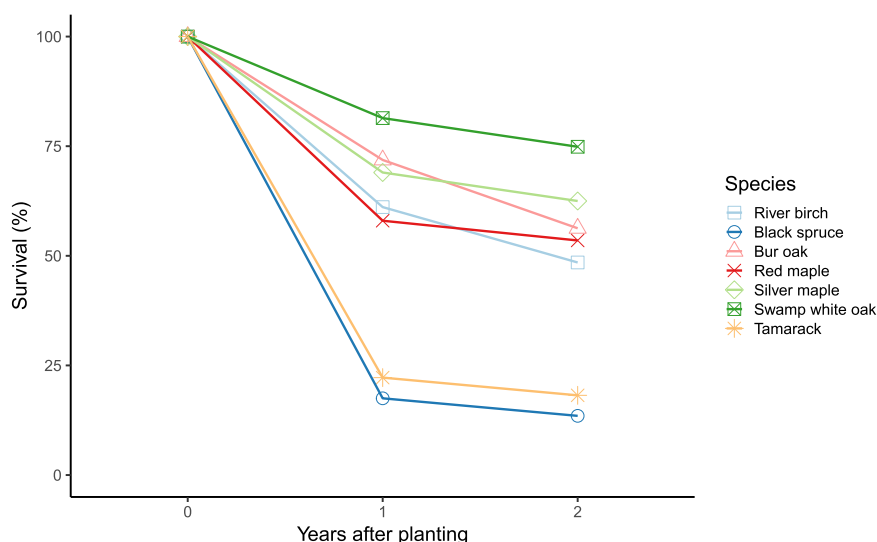


Fig. 2. Percent survival across all sites by number of years after planting for the seven species examined.

$p < 0.001$), CN2 (6.78 cm/yr, $p = 0.002$), and OT1 (4.92 cm/yr, $p = 0.036$) all had significantly greater RGR across species. Flat microsites (0.41 cm/yr, $p = 0.782$) displayed increased RGR compared to hollows, but the relationship was not significant. Hummocks exhibited lower RGR than hollows (-0.71 cm/yr, $p = 0.682$) but as with flat microsites, the relationship was not significant. The height of woody shrubs and seedlings (< 0.001 cm/yr, $p = 0.997$) and the depth of standing water (-0.174 cm/yr, $p = 0.152$) in 2024 were included in the final model but did not have a significant effect on RGR. Removal of these variables from the model caused the AIC to increase greatly, warranting the decision to preserve them in the final model. Additionally, as the distance from mean water table increased, overall RGR across species and stands decreased (-0.13 cm/yr, $p = 0.008$).

Similar to RGR, vegetative competition cover, browse intensity, hydrology during the 2022–2023 and 2023–2024 measurement periods, light availability, and climate during the 2022–2023 and 2023–2024 measurement periods were all found to be insignificant to survival and were not included in the final model. The factors remaining in the final model for survival were stand, species, microsite, browse presence, woody shrub and seedling height in 2024, standing water depth in 2024, and distance from mean water table (Table 6). Compared to stand OT2, seedlings planted in stand CN1 were 0.63 times as likely to survive, but the relationship was not significant ($p = 0.298$). Seedlings planted in stands CN2 ($p = 0.158$) and OT1 ($p = 0.481$) had a 1.77 and 1.37 times greater chance of survival, respectively, than stand OT2 but neither relationship was significant. In relation to black spruce, all species had significantly greater odds of survival. River birch ($p < 0.001$), bur oak ($p < 0.001$), and red maple ($p < 0.001$) displayed 12.31, 11.75, and 9.43 times higher chances of survival, respectively. The most extreme increases in survival probability compared to black spruce were exhibited by silver maple (OR = 26.34, $p < 0.001$) and swamp white oak (OR = 23.07, $p < 0.001$). The second-worst-performing species, tamarack, also had a significantly greater chance of survival than black spruce but to a lesser degree than the other planted species (OR = 3.36, $p < 0.001$). Contrasted with hollows, seedlings planted on flat microsites had higher survival probability, but the effect was not significant (OR = 1.61, $p = 0.088$). However, seedlings planted on hummocks were 3.62 times as likely to survive ($p < 0.001$) than those planted on hollows. The relationship between herbivore browse presence and survival was not significant ($p = 0.306$). None of the competitive groups of vegetation tested were found to have a significant influence on survival. The height of woody shrubs and seedlings and the depth of standing water in 2024 were included in the final model but did not have a significant effect on survival ($p = 0.599$ and $p = 0.631$, respectively). Removal of these variables from the model caused the AIC to increase greatly, warranting the decision to preserve them in the final model.

