Forest adaptation strategies aimed at climate change: Assessing the performance of future climate-adapted tree species in a northern Minnesota pine ecosystem

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ABSTRACT

Climate change is expected to impact the function, health, and productivity of many northern latitude forests, including North American mixed-pine ecosystems. Additionally, forest managers face increasing challenges to sustaining forests in the face of high uncertainty associated with response to climate change. The Adaptive Silviculture for Climate Change (ASCC) project was developed to provide operational-scale research opportunities to assess and demonstrate various adaptation approaches to forest management in regionally important forest types. The ASCC project framework includes three treatments (resistance, resilience, and transition) representing a gradient of silvicultural approaches aimed at climate change. The first of five ASCC installations is located on the Cutfoot Experimental Forest-Chippewa National Forest (CEF), Minnesota USA, in a mixed-species northern pine forest. Using habitat suitability models under projected future climates, as well as expert opinion, we chose eight future climate-adapted species for planting as part of the transition treatment, consisting of four native species to the CEF: eastern white pine (*Pinus strobus* L.), northern red oak (*Quercus rubra* L.), bur oak (*Quercus macrocarpa* Michx.), and red maple (*Acer rubrum* L.); and four novel species to the CEF: white oak (*Quercus alba* L.), bitternut hickory (*Carya cordiformis* Wangenh.), black cherry (*Prunus serotina* Ehrh.), and ponderosa pine (*Pinus ponderosa* C. Lawson). The seedlings were planted under two canopy conditions, a thinned matrix (14–18 $m^2\ ha^{-1}$ residual basal area) and 0.2-ha gap openings (through harvesting). We measured how overstory canopy conditions (gap openings versus a thinned matrix) and understory shrub/herbaceous cover affect species performance. We measured 45 plots over the course of three growing seasons (Spring 2016 – Fall 2018), taking measurements of seedling basal diameter and survival, as well as estimates of understory vegetation density. Our findings highlight strong variations in species performance across treatment conditions. While overstory canopy condition was found to be a weak predictor of seedling survival and growth, our results show post-treatment colonization of understory shrub/herbaceous cover being a strong predictor of seedling survival ($p < 0.001$), with 86.67% (± 8.04; 1 standard error) of seedlings surviving in the lowest understory cover class, and 74.23% (± 3.04) surviving in the highest understory cover class. Seedling growth did not appear affected by understory shrub/herbaceous cover. Additionally, growth and survival varied significantly among native and novel seedlings, with ponderosa pine exhibiting the highest growth rates at 0.31 cm cm^{-1} $year^{-1}$ (± 0.004), while also having the lowest survival of any species at 45.66% (± 1.2). Results from this study can be directly used by managers to inform planting decisions and species selections that align with management planning to promote forest health and sustainably in the face of climate change.

1. Introduction

Climate change is expected to impact the function, health, and sustainability of North American forest ecosystems (Frelich and Reich, 2010; D'Amato et al., 2011; Handler et al., 2014; Fisichelli et al., 2014; IPCC, 2014). Additionally, rapidly changing climate will likely increase the intensity and severity of disturbances such as wildfire, drought, and insect and disease outbreaks that impact these ecosystems (Hanson and Weltzin, 2000; Dale et al., 2001; Soja et al., 2007; Thompson et al., 2009), and add uncertainty as to how forest processes will respond to

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management efforts (Janowiak et al., 2014). One area of particular concern are the mixed-pine forests of the western Great Lakes region of North America, which range from southeastern Manitoba to western Ontario in Canada and central Minnesota to northern Michigan in the USA. These ecosystems, dominated by red pine (*Pinus resinona* Aiton), jack pine (*Pinus banksiana* Lamb.), and eastern white pine (*Pinus strobus* L.), along with a mix of other conifers and deciduous species, hold great ecological, social, and economic value (Ek et al., 2006; Gilmore and Palik, 2006).

Climate projections suggest that the mixed-pine forests of the western Great Lakes region will experience shifts in the seasonality of precipitation (Karl et al., 2008; Frelich and Reich, 2010) with shorter, and generally warmer, wetter winters (IPCC, 2014; Notaro et al., 2014). Additionally, recent climate change assessments suggest that these regions will experience increasing episodic precipitation and flood events, and prolonged dry periods during the growing season (IPCC, 2014; Melillo et al., 2014; Walsh, 2014). As a result, multiple studies have identified potentially significant changes to the future range and distribution of tree species found in these forests (Galatowitsch et al., 2009; Frelich and Reich, 2010; Wang et al., 2016; Iverson et al., 2017; Swanston et al., 2018). Under the current rapidly changing climate, species may not possess the capacity for genetic adaptation at the rate needed to avoid risk of local extinction (Davis and Shaw, 2001; Walther et al., 2002). Other species may simply not propagate quickly enough to expand to climatically suitable habitat in new geographical areas (Swanston et al., 2011; Iverson et al., 2017), or there may be insurmountable anthropogenic barriers to migration (e.g., land development, conversion of forests to agriculture). Additionally, most models suggest that temperate hardwood species' ranges in North America will continue to shift to the north where they may potentially displace historically mixed-pine forest species (Fei et al., 2017; Iverson et al., 2017).

Adult trees can often tolerate a much broader range of climate conditions than seedlings of the same species. Given that the seedling stage is the most vulnerable period for a tree's survival (Davis et al., 1998; Dulamsuren et al., 2010), it is important that we understand how tree species regeneration choices tailored to future climatic conditions may affect the short- and long-term sustainability of these forests. Additionally, it is important that we understand how forest processes such as regeneration and growth are affected by climate change, and how management approaches can be designed or modified to direct stand development to meet management objectives focused on climate adaptation.

Forest managers may need to consider modifying current management approaches to promote a species composition adapted to future climate in order to maintain forest ecosystem productivity and function (Millar et al., 2007; Peterson et al., 2011; Janowiak et al., 2014). Additionally, managers may also need to explore techniques that promote structural heterogeneity within and among forest stands (Millar et al., 2007), as this has been shown to decrease local species extinction and support higher levels of biodiversity and suitable habitat for a wider range of tree species (Naeem and Li, 1997; Lindenmayer et al., 2000). Silvicultural approaches designed to accomplish these outcomes may include some form of multi-cohort management that includes group selection, group retention or variable retention practices (Palik et al., 2014) combined with planting future-adapted species and genotypes (Janowiak et al., 2011).

To address these challenges, the Adaptive Silviculture for Climate Change project (ASCC; Nagel et al., 2017) was developed to provide on-the-ground regional examples of applying climate-adaptive approaches at an operation-scale. In 2015, the first replicated experimental ASCC site was established in a red pine-dominated mixed-pine ecosystem on the Cutfoot Experimental Forest (CEF) on the Chippewa National Forest (CNF) in north-central Minnesota, USA (hereafter MN-ASCC). This ASCC installation includes harvesting and establishment through planting of eight future climate-adapted tree species under different

canopy structural conditions and associated understory vegetation densities. The species planted include four native species currently found on the CEF, and four novel species not currently established on the CEF but are predicted to have increased habitat suitability over time. Furthermore, while these species may be future adapted, it is not yet apparent whether they can establish under the current climate conditions. The ASCC treatments on the CEF create a range of micro-environmental conditions that affords us the opportunity to ask questions regarding survival and growth of regenerating trees under variable stand structures. While still early in the experiment, assessment of early seedling performance is an important measure of likely persistence into the future (Dobbertin, 2005). Specifically, our research questions include: (1) how does survival and growth of planted future-adapted tree seedlings vary among the species under current climate conditions; (2) how does performance (survival, growth) differ between overstory condition (gap versus thinned matrix as created by variable retention harvesting) and among different levels of shrub and herbaceous density; and (3) how does the initial performance of novel species compare to native species?

