ARTICLE

Canopy treatment influences growth of replacement tree species in *Fraxinus nigra* forests threatened by the emerald ash borer in Minnesota, USA

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

Abstract: *Fraxinus nigra* Marsh. (black ash), a dominant tree species of wetland forests in northern Minnesota, USA, is imperiled by the invasive insect emerald ash borer (EAB; *Agrilus planipennis* Fairmaire, 1888). Regeneration of associated tree species is generally low in *F. nigra* forests and could be impacted further by climate change. Proactive management may be critical to maintaining tree cover and ecosystem function following EAB invasion. We investigated the mean height and diameter relative growth rate (RGR) of seedlings of 10 potential replacement tree species, including two from the next southern climate zone projected to be adapted to the future northern Minnesota climate. Seedlings were planted in *F. nigra* wetlands under four canopy treatments: unharvested control, clearcut, girdling *F. nigra* to emulate EAB-induced mortality, and group selection. Mean height and diameter RGR was fastest overall in the clearcut treatment, followed by the girdling, group selection, and control treatments. Depending on species, treatment significantly influenced RGR. Several species projected to be adapted to the future northern Minnesota climate had moderate to rapid mean RGR, including one from the next southern climate zone. Our results suggest that seedling plantings and overstory treatment represent an effective strategy for establishing *F. nigra* replacement tree species as EAB approaches, while reducing future risk from climate change.

Key words: emerald ash borer, black ash wetlands, artificial regeneration, invasive species, climate change.

Résumé : Le frêne noir (*Fraxinus nigra* Marsh.), une espèce d'arbre dominante dans les forêts des milieux humides du nord du Minnesota, aux États-Unis, est menacé à cause d'un insecte invasif, l'agrile du frêne (AF) (*Agrilus planipennis* Fairmaire, 1888). La régénération des espèces compagnes est généralement faible dans les forêts de frêne noir et elle pourrait être davantage affectée par le changement climatique. Un aménagement proactif pourrait s'avérer essentiel pour maintenir le couvert forestier et la fonction de l'écosystème à la suite d'une invasion de l'AF. Nous avons étudié la hauteur relative moyenne et le taux de croissance relatif (TCR) en diamètre des semis de 10 espèces d'arbres qui pourraient remplacer le frêne, incluant deux espèces provenant de la zone climatique voisine au sud qui pourraient éventuellement s'adapter au climat du nord du Minnesota. Des semis ont été plantés dans des milieux humides occupés par le *F. nigra* où quatre traitements du couvert forestier ont été appliqués : témoin non traité, coupe rase, annélation du *F. nigra* pour imiter la mortalité causée par l'AF et jardinage par groupe. La hauteur moyenne et le TCR en diamètre étaient dans l'ensemble plus rapides dans la coupe rase, suivie par l'annélation, le jardinage par groupe et le témoin. Selon l'espèce, le traitement a significativement influencé le TCR. Plusieurs espèces qui pourraient s'adapter au climat du nord du Minnesota ont eu des TCR moyens de modérés à rapides, incluant une espèce provenant de la zone climatique voisine au sud. Nos résultats indiquent que la plantation de semis et le traitement de l'étage dominant constituent une stratégie efficace visant à établir des espèces pour remplacer *F. nigra*, étant donné l'arrivée de l'AF, tout en réduisant les risques futurs associés au changement climatique. [Traduit par la Rédaction]

Mots-clés : agrile du frêne, milieux humides occupés par le frêne noir, régénération artificielle, espèces invasives, changement climatique.

Introduction

Fraxinus nigra Marsh. (black ash), a dominant tree species of the North American wetland forests that range from southeastern Canada (Scott 1995) to the western Great Lakes region of the U.S. and occur extensively in northern Minnesota (Erdmann et al. 1987), is imperiled by the invasive insect emerald ash borer (EAB; *Agrilus planipennis* Fairmaire, 1888). EAB causes lethal girdling damage in all North American *Fraxinus* species (Herms and McCullough 2014). Over 99% of *Fraxinus* trees with a diameter ≥ 2.5 cm died within a decade in EAB-affected southern Michigan

mixed hardwood forests (Herms and McCullough 2014), with few or no newly germinated *Fraxinus* seedlings observed on heavily infested sites (Klooster et al. 2014). While cold winter temperatures appear to slow the intensity of invasion (DeSantis et al. 2013), the regional climate is rapidly warming (Pryor et al. 2014). Thus, in a worst-case scenario, the continued spread of EAB could result in the functional loss of *F. nigra* from the wetland forests that it presently dominates (Pugh et al. 2011).

Tolerant of prolonged seasonal ponding (Erdmann et al. 1987), *F. nigra* helps regulate ecosystem processes by lowering summer

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water tables through evapotranspiration, thus reducing competition from the herbaceous layer and aiding survival of associated tree species (Slesak et al. 2014). Tree species such as *Acer rubrum* L. (red maple), *Betula alleghaniensis* Britton (yellow birch), *Thuja occidentalis* L. (northern white cedar), and *Ulmus americana* L. (American elm) are often minor components of *F. nigra* forests, although advance regeneration of these species is generally low (Palik et al. 2011). Consequently, if *F. nigra* is lost to EAB invasion, few naturally occurring species are poised to replace it (Looney et al. 2015).

Silvicultural treatments such as harvesting and seedling plantings may be critical to maintaining tree cover and ecosystem function following EAB invasion of *F. nigra* wetlands (Iverson et al. 2016). While harvest treatments can promote seedling growth by removing overstory leaf cover that blocks available light from reaching the forest floor (Smith et al. 1996), research suggests that the complete loss of the *F. nigra* overstory to preemptive salvage logging or EAB could raise the water table, invigorate the herbaceous layer, and potentially limit tree seedling establishment (Slesak et al. 2014). The creation of small gaps in the forest canopy via group selection could minimize changes in site hydrology (Slesak et al. 2014), while potentially enhancing light availability to boost seedling growth (Smith et al. 1996). However, a 2-year study in a southeastern Michigan mixed *Fraxinus* spp. forest found no increase over time in understory light availability (measured as gap fraction) in small, hydric plots following loss of the *Fraxinus* overstory (Klooster 2012). It is unclear to what degree partial harvesting or EAB-induced mortality would affect canopy openness over time in northern Minnesota's more expansive *F. nigra* wetland stands.

Beyond the threat of EAB, climate change is predicted to impact upper Great Lakes forests, potentially increasing the frequency and intensity of floods, droughts, and outbreaks of forests pests (Iverson et al. 2016). One projected effect is a reduction in growing-season, wetland water budgets due to increased evapotranspiration from warming temperatures (Galatowitsch et al. 2009). Such a reduction could potentially benefit associated tree species less tolerant of the hydric soil conditions in *F. nigra* wetlands (Iverson et al. 2016). At the same time, suitable climate locales for many tree species are predicted to shift northeastward (Iverson et al. 2008), further threatening the potential for co-occurring tree species to replace *F. nigra*. This scenario suggests that forestry-related assisted range expansion of potential *F. nigra* replacement species should be explored (Looney et al. 2015). Forestry-related assisted range expansion, which proposes northeasterly relocation of tree species within a few hundred kilometres of their current range limits (Pedlar et al. 2012), could promote species capable of maintaining both tree cover and ecosystem function while reducing future risk from climate change (Iverson et al. 2016).

