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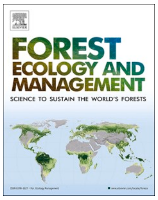

Eighth-year survival and growth of planted replacement tree species in black ash (*Fraxinus nigra*) wetlands threatened by emerald ash borer in Minnesota, USA

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ABSTRACT

Black ash *(Fraxinus nigra*) is native to lowland forests of the western Great Lakes region, USA, where it often comprises a majority of trees. Like all native ash in North America, black ash is threatened by emerald ash borer (EAB; *Agrilus planipennis*), but the impacts from EAB mortality may be particularly severe in these forests given the foundational role of black ash at regulating ecosystem function. Compounding the problem is that associated tree species occur in low abundance and their abundance may be further reduced as habitat declines with climate change. These converging threats point to the need for silvicultural intervention to establish replacement tree species in anticipation of EAB invasion. Here we report on a large-scale management experiment from Minnesota, USA that includes different silvicultural approaches for establishing replacement tree species in black ash forests. Specifically, we examined eighth-year survival and growth of planted seedling in treatments that included clearcutting, group selection, uncut forest, and emulation of EAB mortality by girdling black ash. Species included nine that are native to the ecosystem, two from the next southern climate zone, and one exotic species, Manchurian ash (*Fraxinus mandshurica)*. Among species and treatment combinations, survival was highest for American elm (*Ulmus americana*), averaging around 81% in uncut, group selection, and girdle treatments. Swamp white oak (*Quercus bicolor*), a species from the next southern climate zone, also had high survival in these treatments (ranging from 61% to 79%). Both species had survival under 60% in the clearcut treatment. Most native southern boreal species, as well as Manchurian ash, had low survival (0% to less than 40%) in most treatments. In the clearcut, girdle, and group selection treatments relative diameter and relative height growth was highest for balsam poplar (*Populus balsamifera),* averaging, respectively, around 0.25 mm mm^{-1} yr^{-1} and 0.20 cm cm^{-1} yr^{-1}*,* followed by swamp white oak and red maple (*Acer rubrum*). Non-native Manchurian ash had consistently low growth in all treatments compared to other species. All species had low growth rates in the uncut treatment. An integration of survival and diameter growth pointed to group selection as the treatment that provides the best balance between survival and growth. Our results indicate promising survival and growth of at least some replacement species, including several predicted to be future climate-adapted, as well as a silvicultural approach in group selection that is an effective method to regenerate these species.

1. Introduction

The emerald ash borer (EAB; *Agriulus planipennis*) has killed ash trees (*Fraxinus* sp.) in forests throughout much of eastern North America. For most ash species, EAB causes over 90% mortality of trees over 2.5 cm diameter within a few years after infestation (Klooster et al., 2014). Moreover, ash saplings that may initially be too small to be susceptible during the initial spread of EAB may become vulnerable during

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subsequent recolonization (Aubin et al., 2015). There has been a large amount of research on the impacts of ash mortality on ecosystem function (e.g., Klooster et al., 2018 and references therein; Kolka et al., 2018), but most of this research has come from mixed-species forests where ash makes up a portion, often a minority, of overstory trees (e.g., Kashian and Witter, 2011; Bowen and Stevens, 2018; Klooster et al., 2018; Hoven et al., 2020).

While loss of ash in mixed-species forests may be impactful, changes likely pale in comparison to impacts when a single species of ash makes up the majority of trees (Abella et al., 2019). Such is the case in northern Minnesota, USA where black ash (*Fraxinus nigra*) wetlands occupy 500,000 ha and the species often comprises upwards of 85% of overstory trees (e.g., D'Amato et al., 2018; Palik et al., 2011, 2021). In these ecosystem, black ash is considered foundational (*sensu* Ellison et al., 2005) for its role in modulating hydrology (Diamond et al., 2018), litter quality (Youngquist et al., 2020), and resource availability (Looney et al., 2017a; Youngquist et al., 2017).

Research in these same forests has pointed to a wide-spread lack of other tree species posed to replace black ash in abundance and in its foundational role. While black ash wetlands tend to 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, 2021). Thus, there is little potential for gap-filling in the overstory by other species and limited potential for near-term replacement through release from sub-canopy layers. Moreover, many of the tree species that are found in this ecosystem, including black ash, are climate change vulnerable, with large losses of habitat predicted by the end of the 21st century (Iverson et al., 2016). Two common co-occurring species, American elm (*Ulmus americana*) and northern white-cedar (*Thuja occidentalis*), are also susceptible to introduced Dutch elm disease (Townsend et al., 2005) and heavy deer browsing (Rooney et al., 2002), respectively. Thus, even if establishment of co-occurring species could be encouraged through natural regeneration, their long-term viability as replacements for black ash is questionable (D'Amato et al., 2018).

The characteristics of black ash ecosystems, i.e., dominance by a single species that is at great risk of mortality from an invasive pest, with little potential for near-term replacement by other species, point to potentially large impacts to ecosystem functions (D'Amato et al., 2018; Kolka et al., 2018). A potential shift to undesirable novel ecological conditions underlies an urgent need for evaluation of silvicultural approaches to transition black ash forests to non-EAB host and climate-suitable tree species, likely through artificial regeneration (Looney et al., 2015). Regenerating trees can be challenging in these wetland ecosystems after overstory removal or loss because of increased soil wetness and development of anoxic conditions, so silvicultural approaches also need to consider how to minimize hydrologic impacts.

With this need in mind, in 2011 we established the first of its kind operational-scale trial in North America to evaluate silvicultural approaches for facilitating replacement of black ash by future adapted tree species. Located in northern Minnesota USA, treatments span a range of tree removal including clearcutting, group selection, and mature uncut forest. A fourth treatment was designed to emulate EAB mortality by girdling all black ash. Planted tree species examined include several native to the ecosystem, two that have their northern range limits ~ 150–200 km south of the study area, and a final species, Manchurian ash (*Fraxinus mandshurica*), that is resistant to EAB (Rebek et al., 2008) and is potentially a cultural and ecological replacement for black ash (Looney et al., 2015).

Third-year seedling survival and growth has been reported previously (Looney et al., 2015, 2017a). Here we examine responses after eight growing seasons, to better identify the most promising combination of species and overstory treatments for transitioning these ecosystems to non-EAB host species. Our specific objectives were to i) assess and compare survival of planted seedlings of the various tree species to a gradient of canopy manipulations, including emulated EAB-induced mortality, and ii) compare diameter and height growth rates among species and canopy treatments.

Our expectations were that patterns in survival and growth after eight years would parallel the 3rd year results, specifically that: i) overall survival would be lowest in the clearcut treatment and similar in the other three treatments; ii) species projected to be future climate adapted would have the highest survival in most treatments; iii) growth would be highest in the clearcut treatment, both overall and for most species, due to a more favorable light environment, followed by the girdle, group selection, and uncut treatments, respectively; and iv) the group-selection treatment conveys the best balance of survival and growth overall and for most species.

2. Methods

2.1. *Study area*

This study is located on the Chippewa National Forest in northern Minnesota, USA approximately centered on 47.66° latitude and −94.32° longitude (Fig. 1a). Climate is continental, with most rainfall occurring during between May and September (PRISM Climate Group, 2015). For the 1981 to 2010 period, mean temperature averaged –13.7 and 16.5 °C in January and July, respectively, while mean precipitation averaged 742 mm year^{-1} (PRISM Climate Group, 2015).

