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Restoration of woody plant communities in red pine plantations on abandoned agricultural land in northern Minnesota, USA

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A B S T R A C T

While tree plantations have increased globally, there is growing interest in restoring plantations to native ecosystems. Restoration efforts may be more successful when tree species native to original ecosystems are planted instead of species that are either introduced or native, but off site.

Plantations of red pine (*Pinus resinosa* Ait.) in the western Great Lakes region of North America were commonly established on red pine sites, often after agricultural clearing and abandonment. Red pine is the only species in the overstory, compared to 10 or more species in red pine woodlands. Plantations differ in structure from woodlands, being single-aged versus multi-cohort and having high and spatially-uniform density versus lower and variable density.

Our aim was to contrast changes in structure and woody species composition over a 15-year period in response to two silvicultural approaches in red pine plantations on the Red Lake Wildlife Management Area in northwestern Minnesota, USA. Approaches included: 1) uniform thinning followed by a dispersed retention harvest (dispersed treatment) and 2) variable density thinning followed by an expanding gap irregular shelterwood (aggregated treatment).

Basal area of trees $\geq$10 cm dbh was reduced similarly in both treatments to 9 m^2 ha^{-1}, but there was high within-stand variability (coefficient of variation) in the aggregated treatment (>100%) compared to the dispersed treatment (20%). Understory woody species abundance increased with both treatments, including sapling, large regeneration, and small regeneration layers, with >100% increases. In the sapling layer, the increased abundance (to 2.5 m^2 ha^{-1}) reflected new recruitment into this layer, as there were few saplings before treatment (<0.5 m^2 ha^{-1}). By year 15, the majority of saplings were canopy capable species, while lower regeneration layers contained mixtures of canopy trees, sub-canopy trees, and shrubs.

Composition in the understory changed, but was similar between treatments, including increases in woody shrubs in the small regeneration layer and increases in red pine regeneration in the large regeneration layer. The sapling layer had increased importance of several native tree species, especially in the aggregated treatment.

Both of our silvicultural approaches moved structurally simple, species poor red pine plantations toward a condition reflecting native red pine woodlands, which had mixed-species composition and variably open canopy cover. The treatment using variable density thinning and an irregular shelterwood resulted in greater spatial variability of structure and greater importance of shade-intolerant tree species, both characteristics of native woodlands. While focused on red pine, this approach should have application to conifer restoration more generally.

1. Introduction

Plantations of commercial timber species have increased in extent over the last several decades as global demand for wood increases (Payn et al., 2015; Production Forests: Global Forest Review, 2021). At the same time, there is interest in restoring plantations to native tree species and the plant communities originally found on the site (Kremer et al., 2021). In some cases, particularly in the tropics, this may involve an off-site or non-native tree species being used as a nurse crop to facilitate succession to native species (Griscom and Ashton, 2011; Bechara et al., 2016; Kremer et al., 2021). Alternatively, the plantation tree species may be a component of the original native plant community (e.g., Guariguata et al., 1995; Griscom and Ashton, 2011), but its abundance is unnaturally high, and the structure of the plantation is altered from natural conditions (Kremer et al., 2021).

The latter is often the case for plantations of red pine (*Pinus resinosa* Ait.) in the western Great Lakes region of North America. For instance, in Michigan, Wisconsin, and Minnesota, the estimated area for red pine forests in 2016 was over 800,000 ha and over 76 percent of this was plantation (Palik and D'Amato, 2020). Many of these plantations occur on sites where red pine occurred naturally, specifically those having course textured sandy soils with xeric to dry-mesic moisture regimes (Rudolf, 1990). Moreover, the plantations were sometimes established on abandoned farmland which proved unproductive for agriculture (e.g., Bielecki et al., 2006). Red pine is often the only species in the overstory of the plantations, while historically, over much of its Lake States range, red pine was abundant but occurred often in association with eastern white pine (*Pinus strobus L*) or jack pine (*Pinus banksiana Lamb.),*

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as well as a number of less abundant species, including balsam fir *(Abies balsamea (L.) Mill.)*, white spruce *(Picea glauca (Moench) Voss),* trembling and bigtooth aspens *(Populus tremuloides Michx., P. grandidentata Michx.),* red maple *(Acer rubrum L.),* northern red oak *(Quercus rubra L.),* bur oak *(Quercus macrocarpa Michx.), and* paper birch *(Betula papyrifera (Marsh.)* (Whitney, 1986; Nowacki et al., 1990; Palik and Pregitzer, 1992; Frelich and Reich, 1995; Aaseng, 2003).

Structurally, red pine plantations differ from natural red pine-dominated ecosystems (Bender et al., 1997). Many natural red pine ecosystems are characterized as woodlands, ranging from open barrens on the most xeric sites to closed woodlands on dry-mesic sites (Palik and D'Amato, 2020). Age structures of red pine dominated (mixed-species) ecosystems range from broadly single-cohort to multi-cohort (Bergeron and Brisson, 1990; Drobyshev et al., 2008a; b; Fraver and Palik, 2012). A disturbance regime is characterized by frequent surface fire and infrequent, patchy crown fire (but often less than stand-replacing), which results in the structural conditions described (Palik and D'Amato 2019; 2020). In contrast, like most conifer plantations, red pine plantations are narrowly even-aged and managed to maintain high stocking of crop trees with a closed canopy structure.

To date, there has been limited long-term research aimed at active restoration of red pine plantations back to native woody species and woodland structure. Studies that have occurred have been in areas outside the native range of red pine (Abella, 2010) or on sites and soils not necessarily characteristic native red pine woodland ecosystems (Parker et al. 2001; 2008; Bender et al., 1997; Spitale, 2011), or not focused on restoration of native ecosystems (Vander Yacht et al., 2022). While informative, some of these studies are more akin to an exotic nurse tree approach to facilitate succession to native species (Griscom and Ashton, 2011). One study in southern Ontario CA on abandoned farmland (Newmaster et al., 2006), that was within the range of red pine and included sites on course textured, xeric soils, found that plant communities of plantations were substantially different than native forest (different composition, lower richness, different abundance), but that the difference was lessened at wider tree spacing, presumably due to greater resource availability to other species.

Our aim was to add to understanding silvicultural restoration of post-agricultural red pine plantations, specifically on sites formerly supporting native red pine ecosystems. Our study setting was the Red Lake Wildlife Management Area (RLWMA) in northwestern Minnesota, USA, where red pine plantations were planted on abandoned agricultural land by the Civilian Conservation Corps and the Resettlement Administration in the 1930s and 1940s (Minnesota Department of Natural Resources, 2020). The RLWMA has an interest in restoring plantations to conditions approaching those of the native plant community for wildlife and plant diversity objectives.

Our overall objective was to compare changes in composition and structure over a 15-year period in response to two contrasting silvicultural approaches aimed at restoration: i) uniform thinning and direct seeding of select species, with a subsequent dispersed retention harvest to release regeneration and ii) variable density thinning and direct seeding, with a subsequent retention harvest that approximated an expanding gap irregular shelterwood. We addressed the following questions with an aim of comparing and contrasting responses to the two approaches. Question 1: How do the two silvicultural approaches differ in resultant structural conditions which influence resource availability in the understory? Question 2: Do the approaches result in differing abundance and composition of the woody plant community in the lower structural layers, including regenerating trees and woody shrubs? While the study ecosystem is red pine, our results and conclusions potentially may have application to conifer plantation restoration more broadly.