2. Methods

2.1. Study site

This study is located on the Cutfoot Experimental Forest (CEF) on the Chippewa National Forest in north-central Minnesota, USA, at a latitude of 47°40′N and a longitude of 94°5′W. The climate for the CEF is characterized by cold, long winters and a warm, short growing season. The average temperature at the CEF is 3.9 °C. Maximum summer temperatures can exceed 32 °C while minimum winter temperature can drop below −35 °C. The average July high temperature is 26.5 °C while the average January high temperature is −7.4 °C. The current growing season length is approximately 100–120 days. Average annual rain-equivalent precipitation is 50–64 cm (PRISM Climate Group, 2015). In winter, average total snowfall ranges from 1 to 2 m (Adams et al., 2008). The soils on the site are well-drained medium to fine sandy soils developed from glacial outwash parent material. The soils are typical of this forest type in northern Minnesota (Adams et al., 2008).

The CEF is located within the Northern Minnesota Drift and Lake Plains section of the Laurentian Mixed Forest Province (MNDNR 2003). Most of the CEF forest is classified as dry-mesic mixed woodland (FDn33a) by the Minnesota DNR Native Plant Community Classification System (Aaseng et al., 2011). In this plant community, red pine comprises roughly 85% of the canopy tree abundance, with varying amounts of jack pine (*Pinus banksiana* Lamb.) and eastern white pine. Northern red oak (*Quercus rubra* L.), paper birch (*Betula papyrifera* Marshall), and quaking aspen (*Populus tremuloides* Michx.) are also common forest associates. Less frequently, bur oak (*Quercus macrocarpa* Michx.), balsam fir (*Abies balsamea* L. Mill.), and white spruce (*Picea glauca* Moench Voss) are found in this forest (Table 1). The site index for red pine is 17 m (base age 50). Within the study area, pre-treatment basal area was 32–41 m^2 ha^{-1} with a mean diameter at breast height (1.37 m) of 32 cm. Red pine in the study area are of natural origin, with the majority establishing following a fire in 1918. There is some evidence of older red pine trees that established following fires in 1876, 1888, and 1892. Over the past century, however, fire suppression efforts have eliminated occurrences of wildfire in the study area. Additionally, many climate projections suggest that the CEF, along with much of the Northern Minnesota Drift and Lake Plains, will experience increases in temperature, longer droughts, and more extreme windthrow events (Handler et al., 2014; IPCC, 2014). Climate projections for summer months (June, July, and August) in north central Minnesota suggest temperatures will increase by +3–9 °C (range encompasses low and high CO_2 emission scenarios established by the Intergovernmental Panel on Climate Change [IPCC]; Wuebbles and Hayhoe, 2004;

Table 1
Summary of pre-treatment conditions for all initial overstory trees (DBH ≥ 12.7 cm) from plot data gathered on the MN-ASCC site.

Species	Composition (%)	DBH (cm)	Trees per Hectare	BA (m^2/ha)
Abies balsamea	1.60	16.83	11.25	0.65
Betula papyrifera	1.85	18.54	9.15	0.76
Pinus banksiana	4.06	26.49	23.08	1.66
Picea glauca	1.15	22.67	3.88	0.47
Pinus resinosa	86.31	32.05	129.36	35.29
Pinus strobus	4.51	24.64	11.98	1.84
Populus grandidentata	0.25	30.41	0.42	0.10
Quercus rubra	0.27	14.43	2.66	0.11
Stand	100%	28.88	191.79	40.89

Christensen et al., 2007; Galatowitsch et al., 2009).

2.2. Study design and implementation

The ASCC study design (Nagel et al., 2017) involves three adaptation approaches (resistance, resilience, transition) and a no action control. Management objectives and desired future conditions associated with each adaptation approach were developed into silvicultural treatments that are replicated in each of five blocks, for a total of 20 treatment units (4 treatments × 5 replicates). Each treatment unit is approximately 10 ha while the entire study encompasses approximately 200 ha (Fig. 1). All treatments were harvested during the winter of 2014–2015 on frozen ground conditions with snow cover during most of the harvesting. Mechanical site preparation was performed throughout the transition treatment using a harrow disc in the summer of 2015. The focus of the study documented in this paper is on the transition treatment only, as this is the treatment where the full range of future-climate adapted tree species was planted (Nagel et al., 2017).

The transition treatment aims to actively move the forest toward a condition that is better adapted to future climate conditions by creating a range of establishment conditions across the stand, including both harvested openings (henceforth referred to as gaps) and protected microsites through stand and canopy modifications. The silvicultural approach employed variable retention harvesting that created 0.2-ha gaps, where one or two mature red pine trees were left for ecological and wildlife value within each of the gaps, and thinned the forest matrix (14–18 m^2 ha^{-1} residual basal area). The newly created gaps, defined in size from the canopy drip line, consisted of approximately 20% of the treatment area. Across the matrix, the post-treatment basal area is at the lower end of full stocking for red pine management in this region (Gilmore and Palik, 2006), but is within the zone of low vulnerability when mitigating for growing season drought with density management (Bottero et al., 2017).

2.3. Species selection for planting

Species selected for planting were based on Tree Atlas (Iverson et al., 2008) projections, Minnesota Native Plant and Suitability Guidelines, information gathered through a collaborative workshop, and expert opinion, in order to align with the goals of the transition treatment (Nagel et al., 2017). Species selection focused on promoting an array of species, some of which are native to the ecosystem and projected to maintain future suitable habitat, as well as species that are novel to the ecosystem but projected to have increased habitat suitability (see Table 2 for species silvical descriptions). These species included eastern white pine, red maple (*Acer rubrum* L.), northern red oak, bur oak, white oak (*Quercus alba* L.), bitternut hickory (*Carya cordiformis* Wangenh.*),* black cherry (*Prunus serotina* Ehrh.*),* and ponderosa pine (*Pinus ponderosa* C. Lawson; Table 2). Eastern white pine, red maple, northern red oak, and bur oak are all native components of the ecosystem (MNDNR, 2003), and model projections suggest stable or

increased habitat suitability for these species in the future (Iverson et al., 2008). Bitternut hickory, black cherry, and white oak are all currently found in southern and central parts of Minnesota (MNDRN 2003). However, other than scattered individuals, their ranges do not currently include the study area, though each of these species is projected to have suitable habitat in the study region by the end of the 21st century (Iverson et al., 2008).

Ponderosa pine was selected as a species that is potentially an ecological, social, and economic replacement for red pine, but with greater drought tolerance (Richardson, 2000). While nonnative, ponderosa pine has been occasionally planted across Minnesota over the past 50 years, including at latitudes similar to the study area. Moreover, results from a long-term provenance study initiated in 1968 (Radsliff et al., 1981) suggest that seed sources from the eastern part of the range of ponderosa pine may have reasonable levels of survival and growth in northern Minnesota. We selected the four best performing seed sources from the provenance study, based on the last reported measurements in 1978 (10-year growth and survival; Radsliff et al., 1981), as well as recent visual inspection of the remaining installations. These included seed sources from northwest Nebraska, southeast Montana, and two sources from southwestern South Dakota, USA (Table 2). The eight tree species (including four seed sources of ponderosa pine) were planted in the May of 2015 in the transition treatment units in equal proportions in gaps and the forest matrix. Approximately 310 seedlings per hectare of each species were planted randomly throughout the treatment. Individuals of the same species were planted at approximately 5.5-m spacing. All seedlings were bare-root stock, except the ponderosa pine seed sources which were containerized. Additionally, all deciduous species were grown outside from seed for one year in the nursery prior to planting, while conifer species were grown from seed for two years prior to planting. All species were hand-planted using a planting bar.

2.4. Data collection

Data were collected on 45 permanent plots (nine plots × five blocks) located across the transition treatment units over the course of three growing seasons (May-September; 2016, 2017, and 2018). In each of the five treatment stands, six plots were located within the thinned matrix (basal area of 14–18 m^2 ha^{-1}), while three plots are located in gaps. The locations of all plots were permanently marked, with overstory trees stem-mapped and measured in 2014. The plot layout included a 0.2-ha macro-plot and a series of three nested 0.004-ha subplots. Basal area (m^2 ha^{-1}) was measured in the macro-plots, while shrubs and herbaceous plants (< 30.5 cm height) were tallied on the 0.004-ha subplots. Shrub and herbaceous plant tallies were also performed on the no action control subplots for post-treatment understory vegetation comparison. No action subplots were located in the study control stands where no planting or other management activity occurred.