Palustrine black ash wetlands in the study areas are classified as northern wet black ash swamp (Native Plant Community = WFn55) and northern very wet black ash swamp (NPC = WFn64), according to native plant community classification for the state of Minnesota (Aaseng, 2003). Soil texture of both types ranges from loam and sandy loam derived from glaciofluvial or lacustrine parent materials to clay and silty clay derived from glacio-lacustrine material overlain by approximately 30 cm of muck (Slesak et al., 2014). Study site hydrology is strongly influenced by a confining clay layer, which coupled with flat topography, results in poor drainage (Slesak et al., 2014).

2.2. *Study site*

Within the study area, we identified eight ~ 8 ha experimental blocks dominated by mature black ash forest (Fig. 1b). Four blocks were classified as wet ash swamp (WFn55) and four as very wet ash swamp (WFn64). Pretreatment basal area for trees > 10.0 cm diameter 1.4 m (diameter at breast height or DBH) averaged 20.7 (2.2 = standard error) m^2 ha^{-1} and mean tree density was 477 (50.6) trees ha^{-1} (Looney et al., 2015). On average, black ash comprised 91% of basal area among the blocks, with minor components of balsam fir (*Abies balsamea)*, trembling aspen (*Populus tremuloides)*, bur oak (*Quercus macrocarpa*), American basswood (*Tilia americana*), and American elm. Understory woody species included speckled alder (*Alnus incana* ssp. *rugosa*), beaked hazel (*Corylus cornuta*), and mountain maple (*Acer spicatum*) (Looney et al., 2015), all of which are shrub or subordinate tree species with little potential to replace overstory black ash (Palik et al., 2021).

2.3. *Experimental design*

In each block, four 1.62 ha circular areas, hereafter referred to as stands, were established with random assignment to one of four treatments, including uncut, group selection, clearcut, and girdle (Fig. 1b). Given the historically low levels of commercial harvesting in black ash wetlands, the uncut treatment was intended to approximate areas where harvesting of black ash would not occur, but where underplanting of non-EAB host species may be used in mature black ash forests to increase resilience to EAB (see *2.4 Species Selection* below). The group selection treatment was developed in consultation with the silviculturist from the Chippewa National Forest and consisted of eight 0.04 ha circular plots in each 1.62 ha stand, totaling approximately 20% of stand area in which all trees down to 5 cm dbh were harvested as a group. The treatment was

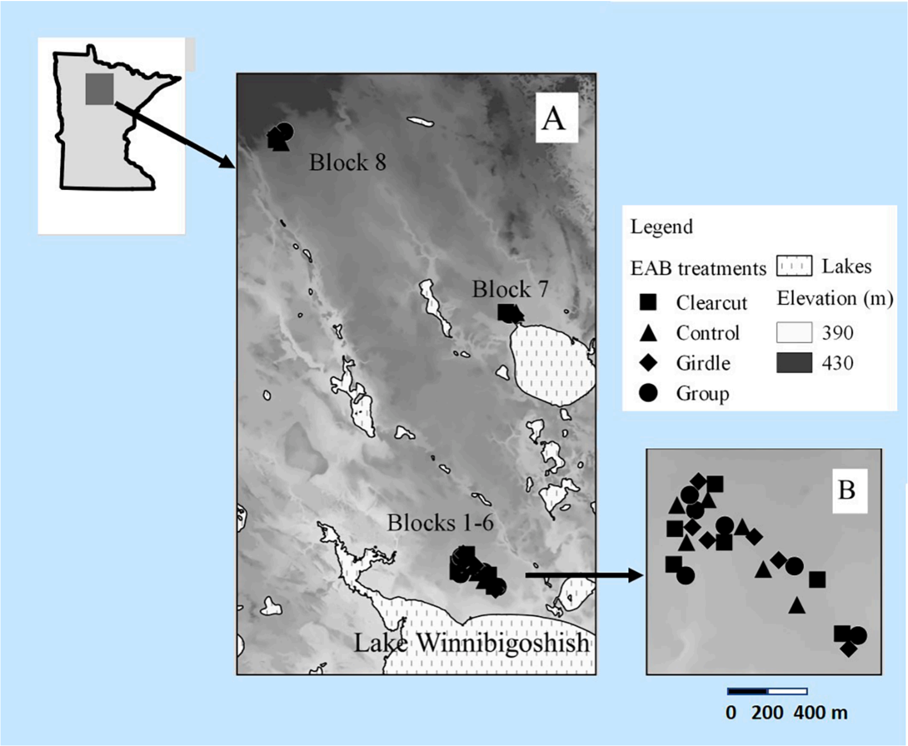

Fig. 1. A. Location of study sites in northern Minnesota, USA. B. Layout of experimental treatments in blocks 1–6, with each treatment replicated once per block. Modified from Looney et al. (2015).

meant to be an emulation of the gap-based natural disturbance regime of the ecosystem (D'Amato et al., 2018). In the clearcut treatment, all trees down to 5 cm dbh were harvested, while smaller woody stems were largely run over by machinery traffic. Finally, the girdle treatment was meant to emulate mortality of EAB: all black ash ≥ 5 cm dbh were girdled using draw knives twice in two successive. Harvesting of the clearcut and group selection treatments was conducted in late winter 2012 under frozen ground conditions using a tracked feller-processor and forwarder, while the girdling treatment was applied in the winters of 2012 and 2013 (Looney et al., 2015). Slash was lopped and scattered over harvested areas.

Average basal area after treatment (trees at least 10 cm dbh) was zero in the clearcut treatment, 16.6 m^2 ha^{-1} in the group treatment, and unchanged in the uncut forest (20.7 m^2 ha^{-1}). Most trees in the girdle treatment died over three to four years; by the time of the current study 90% of girdled black ash were dead, so basal area was comparable to the clearcut. The light environment, as reflected in leaf area index (LAI) two years after treatment, paralleled basal area, being lowest in the clearcut (averaging 11% of the control), moderate, but declining over time in the girdle treatment (69% of the control) and highest in the group selection treatment (85% of the control), with much lower LAI in the center of the group openings themselves (Looney et al., 2017a).

2.4. Species selection

We planted 12 species, ranging from native to novel, as described below (Table 1). Species choice was based on an informal poll that we conducted among researchers, foresters, and wildlife biologists familiar

Table 1
Characteristics of planted species and planting stock.

Species	Shade tolerance[1]	Wetland indicator status[1]	Stock type[2]	Mean height (cm)[3]	Mean diameter (mm)[3]
Red maple[4]	Tolerant	Facultative	Fall 2011: Container (90 cm^3)	17.4 (4.2)	3.7 (0.2)
			Spring 2012: Bare root (1 + 0)	27.5 (10.1)	4.6 (0.3)
Tamarack	Intolerant	Facultative wetland	Container (60 cm^3)	44.9 (2.0)	4.7 (0.2)
Black spruce	Tolerant	Facultative wetland	Container (90 cm^3)	45.3 (1.7)	4.4 (0.1)
Balsam poplar	Intolerant	Facultative wetland	Container (164 cm^3)	50.8 (2.8)	5.0 (0.3)
Eastern cottonwood	Intolerant	Facultative	Bare root (1 + 0)	60.7 (3.3)	5.7 (0.3)
Northern white cedar	Tolerant	Facultative wetland	Container (60 cm^3)	24.2 (1.9)	3.3 (0.2)
American elm	Intermediate	Facultative wetland	Container (1890 cm^3)	103.0 (3.3)	11.2 (0.3)
Yellow birch	Intermediate	Facultative	Container (90 cm^3)	21.8 (0.6)	3.4 (0.6)
Trembling aspen	Intolerant	Facultative	Container (90 cm^3)	21.0 (0.4)	3.1 (0.1)
Hackberry	Tolerant	Facultative	Container (336 cm^3)	37.4 (2.1)	4.6 (0.2)
Swamp white oak	Intermediate	Facultative wetland	Bare root (1 + 0)	33.5 (1.5)	5.3 (0.2)
Manchurian ash	Intermediate[5]	Unknown	Bare root (3 + 0)	68.3 (2.5)	9.8 (0.3)

