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

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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.

Résumé : Les forêts humides de frêne noir (*Fraxinus nigra* Marsh.) du nord du Minnesota, aux États-Unis, sont menacées par un insecte invasif, l'agrile du frêne (*Agrilus planipennis* Fairmaire (AF)). Une option potentielle d'aménagement consiste à encourager la régénération d'espèces d'arbres non hôtes pour maintenir les fonctions de l'écosystème. À l'aide d'une expérience sur le terrain à une échelle opérationnelle, nous avons étudié la survie de 12 espèces alternatives d'arbres en réponse à différents traitements du couvert forestier. Nous avons plantés des semis dans des parcelles de 1,6 ha assignées à quatre traitements du couvert forestier : témoin non traité; jardinage par bouquets (trouées de 0,04 ha occupant 20 % du peuplement); annélation du frêne noir pour imiter la mortalité causée par l'AF; et coupe à blanc. Des plantations à l'automne et au printemps ont été utilisées pour comparer les effets de l'accumulation d'eau au printemps. Le témoin (32,9 %), le jardinage par bouquets (34,5 %) et l'annélation (33,3 %) avaient globalement un taux de survie comparable. Le taux de survie était significativement plus faible (22 %) avec la coupe à blanc. Ensemble, le choix des espèces, le traitement du couvert forestier et la saison de plantation ont engendré un taux de survie qui variait de 0,08 % à 94,1 %. Globalement, les espèces de conifères avaient un faible taux de survie (10,7 %) tandis que certaines espèces dont l'aire de répartition naturelle ne chevauchait pas présentement les forêts nordiques de frêne noir, p. ex. *Quercus bicolor* Willd. (75,5 %), avaient un taux de survie élevé. Si la croissance est limitée par la lumière, le jardinage par bouquets pourrait être efficace pour favoriser le recrutement et supporter une plus grande variété d'espèces. [Traduit par la Rédaction]

Mots-clés : Fraxinus nigra, agrile du frêne, espèces alternatives d'arbres, régénération artificielle, traitements du couvert forestier.

Introduction

Fraxinus nigra Marsh. (black ash) wetland forests in northern Minnesota, USA, are threatened by the introduced Asian insect, emerald ash borer (*Agrilis 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-

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story plant species and provide important habitat for large and small mammals, birds, amphibians, reptiles, and arthropods (Gucker 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 Frelich 2008).

Kashian and Witter (2011) suggest that ash regeneration in southern Michigan's upland, mixed-*Fraxinus* 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 than 99% mortality rate between the estimated start of the outbreak in 1998 and 2010 (Herms and McCullough 2014). Although the nearly pure black ash wetland ecosystems of northern Minnesota (Minnesota Department of Natural Resources (MNDNR) 2003) differ dramatically from the mixed-species stands of southern Michigan (Cohen et al. 2014), such findings suggest that the continued spread of EAB could potentially result in large-scale loss of *F. nigra* from the extensive Minnesota wetland forests it presently dominates (Pugh et al. 2011).

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) (MNDNR 2003). Although advance regeneration of tree species that are not EAB hosts in *F. nigra* wetland forests is presently low (Palik et al. 2011), 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 species 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-intolerant 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* Marshall (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 northerly 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 sustaining ecosystem function in imperiled 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 (0.04 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 Chippewa 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 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). 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 m^2·ha^{-1}, and mean tree density was 477 ± 50.6 trees·ha^{-1}.