2. Methods

2.1. Study area

The Red Like Wildlife Management Area (hereafter RLWMA) is located in northwestern Minnesota, USA (centered on 48.57 N, −95.12 W; Fig. 1). The area encompasses 130,000 ha of mixed subboreal upland and lowland forest types. The surficial geology of the area reflects the drainage of glacial Lake Agassiz and consists of gently rolling to flat topography interrupted by sand and gravel beach ridges (Heinselman, 1963). Parent materials consist of unconsolidated lacustrine deposited silts, clays, sands, and lake-modified till. Mineral soils occur on better drained upland sites formed on lacustrine sands and calcareous glacial till.

The climate of the RLWMA region is humid-continental with short, mild summers and long, cold winters. The average temperatures are 19.6 °C and −16.3 °C for July and January, respectively. Winter low temperatures of −40 °C are common. Average annual precipitation is 57.3 cm, ranging from 1.2 cm in February to 10.3 cm in June. Seventy-two percent of the annual precipitation falls from May through September. Annual snowfall averages 110.7 cm.

2.2. Study ecosystems

Uplands of the study area were cleared of forest and converted to agriculture during Euro-American settlement in the early part of the 20th century. These lands were subsequently abandoned due to poor growing conditions, after which red pine was machine planted in the 1930s to early 1940s at densities of 1994 per ha on a spacing of 1.8 × 2.7 m. Eight stands were selected in 2004 (Fig. 1) from a larger pool of plantations and ranged in size from 5 to 21 ha, with basal areas of 21 to 40 m^2 ha^{-1} of trees ≥10 cm diameter at breast height (diameter at 1.4 m height).

The soil taxonomic class of the study sites were mixed, frigid Aquic Udipsamments. The majority of stands were located on the Hiwood soil series, consisting of very deep, moderately well drained soils that formed in sandy glacial lacustrine or outwash sediments on glacial lake plains or outwash plains. Permeability is rapid. Slopes range from 0 to 12 percent (Soil Survey Staff, 2023). Red pine site index of 17.7 m at age 50.

The original ecosystem of the study sites has been determined from adjacent native ecosystems to be Fire Dependent Northern Dry-Sand Pine Woodland (termed FDn12, based on the state of Minnesota's native plant community classification system; Aaseng, 2003). These were woodlands having an interrupted and variable canopy (50–75% cover) with mature and old stands dominated by red pine and jack pine, with occasional balsam fir and paper birch. Stands often include younger cohorts of red pine, along with eastern white pine, white spruce, and trembling aspen. Northern red oak, bur oak, and red maple can be occasional in the canopy. The more abundant woody shrubs and sub-canopy trees include lowbush blueberry (*Vaccinium angustifolium* Aiton), juneberry (*Amelanchier* spp.), wild rose (*Rosa* spp.), beaked hazelnut (*Corylus cornuta* Marsh.), and bush honeysuckle (*Diervilla lonicera* Mill.).

On average (+/- 1 standard deviation), red pine comprised 94.5 (8.9)% of overstory basal area at the time of stand selection. Balsam fir, paper birch, eastern white pine, jack pine, and white spruce where the most abundant minor species in the overstory, but none of the species occurred in all eight stands or with any abundance. There were very few sapling-sized trees (2.5 ≤ dbh < 10 cm), with the species largely the same as the minor species in the overstory, but also including infrequent willow (*Salix* spp.), balsam poplar (*Populus balsamifera* L.), juneberry, boxelder (*Acer negundo* L.), and speckled alder (*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen).

Trees and woody shrubs in the large regeneration layer (dbh < 2.5 cm and taller than 1 m) were limited and highly variable in abundance, averaging 6219 (8148) ha^{-1}. Species in this layer included most of those listed above for the sapling layer, as well as rose (*Rosa* spp.), beaked

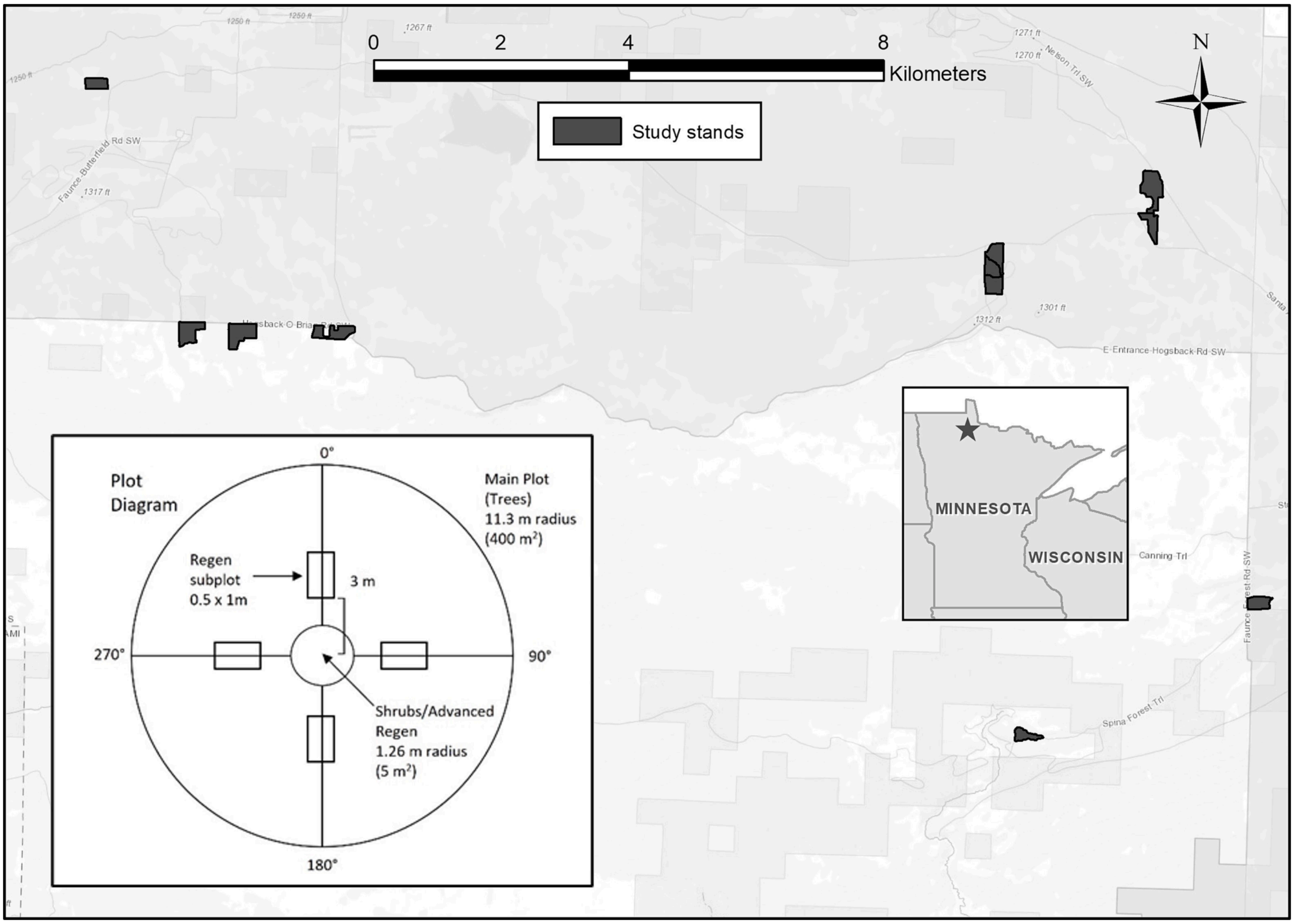

Fig. 1. Location of the Red Lake Wildlife Management Area (RLWMA) in Minnesota, USA, showing study stands within the RLWMA, with an inset of a sampling plot.

hazel, and chokecherry (*Prunus virginiana* L.). Tree and woody shrub density in the small regeneration layer (<1 m tall) averaged around 57,218 (32,052) ha^{-1}, with red pine, balsam fir, rose, juneberry, bush honeysuckle, beaked hazel, and lowbush blueberry being the most common species in this layer.