While no research to date has examined the growth response of planted seedlings of non-EAB-host species in *F. nigra* forests, in a related study, we previously investigated overstory treatment effects on seedling survival (Looney et al. 2015). We found that seedling survival was lowest in clearcuts but roughly equivalent for all species except shade-intolerant *Populus balsamifera* L. (balsam poplar) in unharvested controls, group selections, and girdling treatments, the latter of which were used to emulate multiyear EAB mortality (Looney et al. 2015). Conifer species had low overall rates of survival, while a species whose native range does not presently overlap with northern *F. nigra* forests had a high rate of survival (Looney et al. 2015). However, initial seedling survival does not necessarily translate into an advantage in growth and longer term recruitment to the sapling phase (Shipley et al. 1989).

Therefore, in the current study, we investigated the relative growth response of 10 potential *F. nigra* replacement tree species, several of which are projected to be well adapted to the future climate in northern Minnesota, including two species from the next southern climate zone (Iverson et al. 2016). Seedlings were planted in *F. nigra* wetlands in four canopy treatments: control

(unharvested forest), clearcut (preemptive removal of all trees), girdling of *F. nigra* (to emulate EAB mortality), and group selection (partial canopy removal to facilitate transition to replacement species). Our objectives were to determine (*i*) the effects of simulated EAB-induced mortality and harvesting on canopy openness, as indicated by the leaf area index, (*ii*) the influence of overstory changes from EAB and harvesting on the height and diameter RGR of planted seedlings of *F. nigra* replacement species, and (*iii*) the most promising combination of species and treatment for management strategies to mitigate the effects of EAB under a warming future climate. We predicted that (1) treatment intentions would be confirmed by finding canopy openness lowest in the control, low to intermediate in the group selection, high to intermediate in the girdling, and highest in the clearcut treatment, once girdling-induced ash mortality was complete, (2) RGR would increase with canopy openness for shade-intolerant species such as *P. balsamifera*, while shade-tolerant species such as *A. rubrum* (Niinemets and Valladares 2006) would have relatively higher RGR only in the controls, and (3) group selection and possibly girdling treatments, assuming a shelterwood effect, would support relatively high RGR for a mix of species by providing increased light while limiting the water table rise.

Materials and methods

Study sites and overstory treatments

Study sites were located in *F. nigra* wetlands on the Chippewa National Forest in northern Minnesota, USA (Looney et al. 2015). Climate is continental, with most rainfall occurring during the May–September growing season (PRISM Climate Group 2015). For the 1981–2010 period, mean temperature averaged –13.7 and 16.5 °C in January and July, respectively, while mean precipitation averaged 742 mm·year^{-1} (PRISM Climate Group 2015). The study sites are classified as northern wet *Fraxinus* swamp (WFn55) and northern very wet *Fraxinus* swamp (WFn64) according to native plant community classification for the state of Minnesota (Minnesota Department of Natural Resources (MNDNR) 2003). Soils within the study area are classified as Morph Series: Fine-loamy, mixed, superactive, frigid Typic Glossaqualfs and Wildwood Series: Very-fine, smectitic, non-acid, frigid Histic Humaquepts (Soil Survey Staff, Natural Resources Conservation Service, USDA, 2016). A confining clay layer and flat topography result in poor drainage and spring ponding, with water tables usually falling below the surface by mid-July (Slesak et al. 2014).

Within the study area, we identified eight experimental blocks for treatment installation. Dominant canopy tree age ranged from 150 to 274 years. Pretreatment basal area for trees > 10.0 cm diameter at breast height (DBH) averaged 20.7 ± 2.2 m²·ha^{-1}, with mean tree density of 477 ± 50.6 trees·ha^{-1} (Looney et al. 2015). As the dominant overstory species, *F. nigra* comprised 91% of basal area, with minor components of *Abies balsamea* L. (balsam fir), *Populus tremuloides* Michx. (quaking aspen), *Quercus macrocarpa* Michx. (bur oak), *Tilia americana* L. (American basswood), and *U. americana* (Looney et al. 2015). Midstory shrub species included *Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) Clausen (speckled alder), *Corylus cornuta* Marshall (beaked hazel), and *Acer spicatum* Lam. (mountain maple) (Looney et al. 2015).

In each block, four 1.62 ha (71.8 m radius) circular plots were established. We randomly assigned each plot to one of four treatments: control, clearcut, girdling, and group selection. The control plot was left as unharvested forest. The clearcut treatment was used to evaluate the effects of preemptive removal of all *F. nigra* prior to EAB invasion. The girdling treatment was applied to all *F. nigra* ≥ 6 cm DBH over a 2-year period to emulate multiyear EAB-induced mortality. The group selection treatment, which consisted of eight 0.04 ha (400 m²) circular gaps totaling approximately 20% of plot area, was used to test the efficacy of partial overstory removal to promote seedling growth while limiting the

Table 1. Scientific name, tree species code, stock type, average mean height (±SE), and average basal diameter (±SE) for seedlings of 10 potential *F. nigra* replacement species.

Species	Code	Stock type	Mean height (cm)	Mean basal diameter (mm)
Acer rubrum (planted in 2011)	ACRU	Container (90 cm³)	17.4±4.2	3.7±0.2
Acer rubrum (planted in 2012)	ACRU	Bareroot (1 + 0)	27.5±10.1	4.6±0.3
Celtis occidentalis	CEOC	Container (336 cm³)	37.4±2.1	4.6±0.2
Fraxinus mandshurica	FRMA	Bareroot (3 + 0)	68.3±2.5	9.8±0.3
Larix laricina	LALA	Container (60 cm³)	44.9±2.0	4.7±0.2
Picea mariana	PIMA	Container (90 cm³)	45.3±1.7	4.4±0.1
Populus balsamifera	POBA	Container (164 cm³)	50.8±2.8	5.0±0.3
Populus deltoides	PODE	Bareroot (1 + 0)	60.7±3.3	5.7±0.3
Quercus bicolor	QUBI	Bareroot (1 + 0)	33.5±1.5	5.3±0.2
Thuja occidentalis	THOC	Container (60 cm³)	24.2±1.9	3.3±0.2
Ulmus americana	ULAM	Container (1890 cm³)	103.0±3.3	11.2±0.3

Note: Code = USDA Forest Service FIA tree species code. Under "stock type", values in parentheses correspond to container volume for containerized seedlings and number of years spent in nursery and transplant beds for bareroot stock. Mean height and diameter measurements were taken at the start of the growth study period in fall 2013.

water table rise associated with clearcutting (Erdmann et al. 1987). All treatments were installed in late winter 2012 under frozen ground conditions (Looney et al. 2015).

