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Survival and growth of underplanted replacement tree species in black ash wetlands threatened by emerald ash borer in Minnesota, USA

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Abstract

Black ash (*Fraxinus nigra*) wetlands in the northern US Lake States are threatened by emerald ash borer (EAB), with the impacts expected to be severe because of the foundational role of this species in controlling ecosystem functions. Underplanting before mortality from EAB is one approach being considered to replace black ash and maintain ecosystem functions. We report on third-year survival and growth responses of five underplanted tree species (red maple, silver maple, American elm, balsam poplar, and swamp white oak), to differences in seedling stock size, understory competition, and browse protection. After three years, silver maple and swamp white oak had similarly high survival (>90%), followed by red maple (70–90%) and American elm (50–80%). Balsam poplar had almost no survival. There was no effect of stock size, browse protection, or understory competition on tree survival. Swamp white oak had the highest diameter growth, followed by red maple, silver maple, and American elm. Stock size had a modest effect on growth, while browse protection and understory competition were weak predictors. Relative height growth was negative across all species, indicating a net loss in height from either winter cold damage or browsing. Relative height growth was similar regardless of stock size, browse protection, and understory competition. Our results show promising survival and growth for silver maple and swamp white oak when underplanted in black ash wetlands. However, patterns in height growth suggest that future canopy openings, either via harvests or EAB-induced mortality, may be necessary to recruit replacement species into the canopy.

Keywords Foundational species · Regeneration · Silviculture · Adaptation · Invasive species

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Introduction

The emerald ash borer (EAB; *Agriulus planipennis*) has killed ash trees (*Fraxinus*) in forests throughout much of eastern North America. For most ash species, EAB causes over 90% mortality of trees within a few years after infestation (Klooster et al. 2014), or after a second wave of infestation after trees reach a minimum diameter of around 2.5 cm (Aubin et al. 2015). There has been a large amount of research on ash mortality and impacts to ecosystem function (see references in Klooster et al. 2018; Kolka et al. 2018), but most of this work has been in mixed-species forests where ash makes up 50% or less of overstory basal area (Kashian and Witter 2011; Bowen and Stevens 2018; Hoven et al. 2020).

While loss of ash in mixed-species forests can be impactful to ecosystem function (Flower et al. 2013), impacts are greater in forests where ash makes up most trees in the overstory (Abella et al. 2019). Such is the case in black ash (*Fraxinus nigra* Marsh.) wetlands of the northern Great Lakes region of North America, where the species often comprises upwards of 85% of overstory trees (e.g., Palik et al. 2011; D'Amato et al. 2018; Palik et al. 2021a). In these ecosystems, black ash is considered foundational (Youngquist et al. 2017) for its role in modulating ecosystem structure and function through influences on hydrology (Diamond et al. 2018), litter quality (Youngquist et al. 2020), and resource availability to aquatic detritivores (Youngquist et al. 2017).

There is limited potential for other species to replace black ash in abundance or to assume its foundational role in ecosystem function (D'Amato et al. 2018). While black ash wetlands can be rich in woody species in all structural layers, most species occur in low abundance, are found infrequently in stands across the landscape, or do not attain overstory tree stature (Palik et al. 2012; 2021a). As a result, there is little potential for gap-filling in the overstory by these other species and limited potential for near-term replacement through release from sub-canopy layers. This condition underlies an urgent need to deploy silvicultural approaches to transition black ash wetlands into non-ash tree species (Looney et al. 2015; D'Amato et al. 2018). Due to the lack of adequate natural regeneration, such approaches will include artificial regeneration.

Studies in the US Lake States have examined survival and growth of planted replacement tree species after several types of harvesting in black ash wetlands (Bolton et al. 2018; Palik et al. 2021b). Gap-based partial harvests have proven effective at establishing a variety of replacement species (Palik et al. 2021b), while also maintaining site hydrology observed in undisturbed mature black ash wetlands (Diamond et al. 2018). However, given the vast area of black ash wetlands in the western Lake States of the US, including 500,000 ha in Minnesota, 340,000 ha in Wisconsin, and 270,000 ha in Michigan (Youngquist et al., 2017), it is unlikely that partial harvesting can be used widely to establish replacement species. A more realistic approach for treating a greater area is underplanting in unharvested forest. We are aware of two studies that monitored the survival of replacement species with underplanting, with reasonable survival of mid- to shade tolerant species, although with limited diameter and height growth of seedlings (Bolton et al. 2018; Palik et al. 2021b). The expectation with underplanting is that the replacement tree species can be established before overstory mortality of black ash from EAB occurs, with seedlings being released when resources (primarily light) increase after this mortality.