[1] From USDA, NRCS (2020) and Baker (1949).
[2] Stock type: values in parentheses correspond to container volume or number of years spent in nursery and transplant beds for bare root stock.
[3] Mean (±1 standard deviation) height and diameter measurements were taken at the start of the growth study period in fall 2013.
[4] For red maple, stock type on each planting plot was a mixture of containerized and bare root seedlings.
[5] Kim et al. (2010).

with this ecosystem, but it was also influenced by availability of planting stock from local and regional nurseries. For example, silver maple (*Acer saccharinum*) ranked high as a species to evaluate, but seedlings for the species were not widely available at the time of planting. Nine of the selected species are native to black ash wetlands including: red maple (*Acer rubrum)*, tamarack (*Larix laricina*), black spruce (*Picea mariana*), balsam poplar (*Populus balsamifera*), eastern cottonwood (*Populus deltoides*), northern white cedar, American elm, yellow birch *(Betula alleghaniensis*), and trembling aspen. The seed source for these species was local except for American elm, which came from stock bred for tolerance to Dutch elm disease (*Ophiostoma novo-ulmi*) through controlled pollination between surviving trees on the Chippewa National Forest and the Dutch elm disease tolerant 'Valley Forge' cultivar of American elm (Slavicek and Knight, 2012).

We planted two lowland hardwood species from the next southern climate zone in Minnesota, USA that are projected to have increased habitat suitability with climate warming (Iverson et al., 2016) including hackberry (*Celtis occidentalis*) and swamp white oak (*Quercus bicolor*). Both species have their northern range termini within 150–200 km south of the study area.

Finally, we planted Manchurian ash, a species with resistance to EAB in its native range (Rebek et al., 2008), which includes northeastern and northwestern China, northern Korea, the Far East of Russia, and northern Japan. In one study from northeastern China that examined Manchurian ash, mean temperature and precipitation were very similar to our study area, although mean elevation was nearly double (Zhang et al., 2010). We secured Chinese seed stock for Manchurian ash, obtained from a commercial nursery in Plains, Montana, USA, but we do not have details on the exact source of the seed within the range of the species. The 12 species differed in planting stock type and initial size, as well as wetland indicator status and shade tolerance (Table 1).

2.5. *Planting*

Six 0.04 ha (400 m^2) plots were established as planting areas within each of the 1.62 ha treatment stands. Plots were randomly placed in the uncut, girdle, and clearcut treatments, while in the group selection treatment, four plots were centered in canopy gaps and two were located in the unharvested matrix. A planting bar was used to plant eight rows of seedlings that were spaced 1.25 m apart within rows, with 2.5 m between rows. Most species were randomly allocated to locations within rows and planted on the closest favorable microsite, avoiding small micro-depressions that often hold water in the spring. Due to delayed availability, American elm and Manchurian ash were always located at the western ends of planting rows.

For all species except American elm (see below), 1536 seedlings were planted (8 seedlings per species per plot; 48 seedlings per species per treatment stand). One half the seedlings were planted in fall before harvest and one-half in the spring after harvest. Fall planting was included even though it is not a typical practice in the region because we were concerned about the potential for challenging planting conditions due to wet soils in the spring following harvesting; this proved not to be an issue. For American elm, only 384 seedlings were planted in the fall before harvest (2 seedlings per plot; 12 seedlings per treatment stand), with no spring planting due to a lack of planting stock at the time.

2.6. *Field measurements*

Seedlings were assessed for survival and measured for size after eight growing seasons. At that time, a seedling was considered alive if it had a living shoot, although in some cases this was a new shoot that sprouted after death of an initial shoot. Diameters were measured at the root collar, at the approximate soil surface, using digital calipers to obtain two perpendicular measurements, which were later averaged. Heights were measured from the soil surface to the tip of the tallest live shoot, following along the length of the stem.

2.7. *Analyses*

Seedlings alive after eight growing seasons were summarized for survival, size (see Appendix A), and growth by species and treatment, setting time zero to 2012, under the assumption that mortality before this date was due to planting shock more than treatment influence. As a consequence of this initial mortality and a smaller number of planted American elm, our survival and growth data were imbalanced. For those species that were planted in both fall 2011 and spring 2012, the seedlings were pooled for analysis, since after 8 growing seasons there was little appreciable difference in responses between the planting times. Moreover, for all analyses we pooled blocks classified as wet and very wet ash forest, as preliminary analysis (not shown) indicated no consistent differences between the two types in any response variable.

2.7.1. *Survival*

Binomial survival data were analyzed using a split-plot design, with overstory treatments (the mixed whole-plot factor) nested within the random effect of block. Species (the fixed split-plot factor) were planted within the 0.04 ha plots, nested within overstory treatments. This arrangement differed from a traditional split-plot design in that species were replicated both across and within the 0.04 sample plots, providing added statistical power for testing a species effect on survival. In addition to the main effects of treatment and species, we included the treatment × species interaction in modeling. The near-to-complete mortality of cottonwood, trembling aspen, yellow birch, and northern-white cedar in certain treatments required that these species be omitted from the survival analysis.

The null model was that survival varied as a function of random effects, including block ($N = 8$), treatment nested within block ($N = 32$), and plot ($N = 196$). Alternative models iteratively included the effects of treatment, species, and their interaction. We compared alternative models using corrected Akaike's Information Criterion (Sugiura, 1978; Burnham and Anderson, 2002). Our criteria for considering models plausible were a) ΔAICc ≤ 6 of the best-approximating model, and b) lower AIC compared to nested models (Richards, 2008; Grueber et al., 2011). If models were within 2 AICc, we interpreted the less complex model (Burnham and Anderson, 2002). We considered all models meeting the criteria to warrant inference (Richards, 2008). We also report F and p statistics but relied upon AICc results for selecting the best model.

We modeled discrete survival with a binomial error distribution and a cumulative log–log function. Compared to the more common logit or probit link functions, the cumulative log–log link performs well when events, such as mortality, are highly frequent (Zuur et al., 2009), as was the case for some species in our study. Because this link function is sensitive to the correct coding of outcomes, we recoded data so that seedling mortality was considered an event. We did not weight survival in the group selection treatments by aerial extent of groups vs. matrix (as we did with relative growth; see 2.7.2), as doing so resulted in poor model fit. Models were fit using maximum likelihood. We evaluated model assumptions and assessed model fit using simulated residuals plots (Hartig, 2018). We calculated the ratio of weights (evidence ratio) to intuitively quantify the relative support for the best-approximating model compared to alternative plausible models (Burnham and Anderson, 2002). We calculated pseudo-R^2 statistics for binomial models (Nakagawa and Schielzeth, 2013). We used the glmmTMB package (Magnusson et al., 2018) in R (R Core Team, 2018) for all modeling, and the MuMIn package (Bartoń, 2017) for model comparisons and R^2 calculation. In the event of model support for a fixed factor, we calculated Tukey's post-hoc comparisons to facilitate interpretation with an $\alpha = 0.05$ (Lenth et al., 2020). We report seedling survival summarized to the level of overstory treatments nested within blocks ($N = 32$ for species, $N = 8$ for treatment, and $N = 8$ for species-within-treatment).