Species selection and planting

We planted seedlings of 10 species, seven of which were native to northern Minnesota *F. nigra* forests: *A. rubrum*, *Larix laricina* (Du Roi) K. Koch (tamarack), *Picea mariana* (Mill.) BSP (black spruce), *P. balsamifera*, *Populus deltoides* W. Bartram ex Marshall (eastern cottonwood), *T. occidentalis*, and *U. americana*. We also planted two species from the next southern climate zone that are projected to have increased suitability to northern Minnesota under a warming future climate (Iverson et al. 2008): *Celtis occidentalis* L. (hackberry), which occurs in isolated populations 80 km southwest of the study area (Prasad et al. 2007), and *Quercus bicolor* Willd. (swamp white oak), an often dominant wetland forest species with a northern range limit approximately 150 km southwest of the study sites (Prasad et al. 2007). Finally, we planted seedlings of *Fraxinus mandshurica* Rupr. (Manchurian ash), an Asian species with resistance to EAB and growth form similar to *F. nigra*, which is being tested in efforts to hybridize EAB-resistant Asian – North American ash cultivars (Koch et al. 2012). Shade-intolerant species included *L. laricina*, *P. balsamifera*, and *P. deltoides*, while shade-tolerant species included *A. rubrum*, *C. occidentalis*, *F. mandshurica*, *P. mariana*, *Q. bicolor*, *T. occidentalis*, and *U. americana* (Niinemets and Valladares 2006). *Betula alleghaniensis* Britton (yellow birch) and *P. tremuloides* were also planted but were excluded from the growth analysis due to insufficient survival (Looney et al. 2015). Seedlings of *A. rubrum*, *C. occidentalis*, *L. laricina*, *P. mariana*, *P. deltoides*, and *T. occidentalis* were planted both before harvesting in 2011 and after harvesting in 2012. Seedlings of *Q. bicolor*, *P. balsamifera*, *F. mandshurica*, and *U. americana* were planted only after harvesting in 2012. For the 2011 plantings, we assumed that a winter snowpack would protect the seedlings from mechanical harvesting damage (Looney et al. 2015).

Seedlings of *A. rubrum*, *L. laricina*, *P. mariana*, *P. balsamifera*, *P. deltoides*, and *T. occidentalis* were from locally adapted seed sources, while *C. occidentalis* and *Q. bicolor* were from seed sources from adjacent climate zones. *Ulmus americana* stock was bred for tolerance to Dutch elm disease (*Ophiostoma novo-ulmi* Brasier) by USDA Forest Service researchers through controlled pollination between surviving trees on the Chippewa National Forest and the Dutch elm disease tolerant 'Valley Forge' cultivar of *U. americana* (Slavicek and Knight 2012). Chinese seed stock was used for *F. mandshurica*. All seedling stock was obtained from local commercial nurseries, with the exception of *U. americana*, which was obtained from the USFS Toumey Nursery in Watersmeet, Michigan, and *F. mandshurica*, which was obtained from a commercial nursery in Plains, Montana. Planting stock type differed among

species (Table 1). Containerized seedlings were used for *C. occidentalis*, *L. laricina*, *P. mariana*, *P. balsamifera*, *T. occidentalis*, *U. americana*, and the 2011-planted *A. rubrum* (Looney et al. 2015). Bareroot seedlings were used for *F. mandshurica*, *P. deltoids*, *Q. bicolor*, and the 2012-planted *A. rubrum* (Looney et al. 2015). Stock size also differed among species (Table 1), with containerized seedlings of *P. balsamifera*, *C. occidentalis*, and, in particular, *U. americana* larger than seedlings of other species (Looney et al. 2015).

Six 0.04 ha (400 m²) subplots were established to serve as planting areas within each of the 1.62 ha treatment plots. We randomly distributed subplots in the control, girdling, and clearcut treatments, while in the group selection treatment, four subplots were centered in canopy gaps and two were located in the unharvested matrix. A planting bar was used to plant eight rows of seedlings on the western half of each 0.04 ha subplot. Seedlings were spaced 1.25 m apart within rows, with 2.5 m between rows. Species were randomly allocated to locations within rows in each planting frame and planted on the closest favorable microsite, avoiding wet hollows as allowed by site topography. Due to delayed availability, *U. americana* and *F. mandshurica* were always located at the ends of planting rows. For all species but *U. americana*, 1536 seedlings were planted, distributed as 48 seedlings per species per treatment plot and 8 seedlings per species per planting subplot. For *U. americana*, 768 seedlings were planted, distributed as 24 seedlings per species per plot and four seedlings per subplot (Looney et al. 2015).

Data collection

Leaf area index

We used hemispherical photography within each treatment replicate in July 2013 and July 2015 to assess leaf area index (LAI), which was used as an indicator of overstory cover (Jonckheere et al. 2004). We used a Canon EOS 5D mark II set on aperture priority mode with a Belomo 8 mm fisheye lens, at a tripod height of 1.37 m, which yielded a field of view of 180° and circular image on the 35 mm sensor format. We took photographs from 30 min before sunset to dusk on days with direct sun conditions. We also photographed throughout the day in overcast, diffuse sun conditions. We used a systematic sampling of 12 photo points evenly spaced within each treatment replicate and buffered 10 m from treatment edge. The photo point sampling protocol was applied without variation to all treatments, including the group selection, to accurately assess LAI across the entire area of the treatment replicates. We used Gap Light Analyzer software (Frazer et al. 1999) to estimate LAI and processed images based on a 75° zenith angle to account for midstory foliage. Blue channel images were used to improve distinction between sunlit foliage and sky.

Table 2. Summary of confidence set models for height and diameter growth, based on the Akaike information criterion (ΔAIC ≤ 8).

Response	Factors	AIC	ΔAIC	Relative likelihood	Weights	Evidence ratio
LAI	Treatment	−2184.00	0.00	1.00	0.53	1.00
LAI	Treatment, year	−1.96	0.22	0.89	0.47	1.12
LAI	Null	125.75	127.93	0.00	0.00	>1000
Height RGR	Treatment, species, treatment × species	−2317.96	0.00	1.00	1.00	1.00
Height RGR	Null	−877.42	1440.54	0.00	0.00	>1000
Diameter RGR	Treatment, species, treatment × species	−9554.97	0.00	1.00	1.00	1.00
Diameter RGR	Null	−7407.23	2147.74	0.00	0.00	>1000
Height RGR: group selections	Species, position	−609.73	0.00	1.00	1.00	1.00
Height RGR: group selections	Species	−608.76	0.97	0.62	0.38	2.62
Height RGR: group selections	Null	−120.36	489.37	0.00	0.00	>1000
Diameter RGR: group selections	Species, position	−3000.10	0.00	1.00	1.00	1.00
Diameter RGR: group selections	Null	−2410.60	589.50	0.00	0.00	>1000

Note: Model terms are provided for each model, as well as information-theoretic support compared with the most plausible model in the set.

Seedling measurement

We assessed seedling root collar diameter and height in fall (September–November) 2013, one year after the final plantings, and again in 2015. We used digital calipers to obtain two opposing diameter measurements per stem, which we later averaged. For seedlings with multiple stems at soil level, we recorded the height of each stem while calculating an equivalent root collar diameter based on total stem basal area (Chojnacky and Rogers 1999). We recorded heights of each individual stem originating at or below ground level but used the height of the tallest living stem for analytical purposes. Seedlings were assessed for the presence or absence of deer browse damage in spring 2013, 2014, and 2015.

