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ORIGINAL PAPER

The Perfect Pairing: Early Stand Dynamics in Conventional Aspen and Mixedwood Forests in Northern Minnesota, USA

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Abstract

In North America, mixedwood management is being increasingly considered by natural resource managers as an alternative to single species management for a variety of ecological, economic, and cultural reasons. In northern Minnesota, USA, natural resource managers are increasingly using treatments to establish mixedwood forests in aspen (*Populus tremuloides* Michx, *Populus grandientata* Michx) dominated ecosystems by planting white spruce (*Picea glauca* (Moench). However, little quantitative information is known regarding differences between stand structure and composition in conventional aspen and aspen-white spruce during early stand development. To provide greater clarity for managers, we sampled 40 aspen stands across a chronosequence of 0 – 20 years old in northern Minnesota. Stands received one of two treatments: conventional aspen management (20 stands) or mixedwood management which included planting of white spruce and early release (20 stands). Forest inventory data were collected on seedlings, saplings, overstory trees, and non-tree understory cover. Results found a tradeoff between higher regeneration density in aspen stands, but greater tree diameter growth and structural and compositional diversity in mixedwoods. White spruce-aspen mixedwood systems can provide opportunities for increased ecological services during early stand development without compromising on long-term timber-focused management goals. Study Implications Establishing white spruce-aspen mixedwood forests can be a valuable silvicultural management option for the Lake States region (Michigan, Minnesota, Wisconsin) of the US for managers aiming to transition away from single species systems. Mixedwoods were shown in this study to have higher compositional and structural diversity than monoculture aspen (*Populus* spp.) stands, which other studies indicate can lead to additional ecological benefits such as greater climate resilience, diverse habitat for wildlife, resistance to pests, and diversity of important commercial timber products.

Keywords Stand dynamics · Regeneration · Species diversity · Ecological services · Lake States region · Silviculture · Growth and regeneration

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Introduction

Managers are increasingly considering how to maintain or increase forest biodiversity (Mori et al. 2016). However, forests containing multiple tree species pose the additional challenge of balancing ecological priorities, like biodiversity and environmental services, with economic return. In North America, a mixedwood system, as defined by Kenefic and colleagues (2021), has a mix of hardwood and conifer trees where neither component exceeds 75–80% basal area nor canopy closure. Mixedwood stands typically develop as a mid-successional forest shifts in dominance from a fast-growing hardwood species to a slow growing, shade tolerant conifer species in the decades after a major stand replacing disturbance event like fire or windthrow (Frelich 2008). Mixedwoods can also be artificially reinitiated, and more foresters are intentionally stewarding monoculture stands to shift into mixedwood forests through silvicultural practices (Danneyrolles et al. 2019; Knoke et al. 2007).

Land managers are interested in creating or maintaining mixedwood systems because of their potential economic and ecological benefits, especially in the face of climate uncertainty. Economically, a mixedwood system capitalizes on the niche complimentary hypothesis which theorizes that forests with species differing in shade tolerance, structure, and phenology separate their resource use, potentially optimizing productivity and growth over that of monospecific forests (Lu et al. 2016). Forest productivity has also been shown to be higher in stands with higher species diversity and richness (Zhang et al. 2012) and managing for mixed species allows for better flexibility and adjustment to market volatility and product demands (Knoke et al. 2007). Compared to monoculture stands, mixedwood forests have increased biodiversity of understory plants and habitat diversity for wildlife (Cavard et al. 2011), higher resilience to damage from insect infestations (MacLean & Clark 2021), and increased aboveground carbon stocks (Kabrick et al. 2017). Structural and compositional diversity of mixedwood forests also allow them to be more adaptable to climate change stressors than conifer (softwood) monocultures (Kabrick et al. 2017).

In North America, boreal mixedwood forests stretch across northern regions of the United States and much of Canada and are generally initiated by fast growing hardwood species like trembling aspen (*Populus tremuloides* Michx.) or paper birch (*Betula papyrifera* Marshall) and are joined by conifers including black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.) in later successional stages (Chen & Popadiuk 2002). In the Lake States in the United States (defined as Michigan, Minnesota, and Wisconsin) and in numerous Canadian Provinces, the white spruce-aspen boreal mixedwood composition has become a subject of more recent research, with most of these studies coming from Canada. The topics of these studies range from regeneration and early stand dynamics (e.g., Chhin & Wang 2002, Man et al. 2010, Bokalo et al. 2007, Comeau et al. 2004), to experimental silvicultural and thinning treatments (e.g., Comeau et al. 2023, Comeau 2021, Bjelanovic et al. 2021, Darquié et al. 2024), to tree growth and volume accumulation (e.g., Cortini et al. 2012, Kabzems et al. 2015), to carbon dynamics (e.g.,

Comeau et al. 2005, Payne et al. 2019, Comeau & Bokalo 2024), to climate resilience (MacLean & Clark 2021, Drobyshev et al. 2012).

Historically, aspen and white spruce in the Lake States have been managed separately in single species stands and grown and harvested as valuable forest products (Windmuller-Campione et al. 2020). Aspen is a fast growing but relatively short-lived species with lifespans generally less than 100 years; however, older individuals can be present in the landscape (Doucet 1989). Aspen regenerate rapidly through suckering or seeding, often dominating a site after a disturbance and creating stands that are essentially purely aspen in composition (Brinkman & Roe 1975). There is increased awareness that aspen, across its range, reproduce through both methods and while asexual regeneration is likely more common in our system, we will use the term regenerant to include both sexual and asexual regeneration of aspen (e.g. McDonough 1979, Long & Mock 2012). The standard silvicultural system for aspen is to implement coppice regeneration harvest on a 40-to-60-year rotation with no intermediate treatments (David et al. 2001) with few residual trees to ensure high-light conditions for the regenerating aspen (Mulak et al. 2006). However, there is discussion regarding the trade-offs of residuals in aspen forest types and at what level is aspen regenerants negatively impacted.

