Restoring southern Ontario forests by managing succession in conifer plantations

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ABSTRACT

Thinning and underplanting of conifer plantations to promote natural succession in southern Ontario's forests for restoration purposes was examined in a young red pine (*Pinus resinosa* Ait.) plantation. Eleven years after application of five thinning treatments, seedling diameter, height, and stem volume of planted white ash (*Fraxinus americana* L), red oak, (*Quercus rubra* L.), and white pine (*Pinus strobus* L.) were positively correlated with thinning intensity and size of canopy openings. Percent survival did not differ among thinning treatments. Based on growth and survival responses, field performance of white ash and white pine was superior to red oak. Recommendations for restoring conifer plantations to native forest types are provided.

Key words: acorn predation, direct seeding, *Fraxinus americana*, *Pinus resinosa*, *Pinus strobus*, plantations, *Quercus rubra*, red oak, red pine, underplanting, thinning, white ash, white pine

RÉSUMÉ

L'éclaircie et la plantation en sous-étage dans des plantations de conifères afin de promouvoir une succession naturelle dans les forêts du sud de l'Ontario devant être régénérées ont été étudiées dans le cas d'une jeune plantation de pin rouge (*Pinus resinosa* Ait.). Onze ans après la réalisation de cinq traitements d'éclaircie, le diamètre, la hauteur et le volume de la tige des semis plantés de frêne d'Amérique(*Fraxinus americana* L), de chêne rouge (*Quercus rubra* L.) et de pin blanc (*Pinus strobus* L.) ont été corrélés positivement avec l'intensité de l'éclaircie et la dimension de l'ouverture du couvert. Le pourcentage de survie n'a pas varié en fonction des traitements d'éclaircie. Selon les réactions de croissance et de survie, la performance sur le terrain du frêne d'Amérique et du pin blanc a été supérieure au chêne rouge. Des recommandations sur la régénération des plantations de conifère en espèces indigènes sont formulées dans cet article. .

Mots-clés : disparition des glands, ensemencement direct, *Fraxinus americana*, *Pinus resinosa*, *Pinus strobus*, plantations, *Quercus rubra*, chêne rouge, pin rouge, plantation en sous-étage, éclaircie, frêne d'Amérique, pin blanc

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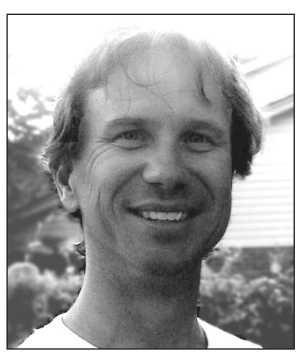

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Introduction

European settlement of eastern North America initiated broad-scale, human-induced forest disturbance. More than three centuries of forest clearing for agricultural production, commercial logging, and urban development have dramatically reduced the total area and fundamentally altered the composition, structure, and distribution of remaining forests (Clawson 1979, Frelich 1995, Foster *et al.* 1998). Forest clearing and human land use practices associated with settlement of southern Ontario have resulted in a similarly dramatic

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change in the region's forest vegetation (Zavitz 1960, Kelly 1974, Borczon 1986, Suffling *et al.* 2003). Growth and migration of the population northward from the shores of Lake Ontario beginning in the 1820s initiated the intensive harvest and widespread clearing of forest lands for agricultural production (Kelly 1974, Borczon 1986, Howard *et al.* 1996). Fires used to clear land or ignited by railroad locomotives or carelessness in cutovers sometimes escaped into adjacent woodlands, further reducing forested land (Kelly 1974, Howard *et al.* 1996). Repeated, high-intensity fire likely reduced the soil nutrient capital, particularly on the relatively coarse-textured soils (Dickmann 1993, Howard *et al.* 1996). Although much of this cleared land was reasonably good for agriculture, large regions with deep glacial deposits of sand and gravel were unfit for even subsistence crop production (Carman 1941, Kelly 1974, Borczon 1986). Cultivation quickly reduced the organic matter content, fertility, and productive capacity of this land. In most cases, these areas were farmed for a brief period and abandoned to erosion by wind and water (Kelly 1974, Borczon 1986, Howard *et al.* 1996).

By 1880, these land use practices had removed 75% to 80% of the native tolerant hardwood and conifer forests of this region (Zavitz 1960, Kelly 1974, Whitney 1986, Delcourt and Delcourt 2000). In areas of glacial outwash soils, this sequence of clearing, farming, and abandonment created unproductive, desert-like wasteland that covered thousands of hectares (Zavitz 1960, Kelly 1974). In some areas, wind action removed the top soil and subsoil, and formed large "blow pits" some 3 m deep that covered 30 ha or more (Borczon 1986). Recognition of the extent and effect of this deforestation resulted in a series of legislative efforts to encourage reforestation to control erosion, protect watersheds, and provide a future source of revenue from the timber produced (Carman 1941, Kelly 1974, Borczon 1986, Kuhlberg 1996, Suffling *et al.* 2003). Beginning in the 1920s, about 102 000 ha of this degraded landscape were reforested (Borczon 1986). In many areas, red pine (*Pinus resinosa* Ait.) was favoured for planting because of its ability to grow on infertile, well drained soils (Wilde and Iyer 1962, Rudolph 1990). The shared experience of exploitive logging and forest clearing for cultivation in the Great Lakes region of the United States during the 19th Century led to parallel reforestation and soil stabilization efforts (Rudolf 1950, Bender *et al.* 1997).

Over time, the forest cover provided by these plantations has improved soil conditions (Wilde 1964, Stone 1975, McPherson and Timmer 2002) and moderated the microenvironment of these once-exposed, degraded lands, creating understory conditions conducive to the natural establishment of more shade-tolerant forest tree species (Russell 1955, Truax *et al.* 2000, McLaughlin 2001, Hewitt and Kellman 2002). Disturbance by thinning and the natural mortality of single or groups of trees in older plantations has stimulated the development of this forest understory and accelerated the succession of these plantations to a more natural forest composition (Young 1933, Russell 1955, Goldblum 1998, McLaughlin 2001, Parker *et al.* 2001). In younger plantations with little disturbance history, very low understory light and thick litter layers impede the establishment of understory vegetation (Russell 1955, Gysel 1966, Anderson *et al.* 1969, Truax *et al.* 2000). These even-aged, symmetrical monospecific stands are perceived by some as "biological deserts" due to their lack of plant and wildlife diversity and aesthetic appeal (Dickmann 1993, Parker *et al.* 2001). These plantations also differ markedly from the native mixed conifer-hardwood forests that occupied much of this region prior to settlement (Delcourt and Delcourt 2000, Parker *et al.* 2001).