Lastly, for every one cm increase in the distance from mean water table, survival probability increased by 2 % ($p = 0.023$), a trend that was consistent across stands.

3.5. Species $\times$ distance from mean water table interactions

Out of the seven species examined, the distance from mean water table only had a significant effect on RGR for black spruce ($p = 0.048$) and tamarack ($p = 0.007$) (Fig. 3). As the DFMWT increased for seedlings of both species across all stands, the overall RGR decreased by 0.18 cm/yr and 0.31 cm/yr for black spruce and tamarack, respectively. In contrast to RGR, the DFMWT had a significant effect on a greater number of species for survival probability, with black spruce ($p = 0.014$), bur oak ($p = 0.001$), red maple ($p < 0.001$), and silver maple ($p = 0.017$) being impacted (Fig. 4). For every one cm increase in DFMWT, the chance of survival increased by approximately 3 % for black spruce, bur oak, and red maple. Similarly, the odds of survival for silver maple increased by approximately 2 % for every one cm increase in DFMWT.

4. Discussion

Identifying the best-performing species and optimum planting conditions is paramount for sustaining forested conditions in black ash wetlands (D'Amato et al., 2018), particularly in the Great Lakes region where natural forest regeneration in these systems is insufficient (Palik et al., 2012, 2021b). Among the seven species we tested, the best-performing species were found to be river birch, silver maple, and swamp white oak, due to their above average growth and survival rates (Table 4; Fig. 2). While both bur oak and red maple exhibited below average growth rates, their above average survival also makes them desirable species for planting in these systems, which can further diversify the planted stand. Surprisingly, black spruce and tamarack had poor survival. Our first hypothesis that microtopography would have a significant effect on survival was confirmed, as seedlings planted on hummocks displayed increased chances of survival (Table 6). We expected light availability to be influential for growth and survival but there was no evidence to support this. Moreover, no evidence was found in support of our third hypothesis that the presence and intensity of herbivory would negatively impact growth and survival (Tables 5 and 6). Lastly, we expected increasing cover and height of vegetative competition to hinder the overall performance of the seedlings planted in this study, but none of the competitive groups tested had a significant influence on either RGR or survival, and the variables for competition height in 2024 were not significant to either response despite remaining in the final models. Our models suggest that the primary drivers behind

Table 6

Final model predictors, coefficients, odds-ratios (ORs), standard error, z-values, and p-values for survival. Group refers to categorical variables with multiple sub-categories. Significant values are marked with a †.

group	variable	estimate	OR	std. error	z-value	p-value	
	intercept	-2.942	0.053	0.626	-4.701	< 0.001	†
stand	CN1	-0.461	0.631	0.443	-1.040	0.298	
stand	CN2	0.571	1.771	0.405	1.410	0.158	
stand	OT1	0.316	1.372	0.449	0.704	0.481	
species	river birch	2.510	12.307	0.530	4.733	< 0.001	†
species	bur oak	2.464	11.747	0.507	4.862	< 0.001	†
species	red maple	2.244	9.434	0.539	4.162	< 0.001	†
species	silver maple	3.271	26.344	0.579	5.647	< 0.001	†
species	swamp white oak	3.139	23.070	0.537	5.848	< 0.001	†
species	tamarack	1.212	3.359	0.480	2.523	< 0.001	†
microsite	flat	0.478	1.613	0.280	1.705	0.088	
microsite	hummock	1.287	3.622	0.387	3.322	< 0.001	†
browse	yes	0.317	1.373	0.310	1.024	0.306	
	SSheight24	0.002	1.002	0.003	0.526	0.599	
	WTdepth24	-0.011	0.989	0.023	-0.480	0.631	
	DFMWT	0.024	1.024	0.010	2.278	0.023	†