Unlike aspen, juvenile white spruce monocultures rarely form without planting despite being a common Lake States species. Spruce regeneration is extremely variable, relying heavily on biotic and abiotic conditions such as an ample seed source, receptive seedbed, moist and cool microclimate, and limited competition from other vegetation (Solarik et al. 2010; Gärtner et al. 2011). Very young white spruce seedlings can experience high mortality from competition with herbaceous plants, shrubs, grasses, overstory trees and their seedlings, and fallen leaves (Comeau et al. 2023; Dobbs 1972; Man et al. 2008). However, once established, the species has a life expectancy of 250 to 300 years, high shade tolerance, low mortality rates of mature trees, and large masting years (Gärtner et al. 2011), explaining their strong presence of up to 30 percent basal area in boreal ecosystems (Rauscher 1984). Due to the variability of natural white spruce regeneration, white spruce seedlings have been extensively planted after harvests in the region since 1930 as the primary regeneration strategy (Lieffers et al. 1996; Rauscher 1984). Seedlings are planted at densities of 800 to 900 trees per acre to regenerate stands and create plantations after clearcut harvests, followed by a thin from below or row thinning at age 30 to 50 years to a basal area between 100 and 140 ft^2 per acre (Rauscher 1984; Minnesota DNR 2008). White spruce stands are generally harvested between 80 and 120 years old for sawlogs using a clearcut regeneration harvest (Minnesota DNR 2008), although many are harvested early at 50 to 60 years due to lack of thinning response or defoliation from pests like eastern spruce budworm (*Choristoneura fumiferana*).

Older aged white spruce plantations still exist in the Lake States, but in more recent decades, forest practitioners have generally moved away from managing white spruce in monoculture systems due to the high initial expense of artificial regeneration, variable success in establishing plantations, the cost of intermediate treatments, inconsistent growth response of spruce to thinning, and chronic annual damage from spruce budworm (Dobbs 1972; Patton et al. 2019). The presence of spruce budworm has been documented in Minnesota since 1954 and in

2023, spruce budworm defoliated or killed about 664,800 acres of fir and spruce forests (Minnesota Forest Health Team 2023). Studies suggest maintaining white spruce in a mixed-species composition with less susceptible trees such as aspen, pine (*Pinus* spp.), or larch (*Larix* spp.) (Mattson et al. 1988), as these mixedwood compositions have been shown to be more resilient to defoliators like eastern tent caterpillar (*Malacosoma disstria*) and spruce budworm (Drobyshev et al. 2012, Reinikainen et al. 2014).

Various Canadian studies have shown that, like other mixedwood compositions, both white spruce and aspen will reinitiate after a disturbance, with aspen dominating the stand for the first 50 to 60 years before white spruce dominates for the ensuing 100 to 200 years (Comeau 2021; Cortini et al. 2012). Over the first 12 years of regeneration, aspen undergo extensive self-thinning, allowing the slower growing, shade tolerant white spruce to persist in the understory for the first few decades (Comeau 2021). This dynamic occurs because, in part, because white spruce and aspen reduce their interspecies competition through shade tolerance separation (Kabzems et al. 1986; Man & Lieffers 1997), physical separation of canopies that prevents damage from inter-crown abrasion (Man & Leiffers 1999), and phenological separation of photosynthetically active periods (Man & Lieffers 1997). Aspen dominant stands also typically have higher rates of litter decomposition and nutrient cycling in the soil, providing additional nutrients for white spruce growth (Gordon 1983). Additionally, aspen's greater growth rate can serve as shelter trees, reducing frost severity and increasing relative humidity to white spruce seedlings (Groot & Carlson 1996; Filipescu & Comeau 2011). Once established, white spruce-aspen mixed stands show ecological benefits such as biomass accumulation even during periods of climate instability (Drobyshev et al. 2012), higher carbon storage and sequestration than in pure white spruce stands (Payne et al. 2019; Comeau & Bokalo 2024), and reduced susceptibility to infestations by insects and pathogens as compared to single species dominated stands (MacLean & Clark 2021), especially when the tree species of mixed forests are more taxonomically distant and when the proportion of non-host trees exceeds that of host trees (Jactel & Brockerhoff 2007).

In summary, there are a variety of economic and ecological motivators for using treatments to establish white spruce-aspen mixedwood in aspen forest types. While much is known about the silvics and ecology of pure aspen stands and white spruce plantations in the Lake States (e.g. Alban 1992; Cleland et al. 2000; Peterson & Peterson 1996), there is relatively little information on white spruce-aspen mixedwood early stand dynamics in this region compared to Canada (Gerlach et al. 2002). Aspen and white spruce both reach range margins within Minnesota and species dynamics can be different at these range extremes (Nienstaedt & Zasada n.d.; Perala n.d.). This study aims to quantify how stand structure, composition, and species diversity differs in early stand development of aspen stands treated conventionally and stands treated to establish white spruce-aspen mixedwoods. Results will provide managers with data to consider how treatments to establish mixedwood systems may fit within their larger landscape level goals.

Methods

Site History

Minnesota represents the transition zone among four major biomes: Laurentian Mixed Forest, Eastern Broadleaf Forest, Prairie Parkland, and Tallgrass Aspen Parklands. The Laurentian Mixed Forest (LMF) Province covers 23 million acres in the northeastern part of Minnesota and extends into northern Wisconsin, Michigan, and Southern Ontario and is characterized by conifer forests, mixed hardwood, and conifer bogs (Minnesota DNR 2023). Aspen, pine, spruce, fir, and northern hardwoods are the most common tree species (Minnesota DNR 2023). The diverse forest ecosystems are related to the diversity of soil types ranging from deep peats to sandy outwash glacial deposits.

Within the LMF, a common native plant community is the Northern Wet-Mesic Boreal Hardwood-Conifer Forest, or MHn44, as defined by the Minnesota Department of Natural Resources (MN DNR) native plant community classification system (ECS) (Minnesota DNR n.d.). After a disturbance, MHn44 forests used to transition from birch and aspen dominance to a mixed composition containing white spruce and balsam fir, but these landscapes were altered by extractive logging conducted by Euro-American settlers who selectively removed eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Aiton), northern white cedar (*Tabebuia heterophylla* (DC.) Britton), spruce, and various hardwoods from Minnesota's northern forests from 1880 to 1910, an era known as the cutover (Windmuller-Campione et al. 2020; Schulte et al. 2007). Slash fires were used after these extractive harvests, allowing aspen to become regionally dominant, a composition that has been maintained in the area due to aspen's adaptation to clearcut regeneration harvest (Schulte et al. 2007).