Analytical methods

To quantify treatment effects on the overstory, we examined LAI for 2013 and 2015. The analysis of LAI included year, treatment, and year × treatment effects as potential factors in candidate models. We examined 2-year height and diameter for 2013 to 2015. We used RGR, based on the differences of natural logarithms of seedling sizes in 2013 and 2015, as the response metric to help control for between-species variation in seedling size (Hunt and Cornelissen 1997). We did not find it necessary to transform height RGR, diameter RGR, or LAI to meet model assumptions. Potential predictors of RGR included species, overstory treatment, absence or presence of browse damage in 2013, and interactions between these factors. Preliminary analysis showed that deer browse did not have a significant influence on either height or diameter RGR; therefore, we excluded browse from the final models. For LAI, as well as for seedling height and diameter RGR, we used multilevel mixed-effects regression to analyze the blocked, repeated measures, split plot design, in which species were nested within overstory treatments. We treated individual treatment replicates as LAI sample units, with repeated LAI measurements (2013 and 2015) nested within each unit. We further analyzed the group selection treatment individually in a separate series of models to examine the effects of planting position (matrix vs. group) on seedling growth by species.

We performed mixed-effects modeling using the nlme package (Pinheiro et al. 2016) for R. For the analysis of seedling growth, random effects included the block effect, as well as seedling plots nested within blocks. For the analysis of LAI, block was the only random effect. We examined plots of model residuals vs. fitted values to evaluate model fit.

We used the Akaike information criterion (AIC) and the information-theoretic approach to evaluate model parsimony rather than base model selection on strict hypothesis tests (Burnham and Anderson 2003). We constructed multiple competing models of LAI, study-wide seedling height and diameter RGR, and seedling RGR within group selections. For each response variable, we compared models with a null, intercept-only model. For model terms with substantial AIC support, we used Tukey's HSD to make post

hoc comparisons of individual factor levels. We also report F-test results for models with high AIC support based on marginal sums of squares.

Results

Leaf area index by treatment

The best-supported LAI model included overstory treatment as the sole predictor but was nearly equivalent to a model that included a year term (ΔAIC = 0.22; Table 2). A model including both year and a year × treatment effect did not have substantial AIC support, defined as ΔAIC ≤ 8 (Burnham and Anderson 2003). In the best-supported LAI model, treatment was a significant predictor (F = 282.5, p < 0.001). Treatment was also a significant predictor in the second-best supported LAI model (F = 288.6, p < 0.001), as was the year effect (F = 10.3, p = 0.018). LAI was lowest in the clearcut, followed by the girdling, group selection, and control treatments (Fig. 1). The model including a year effect suggested that study-wide LAI increased slightly from 2013 to 2015 (Fig. 1), even in the girdling treatment, where *F. nigra* mortality was not complete until 2014 and *F. nigra* sprouts were removed annually. LAI in the clearcut, girdling, and group selection treatments measured 11%, 69%, and 82%, respectively, of LAI in the controls (data not shown).

Overall relative growth rates by treatment

The most parsimonious models of both mean seedling height and diameter RGR for all species combined included species, treatment, and species × treatment. No other competing models for either mean overall height or diameter RGR had substantial AIC support (ΔAIC > 8; Burnham and Anderson 2003). In the best-supported height RGR model, tests of species (F = 45.1, p < 0.001), treatment (F = 13.4, p < 0.001), and species × treatment (F = 11.1, p < 0.001) were significant. The best-supported diameter RGR model also had significant tests for species (F = 126.3, p < 0.001), treatment (F = 7.4, p < 0.001), and species × treatment (F = 11.0, p < 0.001). Within group selections, the best-supported models of both mean overall height and diameter RGR included species and planting position (gap vs. untreated matrix). No other models of mean overall height or diameter RGR within the group selections had substantial AIC support. Species was a significant predictor in both the best-supported group selection models of height RGR (F = 93.3, p < 0.01) and diameter RGR (F = 86.9, p < 0.001). Planting position was also a significant predictor in the best-supported height RGR (F = 12.4, p < 0.001) and diameter RGR (F = 46.7, p < 0.001) models.

For all species combined, the clearcut and girdling treatments had fast and relatively comparable mean height RGR (Fig. 2), although mean diameter RGR was slightly slower in the girdling treatment than in the clearcut. The group selection treatment supported moderate mean overall height and diameter RGR, while mean overall height and diameter RGR in the control treat-

Fig. 1. Mean leaf area index (LAI) for four overstory treatments (mean ± 95% confidence intervals) on *F. nigra* wetland forest study sites in northern Minnesota, USA, in the summers of 2013 and 2015. This figure illustrates the more complex, second-best supported model of LAI. The best-supported model eliminated the year effect, but treatment means over the duration of the study were intermediate between the two sets of values shown here. Letters adjacent to species summarize pairwise comparisons of treatments. Levels not connected by the same letter are significantly different ($p < 0.05$).

Fig. 2. Mean 2-year overall relative growth rate (RGR) for height (cm·cm⁻¹·year⁻¹) and diameter (mm·mm⁻¹·year⁻¹) by treatment for seedlings of potential *F. nigra* replacement species planted in the northern Minnesota *F. nigra* wetland forest (±95% confidence intervals). RGR was based on fall 2015 measurements relative to fall 2013. Letters adjacent to species summarize pairwise comparisons of treatments. Levels not connected by the same letter are significantly different ($p < 0.05$).
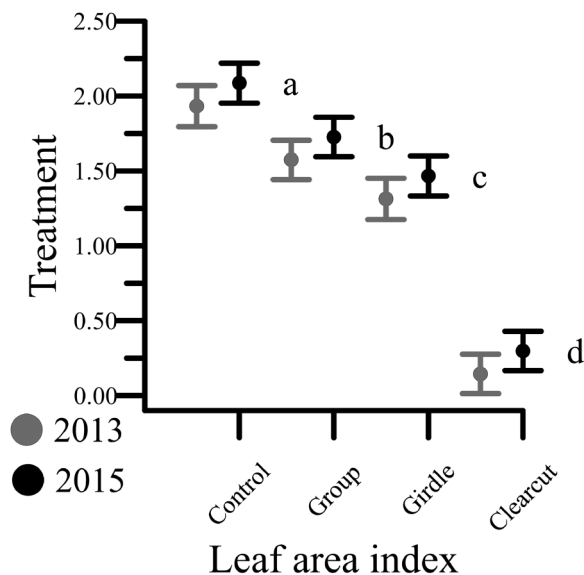
ment was slow but significantly greater than zero. Within the group selection treatment, mean overall height RGR was faster for seedlings positioned within gaps (0.76 cm·cm⁻¹·year⁻¹ ± 0.01) than within the untreated matrix (0.38 cm·cm⁻¹·year⁻¹ ± 0.01), although we found nearly equivalent support ($\Delta AIC = 0.97$) for a model that included species but not seedling position. Mean overall diameter RGR was approximately 50% faster for seedlings planted in gaps (0.09 mm·mm⁻¹·year⁻¹ ± 0.01) than for seedlings planted in the matrix (0.06 mm·mm⁻¹·year⁻¹ ± 0.01; data not shown).

