Managing succession in conifer plantations: converting young red pine (*Pinus resinosa* Ait.) plantations to native forest types by thinning and underplanting

by William C. Parker[1], Ken A. Elliott[2], Daniel C. Dey[1,3], Eric Boysen[4] and Steven G. Newmaster[1,5]

The effects of thinning on growth and survival of white pine (*Pinus strobus* L.), white ash (*Fraxinus americana* L.), and red oak (*Quercus rubra* L.), and understory plant diversity were examined in a young red pine (*Pinus resinosa* Ait.) plantation. Five years after thinning, seedling diameter, height, and stem volume were positively correlated with thinning intensity and the size of canopy openings. Percent survival did not differ among thinning treatments, but was significantly higher in white ash and white pine than red oak. Understory vegetation included 113 species, with species richness increasing with thinning intensity and proximity to neighbouring plant communities. Thinning to create relatively large canopy openings in combination with underplanting can promote the natural succession of young pine plantations to native forest species.

Keywords: direct seeding, plant diversity, natural regeneration, red oak, restoration, white ash, white pine

Les effets de l'éclaircie sur la croissance et la survie du pin blanc (*Pinus strobus* L.), du frêne d'Amérique (*Fraxinus americana* L.) et du chêne rouge (*Quercus rubra* L.) et sur la diversité des plantes en sous-étage ont été étudiés dans une jeune plantation de pin rouge (*Pinus resinosa* Ait.). Cinq années après l'éclaircie, le diamètre, la hauteur et le volume de la tige des semis ont été corrélés positivement avec l'intensité de l'éclaircie et la taille des ouvertures dans le couvert des cimes. Le pourcentage de survie n'a pas différé selon les traitements d'éclaircie, mais il était significativement plus élevé pour le frêne d'Amérique et le pin blanc que pour le chêne rouge. La végétation en sous-étage comprenait 113 espèces, et la diversité des espèces augmentait selon l'intensité d'éclaircie et la proximité de communautés de plantes avoisinantes. Une éclaircie réalisée dans le but de créer d'importantes ouvertures dans le couvert en association avec un regarnissage peut promouvoir la succession naturelle des plantations de jeunes pins vers des espèces forestières indigènes.

Mots-clés: ensemencement direct, diversité des plantes, régénération naturelle, chêne rouge, réhabilitation, frêne d'Amérique, pin blanc

Introduction

Prior to European settlement, most of south-central Ontario was dominated by forest vegetation. The mesic sites were occupied by the tolerant hardwood species of the Great Lakes – St. Lawrence Forest Region (Rowe 1972), dominated by sugar maple (*Acer saccharum* Marsh), red maple (*Acer rubrum* L.), basswood (*Tilia americana* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Delcourt and Delcourt 2000). On the drier sites of this region, eastern white pine (*Pinus strobus* L.) and red oak (*Quercus rubra* L.) increased in frequency, with areas of coarse-textured soils supporting white, red (*Pinus resinosa* Ait.) and jack (*P. banksiana* L.) pine forests (Whitney 1986, Delcourt and Delcourt 2000). Settlement of southern Ontario in the early to mid-1800s initiated the widespread logging of pine and clearing of forests for agriculture (Borczon 1986). By the late 1800s, much of the native forests of this region were eliminated or modified by the new European land use practices.

A large proportion of the forest land brought into cultivation was unsuitable for growing agricultural crops, particularly the coarse-textured soils of the original pine forests. Removal of the protective forest cover and the prevailing agricultural practices often resulted in massive soil erosion, and increased frequency and severity of spring flooding and summer drought. These poor farmlands were ultimately abandoned to further erosion by wind and water, leading to the development of vast areas of desert-like wasteland. Commonly, wind action lifted the light sands forming large "blow pits," depositing the sands in banks downwind. In severe cases, the pits and banks of blow sand areas covered 30 ha or more (Borczon 1986).

At the turn of the century, recognition of the extent and impact of this problem resulted in a series of legislative efforts to encourage reforestation of these degraded forest lands to both control erosion and protect watersheds (Borczon 1986). Red pine was often favoured for planting because of its ability to grow on the infertile, sandy soils. Today, these plantations are an important component of southern Ontario's woodlands. They provide a variety of ecological and social benefits to this mainly urban environment, where little of the original forest remains and forests have been fragmented by development.

The structure and composition of these plantations differ with stand age and history of natural disturbance and management. In older pine plantations, thinning and natural disturbances

[1]Ontario Ministry of Natural Resources, Ontario Forest Research Institute, 1235 Queen St. E., Sault Ste. Marie, ON P6A 2E5. Email: bill.parker@mnr.gov.on.ca
[2]Ontario Ministry of Natural Resources, South Central Science Section, 659 Exeter Rd, London, ON N6E 1L3.
[3]Current Address: U.S. For. Serv. North Central Research Station, 202 Anhueser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA.
[4]Ontario Ministry of Natural Resources, Forest Management Branch, 5th floor, North tower, 300 Water St., Peterborough, ON K9J 8M5.
[5]Current Address: Algoma University College, 1520 Queen St. E., Sault Ste. Marie, ON P6A 2G4.

that opened the canopy encouraged the development of an understory of native hardwood and conifer species. Younger plantations with no overstory disturbance history are largely devoid of understory vegetation, and are viewed by some as "biological deserts" (Mosquin *et al.* 1995).

There is currently great interest in managing the succession of conifer plantations to accelerate their conversion to more natural forest types. The suite of silvicultural treatments needed largely depends on the presence and abundance of advance regeneration of the desired species. In 1993, the Ontario Ministry of Natural Resources in cooperation with the Regional Municipality of Durham developed a research project to identify methods for managing the natural succession of older, previously disturbed, and younger, undisturbed, conifer plantations. In this report, we present the results of a study of the influence of five thinning treatments on: (1) growth and survival of underplanted white pine, red oak, and white ash, and (2) abundance and diversity of naturally regenerated, understory vegetation in a young, 32-year-old red pine plantation.

Materials and Methods

Study Site

This study was established in the Norton Tract of the Durham Regional Forest (43°55'N, 79°10'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 located within a larger 20.3-ha block of pine (white, red, jack, and Scots pine (*Pinus sylvestris* L.)) plantations. The study plantation was established in 1962, with red pine planted at 1.8-m × 1.8-m spacing. Thereafter, the plantation received no further treatment. In 1993, the overstory was pure red pine with average stand basal area, height, and diameter (at 1.3 m) of 54.7 $m^2\ ha^{-1}$, 14 m, and 17 cm, respectively. Very little understory vegetation existed and the forest floor consisted largely of a 5–10 cm litter layer of pine needles. Soils are of the Pontypool Sands soil series, with loamy fine sand soils that have a moderately fresh moisture regime with rapid drainage. The A horizon (upper 25 cm) is a plow layer (Ap), overlying a 50-cm Bm horizon. Carbonates are present beyond 70 cm.