The study region for this project centers around Grand Rapids, Minnesota (47.240410, −93.521255) which is situated within the LMF Province. Grand Rapids experiences very cold, snowy winters and warm summers with an average annual high temperature of 52°F and low of 29°F (usclimatedata.com). The average annual precipitation is 29 inches per year and the average annual snowfall is 57 inches per year (usclimatedata.com).

Site Selection

Potential study sites were identified from a list of 500 spruce-aspen mixedwood and 700 aspen stands managed by UPM Blandin and the MN DNR, all displaying the characteristics of the MHn44 plant community. These mixedwood stands were intentionally created by the land managers of both organizations after conducting a clearcut regeneration harvest with reserves on an existing aspen dominated stand followed by an enrichment planting of white spruce seedlings at a density of 400 to 500 trees per acre (TPA). Aspen naturally regenerated through suckering and seeding. After three to four growing seasons, white spruce seedlings were

mechanically released through brush sawing (gas-powered handheld clearing saws affixed with a steel circular saw blade (personal communication S. Scherer 2025) of the aspen within approximately 3 ft of all conifers. The goal was a complete removal of aspen surrounding the white spruce; a light thinning of aspen in the matrix is also performed with targeted densities between 1,000 and 1,500 TPA (personal communication S. Scherer 2025). No further intermediate treatments occurred after initial releases.

A number of these aspen and mixedwood sites were visited during summer of 2022 to document age class, species composition, structure, and accessibility. Stands were removed if they were less than 10 acres or greater than 80 acres, further than one hour away from Grand Rapids, MN, inaccessible, or lacked the desired composition of species. The resulting 100 candidate stands of each treatment type were sorted into one of four age classes: 0–5 years, 6–10 years, 11–15 years, and 16+ years, with the oldest stands aged at 23 years. Simple random sampling was used to select five stands per age class for each of the treatment types, resulting in 40 stands: 20 pure aspen and 20 mixedwood. Plots were allocated according to stand size, where one plot was added to the baseline of 5 plots for every additional 5 acres (e.g. 10–14.9 acres = 5 plots, 15–19.9 = 6 plots, 20–24.9 acres = 7 plots, etc.). In total, 287 plots (145 aspen and 142 mixedwood) were sampled across the 40 stands (Table S1). Global Positioning System (GPS) coordinates for the plot centers were determined using a grid overlay on the stand maps in ArcGIS (Esri 2024) to ensure equal spacing of about 100 yards between plots. In the field, plot centers were permanently monumented using painted PVC pipes.

Data Collection

At each survey site, a nested fixed-radius plot was established around the monumented center. In $1/20^{th}$ acre plots (23.6 ft radius), large trees with a diameter at breast height (DBH) greater than or equal to 5.0 inches were measured for species, live/dead status, DBH to 0.1 in., and height to 1 ft. Within these plots, a smaller, nested $1/100^{th}$ acre fixed radius plot was created (11.8 ft radius) for mixedwood plots and $1/300^{th}$ acre (6.8 ft radius) for aspen plots. Within these smaller plots, regenerants and saplings were measured. Regenerants were classified as regenerating stems with a height greater than one foot and a DBH less than two inches, while saplings were classified as stems with DBH between two and five inches. Regenerants were tallied and recorded for species and alive/dead status. For saplings, species, live/dead status, and DBH to 0.1" were recorded, and the height of every fifth sapling was measured up to 10 trees per subplot.

Additionally, two 10.8 ft^2 quadrats were placed in each sampling plot, one 15 feet due east and one 15 feet due west from the plot center. Within each quadrat, visual estimates of ground cover percentages were recorded for the following functional groups: trees/shrubs < 5" DBH, ericaceous/small shrubs, woody vines,

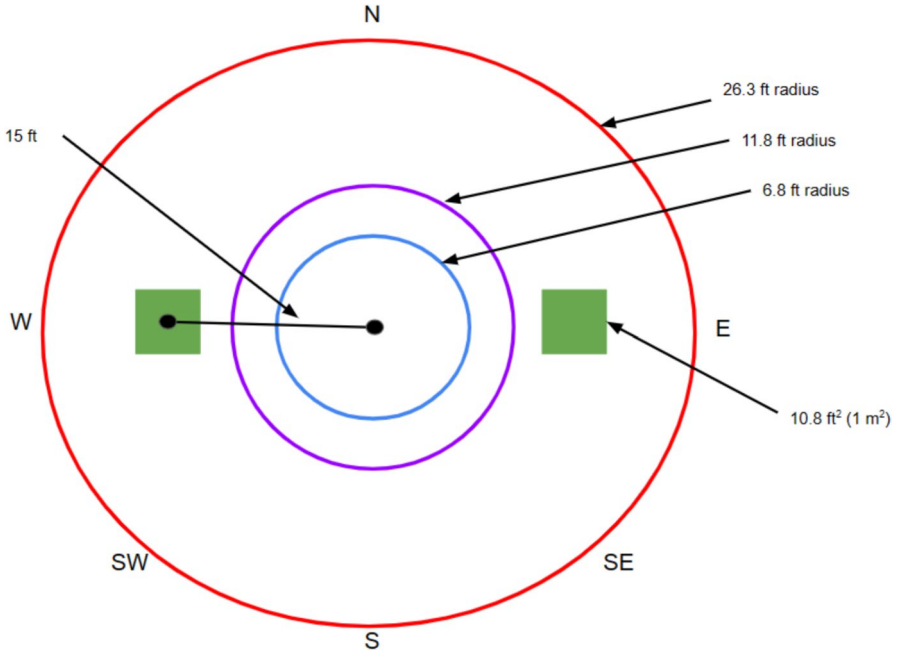


Fig. 1 Plot sample design for mixedwood and pure aspen stands. Larger trees (dbh ≥ 5") were sampled in the largest circular plot with a radius of 26.3 ft (1/20th acre, red circle). Regeneration and saplings (regeneration: height > 1 ft and dbh < 2", saplings: 2" ≤ dbh < 5") were measured in the smaller circular subplot with radius of 11.8 ft (1/100th acre, purple circle) in mixedwood plots and 6.8 ft (1/300th acre, blue circle) in pure aspen plots. Two 10.8 ft^2 (1 m^2) ground cover species plots were located 15 ft from plot center, one to the east and one to the west

ferns and fern allies, graminoids, other herbaceous plants, sphagnum moss, other mosses, standing water, bare ground, rocks, and coarse woody debris (Figure 1).