2.3. Silvicultural approaches

The two silvicultural approaches examined were based on a hybrid variable density thinning/variable retention harvest (Palik et al. 2020). The initial entry for both reduced basal area from a mean (+/- sd) of 31 (8) m^2 ha^{-1} to 19 (3) m^2 ha^{-1}, or an average reduction of 35 (3)%. The two treatment approaches differed in the spatial pattern of harvest and subsequent residual trees. In the initial entry, treatment 1 (hereafter dispersed retention) was a uniform thinning with dispersed retention of the residual trees. Treatment 2 (hereafter aggregated retention) concentrated the removal in 0.13 to 0.20 ha openings, with limited thinning between the openings to facilitate machinery trafficking, resulting in aggregated retention of residual trees. For both treatments, harvesting took place between July and September 2004 using a feller-buncher with whole-tree skidding to a landing outside the stands, where tops and branches were piled. In the aggregated retention treatment, trees were felled into the opening prior to skidding to minimize damage to residual trees. In both treatments, skid routes for trees were established during harvest and were used in the first and the second entry.

All stands were seeded just prior to the initial harvest using an all-terrain vehicle and seed hopper. Seeding before harvest was conducted for ease of application and so that machinery trafficking and log skidding would incorporate seed into the exposed surface mineral soil. The seeding mixture included jack pine (0.05 kg ha^{-1}), eastern white pine (0.14 kg ha^{-1}), and paper birch (0.006 kg ha^{-1}). These species were selected as they were all components of the native plant community for the ecosystem and have the potential to germinate on exposed mineral soil.

The second entry reduced basal area in both treatments to a mean (+/- 1 sd) of 9 (0.9) m^2 ha^{-1}. The harvest took place between July and September 2013 and used a feller-buncher with whole-tree skidding to a landing where tops and branches were piled. In the dispersed retention treatment, harvesting paralleled the initial entry, removing trees uniformly across stands to leave a dispersed residual matrix. In the aggregated retention treatment, existing openings were expanded by 15 to 25% in size, with some thinning between gaps. This sometimes resulted in merging adjacent gaps to form a single larger irregular gap containing scattered residual trees. After the second entry, basal area within the aggregated treatment stands ranged widely, from 0 to 21 m^2 ha^{-1}. In the aggregated treatment, trees were felled away from gaps to avoid damage to advance regeneration in the gaps and both treatments utilized established skid trails from the first entry to minimize damaged to established regeneration.

2.4. Sampling

Woody vegetation was sampled before the initial harvest, from June to August 2004, staying ahead of the harvesting in each of the eight stands. In each stand, eight permanent plot centers were located and monumented to serve as the loci for initial sampling of woody vegetation

(Fig. 1). In the aggregated treatment, plot center number was increased to 16 after harvesting to better capture spatial variability of conditions. Plot centers were distributed randomly across a stand, but at least 30 m from stand boundaries and each other where space allowed. At each point, a fixed 11.3 m radius circular plot (405 m^2) was established and woody stems ≥2.5 cm dbh were measured for species and diameter. This layer was remeasured in years 1, 10, 12 (all after the first harvest), 13, and 15 (both after the second harvest). Large regeneration and shrubs (stems <2.5 cm dbh and ≥1 m tall) were tallied to species in a centrally located 1.26 m radius plot (5 m^2) in each main plot. Small regeneration and shrubs (stems <1 m tall) were tallied to species in four 0.5 m × 1.0 m quadrats) spaced 3 m from plot center. Regeneration and shrub tallies were repeated in years (after initial harvest) 1, 2, 3, 7, 9, 12, and 15. Canopy cover was estimated using a spherical densiometer. Four readings were taken at each sample point facing north, east, south, and west, respectively. Readings were taken at waist height, approximately 1.2 m, and reflect all vegetation above that height. Canopy cover measurement were repeated in years (after initial harvest) 1, 10, 12, and 15.

2.5. Analysis

Plot level data for the overstory (basal area, percent cover), sapling layer (basal area), and large and small regeneration/shrub layers (density) were summarized to the stand-scale for each measurement year. This involved deriving arithmetic means for each variable in each sample year for dispersed treatment stands and weighted means for aggregated treatment stands. In the aggregated treatment stands for each sample year, the weighting procedure consisted of separating measurement plots into canopy condition (opening or matrix), deriving means for that condition, and adjusting means by the proportion of the stand in each condition. Adjusted conditional means were then summed to get the weighted mean for the response variable in a stand.

Repeated measure ANOVA was used to test for treatment differences in response variables over time. We used a two-factor mixed effects model with canopy treatment as the between-subject factor and year of sampling as the within-subject factor. Normality of residuals for treatment main effects and treatment by time interactions were tested with Shapiro-Wilk tests ($p = 0.05$), while homogeneity of variances for treatment and treatment within year were tested with Levine's tests ($p = 0.10$). Square root or log transformations of the data were used if any of the test assumption were not met. Homogeneity of covariance matrices were tested with Box's tests and a conservative alpha of $p \geq 0.001$ was used to protect against type II errors due to low sample size. The conservative Greenhouse and Geisser adjustment was used for all tests for year and interaction of year and treatment. If year was significant, Tukey's HSD contrasts were used to compare years, either pooling treatments or within each treatment if the interaction was significant. Significance of tests for treatment, year, interaction, and contrasts, was assessed at $p \leq 0.10$.

Sapling basal area, large and small regeneration/shrub layer densities were also analyzed in year 15 for treatment effects on abundance of different growth forms, including canopy capable tree species, subcanopy tree species, and woody shrub species. Analyses were done separately for each layer using a two-factor mixed-effect ANOVA model. Assumptions of normality of residuals and homogeneity of variances were tested with Shapiro-Wilk tests ($p = 0.05$) and F-max tests ($p = 0.10$), respectively. Data were square-root or log transformed as needed to meet test assumptions. Tukey's HSD tests were used to compare growth forms for pooled treatments or within treatments if the interaction term was significant. As above, significance of tests was assessed at $p \leq 0.10$.

Nonmetric multidimensional scaling (NMS) was used to graphically display and interpret woody community compositional changes over time within the sapling and large and small regeneration/shrub layers. NMS relaxes assumptions of normality and linear relationships to environmental variables, provides a biologically meaningful view of data, and preserves distance properties among sample units (stands in our case) (McCune and Grace, 2002).

The NMS data matrices consisted of mean treatment stand values (average for the four stands in each treatment) × year combinations (rows) and tree/shrub species that occurred in at least five stands in the structural layer (columns). We chose this approach, rather than ordination of actual treatment stand by year combinations, because some stands contained little or no individuals in a size class before harvest or in the initial years after the first harvest, rendering it impossible to achieve a multi-dimensional NMS solution. The averaging approach resulted in all treatment by year combinations having at least one species in the size class. For all ordinations, data were square root transformed prior to analysis to down-weight the influence of overly abundant species.

Ordinations were run using Sørenson (Bray–Curtis) distance measures and a specification of 6 dimensions and 250 iterations (with actual data) for the initial analysis. The significance of dimensional solutions was assessed using Monte Carlo permutation procedures (based on 249 interactions). Final ordinations were restricted to no more than three dimensions based on stress reduction and examination of scree plots (McCune and Grace, 2002). Pearson correlations of species with axes are noted when p values were 0.70 and greater. NMS was performed using PC-ORD 5.0 software (McCune and Mefford 2006).