Experimental Design and Overstory Treatment Description

The main study area (120 m × 160 m; 79 planted (north-south) rows) was divided into 20, 30-m × 32-m plots (Fig. 1). Each of these plots was further subdivided in half along an east-west line. Following thinning treatments, the southern half of each plot (15 m × 32 m) was planted with single, east-west rows of white pine, red oak, and white ash. The northern subplot was left untreated to monitor the ingress of woody and herbaceous vegetation.

Red pine plantations in the Lake States and Ontario have most commonly been by thinned by row and individual tree selection (Horton and Bedell 1960, Lundgren 1981). In this study, we used row thinning, selection thinning, and creation of small canopy gaps to obtain a range in the intensity and spatial distribution of canopy disturbance. Plots in the main study area were randomly assigned one of five treatments, including an uncut control (CN), with each treatment replicated four times. Single (1R) row thinning removed the first of every four rows and decreased basal area by 25% (residual basal area ~41 $m^2\ ha^{-1}$). Double (2R) row thinning removed the first two of every five rows and reduced basal area by about 40% (~33 $m^2\ ha^{-1}$). All row thinning was applied in a north-south direction. A selection (SLT) treatment reduced basal area by about 44% (~31 $m^2\ ha^{-1}$), by combining single row thinning with removal of 25% of the trees in the three adjacent rows. The final treatment (G1) was designed to better simulate natural canopy disturbances. Small, circular canopy gaps, 7 m in diameter or approximately half the average height of the overstory trees (Hibbs 1982a), were created in plots that also received the SLT treatment. This treatment reduced basal area by about 46% (~30 $m^2\ ha^{-1}$).

A second smaller area (0.4 ha) about 40 m to the west of the main block was later added to the study to more closely examine the effect of planting location on seedling growth (Fig. 1). This area was divided into four, 30-m × 32-m plots. These plots were thinned using the G1 method, but seedlings were planted only within the circular understory opening, hereafter referred to as the G2 treatment.

All thinning was completed in August 1994 using a feller-processor and a wheeled forwarder. The feller-processor consisted of a small, tracked excavator fitted with a cutter head and delimber on a jointed boom. The operator harvested and processed logs along a travel corridor created by the row thinning. The length of the cutter arm allowed the extraction of trees up to 4 m (i.e., 2 rows) away from the cleared rows. Trees were cut, delimbed, cut to ~2.4-m lengths, and stacked in small piles (< 10 logs) along the edge of the removed rows. Cut logs were loaded on the back of the forwarder and removed from the study plots using the same travel corridors as the feller-processor. Logging damage to residual trees was negligible. Disturbance of the forest floor was largely confined to the path shared by the two machines.

The study area is surrounded by a number of potential sources of propagules for understory colonization and natural regeneration (Fig. 1). These areas include white, Scots, red, and jack pine plantations differing in age and understory development. Mature trees in a fence row, and an old field with scattered Scots pine and several hardwood tree species occur along the southern boundary of the plantation. A residential area and small, open woodland occur to the north of these pine plantations. Tolerant hardwood stands 700 m to the west and 1 km to the southeast of the plantation may provide a more distant source of seed.

Artificial Regeneration

In April 1995, all 24 plots were planted with 2+0 bareroot white ash, white pine, and red oak seedlings, and direct seeded with red oak acorns. These species are common to the original forests of the region, adapted to the site, and intermediate in shade tolerance. Seedlings were obtained from St. Williams Nursery (St. Williams, ON). Red oak acorns obtained from a 1994 bulk collection from a local seed source were cleaned of damaged seed, and stratified for 46 days at 2°C. Viability tests indicated germinability of about 90%. Four east-west planting rows were established in the southern half of the 20 plots in the main study area, 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 the same 1.2-m spacing, with five acorns planted to a depth of 2–3 cm in a 10-cm

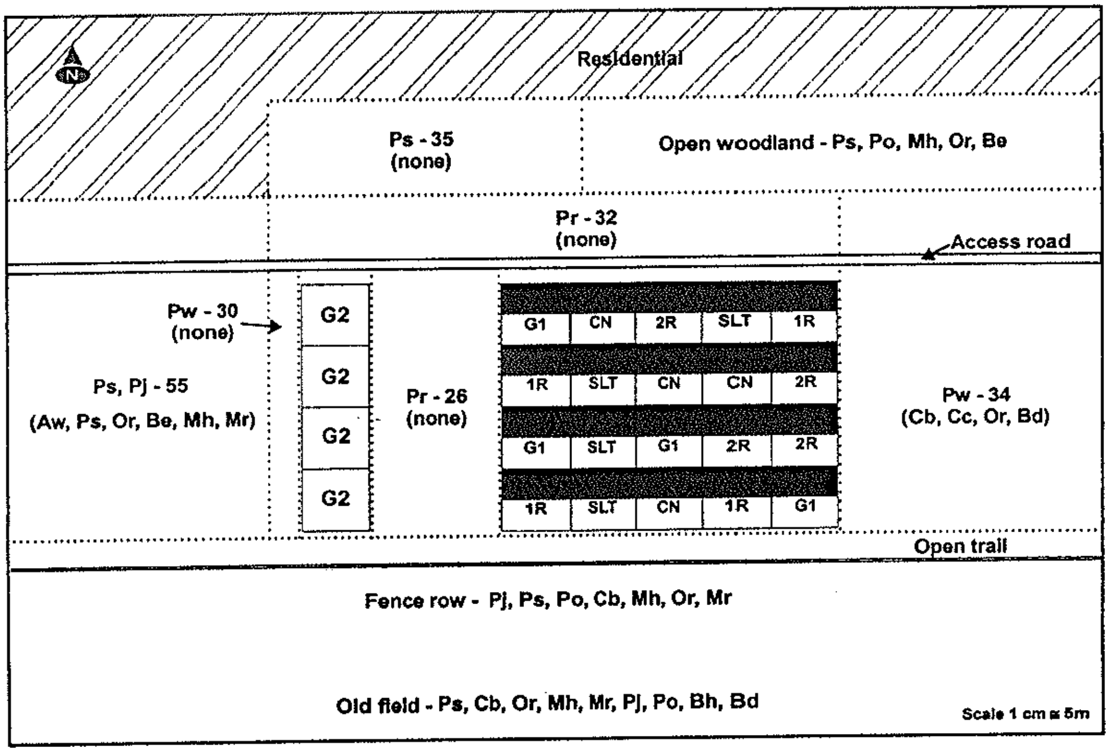

Fig. 1. Thinning treatment location and description of vegetation neighbouring the 32-year-old red pine study plantation. Shading in individual plots refers to the unplanted area. Adjacent pine plantations are identified by species (red (Pr), white (Pw), jack (Pj), and Scots (Ps)) and age. Plantation understory composition of major woody species is noted in parentheses. Species are listed in order of abundance. Open woodland, old field, fence row, and understory tree species codes: white ash (Aw), basswood (Bd), American beech (Be), beaked hazel, (*Corylus cornuta* Marsh) (Bh), black cherry (*Prunus serotina* Ehrh.) (Cb), choke cherry (*Prunus virginiana* L.) (Cc), red oak (Or), sugar maple (Mh), red maple (Ms), *Populus* sp. (Po).