Within the transition treatment macro-plots (matrix and gaps), a subset of 10 planted seedlings per species (or per ponderosa pine seed source) were tagged and monumented during planting in spring 2016 for repeated measurements over time, for a total of 4950 measured seedlings. Immediately following planting, a subsample of 130 randomly selected tagged seedlings of each species and seed source were measured for diameter at the base of their stem to estimate an average initial basal diameter for each species. Variation in diameter was minimal enough for each species that the measure of mean diameter served as the common starting size for each tagged seedling of each species (see Table 2 for initial basal diameters). Following the first growing season (September 2016), seedlings were recorded as dead or alive. In the following spring (2017), each of the tagged seedlings were again recorded as dead or alive to assess overwinter survival. In the fall of 2017 and 2018, both survival and growth were measured, where two measurements of basal diameter (using an electronic diameter caliper) were recorded and averaged for each tagged seedling. Additionally, during each seedling measurement potentially competing vegetation
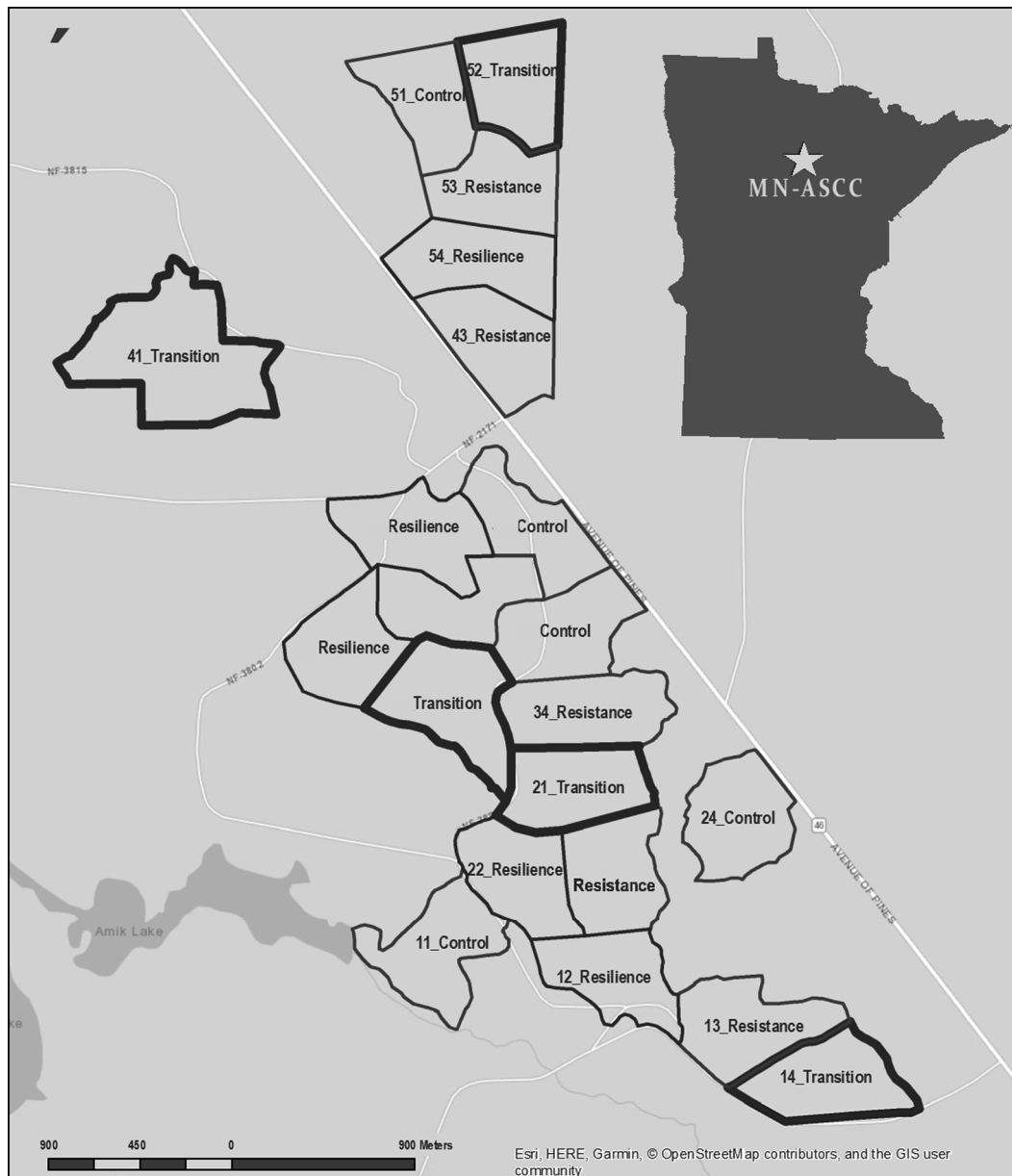
Fig. 1. Map showing location of MN-ASCC within the Cutfoot Experiment Forest, Chippewa National Forest, Minnesota, USA. Map includes all treatments (Resistance, Resilience, Transition, and No Action/Control) each replicated once per block across the five blocks.

ground layer/shrub vegetation (woody and herbaceous species < 100 cm in height) was estimated around each seedling using a 1×1 m^2 quadrat centered over the seedling and categorized into four cover classes (1 = 0–14.9%, 2 = 15–29.9%, 3 = 30–59.9%, 4 = 60–100%).

2.5. Data analysis

To quantify treatment effects, we examined survival and growth of planted seedlings following the 2018 growing season. Relative growth rate (RGR) was used as a response metric to control for between-species variations in initial seedling size. RGR was calculated for basal diameter growth for each species over the 3-year monitoring period using the formula by Fisher (1921), where *D* is the initial and final basal diameter and *t* is the measurement year:

$$\text{RGR} = \frac{\ln D_2 - \ln D_1}{t_2 - t_1}$$

We used generalized linear mixed modeling (GLMM; Pinheiro and

Bates, 2006; Bolker et al., 2009) using the glmmTMB package (Brooks et al., 2017) in the statistical package R (R Core Development Team, 2015) to analyze the blocked, split-plot design. We tested a combination of factors for both RGR and survival as the response variables where overstory condition represented the whole plot factor and species (within each sample plot) represented the split-plot factor. Fixed effects included species, overstory condition (gap versus matrix), understory vegetation cover (categorically grouped), and their interactions, while random effects include block and plot. Survival was modeled using a binomial error distribution (using logit link function), while RGR was modeled using a Gaussian (normal) error distribution. These error distributions were chosen based on the nature of the data. Survival was 1 or 0, hence our use of a binomial error distribution. Conversely, growth was a continuous variable and expressed as a number with fractional values, and is the reason we chose a Gaussian distribution error. We began with the full model (species × overstory condition × understory vegetation cover; where "x" indicates interaction between terms) and then built subsets of this model (Gotelli and

Table 2

Species silvical characteristics for each of the planted tree species on the Cutfoot Experimental Forest in Northern MN, USA as part of the MN-ASCC transition treatment.