Residuals

Residuals refer to mature trees in the stand that were left behind during the previous harvest. Some stands also contained advance regeneration, mostly in the form of sapling sized stems of aspen and other deciduous species. Residual trees in the form of advance regeneration are likely to exert less of an influence on the rest of regeneration layer compared to larger overstory residuals (Oliver & Larson 1996), but because it is challenging to distinguish between these two types of mature trees without any tree age analysis, they have been grouped together in the analysis under the label of "residuals." Residuals were designated if their size was substantially larger than the average tree size for their age class: trees with a DBH greater than 2.3 inches in the first age class, 3.1 in the second, 5 in the

third, and 7.5 in the fourth were designated as residuals. These residual designation cutoffs were determined through field observations based on which ages trees were reaching certain diameter sizes (Figure 3). The overstory dataset was further screened to identify any potential outliers as residuals.

Data Analysis

Data were entered and organized using Microsoft Excel. Data analysis was conducted with R Statistical Software (v2.2.4; R Core Team, 2022) using the tidyverse package (v1.3.0; Wickham et al., 2019) to calculate descriptive statistics. A t-test was used to test differences in tree width, height, density, and mortality between conventional and mixedwood systems for each different stand age class; the goal was to identify differences between treatment type rather than across years, which we would assume would be different due to tree growth and development (Oliver & Larson 1996).

Mixed-effects modeling was used to explore the relationship between aspen tree height (ft) and other tree and site level characteristics to better understand the influence of the selected management approach on stand development. Explanatory variables included DBH (in), live/dead status, trees per acre (TPA), basal area (ft^2/ac), quadratic mean diameter (in), age class, and management type. Mixed-models were also used to investigate the effect of residuals and advance regeneration in the overstory on regenerant abundance in the understory. Aspen regenerant counts from stands in the first age class were regressed against several stand level residual characteristics, including basal area, TPA, quadratic mean diameter, average height (ft), and management type. Note that by definition residuals will be larger than the target size (in this case regenerants), so residual basal area also represented the commonly used metric basal area in larger trees (BAL).

For both modeling efforts, stand was included as a random effect to account for stand-to-stand variability using the lme4 package in R (Bates et al. 2015). Candidate models were compared using Akaike Information Criterion (AIC) (Akaike 1974) and traditional fit statistics, including R^2. In order to meet regression assumptions, tree heights and regenerant counts were transformed using the natural logarithm.

Given the variability present in ecosystems, a p-value of 0.1 was used to determine significance. For documenting significance in tables and figures, p-values between 0.1 and 0.05 were designated with *, between 0.05 and 0.001 with **, and less than 0.001 with ***.

Results

Regenerant Dynamics

There were robust levels of regenerants (> 1 ft height and < 2 in DBH) across all stand ages and treatment types (Table 1); regeneration varied from 20,795

Table 1 Average number of stemss per acre (± standard error) for the total regeneration, aspen, spruce, black ash, red maple, and balsam fir across all age classes for each treatment type

	0–5 years			6–10 years			11–15 years			16+ years		
	Aspen	Mixed		Aspen	Mixed		Aspen	Mixed		Aspen	Mixed	
All Species	20795 (2847)	13536 (2124)	*	8195 (1028)	5247 (860)	**	5352 (730)	1999 (325)	***	2194 (402)	1820 (356)	
Aspen	18687 (1904)	11767 (1577)	**	7405 (630)	3972 (705)	***	3532 (325)	1150 (219)	***	694 (181)	280 (53)	**
White Spruce	8 (8)	267 (43)	***	7 (7)	272 (46)	***	0 (0)	138 (22)	***	0 (0)	100 (23)	***
Black Ash	1429 (493)	748 (306)		520 (210)	369 (141)		1636 (465)	313 (160)	**	197 (105)	671 (307)	
Red Maple	426 (195)	600 (215)		146 (69)	506 (163)	**	29 (16)	284 (110)	**	1114 (307)	534 (111)	*
Balsam Fir	8 (8)	30 (14)		59 (32)	8 (5)		116 (58)	13 (7)		26 (26)	58 (19)	

(±2,847 standard error (SE)) stems per acre in the 0–5 age class to 1,820 (±356) in the 16+ age class. Aspen was the most dominant species across the youngest three age classes in both treatment types, varying from 90% density in the 0–5 age class of pure aspen stands to 15% density in the 16+ age class of mixedwood stands. For both treatment types, aspen, black ash, and red maple were the most common hardwood species observed, and white spruce and balsam fir were the most common conifers, with density ranging from 272 (±46) to 0 (±0) TPA for white spruce and 116 (±58) to 8 (±8) for balsam fir.

There were significantly more regenerants per acre in pure aspen stands for the youngest three age classes compared to mixedwood stands (Table 1). From the 0–5 to the 16+ age classes, regenerant TPA decreased by 89% in pure aspen stands, from 20,795 (±2,847) to 2,194 (±402), and by 87% in mixedwoods, from 13,536 (±2,124) to 1,820 (±356). There were also significantly more aspen stems per acre in pure aspen stands than mixedwoods for all four age classes, with the largest difference being in the 0–5 age class where TPA was 18,687 (±1,904) and 11,767 (±1,577), respectively. The opposite relationship occurred for white spruce, where average regenerant TPA was similar for the 0–5 and 6–10 age classes, at 267 (±43) and 272 (±46), respectively. There was a higher density of white spruce regenerant in mixedwood stands than pure aspen stands in all four age classes, and white spruce was only present in low densities of 8 (±8) and 7 (±7) TPA in the 0–5 and 6–10 age classes of the pure aspen composition, respectively.