To add to this body of information, we established an underplanting trial of five tree species in northern Minnesota, USA in black ash wetlands to provide more information for managers considering this preemptive approach in anticipation of EAB mortality. For each species, we tested differences in seedling stock size (i.e., small vs. larger) given the well-known influence of size on survival and growth (Grossnickle 2012). Browsing by native eastern white-tailed deer (*Odocoileus virginianus*) is a widespread silvicultural issue for forest regeneration in the study area (Patton et al. 2018). Therefore, we assessed seedling performance with and without physical browsing protection.

Our overall objective was to assess survival and growth as related to tree species, planting stock size, and local understory competition around seedlings. Our expectations were that: (1) more shade tolerant species will have better survival, whereas less shade tolerant species, if surviving will have better growth; (2) larger planting stock will have higher survival and growth; (3) survival and growth will be negatively affected by local understory competition; and (4) browse-protected seedlings will have higher survival and growth.

Methods

Study area and sites

We conducted our study in northcentral and northeastern Minnesota, USA, between latitude 46.90–47.71° and longitude −92.74 to −94.33°. Mean annual temperature of the region is approximately 4.0°C. Maximum summer temperatures can exceed 32°C, while minimum winter temperature can drop below −35°C. Mean annual rain-equivalent precipitation is 50–64 cm (PRISM Climate Group, 2014). In winter, average total snowfall ranges from 1 to 2 m. The study area is a glacial moraine landscape dominated by aspen (*Populus* spp.), pine (*Pinus* spp.), maple (*Acer* spp.), paper birch (*Betula papyrifera*), and other conifers (*Abies balsamea*, *Picea glauca*) in the uplands, with black ash and lowland conifers (*Picea mariana* and *Larix laricina*) dominating wetlands in poorly drained landscape positions.

Study sites were selected from two widespread black ash wetland types identified in the region, including northern wet ash swamps and northern very wet ash swamps (Aaseng, 2003), which differ in soil hydrological characteristics, including mean depth to the water table (shallower for very wet) and days of surface water ponding (longer for very wet). Soils of both wetland types are typically Histosols characterized by mucky peats of varying depths underlain by silty clay horizons (Natural Resource Conservation Service, 2019) but may also include mineral soils of varying composition (Slesak et al., 2014). The two wetland types occur in a variety of geomorphic settings in the region, including isolated depressions, extensive lowlands with flat topography, transitions between uplands and conifer wetlands, and riverine settings adjacent to flowing channels (Diamond et al., 2019). We restricted our study to the lowland geomorphic setting, as it is the most extensive in the region and the one most vulnerable to altered hydrology following ash loss (Cianciolo et al. 2021).

We selected twelve black ash sites from a larger pool identified from inventory records of federal, state, and county ownerships (Grinde et al. 2022). All twelve sites had characteristics of both wet ash and very wet ash wetland types, depending on location of the sample plot. Characteristics of the sites are summarized in Table 1. Mean (+/- standard deviation) overstory basal area (trees ≥ 10 cm diameter at 1.4 m height) was 24 (4) m^2 ha^{-1}, with black ash comprising 87 (8) % of basal area (Table 1). Green.

Table 1 Characteristics of study sites. Site values for vegetation are means (+/- 1 standard deviation) of three plots; water table values are means (+/- 1 standard deviation) of three years (2022–2024) based on one well per site

Site	Basal[1] area m^2 ha^{-1}	Percent black ash[2]	Mean diameter (cm)[1]	Saplings[3] ha^{-1}	Seedlings[4] ha^{-1}	Mean daily water table depth (cm)[5]	Days water table within 30 cm of surface[6]
Third River 1	28.6 (5.3)	97 (2)	22.9 (2.5)	898 (621)	21,319 (6229)	−17.9 (4.9)	75 (19)
Third River 2	27.8 (7.4)	88 (13)	25.3 (1.0)	577 (117)	22,608 (555)	−46.3 (14.0)	42 (19)
Third River 3	28.1 (4.3)	86 (4)	22.1 (1.1)	873 (362)	21,133 (9448)	−18.7 (16.3)	43 (32)
Kupcho	23.8 (5.2)	82 (5)	21.8 (2.1)	1433 (544)	23,333 (6704)	−32.9 (13.5)	24 (5)
Wirt	26.7 (9.6)	97 (3)	23.9 (0.3)	675 (371)	16,038 (5095)	−33.3 (4.2)	50 (23)
Hill City	22.9 (0.7)	75 (5)	21.7 (0.6)	997 (803)	28,219 (8906)	−28.6 (17.3)	45 (25)
Kosonen	12.6 (1.5)	81 (13)	19.7 (1.9)	1886 (299)	53,100 (7808)	−7.4 (18.5)	99 (32)
Aitkin 1	30.0 (3.0)	88 (3)	26.8 (0.8)	461 (79)	13,311 (5563)	−46.9 (8.9)	50 (23)
Aitkin 2	27.3 (4.4)	98 (1)	26.4 (2.1)	667 (173)	26,863 (2544)	−35.8 (18.1)	47 (27)
Aitkin 3	20.6 (5.0)	88 (8)	25.2 (1.3)	560 (234)	43,867 (7780)	−42.8 (13.8)	41 (23)
River Road	21.6 (1.3)	72 (17)	21.5 (1.0)	923 (528)	27,600 (9042)	−43.0 (15.6)	48 (25)
Floodwood	19.3 (0.9)	63 (22)	19.1 (0.7)	997 (174)	19,142 (6693)	−21.6 (13.3)	91 (31)
Site mean (sd)	26.0 (4.9)	84 (11)	23.0 (2.5)	912 (404)	26,378 (11408)	−31.3 (12.7)	55 (22)