Species by treatment
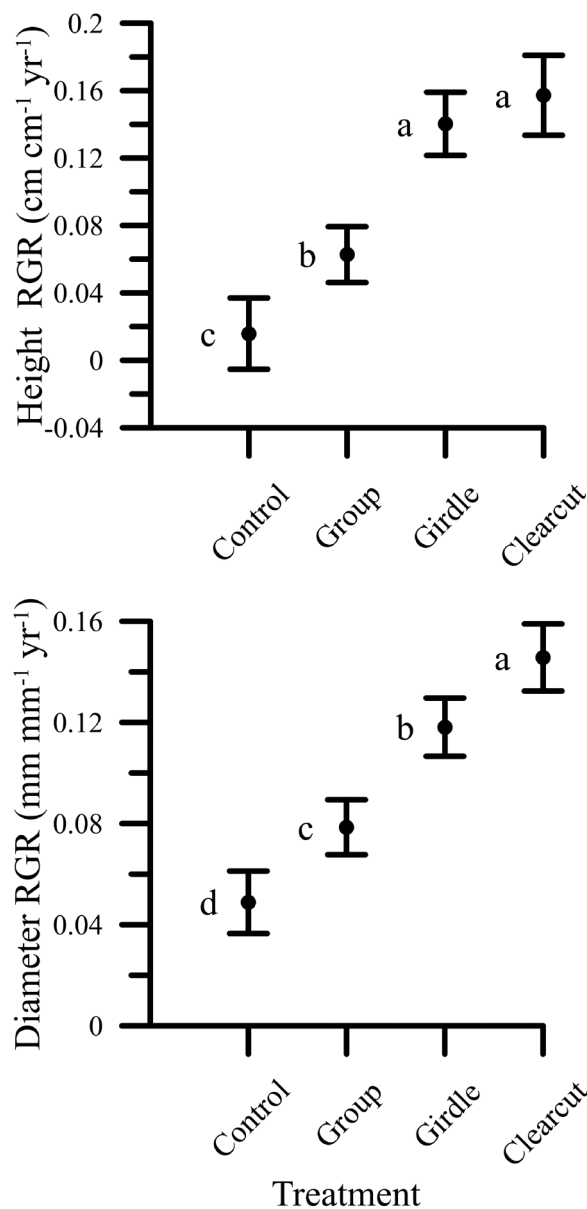
Height RGR

In the control treatment, only *L. laricina*, *P. balsamifera*, *Q. bicolor*, and *A. rubrum* displayed mean height RGR significantly greater than zero (Fig. 3). Mean height RGR for *P. deltoides*, *P. mariana*, *T. occidentalis*, and *C. occidentalis* did not significantly differ from zero, while both *U. americana* and *F. mandshurica* showed significant height loss.

In the clearcut treatment (Fig. 3), *P. balsamifera* and *L. laricina* had the fastest mean height RGR, significantly faster than the third-ranking species, *P. deltoides*. *Thuja occidentalis*, *A. rubrum*, *U. americana*, and *Q. bicolor* had moderate mean height RGR, whereas mean height RGR was minimal (and sometimes negative due to tip dieback) for *F. mandshurica* and *C. occidentalis*.

Within the girdling treatment (Fig. 3), the species with the fastest mean height RGR were *P. balsamifera*, *P. deltoides*, *L. laricina*, and *A. rubrum*. Mean height RGR was slower but still significantly greater than zero for *Q. bicolor*, *F. mandshurica*, *P. mariana*, *U. americana*, and *C. occidentalis*. *Thuja occidentalis* was the only species whose mean height RGR in the girdling treatment was not significantly greater than zero.

Mean height RGR by species was generally slower in the group selection than in clearcut or girdling treatments (Fig. 3). In the group selection treatment, the fastest mean height RGR occurred

in *P. balsamifera*, *L. laricina*, *P. deltoides*, and *Q. bicolor*. Mean height RGR was slow but significantly greater than zero for *A. rubrum* and *T. occidentalis*, not significantly greater than zero for *P. mariana*, *C. occidentalis*, and *U. americana*, and negative for *F. mandshurica*.

Diameter RGR

In the control treatment (Fig. 4), *P. balsamifera* had the fastest mean diameter RGR, followed by *A. rubrum* and *L. laricina*. Mean diameter RGR was slow but significantly greater than zero for *Q. bicolor*, *T. occidentalis*, *U. americana*, and *C. occidentalis*. Mean diameter RGR for *P. deltoides*, *P. mariana*, and *F. mandshurica* was not significantly greater than zero.

Fig. 3. Interaction plot showing mean 2-year species by treatment relative growth rate (RGR) for height (cm·cm^{-1}·year^{-1}; ±95% confidence intervals) for seedlings of 10 potential *F. nigra* replacement species planted in the *F. nigra* wetland forest. Species are displayed on the *y* axis for visibility. RGR was based on fall 2015 measurements relative to fall 2013. Letters adjacent to species summarize pairwise comparisons of species within treatments. Levels not connected by the same letter are significantly different ($p < 0.05$). See Table 1 for species abbreviations.
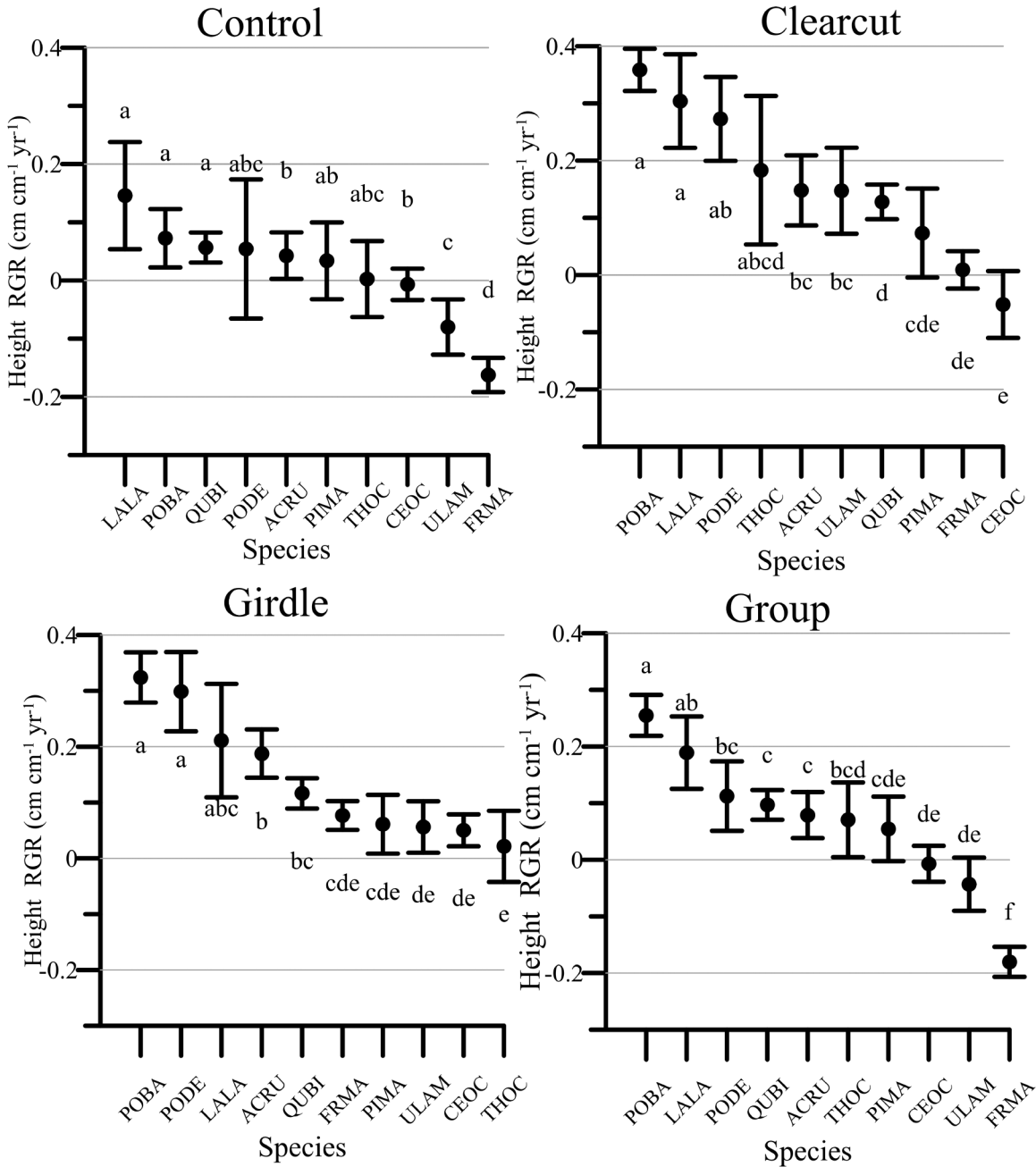
In the clearcut treatment (Fig. 4), *P. balsamifera* had the fastest mean diameter RGR, followed by *P. deltoides* and *L. laricina*. Mean diameter RGR was more moderate for *Q. bicolor*, *U. americana*, *T. occidentalis*, *P. mariana*, and *A. rubrum*. Diameter RGR was slower but significantly greater than zero for *F. mandshurica* and *C. occidentalis*.