Red pine plantations are a prominent feature of the 2 million ha forested area of southern Ontario, a region that comprises 8% (7 million ha) of Ontario's total land area but is home to 91% of the province's 12.6 million people. Despite criticism of these plantations, the variety of ecological and social benefits these woodlands provide to this mainly urban landscape are well recognized (Borczon 1986, Wood 1991, Bender *et al.* 1997, McLaughlin 2001). Thus, conserving these forested areas while developing techniques to restore them to a more natural forest composition and structure is of great interest (Dickmann *et al.* 1987, Bender *et al.* 1997, Parker *et al.* 2001). This need has recently become more important due to the increasing incidence of growth decline and root diseases that threaten younger, pole-sized red pine plantations throughout the Great Lakes Region of North America (McLaughlin 2001, Erbilgin and Raffa 2002).

Comparatively little information on natural succession in conifer plantations is available to assist with development of management options to support restoration to native forest types (Young 1933, Russell 1955, Goldblum 1998, Parker *et al.* 2001). Previously, we reported fifth-year results of a study examining the influence of five thinning treatments on growth and survival of underplanted white pine (*Pinus strobus* L.), red oak (*Quercus rubra* L.), and white ash (*Fraxinus americana* L.), and the abundance and diversity of understory vegetation in a 32-year-old red pine plantation (Parker *et al.* 2001). In this paper, we present the survival and growth response of underplanted tree seedlings for the 11-year period following thinning treatments intended to hasten succession to more natural forest types in these stands. Based on these findings and the results of others, we provide recommendations for management of southern Ontario red pine plantations where restoration is a primary objective.

Materials and Methods

Study site

This study was established in the Norton Tract of the Durham Regional Forest (43° 3′ N, 79° 9′ W). The site is flat to gently rolling and is located on the Oak Ridges Moraine along the divide between the Lake Simcoe and Lake Ontario watersheds. The study area is a 3.2-ha red pine plantation established in 1962. Red pine nursery stock was planted at 1.8 m × 1.8 m spacing and received no further treatment. In 1993, the overstory was pure red pine with an average stand basal area, height, and diameter (at 1.3 m) of 54.7 m^2 ha^{-1}, 14 m, and 16 cm, respectively. Very little understory vegetation existed and the forest floor consisted largely of a 5-cm to 10-cm deep litter layer of pine needles. Soils are of the Pontypool soil series, with loamy fine sands that have a moderately fresh moisture regime with rapid drainage. These soils have poor agricultural potential and are quite sensitive to disturbance and susceptible to erosion (Olding *et al.* 1965). The A horizon (upper 25 cm) is a plough layer (Ap), overlying a 50-cm Bm horizon. Carbonates are present beyond 70 cm. The Pontypool and other soil series of glacial outwash parent material are common to the approximately 1400-km^2 Oak Ridges Moraine region of southern Ontario where many of these conifer plantations were established.

Experimental design and overstory treatment description

The main study area (120 m x 160 m) was divided into 20, 30 m × 32 m adjacent plots arranged in a 4 × 5 grid, with each plot containing 20 rows of about 22 red pine trees. Four plots in the main study area were randomly assigned each of five thinning treatments, including an unthinned control (CN). The relative density (RD) of the stand at time of intervention was 0.69, where a RD of 1.00 is the maximum "biological" density at which self-thinning occurs for trees of a given size (Smith and Woods 1997). Five thinning regimes, which differed in the size and spatial distribution of canopy openings, were designed to reduce RD to 0.40, to maximize pine growth (Smith and Woods 1997). Single row (1R) thinning removed the first of every four rows, decreased basal area by 25% (RD = 0.51), and created five equally spaced rectangular 54 m^2 (1.8 m × 30 m) openings. Additional single row thinnings were planned to gradually reduce RD to 0.40 but were never applied. Double row (2R) thinning, which removed the first two of every five rows, reduced basal area by about 40% (RD = 0.41), and created four, 108 m^2 (3.6 m × 30 m) rectangular openings. All row thinnings were applied in a north-south direction. A selection (SLT) treatment reduced basal area by about 44% (RD = 0.39) by combining 1R thinning with removal of 25% (n = 48) of the trees in the three adjacent rows. The SLT treatment added 48 small (2.5 m^2) single tree canopy gaps to the 1R treatment.

A thinning treatment to simulate natural canopy gap formation (G1) was also applied, and created 7-m diameter circular openings in the overstory (~50% mean overstory height) within stands otherwise thinned using the SLT treatment. These gaps were formed by removing several adjacent trees in the centre of the plots. This treatment reduced basal area by about 46% (RD = 0.39), created a single 38.5-m^2 canopy gap, in addition to the rectangular row openings and single tree canopy gaps. A second smaller area (0.4 ha) about 40 m to the west of the main block was later added to the study. This area was divided into four adjacent 30 m × 32 m plots, and also thinned using the G1 method. A map of treatment plot locations and details about operational aspects of the thinning treatments are reported in Parker *et al.* (2001).

Artificial regeneration

In April 1995, seven months after thinning, each plot was planted with 2+0 bare-root white pine, red oak, or white ash seedlings, or direct seeded with red oak acorns. The underplanted tree species are common to the original forests of the region (Delcourt and Delcourt 2000, Suffling *et al.* 2003), intermediate in shade tolerance (Schlesinger 1990, Wendel and Smith 1990, Dey and Parker 1996), and readily colonize the understory of conifer plantations in the Great Lakes Region (Russell 1955, Goldblum 1998, Truax *et al.* 2000, McLaughlin 2001, Parker *et al.* 2001, Hewitt and Kellman 2002). Preliminary evaluation of soil properties (texture, effective rooting depth, drainage) of the plantation indicated that these three species were well suited for underplanting on the study site (Taylor and Jones 1986, OMNR 2000).

Bare-root seedlings were obtained from St. Williams Nursery (St. Williams, ON). Red oak acorns obtained from a bulk collection from a local seed source were cleaned of damaged seed and stratified for 46 days at 2°C. Viability tests indicated a germinability of about 90%.

