Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened Fraxinus nigra forests in Minnesota, USA

Christopher E. Looney, Anthony W. D'Amato, Brian J. Palik, and Robert A. Slesak

Abstract: Fraxinus nigra Marsh. (black ash) wetland forests in northern Minnesota, USA, are threatened by the invasive insect, emerald ash borer (Agrilus planipennis Fairmaire (EAB)). A potential management option is promoting regeneration of tree species that are not EAB hosts to maintain ecosystem functions. Using an operational-scale field experiment, we examined the survival of 12 alternative tree species in response to different canopy treatments. We planted the seedlings in 1.6 ha plots assigned to four replicated canopy treatments: untreated control, group selection (0.04 ha gaps, 20% of stand), black ash girdling to emulate EAB-induced mortality, and clearcut. Fall and spring plantings were used to compare the effects of spring ponding. Control (32.9%), group selection (34.5%), and girdling (33.3%) treatments had comparable overall seedling survival. Survival in the clear-cut treatments was significantly lower (22%). Species selection, overstory treatment, and season of planting together resulted in survival rates ranging from 0.08% to 94.1%. Conifer species had low overall rates of survival (10.7%), whereas some species with native ranges not presently overlapping with northern F. nigra forests, e.g., Quercus bicolor Willd. (75.5%), had high survival rates. If growth is light-limited, group selection may be effective in promoting recruitment and supporting a larger variety of species.

Key words: Fraxinus nigra, emerald ash borer, alternative tree species, artificial regeneration, canopy treatments.

Introduction

Fraxinus nigra Marsh. (black ash) wetland forests in northern Minnesota, USA, are threatened by the introduced Asian insect, emerald ash borer (Agrilus planipennis Fairmaire (EAB); Pugh et al. 2011). First detected in southern Michigan in 2002, EAB has caused high mortality in Fraxinus populations in other areas of the Great Lakes region (Pugh et al. 2011). Control methods are constrained by lack of EAB resistance in North American Fraxinus spp. (Poland and McCullough 2006). Insecticides are effective but restricted to high-value urban trees, whereas wildland management, to date, has focused without success on quarantine to slow the pace of invasion (Poland and McCullough 2006).

Tolerant of heavily saturated soils and seasonal ponding, F. nigra serves as a foundation species in northeastern Minnesota’s expansive wetland forests (Telander et al. 2015). In other locations in North America, F. nigra occurs in heavily inundated swamp forests (Cohen et al. 2014), poorly drained depressions (Scott 1995), and as an associated species in upland mixed-hardwood forests (Erdmann et al. 1987). As a foundation species in Minnesota, F. nigra plays an important role in regulating ecosystem processes by lowering water tables in summer through evapotranspiration (Telander et al. 2015). In this way, it aids the survival of associated tree species, while allowing a mixture of facultative and obligate wetland species to exist in the herbaceous understory (Lenhart et al. 2012). Fraxinus nigra forests support a wide variety of under-
story plant species and provide important habitat for large and small mammals, birds, amphibians, reptiles, and arthropods (Guckler 2005). _Fraxinus nigra_ is culturally and economically important to northern Minnesota Native American tribes, who use its wood to weave their traditional baskets (Benedict and Freilich 2008).

Kashian and Witter (2011) suggest that ash regeneration in southern Michigan’s upland, mixed-F. nigra forests appears sufficient to offset EAB-related _F. nigra_ mortality, but post-EAB regeneration in _F. nigra_ dominated wetland forests may be considerably lower due to hydrological changes from the loss of the black ash overstory (Palik et al. 2012). A study that examined the effects of logging on _F. nigra_ forests found that the loss of the overstory to clear-cutting raised the water table and promoted growth of the herbaceous layer at the expense of tree regeneration (Erdmann et al. 1987). Even assuming ample _F. nigra_ regeneration, it is uncertain whether the new trees will survive to maturity (Kashian and Witter 2011). On sites near the southern Michigan epicenter of the North American EAB invasion, _F. nigra_ and trees of other _Fraxinus_ spp. with a diameter ≥2.5 cm (1 in) experienced a greater growth rate than _F. nigra_ regeneration, resulting in larger trees with new forest after 10 years (Schuster et al. 2019). In contrast, _F. nigra_ regeneration was minimal in the same forests, suggesting that _F. nigra_ may not be as resilient to EAB as other species (Schuster et al. 2019).

The predicted northeastward shift in suitable habitat in response to climate change (Galatowitsch et al. 2009) suggests that assisted range expansion of _F. nigra_ should be explored as a means of sustaining ecosystem functions over the longer term (Pedlar et al. 2012). Forestry-related assisted range expansion, a variant form of assisted migration (see Williams and Dumroese (2013)), proposes the northern relocation of tree species from or within a few hundred kilometers of their current range limits (Pedlar et al. 2012). As such, it represents a potential tool for maintaining and protecting _F. nigra_ forests and increasing forest resilience to future climate change (Pedlar et al. 2012).

In the event of such a worst-case scenario, a possible management option is promoting increased regeneration of unsusceptible, alternative tree species to maintain forest cover and ecosystem functions (Slesak et al. 2014). Tree species often associated with _F. nigra_ in Minnesota include _Ulmus americana_ L. (American elm), _Acer rubrum_ L. (red maple), _Betula alleghaniensis_ Britton (yellow birch), _Thuja occidentalis_ L. (northern white cedar), _Larix laricina_ (Du Roi) K. Koch (tamarack), and _Picea mariana_ (Mill) Britton, Sterns & Poggenb. (black spruce) (Slesak et al. 2003). Although advance regeneration of tree species that are not EAB hosts in _F. nigra_ wetland forests is currently low, the potential for one or more non EAB host tree species to replace _F. nigra_ has not been adequately explored, and silvicultural approaches for facilitating this replacement have not been investigated.