2.7.2. *Relative growth*

Diameter and height relative growth were compared among treatments and species. Only species with survivors in all or most replicates of at least three treatments were included. These tended to be species with higher survival overall; species with low survival were often missing from at least half the replicates in all treatments. We did include two species, balsam poplar and hackberry, that had survivors in only three and five replicates of one treatment respectively. For these, relative growth was set to zero to maintain a balanced design.

We used relative growth rate to compensate for large differences among species in initial size (Table 1), which would bias comparison of absolute growth rates (Hunt and Cornelissen, 1997). Relative growth rates were calculated as the difference between mean natural logarithm of sizes after eight growing seasons (Appendix A) and size at planting (Table 1), divided by the time interval (following Burdon and Harper, 1980). 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). For the group selection treatment, a weighted mean was calculated for each species in a replicate stand by first averaging growth rates in matrix plots and gap plots separately, then weighting the two means by the proportional area of each condition (0.80 matrix, 0.20 gap), then adding the two values to get the weighted replicate mean.

Analyses were run with a split-plot, randomized complete block analysis of variance, with blocks as the random factor, treatment the fixed main plot factor, and species the fixed split-plot factor. After checking assumptions of normality of residuals and homogeneity of variances, the ANOVAS were run on log-transformed data. If main effects or interactions were significant ($p \leq 0.05$), we used Tukey's HSD for comparisons.

2.7.3. *Integrating survival and growth*

We used a ranking procedure to derive an ordinal metric of performance that integrated survival and growth of treatments and species and generally reflects response to resource environment. For each species individually, we ranked its survival and relative diameter growth among the four treatments from highest (4) to lowest (1). We used relative diameter growth rather than relative height growth because the latter is often influenced by factors other than resource availability, including density, browsing, and tip dieback. The two scores were summed for each species in the treatment; the sum could range from 8 (both survival and growth were highest in the treatment) to 2 (both survival and growth were lowest in the treatment). The species summed scores were then totaled for the treatment, resulting in a number that allowed an ordinal comparison of overall performance among the four treatments.

3. Results

3.1. *Survival*

The best-approximating model of study-wide survival included species, treatment, and the interaction between these factors ($R^2 = 0.30$, evidence ratio = 1). Under this model, the treatment × species interaction ($F = 22.7$, $p < 0.001$), species main effect ($F = 21.2$, $p < 0.001$), and treatment main effect were significant ($F = 14.6$, $p < 0.001$) under conventional null hypothesis significance testing. No other models met our criteria for plausibility ($AICc \geq 6$).

Mean survival was similar among the uncut, girdle, and group selection treatments, while somewhat lower in the clearcut treatment (Fig. 2); only the clearcut and group selection treatment were significantly different from each other. While the overall species effect was significant, the pattern of species survival did vary somewhat among treatments, as reflected in the significant species × treatment interaction, which we focus on below.

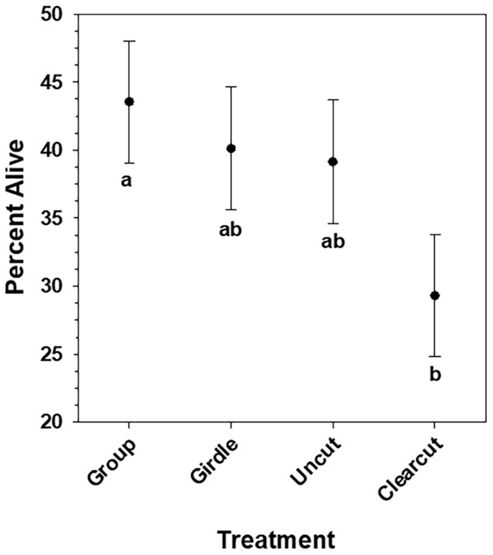

Fig. 2. Planted seedling survival after eight growing seasons by treatment. Value are adjusted means ± standard error (n = 8). Means joined by the same lower-case letters were not significantly different based on Tukey's HSD contrasts ($p \leq 0.05$). Tukey's HSD contrasts are based on adjusted means, correcting for initial imbalances in sample sizes.

The clearcut treatment (Fig. 3a) had the greatest contrasts in individual species survival, relative to the other treatments, but variability was generally high, with only a few significant differences between species. Survival in the clearcut treatment was highest for American elm (55.7 ± 7.6%) and swamp white oak (50.5 ± 4.8%), followed by balsam poplar (32.9 ± 5.0%), tamarack (32.3 ± 7.2%), Manchurian ash (30.4 ± 4.9%), black spruce (20.4 ± 5.9%), red maple (16.0 ± 4.6%), and hackberry (5.1 ± 2.4%). The remaining species, including trembling aspen, eastern cottonwood, northern white-cedar, and yellow birch, had low survival (generally below 5%) and small sample size, so were excluded from the analysis.

Within the girdle treatment (Fig. 3b), American elm (81.4 ± 4.3%) survival was significantly higher than all other species. Swamp white oak (62.0 ± 4.3%) had similar survival as Manchurian ash (57.8 ± 4.5%) and both were significantly higher than all the remaining species. Survival of hackberry (41.0 ± 5.1%) and red maple (33.7 ± 5.5%) were similar and both were significantly higher than the remaining species, including balsam poplar (14.5 ± 3.9%), black spruce (13.6 ± 4.0%), and tamarack (8.9 ± 4.0%), which were not significantly different from each other. The remaining species all had low survival (below 5%) and small sample sizes and were omitted from the analysis.

In the group selection treatment (Fig. 3c), American elm (81.4 ± 4.4%) and swamp white oak (72.6 ± 3.5%) had similarly high survival and both were significantly higher than all the remaining species. These species were followed by hackberry (43.3 ± 5.2%) and red maple (43.2 ± 5.5%), which were significantly higher than all remaining species, except tamarack (27.7 ± 6.0%). The latter was not significantly different from Manchurian ash (27.9 ± 4.8%), balsam poplar (21.9 ± 4.5%), or black spruce (13.9 ± 4.2%). As in the previous treatments, the remaining species had low survival and small sample size and were not included in the analysis.

Finally, in the uncut treatment (Fig. 3d), American elm (81.4 ± 4.4%) and swamp white oak (79.2 ± 3.0%) had highest mean survival and were not significantly different from each other, but were significantly higher than all remaining species. Hackberry (62.7 ± 4.3%) had the next highest survival and was significantly different from all the remaining species. Red maple (41.8 ± 5.4%) had the next highest survival and was significantly different that all remaining species. Manchurian ash (21.5 ± 4.4%) and tamarack (10.8 ± 4.3%) did not differ from each other, but ash was significantly higher than remaining species, including black spruce (7.9 ± 3.0%) and balsam poplar (2.9 ±