Species Planted	Code	Seedling Seed Source Location	Starting Basal Diameter (mm) ± SE	Current MN Range	Moisture Stress Tolerance	Competition Tolerance	Shade Tolerance	Fire Tolerance
				Species Silvical Characteristics[†]				
Eastern white pine *Pinus strobus*	WP	Oconto Country, WI	5.48 (± 0.15)	Northern MN	Moderate	Low	Intermediate	Low
Red maple *Acer rubrum*	RM	Pine County, MN	2.67 (± 0.10)	Throughout MN	Low	High	Tolerant	Very Low
Northern red oak *Quercus rubra*	RO	Pine County, MN; Morrison County, MN	6.29 (± 0.18)	Throughout MN	Moderate-Low	Moderate	Intermediate	Very Low
Bur oak *Quercus macrocarpa*	BO	Mille Lacs County, MN Beltrami County, MN	5.4 (± 0.15)	Throughout MN	Moderate-High	Moderate	Intermediate	Moderate
White oak *Quercus alba*	WO*	Mille Lacs County, MN; Todd County, MN	5.77 (± 0.15)	Southeastern MN	Moderate-High	High	Intermediate	Moderate
Bitternut hickory *Carya cordiformis*	BH*	Allegan County, MI	5.18 (± 0.12)	Southeastern MN	Moderate-High	Moderate	Intermediate to Intolerant	Very Low
Black cherry *Prunus serotina*	BC**	Grant County, WI	5.8 (± 0.19)	Southeastern MN	Moderate	High	Intolerant	Low
Ponderosa pine *Pinus ponderosa*	SD1* SD2* MT* NEB*	Shannon County, SD; Todd County, SD; Rosebud County, MT; Dawes County, NE	5.1 (± 0.18) 5.12 (± 0.18) 5.44 (± 0.19) 5.09 (± 0.18)	Novel, plantations in southern and western MN	High	Low	Very Intolerant	High

[†]Information gathered from Burns & Honkala's *Silvics of North America* (1990).
* Not currently found on the Cutfoot Experimental Forest.
** Found infrequently on the Cutfoot Experimental Forest.

Ellison, 2004). In total, we examined eight models of different configurations for both survival and RGR. We examined each model for linearity and normality of residuals using regression diagnostics based on analyses of residuals. Normality of residuals was only tested for Gaussian error distributions. Following inspection of residuals, we determined no major transformations of the response variables were needed.

Akaike information criterion (AICc; Forster and Sober, 1994; Sugiura, 1978) was used to evaluate the explanatory predictive power for each model. Models were considered to have strong support when ΔAIC values were less than seven (Burnham and Anderson, 2002). Multi-model inferences were based on comparisons of a priori models using the MASS package in R (Venables and Ripley, 2002) to provide F-statistics and P-values for model fixed effects based on Type III sums of squares. We compared multiple competing models of basal diameter RGR and survival and ranked them according to change in AICc (ΔAICc). We included a null, intercept-only model for each response variable. Based on AIC support, the best-supported model was chosen for our response variables and used for post hoc testing (using Tukey's HSD) to compare factor levels. The lsmeans package (Lenth, 2016) in the statistical package R was used to interpret model effects in the presence of interactions among the main effects. For all post-hoc tests, we set a significance threshold (α = 0.05) to test for differences in our main effects. In addition to seedling analyses, we explored the relationship between overstory density (basal area) and understory density (plant tally) in matrix, gap, and no action control plots using linear regression.

3. Results

3.1. Seedling survival

Several models for seedling survival, consisting of different combination of predictors, had similar support ((ΔAIC < 7; Table 3). We chose the second model (survival ~ species × overstory condition + understory vegetation cover; Weight = 0.40) as it included all of our hypothesized predictors to allow for further analysis and post hoc testing of each response variable. Survival varied significantly by species (F = 31.1, p < 0.001) and understory vegetation cover (F = 69.8, p < 0.001). Overstory condition was not found to be a significant predictor (F = 0.5, p = 0.45); however, we did find significant species × overstory condition interaction (F = 1.1, p < 0.01).

Mean (± 1 standard error) survival of all species following the third growing season (2016–2018) was 77.9% (± 2.35%). Survival varied significantly among species within each overstory condition (p < 0.001; Fig. 2). Bur oak, white oak, bitternut hickory, and black cherry had the highest levels of survival (99.77% ± 1.76, 98.0% ± 2.76, 97.1% ± 3.21, and 96.2% ± 3.61, respectively). Red maple, northern red oak, and eastern white pine also had relatively high survival, all exceeding 90% across overstory conditions (94% ± 4.4, 92.4% ± 4.74, and 92.4% ± 4.86, respectively). There was a substantial decline in survival for the ponderosa pine seed sources in both the gaps and matrix (Fig. 2), with each of the four seed sources having lower than 50% mean survival by the end of the third growing season. Collectively, South Dakota seed sources (SD1 and SD2) had the highest levels of survival for ponderosa pine, at 49.6% (± 9.0) and 48.2% (± 9.0). The Montana (MT) seed source had 45.8% (± 4.6%) survival, while the Nebraska (NEB) source had the lowest survival at 42.7% (± 4.6).

Pooled across species, seedlings planted in gaps had mean survival of 77.0% (± 3.9), while seedlings planted in the forest matrix had mean survival of 78.3% (± 2.76). Of all species, only bitternut hickory, red maple, eastern white pine, and ponderosa pine-NEB had significant differences (p = 0.05) in survival between gap and matrix (Fig. 3). Among those with differences in seedling survival between overstory condition, only bitternut hickory exhibited higher survival in gaps. All of the other species (red maple, eastern white pine, and ponderosa pine-NEB) had higher survival under the matrix overstory condition (Table 4).

Post-treatment shrub density was strongly negatively correlated ($R^2 = 0.75$) to overstory basal area ($m^2\ ha^{-1}$), where high levels of shrub cover were found under low basal areas (i.e., gaps), and low

Table 3
Summary of confidence set models for survival, based on the Akaike information criterion (ΔAICc ≤ 7). "x" symbols indicate an interaction between connected terms. "+" symbols indicate an additive term.

Response	Factors for Survival Response	AICc	ΔAICc	Weights
Survival	Understory vegetation cover × species	3422.03	0.00	0.43
Survival*	Species × overstory condition + understory vegetation cover	3422.14	0.11	0.40
Survival	Understory vegetation cover × species + overstory condition	3423.88	1.85	0.17
Survival	Species	3503.88	81.85	0.00
Survival	Species + overstory condition	3505.36	83.33	0.00
Survival	Species × overstory condition	3514.93	92.90	0.00
Survival**	Understory vegetation cover × species × overstory condition	3765.96	343.93	0.00
Survival	null	4166.26	744.23	0.00

* Model used for analyses.
** Full model including all main effects terms.

levels of shrubs were found under high basal areas (Fig. 4). Pooled across species, survival varied significantly among the shrub/herbaceous cover classes (p < 0.05), ranging from a high of 86.67% (± 8.04) in cover class 1 to a low of 74.23% (± 3.04) in cover class 4 (Fig. 5).

Collectively, native species (northern red oak, bur oak, eastern white pine, and red maple) had 94.77% (± 0.6) average survival, compared to 77.85% (± 0.7) average survival for all novel species combined (bitternut hickory, black cherry, white oak, ponderosa pine). However, relatively low survival of novel species as a group can largely be attributed to low survival of ponderosa pine (the four seed sources pooled), which had significantly lower survival (p < 0.001; 45.66 ± 1.2%) compared to the other novel species (97.03 ± 0.5%; Fig. 5.)

3.2. Seedling growth

The best-supported model for relative growth rate (RGR) included species (F = 95.3, p < 0.001), and species × overstory condition ((F = 3.1, p < 0.001; Weight = 0.99). All other models, including those with understory vegetation density as a main effect, exhibited negligible support (ΔAIC < 7; Table 5).

Mean diameter RGR from May 2016 to September 2018 was 0.079 cm cm^{-1} year^{-1} (± 0.002), but this varied significantly among species. Eastern white pine and red maple had RGR's of 0.13 cm cm^{-1} year^{-1} (± 0.003) and 0.11 cm cm^{-1} year^{-1} (± 0.003), respectively.

Bur oak, white oak, and northern red oak each had moderate levels of RGR, at 0.048 cm cm^{-1} year^{-1} (± 0.003), 0.038 cm cm^{-1} year^{-1} (± 0.003), and 0.032 cm cm^{-1} year^{-1} (± 0.004 SE), respectively. Black cherry and bitternut hickory had the lowest RGR's of any species, across both gaps and matrix. As a group, ponderosa pine exhibited the highest levels of growth of any species. The MT and SD1 seed sources had significantly higher RGR's of any species, across both gaps and matrix (Fig. 6).