Silvicultural strategies such as artificial regeneration and overstory treatments have been suggested to restore sites impacted by introduced disturbance agents (Dix et al. 2010). Overstory treatments can greatly enhance the potential for both natural and artificial regeneration success (Smith et al. 1997). For example, clearcuts may aid the establishment of shade-tolerant species, whereas group selection or shelterwood harvests can be used to make more subtle adjustments to the amount of light that reaches the forest floor, as well as to ameliorate changes in site hydrology (Slesak et al. 2014) and microclimate effects (Smith et al. 1997). Although experience with artificial regeneration in wetland forests has been limited to date, artificial regeneration combined with canopy treatment increased the recruitment of associated tree species in _Salix nigra_ Marsh (black willow) wetland forests, with species selection exerting a greater influence on regeneration success than canopy treatment type (Dulohery et al. 2000).

The design of strategies to mitigate the effects of EAB-induced mortality on _F. nigra_ ecosystems must take into account the uncertainties associated with climate change (Pedlar et al. 2012). If global emissions increases continue on their current path (Walsh et al. 2014), temperatures in northern Minnesota could rise by as much as 2.7 °C during the next half-century (Pryor et al. 2014), causing suitable climate locales for many tree species to shift 400–500 km NNE (Galatowitsch et al. 2009). Despite a projected slight increase in spring precipitation (Pryor et al. 2014), decreased summer rainfall and higher evapotranspiration rates would likely reduce wetland water budgets during the summer growing season (Galatowitsch et al. 2009), potentially benefitting less flood-tolerant _F. nigra_ associated tree species (MacFarlane and Meyer 2005).

The predicted northeastward shift in suitable habitat in response to climate change (Galatowitsch et al. 2009) suggests that assisted range expansion of wetland tree species should be explored as a means of sustaining ecosystem functions over the longer term (Pedlar et al. 2012). Forestry-related assisted range expansion, a variant form of assisted migration (see Williams and Dumroese (2013)), proposes the northern relocation of tree species to or within a few hundred kilometers of their current range limits (Pedlar et al. 2012). As such, it represents a potential tool for maintaining and protecting _F. nigra_ forests and increasing forest resilience to future climate change (Pedlar et al. 2012).

In terms of _F. nigra_ forests, assisted range expansion could both extend the potential pool of available tree species for maintaining post-EAB forest cover and promote tree species diversity to reduce risk from climate change and other forest threats (Pretzsch 2005).

With these considerations in mind, we used an operational-scale field experiment in _F. nigra_ wetlands to examine the survival of spring and fall plantings of 12 alternative tree species in response to four canopy treatments: uncut forest (control), girdling of all _F. nigra_ ≥ 6 cm diameter at breast height (DBH) to emulate EAB-induced mortality, group selection (0.64 ha gaps covering 20% of plot), and clear-cutting (1.6 ha patches). We used both spring and fall plantings to assess the effects of extensive spring ponding on seedling establishment. Our objectives were to determine (i) the survival response of planted seedlings to canopy manipulations and emulated EAB-induced mortality, and (ii) the most promising combination of species, overstory treatment, and planting season to inform diversification strategies.

**Materials and methods**

**Study sites and overstory treatments**

We investigated the survival of potential _F. nigra_ replacement species using an operational-scale field experiment set in _F. nigra_ wetlands in the Chipewa National Forest in northern Minnesota, USA (Fig. 1). The climate is continental, with 1981–2010 high temperatures averaging −8.9 and 25.4 °C in January and July, respectively (PRISM Climate Group 2015). Mean precipitation for the same period was 742 mm-year⁻¹, with the majority of precipitation occurring from May through September. Plant communities at the sites are classified as WFn55 (northern wet _Fraxinus_ swamp) grading into WFn64 (northern very wet _Fraxinus_ swamp), based on Minnesota native plant community classification (MNDNR 2003). Soil texture varies from loam and sandy loam derived from glacio-fluvial 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). Ponding occurs in the early part of the May to September growing season, with water tables typically declining below the ground surface by mid-July (Slesak et al. 2014). Water table fluctuations are largely dependent on precipitation (particularly snowmelt) and evapotranspiration, with only a very low absolute amount of shallow subsurface flow occurring (Slesak et al. 2014).

We divided the study area into eight experimental blocks based on preliminary observations of site moisture, proximity, and stand history. Most stands in blocks 1–6 were predominantly even aged, whereas blocks 7 and 8 had multi-aged structures (A.W. D’Amato and M. Reinikainen, unpublished data). Before treatment, basal area for trees >10.0 cm in diameter averaged 20.7 ± 2.2 m²·ha⁻¹, and mean tree density was 477 ± 50.6 trees·ha⁻¹.

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The predominant overstory species was *F. nigra*, which comprised 91% of basal area, with minor components of *U. americana*, *Tilia americana* L. (American basswood), *Abies balsamea* (L.) Mill. (balsam fir), *Populus tremuloides* Michx. (quaking aspen), and *Quercus macrocarpa* Michx. (bur oak).

Within each block, four 1.62 ha (radius, 71.8 m) circular plots were established, one of which was left as uncut forest to serve as a control, whereas each of the other plots received one of three treatments. To emulate EAB-induced tree mortality, which research suggests may not occur for several years after infestation depending on tree carbohydrate reserves (Knight et al. 2010), a girdling treatment was applied to all *F. nigra* ≥ 6 cm DBH. A group selection treatment, consisting of six 0.04 ha (400 m²) circular gaps totaling a cleared area of approximately 20% of the 1.62 ha plot, was installed to test the potential for promoting regeneration through partial overstory removal prior to EAB invasion while limiting the water table rise associated with clear-cutting (Erdmann et al. 1987). A clear-cut treatment, involving the removal of all trees, was installed to evaluate the effects of preemptive salvage logging. All treatments were implemented in late winter 2012 under frozen ground conditions.