In the girdling treatment, *P. balsamifera*, *P. deltoides*, and *L. laricina* had the fastest mean diameter RGR (Fig. 4). Mean diameter RGR was moderate for *A. rubrum*, *Q. bicolor*, *U. americana*, and *T. occidentalis*. *Thuja occidentalis*, *C. occidentalis*, *P. mariana*, and *F. mandshurica* had the slowest mean diameter RGR in this treatment, although their growth rates were significantly greater than zero.

In the group selections, *P. balsamifera* again had the fastest mean diameter RGR, followed by *L. laricina*, *P. deltoides*, and *Q. bicolor*. Mean diameter RGR was slower but significantly greater than zero for *A. rubrum*, *P. mariana*, *T. occidentalis*, *U. americana*, and *C. occidentalis*. For *F. mandshurica*, mean diameter RGR was not significantly greater than zero.

Discussion

Overall, we found that seedlings planted in clearcuts had the fastest mean height and diameter RGR, with growth rates generally declining as treatment LAI increased from girdling to group

Fig. 4. Interaction plot showing mean 2-year species by treatment relative growth rate (RGR) for diameter (mm·mm⁻¹·year⁻¹; ±95% confidence intervals) for seedlings of 10 potential *F. nigra* replacements species planted in the *F. nigra* wetland forest. Species are displayed on the *y* axis for visibility. RGR was based on fall 2015 measurements relative to fall 2013. Letters adjacent to species summarize pairwise comparisons of species within treatments. Levels not connected by the same letter are significantly different ($p < 0.05$). See Table 1 for species abbreviations.
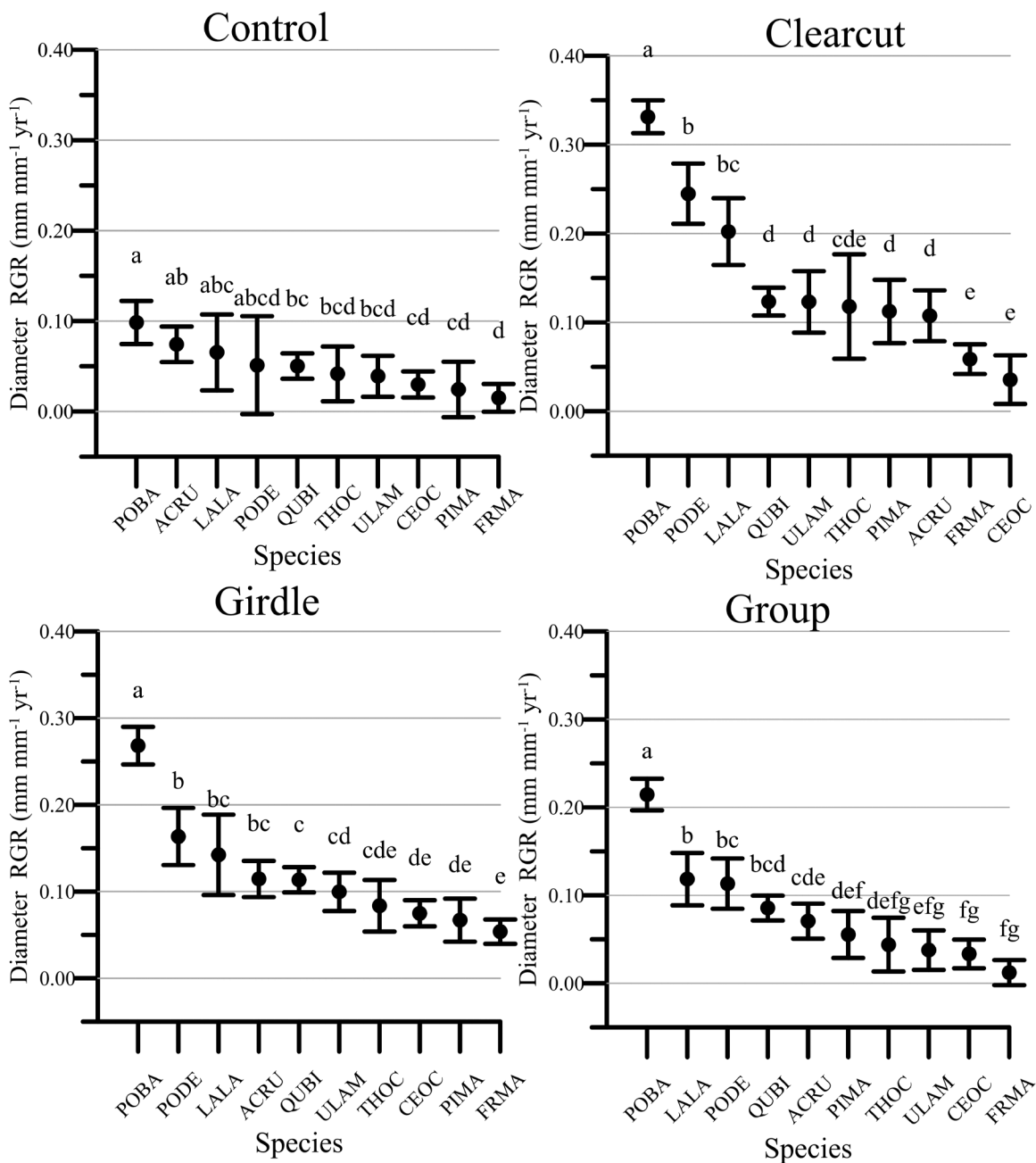
selection to control treatments. Mean height and diameter RGR were strongly influenced by an interaction between species and overstory treatment. In terms of individual species, *P. balsamifera* had the fastest rates of mean height and diameter RGR in all treatments except the controls, where it ranked second for height RGR. While these results suggest great potential for this species, mean RGR must be weighed against survival and projected shifts in suitable future habitat with changing climate when determining the most favorable combination of treatment and *F. nigra* replacement species to mitigate the impacts of EAB. In the discussion that follows, we consider these factors, drawing on the results of an earlier study of seedling survival from the same experiment (Looney et al. 2015).