3. Results

3.1. Overstory structure

Mean basal area of the overstory (trees ≥ 10 cm dbh) varied significantly over time (Fig. 2a; $p < 0.001$), but not between treatments ($p = 0.610$), nor was the interaction between the two significant ($p = 0.744$). Basal area was significantly reduced by the initial harvest ($p < 0.001$), increased slightly (but significantly) by years 10 and 12 ($p = 0.087$, 0.019, respectively), and was reduced again significantly after the second harvest in year 13 ($p < 0.001$), but had not increased in year 15 over year 13 values ($p = 0.853$).

In contrast, there were significant effects of treatment on within-stand variability of basal area, as measured by mean coefficient of variation (cv) in basal area (Fig. 2a inset). The interaction between treatment and time was significant ($p < 0.001$). Within treatments, there were no significant year effects on mean cv for the dispersed treatment ($p = 0.287$), while the effect of year was significant for the aggregated treatment ($p = 0.001$). Within the aggregated treatment, mean cv in all years after the initial treatment was significantly higher than pretreatment ($p < 0.001$). Mean cv in years 1, 10, and 12 did not differ from each other ($p = 0.990$), but were all less than cv in years 13 and 15 ($p < 0.001$), which did not differ from each other ($p = 0.923$). Within years, mean cv did not differ between treatments prior to the initial harvest ($p = 0.443$), but means did differ between treatments in all other years ($p < 0.001$), being consistently higher in the aggregated treatment.

Mean canopy openness did not differ between treatments (Fig. 2b; $p = 0.649$), nor was the interaction with year significant ($p = 0.428$). Canopy openness did vary significantly over time ($p < 0.001$). Percent open canopy was significantly lower before the initial harvest compared to all subsequent years ($p < 0.001$). Year 1 canopy openness was significantly higher than years 10 and 12 ($p = 0.005$, 0.004, respectively), while the later did not differ from each other ($p = 0.99$). There was a substantial increase in canopy openness after the second harvest in year 15, which was significantly different than all earlier years ($p < 0.001$).

As with basal area, there were significant effects of treatment and time on within-stand variability of canopy openness, as measured by mean coefficient of variation (Fig. 2b inset). The interaction between treatment and time was not significant ($p = 0.292$), so main effects were examined. Mean cv was significantly higher for the aggregated treatment compared to the dispersed treatment ($p = 0.049$). The overall

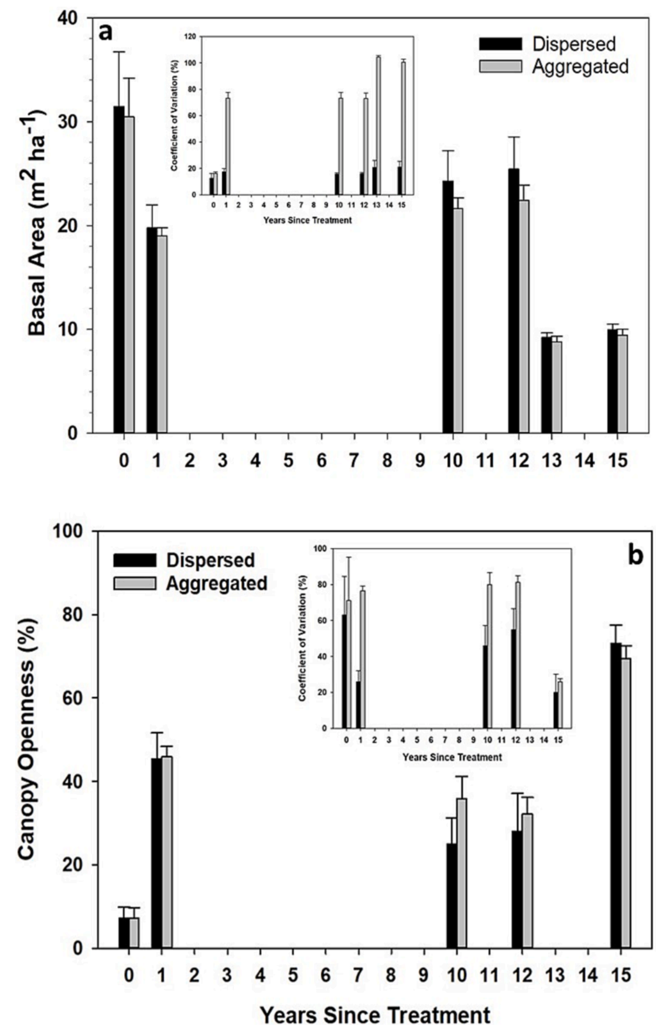

Fig. 2. Changes in a) canopy basal area and b) canopy openness over time in two silvicultural treatments in red pine plantations. Values are means + one standard error of four treatment stands. Insets are mean coefficient of variation in response variables.

effect of year was significant ($p = 0.018$), with year 15 significantly less than all other years ($p < 0.001$ to 0.045), with none of the earlier years differing significantly from each other ($p = 0.497$ to 0.992).

3.2. Woody species development

Woody species abundances increased over time in all structural layers in response to treatments, but were similar between treatments. In the sapling layer, treatment effect was not significant ($p = 0.238$), although there was a trend towards greater basal area of saplings in the later years that was muted by the variability in the aggregated treatment (Fig. 3a). The interaction of treatment and time was not significant ($p = 0.135$), so treatments were pooled to compare years. Sapling basal area did not differ between pre-treatment and year 1 ($p = 0.999$), but increased significantly by years 10–15, which were all significantly greater than years 0 and 1 ($p = 0.071$ to < 0.001), but not significantly different from each other ($p = 0.72$ to 0.999). Year 10 was less than year 15 ($p = 0.014$), while year 12,13, and 15 were not significantly different from each other ($p = 0.278$–0.999).

Stem density in the large regeneration/shrub layer did not differ significantly between treatments ($p = 0.374$), although there was a trend towards higher density in the aggregated treatment (Fig. 3b). The interaction of treatment and time was not significant ($p = 0.676$), so treatments were pooled to compare the effect of years, which was significant ($p = 0.002$). Density before treatment (year 0) and years 1–3 and 7 did not differ significantly ($p = 0.690$ to 0.999), but all were significantly lower than years 9,12, and 15 ($p = 0.018$ to < 0.001), which did not differ among themselves ($p = 0.990$).

Density in the small regeneration/shrub layer did not differ significantly between treatments ($p = 0.804$; Fig. 3c). The interaction of treatment and time was not significant ($p = 0.603$), so treatments were pooled to compare years, which was significant ($p = 0.052$). Densities were highly variable in most years, but increased from before treatment (year 0) through subsequent years, but with only a few differences being significant. Year 0 and years 1–3 did not differ significantly ($p = 0.202$ to 0.999), but year 0 was significantly less than years 7, 9, and 15 ($p = 0.018$ to < 0.001).

3.3. Growth form differences in year 15

In year 15, basal area of saplings differed by growth form (Fig. 4a; $p < 0.001$), but not treatment ($p = 0.500$). Although the interaction was significant ($p = 0.079$), the pattern within treatments was similar; basal area of canopy capable tree species was much higher than subcanopy tree species ($p = 0.017$ and 0.002 for dispersed and aggregated, respectively). There were no woody shrub species in the sapling layer in the dispersed treatment in year 15 and very few in the aggregated treatment, so that shrub species in this size class were not included in the analysis.