In the main study area, the northern half of each plot was left unplanted and used to monitor the ingress of natural regeneration of woody, herbaceous, and cryptogam species (Parker *et al.* 2001). Four east-west planting rows were established in the southern half of the 20 plots, with 3-m spacing between rows. A single species was planted in each row, with 1.2-m spacing between planting spots. From north to south, the first three rows were always planted with white pine, red oak, and white ash. The fourth row was seeded with red oak acorns at a 1.2-m spacing, with five acorns planted to a depth of 2 cm to 3 cm in a 10-cm × 15-cm planting spot. The four G2 plots in the adjacent study area were planted only within the circular canopy openings. Five seedlings per species and five groups of four acorns were randomly planted within this opening.

Total seedling height, basal stem diameter (0.5 cm above ground line), and survival were measured at the end of each growing season from 1995 to 1999 (years 1 to 5) and in 2005 (year 11). Diameter of seeded red oak was not measured in year 1. Stem volume index (SVI) was estimated assuming a conical shape for main stems. Where more than one acorn successfully formed a seedling at a given sowing location, only the height and diameter of the largest seedling was measured. The incidence of browsing damage and terminal shoot dieback was also noted for each seedling for the 3rd- to 5th- and 11th-year assessments.

Seedling relative stem volume growth increment (RV) for growing seasons 2 to 5 (RV1) and 5 to 11 (RV2) was estimated as the ratio of incremental change in SVI during this period to the total SVI at the end of the period. The RV estimates do not include seedlings that suffered browsing or mechanical damage to the main stem during the relevant growth period and therefore represent maximum attainable values.

Overstory characteristics

Post-thinning canopy characteristics were estimated to examine their relationship with seedling growth responses. In fall 1996, one growing season after thinning, leaf area index (LAI), diffuse non-interceptance (DIFN), and photosynthetic photon flux density (PFD) of each treatment plot were measured on a uniformly overcast day using a LAI-2000 plant canopy analyzer (LiCor, Inc., Lincoln, NE, USA) (Deblonde *et al.* 1994, Machado and Reich 1999). The DIFN value was used as an estimate of percent canopy openness. Eleven instantaneous measurements at 1 m above the ground were collected along a systematic transect through each of the 24 plots to estimate plot-averaged values of LAI, DIFN, and PFD. Mean daily percent PFD (%PFD) was estimated as the ratio of below- to above-canopy PFD readings (Messier and Puttonen 1995). In the G2 plots, %PFD was determined only within the canopy gaps (n = 11).

Statistical analyses

The GLM procedure of SAS (SAS Institute Inc., Cary, NC) was used for analysis of variance (ANOVA) of treatment effects on height and basal diameter of underplanted seedlings within the main study area using treatment plot means as primary data. The following mixed general linear model was used:

$$[1] \quad Y_{ijk} = \mu + T_i + P_{(i)j} + S_k + TS_{ik} + SP_{(i)jk}$$

with thinning (T) and species/seedling type (S) as fixed factors, and plot (P) identified as a random factor. F tests and Tukey-Kramer mean comparison tests of T effects used P as the mean square error term, while SP was used as the error term for testing of S and TS effects. A Tukey-Kramer test was used for mean comparisons only when the main treatment effect was significant ($p \leq 0.05$). One-way AVOVA and a simplified linear model were used to determine single-factor effects (T or S) on seedling height and diameter. Either the T or S term (including interactions) was dropped from the model and ANOVA within a given thinning treatment or species conducted using P as the error term for all tests. Residual analysis confirmed that data met ANOVA assumptions of constant variance and normal distribution of error.

Analysis of variance was inappropriate for testing T and S effects on percent seedling survival, RVR1, and RV2 due to strong deviation from a normal distribution observed for these variables. Instead, separate, nonparametric one-way ANOVA, the NPAR1WAY procedure of SAS, and a Kruskal-Wallis test were used to determine single main factor effects (T or S) on RV1, RV2, and percent seedling survival. Mean comparison tests among thinning treatments and species were determined using a Students-Newman-Keuls test ($p \leq 0.05$) (Glantz 1992). Species differences in survival within individual thinning treatments were determined using this same procedure. The relatively small number of surviving seeded oak seedlings and seedlings free of significant browsing by year 11 precluded more detailed analysis of treatment effects on RVR1 and RVR2.

Thinning treatment effects on post-harvest LAI, DIFN, and %PFD were quantified using one-way ANOVA, the GLM procedure, and the mixed general linear model:

$$[2] \quad Y_{ij} = \mu + T_i + P_{(i)j}$$

with P(i)j as a random factor. Treatment plot means were used as primary data and $P_{(i)j}$ used as the mean square error term for the F test and Tukey-Kramer mean comparison test ($p \leq 0.05$).

The relationship of LAI, DIFN, and %PFD with RV1, RV2, and 5th- and 11th-year SVI and percent survival was quantified for each species with the CORR procedure of SAS and Pearson product-moment correlation coefficients (r), using treatment plot means as primary data. The relationship between 11th-year seedling survival and SVI with distance from canopy openings was examined by estimating the mean response of seedlings in the G1 treatment grouped by location in a planting row. Eight relative planting position classes were formed, consisting of three seedlings occupying consecutive planting spots within a row of 24 trees in an east-west direction (i.e., position 1 = trees 1–3; position 2 = trees 4–6, etc.). Percent survival and mean SVI were calculated for each position class (three trees per four treatment plots; maximum n = 12). A three-parameter Gaussian function was fit to the relationship of percent survival and SVI with position class using SigmaPlot version 9.1 (Systat Software Inc., San Jose, CA). Significant relationships between seedling response and relative planting position were assumed where the coefficient of determination (r^2) for these functions was $r^2 \geq 0.60$.

The location of G2 plots outside the main study area and differences in planting patterns precluded their inclusion in formal analysis of thinning effects. Instead, treatment means and standard errors (SE) are presented for comparison with the other thinning treatments. Correlation analysis included %PFD from the G2 treatment because plot-averaged values for growth and light were measured in the same understory location.