The TPA of dead aspen regenerants differed significantly between treatment types in the 6–10, 11–15, and 16+ age classes, with pure aspen stands having

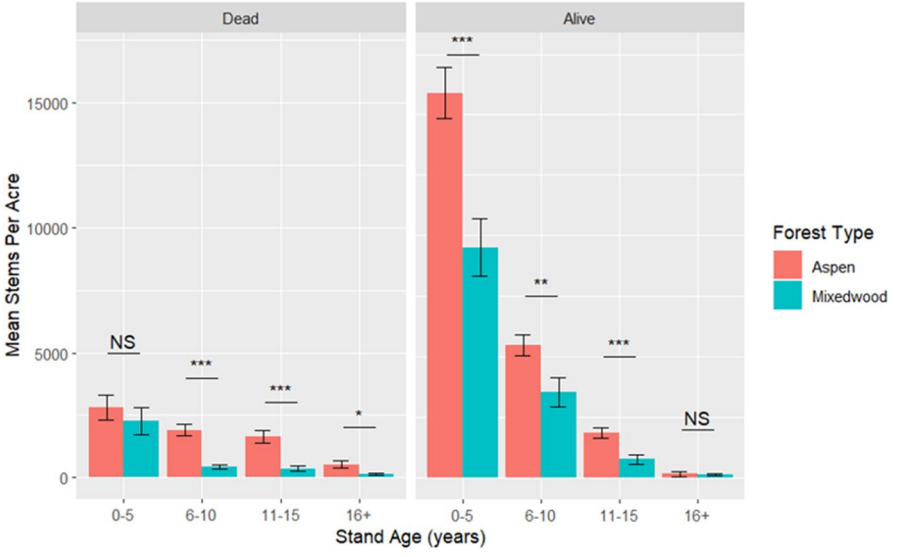


Fig. 2 Mean stems per acre (± standard error) of dead and alive aspen regeneration in each stand age class for both the aspen and mixedwood treatment types. For indicating significance, *p*-values between 0.1 and 0.05 are designated with *, between 0.05 and 0.001 with **, and less than 0.001 with ***

more dead stems than mixedwoods (Figure 2). For the 16+ age class, 75% and 53% of the total aspen regenerants were dead in the aspen and mixedwood stands, respectively. Comparatively, in the 0–5 age class, only 15% and 19% of aspen were dead in the aspen and mixedwood stands, respectively.

Sapling Composition

The sapling (2" ≤ DBH < 5") layer had a similar composition to the regenerants layer where aspen, white spruce, balsam fir, and red maple were the most common species recorded (Table 2). Aspen was the most dominant species in the overstory in both treatment types, ranging from 56% to 100% of the sapling TPA. White spruce was less dominant in the sapling layer, especially in pure aspen stands where there were zero spruce saplings in all age classes. In mixedwood stands, spruce saplings contributed as little as 0% TPA in the 0–5 age class and as high as 24% in the 16+ stands.

Sapling DBH was, on average, greater in mixedwood stands than in pure aspen (Table 2). For aspen saplings, average DBH was 5% to 9% larger in mixedwood stands than in pure aspen stands depending on the age class. This difference in DBH was significant in the 6–10 and 11–15 age classes where DBH was 2.27 (±0.03) and 2.81 (±0.06) inches in conventional aspen, but 2.43 (±0.03) and 3.08 (±0.08) inches in mixedwood, respectively. Opposite of DBH, sapling height was on average greater in pure aspen stands than in mixedwoods, significantly so in the 11–15 and 16+ age classes, where heights in conventional aspen stands were 33.33 (±0.52) and 37.62 (±0.80) feet respectively, but only 28.96 (±0.40) and 32.26 (±0.75) in mixedwood. In all but the 0–5 age class, total sapling TPA was 18% to 47% greater in pure aspen stands than mixedwoods, and basal area was 1% to 44% greater. TPA and basal area of aspen saplings was also, on average, greater in pure aspen stands than in mixedwoods in the oldest three age classes. Aspen sapling TPA ranged from 439 (±86) to 1,306 (±157) for pure aspen stands, but only 369 (±44) to 641 (±73) for mixedwoods, and basal area ranged from 12.47 (±2.58) to 61.19 (±9.71) ft^2/ac for aspen and 12.14 (±1.56) to 35.03 (±3.86) ft^2/ac for mixedwoods.

Overstory Structure and Composition

Most regenerated stems that were recruited into the overstory did not reach tree (DBH ≥ 5") size until the 16+ age class for both treatment types (Table 3). In the 16+ age class, the DBH and height of aspen trees did not differ significantly between treatment types, but was slightly greater in mixedwoods, where DBH and height were 5.89 (±0.4) inches and 53.43 (±0.54) feet in pure aspen, respectively, and 5.95 (±0.03) inches and 53.85 (±0.40) feet in mixedwood. Mixedwood stands also had higher TPA and basal area on average with 166 (±17) TPA and 32.62 (±3.57) ft^2/ac of basal area, while aspen had 150 (±21) TPA and 28.87 (±4.12) ft^2/ac of basal area.