By year 15, density in the large regeneration/shrub layer (Fig. 4b) did not differ by treatment ($p = 0.664$) or growth form ($p = 0.314$), but the interaction between the two was significant ($p = 0.071$). Within the dispersed treatment, density of canopy capable tree species was much higher than subcanopy tree species and shrubs ($p = 0.050$ and 0.067, respectively), while density of the latter growth forms did not differ ($p = 0.981$). Within the aggregated treatment, density of growth forms did not differ significantly ($p = 0.830$ to 0.986).

In year 15, density in the small regeneration/shrub layer (Fig. 4c) did not differ by treatment ($p = 0.597$), nor was the interaction between treatment and growth form significant ($p = 0.290$), so treatments were pooled to compare growth form differences, which was significant ($p < 0.001$). For both treatments, the density of canopy capable tree species and subcanopy tree species did not differ ($p = 0.673$), but both were significantly less than the density of shrubs ($p < 0.001$ and 0.003 for canopy trees and subcanopy trees, respectively).

3.4. Compositional changes in the understory

A total of thirty-three woody taxa (four of which were identified only to genus) were sampled during the study (Appendix 1), with 20 of these reported to be native to the original ecosystem. Of the 20, twelve were tree species and eight were woody shrubs. Most taxa occurred in only a subset of stand-by-year combination, hence frequency of occurrence was always <100% (Appendix 1). The NMS ordinations by vegetation layer, i.e., sapling, large regeneration/shrub, small regeneration/shrub, used only the taxa that occurred in that respective layer.

For the sapling layer, NMS converged on a two-axis solution, explaining 98% of variation in composition between treatments and over time. Final stress was 1.589, and instability was<0.00001. There was a pattern of compositional change over time away from the pre-treatment composition, evident on NMS axis 1 for both treatments (Fig. 5a). This was more evident for the aggregated treatment, which was also separated from the dispersed treatment on NMS axis 2 (Fig. 5a). A number of species were highly (positively) correlated with NMS axis 1 (Table 1), reflecting an increase in their importance over time, including balsam poplar, eastern white pine, red pine, paper birch, jack pine, and pin cherry. Several of these species were negatively correlated with NMS axis 2 (Table 1), reflecting greater importance in the aggregated treatment, including chokecherry, jack pine, paper birch, and red pine, while

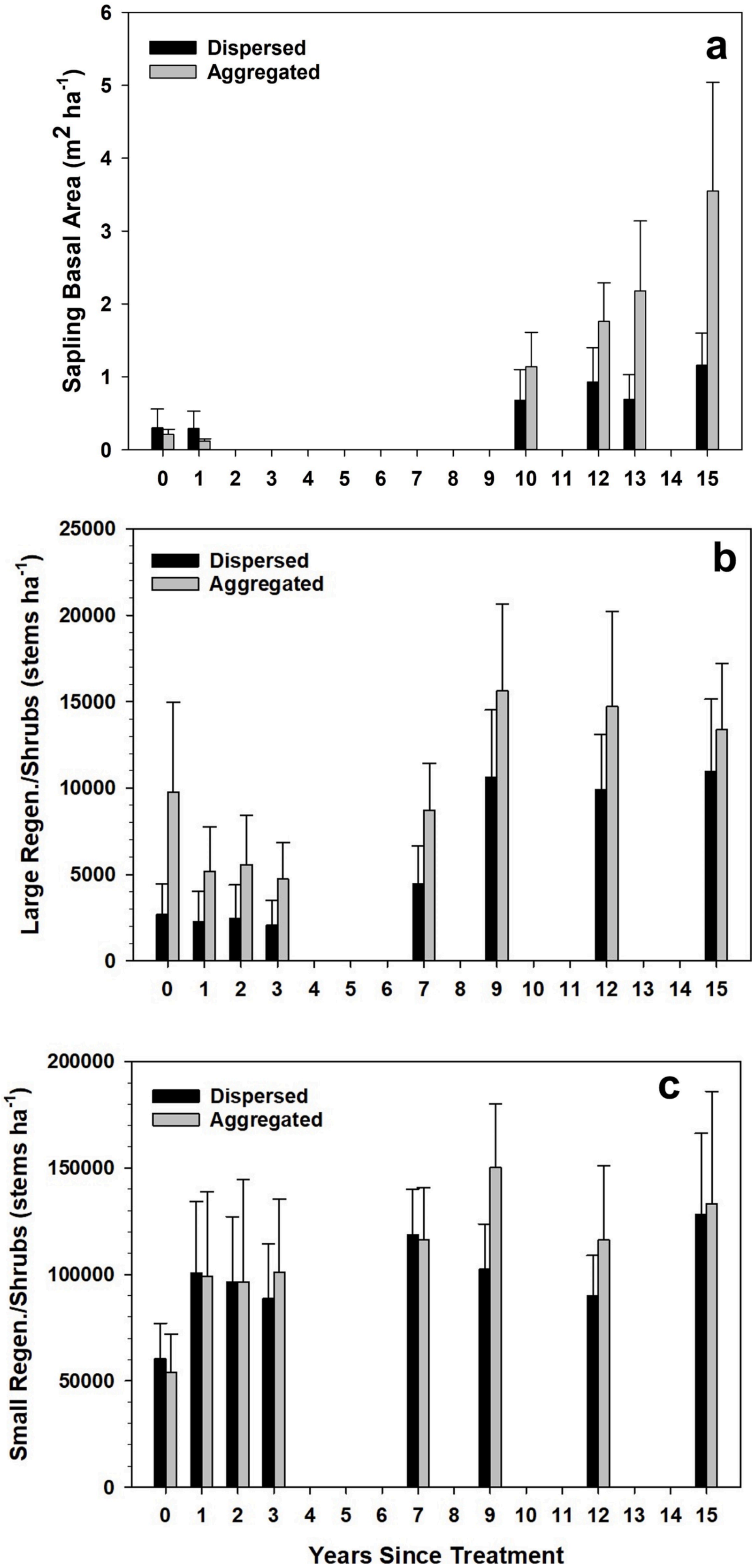

Fig. 3. Changes in a) sapling basal area, b) large regeneration (trees and woody shrubs), and c) small regeneration (trees and woody shrubs) density over time in two silvicultural treatments in red pine plantations. Values are means +/- one standard error of four treatment stands.