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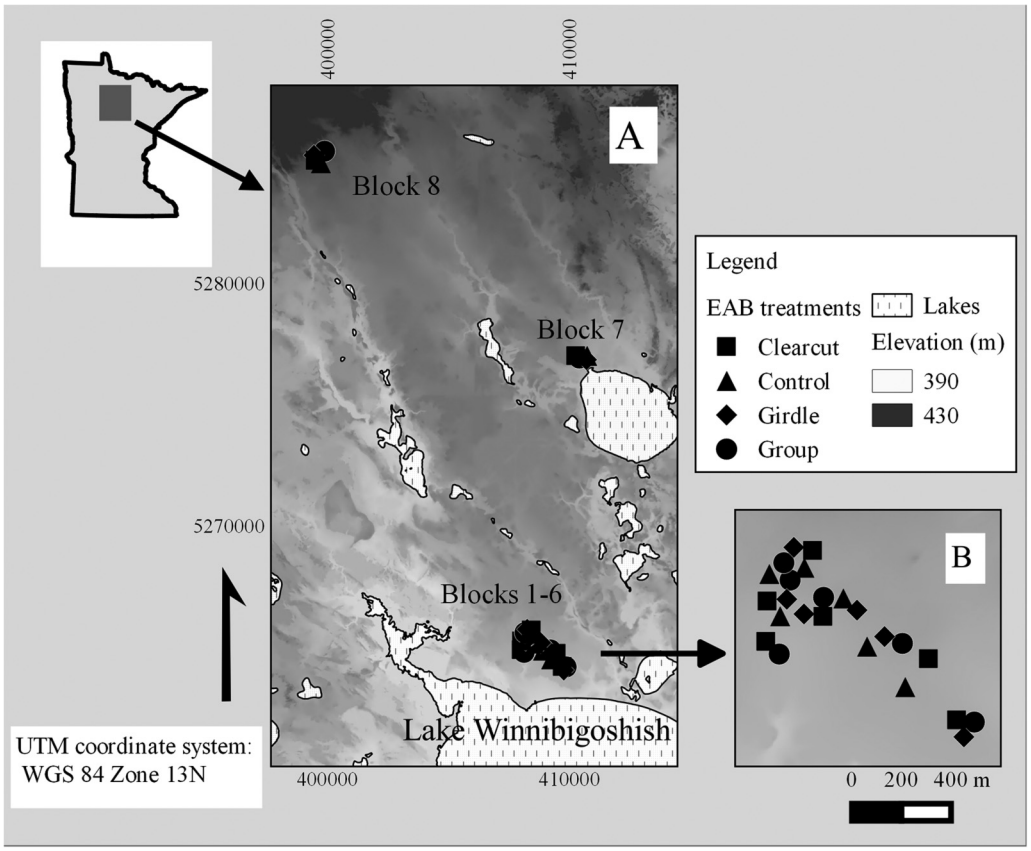
Fig. 1. (A) Map showing location of study sites near and within the Lake Winnibigoshish watershed, an area of low relief in Minnesota, USA. (B) Illustration of approximate layout of overstory treatment plots in blocks 1–6 (symbols not to scale), with each treatment replicated once per block. Blocks 7 and 8 were similar in layout to blocks 1–6.



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 m^2) 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. laricina*, *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* L. (hackberry), of which isolated populations presently occur in the study area, and *Quercus bicolor* Willd. (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. laricina*, *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

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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.

Species	Mean basal diameter (mm)	Mean stem length (cm)	Stock type
Acer rubrum	4.7 (0.17)	22.1 (1.13)	Container (90 cm^3)
Betula alleghaniensis	3.4 (0.55)	21.8 (0.63)	Container (90 cm^3)
Celtis occidentalis	5.1 (0.14)	44.7 (1.37)	Container (336 cm^3)
Fraxinus mandshurica	9.1 (0.26)	78.7 (1.28)	Bareroot (3+0)
Larix laricina	3.9 (0.09)	28.5 (0.86)	Container (60 cm^3)
Picea mariana	3.9 (0.08)	42.4 (0.66)	Container (90 cm^3)
Populus balsamifera	3.5 (0.08)	29.8 (0.73)	Container (164 cm^3)
Populus deltoides	4.5 (0.11)	38.6 (1.18)	Bareroot (1+0)
Populus tremuloides	3.1 (0.05)	21.0 (0.38)	Container (90 cm^3)
Quercus bicolor	4.7 (0.13)	25.4 (0.64)	Bareroot (1+0)
Thuja occidentalis	2.6 (0.77)	23.2 (0.37)	Container (60 cm^3)
Ulmus americana	10.3 (0.50)	95.4 (0.98)	Container (1890 cm^3)

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.