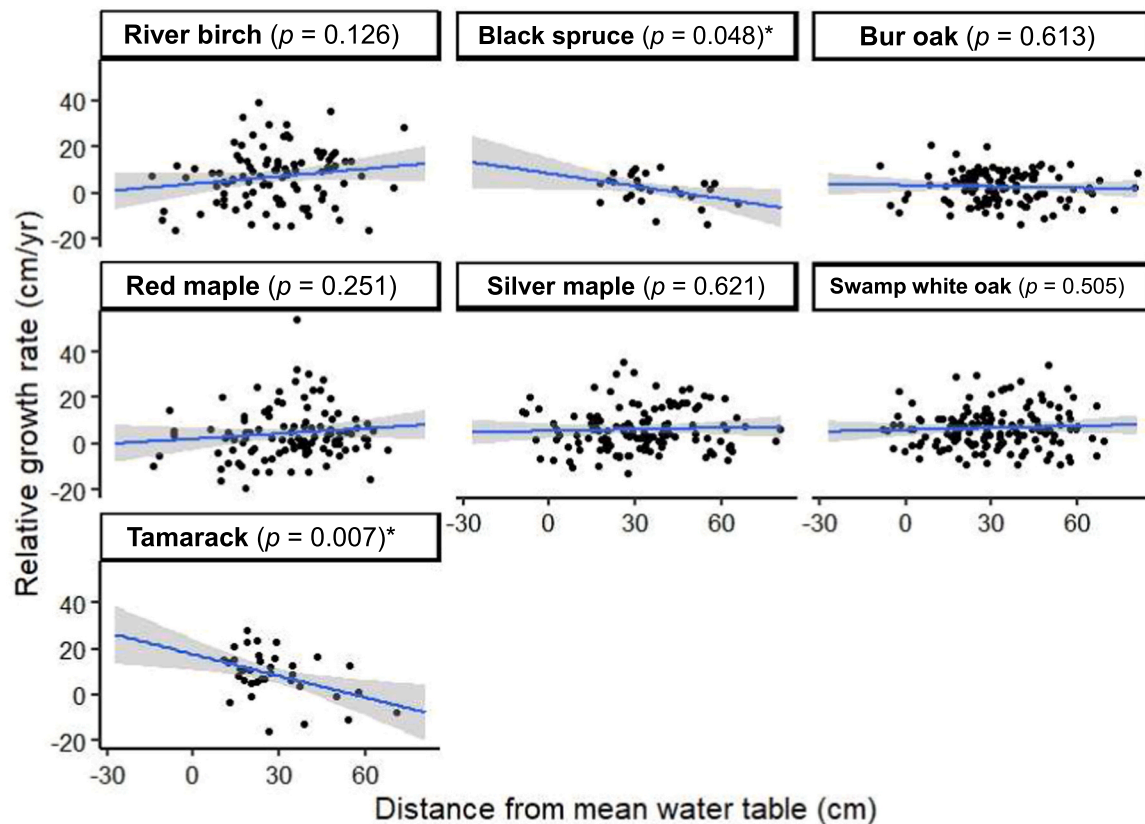


Fig. 3. The relationship between relative growth rate (RGR) and the distance from mean water table (DFMWT) of each seedling, broken down by species. Standard error for each estimate is depicted in grey. *P*-values for the estimate of DFMWT for each basic linear model are in parentheses next to species name. *P*-values marked with a * are significant.

growth were stand and distance from mean water table, while the primary drivers behind survival were species, microtopography, and distance from mean water table.

4.1. Post-EAB stand conditions

Overstory surveys conducted two years after planting highlight the destructive impact of EAB on black ash-dominated wetlands (Table 1). The complete overstory ash mortality at the Ottawa National Forest sites and the low overstory ash mortality at the Chequamegon-Nicolet National Forest sites is likely due to longer confirmed EAB presence in northern Michigan compared to northern Wisconsin (EAB Information Network, 2025). Further, the lower overstory mortality of ash in the Chequamegon-Nicolet stands is likely to mirror that of the Ottawa stands within the next few years due to the 100 % EAB infection rate of all ash trees surveyed at these sites. Despite these stark differences in overstory mortality, only stand OT2 had significantly lower seedling survival rates than CN1 and OT1, while CN2 did not have significantly different survival from the other three stands (data not shown). These results imply that there may be sufficient time within the first few years post-EAB invasion and/or EAB-induced canopy mortality where non-ash seedlings can be planted and establish themselves before the drastic changes in hydrology (Slesak et al., 2014; Van Grinsven et al., 2017; Shannon et al., 2022) and vegetation (Davis et al., 2017; Looney et al., 2017b) arise.