[1]Stems ≥ 10 cm diameter; [2]Percent of basal area; [3]2.5 cm ≤ diameter < 10 cm; [4]< 2.5 cm diameter including trees and woody shrubs; [5]Mean daily depths relative to the surface from April to October; [6]Mean number of days from April to October.

ash (*Fraxinus pennsylvanica*), which is also susceptible to EAB, was a minor component in some sites. Other co-occurring tree species occurring in small amounts included northern white cedar (*Thuja occidentalis*), American elm (*Ulmus americana*), and quaking aspen (*Populus tremuloides*) (Palik et al. 2021a). Additional criteria for site selection included (1) stands were large enough to establish three 0.08 ha circular plots for planting (see below); (2) no evidence of recent cutting or mortality of trees; (3) no ditches, roads, or trails in the sample area and (4) dominated by mature trees. The average size of selected wetlands was 5.6 ha.

Species selection

We planted five tree species to evaluate as potential functional replacements for black ash (Table 2). Three species are native to black ash ecosystems, including red maple (*Acer rubrum)*, balsam poplar (*Populus balsamifera*), and American elm (*Ulmus americana*). One species, silver maple (*Acer saccharinum*), is native to the region, but is rare in black ash ecosystems occurring in the extensive flat geomorphic setting. The last species, swamp white oak (*Quercus bicolor*), is novel to the region, having its northern range terminus approximately 200 km south of the study area. However, it is projected to have increased habitat suitability in the study region with climate warming (Iverson et al., 2016).

Species choice was based on a combination of desired traits, including: (1) capability of growing to dominant canopy position, (2) mid- to long-life span (e.g., >140 years), and

Table 2 Characteristics of planted species

Species	Co-occurring, native, or novel[1]	Stock type	Seed source	Shade tolerance	Wetland indicator status
Red maple	Co-occurring	Bare-root seedlings	Southern Minnesota	Intermediate	Facultative
Balsam poplar	Co-occurring	Stem cuttings	Northern Minnesota	Intolerant	Facultative wetland
Silver maple	Native	Bare-root seedlings	Southern Minnesota	Tolerant	Facultative wetland
American elm	Co-occurring	Bare-root seedlings	Princeton cultivar	Intermediate	Facultative wetland
Swamp white oak	Novel	Bare-root seedlings	Northern Iowa	Intermediate	Facultative wetland

[1] Co-occurring in black ash wetlands occupying flat geomorphic settings; native to the region, but not the study ecosystem; novel to the region.

(3) except for American elm, has no major health issues in the region. For American elm, which is impacted by Dutch elm disease (*Ophiostoma novo-ulmi*), we used the Princeton cultivar which has shown tolerance of DED in the region (Slavicek and Knight, 2012). The final trait of interest was wetland indicator status. All species except red maple are facultative wetland species, i.e., mostly occur in wetlands, with red maple classified as facultative, i.e., occurring equally in wetlands and uplands (USDA Natural Resource Conservation Service (2020). The species varied in shade tolerance ranking (Table 2), including one intolerant species, three intermediate species, and one tolerant species (USDA Natural Resource Conservation Service (2020). Our inclusion of the shade-intolerant balsam poplar for underplanting was informed by regional managers reporting initial success of underplanted balsam poplar cuttings in our study area.