In the youngest three age classes, residual trees made up 94% to 100% of the overstory trees, but only consisted of 25% of the overstory by the 16+ age class

Table 2 Summary table of the mean dbh (in), height (ft), TPA, and BA/ac (ft^2/ac) (± standard error) of measured saplings (2" ≤ dbh < 5") across treatment type and age class

	0–5 years			6–10 years			11–15 years			16+ years		
	Aspen	Mixed		Aspen	Mixed		Aspen	Mixed		Aspen	**Mixed**	
All Species												
DBH (in)	2.13 (0.09)	2.09 (0.02)		2.28 (0.03)	2.41 (0.03)	***	2.82 (0.06)	3.04 (0.05)	**	3.18 (0.08)	3.23 (0.05)	
Height (ft)	-	22.25 (0.97)		24.55 (0.45)	23.73 (0.44)		33.33 (0.52)	28.96 (0.40)	**	37.62 (0.80)	32.26 (0.75)	**
TPA	24 (13.30)	88 (26.74)	**	453 (89)	397 (45)		1345 (156)	747 (81)	**	1114 (161)	693 (60)	**
BA/ac (sqft/ac)	0.59 (0.33)	2.11 (0.65)	**	12.95 (2.67)	12.85 (1.60)		61.39 (8.18)	39.65 (4.18)	**	65.87 (9.70)	42.1 (3.86)	**
Recruited Aspen												
DBH	-	2.09 (0.02)	-	2.27 (0.03)	2.43 (0.03)	***	2.81 (0.06)	3.08 (0.05)	***	3.27 (0.01)	3.45 (0.07)	*
Height	-	22.25 (0.97)	-	24.55 (0.45)	24.57 (0.37)		33.33 (0.52)	30.64 (0.29)	**	38.40 (0.88)	39.06 (0.95)	
TPA	0 (0)	88 (27)	**	439 (86)	369 (44)		1306 (157)	641 (73)	***	977 (159)	385 (44)	***
BA/ac	0 (0)	2.11 (0.65)	**	12.47 (2.58)	12.14 (1.56)		59.33 (8.24)	35.03 (3.86)	**	61.19 (9.71)	26.63 (3.30)	**
Recruited Spruce												
DBH	-	-	-	-	2.2 (0.08)	-	-	2.57 (0.10)	-	-	3.10 (0.08)	-
Height	-	-	-	-	12.40 (1.01)	-	-	16.67 (0.73)	-	-	19.55 (0.42)	-
TPA	0 (0)	0 (0)	-	0 (0)	14 (7)	**	0 (0)	59 (18)	**	0 (0)	163 (29)	***
BA/ac	0 (0)	0 (0)	-	0 (0)	0.37 (0.19)	**	0 (0)	2.21 (0.72)	**	0 (0)	8.99 (2.01)	***
Other Species												
DBH	2.13 (0.09)	-	-	2.45 (0.35)	2.12 (0.06)		3.05 (0.39)	3.03 (0.14)		2.49 (0.7)	2.79 (0.09)	*
Height	-	-	-	-	-	-	26.30 (0)	26.07 (2.99)		33.10 (1.77)	29.29 (0.96)	
TPA	24 (13)	0 (0)		15 (10)	14 (7)		39 (23)	47 (16)		137 (61)	144 (41)	
BA/ac	0.59 (0.33)	0 (0)		0.49 (0.36)	0.34 (0.18)		2.06 (1.27)	2.41 (0.81)		4.68 (2.00)	6.48 (1.72)	

Table 3 Summary table of the mean dbh (in), height (ft), TPA, and BA/ac (ft^2/ac) (± standard error) of measured trees (dbh≥ 5") across treatment type and age class. All overstory refers to every tree recorded, recruited aspen and recruited spruce are individuals that regenerated into the over story, and residuals are all species of mature trees that were left behind during the last regeneration harvest

	0–5 years			6–10 years			11–15 years			16+ years		
	Aspen	Mixed		Aspen	Mixed		Aspen	Mixed		Aspen	Mixed	
All Overstory												
DBH (in)	8.59 (0.57)	5.25 (0.68)	***	7.37 (0.45)	5.37 (0.42)	**	7.23 (0.25)	6.24 (0.15)	**	6.73 (0.12)	6.34 (0.07)	**
Height (ft)	53.18 (2.76)	40.18 (2.98)	*	43.98 (1.62)	34.60 (1.21)	***	48.11 (1.29)	40.93 (0.91)	***	54.57 (0.55)	52.13 (0.45)	***
TPA	55 (22)	65 (18)		25 (11)	66 (13)	**	57 (15)	71 (15)		204 (22)	258 (20)	*
BA/ac (sqft/ac)	10.84 (4.14)	6.48 (1.95)		6.89 (2.02)	7.5 (1.44)		15.74 (3.69)	14.31 (2.97)		56.28 (7.22)	57.51 (4.58)	
Recruited Aspen												
DBH	-	-		-	-		5 (0)	5 (0)		5.89 (0.4)	5.95 (0.03)	
Height	-	-		-	-		48.30 (0)	43.17 (2.17)		53.43 (0.54)	53.85 (0.40)	
TPA	0 (0)	0 (0)		0 (0)	0 (0)		1 (1)	2 (1)		150 (21)	166 (17)	
BA/ac	0 (0)	0 (0)		0 (0)	0 (0)		0.01 (0.09)	0.26 (0.14)		28.87 (4.12)	32.62 (3.57)	
Recruited Spruce												
DBH	-	-		-	-		-	-		-	5.26 (0.06)	
Height	-	-		-	-		-	-		-	29.63 (1.23)	
TPA	0 (0)	0 (0)		0 (0)	0 (0)		0 (0)	0 (0)		0 (0)	5 (2)	**
BA/ac	0 (0)	0 (0)		0 (0)	0 (0)		0 (0)	0 (0)		0 (0)	0.81 (0.32)	**
Residuals												
DBH	8.59 (0.57)	5.25 (0.68)	***	7.37 (0.45)	5.37 (0.42)	**	7.29 (0.25)	6.32 (0.16)	**	10.04 (0.40)	7.84 (0.23)	***
Height	53.18 (2.76)	40.18 (2.98)	**	43.98 (1.62)	34.60 (1.21)	***	48.34 (1.30)	41.10 (0.96)	***	60.94 (1.63)	51.52 (1.27)	***
TPA	55 (22)	65 (18)		25 (11)	66 (13)	**	56 (15)	67 (14)		41 (10)	72 (10)	**
BA/ac	10.84 (4.14)	6.48 (1.95)		6.89 (2.02)	7.5 (1.44)		15.57 (3.68)	13.8 (2.81)		24.76 (6.87)	21.58 (3.07)	

(Table 3). Residual and advanced regeneration trees were present at a TPA range of 25 (±11) to 72 (±10) depending on age class, and basal area of 6.48 (±1.95) ft^2/ac in the 0–5 mixedwood age class to 24.76 (±6.87) ft^2/ac in the 16+ aspen age class. In all age classes, the residual trees in the pure aspen stands had significantly greater average DBH and heights, ranging from 7.29 (±0.25) to 10.04 (±0.40) inches for DBH and 43.98 (±1.62) to 60.94 (±1.63) feet for height, but 5.25 (±0.68) to 7.84 (±0.23) inches and 34.60 (±1.21) to 51.52 (±1.27) feet in mixedwoods.