Seedlings planted in gaps (all species pooled) had a mean RGR of 0.084 cm cm^{-1} year^{-1} (± 0.003), while species planted in the forest matrix had a mean RGR of 0.076 cm cm^{-1} year^{-1} (± 0.002). Species having significantly higher (p < 0.05) RGR in gaps than matrix include all of the ponderosa pine seed sources and bitternut hickory (Fig. 7).

Understory vegetation cover was found to be a weak predictor of RGR and therefore not analyzed for significant differences among the shrub/herbaceous cover classes. No significant differences in growth were observed between novel species and native species, with RGR's of 0.156 cm cm^{-1} year^{-1} (± 0.004) and 0.162 cm cm^{-1} year^{-1} (± 0.004), respectively. However, when ponderosa pine is removed from the novel group, growth rates decrease precipitously for the novel group, across both gaps and matrix. Ponderosa pine, as a group, had significantly higher RGR than the native or novel species, with a species average RGR of 0.35 cm cm^{-1} year^{-1} (± 0.007) in gaps and 0.29 cm cm^{-1} year^{-1} (± 0.005) in the matrix (Fig. 8).
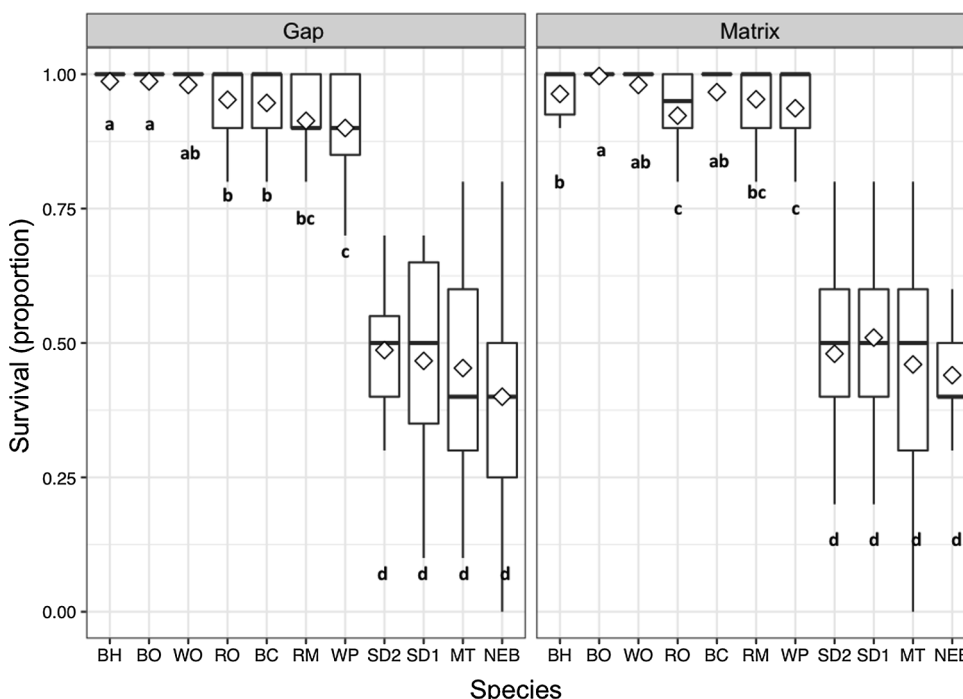
Fig. 2. Boxplots of species showing 3-year survival for 11 species/seed sources planted across the transition treatment's overstory conditions (gap and matrix) on the MN-ASCC site. The box spans the upper and lower quartiles while the lines represent the maximum and minimum values. The white diamonds in each plot represent the mean while the black horizontal line represents the median value. Letters adjacent to species indicate pairwise comparisons of species. Boxplots not connected by the same letter are significantly different (p < 0.05). See Table 2 for species codes.
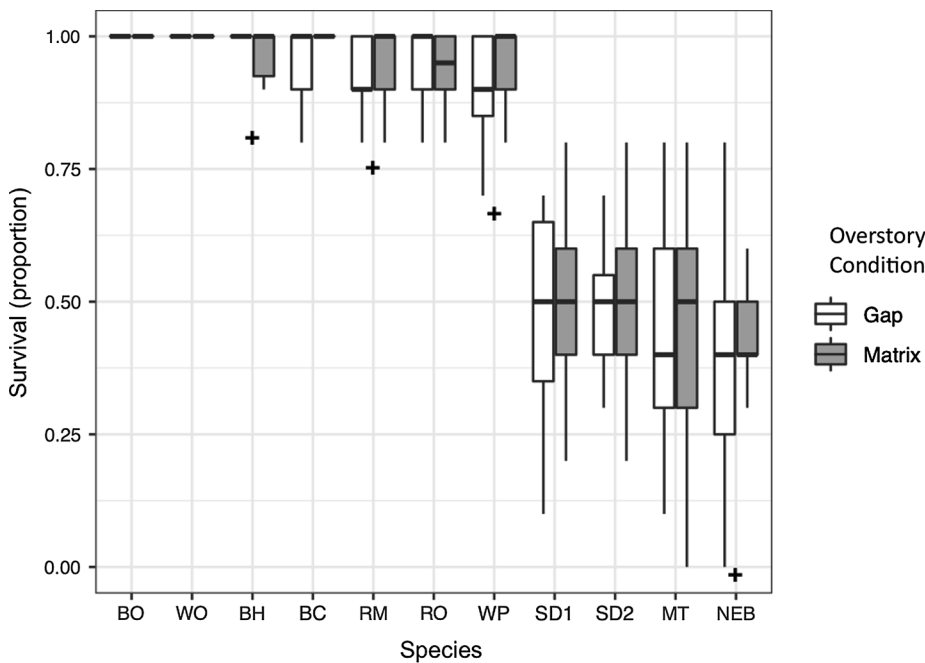
Fig. 3. Boxplots comparing differences in 3-year survival across the overstory conditions (gap versus matrix) in the transition treatment on the MN-ASCC site. The box spans the upper and lower quartiles while the lines represent the maximum and minimum values. The white diamonds in each plot represent the mean while the black horizontal line represents the median value. Plus (+) signs below each species boxplot indicate a significant difference in survival between overstory conditions for that species (p < 0.05). See Table 2 for species codes.

4. Discussion

Our study found substantial variation in survival and growth among planted seedlings of future climate-adapted tree species in the MN-ASCC transition treatment. Variation in performance can likely be attributed to their silvical differences. Species that performed the best (e.g., eastern white pine and bur oak) likely possess more favorable silvical characteristics (i.e., shade and soil moisture tolerance; Table 2), which allowed them to perform better across heterogeneous stand conditions, even with high levels of competition from understory vegetation.

4.1. Seedling survival and growth across species

Individual species survival and growth varied significantly after

three growing seasons. Collectively, ponderosa pine had the highest RGR among all species, while also having significantly lower survival among all species, regardless of overstory conditions. Other species, such as bitternut hickory, black cherry, and the oak species exhibited much lower growth rates, while having much higher levels of survival, regardless of overstory condition. Thus, our results show RGR was not indicative of a species survivability through the first three growing seasons. For many species, seedlings with high initial survival often invest in below-ground growth preferentially over above-ground growth, whereas species with high early above-ground growth often have relatively low survival (Kneeshaw et al., 2002). This is a common trend in our study where species with the highest RGRs (e.g., ponderosa pine) also had the lowest survival. These results support previous research examining growth strategies of "early colonizer" species (e.g., *Pinus*), which have been shown to outcompete more shade tolerant

Table 4
Summary of planted species/seed source survival and growth.