Seedling planting and monitoring

In each of three 0.08 ha circular plots per site, we planted one hundred seedlings consisting of ten individuals of each of five species by two sizes. We split planting plots into two equal halves and assigned to either browse protection or unprotected such that half of the seedlings of each species by size combination were planted in each half.

The size differences were not large, except for American elm (Fig. 1). Size was based on height alone for red maple, silver maple, and swamp white oak, which were all one-year-old seedlings (1 − 0 stock). American elm stock differed in both height and age; small seedlings were one year old (1 − 0 stock), while large seedlings were three-years-old (3 − 0 stock). Balsam poplar was established from stem cuttings (Landhausser 2003), with the size difference based on length of the cutting. Small and large cuttings came from the same stems, with the former coming from the bottom 30 cm and the latter coming from the terminal 60 cm. The cuttings had 2.5 cm of bark shaved off the rooting end which was dipped into a powdered

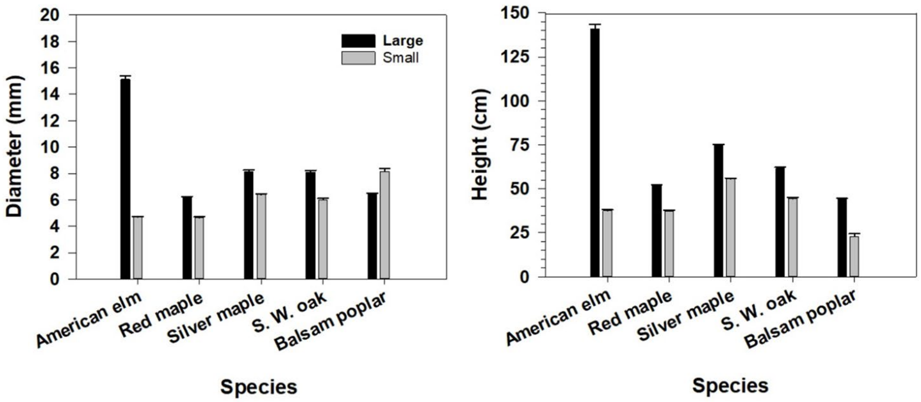

Fig. 1 Diameters and heights of planted species in fall 2022 in northern Minnesota USA black ash wetlands. Sizes at the time of planting in spring 2022 were not available. Values are means (standard errors) of twelve sites

rooting hormone (DesRochers et al. 2004) and planted approximately 15 cm below the soil surface.

We planted seedlings in May 2022 along rows radiating at 15-degree intervals from the plot center towards the plot boundary, with planting locations starting 6 m from plot center, spaced at 1. 5 m intervals, ending at 12.0 m from center. Each planting row consisted of five seedlings of a species by stock size. Each half plot contained 10 rows (5 species by 2 stock sizes). We marked each planting location with a colored pin flag corresponding to each of the five species. Seedlings were planted at the best location within planting cells of approximately 1.5 m^2 in size, with areas that were unplantable due to obstructions from rocks, deadwood, or standing water being avoided. If there were no suitable planting locations within a given planting cell, then that location was skipped and planting advanced to the next cell on the line. Each seedling had a wire with an aluminum tag loosely tied around its base, with a unique number that identified the species, size, and browse protection.

Browse protection was added in fall 2022. Protection consisted of cages made of plastic fencing supported by bamboo or lath stakes on at least two sides of the seedling, with the fencing stapled to stakes to form a 15 cm diameter tube extending at least 20 cm above the terminal bud. We inspected and repaired the cages as needed in spring and fall of both 2023 and 2024.

Seedlings were measured at the end of each growing season in 2022, 2023, and 2024. Observations included survival, height, basal diameter, and evidence of browse damage. We measured height to the nearest cm from the base at ground level to the tallest terminal bud on the main stem or on a branch if the terminal leader was damaged. We measured basal diameter to the nearest mm near ground level just above the root collar using digital calipers in two perpendicular directions. Evidence of browsing reported here was assessed in fall 2024 on the current year's growth. Note that balsam poplar had less than 4% survival study-wide by fall 2024 (data not shown) and we did not include it in statistical analyses.

Vegetation sampling

Within each plot, understory vegetation was estimated around each planted seedling in summer 2023 as a measure of local competition. For this, we centered a circular 0.56 m radius plot on each seedling. We estimated total herbaceous cover by categorical classes representing cover ranges, including 1 = trace, 2 = 1–5%, 3 = 6–15%, 4 = 16–30%, 5 = 31–60%,6 = > 60%. Understory woody stem density was tallied in each sample plot by two size classes: 15 cm to 1.5 m in height and > 1.5 m in height to 2.5 cm diameter. Preliminary analysis revealed similar patterns of distribution and response across both classes, so they were combined for subsequent analyses to simplify interpretation. Distributions of herbaceous cover and woody density were highly skewed, as most plots had high herbaceous cover (94% of individual plots had cover categories 5 or 6) and low woody density (2.6 ± 3.2, mean ± SD, range 0–44).