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).

Within each of the 1.62 ha treatment plots, we established six 0.04 ha (400 m^2) subplots to serve as planting areas. In the group selection treatments, we centered four planting subplots within canopy gaps and dispersed two of them beneath undisturbed canopy. Using a planting bar (Smith et al. 1997), we planted eight rows of seedlings on the western half of each 0.04 ha subplot. The positions of species within rows were randomly allocated to planting locations within a planting frame, with 1.25 m spacing between seedlings within rows and 2.5 m separation between rows. Given the importance of microsites to seedling survival in lowland systems, we planted each seedling on the closest favorable microsite to the randomly allocated planting location, avoiding hollows to the fullest extent possible given site topography. Random planting positions were not used for two species, *U. americana* and *F. mandshurica*, which were always located at the end of planting rows due to their late availability. For each species that received both spring and fall plantings, a total of 1536 seedlings was planted, distributed as 48 seedlings·species^{-1}·treatment plot^{-1} and 8 seedlings·species^{-1}·planting subplot^{-1}. For *U. americana*, which was planted only in spring, a total of 768 seedlings were planted, with 24 seedlings·species^{-1}·treatment plot^{-1} and 4 seedlings·planting subplot^{-1}. We assessed seedling survival at the beginning (May or June) and end (September or October) of each growing season from fall 2012 through fall 2014. We also inspected seedlings for the presence or absence of browse damage in spring 2013.

Analytical methods

We examined seedling survival for the final census period (fall 2014) using mixed-effects logistic regression. We analyzed the experiment as a split-plot design, with species and season of planting nested within overstory treatments. Random effects included 0.4 ha planting subplots nested within 1.62 ha treatment plots and experimental blocks. We initially modeled overall survivorship, excluding *U. americana* from the model, due to lack of spring plantings. Fixed factors included species, treatment, season of planting, and first-order interactions; we did not test second-level interactions due to difficulty of interpretation. The species with lowest survivorship, *B. alleghaniensis*, served as the reference level for species; the control served as the reference level for overstory treatment. Due to the large number of species and complexity of the analysis, we created individual-species models to more thoroughly investigate within-species treatment and seasonal effects. Because our analysis of *U. americana* was restricted to individual-species models, this species was not formally compared with the other 11 species.

We used backwards elimination to build initial sets of models, except in cases of significant interactions but insignificant main effects. We used Akaike's information criterion (AIC) to compare model parsimony for a given response variable and assessed overall model performance by calculating the area under the receiver operator characteristic (ROC) curve. In the event of a significant interaction but insignificant main effect, we calculated AIC of the model without the main effect but later refit the model to aid interpretability. We considered models with $\Delta AIC \leq 2$ to have similar support (Burnham and Anderson 2003). We performed posthoc tests of species means, using Sidak adjustments for multiple comparisons. Mixed-effect logistic regressions were performed with the xtmelogit 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. mandshurica*, 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.

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 weight of evidence ($\Delta AIC > 10$) for alternatives. Random block and subplot effects were significant for all models in Wald χ^2 tests (data not shown). Block effects accounted for more random variation than within-treatment subplot effects.

The mean overall survival rate for all species for all treatments and planting seasons was 30.7% ± 0.3% (Table 2). Mean overall survival by species across treatments and seasons was highest for *Q. bicolor* (75.5% ± 1.1%), *U. americana* (74.8% ± 2.1%), *F. mandshurica* (73.3% ± 1.1%), and *C. occidentalis* (52.9% ± 1.3%). In contrast, mean overall survival across treatments and seasons was lowest for *B. alleghaniensis* (3.9% ± 0.5%) and *P. tremuloides* (4.8% ± 0.5%).

Overstory 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 mandshurica* 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%),

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Table 2. Mean survival (± standard error (SE)) by treatment and planting season with overall means for seedlings of 12 tree species.