Results

Thinning effects on seedling survival

Thinning treatments differed significantly in post-thinning LAI, DIFN, and %PFD, and these values were generally proportional to the percentage of basal area removed (Table 1). Seedling survival decreased significantly between the 1st, 5th, and 11th growing seasons, but did not differ among thinning treatments within a given growing season (Table 2). Percent seedling survival was significantly lower in year 11 than year 1 for all species. Differences in seedling survival among species over the study period can generally be ranked as white ash > white pine > planted oak >> seeded oak. Within thinning treatments, however, survival of seeded oak did not differ significantly from planted oak, but was sometimes lower than white ash and white pine (Fig. 1). Survival of all species was uniformly high when planted in the centre of canopy gaps in the G2 treatment.

Seedling survival in the 5th and 11th growing seasons was not significantly correlated with LAI, DIFN, or %PFD for any species. Seedling survival response within thinning treatments was related to seedling location relative to canopy gaps in year 11, (Fig. 2). Apparent higher survival in or near open-

Table 1. Estimated basal area and mean (± 1 SE in parentheses) values for leaf area index (LAI), percent open sky (DIFN), and percent sunlight (%PFD) for six thinning treatments. Understory %PFD for the G2 treatment was measured within the canopy gap only. Means in a column followed by the same letter are not significantly different ($p \leq 0.05$).

Treatment	Basal area ($m^2\ ha^{-1}$)	LAI	DIFN	(%) %PFD
Control (CN)	55.0	3.14 (0.09) a	6.7 (0.5) c	6.7 (0.4) b
1 row (1R)	41.0	2.31 (0.19) b	14.6 (2.2) bc	13.3 (0.8) ab
2 row (2R)	33.0	1.48 (0.27) c	30.1 (6.4) a	17.7 (2.0) a
Selection (SLT)	31.0	2.07 (0.15) bc	18.2 (1.6) abc	16.1 (2.1) a
Gap (G1)	30.0	1.69 (0.14) bc	24.5 (3.2) ab	16.8 (3.1) a
Gap (G2)	30.0	1.71 (0.25)	28.7 (5.7)	33.5 (6.7)

ings was observed only for red oak. In seeded oak, both initial seedling emergence and 11th-year survival improved inside and near the western side of the canopy gaps of the G1 treatment. As well, seeded oak survival appeared higher when acorns were planted within the canopy gap of the G2 treatment. Planted red oak also exhibited a notable, but comparatively weaker, trend towards higher survival near the centre of canopy gaps in the G1 treatment.

Table 2. Mean (± 1 SE) for seedling survival in the 1st, 5th, and 11th growing seasons after treatment application for data pooled by (a) thinning treatments and (b) species. Means followed by the same letter are not significantly different ($p \leq 0.05$). The G2 treatment was not included in analysis of treatment effects or mean comparison tests.

Seedling survival (%)			
Treatment	Year 1	Year 5	Year 11
a) Thinning			
Control (CN)	80.0 (7.9)	63.9 (7.7)	47.1 (7.7)
1 Row (1R)	82.5 (7.7)	77.7 (7.6)	70.4 (7.2)
2 Row (2R)	78.9 (7.4)	72.8 (7.4)	66.5 (7.8)
Selection (SLT)	77.4 (9.2)	69.5 (8.6)	56.6 (8.8)
Gap and SLT (G1)	83.2 (7.5)	76.0 (6.8)	66.8 (7.0)
Gap (G2)	97.5 (1.7)	93.8 (3.0)	91.3 (3.2)
(b) Species[a]			
White ash	100.0 (0.0)a	96.7 (0.8)a	90.0 (3.3)a
White pine	100.0 (0.0)a	89.2 (2.2)b	78.9 (3.1)b
Planted oak	92.1 (1.7)b	75.5 (4.3)c	60.5 (5.8)c
Seeded oak	29.5 (3.6)c	26.6 (3.0)d	20.0 (2.6)d
(c) Total mean[a]	83.2 (7.5)a	76.0 (6.8)b	66.8 (7.0)c

[a]Pooled species and overall means do not include G2 treatment.

Thinning effects on seedling growth

Canopy disturbance and improved understory light following thinning significantly influenced seedling growth, which varied with time after treatment and differed among species (Fig. 3, Table 3). Thinning had little effect on early seedling growth but significantly changed RV1 and 5th- and 11th-year seedling stem diameter and height. Species differences in initial (first growing season) height of underplanted seedlings were associated with the slightly taller white ash planting stock. Thereafter, seedling growth responses pooled over thinning treatments were generally higher in white ash and white pine than planted and seeded red oak (Table 3). When significant differences in seedling growth were observed among species within a given thinning treatment, white ash and/or white pine were typically larger than seeded oak (Fig. 3).

Post-thinning LAI, DIFN, and %PFD all influenced 5th- and 11th-year seedling growth responses, which differed somewhat among species (Table 4). Seedling SVI and RV were positively correlated with DIFN and %PFD, and negatively correlated with LAI, with white pine growing showing the strongest relationship with these three variables. Seedling growth response within thinning treatments was also influenced by understory location relative to canopy openings—seedlings were generally larger in or near openings. This is illustrated by variation in SVI with planting position in the G1 treatment (Fig. 4). White ash, white pine, and planted red oak seedlings had a larger SVI when planted inside or near the canopy gap than when planted further from the gap. Lack of SVI response in seeded red oak may be because this planting row is furthest from the gap. Seedlings of all species had larger 5th- and 11th-year diameter and height in the G2 than the G1 treatment (Table 3).