Data summary

Planted seedling survival, expressed as the actual percentage of individuals remaining in fall 2024, was assessed after the three growing seasons. Seedling size (mean base diameter and height) were summarized in fall 2022 and again in fall 2024, after one and three growing seasons, respectively. For analysis these variables were summarized to the plot level and plots were averaged to derive site level metrics.

Growth was assessed between fall 2022 and 2024 using only individuals that were alive in fall 2024. For this, we calculated relative diameter and height growth rates to compensate for the differences in initial sizes among species and stock size (Table 1), which would bias comparison of absolute growth rates (Hunt and Cornelissen, 1997). We calculated relative growth rates as the difference between natural logarithms of individual seedling sizes in fall 2024 and fall 2022, divided by the time interval of two years (following Burdon and Harper, 1980), with values then averaged to the plot and site level. This approach, i.e., sizes transformed before averaging, as opposed to the more typical approach of transforming averages, avoids bias associated with increasing variance in size over time (Hoffmann and Poorter, 2002).

Statistical analysis

Generalized linear mixed models were used to evaluate the predictors of survival and relative growth rate using lme4 package (Bates et al. 2015). Species, stock size, and browse protection were modelled as fixed effects (all predictor combinations were evaluated), while site was a random effect. Models penalized for complexity were compared using Akaike Information Criterion (AIC) and the most parsimonious model was selected as the final model if $\delta\text{AIC} < 7$. To facilitate interpretation, simple linear models were used to visualize the effects of key predictors. Assumptions of ANOVA were evaluated using Levene's test for homogeneity of variance. Key comparisons were also evaluated for sensitivity using a non-parametric approach, Welch's Heteroscedastic test with Games-Howell post-hoc tests using onewaytests (Dag et al. 2018) and rstatix (Kassambara 2022), respectively. Understory woody density and herbaceous cover were not included in the mixed models because of the violated distributional assumptions which could not be alleviated by any transformation; however, we tested their individual effects, within the limited range observed in this study, using non-parametric regression analysis. Analyses were done in the R environment (R Core Team, 2022, version 4.1.3).

Results

Browse occurrence

Protective cages reduced browse damage on seedlings as assessed in fall 2024 (Fig. 2). The occurrence of some browse damage even on protected seedlings is a result of the enclosures failing due to heavy snow loads and/or disruption by American black bears (*Ursus americanus*) which were attracted to the cages.

Survival

Mean survival after three years was 71% (median 80%) when pooled across all plots and species. Note this does not include balsam poplar which was removed from analysis due to almost complete mortality (<4% survival). Seedling survival was best explained by the mixed model including species and site (Table S1). Post-hoc comparisons showed significant differences in survival rates for all species pairs (Tukey $P<0.0001$), except between silver maple and swamp white oak, which did not differ ($P=0.77$). Although Levene's test demonstrated significant heterogeneity in survival across species ($P<0.0001$), results of non-parametric tests were identical to parametric tests (Welch's $P<0.0001$, Games-Howell $P<0.0001$) for all comparisons except silver maple and swamp oak, which again was not significant, indicating that the survival response to species was not overly sensitive to violation of distributional assumptions.

Silver maple and swamp white oak had the highest survival (>90%) among all species (Fig. 3), followed by red maple (70–90%) and American elm (50–80%). As confirmed by our model, survival did not differ by stock size (Fig. 3). Browse protection was not included in the top mixed models based on AIC and was not significant in the simple linear model

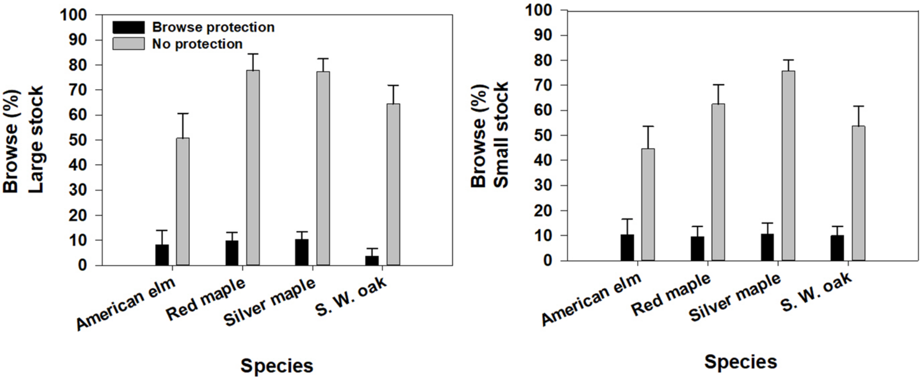

Fig. 2 The percentage of planted seedlings with evidence of browse damage in fall 2024 in northern Minnesota USA black ash wetlands. Values are means (standard errors) of $n=12$ sites except for American elm ($n=10$ to 12 sites)