		Treatment				Planting season	
Species	Overall	Clearcut	Control	Girdle	Group	Fall	Spring
ACRU	27.8d (1.1)	14.7a (1.8)	33.3b (2.4)	29.6b (2.3)	33.5b (2.4)	17.5a (1.4)	37.9b (1.7)
BEAL	3.9a (0.5)	0.3a (0.3)	3.9b (1.0)	4.9b (1.1)	6.5b (1.3)	2.6a (0.6)	5.2b (0.8)
CEOC	52.9f (1.3)	17.3a (1.9)	76.7d (2.2)	66.1c (2.4)	51.6b (2.5)	51.0a (1.8)	54.8a (1.8)
FRMA	73.3g (1.1)	56.5a (2.5)	74.4b (2.2)	84.4c (1.8)	78.3bc (2.1)	83.7b (1.3)	62.7a (1.7)
LALA	9.6b (0.8)	8.1a (1.4)	8.1a (1.4)	7.3a (1.3)	14.8b (1.8)	14.0b (1.3)	5.2a (0.8)
PIMA	19.1c (1.0)	11.4a (1.6)	17.4ab (1.9)	24.9c (2.2)	22.7bc (2.1)	5.6a (0.8)	32.6b (1.7)
POBA	36.0e (1.2)	39.3bc (2.5)	28.5a (2.3)	31.2ab (2.4)	45c (2.5)	46.5b (1.8)	25.4a (1.6)
PODE	11.0b (0.7)	11.6b (1.5)	5.3a (1.1)	10.9b (1.5)	16b (1.7)	9.6a (1.0)	12.2a (1.1)
POTR	4.8a (0.5)	7.6b (1.4)	0.3a (0.3)	3.2a (0.9)	8.4b (1.4)	2.9a (0.6)	6.8b (0.9)
QUBI	75.5g (1.1)	68.2a (2.4)	83.2b (1.9)	74.4a (2.2)	76.5ab (2.1)	85.5b (1.3)	65.3a (1.7)
THOC	12.4b (0.8)	4.2a (1.0)	16.1b (1.9)	15.5b (1.8)	13.8b (1.8)	7.2a (0.9)	17.6b (1.4)
ULAM	74.8 (2.1)	31.8a (4.5)	93b (2.6)	91.3b (2.8)	87b (3.4)	74.8 (2.1)	N/A
Total	30.7 (0.3)	22.1a (0.6)	32.9b (0.7)	33.3b (0.7)	34.5b (0.7)	32.0a (0.5)	29.4a (0.5)

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*; CEOC, *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.