Species Planted	Species Code	Overstory Condition	Initial number of seedlings measured	3-Year Survival	Survival (%) (± SE)	Basal Diameter RGR (± SE)
Eastern white pine	WP	Gap	150	135	90.00 ± 9.68	0.29 ± 0.011
Pinus strobus		Matrix	300	281	93.67 ± 5.58	0.25 ± 0.008
Red maple	RM	Gap	150	137	91.33 ± 9.17	0.24 ± 0.013
Acer rubrum		Matrix	300	286	95.33 ± 4.92	0.23 ± 0.008
Bur oak	BO	Gap	150	149	99.33 ± 4.23	0.11 ± 0.012
Quercus macrocarpa		Matrix	300	299	99.67 ± 2.16	0.09 ± 0.007
White oak	WO*	Gap	150	147	98.00 ± 5.45	0.09 ± 0.012
Quercus alba		Matrix	300	294	98.00 ± 3.51	0.07 ± 0.008
Northern red oak	RO	Gap	150	142	94.66 ± 7.91	0.06 ± 0.014
Quercus rubra		Matrix	300	276	92.00 ± 6.15	0.06 ± 0.009
Black cherry	BC**	Gap	150	142	94.66 ± 7.61	0.04 ± 0.015
Prunus serotina		Matrix	300	291	97.00 ± 4.09	0.05 ± 0.010
Bitternut hickory	BH*	Gap	150	148	98.67 ± 4.88	0.01 ± 0.013
Carya cordiformis		Matrix	300	289	96.33 ± 4.45	0.04 ± 0.007
Pondorosa pine - MT	MT*	Gap	150	68	45.33 ± 15.42	0.43 ± 0.014
Pinus ponderosa		Matrix	300	138	46.00 ± 10.98	0.36 ± 0.007
Pondorosa pine - SD1	SD1*	Gap	150	70	46.67 ± 15.45	0.37 ± 0.015
Pinus ponderosa		Matrix	300	153	51.00 ± 11.02	0.31 ± 0.008
Pondorosa pine - SD2	SD2*	Gap	150	73	48.67 ± 15.49	0.28 ± 0.012
Pinus ponderosa		Matrix	300	144	48.00 ± 11.02	0.24 ± 0.008
Pondorosa pine - NEB	NEB*	Gap	150	60	40.00 ± 15.19	0.31 ± 0.013
Pinus ponderosa		Matrix	300	132	44.00 ± 10.94	0.25 ± 0.009

* Novel to the Cutfoot Experimental Forest.
** Found infrequenty on the Cutffot Experimental Forest.
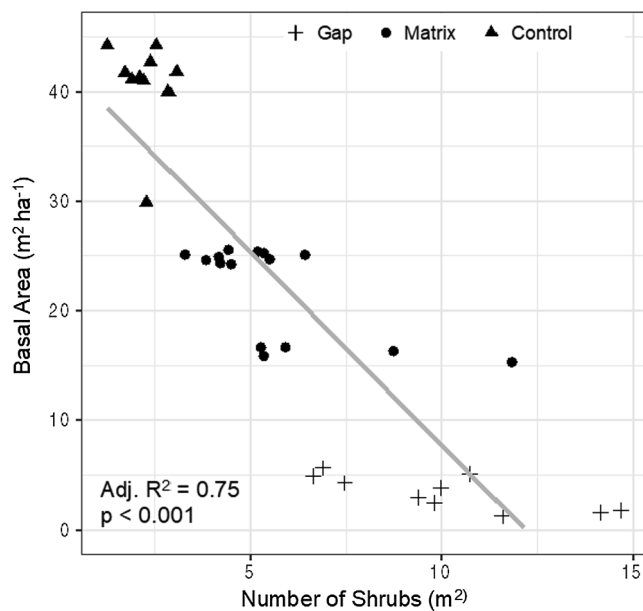
Fig 4. Average number of shrub stems (per m^2) and overstory basal area (m^2/ha). Symbols represent different overstory conditions, including the control plots. Measurements were taken in during the 2018 growing season on the MN-ASCC site, Cutfoot Experimental Forest in northern MN, USA.

species and establish a higher position in the canopy, particularly when resources are abundant (Bond, 1989; Bloor and Grubb, 2003; Seiwa, 2007). This growth strategy of investing heavily in initial growth may also lead to seedlings being more vulnerable to environmental stressors, and thus resulting in higher levels of mortality.

4.2. Overstory condition and understory Shrub/Herbaceous cover

Overstory condition interacted with species on both best-supported

models for survival and RGR, and was found to be a strong predictor of survival. Overstory condition was found to affect survival in five species/seed sources: ponderosa pine-SD1, ponderosa pine-NEB, eastern white pine, red maple, and bitternut hickory. Of all those species, only bitternut hickory had higher survival in gaps than matrix plots. However, we would expect greater differences in survival across overstory condition for all species if seedlings had been planted under a wider range of canopy conditions (Canham, 1988; McCarthy et al., 2001). For instance, given that the transition matrix was harvested at or below the lower level of stocking on the regional red pine stocking chart (Gilmore and Palik, 2006), seedlings in the thinned matrix still received relatively high amounts of sunlight compared to pre-treatment conditions. The oak species (i.e., white oak, northern red oak, bur oak), having more intermediate levels of shade tolerance, exhibited very little difference in survival between the gap and matrix plots.

Following harvesting and site preparation of the transition treatment gaps, there was a rapid colonization of understory vegetation, particularly bracken fern (*Pteridium aquilinum* var. *latiusculum*), wild red raspberry (*Rubus idaeus* L.), and beaked hazel (*Corylus cornuta* Marshall), and other herbaceous vegetation. The understory cover was strongly negatively correlated to overstory canopy cover (Fig. 5), as would be expected where higher resource environments (e.g., light) favor establishment of these species. We suspect that mechanical site preparation contributed to rapid colonization by shrubs and herbaceous vegetation due to the exposure of bare soil and inadvertently spreading seeds by the equipment. Moreover, site preparation was performed relatively evenly throughout the transition treatment, suggesting the overstory canopy density heavily influenced understory vegetation growth, which is consistent with previous studies examining post-harvest re-colonization of understory vegetation (McConnell and Smith, 1970; Löf et al., 2007; Ares et al., 2010). Our analyses showed shrub/herbaceous cover was a strong predictor for seedling survival. Collectively, seedlings had substantially lower survival under the highest understory shrub/herbaceous cover classes, while survival was nearly uniform when understory shrub/herbaceous cover levels were low (below 30% cover). However, RGR was less affected by shrub/
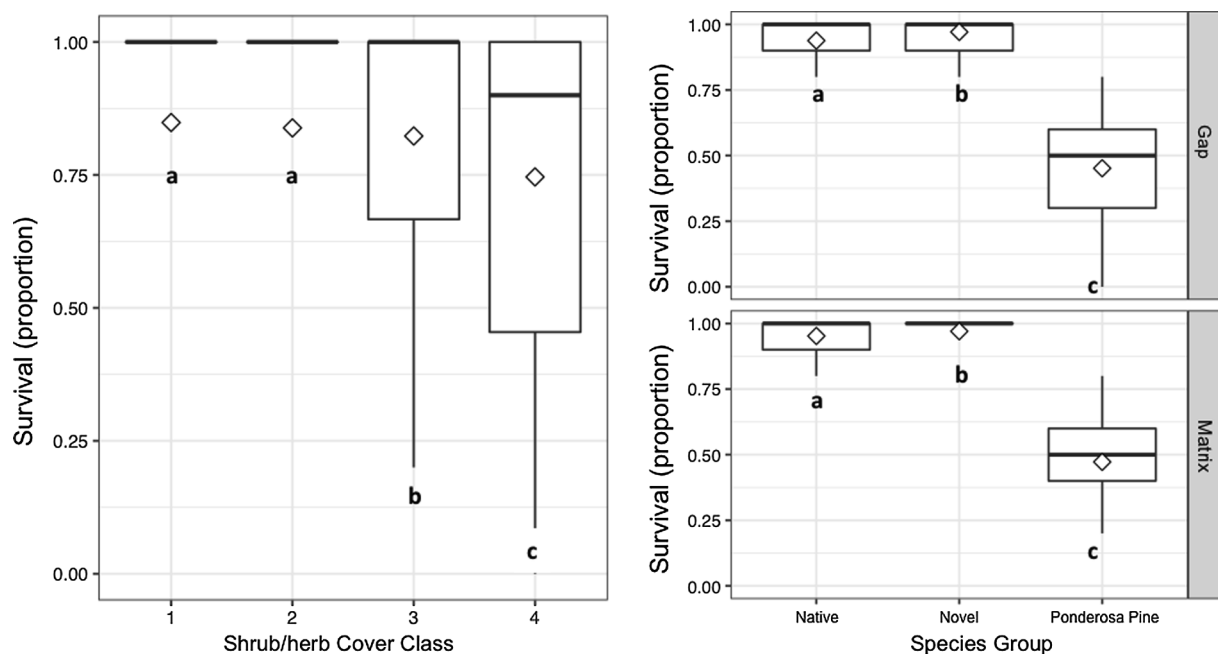
Fig. 5. Boxplots showing combined species survival under each of the vegetation (shrub/herbaceous) cover classes (left; 1 = 0–14.9%, 2 = 15–29.9%, 3 = 30–59.9%, 4 = 60–100%) and pooled species native/novel/ponderosa pine groups (right). The box spans the upper and lower quartiles while the lines represents the maximum and minimum values. The white diamonds in each plot represent the mean while the black horizontal line represents the median value. Letters adjacent to cover class indicate pairwise comparisons of seedling survival across each cover class. Levels not connected by the same letter are significantly different (p < 0.05).