× 15-cm planting spot. The four G2 plots were planted only within the circular canopy openings. Five seedlings per species and five groups of four acorns were randomly planted within this opening.

Height and diameter (2 cm above ground) of underplanted seedlings were measured shortly after planting to provide baseline data for future growth comparisons. Height, diameter, and survival of underplanted seedlings were measured at the end of each growing season from 1995–1999. The number of oak seedlings, the height and diameter of the largest seedling, and survival were determined for each acorn planting spot.

The relative increase in seedling stem size since time of planting was estimated by the ratio of incremental change in height, diameter, or volume since the first measurement date to the total measured in 1999 (year 5). Relative height growth rate was integrated over the entire five-year, post-treatment period. Relative diameter and volume growth were integrated over a four-year period since diameter was not measured on seeded red oak until the second year after planting.

Understory vegetation and plant diversity

A comprehensive botanical survey of all understory plant species was conducted in August 1999, five years after thinning. Four, 10-m × 10-m plots were located in each of the 24 treatment plots (two in the north (unplanted), two in the south (planted) subplot). Percent cover (i.e., abundance) was estimated for each species relative to the 100-m^2 plot. Frequency of occurrence by species was estimated as the proportion of the 16, 100-m^2 plots per treatment that had at least one individual present. Each plant species identified in the 96 plots was assigned a layer code: (1) dominant tree (>10 m), (2) subdominant tree (<10 m), (3) woody vegetation (trees, shrubs, vines), 2.0–10.0 m, 0.5–2.0 m, or < 0.5 m in height, (4) herbs, grasses, and sedges, and (5) cryptogams (pteridophytes, bryophytes, lichens). The species rarity ranking, species nomenclature, and exotic status follow the Ontario Plant List (Newmaster *et al.* 1998). For comparative purposes, understory vegetation was also surveyed in four locations within a nearby 70-year-old conifer plantation. Alternate rows of white and red pine were planted in 1929, and the plantation thinned at 32, 42, and 55 years. In 1993, the plantation had an average basal area of 31 $m^2\ ha^{-1}$ and height of 28 m, with abundant advance reproduction of woody species.

Species richness (Fisher *et al.* 1942, McIntosh 1967, Peet 1974) was used as a measure of plant diversity. Mean species richness (i.e., the mean number of species present) was calculated for each thinning treatment, plots grouped by the number (0,1, 2–3) of plot borders, "edges," adjacent to plant communities neighbouring the study area, and for functional plant groups: woody, herbaceous (herbs, grasses, sedges), and cryptogams.

Overstory characteristics

In fall 1996, a LAI-2000 plant canopy analyzer (LiCor, Inc., Lincoln, NE, USA) was used to estimate leaf area index (LAI)

Table 1. Thinning intensity, estimated size and number of canopy openings, and plot-averaged values for mean (± 1 SE) leaf area index (LAI), percent crown closure, and percent PPFD in the understory for six thinning treatments[1]

Treatment	Thinning intensity (%)	Average number and opening area (m^2)	LAI	Crown closure (%)	Daily PPFD (% full sunlight)
Control (CN)	0	0	3.14 (0.09)	93.2 (0.5)	6.7 (0.2)
1 row (1R)	25	5, 108	2.31 (0.19)	85.4 (2.2)	13.3 (0.6)
2 row (2R)	40	4, 162	1.67 (0.27)	75.2 (5.2)	17.7 (0.9)
Selection (SLT)	44	5, 108 48, 2.5	2.07 (0.15)	81.8 (1.6)	16.1 (0.7)
Gap (G1)	46	1, 38.5 65, 2.5	1.69 (0.14)	75.5 (3.2)	16.8 (0.9)
Gap (G2)	46	1, 38.5 65, 2.5	1.71 (0.25)	71.3 (5.7)	33.5 (1.9)

[1]Estimates of average canopy opening size and number assume 2-m × 2-m spacing, fully stocked conditions, and roughly circular crowns of overstory red pine that did not overlap at time of thinning. Canopy openings for 1R and 2R thinnings are rectangular, G1 and G2 are circular, and those for SLT are a combination of both.

and percent crown closure of each treatment plot. Eleven instantaneous measurements at 1 m above the ground, collected along a systematic transect through each of the 24 plots, were used to estimate plot-averaged treatment values. All measurements were made on a completely overcast day. A LI-190s quantum sensor attached to the canopy analyzer was used to measure photosynthetic photon flux density (PPFD: light intensity between 400–700 nm). Periodic above canopy PPFD measurements were made in an adjacent opening. Mean daily percent PPFD in the understory was estimated as the ratio of below to above canopy PPFD (Messier and Puttonen 1995). All PPFD measurements in the main treatment area were collected at the same time and position as canopy measurements (n=11). In the G2 plots, PPFD was measured only within the canopy gap (n=11).

Statistical analysis

The GLM procedure of SAS (SAS Institute Inc. 1989) was used for analysis of variance (ANOVA) of treatment effects on growth and survival of artificial regeneration within the main study area. The following mixed general linear model was used,

$$u_{ijk} = T_i + P_{(i)j} + S_k + TS_{ik} + PS_{(i)jk} + E_{(ijk)l}$$

with thinning (T) and species/seedling type (S) as fixed factors, and plot (P) identified as a random factor. A Tukey-Kramer test was used for mean comparisons. Variance in percent survival data was stabilized using an arcsine square root transformation. Because the G2 plots were established outside the main study area, and were underplanted with fewer seedlings per species, this treatment was not included in the ANOVA. Instead, treatment means and standard errors (SE) were used for comparison of G2 with the other thinning treatments. Non-parametric statistics and a Kruskal-Wallis test were used for analysis of understory species richness because of non-homogeneity of variance (Lavene statistic, $p \leq 0.05$). The relationship between thinning intensity (i.e., percent basal area reduction) and mean LAI, percent crown closure, and understory PPFD was examined using Pearson product-moment correlation coefficients. For the G2 treatment, basal area reduction was set to 46% for correlation analysis with plot-averaged LAI and percent crown cover. A basal area reduction of 100% was used for correlation analysis with daily understory PPFD, since PPFD was measured only within the canopy gaps in these plots.