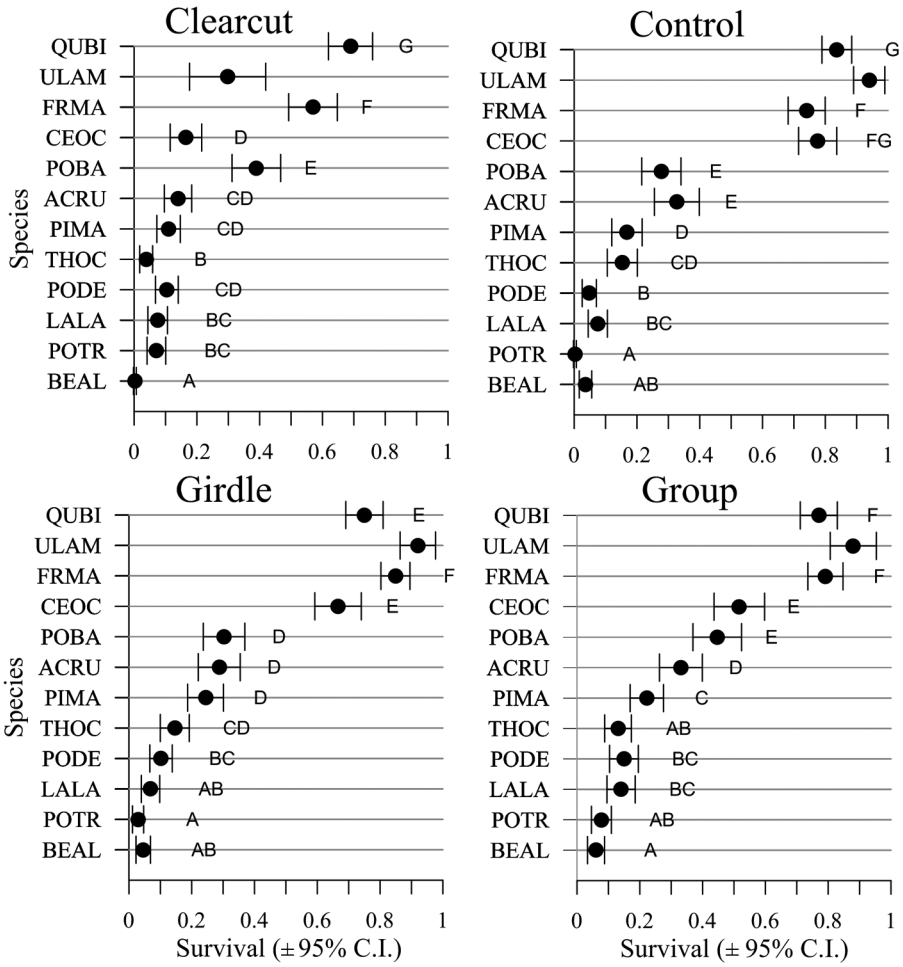

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Fig. 3. Interaction plot of the influence of overstory treatment and season of planting on average seedling survival (mean ± 95% confidence interval (C.I.)), as of fall 2014. Uppercase letters represent pairwise comparisons of treatments performed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

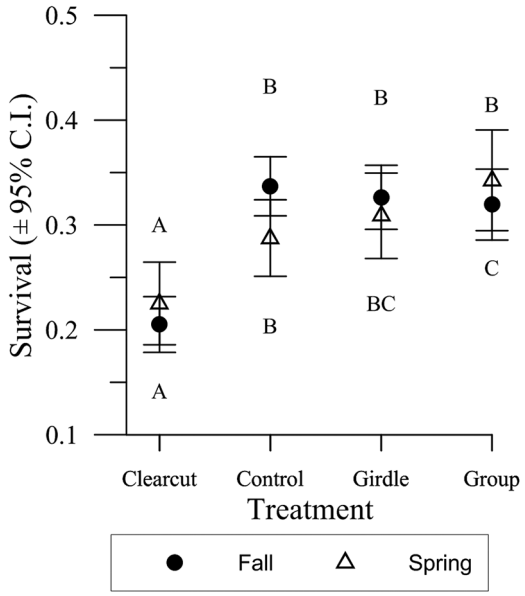
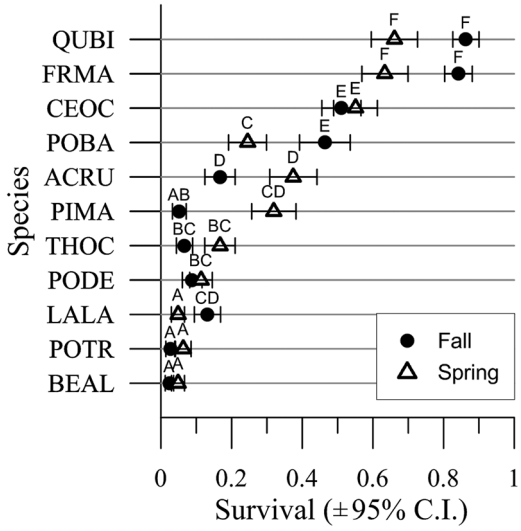


Fig. 4. Interaction plot of the survival of spring and fall plantings of seedlings of 12 tree species (mean ± 95% confidence interval (C.I.)), as assessed in fall 2014. Uppercase letters represent pairwise comparisons of species performed separately for each season; species not connected by the same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



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.