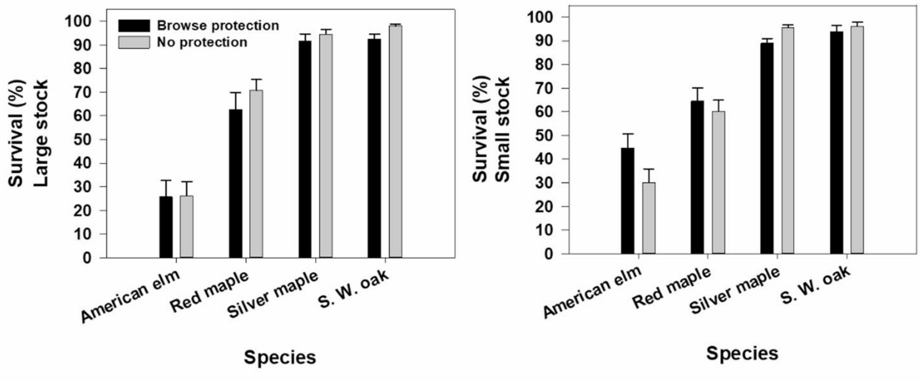

Fig. 3 Survival (%) of planted replacement species (actual proportion surviving) after three growing seasons in northern Minnesota USA black ash wetlands. Values are means (standard errors) that were derived by hierarchically averaging at plot level and then at the site level

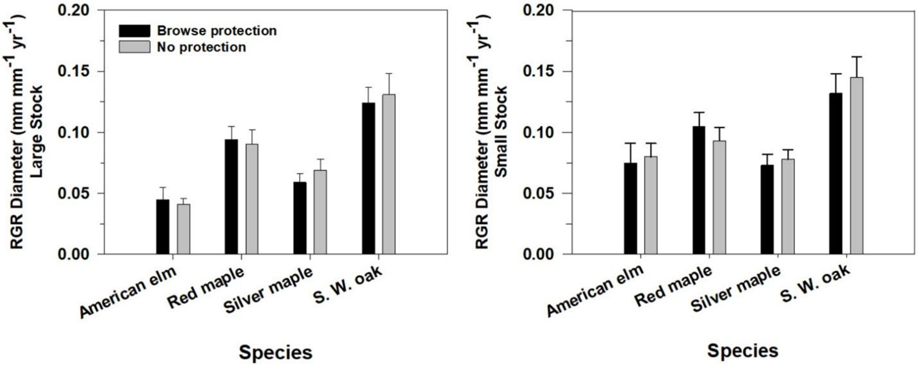

Fig. 4 Relative diameter growth of planted replacement species between fall 2022 and fall 2024 in northern Minnesota USA black ash wetlands. Values are means (standard errors) of values that were hierarchically averaged at plot level and then at the site level

($P=0.86$). Finally, survival was only negligibly correlated with local understory competition within the limited range observed in this study (herbaceous cover Kendall $\tau=0.07$, $P=0.03$; woody density $\tau=0.07$, $P=0.02$).

Growth

The best approximating model for relative diameter growth included species and stock size (Fig. 4, Table S1). In a simplified model, the effect of species was greater than effect of size (multiple regression: size F = 9.2, $P=0.003$; species F = 43.7, $P<0.0001$; $\eta^2=0.01$ and 0.21 for size and species, respectively). All species pairs were significantly different (Welch's $P<0.0001$, Games-Howell post hoc $P<0.0001$), except for American elm and silver maple (Games-Howell $P=0.74$).