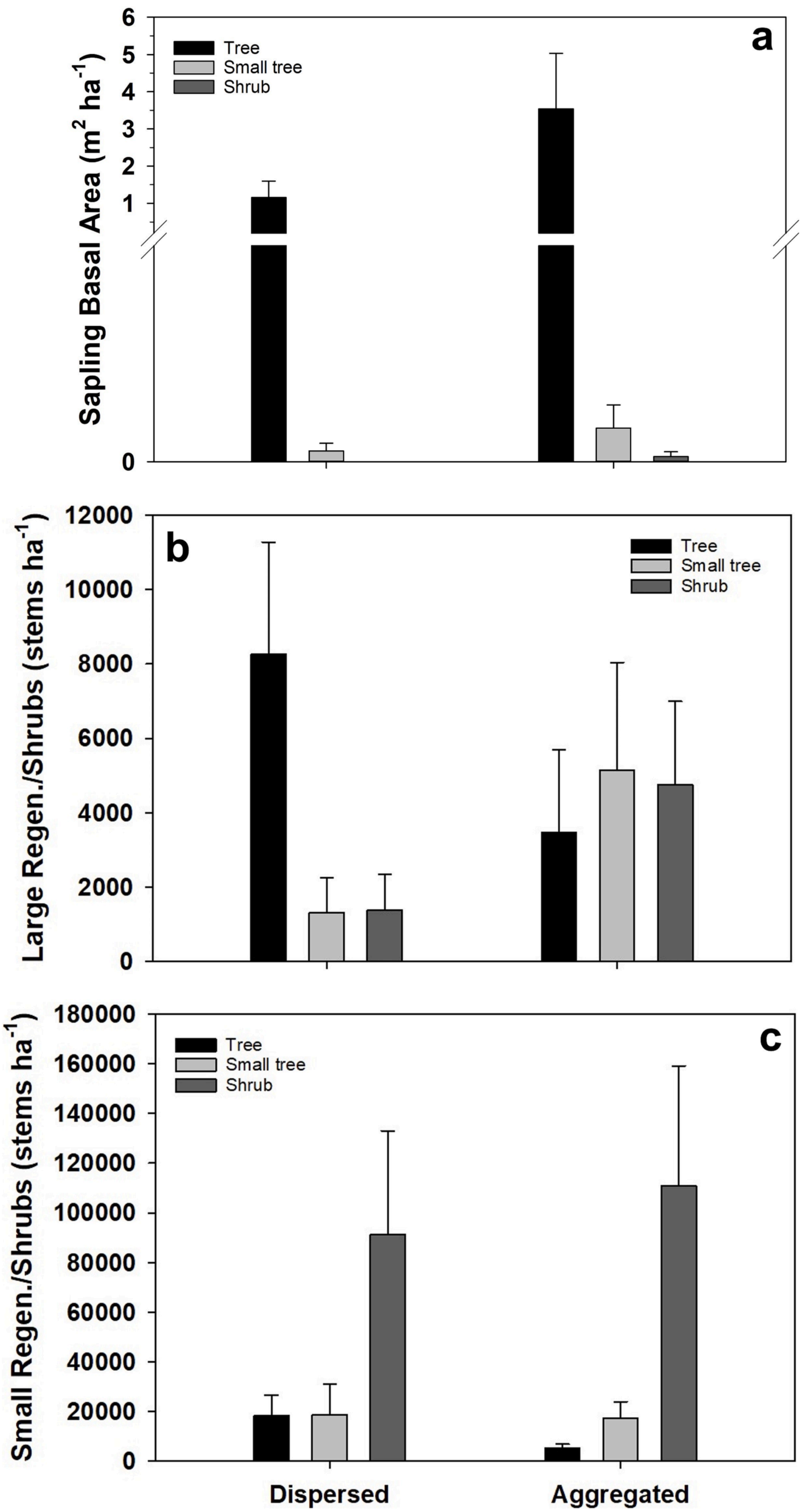

Fig. 4. Sapling basal area (a) and large (b) and small (c) regeneration layer density in different woody plant growth forms and treatment at year 15 in red pine plantations. Values are means +/- one standard error of four treatment stands. Trees are species capable of reaching the main canopy, small trees are subcanopy species, and shrubs are woody species growing in the understory.

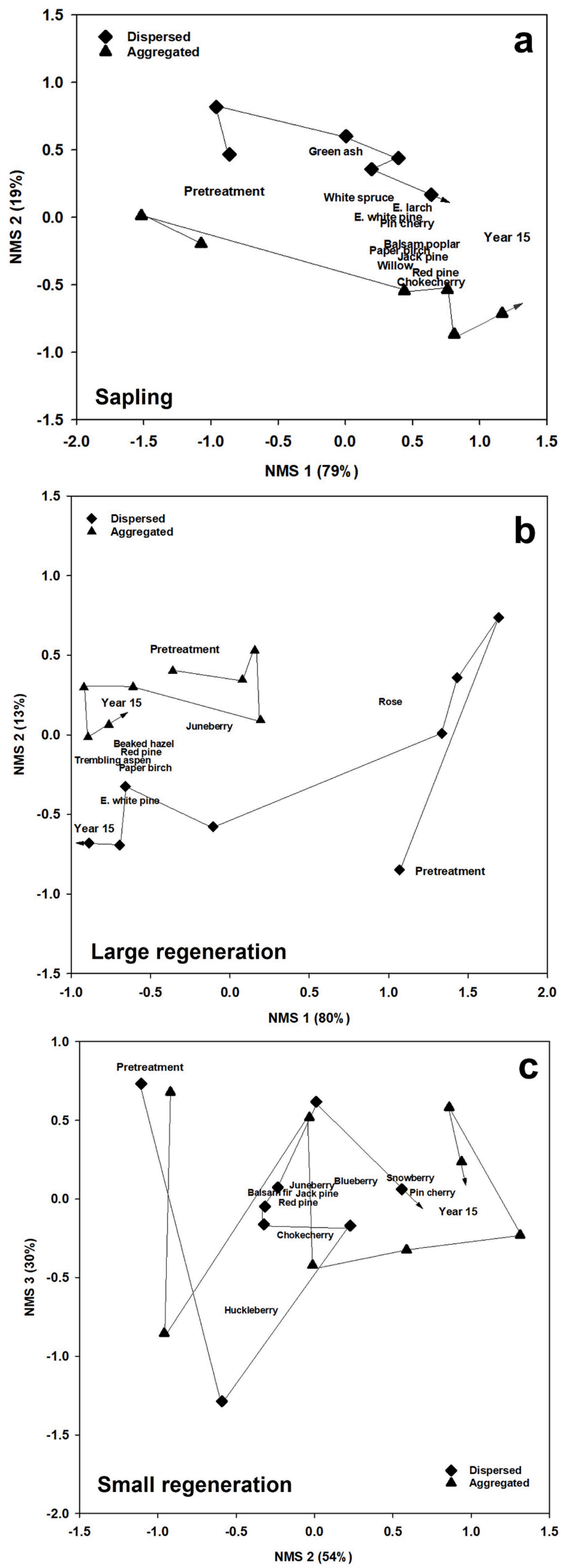

Fig. 5. NMS ordination biplots of understory compositional change in two silviculture approaches over 15 years in red pine plantations in the sapling (a), large (b), and small (c) regeneration layers Values are mean ordination score for four treatment stands.

green ash (*Fraxinus pennsylvanica* Marsh.) was positive correctly with axis 2, reflecting greater importance in the dispersed treatment.

In the large regeneration/shrub layer, NMS converged on a two-axis solution, explaining 92% of variation in composition between treatments and over time. Final stress was 8.195 and instability was<0.00001. Patterns of compositional change in this vegetation layer were difficult to interpret (Fig. 5b). The aggregated and dispersed treatments were different in composition from each other before treatment and in the first years after the initial harvest, reflected in the separation of treatments in the early years on NMS axis 1. This was due to greater abundance of rose in the dispersed treatment and greater abundance of red pine and beaked hazel in the aggregated treatment (Table 1). Over time, the dispersed treatment converged on the aggregated treatment, reflecting an increase in importance of red pine and beaked hazel. There was some separation of the dispersed treatment from the aggregated treatment in the later sample years, reflected an increased importance of eastern white pine in the dispersed treatment (Fig. 5b).

In the small regeneration/shrub layer, NMS converged on a three-axis solution, explaining 92% of variation in composition between treatment and over time. NMS axes 2 and 3 explained most of this variation (84% of the total). Final stress was 8.113 and instability was <0.00001. Patterns of compositional change in this vegetation layer were similar between treatments (Fig. 5c). Pretreatment composition reflected greater importance of red pine and balsam fir compared to later years, with the latter having an increase in importance of several woody shrubs, including snowberry (*Symphoricarpos albus* (L.) S.F. Blake) and lowbush blueberry (Table 1). There was a distinct, although short-lived compositional change in the first year after the initial harvest for both treatments, reflected in a negative correlation of velvetleaf huckleberry (*Vaccinium myrtilloides* Michx.) and chokecherry with NMS axis 3 (Table 1).