Results

The closed canopy of the unthinned, CN plots had an average LAI of 3.14, 93.2% crown closure, and daily understory PPFD of about 7% of full sunlight (Table 1). The four thinning treatments created canopy openings of different number and size, reduced plot-averaged estimates of LAI and percent crown closure, and increased understory light levels (Table 1). The highest plot-averaged value of daily PPFD was ~18% in the 2R treatment, but daily PPFD within canopy gaps of the G2 plots averaged 34%. A significant correlation existed between thinning intensity and LAI ($r = -0.93$, $p \leq 0.008$), percent crown closure ($r = -0.86$, $p \leq 0.03$), and daily PPFD ($r = 0.99$, $p \leq 0.0001$).

Artificial regeneration

Reduction in overstory basal area in the main study area had a significant, positive effect ($p \leq 0.05$) on seedling stem diameter, height, and volume, but not until the third growing season after thinning. Five years after planting, seedlings were generally larger in the 2R and G1 treatments and smaller in the CN and SLT treatments (Table 2). Thinning also had a strong effect on relative diameter ($p \leq 0.03$), height ($p \leq 0.04$), and volume ($p \leq 0.08$) growth rates, with seedlings in the 2R, 1R, and G1 treatments exhibiting a proportionally larger increase in size than those in the unthinned, CN plots (Table 2). By comparison, seedlings growing within canopy gaps in the G2 plots were much larger and exhibited higher relative growth rates.

Seedling stem size differed significantly ($p \leq 0.05$) among species in all five growing seasons. Initially, species variation in stem size was largely due to the smaller size of direct seeded red oak germinants relative to nursery stock. By year five, seedling diameter, height, and volume were generally larger for ash and pine than both types of oak seedlings (Table 2). Stem relative growth rates also differed among species in all five growing seasons ($p \leq 0.01$), and tended to be lower in ash and oak planting stock than in pine and the direct seeded oak (Table 2). The general similarity in comparative growth response to thinning intensity among species is illustrated in Fig. 2.

Seedling survival ranged from 76 to 95% among thinning treatments in the first growing season after planting and declined slightly by year five (Table 3). Stem dieback followed by sprouting from the root collar occurred in 5.3% of the oak and 1.4% of the ash seedlings in the year of planting. Seedling survival was not influenced by thinning but differed ($p < 0.0001$)

Table 2. Mean (± 1 SE) for several stem growth parameters for data pooled for thinning treatment (a) and species (b). Means followed by the same letter are not significantly different ($p \leq 0.05$). The G2 treatment was not included in ANOVA and mean comparison tests

	Seedling stem size (5 yr)			Stem relative growth rate		
	Height (cm)	Diameter (mm)	Volume (cm^3)	Height (5 yr)	Diameter (4 yr)	Volume (4 yr)
a) Thinning						
CN	38.9(1.7)^{b}	5.7(0.2)^{b}	6.9(1.4)^{b}	0.38(0.02)^{c}	0.12(0.01)^{c}	0.22(0.01)^{a}
1R	54.8(1.6)^{ab}	7.5(0.2)^{b}	12.2(1.0)^{b}	0.55(0.02)^{ab}	0.28(0.01)^{ab}	0.38(0.01)^{a}
2R	72.3(2.4)^{a}	10.0(0.3)^{a}	32.0(3.1)^{a}	0.65(0.02)^{a}	0.40(0.02)^{a}	0.48(0.02)^{a}
SLT	47.1(1.4)^{b}	6.6(0.2)^{b}	7.9(0.6)^{b}	0.46(0.03)^{bc}	0.23(0.01)^{bc}	0.32(0.02)^{a}
G1	55.7(1.6)^{ab}	8.0(0.2)^{ab}	13.5(1.0)^{b}	0.56(0.02)^{ab}	0.32(0.01)^{ab}	0.39(0.02)^{a}
G2	97.9(5.3)	12.6(0.5)	56.9(6.8)	0.71(0.03)	0.48(0.02)	0.56(0.02)
(b) Species						
White ash	57.0(1.8)^{a}	7.8(0.2)^{ab}	19.3(2.0)^{a}	0.31(0.02)^{c}	0.23(0.01)^{b}	0.27(0.02)^{b}
White pine	62.7(1.2)^{a}	8.7(0.2)^{a}	17.1(1.0)^{ab}	0.71(0.01)^{a}	0.32(0.01)^{a}	0.44(0.01)^{a}
Red oak (p)*	45.8(1.4)^{b}	6.9(0.1)^{b}	9.0(0.7)^{ab}	0.54(0.02)^{b}	0.25(0.01)^{ab}	0.36(0.02)^{ab}
Red oak (s)*	38.9(2.1)^{b}	5.3(2.1)^{c}	5.2(0.8)^{b}	0.66(0.02)^{ab}	0.36(0.02)^{a}	0.45(0.02)^{a}

*Planted (p) and seeded (s) red oak.