**Artificial regeneration**

We investigated the potential success of the following nine co-occurring tree species native to *F. nigra* forests in northern Minnesota: *B. alleghaniensis*, *Populus balsamifera* L. (balsam poplar), *L. larticata*, *Populus deltoides* W. Bartram ex Marshall (eastern cottonwood), *P. tremuloides*, *T. occidentalis*, *T. americana*, *Acer rubrum* L. (red maple), and *U. americana* (MNDNR 2003). In addition, we investigated two species with generally more southerly ranges: *Celtis occidentalis* (hackberry), of which isolated populations presently occur in the study area, and *Quercus bicolor* Wild. (swamp white oak), whose northern range limit lies approximately 150 km SW of the study sites (Prasad et al. 2007) and that, like *F. nigra*, occurs as a dominant species in wetland forests in the northerly parts of its range. Finally, to test its ability to survive local site conditions, we included *Fraxinus mandshurica* Rupr. (Manchurian ash), an EAB-resistant East Asian species closely related phylogenetically to *F. nigra* (Whitehill et al. 2010). *Fraxinus mandshurica* was included at the suggestion of USFS resource managers and members of local Native American tribes, who rely on *F. nigra* for their traditional basketry (A.W. D’Amato, personal communication), as well as to inform ongoing efforts to hybridize Asian and North American *Fraxinus* spp. to produce EAB-resistant cultivars (Koch et al. 2012).

Seedlings of species other than *Q. bicolor*, *P. balsamifera*, *F. mandshurica*, and *U. americana* were planted both prior to winter harvesting in fall 2011 (late August to late September) and after harvesting in spring 2012 (May to mid-June) so as to compare the effects of planting season. Seedlings were planted before harvesting with the assumption of sufficient snowpack to protect them from mechanical damage during the harvest treatments. Due to logistical constraints, fall plantings of *Q. bicolor*, *P. balsamifera*, and *F. mandshurica* were delayed until after harvesting in 2012, whereas *U. americana* was planted in spring 2012 only. Container seedlings included fall-planted *A. rubrum*, as well as *B. alleghaniensis*, *C. occidentalis*, *L. larticata*, *P. mariana*, *P. balsamifera*, *P. tremuloides*, and *T. occidentalis*, whereas bare-root stock seedlings included spring-planted *A. rubrum*, *F. mandshurica*, *P. deltoides*, and *Q. bicolor* (Table 1). *Ulmus americana* seedlings came from stock bred for tolerance to Dutch elm disease (*Ophiostoma novo-ulmi* Brasier) through crossing local seed sources from the Chippewa National Forest.
with the “Valley Forge” cultivar of *U. americana*, which exhibits proven tolerance to the disease (Townsend et al. 2005). Because similarly sized stock was unavailable, *U. americana* seedlings were considerably larger in mean basal diameter, stem length, and container size than seedlings of other species (Table 1).

    Table 1. Mean basal diameter (± standard error (SE)), mean stem length (±SE), and stock type at planting for seedlings of 12 potential *Fraxinus nigra* replacement tree species, based on a random sample of 100 seedlings per species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean basal diameter (mm)</th>
<th>Mean stem length (cm)</th>
<th>Stock type</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acer rubrum</em></td>
<td>4.7 (0.17)</td>
<td>22.1 (1.13)</td>
<td>Container (90 cm³)</td>
</tr>
<tr>
<td><em>Betula alleghaniensis</em></td>
<td>3.4 (0.55)</td>
<td>21.8 (0.63)</td>
<td>Container (90 cm³)</td>
</tr>
<tr>
<td><em>Celtis occidentalis</em></td>
<td>5.1 (0.14)</td>
<td>44.7 (1.37)</td>
<td>Container (336 cm³)</td>
</tr>
<tr>
<td><em>Fraxinus mandschurica</em></td>
<td>9.1 (0.26)</td>
<td>78.7 (1.28)</td>
<td>Bareroot (3+0)</td>
</tr>
<tr>
<td><em>Larix laricina</em></td>
<td>3.9 (0.09)</td>
<td>28.5 (0.86)</td>
<td>Container (60 cm³)</td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td>3.9 (0.08)</td>
<td>42.4 (0.66)</td>
<td>Container (90 cm³)</td>
</tr>
<tr>
<td><em>Populus balsamifera</em></td>
<td>3.5 (0.08)</td>
<td>29.8 (0.73)</td>
<td>Container (164 cm³)</td>
</tr>
<tr>
<td><em>Populus deltoides</em></td>
<td>4.5 (0.13)</td>
<td>38.6 (1.18)</td>
<td>Bareroot (1+0)</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>3.1 (0.05)</td>
<td>21.0 (0.38)</td>
<td>Container (90 cm³)</td>
</tr>
<tr>
<td><em>Quercus bicolor</em></td>
<td>4.7 (0.13)</td>
<td>25.4 (0.64)</td>
<td>Bareroot (1+0)</td>
</tr>
<tr>
<td><em>Thuja occidentalis</em></td>
<td>2.6 (0.77)</td>
<td>23.2 (0.37)</td>
<td>Container (60 cm³)</td>
</tr>
<tr>
<td><em>Ulmus americana</em></td>
<td>10.3 (0.50)</td>
<td>95.4 (0.98)</td>
<td>Container (1890 cm³)</td>
</tr>
</tbody>
</table>

*Note:* Values in parentheses under stock type correspond to container volume for containerized seedlings and number of years spent in nursery and transplant beds for bare-root stock. Measurements were taken prior to planting for all species but *U. americana*, which was measured just after planting.