Diameter Distribution

All forest age classes and treatment types had unimodal distributions (Figure 3). However, the shape of the unimodal diameter distribution between the aspen and mixedwood treatment types varied most in the first three age classes. In the 0–5 age class, residual trees in the aspen treatment were limited and few. Conversely, in the mixedwood treatment, there were more aspen in the 1-inch diameter class. In the 6–10 year old and 11–15 year old age classes, the conventionally treated aspen stands have higher densities in the 1 to 2 inch diameter classes compared to the mixedwood treatment stands at these same ages (Figure 3, Table 3). Yet, in mixedwood treatment, spruce and other species including oaks and balsam fir compose a small but notable density in the 1 to 2 inch size classes. This representation increases in the oldest age class for the mixedwood treatment. The diameter distributions at 16+ years also become similar between the mixedwood and aspen treatments, the notable difference being the presence of white spruce in the mixedwood treatment (Figure 3).

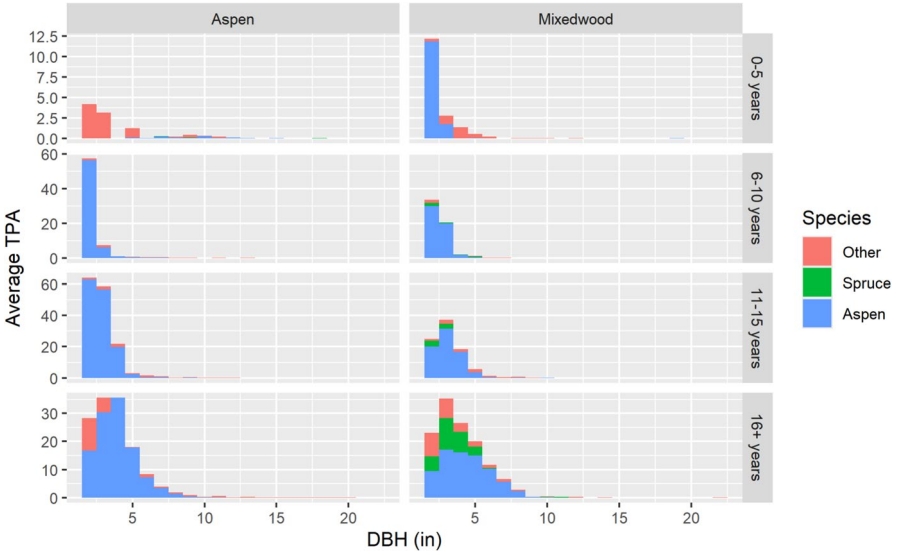


Fig. 3 Diameter distributions of aspen, white spruce, and all other species combined showing average trees per acre (TPA) for each treatment type and age class combination

Mixed-Model Analysis

Comparison of several candidate aspen height models resulted in a model with DBH, live/dead status, stand basal area, age class, and management type as significant (p-values < 0.1) explanatory variables of the natural log of height (Table 4) and an $R^2 = 0.779$. Exponentiating the coefficients showed that height was estimated to increase by exp(0.10538) = 1.11 or 11% for every additional inch of DBH and by 0.03% for each additional ft^2/ac of basal area. Although the first two age classes were not significantly different, on average the third and fourth age classes were estimated as 24% and 47% taller, respectively. Live aspen trees were 17% taller on average than dead aspen trees, and aspen under mixedwood management averaged 6% less height than conventional aspen.

Several candidate models were explored to quantify the relationship between aspen regenerants in the first age class with residual tree and site conditions. After sequentially removing non-significant terms, results showed that residual variables basal area, TPA, quadratic mean diameter, and average height did not affect the number of aspen regenerants (p-values > 0.1). In addition, the most parsimonious model (based on AIC) only included management type as a predictor (Table 4). Exponentiating this coefficient estimated that mixedwood stands had 55% less aspen regenerants than conventionally managed stands.

Table 4 Mixed-effects model results for aspen height and regeneration. Both response variables were natural log transformed and are in ln(ft) and ln(count), respectively. Diameter breast height (DBH) was in inches and basal area in ft^2/ac. Stand was included as a random effect, and standard deviations (σ) are given for the group and residual variation

Response Variable	Explanatory Variables	Coefficients	p-values	
Ln.Height	Intercept	2.77616	< 0.001	***
	DBH	0.10538	< 0.001	***
	Basal area	0.00034	0.0122	**
	Age class 2	0.02929	0.6710	
	Age class 3	0.21428	0.0014	**
	Age class 4	0.38280	< 0.001	***
	Status (live)	0.15930	< 0.001	***
	Management (mixed)	-0.06173	0.0518	*
	σ (stand)	0.0706		
	σ (residual)	0.1451		
Ln.Regeneration	Intercept	9.79738	< 0.001	***
	Management (mixed)	-0.79328	0.0287	**
	σ (stand)	0.5324		
	σ (residual)	0.4535		

Discussion

Aspen management within the Great Lakes region has been greatly shaped by land use history, the development of strong forest product markets, and the silvics of aspen, resulting in aspen being widely distributed across the region (Windmuller-Campione et al. 2020, Gifford et al. 2024). However, management practices (shorter rotation coppice systems) have resulted in lower tree species diversity compared to the aspen forest type prior to European colonization in the region (Cleland et al. 2000). Managers are interested in increasing long-lived conifers within the region and increasing tree species diversity to support ecological and economic resilience through implementing a mixedwood system with white spruce and aspen. Our results highlight that planted white spruce can survive and many will reach the sapling stage by 16–20 years (Table 2), providing justification for the increased cost of planting and release treatments. Additionally, aspen met minimum thresholds for fully stocked stands across all age classes; both the conventional and mixedwood treatments had over 10,000 TPA of aspen on average in the youngest age class (Table 1). Research from the Great Lakes Region shows that the density of regenerating aspen stems per acre can range from 5,000 to 70,000 two years post-harvest (David et al. 2001; Baughman 2019), with a density of at least 1,000 stems per acre after three growing seasons considered adequate stocking (Minnesota DNR 2016).