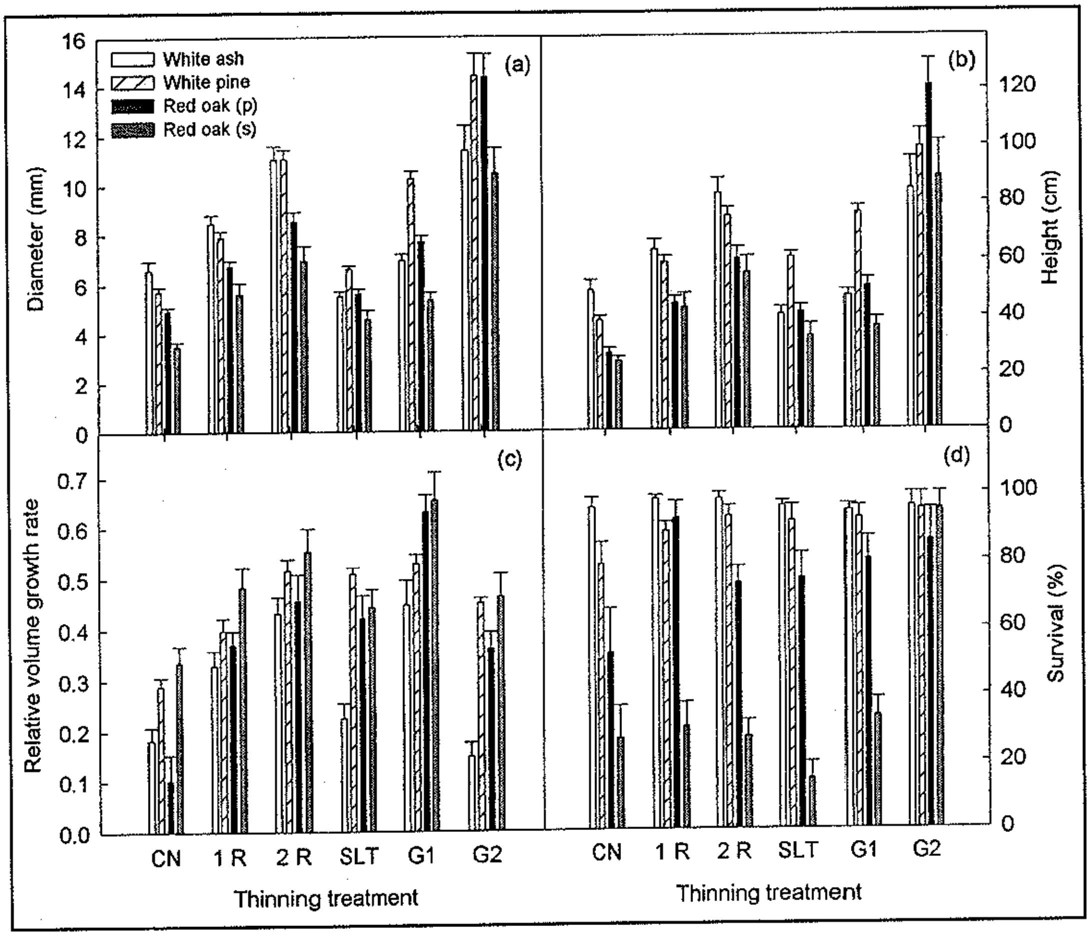

Fig. 2. Mean (± 1 SE) diameter (a), height (b), relative stem volume growth rate (c), and percent survival (d) of underplanted tree seedlings five years after thinning. Red oak seedlings are separated into planted (p) and seeded (s) populations.

among species in years one and five and was ranked as follows: ash = pine > planted oak >> seeded oak (Table 2). Fifth year survival of ash was uniformly high (>95%) for all treatments, while survival of pine and planted oak seedlings was enhanced by heavier thinning (Fig. 2). With the exception of the G2 treatment, only about 30% of the acorn planting spots produced at least one seedling the first growing season, as compared with about 90% survival for the planted oak (Fig. 2). Thereafter, survival of oak germinants was higher than that of planted oak.

Seedling growth response was also influenced by understory location relative to canopy gaps in the G1 and G2 treatments. White pine seedlings planted in the northern-most row in each plot were exposed to relatively high light levels in the canopy opening of G1 plots, and were larger than ash and oak seedlings (Fig. 2, 3). The size of pine seedlings declined to the east and west of plot centre as planting rows passed into the more shaded conditions of the selectively thinned portion of the plot (Fig. 3). By comparison, white ash seedlings planted in the third row were not exposed to the gap environment, and were similar in size to ash in the SLT treatment (Fig. 3). All three species exhibited best growth when planted beneath the canopy gaps in the G2 plots.

Table 3. Results of a Tukey-Kramer multiple comparison test of mean differences in percent survival one and five years after planting. Means (± 1 SE) are presented for data pooled for (a) thinning and (b) species. Means lacking superscripts or sharing the same superscript are not significantly different ($p \leq 0.05$). Data from the G2 thinning treatment were not included in ANOVA for thinning effects or in means by species

	Survival (%)	
	Year 1	Year 5
(a) Thinning		
CN	79.4 (7.8)	63.6 (7.7)
1R	82.3 (7.5)	77.5 (7.4)
2R	77.9 (7.5)	73.0 (7.4)
SLT	76.3 (9.2)	69.2 (8.6)
G1	82.7 (7.5)	75.2 (6.7)
G2	95.4 (2.1)	92.9 (3.0)
(b) Species		
White ash	99.4 (0.4)[a]	96.1 (0.8)[a]
White pine	100 (0.0)[a]	89.2 (2.1)[a]
Red oak (p)	90.2 (2.0)[b]	74.8 (4.2)[b]
Red oak (s)	29.2 (3.7)[c]	26.7 (3.1)[c]

Understory vegetation

The understory vegetation survey identified 113 plant species in the young pine plantation (Table 4), but total percent cover was low (Appendix 1). More total species were present in the CN plots than any other thinning treatment, 22 of which only occurred in these undisturbed plots (Table 4). About 22% of the total species present in the study area were exotic, with the percentage of non-native species ranging from 24–32% among thinning treatments. By comparison, the understory vegetation in the older, previously disturbed plantation was more diverse and abundant, and included *Heuchera americana* L. and *Polytrichum formusum* Hedw., species listed as very rare and uncommon to Ontario, respectively (Table 4, Appendix 1). Exotic species, predominantly herbaceous, were also common in the older plantation. Of the 167 plant species identified at both plantations, 26 were unique to the young plantation, while 56 occurred only in the older plantation.

Thinning had a significant effect ($p < 0.01$) on plant diversity, with species richness increasing at higher thinning intensity (Fig. 4a). The response of species richness to thinning differed among functional plant groups (Fig. 4b). Richness of woody species was higher in the gap thinning treatments and herbaceous species exhibited a trend toward increased richness with heavier thinning. In contrast, species richness of cryptogams was reduced by thinning (Fig. 4b). The number of plot edges bordering other vegetation types had a positive, significant ($p < 0.001$) effect on floral diversity. Species richness averaged 14 ± 6, 25 ± 4, and 48 ± 7 in plots with 0, 1, and 2–3 exposed edges, respectively. Mean species richness of the older plantation was significantly higher than all but the G2 treatment of the younger plantation and also had a much higher richness of cryptogams (Fig. 4).

Natural regeneration of woody species was represented by 14 tree and 14 shrub species, but percent cover (total and for individual species) was uniformly low (<1–2 %) for all treatments (Appendix 1). The most common woody species were red pine and two exotic shrub species, *Rhamnus cathartica* L. and *Rubus idaeus* L. The ingress and development of natural regeneration of woody species has proceeded slowly, with lower abundance and richness observed in the larger size classes (Fig. 5). A slightly larger number of woody species was present in the older plantation, with richness and percent cover being much higher than the young plantation for all three height classes (Table 4, Fig. 5).