Results

Overall survival

The model of seedling survival, as measured in fall 2014, included overstory treatment, species, season, species × treatment, and species × season. We present only the most parsimonious models due to the high number of candidate models and the low interpretability. We considered models with ΔAIC ≤ 2 to have similar support (Burnham and Anderson 2003). We performed post hoc tests of species means, using Sidak adjustments for multiple comparisons. Mixed-effect logistic regressions were performed with the xtlogit command in Stata 12 (StataCorp 2011).

We graphically examined trends in mortality between census periods, treatments, and species. We used the ltable command in Stata 12 (StataCorp 2011) to construct life tables of biannual, fall and spring census data, starting in fall 2012 and continuing through fall 2014. Despite the delayed planting of *Q. bicolor*, *F. mandschurica*, and *P. balsamifera*, we used survival as of fall 2012 as the starting point for all species, with the caveat that more recent plantings entered the study period with less time to die.

Ovystery treatment × species interactions

Survival varied significantly by treatment (*F* = 13.01, *p* < 0.001) and species (*F* = 129.6, *p* < 0.001). However, due to a significant species × treatment interaction (*F* = 13.84, *p* < 0.001), the rank order of species in terms of survival varied between treatments (Fig. 2). Mean overall survival rates, adjusted for the effects of species and season, were generally comparable in the control (32.9% ± 0.7%), girdle (33.3% ± 0.7%), and group selection (34.5% ± 0.7%) treatments (Table 2). Among the top-surviving species, *U. americana* (93% ± 2.6%), *Q. bicolor* (83.2% ± 1.9%), and *C. occidentalis* (76.7% ± 2.2%) achieved their highest rates of survival in the control treatments. *Ulmus americana* and *Q. bicolor* also achieved survival rates above 75% in the girdle and group selection treatments. *Fraxinus mandschurica* showed highest survival in the girdle treatments (84.4% ± 1.8%), followed by the group selection (78.3% ± 2.1%) and the control (74.4% ± 2.2%) treatments.

Overall survival was significantly lower in the clearcuts (22.1% ± 0.6%; Table 2; Fig. 2). Seedling survival rates were lowest in the clearcuts for a full two-thirds of the species planted: *U. americana* (31.8% ± 0.5%), *Q. bicolor* (68.2% ± 0.2%), *C. occidentalis* (17.3% ± 0.2%),
Table 2. Mean survival (± standard error (SE)) by treatment and planting season with overall means for seedlings of 12 tree species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Overall Clearcut</th>
<th>Control</th>
<th>Girdle</th>
<th>Group</th>
<th>Planting season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fall</td>
<td>Spring</td>
<td>Fall</td>
<td>Spring</td>
<td></td>
</tr>
<tr>
<td>ACRU</td>
<td>17.5a (1.4)</td>
<td>37.9b (1.7)</td>
<td>14.7a (1.8)</td>
<td>29.6b (2.3)</td>
<td>33.5b (2.4)</td>
</tr>
<tr>
<td>BEAL</td>
<td>3.9a (0.5)</td>
<td>0.3a (0.3)</td>
<td>3.9b (1.0)</td>
<td>4.9b (1.1)</td>
<td>6.5b (1.3)</td>
</tr>
<tr>
<td>CECO</td>
<td>52.9f (1.3)</td>
<td>17.3a (1.9)</td>
<td>76.7d (2.2)</td>
<td>66.1c (2.4)</td>
<td>51.6b (2.5)</td>
</tr>
<tr>
<td>FRMA</td>
<td>73.3g (1.1)</td>
<td>56.5a (2.5)</td>
<td>74.4b (2.2)</td>
<td>84.4c (1.8)</td>
<td>78.3b (2.1)</td>
</tr>
<tr>
<td>LALA</td>
<td>9.6b (0.8)</td>
<td>8.1a (1.4)</td>
<td>8.1a (1.4)</td>
<td>7.3a (1.3)</td>
<td>14.8b (1.8)</td>
</tr>
<tr>
<td>PIMA</td>
<td>19.1c (1.0)</td>
<td>11.4a (1.6)</td>
<td>17.4ab (1.9)</td>
<td>24.9c (2.2)</td>
<td>22.7bc (2.1)</td>
</tr>
<tr>
<td>POBA</td>
<td>36.0e (1.2)</td>
<td>39.3bc (2.5)</td>
<td>28.5a (2.3)</td>
<td>31.2ab (2.4)</td>
<td>45c (2.5)</td>
</tr>
<tr>
<td>PODE</td>
<td>11.0b (0.7)</td>
<td>11.6b (1.5)</td>
<td>5.3a (1.1)</td>
<td>10.9b (1.5)</td>
<td>16b (1.7)</td>
</tr>
<tr>
<td>POTR</td>
<td>4.8a (0.5)</td>
<td>7.6b (1.4)</td>
<td>0.3a (0.3)</td>
<td>3.2a (0.9)</td>
<td>8.4b (1.4)</td>
</tr>
<tr>
<td>QUBI</td>
<td>75.5g (1.1)</td>
<td>68.2a (2.4)</td>
<td>83.2b (1.9)</td>
<td>74.4a (2.2)</td>
<td>76.5ab (2.1)</td>
</tr>
<tr>
<td>THOC</td>
<td>12.4b (0.8)</td>
<td>4.2a (1.0)</td>
<td>16.1b (1.9)</td>
<td>15.5b (1.8)</td>
<td>13.8b (1.8)</td>
</tr>
<tr>
<td>ULAM</td>
<td>74.8 (2.1)</td>
<td>31.8a (4.5)</td>
<td>93b (2.6)</td>
<td>91.3b (2.8)</td>
<td>87b (3.4)</td>
</tr>
<tr>
<td>Total</td>
<td>30.7 (0.3)</td>
<td>22.1a (0.6)</td>
<td>32.9b (0.7)</td>
<td>33.3b (0.7)</td>
<td>34.5b (0.7)</td>
</tr>
</tbody>
</table>