4. Discussion

The aim of our study was to examine how silvicultural approaches that involved different spatial patterns of thinning and regeneration harvesting influenced the development of woody plant communities in red pine plantations established on abandoned agricultural lands. While there are a handful of studies that share this aim (e.g., Bender et al., 1997, Parker et al., 2001; 2008, Abella, 2010), none that we found were long-term in tenure and only one took place within the native range of red pine and on ecologically appropriate course-textured soils (Newmaster et al., 2006).

Our 15-year study was located within the range of red pine in northwestern Minnesota, USA and on sites formerly occupied by dry-mesic red pine woodlands. These ecosystems have an interrupted and variable canopy (50–75% cover), with mature and old stands dominated by red pine and jack pine, lessor amounts of balsam fir, paper birch, eastern white pine, white spruce, and trembling aspen, and with northern red oak, bur oak, and red maple occasional in the canopy (Aaseng, 2003). For this study, we compared two contrasting silvicultural treatments designed to transition red pine plantations to an overstory structure more representative of natural open-canopy woodlands and to a composition reflective of the woody plant community formally occupying these sites. The treatments both employed thinning and regeneration harvesting, but differed in the spatial pattern of residual trees, from uniform thinning with dispersed retention to gap-focused cutting with aggregate retention that approximated an expanding gap irregular shelterwood (*sensu* Raymond et al., 2009). Based on the different spatial patterns of harvest and retention in these treatments, we expected different responses in development of structure and compositional change in subcanopy layers, including trees and woody shrubs.

Table 1
Woody species Pearson correlations with NMS axes. Only species used in the respective NMS ordinations are included (see Appendix 1 for a complete list of species).

Species	Ecosystemnative[1]	Sapling[2]		Large regeneration[3]		Small Regeneration[4]	
		NMS 1	NMS 2	NMS 1	NMS 2	NMS 2	NMS 3
Green ash	N	−0.08	0.87				
Paper birch	Y	0.86	−0.82	−0.6	−0.4	0.12	0.08
Eastern larch	N	0.62	0.14				
White spruce	Y	0.28	0.63	0.35	−0.29		
Jack pine	Y	0.94	−0.75	−0.36	0.16		
Red pine	Y	0.82	−0.84	−0.94	−0.35	−0.70	−0.22
Eastern white pine	Y	0.71	0.002	−0.57	−0.71		
Balsam poplar	N	0.86	−0.53				
Trembling aspen	Y			−0.55	−0.21		
Balsam fir	Y	0.40	0.52	0.32	0.42	−0.69	0.12
Juneberry	Y	0.01	0.26	−0.51	0.60	0.01	0.57
Pin cherry	N	0.77	−0.03			0.64	0.05
Chokecherry	Y	0.67	−0.90	0.19	−0.52	−0.17	−0.72
Beaked hazel	N			−0.80	−0.22	0.26	−0.19
N. Bush honeysuckle	Y					0.32	−0.51
Fly honeysuckle	N					0.17	−0.49
Rose species	Y			0.76	0.29		
Willow species	Y	0.43	−0.66	−0.51	0.26		
Snowberry	Y					0.78	0.22
Lowbush blueberry	Y					0.79	0.39
Velvetleaf huckleberry	Y					−0.37	−0.81

[1] Denotes a species listed as occurring in the natural (pre-agriculture) northern dry-sand pine woodland ecosystem (Aaseng 2003).
[2] Sapling sized trees (2.5 cm $\leq$ dbh $<$ 10 cm). Note, two species of large shrub occurred rarely in this size class.
[3] Trees and woody shrubs (dbh $<$ 2.5 cm and $\geq$ 1.0 m tall).
[4] Trees and woody shrubs ($<$1.0 m tall).

4.1. Canopy structural development

We asked how the two silvicultural approaches resulted in different structural conditions in the overstory, as a measure reflective of resource availability for subcanopy layers, including regenerating trees and woody shrubs. Both basal area and canopy openness varied over time, reflecting removal with the harvests, but the stand-level means did not differ between the two treatments. However, within-stand variation in both measures of overstory structure did differ significantly between treatments, with both being significantly more variable within the aggregated treatment stands. This suggests there were more high resource availability environments in this treatment, including light and soil resources, but also more variation in resources, compared to the dispersed retention treatment. A similar result has been found in other variable retention harvesting studies in pine ecosystems (Palik et al., 2003; Boyden et al., 2012; Montgomery et al., 2013).

Both treatments served to reduce basal area and increase canopy openness in these dense plantations to a structure thought to be more characteristics of natural woodland structure. However, as the natural woodland structure is characterized by a patchy and variable canopy, ranging from 25 to 100% cover in mature stands (Aaseng, 2003), it is likely that the aggregated treatment brought the plantations closer to the natural model faster than the dispersed treatment. In addition, the aggregate treatment approach included larger openings, which in the natural ecosystem often results from a patchy, mixed-severity fire regime (Palik and D'Amato, 2019; 2020). While we did not measure resource availability directly, we expected these different structures to reflect differences in resource environments, as has been found in other studies in red pine ecosystems (Boyden et al., 2012) and to translate into differences in the development of woody plant communities in the understory, as observed in similar red pine ecosystems (Roberts et al., 2016; 2017).

4.2. Understory woody plant communities

We asked if the treatments would result in different abundances and composition of the regenerating and understory woody plant community, including canopy capable trees, subcanopy trees, and woody shrubs. The expectation being that the differences in variability of canopy structure noted above should translate into different resource environments that influence compositional dynamics.

In general, both treatments led to increases in the abundance of woody stems in all understory layers. Notably, given the low pretreatment abundance of saplings, which were non-existent before treatment, the increase in sapling basal area that occurred in both treatments was due to new recruitment into the size class from lower layers and regeneration initiating after the initial harvest. By year 15, the overwhelming majority of saplings were canopy capable trees, indicating that a new cohort of trees either established or was released from the lower layers by the treatments. This cohort of trees was also evident in the large regeneration layer in both treatments, although the aggregated treatment also had substantial subcanopy trees and shrubs. In contrast, the small regeneration layer in both treatments is best described as a matrix of high shrub density with a lower density of regenerating tree species recruiting to the large regeneration class.

There is not a lot of quantitative information on the understory structure of the red pine woodlands. However, given the potential for frequent surface fire in these and similar ecosystems (Stambaugh et al., 2021), it seems unlikely that a dense understory, especially of woody shrubs, would be a common feature. Spatially patchy understory development, including younger cohorts of trees, was more descriptive of natural structure and while both treatments facilitated the development of a new cohort of trees and woody shrubs, there were some differences, as noted below, in composition changes between treatments.

4.3. Woody understory composition

Compositional changes differed depending on silvicultural treatment and vegetation layer, reflecting differences in stand-scale understory resource environments. Both treatments approaches led to increased importance of several canopy capable tree species in the sapling layer, including paper birch, eastern white pine, red pine, balsam poplar, jack pine, but a clear distinction between treatments was evident by year 10 onward, with greater importance of these mostly shade intolerant species in the aggregated treatment, while the dispersed treatment had greater abundance of mid-tolerant green ash. We surmise that the aggregated treatment favored the intolerant species due to a greater proportion of high-light neighborhoods similar to findings in other studies of pine ecosystems (Palik et al., 2003; Boyden et al., 2012).