Discussion

Forest canopies have a substantial influence on the understory environment, buffering temperature changes, reducing light intensity, changing the spectral quality of solar radiation, and intercepting a significant proportion of precipitation (Anderson *et al.* 1969, Aussenac 2000). The growth and abundance of understory vegetation beneath intact forest canopies are strongly limited by heavy shade, reduced precipitation inputs, and root competition for moisture with overstory trees (Anderson *et al.* 1969, Canham *et al.* 1990, Bazzaz and Wayne 1994). Increased light, soil moisture, and nutrient availability and creation of microsites for colonization associated with canopy disturbance promote understory succession, dependent on the inten-

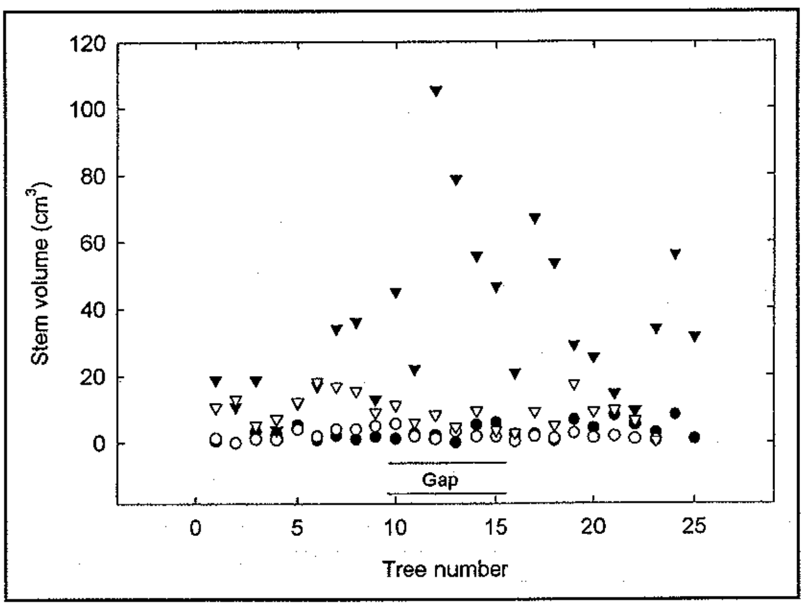

Fig. 3. Relationship of stem volume of white ash (circles) and white pine (triangles) seedlings with position along a planting row in plots thinned with the G1 (solid symbols) and SLT (open symbols) treatments. The approximate location and diameter of the canopy gap of the G1 plot relative to the planting row is noted. Planting rows were oriented in an east-west direction.

Table 4. Summary of the understory vegetation survey for the study area and neighbouring, older red pine plantation (CN2). The number of unique, exotic, and total species for three plant functional groups are presented by thinning treatment and plantation. Unique refers to species that only occur in plots of a given thinning treatment or a given plantation

		Thinning treatment						Plantation	
Species group	Class	CN	1R	SLT	2R	G1	G2	Study area	CN2
Woody	Unique	6	0	0	0	0	0	5	11
	Exotic	3	3	3	2	3	3	3	3
	Total	27	19	14	12	17	17	28	34
Herbaceous	Unique	6	0	3	0	0	0	18	31
	Exotic	22	15	14	11	19	19	25	24
	Total	39	35	30	25	38	38	51	63
Cryptogams	Unique	10	0	0	2	0	0	3	10
	Exotic	0	0	0	0	0	0	0	0
	Total	28	20	10	18	21	21	34	43
All species	Unique	22	0	3	2	0	0	26	52
	Exotic	25	18	17	13	22	22	28	27
	Total	94	74	54	55	78	76	113	140

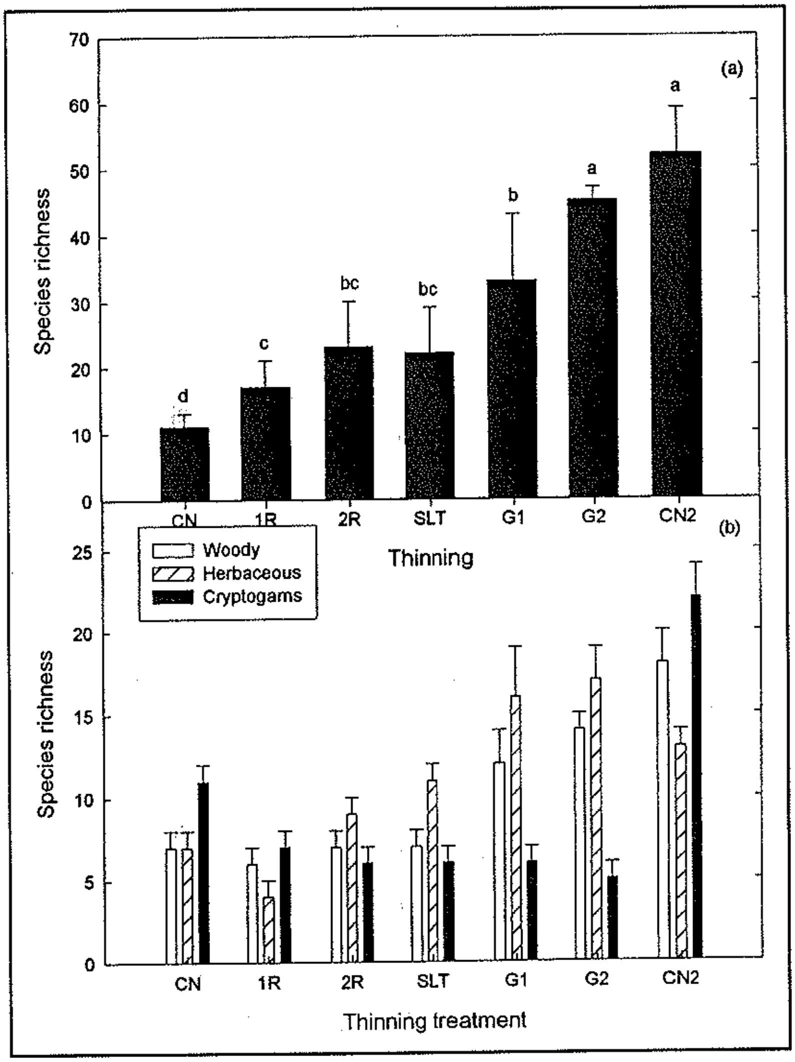

Fig. 4. Mean (± 1 SE) species richness for understory vegetation (a) and plant functional groups (b) five years after thinning. The 70-year-old plantation is identified as CN2. Vertical bars in (a) sharing the same letter are not significantly different based on a Kruskal-Wallis test ($p < 0.05$).

sity of disturbance (Connell 1989, Bazzaz and Wayne 1994, Coates and Burton 1997).