Shoot dieback due to resource limitations and/or environmental stress ranged from 2% to 5% in a given year, with no apparent trend among species or thinning treatments. Dieback in growing seasons 3 to 5 averaged 1.7%, 1.9%, 4.0%, and 5.7% in sown oak, white pine, white ash, and planted oak, respectively. Browsing of shoot tips showed no clear relation-

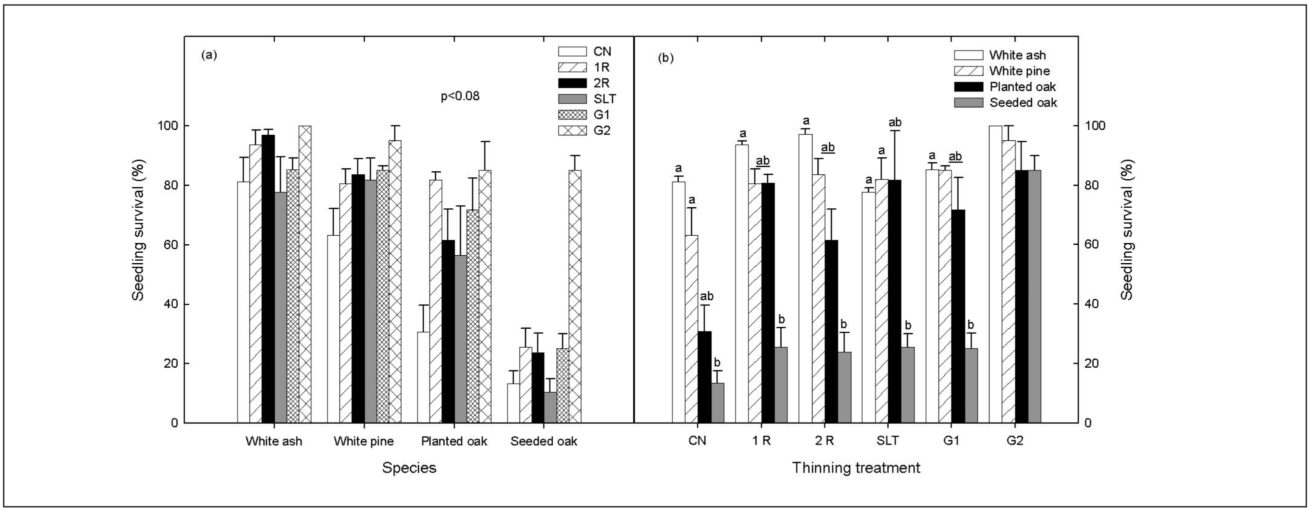

Fig. 1. Mean (± 1 SE) percent seedling survival for underplanted tree species 11 years after thinning treatments. Vertical bars lacking or sharing the same letter within a given thinning treatment or species are not significantly different ($p \leq 0.05$). Underlined letters refer to adjacent vertical bars and are used for clarity. Growth data for the G2 treatment were not included in statistical analysis; mean values are presented for comparative purposes only. Thinning treatment codes as defined in text.

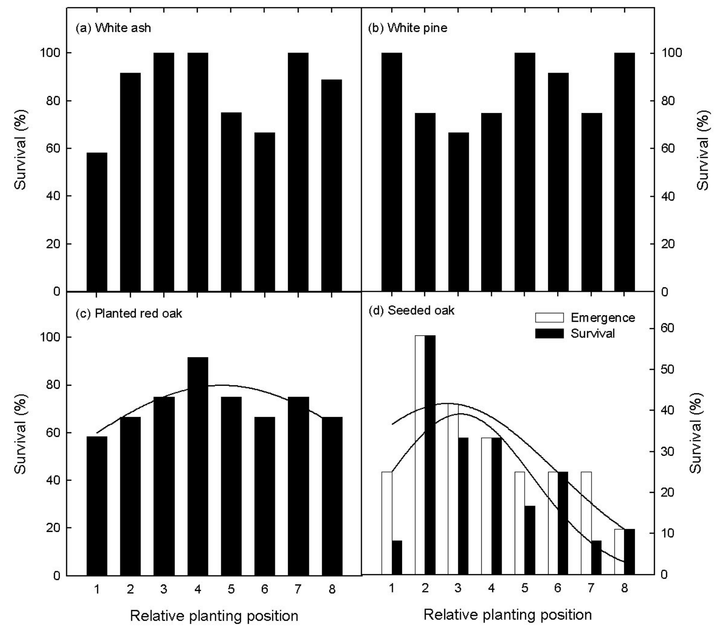

Fig. 2. Relationship of mean seedling survival 11 years after thinning treatment with planting position for (a) white ash, (b) white pine, (c) planted oak, and (d) seeded oak. The relationship of total red oak seedling emergence from planted acorns in the first growing season after treatment with relative planting position is also shown. Each observation represents the percentage of planting spots with a living seedling in three consecutive planting spots in an east-west direction (right to left on x axis) in the four replicate G1 plots (maximum n = 12). Gaussian curve fits to the relationship between seedling response and planting position are shown only where the coefficient of determination (r^2) for these functions was $r^2 \geq 0.60$.

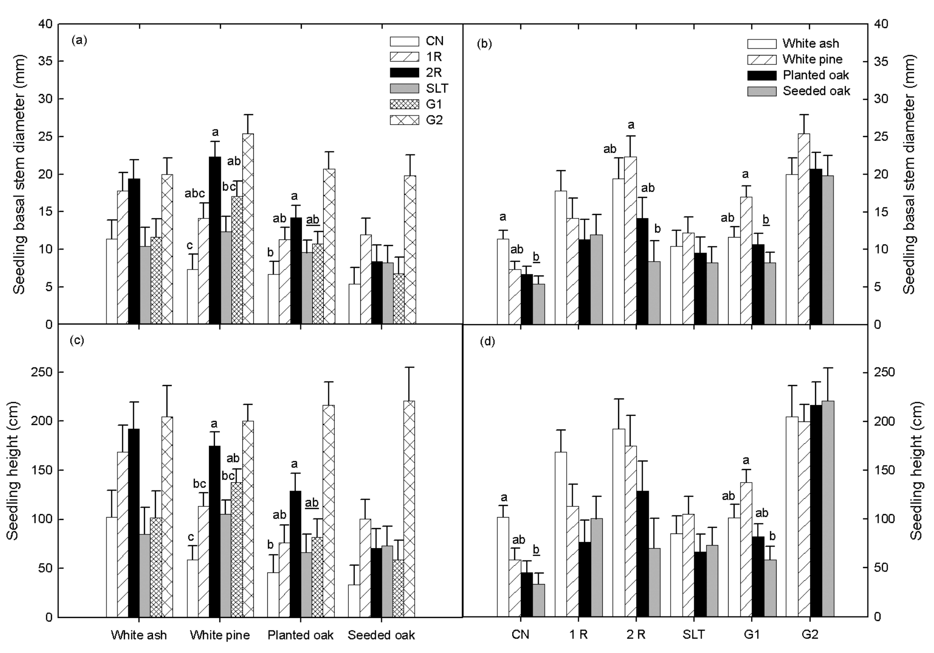

Fig. 3. Least square mean (± 1 SE) basal stem diameter (a, b) and total seedling height (c, d) for underplanted tree species 11 years after thinning treatments. Vertical bars lacking letters or sharing the same letter within a given thinning treatment or underplanted species indicates means are not significantly different ($p \leq 0.05$). Underlined letters refer to adjacent vertical bars and are used for clarity. Growth data for the G2 treatment were not included in statistical analysis; mean values are presented for comparative purposes only. Thinning treatment codes as defined in text.