Understory surveys for naturally occurring seedlings conducted in these stands two years after planting echoed previous findings on post-EAB forest regeneration (Table 2). Looney et al. (2017b) measured the natural regeneration of black ash stands in northern Minnesota subjected to silvicultural treatments that mimicked EAB invasion and found that the seedling density of black ash was far below the recommended

amount for successful restocking post-harvest, even when combined with other non-ash species. Also in northern Minnesota, Palik et al. (2012), (2021b) found that black ash and other co-occurring woody species had inadequate presence in the seedling layer to replace the black ash in the canopy anticipated to experience widespread mortality. In our study, all four stands fell short of recommended stocking densities for natural regeneration of black ash post-harvest (Erdmann, 1987), even when combining all canopy species surveyed in the understory. The majority of the natural seedlings in CN1 and in CN2 were shrubs from the genus *Rubus* that are incapable of growing into the vacated canopy after ash mortality, mirroring previous findings of non-canopy species dominance post-EAB invasion (Palik et al., 2012; Davis et al., 2017; Looney et al., 2017b). Our results indicate that artificial regeneration will be necessary in these stands to supplement the lack of natural regeneration and maintain these wetlands as forested.

4.2. Species performance

Species that performed well in our planting sites (Table 4; Fig. 2) also had high rates of survival and growth in other experimental plantings. Red maple previously performed well when planted in northern Wisconsin and silver maple previously performed well when planted in northern Michigan (Bolton et al., 2018). Additionally, red maple and swamp white oak displayed high survival and growth rates in plantings in black ash wetlands in northern Minnesota (Palik et al., 2021a). River birch, red maple, silver maple, and swamp white oak were some of the most flood-tolerant species in terms of survival rates in a greenhouse setting (Keller et al., 2023), although these results do not factor in the biological complexity associated with planting in natural settings. Moreover, red maple, silver maple, and swamp white oak are all projected to have increased suitable habitat in the Great Lakes region with