Note: Overall, species survival for all treatments and seasons. Lowercase letters adjacent to means represent pairwise comparisons of treatments and seasons based on individual-species models, adjusted for interactions when present. Levels not connected by the same lowercase letter are significantly different (p < 0.05). ACRU, *Acer rubrum*; BEAL, *Betula alleghaniensis*; CECO, *Celtis occidentalis*; FRMA, *Fraxinus mandshurica*; LALA, *Larix laricina*; PIMA, *Picea mariana*; POBA, *Populus balsamifera*; PODE, *Populus deltoides*; POTR, *Populus tremuloides*; QUBI, *Quercus bicolor*; THOC, *Thuja occidentalis*; ULAM, *Ulmus americana*. For ULAM, there was no spring planting, with a bivariate model only; the mean (±SE) includes *U. americana*, whereas pairwise comparison excludes *U. americana*. N/A, not applicable.

Fig. 2. Interaction plot of the survival of seedlings of 12 tree species planted under clear-cut, control, girdle, and group selection overstory treatments (mean ± 95% confidence interval (C.I.)), as assessed in fall 2014. Uppercase letters represent pairwise comparisons of species performed separately for each treatment; species not connected by the same letter are significantly different (p < 0.05). See Table 2 for species abbreviations.
A. rubrum to those of fall plantings for P. mariana respectively), L. laricina rates for Table 2). Fall survival rates were also higher than spring survival (46.5% ± 2.5% vs. 25.4% ± 1.6%, respectively), and P. balsamifera effects (Table 2). Survival rates of spring plantings were superior partially contingent on treatment due to significant interaction (85.5% ± 1.3% vs. 65.3% ± 1.7%, respectively) but were Q. bicolor planted (Table 3). Survival rates were superior for fall-planted vs. spring- C. occidentalis and fall, with the exception of cant predictor of survival for all species planted in both spring (33.7% ± 1.4% vs. 28.7% ± 1.9%, respectively; Table 2). Survival rates were superior for fall-planted vs. spring-planted L. laricina (0.3% ± 0.3%) which was planted only in group selection treatments.

Planting season × treatment and planting season × species interactions

Although planting season did not have a significant main effect on overall survival (F = 1.79, p = 0.18), it interacted significantly with treatment (F = 13.83, p < 0.001; Fig. 3) and species (F = 60.4, p < 0.001; Fig. 4). When controlling for species effects, spring plantings in group selection treatments had significantly higher survival than in controls, whereas girdle treatments had intermediate survival. In contrast, the control, girdle, and group selection treatments were comparable for fall plantings. Mean survival in clearcuts was significantly lower in both spring and fall compared with other treatments (Fig. 3). When U. americana, which was planted only in spring, was excluded from the multi-species regression model, overall survival was higher for fall plantings than for spring plantings (33.7% ± 1.4% vs. 28.7% ± 1.9%, respectively; Table 2).

In terms of individual species, planting season was a significant predictor of survival for all species planted in both spring and fall, with the exception of C. occidentalis and P. deltoides (Table 3). Survival rates were superior for fall-planted vs. spring-planted F. mandshurica (56.5% ± 0.3%), A. rubrum (14.7% ± 0.2%), P. mariana (11.4% ± 1.6%), T. occidentalis (4.2% ± 0.1%), and B. alleghaniensis (0.3% ± 0.3%). Although L. laricina also did poorly in the clearcuts (8.1% ± 1.4%), it had comparably low survival rates in the control (8.1% ± 1.4%) and girdle (7.3% ± 1.4%) treatments. In contrast, survival rates were lowest in the controls for shade-intolerant P. balsamifera (28.5% ± 2.3%), P. deltoides (5.3% ± 1.1%), and P. tremuloides (0.3% ± 0.3%), which survived better in the clearcuts. Survival of P. balsamifera (45% ± 2.5%) was highest in the group selection treatments.

Treatment × species × planting season interactions

Although planting season did not have a significant main effect on overall survival (F = 1.79, p = 0.18), it interacted significantly with treatment (F = 13.83, p < 0.001; Fig. 3) and species (F = 60.4, p < 0.001; Fig. 4). When controlling for species effects, spring plantings in group selection treatments had significantly higher survival than in controls, whereas girdle treatments had intermediate survival. In contrast, the control, girdle, and group selection treatments were comparable for fall plantings. Mean survival in clearcuts was significantly lower in both spring and fall compared with other treatments (Fig. 3). When U. americana, which was planted only in spring, was excluded from the multi-species regression model, overall survival was higher for fall plantings than for spring plantings (33.7% ± 1.4% vs. 28.7% ± 1.9%, respectively; Table 2).