Table 3. Mean seedling diameter, height, and relative volume growth rate (RV1, RV2) for data pooled for thinning treatments (a) and species (b). Means followed by the same letter are not significantly different (p ≤ 0.05). The G2 treatment was not included in ANOVA and mean comparison tests. Pooled species means do not include G2 treatment.

	Diameter (mm)		Height (cm)		Relative volume growth rate	
Treatment	Year 5	Year 11	Year 5	Year 11	RV1[a]	RV2[a]
a) Thinning						
Control (CN)	5.3 c	7.7 d	35.0 c	59.9 d	0.45 d	0.57 c
1 Row (1R)	7.1 b	13.8 ab	51.8 b	114.6 ab	0.67 c	0.80 a
2 Row (2R)	9.3 a	16.1 a	67.3 a	141.6 a	0.78 a	0.76 a
Selection (SLT)	6.2 bc	10.1 cd	44.1 bc	82.5 cd	0.62 c	0.65 b
Gap and SLT (G1)	7.5 b	11.5 bc	52.0 b	94.8 bc	0.68 b	0.70 b
Gap (G2)	12.7	21.9	98.2	210.5	0.84	0.74
(b) Species						
White ash	7.8 ab	14.1 a	56.8 a	130.0 a	0.53 c	0.73 a
White pine	8.6 a	14.6 a	61.8 a	117.9 a	0.71 ab	0.72 b
Planted oak	6.8 bc	10.5 b	44.4 b	79.7 b	0.60 bc	0.65 b
Seeded oak	5.1 c	8.2 c	37.2 b	67.2 b	0.74 a	0.68 b

[a]RV1: relative volume growth rate, growing seasons 2 to 5, RV2: relative volume growth rate, growing seasons 5 to 11.

Table 4. Correlation coefficients for the relationship between leaf area index (LAI), percent open sky (DIFN), and percent sunlight (%PFD) and seedling growth responses for (a) white ash, (b) white pine, (c) planted red oak, and (d) seeded red oak. Significant correlations (p ≤ 0.05) are noted in bold type. Correlations are based on plot mean values (n = 20), and include the G2 treatment only for %PFD (n = 24).

	LAI	DIFN	%PFD
(a) SVI[a] (year 5)	**-0.45**	**0.59**	0.27
RV1[a]	**-0.53**	**0.58**	0.33
SVI (year 11)	-0.35	**0.48**	0.25
RV2[a]	-0.05	0.11	0.15
(b) SVI (year 5)	**-0.78**	**0.77**	**0.71**
RV1	**-0.86**	**0.77**	**0.53**
SVI (year 11)	**-0.74**	**0.79**	**0.73**
RV2	**-0.83**	**0.62**	0.38
(c) SVI (year 5)	**-0.63**	**0.62**	**0.76**
RV1	**-0.72**	**0.68**	**0.43**
SVI (year 11)	**-0.52**	**0.53**	**0.78**
RV2	-0.20	0.20	0.14
(d) SVI (year 5)	-0.44	0.41	**0.81**
RV1	-0.49	0.44	**0.46**
SVI (year 11)	0.14	-0.16	**0.62**
RV2	-0.12	0.04	0.30

[a]SVI: stem volume index, RV1: relative volume growth rate, growing seasons 2 to 5, RV2: relative volume growth rate, growing seasons 5 to 11.

ship with thinning treatment and affected fewer than 3% of all seedlings in the first five growing seasons. In year 11, 15% of underplanted seedlings were browsed, with almost 25% of planted red oak and white ash seedlings, 7% of sown oak, and fewer than 2% of white pine showing damage.

Discussion

Thinning effects on survival and growth responses

Canopy disturbance by natural agents and human activities stimulates the establishment and growth of understory vegetation through improved resource (light, water, nutrients) availability and microclimatic conditions proportional to the intensity of disturbance and size of canopy openings created (Coates and Burton 1997, Aussenac 2000, Raymond *et al.* 2006). Generally, larger canopy openings create a microenvironment conducive to establishment and growth of more shade-intolerant tree species (McClure *et al.* 1993, Dale *et al.* 1995, Wright *et al.* 1998). The thinning treatments applied in our study created residual stands with canopy gaps that differed in size, shape, and spatial distribution, with only marginal improvement in understory light conditions.

Light levels within the CN treatment averaged 7%, similar to that reported for unmanaged red pine plantations in the Lake States (Goldblum 1998, Buckley *et al.* 1998). Thinning increased %PFD from 13% to 33% depending on its intensity and pattern. Seedling growth responses to thinning varied among species but were strongly correlated with post-thinning LAI, DIFN, and %PFD. However, only within or near canopy openings in the G1 and G2 did understory light approach the 40% to 50% sunlight needed to support positive to maximum shoot growth and high RV of the regenerated species (Sander 1990, Schlesinger 1990, Wendel and Smith 1990). Although plot-averaged %PFD was only about 18%, the comparatively higher growth response observed in the 2R treatment may be attributable to more favourable understory conditions in the larger strip openings created. Heavier thinning and/or creation of larger openings in red pine plantations results in comparatively greater increases in light, moisture, and nutrient availability and mean air and soil temperature (Anderson *et al.* 1969, Law *et al.* 1992, Kim *et al.* 1996, Buckley *et al.* 1998), and likely would have improved seedling growth in our study.