Thinning increased plot-averaged daily PPFD from ~7 to 18% sunlight and improved the growth of underplanted seedlings, but understory light levels were much lower than the 40% sunlight needed for maximum shoot growth of the planted species (Sander 1990, Schlesinger 1990, Wendel and Smith 1990). Only within the canopy gaps of the G1 and G2 treatments where daily

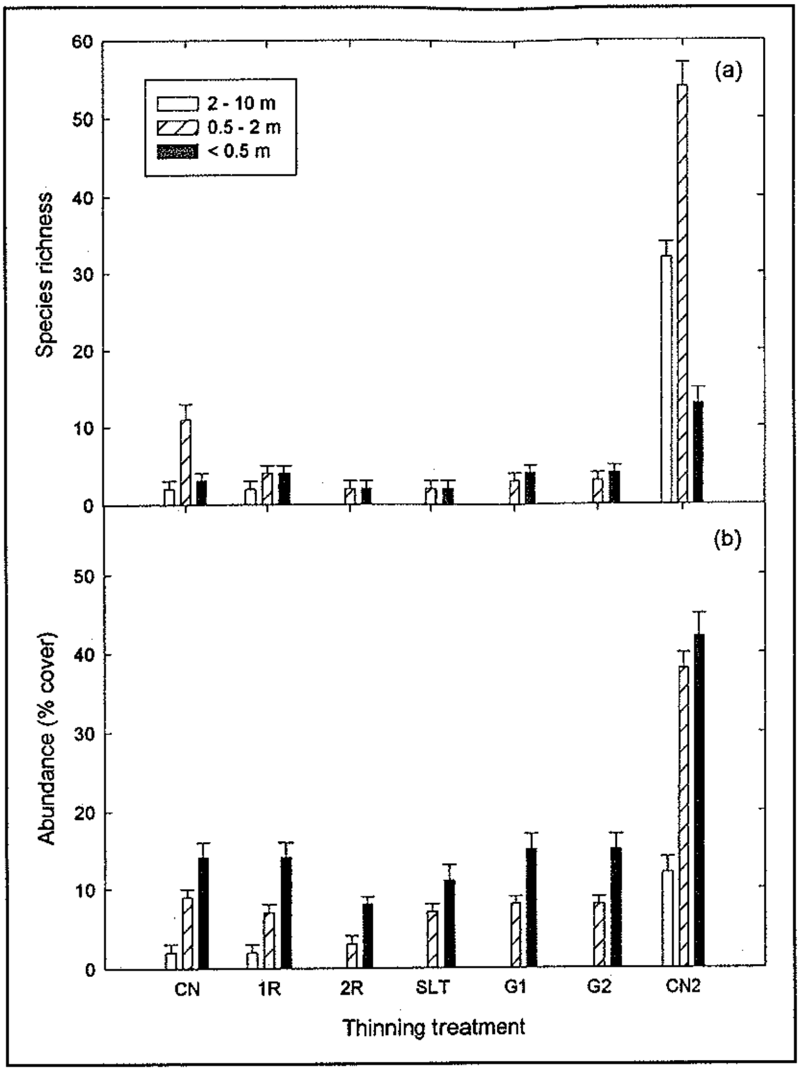

Fig. 5. Mean (± 1 SE) species richness (a) and abundance (b) for woody vegetation of three height classes. The 70-year-old plantation is identified as CN2.

PPFD was as high as 34%, or perhaps in localized microsites of other treatments, did thinning result in light levels high enough to support vigorous shoot growth. For example, seedling diameter and height were about 50% larger and volume four times larger in the 2R than the SLT treatment despite comparable residual basal areas (Fig. 2). This is likely because light availability increased more in the larger canopy openings of the 2R treatment (Canham *et al.* 1990, Bazzaz and Wayne 1994), and in the area immediately surrounding the gap (i.e., the "extended gap") (Canham *et al.* 1990, Tryon *et al.* 1992).

Averaged over all thinning treatments, the growth potential of underplanted white pine was somewhat higher than for white ash and red oak seedlings. Although white ash seedlings can survive in heavily shaded forest understory, shoot growth is greatly reduced (Schlesinger 1990). Red oak seedlings growing in resource-limited environments have an inherently slow shoot growth habit associated with the preferential allocation of carbohydrate to root systems (Dey and Parker 1996). The higher relative shoot growth performance of pine was also related to more frequent shoot dieback in the two hardwood species. As many as 8% of the ash and oak seedlings exhibited partial stem dieback each year, but this occurred in <2% of the pine.

Only slight growth differences were observed between direct seeded and planted oak. However, oak regeneration by seeding was substantially decreased by predation of acorns and young germinants. Partially consumed acorns and shell fragments were observed near many of the seeding spots at the end of the first growing season, suggesting small mammals were the primary source of this mortality. Better initial survival of seeded oak in the understory openings of the G2 plots is likely attributable to a more favourable environment for germination and early growth (Ashton and Larson 1996). Lack of protective overstory cover and higher exposure to predators in these openings may also have deterred herbivory (Webb and Willson 1985, Wright *et al.* 1998).

Understory vegetation

Thinning of conifer stands, including red pine, is often associated with increased diversity and abundance of understory flora (Dickmann *et al.* 1987, Bender *et al.* 1997, Thomas *et al.* 1999, Thysell and Carey 2000). In our study, understory species richness was positively related to thinning intensity and proximity to sources of seed, spores, etc., but frequency and abundance were low. Unfortunately, many of the 113 species found in the understory were exotic (25%) and/or invasive species common to the urban and agricultural landscapes of southern Ontario. These competitive species may displace or reduce populations of native species and significantly impede the conversion of conifer plantations to more natural forest conditions (Hobbs and Huenneke 1992, Bell and Newmaster 1998).

Thinning effects on understory species richness, percent cover, and frequency were attributable to harvesting disturbance of the forest floor, propagule availability, and, to a lesser extent, improved microenvironment for germination and establishment. Disturbance of the pine needle litter layer and exposure of mineral soil by logging activities was confined to small, localized areas. The availability of this substrate, the preferred seedbed of early and mid-successional tree species, was short-lived, being re-covered with litter within two or three years of thinning. The increased richness of woody and herbaceous species observed at higher thinning intensities was probably due in part to greater disturbance to the forest floor in the more heavily thinned plots. Localized increases in light, temperature, and precipitation beneath canopy openings may have encouraged germination and establishment on these substrates (Anderson *et al.* 1969, Peterson and Pickett 2000). Once established, however, the relatively low understory PPFD hindered the development of natural regeneration except in microsites located within small canopy openings.

The distance between the plantation and sources of propagules also limited colonization of the understory as indicated by the positive relationship between species richness and the number of edges of individual treatment plots. Migration of wind-dispersed tree species from neighbouring plant communities was probably confined to within 20–30 m of the parent tree (LePage *et al.* 2000). The relatively high frequency of *Prunus*, oak, *Cornus*, *Rhamnus*, and *Rubus* in the understory suggests that animals played an important role in the migration of woody species at our study site. Only natural regeneration of red pine was relatively abundant, due to seed from the overstory in large enough amounts to colonize mineral soil patches and to overcome the low receptivity of the litter layer (Ribbens *et al.* 1994, Reader *et al.* 1995).

Limited delivery of propagules, particularly by woodland herbs, to microsites of low receptivity greatly delayed understory colonization (i.e., low frequency and abundance) by desirable herbaceous species. Immigration of these species occurs infrequently due to their low reproductive output and poor adaptation for long-distance seed dispersal (Matlack 1994, Cain *et al.* 1998). Once established, these species exhibit gradual expansion and infill by clonal spread and seeds (Matlack 1994, Meier *et al.* 1995). These life history characteristics render these species susceptible to competition from exotic and ruderal species better adapted for aggressive colonization following disturbance.