In terms of individual species, planting season was a significant predictor of survival for all species planted in both spring and fall, with the exception of C. occidentalis and P. deltoides (Table 3). Survival rates were superior for fall-planted vs. spring-planted F. mandshurica (83.7% ± 1.7% vs. 62.7% ± 1.3%, respectively; Table 2). Fall survival rates were also higher than spring survival rates for L. laricina (14.03% ± 1.3% vs. 5.2% ± 0.8%, respectively), P. balsamifera (46.5% ± 2.5% vs. 25.4% ± 1.6%, respectively), and Q. bicolor (85.5% ± 1.3% vs. 65.3% ± 1.7%, respectively) but were partially contingent on treatment due to significant interaction effects (Table 2). Survival rates of spring plantings were superior to those of fall plantings for A. rubrum (37.9% ± 1.7% vs. 17.5% ± 1.4%, respectively), P. mariana (32.6% ± 0.8% vs. 5.6% ± 1.7%, respec-

Fig. 3. Interaction plot of the influence of overstory treatment and season of planting on average seedling survival (mean ± 95% confidence interval (C.I.)), as of fall 2014. Uppercase letters represent pairwise comparisons of treatments performed separately for each season; treatments not connected by the same letter are significantly different (p < 0.05). See Table 2 for species abbreviations.

Fig. 4. Interaction plot of the survival of spring and fall plantings of seedlings of 12 tree species (mean ± 95% confidence interval (C.I.)), as assessed in fall 2014. Uppercase letters represent pairwise comparisons of species performed separately for each season; species not connected by the same letter are significantly different (p < 0.05). See Table 2 for species abbreviations.

Table 3. Summary of results for best-supported models of individual-species survival.

<table>
<thead>
<tr>
<th>Model</th>
<th>Treatment</th>
<th>Season</th>
<th>Treatment × season</th>
<th>F statistic</th>
<th>p statistic</th>
<th>ROC</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACRU</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>N.S.</td>
<td>30.95</td>
<td>&lt;0.001</td>
<td>0.76</td>
</tr>
<tr>
<td>BEAL</td>
<td>0.007</td>
<td>0.009</td>
<td>N.S.</td>
<td>4.69</td>
<td>&lt;0.001</td>
<td>0.81</td>
</tr>
<tr>
<td>CEOC</td>
<td>&lt;0.001</td>
<td>N.S.</td>
<td>N.S.</td>
<td>85.5</td>
<td>&lt;0.001</td>
<td>0.76</td>
</tr>
<tr>
<td>FRMA</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>N.S.</td>
<td>41.2</td>
<td>&lt;0.001</td>
<td>0.77</td>
</tr>
<tr>
<td>LALA</td>
<td>0.002</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>11.81</td>
<td>&lt;0.001</td>
<td>0.76</td>
</tr>
<tr>
<td>PIMA</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>42.73</td>
<td>&lt;0.001</td>
<td>0.81</td>
</tr>
<tr>
<td>POBA</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>18.99</td>
<td>&lt;0.001</td>
<td>0.74</td>
</tr>
<tr>
<td>PODE</td>
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<td>N.S.</td>
<td>N.S.</td>
<td>8.69</td>
<td>&lt;0.001</td>
<td>0.74</td>
</tr>
<tr>
<td>POTR</td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>8.44</td>
<td>&lt;0.001</td>
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<tr>
<td>QUBI</td>
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<td>&lt;0.001</td>
<td>14.84</td>
<td>&lt;0.001</td>
<td>0.74</td>
</tr>
<tr>
<td>THOC</td>
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<td>&lt;0.001</td>
<td>N.S.</td>
<td>16.61</td>
<td>&lt;0.001</td>
<td>0.77</td>
</tr>
<tr>
<td>ULAM</td>
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<td>N/A</td>
<td>N.S.</td>
<td>30.61</td>
<td>&lt;0.001</td>
<td>0.89</td>
</tr>
</tbody>
</table>

Note: Potential model terms included treatment, season, and the treatment × season interaction. Significant terms have corresponding p values, whereas non-significant terms are designated N.S. Overall model F statistics, p values, and area under the receiver operating curve (ROC) are also provided. Species abbreviations are provided in Table 2. N/A, not applicable.

Treatment × species × planting season interactions

For P. balsamifera, Q. bicolor, and L. laricina, there was a significant three-way interaction among species, treatment, and planting season (Table 3). Except in the clear-cut treatments, fall plantings of Q. bicolor and L. laricina had higher survival, whereas survival of spring-planted P. balsamifera was lower in the control and girdle treatments.

Trends and patterns

Plots of mean survival by census period (Fig. 5) illustrate that differences in survival among overstory treatments were evident by fall 2012 and remained consistent through the end of the observation period in fall 2014. In fall 2012, overall survival was
Fig. 5. Plot of life table estimates showing proportion of overall seedlings planted surviving under clear-cut, control, girdle, and group selection treatments (mean ± 95% confidence interval [C.I.]), with survival assessed in spring and fall, beginning in fall 2012. Median life expectancy = the point at which survival falls below 0.5.

Discussion

Overstory treatments

With the exception of the three shade-intolerant species, i.e., P. balsamifera, P. deltoides, and P. tremuloides (Ninemets and Valladares 2006), clear-cutting was the least-successful canopy treatment for promoting survival of the various species of planted seedlings, a finding that is consistent with Erdmann’s (Erdmann et al. 1987) observation that clear-cutting black ash forest may result in loss of tree regeneration due to rising water tables. In a study examining the effectiveness of a willow overstory on hardwood restoration similarly found that overstory removal was counterproductive to artificial tree regeneration, increasing microclimatic extremes, herbaceous layer cover, and seedling mortality (Dulohery et al. 2000). Wang et al. (2013) concluded that F. mandshurica growing in its native range faced heavy root competition from herbaceous species, particularly when grown without a forest overstory. Not only may the increased light availability from clear-cutting indirectly interfere with seedling survival by increasing competition from the herbaceous layer, but Royo and Carson (2006) suggested that clear-cutting F. nigra swamps may result in a recalcitrant understory layer with long-term effects on the reestablishment of forest cover. Based on these findings, the regeneration response in F. nigra forests in the presence or absence (i.e., competition control) of a dense herbaceous layer should be examined in greater detail.