The three mid-tolerant species established in our study are commonly managed using shelterwoods and group selection silvicultural systems (Hannah 1988, 1991; OMNR 2000; Raymond *et al.* 2006) and are well-suited to underplanting after thinning conifer plantations (Buckley *et al.* 1998, Truax *et al.* 2000, Paquette *et al.* 2006). Seedling growth of all species was improved by increased light levels following thinning. By comparison, survival was less responsive to thinning and did

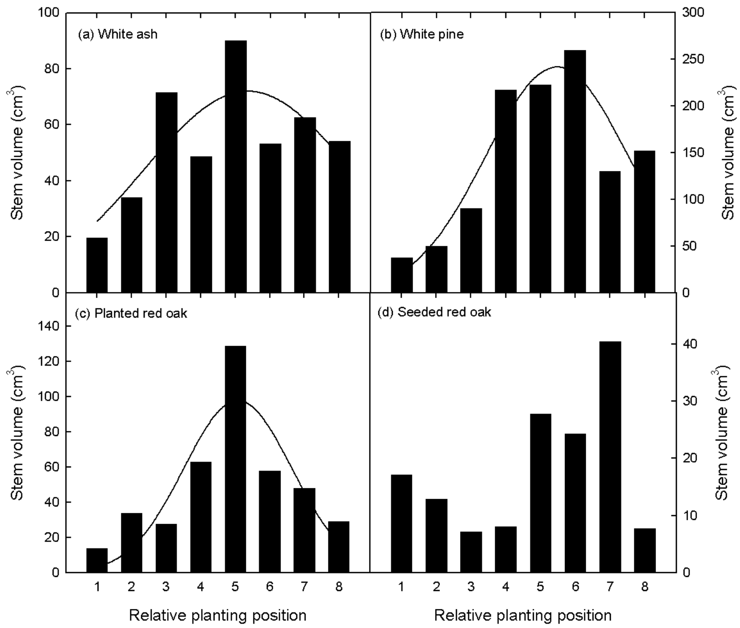

Fig. 4. Relationship of mean seedling stem volume 11 years after treatment with planting position for (**a**) white ash, (**b**) white pine, (**c**) planted oak, and (**d**) seeded oak. Each observation represents the mean stem volume of living seedlings in three consecutive planting spots in an east–west direction (right to left on x axis) in the four replicate G1 plots (maximum n = 12). Gaussian curve fits to the relationship between seedling response and planting position are shown only where the coefficient of determination (r^2) for these functions was $r^2 \geq 0.60$.

not differ among treatments, nor was it related to post-thinning LAI, DIFN, or %PFD. These results are consistent with results of a recent meta-analysis of the growth and survival response of underplanted mid-tolerant species in deciduous temperate forests that indicated height growth exhibited a greater sensitivity to overstory density than survival (Paquette *et al.* 2006).

Based on growth and survival over all thinning treatments in our study, underplanting performance can be ranked as white ash > white pine > red oak, which corresponds with results from other comparative studies of these species (Johnson 1976, Gottschalk and Marquis 1982, Tworkowski *et al.* 1986, Cogliastro *et al.* 1990, Kruger and Reich 1997, Ward *et al.* 2000, Tripler *et al.* 2002). The superior performance of white ash is likely related in part to its well-developed shade tolerance in the seedling stage (Schlesinger 1990). The comparatively poor height and diameter growth of red oak seedlings observed in our study may be related to its recurrent shoot dieback habit and comparatively high allocation of carbohydrate to root over shoot biomass production (Tworkowski *et al.* 1986, Canham *et al.* 1996, Dey and Parker 1996).

Although inherent species differences in capacity for survival and growth response to improved light conditions were important to underplanting performance, these results were confounded somewhat by damage from repeated browsing. Shade tolerance is also strongly associated with storage of non-structural carbohydrate reserves adequate to support seedling recovery from herbivory and other tissue damage suffered in the understory (Kobe 1997, Canham *et al.* 1999). Browsing of tree seedlings by white-tailed deer (*Odocoileus virginianus*) is a serious impediment to regeneration in many areas of North America where deer density is relatively high (> 10 to 15 km^{-2}) (Horsley *et al.* 2003, Rooney and Waller 2003). Deer populations in the region of the study site are estimated at 5 km^{-2} but local pockets of higher density in southern Ontario are common. Species differences in ability to produce new shoot and foliage to replace that lost by browsing may have affected the survival and growth responses to thinning observed in our study.

Regeneration of red oak and other upland oaks by direct seeding is generally less successful than planting due to acorn predation by rodents (Dey and Buchanan 1995). In our study, high seed viability coupled with visual evidence of significant acorn herbivory shortly after sowing suggests predation by small mammals was partially responsible for the low initial survival of seeded red oak. Although increased foraging by small mammals has been reported in habitats with more protective cover from predation (Webb and Willson 1985, Wright *et al.* 1998), red oak acorn consumption and removal by rodents in an oak–pine forest did not differ between intact forest and canopy gaps much larger than in our study (Plucinski and Hunter 2001). Higher seedling emergence and survival observed in the more exposed understory locations in the canopy gaps of the G1 and G2 plots may also be attributable to a more favourable environment for seed germination (Ashton and Larson 1996). Once emerged, seeded red oak exhibited survival (~73%) and size comparable to that of planted oak, suggesting direct seeding in pine plantations may be a viable regeneration option provided significant acorn predation can be avoided (Dey and Buchanan 1995).

Conclusions and Management Recommendations

Southern Ontario red pine plantations provide valuable forest cover in a heavily populated, fragmented landscape with less than 30% of the land covered by forest (Borczon 1986, Suffling *et al.* 2003, OMNR 2006). Although these pine plantations are well suited to even-age, intensive forest management to maximize timber production (Rudolph *et al.* 1984, Woods and Penner 2000, Gilmore and Palik 2005), management objectives must balance financial return for timber with wildlife habitat, recreational opportunities, watershed protection, and other values of these areas. When restoration is also a management objective, the results of our study and others suggest that underplanting and earlier, heavier thinning (i.e., to a residual basal area of 16 to 21 m^2 ha^{-1}) can help to establish a vigorous understory of mid-tolerant tree species while supporting timber production objectives (Dickmann *et al.* 1987, Bender *et al.* 1997).