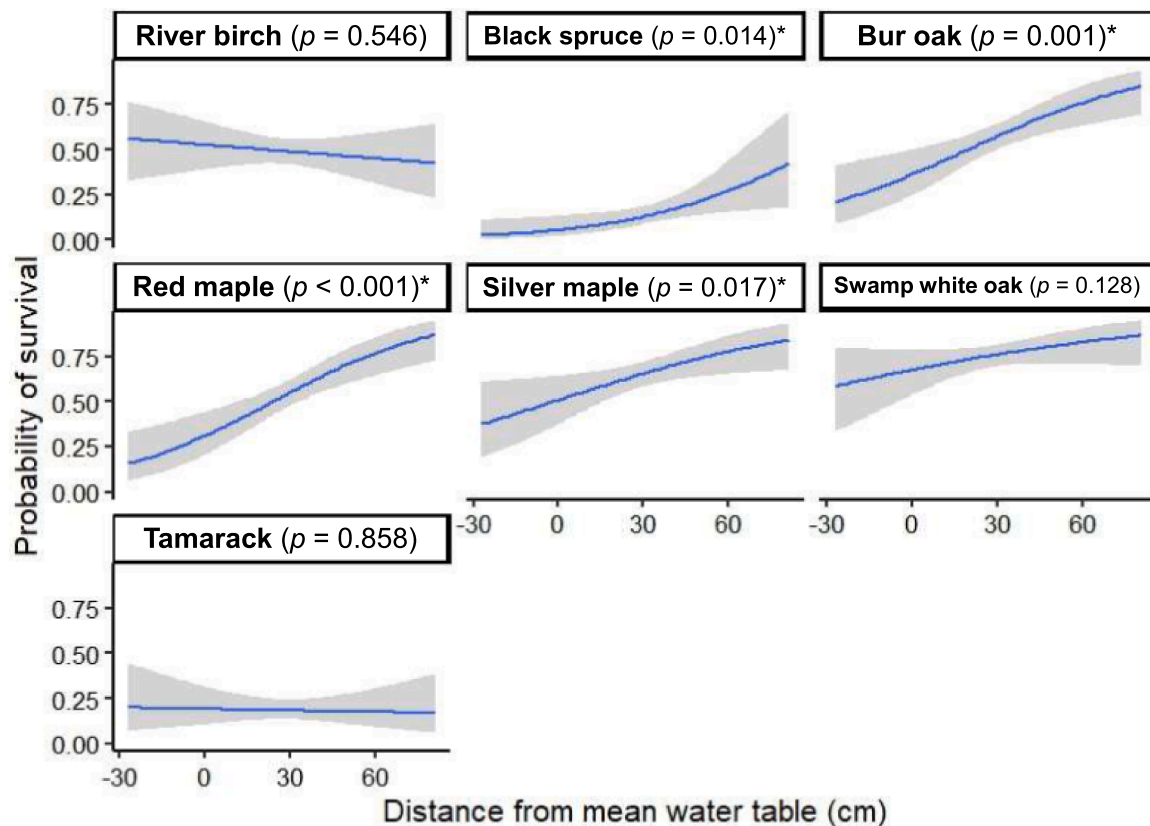


Fig. 4. The relationship between the probability of survival and the distance from mean water table (DFMWT) of each seedling, broken down by species. Standard error for each estimate is depicted in grey. P -values for the estimate of DFMWT for each generalized linear model in the binomial distribution are in parentheses next to species name. The p -values marked with a * are significant ($p < 0.05$).

future climate change (Iverson et al., 2016), further solidifying them as viable candidates for planting in these ecosystems. The poor performance of black spruce and tamarack in our study was unexpected, as their prevalence in inundated peatlands (Lieffers and Rothwell, 1986) would imply that these species would be capable of surviving and growing in the flooded conditions of black ash-dominated systems as well. However, our findings on these species are not isolated to our sites. Similar to our results, black spruce and tamarack had the lowest survival rates when planted in northern Minnesota (Palik et al., 2021a), and no tamarack survived the first three years after planting in a previous study in the Ottawa National Forest (Bolton et al., 2018). Black spruce displayed poor survival and growth across flooding treatments in a greenhouse setting (Keller et al., 2023) and is projected to experience a large decrease in suitable habitat in the region due to climate change (Iverson et al., 2016). While tamarack did exhibit the highest average growth in our study (Table 4), survival rates were less than 20 % (Fig. 2), and the species is projected to perform poorly under future climate change (Iverson et al., 2016).

4.3. Factors influencing seedling performance

Our results suggest that the main driver behind both growth and survival of seedlings underplanted in these black ash wetlands is site hydrology. The four stands were significantly different for growth of the seedlings but not for seedling survival. However, our results imply that the primary difference between stands was hydrology, with multiple significant groups arising for all the hydrological variables examined (Table 3). The most important hydrological factor that persisted in the final models was the distance from mean water table (Tables 5 and 6). Across all species and stands, growth decreased as the distance from mean water table increased. When investigated at the species level, this

was less important for growth than for survival, as only black spruce and tamarack growth were hindered with increasing distance (Fig. 3). In the case of black spruce, hydrology represented a tradeoff where growth decreased but survival probability increased (Fig. 4) with greater distance from mean water table. Tamarack showed a similar trend in reduced growth with increasing distance from mean water table, but odds of survival were low for all distances from water table. Bur oak, red maple, and silver maple, three of the best-performing species, all displayed significant increases in survival chance with increasing distance from mean water table. Three years after planting in northern Minnesota, Looney et al. (2015) reported lower overall survival of seedlings planted in clearcut stands compared to untreated controls as a likely result of elevated water tables and increased periods of seasonal inundation (Slesak et al., 2014). In these same stands eight years after planting, Palik et al. (2021a) confirmed a continued reduction in seedling survival in clearcut stands with higher water tables compared to uncut controls. Swamp white oak displayed high survival across overstory treatments and consequential hydrologic regimes (Looney et al., 2015; Palik et al., 2021a), while red maple was sensitive to changes brought by clearcut and girdle treatments (Palik et al., 2021a). This corroborates our findings that swamp white oak had high overall survival and was not significantly impacted by site hydrology, and that red maple experienced greater odds of survival with increasing distance from mean water table (Fig. 4).