Table 5
Summary of confidence set models for basal diameter growth (RGR), based on the Akaike information criterion (ΔAICc ≤ 7). "x" symbols indicate an interaction between connected terms. "+" symbols indicate an additive term.

Response	Factors for Basal Diameter RGR Response	AICc	ΔAICc	Weights
Basal Diameter RGR*	Species × overstory condition	−12832.68	0.00	0.99
Basal Diameter RGR	Species + overstory condition	−12822.62	10.06	0.01
Basal Diameter RGR	Species	−12822.10	10.58	0.00
Basal Diameter RGR	Species × overstory condition + understory vegetation cover	−12803.87	28.81	0.00
Basal Diameter RGR**	Understory vegetation cover × species + overstory condition	−12792.04	40.65	0.00
Basal Diameter RGR	Understory vegetation cover × species	−12791.21	41.47	0.00
Basal Diameter RGR	Overstory condition	−12041.11	791.57	0.00
Basal Diameter RGR	null	−10748.93	2083.75	0.00

* Model used for analyses.
** Full model including all main effects terms.

herbaceous cover, with mean RGR of all species nearly uniform across all shrub/herbaceous cover classes. Previous studies in this forest type have shown competing shrubs and herbaceous cover lower available moisture and nutrients in the soil in addition to reducing the amount of sunlight that tree seedlings receive, and thus result in lower survival and reduced growth (Saunders and Puettmann, 1999; Montgomery et al., 2013). However, in this study, competition from understory shrub/herbaceous cover appears to only affect tree species survival.

4.3. Future-adapted species – native versus novel

As part of the MN-ASCC project, we planted four species novel to the study area: black cherry (having only scattered individuals growing in the region), bitternut hickory and white oak (both with native populations located within 100 km to the south of the CEF), and ponderosa pine (with the nearest native populations located 200 km west of the CEF). We planted ponderosa pine as a potential replacement species for red pine (if suitable habitat declines precipitously in the future), given the physiological and ecological similarities between the two species. While similar in some respects, ponderosa pine is considered a more fire-adapted and drought-tolerant species than red pine (Kolb and Robberecht, 1996; Richardson, 2000; Niinemets and Valladares, 2006; Ganey and Vojta, 2011). These characteristics align with predicted future disturbance patterns for northern Minnesota including larger, more

intense wildfire and longer periods of drought (Handler et al., 2014; IPCC, 2014). This was an important consideration in selecting ponderosa pine for inclusion in this study as we aimed to increase species diversity, and particularly those that will likely be adapted to future disturbance regimes and climate conditions.

The four ponderosa pine seed sources were selected from locations on the easternmost extremes of the species' current range. The source areas vary in latitude, elevation, and climate (annual temperature and precipitation averages). We hypothesized that seedlings from the nearest seed source locations to the CEF in north-central Minnesota would have higher levels of growth and survival. However, as our results indicate, the Montana seed source exhibited significantly more growth than the other seed sources. While the Montana seed source is the furthest away, it is also the most northerly of the four seed sources. This suggests that matching the seed source latitude, along with its environmental parameters (e.g., temperature extremes, growing season lengths), is likely more important than geographic proximity, at least when considering growth potential. We found no evidence of differences in survival among the ponderosa pine seed sources.