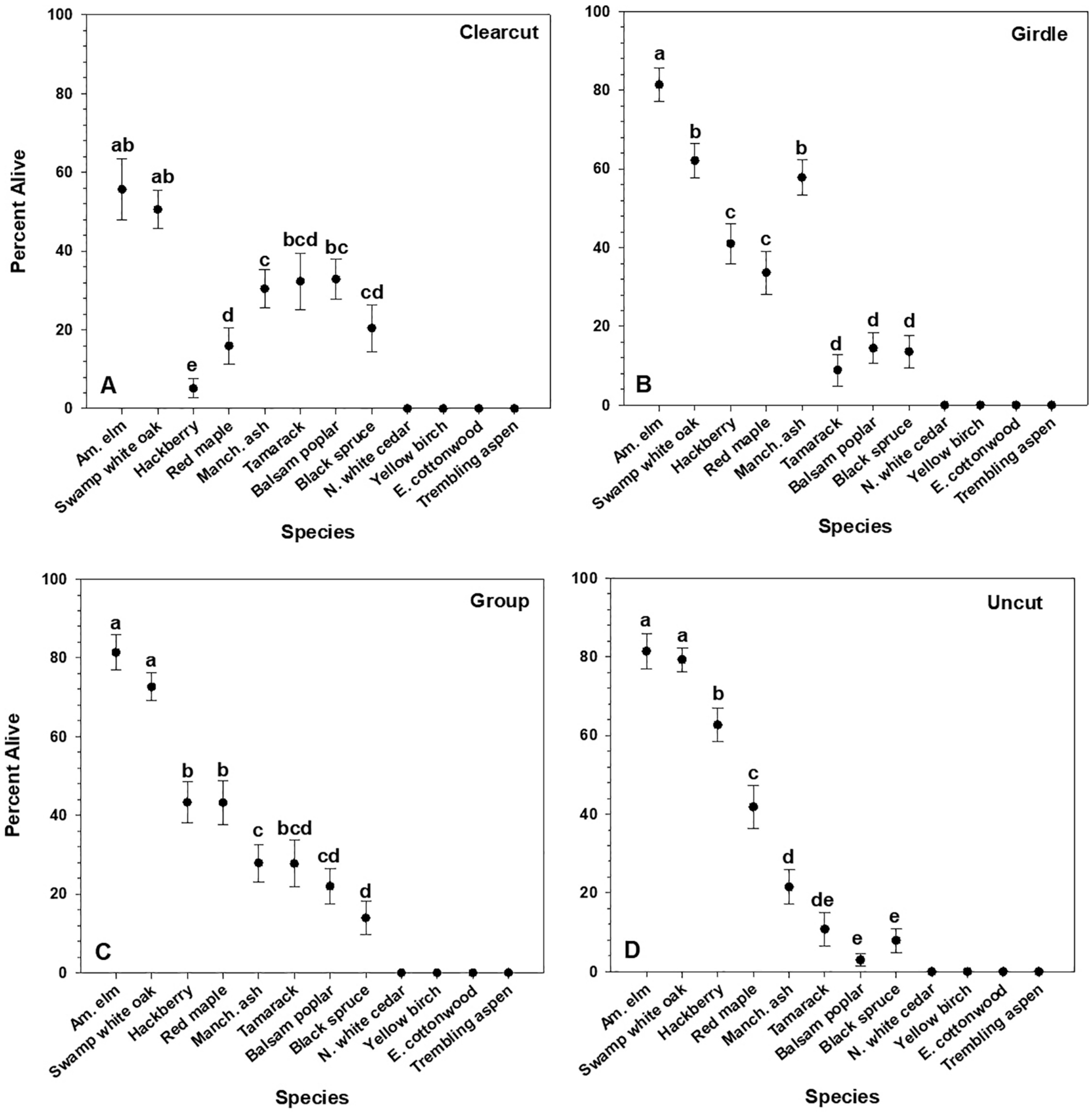

Fig. 3. Planted seedling survival after eight growing seasons by treatment and species. Values are adjusted means ± standard error (n = 8). Within each treatment, means joined by the same lower-case letters were not significantly different based on Tukey's HSD contrasts ($p \leq 0.05$). Tukey's HSD results are based on adjusted means, correcting for initial imbalances in sample sizes. Species without a value in the figure had low survival and low replication and were not included in the analysis.

1.6%), but tamarack did not differ from these latter two species. The remaining species, including northern white-cedar, yellow birch, trembling aspen, and eastern cottonwood, all had very low survival and were not compared statistically due to small sample size.

3.2. Relative growth rate

Species included in analysis of relative diameter growth (RDG) and relative height growth (RHG) rates included American elm, swamp white oak, hackberry, Manchurian ash, red maple and balsam poplar. For both RDG and RHG respectively, treatment ($F = 35.5$, 13.1; $p < 0.0001$), species ($F = 87.0$, 61.5; $p < 0.0001$), and their interaction ($F = 11.7$, 8.0; $p < 0.0001$) were significant.

Overall, the group selection treatment had the highest mean RDG and RHG, followed by the clearcut and girdling treatments, which had comparable growth, while mean RDG and RHG in the uncut treatment were lowest (Fig. 4). While there was an overall species effect, we focus below on comparisons of species within each treatment, given the significant interaction term.

Diameter and height relative growth rates were significantly higher for balsam poplar than all other species in the clearcut, girdle, and group selection treatments, while the species had low growth rates in the uncut treatment (Figs. 5 and 6). In the clearcut treatment, diameter and height RGRs were low for all other species included in the analyses and often not significantly different from each other (Figs. 5 and 6). In both the girdle and group selection treatments, diameter and height RGRs of swamp white oak and red maple were similar to each other and often significantly higher than American elm, hackberry, and Manchurian ash (Figs. 5 and 6), which generally were not significantly different from each other. The exception was Manchurian ash RHG in the group treatment, which was negative due to shoot dieback, likely from cold exposure. Finally, in the uncut forest, there were some significant

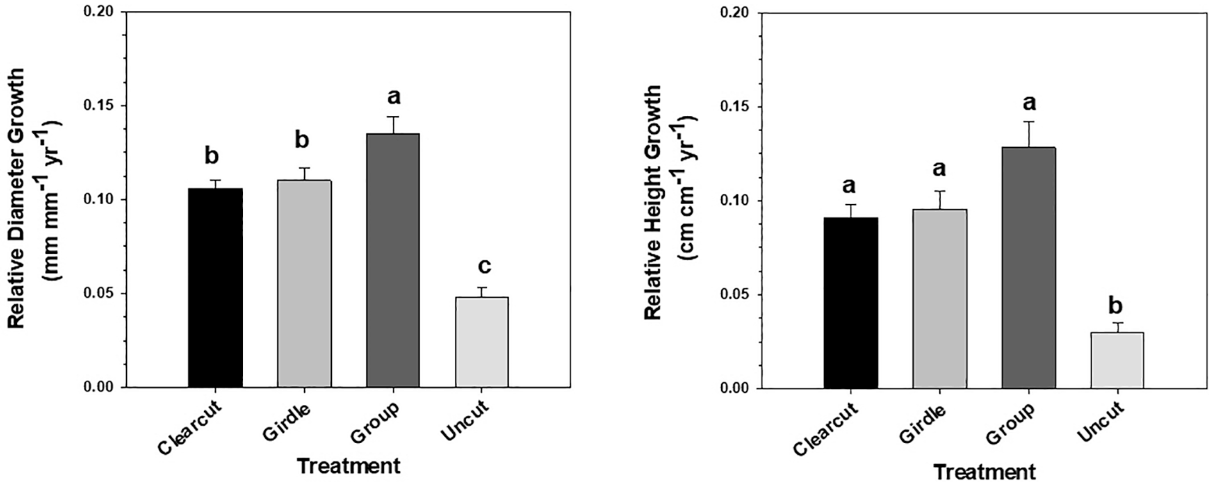

Fig. 4. Relative diameter and height growth rates over eight growing seasons by treatment. Values are means ± standard error (n = 8). Bars with the same lower-case letters were not significantly different based on Tukey's HSD contrasts ($p \leq 0.05$).

differences among species in RDG and RHG, notably negative mean height growth of Manchurian ash, but largely both RDG and RHG were low similarly among species (Figs. 5 and 6).