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* (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%, respectively), *B. alleghaniensis* (5.2% ± 0.8% vs. 2.6% ± 0.5%, respectively), *T. occidentalis* (17.6% ± 1.4% vs. 7.2% ± 0.9%, respectively), and *P. tremuloides* (6.8% ± 0.9% vs. 2.9% ± 0.6%, respectively) but only slightly better for *C. occidentalis* (54.8% ± 1.8% vs. 51.0% ± 1.8%, respectively) (Table 2).

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

Model	Treatment	Season	Treatment × season	*F* statistic	*p* statistic	ROC
ACRU	<0.001	<0.001	N.S.	30.95	<0.001	0.76
BEAL	0.007	0.009	N.S.	4.69	<0.001	0.81
CEOC	<0.001	N.S.	N.S.	85.5	<0.001	0.76
FRMA	<0.001	<0.001	N.S.	41.2	<0.001	0.77
LALA	0.002	<0.001	<0.001	11.81	<0.001	0.76
PIMA	<0.001	<0.001	N.S.	42.73	<0.001	0.81
POBA	<0.001	<0.001	<0.001	18.99	<0.001	0.74
PODE	<0.001	N.S.	N.S.	8.69	<0.001	0.74
POTR	<0.001	<0.001	N.S.	8.44	<0.001	0.87
QUBI	<0.001	<0.001	<0.001	14.84	<0.001	0.74
THOC	0.012	<0.001	N.S.	16.61	<0.001	0.77
ULAM	<0.001	N/A	N.S.	30.61	<0.001	0.89

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

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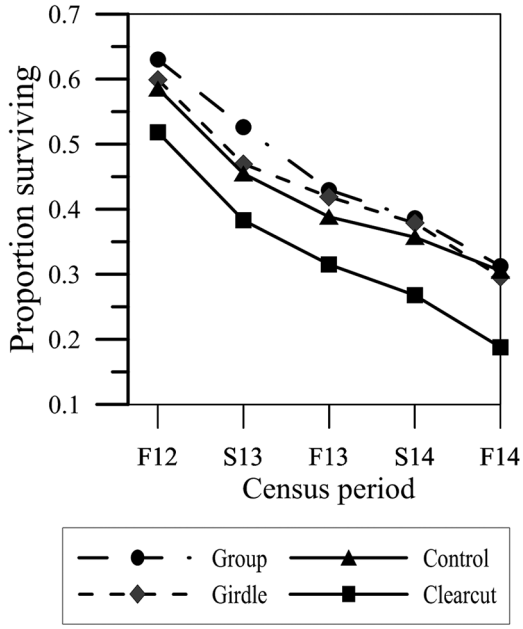
Fig. 5. Plot of life table estimates showing proportion of overall seedlings planted surviving under clear-cut, control, girdle, and group selection treatments (mean ± 95% confidence interval (C.I.)), with survival assessed in spring and fall, beginning in fall 2012. Median life expectancy = the point at which survival falls below 0.5.



lowest in the clearcuts but above 50% for all treatments. In contrast, survival in the clearcuts had fallen steadily to under 20% by fall 2014, whereas nonclear-cut treatments had fallen to an average of about 30%.

Some early patterns of individual species survival demonstrated similar consistency (Fig. 6). As might be expected, fall 2012 seedling survival was highest for *F. mandshurica* (98.6% ± .03%), *Q. bicolor* (95.9% ± 0.5%), and *U. americana* (86.2% ± 1.7%), i.e., the three species for which fall plantings were delayed until immediately prior to the fall 2012 census. However, at the close of the study in fall 2014, survival rates remained above 70% for all three species. *Celtis occidentalis*, which had a fall 2012 survival rate of 73.0% ± 1.3%, was the only spring-planted species still above its median life expectancy in fall 2014 (52.9% ± 1.3%). As early as fall 2012, heavy mortality had reduced survival to below 50% for *A. rubrum* (49.2% ± 1.3%), *B. alleghaniensis* (33.6 ± 1.2%), and *P. tremuloides* (24.6% ± 1.1%), as well as for the three conifer species, *T. occidentalis* (47.2% ± 1.3%), *P. mariana* (38.8% ± 1.2%), and *L. laricina* (17.8% ± 1.0%). By the end of the observation period, all three conifer species had survival rates below 20%.