Control, group selection, and girdle treatments showed equivalent overall survival for the first several years after planting for the four top-surviving species, Q. bicolor, F. mandshurica, U. americana, and C. occidentalis. However, the long-term efficacy of growing replacement species under an intact F. nigra overstory, as in the control, is unknown. As seedlings mature, the negative impacts of shading in the control plots may replace facilitative effects during establishment (Callaway and Puignaire 2007). In the group selection treatments, we found simultaneously high survival of shade-tolerant species such as C. occidentalis and improved success of shade-intolerant Populus spp. and L. laricina compared with the control treatments. If growth is light-limited, group selection could be effective at both promoting development and supporting a larger variety of species. In addition, water table responses (shallower depth and longer duration of ponding) in the group selection treatments were negligible and very similar to controls (Slesak et al. 2014), suggesting that the residual overstory in these treatments is ameliorating the degree of inundation experienced by seedlings. Comparable survival in the girdle treatments suggests that planting immediately prior to EAB invasion could achieve a shelterwood effect, with seedlings initially benefitting from overstory microclimatic effects (Aussenac 2000) but later released following the loss of the canopy (Smith et al. 1997). However, a concurrent rise in the water table following girdling (Slesak et al. 2014) may offset any positive benefits of a shelterwood effect.

Species survival

Mortality rates were high in the first year of the study, with the majority of species having less than 50% survival in the growing season immediately after harvest. Mortality rates over the rest of the study declined, generally maintaining the relative species differences that were apparent by fall 2012. First-year seedling survival was likely impacted by a series of unusual climate events. Fall 2011 marked the onset of a moderate to severe drought, which persisted through 2012 and translated into below average 2011–2012 snowfall (average Palmer Drought Severity Index = 2.63, National Climate Data Center 2015). Reduced snow cover can subject the rooting zone to lower temperatures and dramatically increase vulnerability to frost heaving (Bergsten et al. 2001), visual
evidence of which was reported by the field crew in fall 2012. Below average snow cover may also have exposed seedlings in the clear-cut and group selection treatments to logging damage, as 2011 fall plantings were installed prior to harvesting with the expectation of a protective snowpack, so that no additional provisions were assumed to be necessary for their protection. In addition, a record warming trend in March 2012 disrupted the dormancy period and resulted in a prolonged freeze–thaw cycle (National Climate Data Center 2015). Finally, unusual flooding occurred when 12.7 cm of rain fell on the study area in a 24-hour period on 19–20 June 2012 (National Climate Data Center 2015).

*Quercus bicolor*, *F. mandshurica*, and *P. balsamifera*, half of which were planted in the fall after harvest, and *U. americana*, which was planted only in the spring after harvest, entered the study period with higher survival. Nevertheless, survival rates for these species remained comparatively stable through subsequent measurement periods, suggesting inherently higher overall survival rates. The high survival rate of *U. americana* was comparable with that found in a previous study that examined experimental plantings of the species in *Fraxinus* forests in Ohio (Knight et al. 2012). *Ulmus americana*’s high survival rate may reflect both suitability to *F. nigra* forests and the large average size of seedlings in both studies (Knight et al. 2012). Large seedling size may confer an advantage in wetlands by elevating leaves above standing water (Knight et al. 2012), which may also explain, in part, the high survival rates of non-native *Q. bicolor* and *F. mandshurica* compared with naturally occurring species with smaller planting stock such as *B. alleghaniensis* and *T. occidentalis*. Similarly, root growth increases seedlings’ ability to compete for soil resources, store carbohydrates (Smith et al. 1997), and escape damage from frost heaving (Goulet 1995). Thus, *P. balsamifera*, which was smaller than lower surviving *P. deltoides* in terms of preplanting mean basal diameter and stem length, may have benefitted from superior root development due to its larger container size.

Nevertheless, our findings suggest *U. americana*, *Q. bicolor*, and *C. occidentalis* appear to hold promise as *F. nigra* replacement species in the ecosystems examined. *Ulmus americana* was common in the study ecosystems before the spread of Dutch elm disease (M. Reinikainen and A.W. D’Amato, unpublished data), and the availability of Dutch elm disease-resistant cultivars makes its reintroduction feasible. The long-term ability of *Q. bicolor* and *C. occidentalis* to grow and naturally reproduce in *F. nigra* wetlands has not yet been tested, whereas *C. occidentalis* has shown low natural regeneration in standing water and may be growth limited on wet sites (Krajecek and Williams 1990). However, *Q. bicolor* seedlings have previously demonstrated high survival and positive growth under open, flooded conditions (Kabrick et al. 2012). Furthermore, a predicted decrease in precipitation and shift in suitable habitat to the NNE with warming climate could make both species excellent candidates for assisted range expansion in the longer term (Williams and Dumroese 2013). In the short term, these species might also serve as a “nurse crop” (Landhäusser et al. 2003), regulating water tables and microclimatic conditions until more suitable species can be established.