While ponderosa pine fared quite well with regards to growth, the other novel species (i.e., bitternut hickory, black cherry, and white oak) tended to exhibit much slower growth rates. In fact, bitternut hickory, black cherry, and white oak were among the species with the least amount of overall growth. These species did, however, have very high
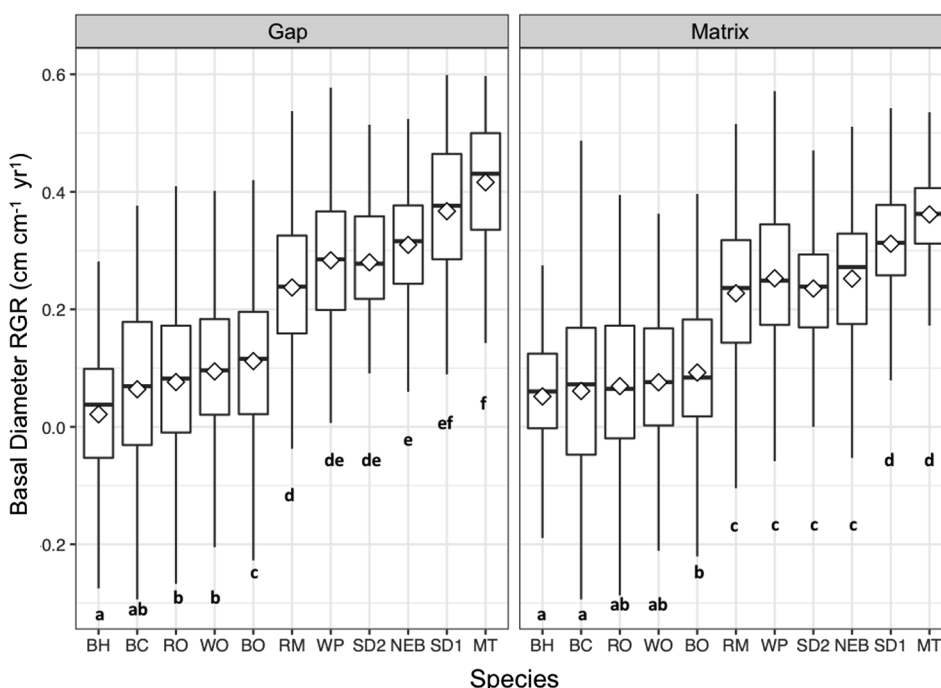
Fig. 6. Boxplots across species showing 3-year basal diameter relative growth rates (RGR) for the 11 species/seed sources planted in the transition treatment's overstory conditions on the MN-ASCC site. The box spans the upper and lower quartiles while the lines represent the maximum and minimum values. The white diamonds in each plot represent the mean while the black horizontal line represents the median value. Letters adjacent to species indicate pairwise comparisons of species. Boxplots not connected by the same letter are significantly different (p < 0.05). See Table 2 for species codes.
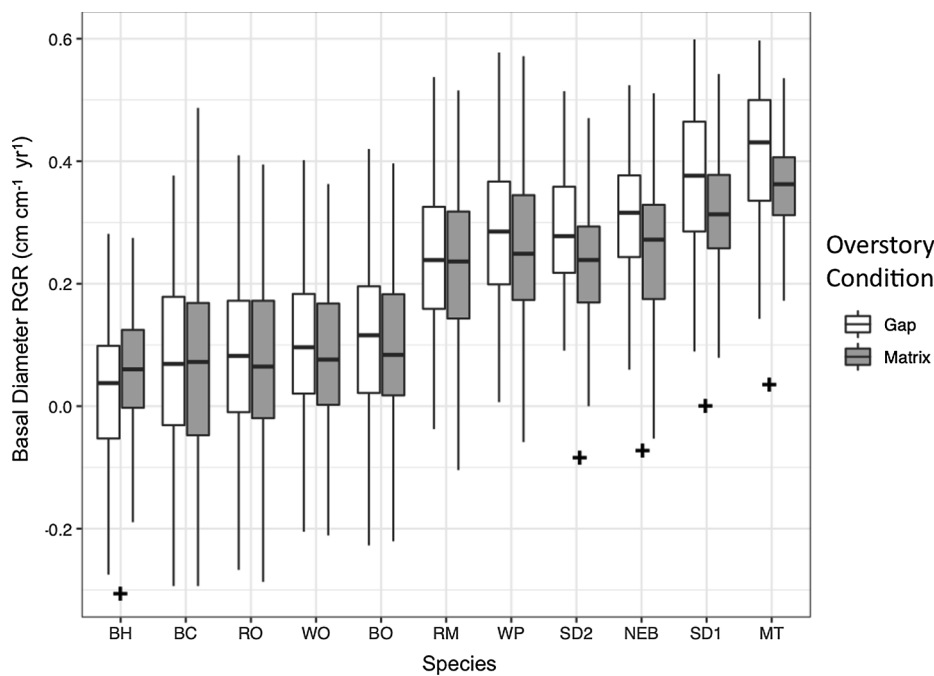
Fig. 7. Boxplots comparing 3-year basal diameter RGR among species and between overstory conditions (gap versus matrix) in the transition treatment on the MN-ASCC site. The box spans the upper and lower quartiles while the lines represent the maximum and minimum values. The white diamonds in each plot represent the mean while the black horizontal line represents the median value. Plus ($+$) signs below the species boxplot indicate a significant difference in survival between overstory conditions (gap versus matrix) for that species ($p < 0.05$). See Table 2 for species codes.
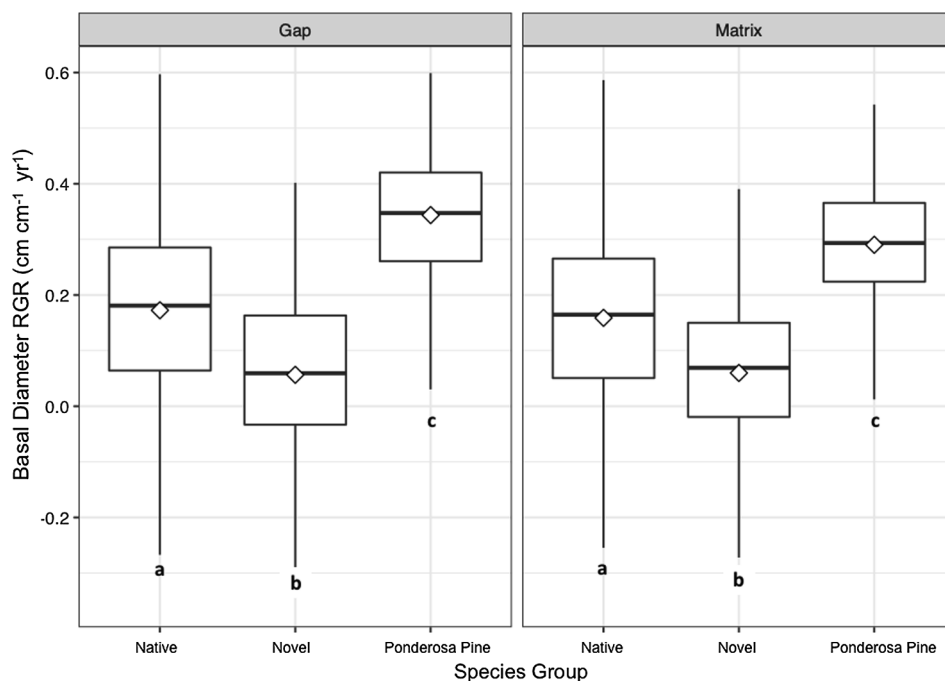
Fig. 8. Boxplots showing RGR's of pooled species native/novel/ponderosa pine groups across overstory conditions. The box spans the upper and lower quartiles while the lines represent the maximum and minimum values. The white diamonds in each plot represent the mean while the black horizontal line represents the median value. Letters adjacent to cover class indicate pairwise comparisons of seedling survival across each cover class. Levels not connected by the same letter are significantly different ($p < 0.05$).

levels of survival following the first three growing seasons (each species had > 95% survival), and are among those with highest overall levels of survival across all species. Though ponderosa pine significantly outgrew the native and novel species, we observed a much lower level of survival for ponderosa pine when compared with the other species groups, regardless of overstory condition (Fig. 5). We observed a similar trend in species overall performance, where those with higher levels of survival had lower overall growth, while species with lower survival exhibited higher levels of growth. This occurred regardless of whether species were native or novel to the study area.

The novel species in this study were selected because they were deemed potentially adaptive to future climate projections, not necessarily the current climate of northern Minnesota. Therefore, a planted novel species growing on the CEF may be experiencing less-than-favorable current climate conditions. However, with a strong understanding of individual species' silvical characteristics, we may be able to better understand how they will likely respond to (or tolerate) conditions associated with new species assemblages and climate conditions.

4.4. Implications

This study presents an early assessment of seedling survival and growth under a silvicultural strategy aimed at promoting future climate-adapted forests. With this *transition* strategy, stand heterogeneity was achieved through gap creation and matrix thinning, creating a range of establishment conditions that benefit a broad range of species, each with differing silvical characteristics. Large planting efforts,

especially with non-traditional (and not readily available) species, can be a costly investment. It is important for managers to understand the tradeoffs of planting future climate-adapted species in contemporary environments. Furthermore, if management plans are focused on planting for the future, managers will need to consider how future climate-adapted species will perform in current climates and in the near future. For example, certain novel species such as black cherry or bitternut hickory, which are currently growing in parts of southern and central Minnesota (and slowly migrating into parts of the CEF), may not see their optimal habitat in northern Minnesota for decades to come. As a result, these species may not exhibit their full potential on the site with the current climate, and managers may need to be patient in looking to the future for these species to thrive. Inherently, this is one of the challenging aspects of species range expansions, and one could argue that if planting future climate-adapted species is to occur, it should focus on species with wide ecological amplitudes.

We consider species with moderate levels of growth and high levels of survival to be among the top performing species in our study. These species include bur oak, white oak, eastern white pine, and red maple. Although ponderosa pine significantly outgrew all the other species, the low levels of survival dramatically reduced its overall performance when compared to the other species. Our results suggest that species performance is at least partly related to a species ability to tolerate shade and competition, particularly from wild red raspberry and beaked hazel, both of which likely limited tree seedling survival in this study. These are important considerations as managers continue to seek answers in regards to future planting efforts in mixed-pine forests.

Given that our results already show higher levels of survival across the novel species we planted (excluding ponderosa pine) compared with planted native species, it may be reasonable for managers to consider unconventional species compositions under climate change, and begin planting novel future-adapted species (e.g., in this study, bitternut hickory, black cherry, and white oak) as part of an adaptive management strategy focused on *transition*. Additionally, we believe that the silvicultural approaches applied as part of the MN-ASCC transition treatment (e.g., planting a suite of both native and novel future climate-adapted species) may also serve as a useful model for similar studies in other forest types to address the challenges and uncertainties associated with forest sustainability and climate change.

5. Funding statement

Declaration of Competing Interest

We declare no competing financial, professional, or personal interests that might have influenced the performance or presentation of the work described in this manuscript.

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