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 companion study on our experimental sites, Slesak et al. (2014) found that clear-cutting caused a significant rise in the water table and duration of ponding during the subsequent growing seasons, which could subject seedlings to greater inundation, waterlogging, and hypoxic conditions. Given the high observed first-year seedling mortality rates across sites, ponding may exert a strong control on survival during seedling establishment but decline in importance thereafter. The early death of seedlings planted on microsites that become inundated due to black ash mortality, combined with greater seedling size over time, may also reduce demonstrated sensitivity to soil saturation in subsequent years (Jones and Sharitz 1998).

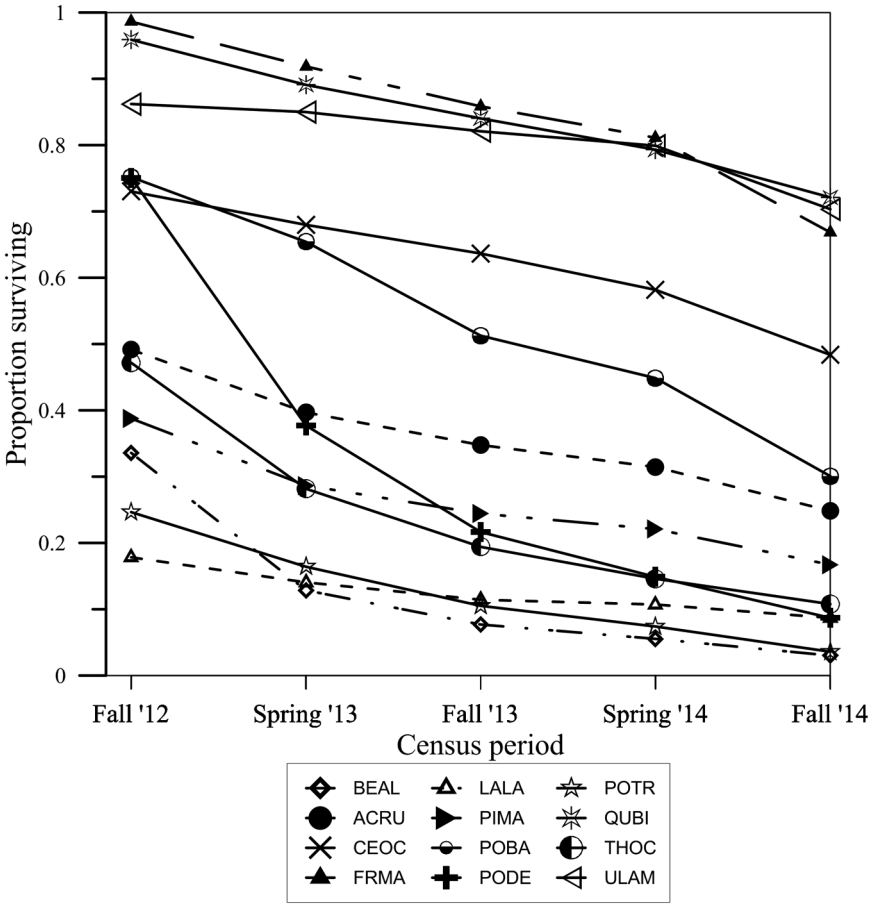
The low survival rates of all but the shade-intolerant *Populus* spp. in the clear-cut treatments also suggests that greater light availability had a negative influence on seedling survival, presumably through its effect on the degree of understory competition. Slesak et al. (2014) noted that the herbaceous understory in our experimental plots responded vigorously to clear-cutting 2 years after treatment, a response we also observed in the third year. 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 Pugnaire 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

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.



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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

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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 (Goulet 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 1988), 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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