3.3. *Integrating survival and growth*

Our ordinal ranking of performance that integrated survival and relative diameter growth rate (RDG) was based on the six species we identified as having generally higher survival, including American elm, swamp white oak, hackberry, red maple, Manchurian ash, and balsam poplar (Table 2). At the treatment level, the summed integrated scores (sum of column C within each treatment) indicated that the overall best performance was associated with the group selection treatment, followed by the girdle, clearcut, and uncut treatments, respectively. The group selection score reflected both high summed survival (sum of column A) and growth (sum of column B) compared to the other treatments, although the summed survival score was nearly the same as in the uncut treatment.

At the species level, four of the six species had their highest integrated score (column C value for each species) in the group selection treatment, including swamp white oak, hackberry, red maple, and American elm, while the high score for balsam poplar was shared by both the group selection and clearcut treatments. Manchurian ash had high scores in both the clearcut and girdle treatments. While the uncut treatment had the lowest summed integrated score (sum of column C), two species had their highest survival ranking in the treatment, including swamp white oak and hackberry (column A score for each species in the treatment).

4. Discussion

Our motivation for examining planted tree survival and growth in this study is the expectation that black ash may be lost from the regional landscape due to emerald ash borer (EAB), at least from the standpoint of reaching reproductive maturity, although it may persist through stump sprouting (Aubin et al., 2015). Moreover, regionally there is limited potential for replacement by existing co-occurring species (Palik et al., 2012, 2021). Identifying which species and which silvicultural approach results in the best combinations of survival and growth of planted trees is needed to offer guidance on how to maintain black ash wetlands in a forested condition (D'Amato et al., 2018).

4.1. *Survival*

We expected survival after eight growing seasons to parallel third-year results (Looney et al., 2015), specifically that overall survival would be lowest in the clearcut treatment and similar in the girdle, group selection, and uncut forest treatments. This expectation was confirmed, although only the clearcut and group selection treatments were significantly different from each other by the eighth year. With some exceptions, most species also had their lowest survival in the clearcut treatment, although our analytical approach did not allow a direct statistical comparison among treatments for individual species. The exceptions to lowest survival in the clearcut treatment included balsam poplar and tamarack, both species that are rated as intolerant of shade (Burns and Honkala, 1990a,b). Accordingly, these species had lowest survival in the uncut treatment.

The lower overall survival in the clearcut treatment likely reflects the dramatic changes in hydrology and herbaceous plant communities that result in challenging competitive and environmental conditions for tree seedlings (Looney et al., 2015). After clearcutting in our study, and even after selective cutting of only black ash in other studies (Van Grinsven et al., 2017), water tables were nearer the surface for longer periods of the growing season compared to the uncut forest and the group selection treatment (Slesak et al., 2014; Diamond et al., 2018). Excessive soil moisture likely inhibits plant growth by creating anoxic conditions for roots (Trettin et al., 1995). Moreover, there was greater herbaceous growth in the clearcut treatment (Looney et al., 2017b), a response also found in a study in Michigan, USA that removed only black ash (Davis et al., 2017). In our study, and similarly in others (Van Grinsven et al., 2017; Davis et al., 2017), hydrologic and herbaceous responses in the girdle treatment became similar to those in the clearcut treatment, although slightly delayed because of protracted mortality of girdled black ash. Given that overall survival in the girdle treatment was not as low as in the clearcut, this suggests that planted seedlings are now established in the girdle treatment and have not been impacted to the same degree by the changing hydrologic and competitive conditions.

We also expected, based on third-year results, that species projected to be future-climate adapted would have equal or superior survival as southern boreal species that are native to black ash ecosystems. This expectation was confirmed, with highest survival in most treatments for American elm, swamp white oak, hackberry, and red maple. Other studies in the region have also found high survival for at least some of these same species in black ash wetlands (Bolton et al., 2018). All four of these species are predicted to have increasingly favorable habitat in the study region with a warming climate (Iverson et al., 2016). In fact, mean

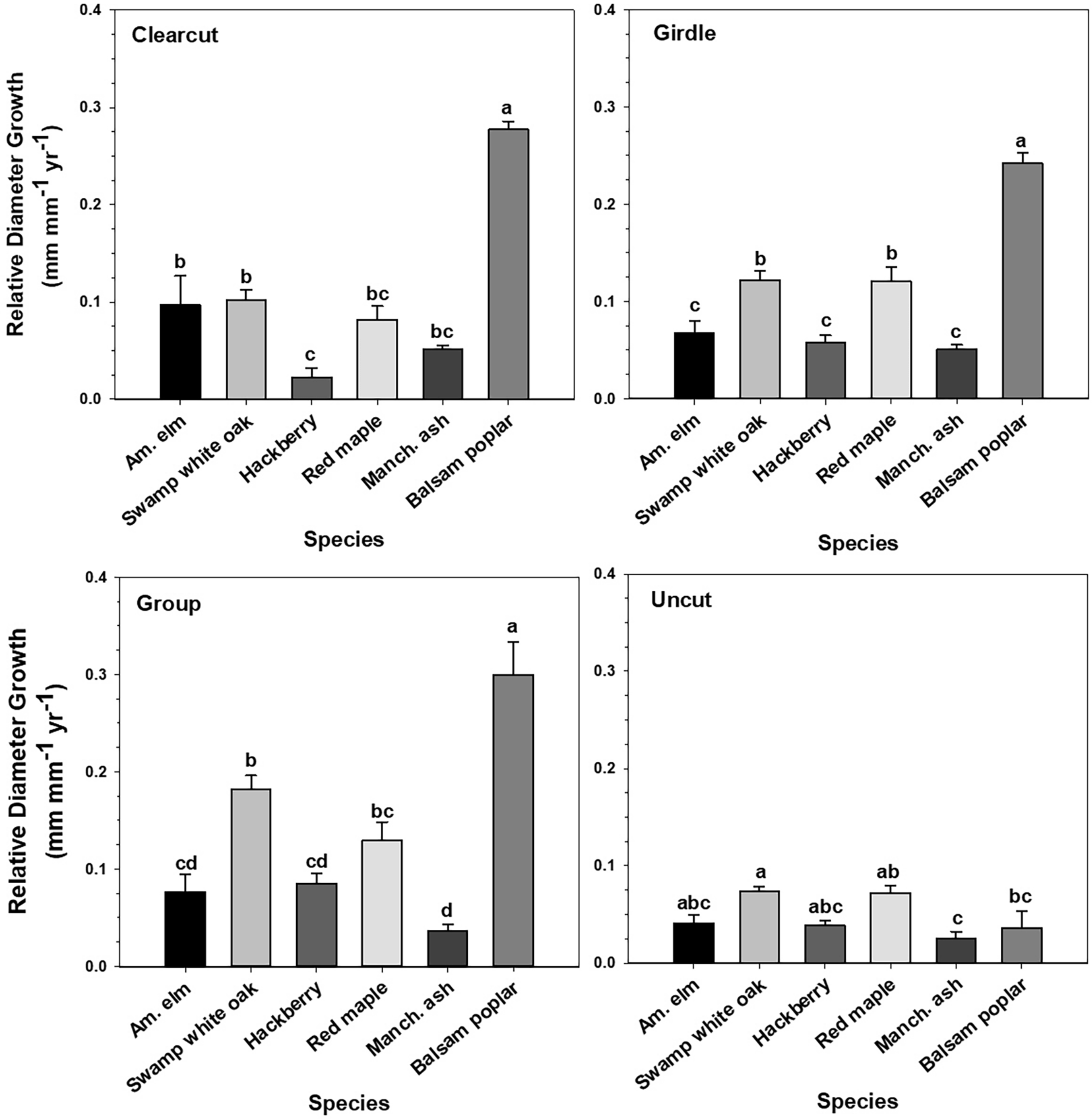

Fig. 5. Relative diameter growth over eight growing seasons of tree seedlings comparing species within treatments. Values are means ± standard error (n = 8). Bars within a treatment with the same lower-case letters were not significantly different (Tukey's HSD, p ≤ 0.05).

annual temperature of the study region has already increased at least 1.2 °C over the last 100 + years (Handler et al., 2014), with more recent assessments reporting an even larger increase of 2.0 °C; the increase likely already favors these more southerly distributed species. American elm and swamp white oak also are facultative wetland species (Table 1), which also likely reflects their adaptation to conditions in black ash lowland forests.