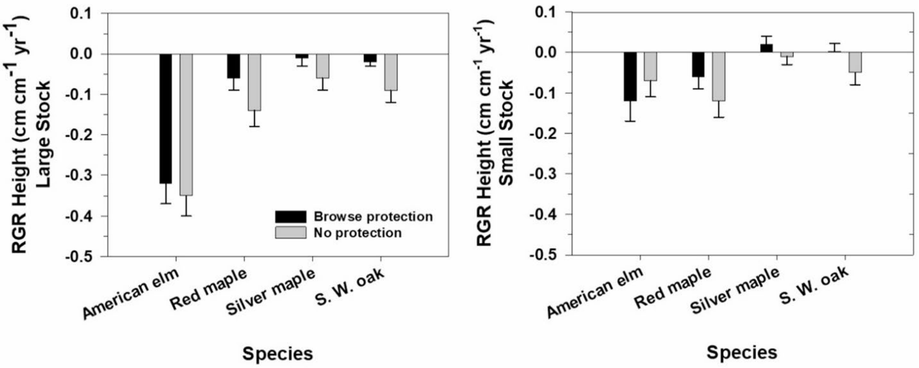

Fig. 5 Relative height growth of planted replacement species between fall 2022 and fall 2024 in northern Minnesota USA black ash wetlands. Values are means (standard errors) of values that were hierarchically averaged at plot level and then at the site level

Swamp white oak had the highest relative diameter growth among all species (Fig. 4), followed by red maple, and then silver maple and American elm, which did not differ. Relative diameter growth was slightly higher for the smaller stock size (multiple regression $P=0.0009$ for size, $P<0.0001$ for species, interaction NS). Browse protection was not included in any of the top mixed models. Also, diameter growth was not significantly related to local understory competition within the limited range of the understory observed in this study (Kendall $P=0.06$ for herbaceous cover, 0.07 for woody density).

Mean relative height growth was negative or near zero for all species, and 47% of individuals lost height during the two-year period of measurement (Fig. 5). However, the values of these reductions were quite small, meaning there was not much height change over the period of record. Like relative diameter growth, species and stock size were the best predictors of relative height growth in mixed models (Table S1). Of the four surviving species, swamp white oak and silver maple lost less height compared to red maple and American elm (Fig. 5; Welch's $P<0.0001$, Games-Howell $P=0.41$ for silver maple-swamp white oak comparison, and P-value ranging from 0.016 to <0.0001 for other pairwise comparisons). Relative height growth was similar regardless of stock size except for large stock American elm, which had a much larger height loss than small stock (Fig. 5). Browse protection had small and inconsistent effects on height growth (Fig. 5). Height growth was not correlated with local understory competition (Kendall $P=0.28$ for herbaceous cover, $P=0.72$ for woody stem density).

Discussion

Survival and growth of species

We evaluated five tree species as potential ecological replacements for black ash, including red maple, silver maple, American elm, balsam poplar, and swamp white oak. All are facultative wetland species except red maple, which is rated as facultative. These species should be well suited to wetland conditions. The species differed in qualitative shade tolerance rating, and we expected survival would increase with shade tolerance when underplanting in mature forest. Survival results partially confirmed our expectations. Balsam poplar had almost no survival, which is consistent with research showing this shade intolerant species surviving poorly when planted in the forest understory (Landhäusser and Lieffers 2001). However, our plantings consisted of stem cuttings rather than actual seedlings and it may be that these cuttings had a lower potential to establish than rooted seedlings in seasonally wet organic soil. Also, our inexperience with using this technique may have led to reduced survival. These results suggest a need to investigate alternative methods for improving establishment and survival, particularly in challenging site conditions.

Red maple, rated intermediate in shade tolerance, had survival of 60–80%, as did intermediate American elm small stock, while larger stock had lower survival of 35–40%. Silver maple is rated a shade tolerant species, and it did have nearly 100% survival in our study, but so did swamp white oak, which is rated as having intermediate shade tolerance. However, this latter result is consistent with findings on artificial regeneration of swamp white oak in a bottomland hardwood setting, where survival after five years with underplanting was similar (80%) as with partial cutting, and even higher than survival in clearcuts (Hayford et al. 2024). We did not measure leaf area or light availability, nor did Hayford et al. (2024), but it may be that understory light environments were not limiting in the wetland settings examined in our two studies. Black ash wetlands generally have lower leaf area than other forest types (Telander et al. 2015), which may provide greater opportunity to underplant less shade-tolerant species, like swamp white oak.

We expected that less shade-tolerant species would exhibit greater growth, assuming they were able to survive. This proved the case for swamp white oak, which had the highest diameter growth of all species and, along with silver maple, was less likely to lose height than red maple and American elm. Swamp white oak and silver maple did not change much in height over the two-year period of monitoring. Our results for swamp white oak seedlings are consistent with increases in basal diameter and height in the bottomland hardwood forests studied by Hayford et al. (2024), where growth was highest in the uncut control, compared to partially cut and clearcut forest.