Tree species for underplanting should be chosen based on soil and site conditions, landscape history of the area, and ability to prosper under moderate understory light levels beneath a partial canopy (OMNR 2000). We recommend that initial thinning for restoration of young red pine plantations combine row removal for access with group selection thinning to create canopy gaps. The specific number of rows removed or diameter of canopy gaps would depend on the microenvironment best suited to the shade tolerance and autecology of the target species. Applied in this way, thinning regimes would optimize growth of target species, while minimizing growth of anticipated competing species (Coates and Burton 1997, Paquette *et al.* 2006). The opening diameter to height ratios (G1, G2 = 0.50; 1R = 0.13; SLT ~ 0.13; 2R = 0.26) in our study did not provide understory light levels needed to obtain maximum height growth. When mid-tolerant species will form the future forest, row thinning widths and gap diameters of 1.5 to 2.0 times the height of the overstory will provide light levels of 15% to 60% sunlight needed for competitive to maximum rates of height growth and canopy recruitment of these species (Fig. 5) (Miller *et al.* 1995, OMNR 2000). However, selection of canopy opening size should be tempered by the abundance and species composition of competition anticipated in a given plantation. The risk of frost and high temperature stress increases with gap size and partial harvest intensity, thus thinning should also be tailored to the temperature stress tolerances of the preferred species of regeneration (Carlson and Groot 1997, Strong *et al.* 1997, Buckley *et al.* 1998, Raymond *et al.* 2006).

Selection of optimal thinning regime depends on whether stands will be regenerated naturally, by planting, or a combination of both methods. Seed germination, seedling emergence, and early seedling establishment of natural regeneration of small-seeded, mid-tolerant species are favoured in sheltered microsites created by lighter thinning, or in smaller gaps, in particular, the southern and western portions of gaps (Wright *et al.* 1998, Raymond *et al.* 2006) (Fig. 5). Some form of forest floor disturbance to create seedbeds and stimulate the soil seed bank will also be needed to enhance natural regeneration, particularly where the littler layer is thick

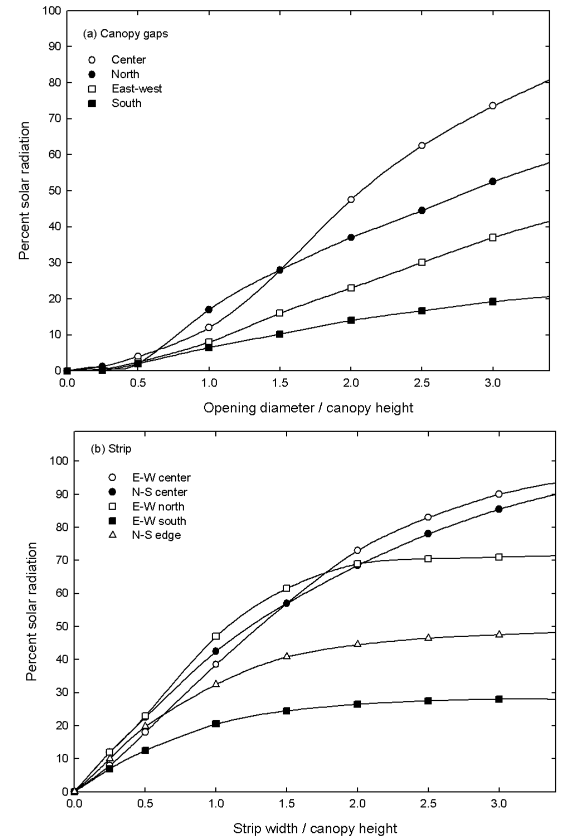

Fig. 5. Variation in estimated relative solar radiation with understory location in (a) circular canopy gaps and (b) strip clearcuts as affected by the ratio of gap diameter or strip width to mean canopy height (adapted from Aussenac 2000).

(LePage *et al.* 2000, Parker *et al.* 2001, Prévost and Pothier 2003). Where direct seeding of red oak is preferred, seeding density should be at least twice the normal planting density and combined with measures to reduce predation (Dey and Buchanan 1995). In contrast, the growth and survival of planted seedlings is favoured by the warmer, higher light environments of more heavily thinned plantations, larger gaps, and more northern and eastern portions of gaps (Coates 2000, Raymond *et al.* 2006). Planting of species mixtures at 1-m to 2-m spacing within and around openings in combination with methods to stimulate natural regeneration can be used to increase understory diversity.

Selection of species for restoration should also consider the risk of damage and mortality from native and exotic pathogens. Although white ash performed well in underplanting, it is extremely vulnerable to future attack and mortality from the emerald ash borer (*Agrilus planipennis* Fairmire), a recently introduced invasive insect species. This insect now occurs in southwestern Ontario and lower Michigan and its expected spread poses a serious threat to all North American ash species (OMNR 2007). When white pine is selected for underplanting, thinning regimes must be modified to minimize the risk of blister rust (*Cronartium ribicola*

J.C. Fischer), a serious exotic pathogen of all five-needled pines of North America (Maloy 1997). Unfortunately, the relationship of overstory structure with blister rust infection is still poorly understood (Ostry 2000). Small-diameter openings (less than the height of the surrounding forest) are not recommended, particularly when located in low lying areas or at the base of slopes. These openings collect cool air and have abundant dew formation, which persists due to insufficient direct sunlight in the understory, creating an ideal microclimate for rust infection (Van Arsdel 1961, Hodge *et al.* 1989, Katovich *et al.* 1993). A compromise that balances growth potential with the risk of mortality from blister rust is possible: underplant white pine in areas selectively thinned to create uniform shelterwoods that reduce dew formation but transmit sufficient light to support acceptable growth and survival.

Focus thinning to create canopy gaps in areas where growth and condition of overstory pine trees is poor (Miller *et al.* 1995). In stands suffering pocket decline, thinning prescriptions, regeneration activities, and species selection must carefully balance restoration objectives with the need to minimize the incidence and spread of disease centres and associated decline (McLaughlin 2001, Erbilgin and Raffa 2002). Some of the material removed in these early thinnings may not be merchantable for traditional products but may have value for bioenergy or can be left on site to increase structural diversity in the form of snags, cavity trees, and downed woody material.

Where possible, deviate from traditional row and selection removal of the overstory in initial and subsequent thinning (Gilmore and Palik 2005). Variable density thinning can be used to create multiple tree openings of the size needed to achieve target light levels interspersed within a matrix of more aggregated canopy tree retention. This residual spatial pattern will increase structural complexity, promote biodiversity, improve wildlife habitat, and enhance the aesthetic value of these stands for recreational and educational use (Bender *et al.* 1997, Hartley 2002, Gilmore and Palik 2005). This approach when combined with permanent retention of selected large overstory red pine will also create residual stands more similar in structure to those formed by natural disturbance (Gilmore and Palik 2005).

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