American elm and red maple are native components of black ash ecosystems in the region, while swamp white oak and hackberry have the northern termini of their distribution approximately 150–200 km to the southeast (Burns and Honkala, 1990b), but appear, in terms of survival, to be candidates for assisted migration (e.g., Pedlar et al., 2012). A caveat to high survival of American elm is that planting stock for this species was larger than all other species, including diameter, height and volume, and likely older than the 2–3 years that is typical of seedlings used in reforestation. Others have noted that larger planting stock likely conveys a survival advantage to seedlings planted in black ash wetlands (Bolton et al., 2018). In contrast, the other species with high survival on our study, swamp white oak, hackberry, and red maple, where no larger, and sometimes smaller, than species with lower survival, so their responses were apparently unrelated to size of planting stock.

4.2. *Growth*

We expected that growth rates would be highest in the clearcut treatment, both overall and for most species, due to a more favorable light environment, followed in order by the girdle, group selection, and uncut treatments, reflecting a gradient of decreasing light availability (Looney et al., 2017a). This expectation was not confirmed, which differed from the third-year results (Looney et al., 2017a). Rather, we found that both diameter and height relative growth rates overall were highest in the group selection treatment, followed by the girdle and clearcut treatments, although the differences were only significant for

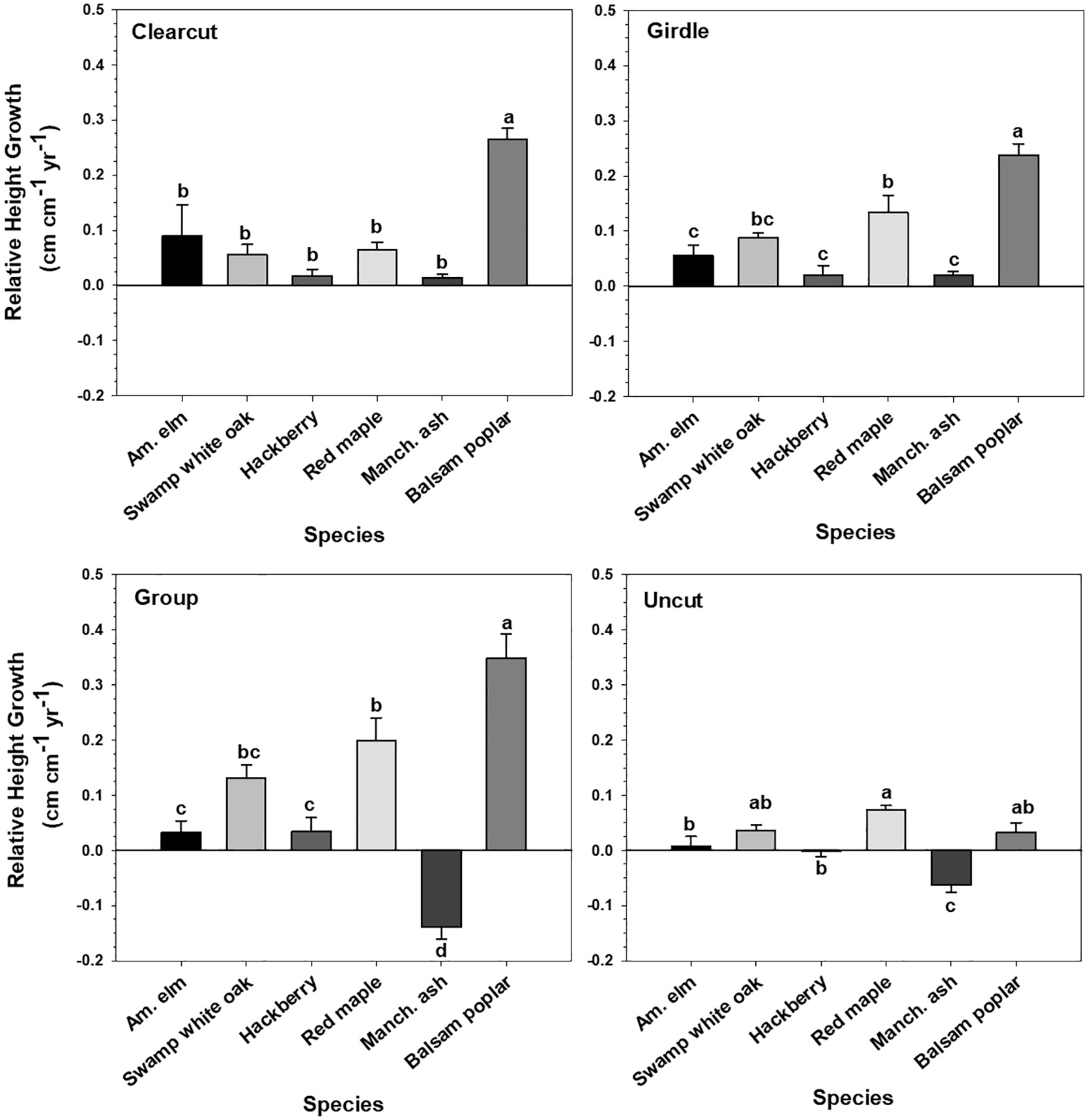

Fig. 6. Relative height growth rates over eight growing seasons of planted tree seedlings compared within treatments. Values are means ± standard error (n = 8). Bars with the same lower-case letters were not significantly different (Tukey's HSD, $p \leq 0.05$).

diameter growth. Growth in all three of these treatments was significantly higher than the uncut treatment.

Of the six species analyzed for growth rates, four had their highest diameter and height growth rates in the group selection treatment, although sometimes only marginally higher than another treatment, including swamp white oak, hackberry, red maple, and balsam poplar. We hypothesize that over eight years, growth in the more open clearcut treatment, and eventually in the girdle treatment, may be inhibited by a higher water table, compared to the group selection treatment, which has a hydrologic regime that largely tracked that of the uncut forest (Diamond et al., 2018). Herbaceous and shrub competition may also increasingly impact seedling growth in the more open clearcut and girdle treatments. By 2015, clearcuts had distinctly higher cover of graminoids, especially bluejoint (*Calamagrostis canadensis*; Looney et al., 2017b).

4.3. *Integrating survival and growth*

Ultimately, success of tree regeneration is a function of both survival and growth. Determining which species and silvicultural approach are most promising for adapting black ash wetlands to non-EAB host tree species requires an ongoing assessment that integrates these metrics. Our integrated metric of performance based on ordinal ranking of survival and relative diameter growth rate indicates that the group selection treatment had the best overall performance, with four of six species having their best integrated performance in the treatment. The group selection treatment was followed by the girdle treatment, then the clearcut, and lastly the uncut forest. As noted below, the performance responses for treatments, and their ranking compared to each other, often reflect differing patterns of survival and growth among the treatments.