To meet regeneration requirements, managers have conventionally focused on a coppice system with limited residuals to successfully regenerate aspen due to the species' shade intolerance (Doucet 1989; David et al. 2001; Brinkman et al. 1975). Perala (1977) found that as little as 10 to 15 ft^2/ac basal area can reduce aspen regeneration growth by 35 to 40%. Other researchers encourage leaving no more than 20 dispersed mature residual trees per acre during a harvest (Baughman 2019). However, more recent research has quantified that leaving aggregated residuals that meet Minnesota's best management practices of 5% of canopy trees retained by areas in 0.25 acres groups maintained adequate aspen regeneration within 0 to 16 feet of the aggregated residuals (Curzon et al. 2017). Similarly in our study's sampled stands which were operationally harvested and met Minnesota's best management practices with residual density, we observed no relationship among aspen regeneration density in the youngest stands (0–5 years) with residual basal area, density, or tree size. Early release treatments successfully reduced aspen regenerate density; there was significantly less aspen regeneration in the mixedwood compared to the aspen treatments (see methods; Table 1). Our results provide additional support that leaving the recommended density of residuals trees does not significantly reduce aspen regeneration while maintaining critical bird and small mammal diversity (Grinde et al. 2020, Merrill et al. 1998).

While aspen stands in the region can have initial densities of over 10,000 stems per acres in the first five years, this density is not maintained over time. Conventional aspen stands have been documented to undergo extensive self-thinning in early stages of development due to density-dependent mortality, reducing to 2,000 to 4,000 stems per acre ten years after harvest (David et al. 2001). Mortality was witnessed in both treatment types, but overall dead regenerant density was higher in conventional aspen than in mixedwood treatments, even in the older age classes (Figure 2), indicating more density-dependent mortality is occurring in aspen treatments than in mixedwoods due

to a lack of early release treatments. Dead aspen regenerants were also significantly shorter than live regenerants, showing how density-dependent thinning is allowing the surviving regenerants to continue putting on substantial growth (Table 4). Bokalo and colleagues (2007) found similar results, where higher starting stand densities were associated with the highest rates of regenerant mortality in spruce-aspen mixedwoods. Multiple studies have also explored the size-density effects of both conventional aspen and white spruce-aspen mixedwood stands, showing how thinning, or decreasing the density, of aspen at early stand ages increases the diameter and height growth of the unthinned trees (Bokalo et al. 2007; Kabzems et al. 2015; Comeau 2021; Comeau & Bokalo 2024), with the tradeoff that the unthinned stands maintain a higher volume than thinned stands (Sorensen 1968; Rice et al. 2001). In our mixedwood sites, white spruce regenerants were released via brush sawing after three to four growing seasons, simultaneously thinning the aspen regenerants. Consistent with previous studies, after 20 years of growth, our "thinned" mixedwood treatments had greater average stem DBH, and "unthinned" aspen treatments had a significantly greater stand density, as seen through their higher TPA and basal area (Table 2). Similar results with increased aspen diameter growth in thinned mixedwood stands were recorded in Alberta, Canada (Bjelanovic et al. 2021). Our height modeling also showed results consistent with expected height development where height in mixedwoods was 6% less than in conventional aspen treatments, indicating that trees in mixedwoods have adequate growing space to allocate growth to diameter rather than height, whereas the trees in the dense pure aspen treatments are more prone to becoming spindly (Table 4).

One concern of mixedwood management is the survival and growth of white spruce given cost of planting and release. In other mixedwood aspen-white spruce systems, understory vegetation such as shrubs, herbaceous plants, grasses, and aspen regenerants can slow the diameter and height growth of the spruce regenerants (Man et al. 2008). This can lead to increased vulnerability to browse and other disturbance agents (Comeau et al. 2004) leading to higher spruce mortality and reducing the proportion of spruce in mature mixed stands (Kabzems et al. 2015; Kenefic et al. 2021). While there was some initial mortality of white spruce, our first two age classes averaged 270 (±45) stems per acre which is just below the stocking levels of 300 to 400 stems per acre after tree growing season (Table 1) (Minnesota DNR 2016). Planting stress (Man & Greenway 2010), interspecies competition with aspen (Dobbs 1972), and incidental damage during the brush sawing treatment are likely causes of the observed regenerant mortality during the first few years of growth. Additionally, compared to aspen-white spruce mixedwood studies within more of the central range of the boreal forest, Minnesota represents the southern extend and the intensity of a summer drought on newly planted white spruce may influence future survival and impact natural regeneration of white spruce (Chhin & Wang 2008, but see Man & Greenway 2013). Natural regeneration of white spruce can be extremely difficult even during a mast year. In Alberta, Canada, natural regeneration survival was only 15% compared to over 95% of planted white spruce seedlings (Stewart et al. 2000). Natural regeneration may be even lower with increased potential for summer drought (Chhin & Wang 2002, Gärtner et al. 2011). It will be important to continue monitoring to document longer term survival to better understand dynamics at the southern extent of the boreal forest biome.

Mixedwood management represents a potential tool for increasing species and structural diversity of stands during early stages of development while maintaining sufficient aspen regeneration in Minnesota (Table 1, Table S2). These structural and compositional differences are also indicative of the ecological benefits of mixedwood forests on the landscape level, such as more diverse wildlife habitat, climate change resilience, resistance to insect outbreaks, and increased carbon storage (Kenefic et al. 2021). Additional studies will be needed to identify timing, intensity, and frequencies of silvicultural treatments required to manage these systems at the southern extent of their range and better understand how to leverage the silvics of these species when implementing mixedwood management given the increased cost of planting and release (see Darquié et al. 2024). Overall, mixedwood systems provide another tool within a forest manager's toolbox to expand the range of ecosystem services provided by the aspen forest type.

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Data Availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interest The authors declare no competing interests.

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