Selectively planting on hummocks or creating hummocks to plant on, known as mounding, when artificially regenerating forested wetlands is an established practice in the Great Lakes region and parts of Canada (Londo and Mroz, 2001). While microtopography did not have a significant impact on overall growth in our study (Table 5), there was evidence that higher elevation microsites improved survival for planted seedlings (Table 6). Additionally, ANOVA results indicate that microsite

is tied with hydrology, as hollows consistently displayed the greatest proportion of time where water was above or within 10 cm below the soil surface and exhibited the lowest distance from the mean water table, while hummocks consistently displayed the opposite effect (Table 3). Bur oak, red maple, and silver maple had greater survival rates in northern Michigan when planted on hummocks compared to hollows, and with the exception of red maple, experienced higher average growth in hollows (Bolton et al., 2018). In this same study, red maple planted in northern Wisconsin had the highest survival and average growth when planted on constructed hummocks compared to natural or scarified hummocks. While individual species may respond differently to microtopography in terms of growth, our results suggest that planting seedlings on hummocks provides the greatest benefit to overall seedling survival in forested wetlands.

Shade tolerance in tree species is generally understood as a compromise between the capability to survive in low light environments and the potential for growth in high light environments (Kobe et al., 1995). Niinemets and Valladares (2006) qualified shade tolerance of North American trees and shrubs, with river birch and tamarack being classified as shade-intolerant; bur oak, red maple, silver maple, and swamp white oak having intermediate tolerance; and black spruce being fully shade-tolerant. Thus, our finding that light availability to seedlings was not an important factor in determining survival or growth was unexpected. In contrast to our study, Looney et al. (2017a) found that increased light availability to planted seedlings across different silvicultural treatments resulted in higher overall growth rates, with growth rates decreasing in stands that were uncut or girdled. Further, in these same stands Looney et al. (2015) reported that survival rates were lower for all seedlings except *Populus* spp. planted in treatments with higher light availability (i.e., clearcuts), presumably due to the positive response of natural understory vegetation to increased light. It is possible that the effects of light availability are masked by the strong impact of hydrology on seedling performance, similar to the findings of Keller et al. (2024) where light reduction in a controlled environment had no significant effect on survival or growth of planted seedlings. Additionally, the time period in which we recorded light data in the field was much shorter than previous studies and could inadequately describe the true light conditions at each site. Therefore, our finding that light availability was unimportant to seedling performance should be taken with caution and put into context with previous work that assessed the response of planted seedlings to differing amounts of light from the canopy.

Our finding that naturally occurring vegetative competition was not significant to seedling performance was also unanticipated. The potential of herbaceous or shrub species to inhibit tree seedling establishment is well-documented (Royo and Carson, 2006; Gilliam, 2007). Beyond competition for resources, tree seedlings must compete with other vegetation for sunlight from the canopy, where stunted height growth and diminished crown development are direct results of decreased light availability (Bartlett and Remphrey, 1998). Hence, we expected both cover class and maximum height of at least one competitive group to have a significant influence on the overall survival and growth of seedlings. Woody shrub and seedling height and depth of standing water in 2024 were the only vegetative competition cover factors that influenced growth and survival, but the effect was not significant to either response (Tables 5 and 6). The estimates for these predictors would otherwise imply miniscule increases in growth and survival chance due to woody shrub and seedling height, and small decreases in growth and survival chance due to standing water depth. Similar to our findings, Davis et al. (2017) found no association between natural tree seedling establishment and increased herbaceous cover for three years post-treatment in stands subjected to silvicultural treatments that mimicked EAB-induced mortality. Contrary to our results, Engelken et al. (2020) reported that tree seedling and sapling density were inversely related to herbaceous vegetation density in southern Michigan ash stands invaded by EAB between 2000 and 2017, with one quarter of

their study sites containing greater than 95 % herbaceous plant coverage and no tree seedlings. Therefore, our results may reflect that it is too early to detect the influence of vegetative competition on the planted seedlings within these stands, and that competition may increase in the future as the post-EAB understory community continues to change.