The group selection response was largely the result of several species having moderate to high rankings for survival, combined with high

Table 2

Ordinal ranking of species among treatments from high to low (4 to 1) based on survival and relative diameter growth (RDG). Each species is ranked independently, separately for survival and growth, from highest to lowest value among the four treatments.

	Clearcut			Girdle		
	A Survival	B RDG	C Sum	A Survival	B RDG	C Sum
American elm[1]	1	4	**5**	3	2	**5**
Swamp white oak	1	2	**3**	2	3	**5**
Hackberry	1	1	**2**	2	3	**5**
Red maple	1	2	**3**	2	3	**5**
Manchurian ash	3	4	**7**	4	3	**7**
Balsam poplar	4	3	**7**	2	2	**4**
Sum	**11**	**16**	**27**	**15**	**16**	**31**
	Group Selection			Uncut		
	A Survival	B RDG	C Sum	A Survival	B RDG	C Sum
American elm	3	3	**6**	3	1	**4**
Swamp white oak	3	4	**7**	4	1	**5**
Hackberry	3	4	**7**	4	2	**6**
Red maple	4	4	**8**	3	1	**4**
Manchurian ash	2	2	**4**	1	1	**2**
Balsam poplar	3	4	**7**	1	1	**2**
Sum	**18**	**21**	**39**	**16**	**7**	**23**

[1] Note that American elm had identical survival in three or the four treatments, so its ranking was averaged for these.

rankings of growth. The uncut forest had a nearly identical overall survival score, however, not surprisingly, growth was generally ranked low for all species in the uncut forest, likely reflecting the low light availability in the treatment (Looney et al., 2017a).

It is likely that differing patterns of integrated survival and growth among the four treatments reflect both competition for resources between the planted seedlings and neighboring vegetation, as well as facilitation of seedlings through amelioration of harsh environmental conditions by this same vegetation (Montgomery et al., 2010; Wright et al., 2014). The clearcut treatment, while providing a high light environment (Looney et al., 2017a) that should favor growth, may also present challenging competitive and environmental conditions that may lower survival. Reduced survival may result from increased height of herbaceous vegetation (Looney et al., 2017b) and the substantial and ongoing rise in water table and delay in drawdown in the treatment (Slesak et al., 2014; Diamond et al., 2018).

In contrast, the uncut treatment, while having relatively lower light availability compared to the other treatments, which likely reduces growth, had an unaltered hydrologic regime that included water tables falling earlier and to greater depths during growing season (Diamond et al., 2018), minimizing the development of anoxic soil conditions. Thus, while having lower light availability, the treatment was less hydrologically stressful for seedlings. Moreover, leaf area in black ash wetland forests is considerably lower than most other forest ecosystems (LAI = 2.1–2-5; Telander et al., 2015), which may have allowed a higher level of light reaching understory seedlings than typically observed in uncut forest systems.

The girdle treatment (i.e., emulation of EAB) developed hydrological conditions similar to the clearcut over several years, that is, water tables were at or above the surface for longer periods of time during the growing season (Diamond et al., 2018). A similar response has been noted in other studies of black ash wetlands after girdling (Van Grinsven et al., 2017). While the treatment did not have an exceptionally good survival score, it was higher than in the clearcut treatment, likely reflecting the delay in hydrologic change as girdled black ash trees died over three to four years. This coupled with eventual higher light availability likely resulted in moderate rankings of growth for several species. The lack of ground disturbance from harvest machinery in the girdle treatment could also have influenced regeneration dynamics (Roberts, 2007). However, hydrology and light are more plausible drivers of seedling performance given that winter harvesting minimized soil impacts.

Finally, the group selection treatment included positive aspects of several of the other treatments that likely contributed to its overall highest performance ranking. Post-harvest hydrology with group selection has largely been unchanged from the uncut forest (Slesak et al., 2014; Diamond et al., 2018), thus the inhibitive impacts of a higher water table on survival are avoided. While light availability was not as high stand-wide as in the clearcut, it was still significantly higher than in the uncut forest (Looney et al., 2017a), resulting in moderate to high growth rankings.

5. Management implications

There is a growing sense of urgency in the western Great Lakes region of North America to work proactively to establish site appropriate tree species through silvicultural treatment before widespread loss of black ash from EAB and degradation into non-forested conditions (D'Amato et al., 2018; Diamond et al., 2018). The problem is particularly acute given the foundational-species role black ash plays in these ecosystems (Youngquist et al., 2017) and the accumulating evidence for insufficient abundance of co-occurring woody species to replace black ash naturally after mortality from EAB (Palik et al., 2012, 2021).

Our results point to group selection as an appropriate regeneration system to use in the transition to non-EAB host tree species. Group selection has several advantages over clearcutting or a no-cutting approach. First, it emulates the natural gap-based disturbance regime of this ecosystem (D'Amato et al., 2018), which may help sustain other biotic components of the forest that depend on this dynamic. Second, at least at the level of removal we examined, group selection prevents hydrologic alteration that results from loss of transpiration (Diamond et al., 2018) and thus avoids inhibitive anoxic soil conditions. Finally, group selection provides focused high-light neighborhoods in a treated stand, with increased growth of tree reproduction in and near these openings. Unfortunately, it still may prove challenging to transition approximately 500,000 ha of this ecosystem in northern Minnesota, USA to non-EAB host species using group selection prior to EAB arrival.

Our results also point to several species of trees that may be established successfully using a group selection regeneration system, notably red maple, balsam poplar, hackberry, and swamp white oak. The first two species are native to the ecosystem; both may be suitable choices for regeneration, although balsam poplar habitat suitability is expected to decline substantially with climate change (Iverson et al., 2016), making its long-term viability questionable. Hackberry and swamp white oak are predicted to have increasing habitat suitability in the study region (Iverson et al., 2016) and, in fact, based on our results, conditions may already be suitable for these species. American elm is also a native component of black ash wetlands and likely was more abundant prior to Dutch elm disease (Barnes, 1976); disease tolerant cultivars may be a viable choice for replacement of black ash. The American elm cultivar we used did have poor relative height growth resulting from top dieback from winter exposure; other cultivars may be better suited to current winter conditions (Jim Slavicek, personal communication).

We were restricted by the range of stock types and species that were available for us to evaluate, since regional nurseries do not produce many species for wetland settings. As such, future operational-scale application of "adaptation plantings" such as those examined in this study, will require refocusing of nursery production towards species with the potential to maintain critical functional roles in black ash wetland ecosystems.

Our focus on potential replacement tree species in black ash wetlands can have wider relevance to thinking about management actions in other ecosystems facing threats from invasive pests, such as forests of eastern USA where the introduced hemlock woolly adelgid (*Adelges tsugae*) has removed eastern hemlock (*Tsuga canadensis* (L.) Carrière), resulting in changes to ecosystem structure and function (Ellison et al., 2005). In reality, it will be increasingly difficult to stop threats to foundational tree species, suggesting that active management to establish replacement species so as to provide continuity of function will become a recurrent management goal.

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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CRediT authorship contribution statement

B.J.P., A.W.D., R A.S. co-designed the project, organized fieldwork, and supervised data interpretation, and analysis and co-wrote the majority of the manuscript. D.K. identified sites and established the harvest layout. D.K. and J.K. conducted the field work and data summarization. C.L. conducted the survival analysis and wrote the corresponding sections of the manuscript. All authors reviewed and edited the final manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.118958.

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