Composition in the large regeneration layer differed between treatments before harvesting, with more red pine in the aggregated treatment initially, but converged over time with increased abundance of red pine, as well as eastern white pine and beaked hazel in the dispersed treatment. In contrast, the small regeneration layer had relative decreases in canopy capable trees species importance over time and increases in several woody shrubs.

Canopy capable trees species establishing in the study were components of the native ecosystem that occurred on these sites before agricultural clearing. Exceptions include balsam poplar and green ash. In the subcanopy, both chokecherry and pin cherry increased in importance. Chokecherry is common in the native ecosystem (Aaseng, 2003) and has been found in red pine plantations and forests in the Lake States (Dickmann et al., 1987; Noyce and Coy, 1990; Bender et al., 1997). There is no record of pin cherry occurring in the native ecosystem we studied and it is also uncommon in abandoned agricultural sites (Marks, 1974). However, it is known to germinate from long-lasting buried seed, which may account for its presence in our study sites (Marks, 1974).

5. Management application

Silvicultural thinning and regeneration harvesting in pine plantations to restore native ecosystem composition and structure has been examined in other studies (e. g., Abella, 2010; Parker et al., 2001; 2008). However, in many of these, the plantation species is not native to the region or the soil type. As such, the template for restoration (i.e., the plantation), is measurably different that the original native plant community of the ecosystem. In our study, we began with a template that was much closer to the original native plant community, at least in overstory composition, but also to some degree, the understory plants that were present in the stands or near-by. This situation can result in more rapid restoration of structure and composition compared to an approach that begins with off-site or non-native species (e.g., Kremer et al., 2021).

The results of our study suggest combinations of direct seeding of tree species, followed by silvicultural thinning, and then later regeneration harvests, can move structurally simple plantations towards the spatially variable structure and species rich composition of the native pine woodlands that occurred on the study sites. While both our silvicultural approaches were successful in accomplishing this, the deliberately more spatially variable aggregated thinning, followed by an expanding gap, irregular shelterwood, moved the plantations closer to the natural model faster than did the more uniform thinning approach. With both approaches, we were able to harvest similar volumes of red pine sawtimber and poles, an outcome of importance to many foresters in the region, who never-the-less may also be interested in restoration and sustainability of wildlife habitat and plant species diversity.

An important caveat for management is that our silvicultural approach for native woodland restoration has not, to date, included reintroduction of low intensity surface fire. It is accepted that frequent fires were integral to the structure and function of red pine dominated woodlands (Bergeron and Brisson, 1990; Aaseng, 2003; Drobyshev et al., 2008a; Stambaugh et al., 2021), serving to limit the abundance of shrubs and the density of regenerating trees, reduce fuels, and expose mineral soil (Palik and D'Amato, 2020). As such, without reintroduction of something approaching a natural fire regime, or surrogate treatments such as mechanical shrub removal and mineral soil exposure (McIver et al., 2012), the compositional and structural responses we document may be short-lived.

CRediT authorship contribution statement

Brian J. Palik: Conceptualization, Writing – original draft. **Douglas N. Kastendick:** Data curation, Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix

Woody species occurrence in different vegetation layers and silvicultural treatments. Values are percent occurrence in stand-by-year combinations for each treatment (24 observations for saplings and 32 for large and small regeneration).

Species	Form	Ecosystem native[1]	Sapling[2]		Large regeneration[3]		Small regeneration[4]	
			Dispersed	Aggregated	Dispersed	Aggregated	Dispersed	Aggregated
Green ash (*Fraxinus pennsylvanica* Marsh.)	Large tree	N	33	0	0	0	0	0
Red maple (*Acer rubrum* L.)	Large tree	Y	0	0	0	0	6	6

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Species	Form	Ecosystem native[1]	Sapling[2]		Large regeneration[3]		Small regeneration[4]	
			Dispersed	Aggregated	Dispersed	Aggregated	Dispersed	Aggregated
Paper birch (*Betuta papyrifera* Marsh.).	Large tree	Y	63	79	31	28	28	25
Eastern larch (*Larix laricina (*Du Roi) K. Koch)	Large tree	N	17	13	0	0	0	0
White spruce (*Picea glauca* (Moench) Voss)	Large tree	Y	71	75	25	0	28	0
Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.)	Large tree	Y	4	8	0	0	0	0
Jack pine (*Pinus banksiana* Lamb.)	Large tree	Y	58	75	13	19	28	6
Red pine (*Pinus resinosa* Ait.)	Large tree	Y	58	79	28	50	88	97
Eastern white pine (*Pinus strobus* L.)	Large tree	Y	58	42	22	9	56	31
Balsam poplar(*Populus balsamifera* L.)	Large tree	N	33	29	0	0	0	0
Bigtooth aspen (*Populus grandidentata* Michx.)	Large tree	N	0	4	0	0	0	0
Trembling aspen (*Populus tremuloides* Michx.)	Large tree	Y	0	38	3	16	22	6
Bur oak (*Quercus macrocarpa* Michx.)	Large tree	Y	0	0	0	0	0	6
Balsam fir (*Abies balsamea* (L.) Mill.)	Small tree	Y	96	100	19	19	56	38
Boxedler (*Acer negundo* L.)	Small tree	N	13	0	0	0	0	0
Serviceberry (*Amelanchier* spp.)	Small tree	Y	13	8	63	63	72	75
Pin cherry (*Prunus pensylvanica* L. f.)	Small tree	N	21	21	0	19	22	16
Chokecherry (*Prunus virginiana* L.)	Small tree	Y	4	24	22	28	50	56
Speckled alder (*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen)	Shrub	N	0	4	0	0	6	6
Beaked hazel (*Corylus cornuta* Marsh.)	Shrub	Y	0	0	28	38	53	47
American hazel (*Corylus americana* Walter)	Shrub	N	0	0	0	0	19	16
Bush honeysuckle (*Diervilla lonicera* Mill.)	Shrub	Y	0	0	0	0	72	69
Fly honeysuckle (*Lonicera canadensis* W. Bartram ex Marshall)	Shrub	N	0	0	0	0	28	22
Gooseberry (*Ribes* spp.)	Shrub	N	0	0	0	0	3	0
Blackberry (*Rubus allegheniensis* Porter)	Shrub	N	0	0	0	0	16	13
American red raspberry (*R. idaeus* L.)	Shrub	Y	0	0	0	0	3	13
Grayleaf red raspberry (*R. idaeus L. ssp strigosus* (Michx.) Focke	Shrub	N	0	0	3	22	47	50
Rose species (*Rosa* spp.)	Shrub	Y	0	0	13	3	94	75
Willow species (*Salix* spp.)	Shrub	Y	8	29	9	38	41	53
Snowberry (*Symphoricarpos albus* (L.) S.F. Blake)	Shrub	Y	0	0	0	0	28	28
Lowbush blueberry (*Vaccinium angustifolium* Aiton)	Shrub	Y	0	0	0	0	69	69
Velvetleaf huckleberry (*Vaccinium myrtilloides* Michx.)	Shrub	Y	0	0	0	0	19	22
Viburnum spp.	Shrub	N	0	0	0	0	25	3

[1]Denotes a species listed as occurring in the natural (pre-agriculture) northern dry-sand pine woodland ecosystem (Aaseng 2003).
[2]Sapling sized trees (2.5 cm $\leq$ dbh $<$ 10 cm). Note, only two species of large shrubs occurred rarely in this size class.
[3]Trees and woody shrubs (dbh $<$ 2.5 cm and $\geq$ 1.0 m tall).
[4]Trees and woody shrubs ($<$1.0 m tall).

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