In the eastern United States, white-tailed deer can greatly suppress tree seedling establishment, survival, and growth through selective browsing (Horsley et al., 2003; Côté et al., 2004; Bradshaw and Waller, 2016). Another common herbivore in this region, snowshoe hare, shows considerable overlap with deer in preferential browsing of woody species in forest understories (Telfer, 1972). The lack of evidence to support our third hypothesis that herbivore browsing presence and intensity would significantly affect seedling performance was contrary to our expectations. Browse presence and intensity were not influential to overall growth (Table 5), and while browse presence was included in the final model for survival, the effect was not significant (Table 6). The OR would otherwise signify increased chances of survival for seedlings that were browsed by white-tailed deer and/or snowshoe hare. This is a possible instance of survivorship bias in that we recorded herbivore browse on both living and dead seedlings two years after planting, where some individuals may have died within the first year before herbivores could use them as a food source, leading to a higher proportion of browse on living seedlings compared to dead seedlings. Similar to our findings, Bolton et al. (2018) found no statistical differences in survival or growth between herbivore exclusion treatments in northern Wisconsin. Looney et al. (2017a) determined that the presence or absence of deer browse on planted seedlings was not significant to radial or height growth rates for three years after planting in northern Minnesota. Akin to the observation of Bolton et al. (2018), it may be too early to detect the impacts of herbivore browsing pressure on the seedlings planted in this study.

4.4. Management considerations

In summary, we found that most of the planted species were capable of reasonable survival and growth rates despite the challenges presented by planting position and site hydrology. While the best-performing species in this study would be viable candidates for future ash replacement plantings, we recognize that the species assemblages for plantings will vary depending on management goals. Dumroese et al. (2015) discussed the advantages and disadvantages of strategies such as assisted migration of alternative species, genetic manipulation of threatened species, and ecological restoration focused on retaining the specific functionality of forests, while emphasizing the importance of putting these different strategies into context with the short- and long-term objectives of regional land management. Surveys of forestry professionals in New England revealed that both loggers and foresters in this region placed a higher priority on regenerating economically valuable species than regenerating species diversity in ash stands impacted by EAB (Markowski-Lindsay et al., 2023). In this same study, it was found that loggers were more than twice as likely to prioritize regenerating economically valuable species than foresters. Range expansion northward of species co-occurring with black ash in the southern portion of its native range has been suggested as a form of climate change resiliency (Iverson et al., 2016), with examples from our study being river birch, silver maple, and swamp white oak. Overall, selecting species to use in artificial regeneration plantings is particularly difficult in the case of black ash, since its regulation of wetland hydrology (Slesak et al., 2014) may be replaced by other wetland-adapted species, but its importance as a cultural resource to indigenous peoples and use in traditional basket-making cannot be replicated (Costanza et al., 2017; Siegert et al., 2023). Thus, planting initiatives should consider a wide range of perspectives and objectives that account for the ecological, economic, and cultural aspects of post-EAB forested wetlands.

5. Conclusions

Our results indicate that without artificial regeneration, the black ash stands examined in this study are at risk of converting to dominance of herbaceous or shrub species, especially in the northern Wisconsin sites as the black ash in the canopy begin experiencing mortality with insufficient tree seedling densities in the understory. Understanding site hydrology is important to seedling success, primarily by examining the water table levels within a site over time. However, planting on higher elevation microsites can greatly improve survival for the first two years after planting, which itself is an important indicator of future success. River birch, bur oak, red maple, silver maple, and swamp white oak all showed high survival and growth when planted in ash wetlands that were recently invaded by EAB. The success of these species in the planted stands despite the challenging conditions solidifies underplanting as an effective silvicultural strategy to combat the ecosystem changes brought about by EAB invasion. Continued monitoring is needed to understand the true influence of competing vegetation, herbivory, and light availability on the planted seedlings as they persist in the forest understories.

Author contributions

Conceptualization, D.B., K.H., R.K., and F.L.; Methodology and Analysis, S.D., D.B., K.H., R.K., G.B., and F.L.; Writing – Original Draft Preparation, S.D.; Writing – Review and Editing, D.B., K.H., R.K., and F.L.; Funding acquisition, S.D., D.B., K.H., R.K., and F.L.

CRediT authorship contribution statement

Seth W. Davenport: Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation. **Dustin R. Bronson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Kathryn Hofmeister:** Writing – review & editing, Supervision,

Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Randall K. Kolka:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Grady Boyle:** Methodology, Formal analysis. **Fengjing Liu:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Supplementary Materials

N/A

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.