Diameter growth rates of silver maple, red maple and small stock American elm were moderate compared to swamp white oak. Large stock American elm had the lowest diameter growth rates of all species-size combinations, as well as large losses of height. We attribute the latter to the tall initial size of the plantings, averaging 150 cm (Fig. 1), which placed their leaders above the snow line in the winter, such that they suffered cold-related shoot dieback. Studies in northern latitudes of cold tolerance and shoot injury of American elm cultivars bred for tolerance of Dutch Elm Disease support this interpretation of shoot dieback (Schaberg et al. 2021).

Stock size

Our expectation was that larger planting stock would have higher survival and growth than smaller stock, as larger stock may facilitate acquisition of growth-limiting resources (light, water, nutrients; Pinto et al. 2011). However, this was not the case for either survival or growth, as there were no significant differences between stock sizes, (except for American elm which we attribute for cold damage as noted above). The relationship between increasing seedling diameter and both survival and growth is well documented (Grossnickle 2012).

That we did not see this may reflect the minimal diameter differences between small and large stock seedlings or large variation in survival and growth in both size classes.

The relationship between seedling height and survival may depend on the resource environment, particularly light availability. In higher light environments, taller seedlings may have greater access to light and should have higher survival (Grossnickle 2012). When planted in an understory, as in our study, larger stock size may not confer an advantage in light acquisition. As with diameter, there was minimal difference in heights between large and small stock for most species, limiting any potential height advantage.

Understory competition

We expected survival and growth would be negatively affected by local understory competition around the seedlings, particularly in the lower basal area and leaf area wetlands of our study. This competitive impact was not strong, as our measures of understory competition, including densities of woody stems and cover of herbaceous vegetation, were of minor importance in survival and growth models. However, there was a limited gradient of woody density and herbaceous cover in this study, as most plots had uniformly high herbaceous cover and low woody density, making it difficult to relate these predictors to seedling performance outside of the observed range. Future studies that manipulate vegetation around planted seedlings (e.g., vegetation removal vs. retention) are needed to clarify the effect of plant competition in these environments.

Browsing impacts

We expected that browsing by eastern whitetail deer would reduce survival and growth of all species. There was evidence that seedlings were browsed and that protective cages reduced the incidence of browsing. However, there was less evidence that differences in survival could be attributed to browse damage or protection from this damage. There was no indication that protection from browsing influenced either diameter or height growth. The damage to cages noted earlier may explain negative height growth despite the clear benefit of protection. It is important to recognize that we did our browse damage assessment on seedlings that survived until the final measurement in fall 2024. It is possible that growth of unprotected seedlings that died in the previous two years had reduced growth rates compared to protected seedlings.

Guidance for management

Underplanting in mature black ash wetlands is not a widespread practice under typical silvicultural programs. However, the threat from EAB to the over 1 million ha of this resource in the northern US Lake States is an unprecedented event that calls for approaches to hasten the establishment of new trees to maintain ecosystem functions. Our results show promise for this approach, using flood tolerant tree species (Keller et al. 2023) that are available from regional nurseries. Moreover, of the five species evaluated, three of them, including red maple, silver maple, and swamp white oak, are expected to have increasingly favorable habitat in the northern Minnesota with climate change (Iverson et al. 2016), with the latter representing new habitat north of its range terminus approximately 200 km to the south.

American elm may be an option if managers can secure DED tolerant stock that is also cold hardy. Balsam poplar is a common species in black ash wetlands but is not projected to maintain habitat with climate change (Iverson et al. 2016) and it may be difficult to establish without substantial overstory removal to increase resources availability (Palik et al. 2021b). Larger stock sizes, which may be more expensive to procure and potentially more difficult to plant, may not enhance survival or growth, although our differences in stock sizes were generally not large, which may have led to the similar performance between sizes that we observed. Our results also indicate that protection from ungulate browsing or competition control around seedlings may not be cost effective given their limited enhancement of survival and growth, although longer-term results may prove otherwise.

Ultimately, the ability of underplanted seedlings to persist until the loss of the ash overstory is of greatest interest, as light conditions will become more favorable to growth. Longer-term results will be useful to determine how far in advance of EAB mortality underplanting can occur, particularly for less shade-tolerant species that may ultimately require greater levels of understory light to recruit to canopy positions. At the same time, there is potential for water tables to rise following ash loss (Slesak et al. 2014, Diamond et al. 2018) which may disfavor continued survival and growth. Continued monitoring at these sites as EAB invades will help determine the utility of underplanting as a mitigation strategy.

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Data availability Data and analysis are provided within the manuscript and in a supplementary information file and are availble from authors.

Declarations

Conflict of interest The authors declare no conflict of interest.

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