Leaf area index and overall relative growth rates by treatment

Untreated control plots had relatively low LAI compared with other regional forest types, with mean LAI less than 50% that of nearby *A. rubrum* forests (Fassnacht and Gower 1997). While many regional *F. nigra* stands have experienced ash decline and canopy dieback (Palik et al. 2011), this was not the case on our study stands, so these lower values likely reflect the more open conditions of wetland forests and low tree-level LAI associated with even healthy *F. nigra*. Despite relatively open canopies compared with some other forest types (Fassnacht and Gower 1997), canopy cover, as indicated by LAI, nevertheless appeared high enough to suppress mean RGR for all species, which was slower in the con-

trol than in the clearcut, girdling, or group selection treatment. Low overall mean RGR in the control contrasted with our earlier study's finding of relatively high overall survival (32.9% ± 0.7%) in this treatment (Looney et al. 2015). Intact canopies may initially benefit seedling survival by suppressing competing vegetation but will hinder growth and survival over time in the boreal forest (Lieffers et al. 1996).

Clearcuts, which involved the removal of living trees and snags, as well as the incidental reduction of midstory shrubs, had the lowest LAI of any treatment. Although harvested *F. nigra* vigorously resprouted (Slesak et al. 2014), LAI in clearcuts measured just 11% of LAI in unharvested controls at the end of the study. Clearcut treatments also had the highest mean overall height and diameter RGR, largely driven by shade-intolerant species, which generally perform best in the open conditions (Youngblood and Titus 1996). In contrast, our related work found that the clearcut treatment had lowest overall seedling survival (22.1% ± 0.6% compared with 30.7% ± 0.3% for all treatments combined; Looney et al. 2015). Higher initial seedling mortality but faster mean RGR in the clearcut treatment may reflect elimination of seedlings from harsher microsites (Jones and Sharitz 1998) and (or) competition from an observed increase in herbaceous vegetation (Slesak et al. 2014).

The girdling treatment, used to emulate multiyear EAB-induced mortality, left a substantial amount of residual cover, as indicated by LAI measurements that were only 30% lower than controls. Girdling treatment LAI increased slightly along with that of other treatments between 2013 and 2015, despite complete mortality of the ash canopy by 2014 and annual removal of *F. nigra* sprouts (Slesak et al. 2014). In a 2-year study, Klooster (2012) similarly found that understory light availability did not increase over time in response to EAB-induced *Fraxinus* mortality on hydric sites in southeastern Michigan forests. Because girdling did not remove midstory shrubs, their leaf production may have been stimulated by increased light, offsetting the loss of overstory LAI. Girdling treatments supported mean overall RGR second only to the clearcuts. In our earlier study, we found that girdling treatments supported overall relatively high survival (33.3% ± 0.7%) of a mix of tree species (Looney et al. 2015). While Slesak et al. (2014) observed significant water table rise and high graminoid cover in clearcut treatment one year after harvesting, they noted that water table rise did not reach similar levels in the girdling treatment until the second year. The greater residual LAI of the girdle treatment also appeared to suppress herbaceous layer height growth and graminoid cover relative to the clearcut treatment (C.E. Looney, unpublished data). Depending on the intensity of infestation (Klooster et al. 2014), multiyear EAB-induced mortality could potentially provide a shelterwood effect that permits seedlings to survive to sufficient size to withstand the slightly delayed water table rise (Slesak et al. 2014).

Group selection resulted in a more moderate reduction in overstory cover, as indicated by an 18% reduction in LAI. LAI increased between years at a rate similar to that of other treatments, suggesting that rapid gap closure from lateral canopy growth did not occur. Nonetheless, the group selection treatment had the slowest mean overall RGR of any treatment but the control. In comparison, we previously found relatively comparable overall survival in group selection (34.5% ± 0.7%), girdling (33.3% ± 0.7%), and control (32.9 ± 0.7%; Looney et al. 2015). Because only four of the six planting subplots in the group selection treatment were situated within gaps, mean LAI above the seedlings was lower than indicated by the systematic LAI sampling, which did not directly overlap with the randomly located seedling plots. Further analysis revealed some evidence of greater mean overall RGR in gaps but nearly equivalent AIC support for seedling species alone as the factor responsible for RGR differences within group selections. The modest gap sizes used in this treatment, the study area's high latitude, and a surrounding matrix of mature trees likely limited

seedling exposure to direct sunlight (Canham et al. 1990) and, thereby, the effectiveness of this treatment in increasing RGR.

Species by treatment

Populus balsamifera had the fastest mean height RGR in all treatments except the controls, where it ranked second, as well as the fastest mean diameter RGR in all treatments. In our companion study, *P. balsamifera* had moderate overall survival (36.0% ± 1.2%) (Looney et al. 2015). These findings support the observation that rapid growth appears to promote survival in *Populus* spp. (Kobe et al. 1995). Research into age structure and gap dynamics of *Populus* stands suggests that *P. balsamifera* may regenerate in the partial sun of gaps and form uneven-aged stands (Cumming et al. 2000). Although *P. balsamifera* is generally classified as shade-intolerant (Niinemets and Valladares 2006), comparatively low LAI in *F. nigra* stands may permit growth of this species even in controls at the cost of somewhat reduced survival (Looney et al. 2015). In contrast to the RGR and survival results, *P. balsamifera* may not be adaptable to northern Minnesota conditions under a warming climate (Iverson et al. 2008), suggesting that it may have limited long-term viability as an *F. nigra* replacement species.

The shade-intolerant species *L. laricina* (Niinemets and Valladares 2006) had among the fastest mean height and diameter RGR in every treatment, while shade-intolerant *P. deltoides* (Niinemets and Valladares 2006) had fast mean height and diameter RGR in all treatments but the controls. However, in the previous study, *L. laricina* and *P. deltoides* were among the species with the lowest survival, averaging just 9.6% ± 0.8% and 11.0% ± 0.7%, respectively, across all treatments (Looney et al. 2015). The small sample sizes of low-surviving species resulted in high levels of variation in RGR, as evidenced by the error bars in Fig. 3.