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Appendix A

Table A.1

Total daily precipitation (ppt), minimum temperature (tmin), and maximum temperature (tmax) of stands 1 and 2 in the Chequamegon-Nicolet (CN1 and CN2) and stands 1 and 2 in the Ottawa (OT1 and OT2) National Forests, as well as the mean across all stands. Time periods are divided by the number of years after planting (YAP) with the respective calendar year in parentheses. Daily normals from 1991 to 2020 are displayed at the top. All data sourced from Oregon State PRISM software

time	climate variable	CN1	CN2	OT1	OT2	mean
30 yr daily normals	total ppt (mm)	871.7	862.6	807.7	807.1	837.3
	tmin (°C)	-18.1	-18.0	-14.6	-14.7	-16.3
	tmax (°C)	25.6	25.6	26.2	26.2	25.9
0 YAP (2022)	total ppt (mm)	836.4	902.7	1015.2	1002.6	939.2
	tmin (°C)	-33.6	-33.7	-28.4	-28.5	-31.1
	tmax (°C)	34.2	34.2	36.2	36.3	35.2
1 YAP (2023)	total ppt (mm)	965.1	922.1	763.2	762.4	853.2
	tmin (°C)	-30.7	-30.3	-23.7	-23.7	-27.1
	tmax (°C)	33.6	33.3	36.2	36.1	34.8
2 YAP (2024)	total ppt (mm)	870.0	984.3	844.2	838.4	884.2
	tmin (°C)	-28.2	-27.6	-21.1	-28.2	-26.3
	tmax (°C)	32.0	32.2	34.0	32.0	32.6

Table A.2

The mean water level (WL) in relation to the soil surface, the elevation of the hydrological monitoring well at the soil surface, and the mean water table elevation (WTE) of each planted site. Water levels within wells were averaged across the duration of the study from 2022 to 2024

stand	mean WL (m)	well elevation (m)	mean WTE (m)
CN1	-0.16596	462.433	462.267
CN2	-0.04282	458.402	458.359
OT1	-0.03071	266.809	266.778
OT2	-0.02608	265.579	265.553

Appendix B

Table B.1

The condition of planted stands in the Chequamegon-Nicolet National Forest (CN1 and CN2) and the Ottawa National Forest (OT1 and OT2) two years after planting. Total basal area (BA) in ft²/ac, the percent of BA occupied by black ash (*Fraxinus nigra*; FN), the percent of BA occupied by dead FN, the percent of FN with signs of EAB, and the mean diameter at breast height (DBH) in inches of FN trees

stand	total BA	% BA FN	% BA dead FN	% FN with EAB	mean FN DBH
CN1	213	42	0	100	8.7
CN2	140	81	5	100	12.9
OT1	183	58	58	100	10.6
OT2	220	41	41	100	13.0

Table B.2

The amount of stems per acre of woody seedlings less than 3.3 ft in height and less than 1 in. diameter organized by stand. Canopy species marked with a *

species	CN1	CN2	OT1	OT2
balsam fir (<i>Abies balsamea</i>)*	51	0	0	0
red maple (<i>A. rubrum</i>)*	860	51	304	152
sugar maple (<i>A. saccharum</i>)*	0	51	0	202
yellow birch (<i>B. alleghaniensis</i>)*	759	304	0	0
paper birch (<i>B. papyrifera</i>)*	0	0	101	0
musclewood (<i>Carpinus caroliniana</i>)	0	51	0	0
beaked hazelnut (<i>Corylus cornuta</i>)	101	101	0	0
black ash (<i>F. nigra</i>)*	1012	51	202	455
winterberry holly (<i>Ilex verticillata</i>)	0	0	253	0
currants (<i>Ribes</i> spp.)	0	354	152	0
brambles (<i>Rubus</i> spp.)	2630	2985	0	101
American elm (<i>Ulmus americana</i>)*	0	51	0	51
Canopy species total	2681	506	607	860
All species total	5413	3996	1012	961

Data availability

Data will be made available on request.

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Glossary

- AIC: Akaike Information Criterion
 DEM: digital elevation model
 DNR: Department of Natural Resources
 EAB: emerald ash borer
 ET: evapotranspiration
 FN: *Fraxinus nigra* (black ash)
 GLM: generalized linear model
 OR: odds ratio
 PPFD: photosynthetic photon flux density
 RGR: relative growth rate