Given the relative success of *C. occidentalis* and *Q. bicolor*, which were respectively planted at or beyond the northern limits of their present ranges, assisted range expansion could improve the available species pool for maintaining long-term forest cover in the

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**Fig. 6.** Plot of life table estimates of survival (mean ± 95% confidence interval (C.I.)) for seedlings of 12 tree species, with survival assessed in spring and fall, beginning in fall 2012. Median life expectancy = the point at which survival falls below 0.5. Six species entered the study with survival rates below this level, suggesting a median life expectancy of less than one growing season. See Table 2 for species abbreviations.
post-EAB F. nigra wetlands (Pedlar et al. 2012). Because Q. bicolor occurs, like F. nigra, both as an associated species in mixed-hardwood forests and a dominant species in more northerly wetland forests (Snyder 1992), its functional traits should be explored to determine if it might potentially fill F. nigra’s niche in very wet northern ecosystems. At present, an insufficient number of degree days for flowering success appears to define the northern range limit of Q. bicolor (Morin et al. 2007), as opposed to lack of physiological tolerance, suggesting that the species might become better suited to northern Great Lakes forests as the growing season lengthens with climate change (Pryor et al. 2014). Future research might also explore whether there are other wetland forest dominant or co-dominant species with similar range distributions currently limited by phenology.

**Populus balsamifera** and **F. mandshurica** are more problematic. **Populus balsamifera**, a minor forest component on our study sites prior to treatment, achieved less than a 50% 3-year survival rate under the best combination of treatment and planting season. Moreover, even if the population of **P. balsamifera** could successfully be increased in the near term, the species is predicted to suffer heavy declines in Minnesota as a result of climate change (Iverson et al. 2008). **Fraxinus mandshurica**, which more typically occurs on sites with well-drained soils, had an impressively high rate of survival, possibly reflecting exposure to harsher winter conditions within much of its native range compared with our study area (Qian et al. 2003). However, we are not advocating for its assisted migration into North American black ash wetland forests, an intercontinental species introduction that could pose unknown and unacceptable risks such as the development of invasive behavior and other interactions with native species (Pedlar et al. 2012). Our results do, however, indicate that as part of a crossbreeding program to develop EAB-resistant **F. nigra**, pure **F. mandshurica** appears inherently tolerant of northern Minnesota growing conditions, although it may suffer winter dieback if not covered by an insulating layer of snow (A.W. D’Amato, personal observation).

Replacing **F. nigra** with **L. laricina**, a naturally occurring conifer species in northern Minnesota forests (MNDNR 2003), has been suggested for the study areas (University of Minnesota Extension and MNDNR 2011). However, the relative success of angiosperm replacement species suggests that **F. nigra** forests after EAB invasion could avoid the dramatic changes associated with conversion to a conifer-dominated forest. Such changes with conversion from one life-form to another have been observed in other North American forests affected by invasive insects (Ford et al. 2012).

**Planting season**

We found that the season of planting can influence survival in combination with overstory management and (or) species selection. Although fall plantings did not show higher survival in clearcuts and group selections, they resulted in significantly higher survival in controls. Although harvesting-related mechanical damage to 2011 fall-planted seedlings likely contributed to this result, fall plantings, in general, may face higher risk of frost heaving in harvest treatments than in closed forests due to reduced overstory cover and soil scarification (Goulert 1995). Although Hansen (1986) found that fall plantings of **P. deltoides** hybrids in Wisconsin resulted in higher mortality, which the author attributed to frost heaving, we found no significant difference between seasons when using standard **P. deltoides** stock on wetter, nonintensively managed sites. Among the conifer species, we found that fall-planted **L. laricina** had higher survival except in clearcuts, whereas **P. mariana** and **T. occidentalis** showed the opposite pattern. Takyi and Hillman (2000) reported similar survival between spring and fall plantings of **L. laricina** and **P. mariana** grown in clearcuts. Examining only seedlings in the clearcuts, we found no difference in survival for **L. laricina** between seasons but significantly lower survival of **P. mariana**. The unusually low snowfall of winter 2011–2012 may have promoted desiccation in the evergreen **P. mariana** seedlings tested in this study (Christersson and von Fircks 1998), while providing little protection from deer herbivory and machine traffic during harvesting. Operationally, we found that fall planting was more efficient due to improved accessibility with drier soil conditions.

**Conclusions**

Our results indicate that planting of tree species that are not EAB hosts, both with and without overstory harvest treatments, is a potentially viable management option for sustaining forest cover and ecosystem services in **F. nigra** wetlands threatened by EAB invasion. Although our results suggest that clear-cutting, as is used with preemptive salvage logging, negatively impacted the survival of 9 of 12 species we tested, unanticipated mechanical damage to seedlings during harvesting may have worsened survival in clearcuts and group selections. Nonetheless, control, group selection, and girdling treatments (which are emulative of planting just prior to EAB infestation) showed roughly equivalent seedling survival responses for the first several years. By maintaining overstory cover while locally increasing understory light availability, group selection could be effective in promoting seedling development, while supporting a wider variety of tree species and maintaining hydrologic conditions similar to the uncut forest and favorable to seedling establishment. Species selection will be critical to the success of any future planting effort, with conifer and shade-intolerant hardwood species showing generally low survival rates. The more robust seedling stock of high-surviving species such as **U. americana**, **Q. bicolor**, and **F. mandshurica** suggests that future research and planting efforts should prioritize stock quality. Toward this end, small preliminary plantings that test the survival of seedlings from several different stocktypes could aid in better matching stock attributes for individual species with local site requirements (see Landis et al. 2010). Although damage during winter harvesting may have reduced the overall effectiveness of fall plantings, our results nevertheless suggest that planting season should be determined based on species and overstory treatment type to assure the greatest chance of seedling survival. Further research is needed to predict how factors such as herbaceous plant communities and herbivore activity may interact with overstory management and artificial regeneration. In addition to survival, growth rates and fecundity of replacement species over longer time periods with different management options need to be evaluated.

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**References**