In contrast, shade-tolerant *A. rubrum* (Niinemets and Valladares 2006) had moderate mean height RGR in all treatments and fast to moderate diameter RGR in control, girdling, and group selection treatments. Our companion study found that *A. rubrum* had above-average survival in the control (33.3% ± 2.4%), girdling (29.6% ± 2.3%), and group selection (33.5% ± 2.4%) treatments (Looney et al. 2015). The combined results are in agreement with a general understanding of shade tolerance as a trade-off between survival in low light and potential for growth in open conditions (Kobe et al. 1995). *Acer rubrum* shows plasticity in growth allocation under different light regimes but often grows less rapidly than shade-intolerant species (Abrams 1998). *Acer rubrum* is projected to be adapted to the future climate of the northern Great Lakes region (Prasad et al. 2007) and, thus, could represent a viable present and future *F. nigra* replacement species.

Shade-intermediate *U. americana* (Niinemets and Valladares 2006), a species that was widespread in *F. nigra* forests before Dutch elm disease (Iverson et al. 2016), had among the highest survival (74.8% ± 2.1%) of all species in all treatments in our previous study (Looney et al. 2015). In the present study, mean height RGR was moderate in clearcut and girdling treatments but not significantly greater than zero in the control and group selection treatments. Mean diameter RGR was slow in all treatments, although significantly greater than zero. These results support the observation of Chen (1997) that height growth appears negatively correlated with shade tolerance, but the relationship between diameter growth and shade tolerance is less clear. Based on climate parameters alone, a large increase in habitat suitability and potential abundance is projected for *U. of americana* in the study region as the climate warms (Iverson et al. 2016). However, although we planted Dutch elm disease tolerant stock, it should be noted that there is a risk that the disease could overcome tolerance (Slavicek and Knight 2012). Consequently, while *U. americana* appears to be a viable *F. nigra* replacement species, it is uncertain whether planted seedlings could survive to occupy the overstory.

In addition to species native to our study ecosystems, we investigated the replacement potential of *C. occidentalis* and *Q. bicolor*,

species from the next southern climate zone that are projected to be adapted to the future climate of the northern Great Lakes region (Iverson et al. 2008). Although we previously found moderately high survival for *C. occidentalis* (52.9% ± 1.3%; Looney et al. 2015), the species showed limited mean RGR in all treatments. A dendrochronological study of *C. occidentalis* at its northern range limit in Quebec found growth declines in association with low maximum temperature and heavy precipitation (Houle and Bouchard 1990). In comparison, *Q. bicolor* had high mean survival (75.5% ± 1.1%; Looney et al. 2015) with moderately rapid mean height and diameter RGR across treatments, although partial overstory removal may be necessary for longer term seedling viability in northeastern *Quercus* species (Dey et al. 2008). Positive growth under the full sun and waterlogged conditions of the clearcuts is consistent with the results of a previous study conducted within *Q. bicolor*'s natural range (Kabrick et al. 2012). At present, the northern range limit of *Q. bicolor* may be defined by insufficient degree days for flower maturation rather than lack of cold tolerance (Morin et al. 2007). Given a projected increase in the length of northern Minnesota's growing season with warming climate (Iverson et al. 2016), *Q. bicolor* could represent a viable future *F. nigra* replacement species.

Finally, we evaluated the response of *F. mandshurica*, an Asian species that is EAB-resistant, to northern Minnesota *F. nigra* forest conditions. While we previously found high survival for *F. mandshurica* (73.3% ± 1.1%; Looney et al. 2015), mean height RGR for this species was significantly above zero only in the girdling treatment. A previous study of *F. mandshurica* in its native range suggests that the species may be sensitive to herbaceous competition (Wang et al. 2013). The decreased cover and delayed mortality of the girdling treatment may produce a shelterwood effect, allowing this species to outgrow the herbaceous layer prior to the senescence of the *F. nigra* canopy (Lieffers et al. 1996). Zero or negative growth might also be due to cold damage (Chen and Chen 1999), as we observed tip dieback (C.E. Looney, personal observation).

Other factors affecting seedling performance

An unusually low winter snowpack in 2011–2012 may have decreased protection of 2011-planted seedlings from harvesting machinery (Looney et al. 2015). In addition, limited snowpack increases soil freezing and frost heaving (Goulet 1995). Although frost heaving would likely have resulted in the outright mortality of most seedlings, some may have survived but suffered damage from root system loss or partial excavation (Goulet 1995).

Variations in seedling stock may also have contributed to differences in performance. Containerized seedlings may have a growth advantage over bareroot stock through reduced transplant shock (Wilson et al. 2007). Larger seedlings typically exhibit more rapid growth and are able to compete more effectively with herbaceous competition for light (Jobidon et al. 1998). Stature is likely also important in *F. nigra* wetlands as it reduces submergence of aboveground tissues during seasonal ponding (Knight et al. 2012). Additionally, we were only able to evaluate a single provenance of stock for each species. Matching stock to site requirements may improve planting success (Landis et al. 2010). It is recommended that future research evaluate the potential for assisted range migration of southern genotypes of *P. balsamifera* to northern Great Lakes *F. nigra* forests, as well as explore the potential growth benefits of herbaceous understory control to reduce competition (Wang et al. 2013).

Conclusions

Overstory treatment, in combination with species, influenced mean height and diameter RGR of planted seedlings in *F. nigra* wetlands in northern Minnesota, USA. Clearcutting promoted rapid mean RGR, especially of shade-intolerant species, but this treatment also precipitated an immediate rise in the water table

(Slesak et al. 2014), as well as low overall survival (Looney et al. 2015). Furthermore, flooded hardwood markets and or future quarantines of the movement of *F. nigra* lumber may render salvage harvesting uneconomical following EAB invasion (Herms and McCullough 2014). While our previous study found that planting in controls resulted in high survival, it appears unviable for long-term growth in the absence of some disturbance. However, results for the girdling treatments suggest that planting under undisturbed canopy once EAB invasion becomes imminent in a region may produce a shelterwood effect that delays water table rise and supports relatively high growth and survival for a variety of species. Group selection was no more effective than girdling in promoting growth but could potentially offset planting costs, assuming that timber markets are available, while encouraging better survival than the clearcut treatment. Species with a combination of moderate to rapid mean height and diameter RGR and relatively high survival, based on the results of our previous study, included *P. balsamifera* (all treatments), *A. rubrum* (all but the clearcut treatment), *Q. bicolor* (all treatments), and *U. americana* (clearcut and girdling treatments). When projected shifts in suitable habitat due to warming climate were also considered, *A. rubrum*, *Q. bicolor*, and *U. americana* appear viable under both present and future conditions, while *P. balsamifera* may represent only a near-term solution. It should further be noted that even if Dutch elm disease tolerant *U. americana* stock is used, there is a risk that the disease could overcome tolerance (Slavicek and Knight 2012).

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