Species richness of herbs, grasses, and sedges was higher at greater thinning intensities but lower diversity was evident in the older plantation. These species are favoured by the improved light and soil moisture conditions of canopy gaps, but they decrease in frequency with time after disturbance as woody species begin to dominate the understory (Anderson *et al.* 1969, Moore and Vankat 1986, Thomas *et al.* 1999). Conversely, cryptogam richness was higher in the sheltered understory microenvironments of the CN plots. Most of the plant species unique to this treatment were bryophytes. Many of these forest mesophytes are quite sensitive to drier, more exposed environments (Newmaster *et al.* 1998, Andersson and Hytteborn 1991), and decrease in abundance after relatively heavy thinning (Dickmann *et al.* 1987, Alaback and Hermann 1988). The older study plantation also had comparatively high cryptogam species richness, a common feature of later successional forest stands (Söderström 1988, Lesica *et al.* 1991, Newmaster *et al.* 1999). The greater microhabitat heterogeneity and moderate, humid understory microclimate of older stands are thought to favour the establishment of cryptogam species with slow growth, limited dispersal, and specialized substrate and microenvironmental needs (Pike *et al.* 1975, Rambo and Muir 1998).

Conclusions and Management Recommendations

Red pine plantations are well suited to even-aged, intensive forest management. Thinning of red pine plantations is commonly used to increase diameter and volume growth of selected crop trees, avoid mortality, and shorten the technical rotation (Lundgren 1981, Woods and Penner 2000). Future volume yields depend on the residual density, thinning method, thinning interval, and age at which the first thinning occurs (Lundgren 1981, Woods and Penner 2000). Many of these same factors have a strong influence on the diversity, abundance, and development of understory vegetation in red pine plantations (Rudolph *et al.* 1984, Dickmann *et al.* 1987, Bender *et al.* 1997). The results of our study suggest that "early" thinning of red pine plantations can help to produce high-value timber and enhance artificial and natural regeneration of native tree species.

Thinning red pine plantations to maintain a residual basal area of 25–30 m^2 ha^{-1} is recommended in Ontario and the Lake States for maximum volume production (Lundgren 1981, Rudolph *et al.* 1984, Smith and Woods 1997). However, where conversion is the primary objective and the merchantability of first removal is not a concern, thinning can be heavier and begin earlier, i.e., after crown closure. A residual basal area of 16–21 m^2 ha^{-1} may be a reasonable compromise between timber production and improved understory development (Dickmann *et al.* 1987, Bender *et al.* 1997). This objective can be achieved using a combination of underplanting and/or scarification, row removal, selection thinning, and canopy gap creation. Row removal is an appropriate method for initial thinning as it permits access for future thinning and accommodates selective removal of additional trees. Where windthrow is not a concern, double row removal and selection in the remaining three rows can be considered.

Alternatively, fourth row removal can be used in combination with selective thinning and canopy gap creation to promote succession and improve the quality of residual red pine. However, to reduce windthrow risk, no more than 25% of the remaining area should be placed in canopy gaps in the first thinning, and gaps should be linked to the cleared rows for access. Where possible, these openings should be located in areas where growth and condition of canopy trees is poor. Gap diameters of 50–100% of the height of the overstory are closer to the optimum size for canopy recruitment of mid-tolerant tree species (Hibbs 1982a,b; Coates 2000). Where gap thinning is preferred, desirable, mid-tolerant species mixtures can be planted with 1–2 m spacing, primarily within gaps for maximum growth. Natural regeneration can be encouraged by scarifying to expose mineral soil. Where nearby seed sources are limited, a combination of scarifying and underplanting may be needed to promote the establishment of desirable species.

Further thinning should occur when stand density approaches the mortality initiation line of density management diagrams (about every 10 years) (Smith and Woods 1997). This thinning should improve spacing and quality of the residual trees, while creating additional, larger canopy gaps to promote natural regeneration. After two to three thinnings, or when red pine has reached rotation age, management efforts should focus on removing valuable, mature individuals and releasing advance reproduction.

Management of conifer plantations should be tailored to promote non-timber values as well, particularly in heavily developed, fragmented landscapes with few woodlands remaining. Early thinning to a lower residual density than recommended for maximum volume production will promote understory succession of woody and herbaceous plant species, increase the floral diversity of the plantation, and improve the visual appearance of these spatially symmetric monocultures (Dickmann *et al.* 1997). Special efforts should be made to limit the ingress and growth of exotic species. Subsequent thinning should not remove all the remaining canopy trees for timber. Retention of large red pine trees at variable spacing will increase the structural complexity of stands, promote biodiversity, improve wildlife habitat, and create a more aesthetically pleasing forest setting for recreational and educational use (Hansen *et al.* 1991, Bender *et al.* 1997, Hayes *et al.* 1997).

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Appendix 1. Percent cover (%), frequency of occurrence (F), and species rarity ranking (SR) of understory vegetation by thinning treatment. SR: S1, extremely rare; S2, very rare; S3, uncommon; S4, common; S5, very common; SE, exotic (Newmaster *et al.* 1998)

	Thinning treatment														
	CN		1R		SLT		2R		G1		G2		CN2		
Species	%	F	%	F	%	F	%	F	%	F	%	F	%	F	SR
Trees > 10 m															
Pinus resinosa	75	1.00	65	1.00	65	1.00	75	1.00	65	1.00	60	1.00	75	1.00	S5
Acer rubrum													15	0.20	S5
Pinus strobus													10	0.20	S5
Trees < 10 m															
Pinus resinosa	<1	1.00	<1	1.00	<1	1.00	<1	1.00	<1	1.00	<1	1.00	2	1.00	S5
Populus grandidentata	2	0.25	<1	0.25	<1	0.13	<1	0.13	<1	0.31	<1	1.00	4	0.19	S5
Pinus strobus	<1	1.00	<1	1.00	<1	0.50	<1	1.00	<1	1.00	<1	1.00	2	0.50	S5
Quercus rubra	<1	1.00	<1	1.00	<1	1.00	<1	0.50	<1	1.00	<1	1.00	2	0.75	S5
Acer negundo	<1	0.50	<1	0.06	<1	0.06	<1	0.06	<1	0.13	<1	0.13	1	0.25	S5
Fraxinus americana	<1	0.50	<1	1.00	<1	0.50	<1	1.00	<1	0.94	<1	1.00	2	0.25	S5
Populus alba	<1	0.50	<1	0.06	<1	0.50	<1	0.06	<1	0.44			<1	0.06	SE
Abies balsamea	<1	0.13											2	0.19	S5
Acer rubrum	<1	0.13											2	0.50	S5
Acer saccharum	<1	0.06	<1	0.44	<1	0.50	<1	0.25	<1	0.31	<1	1.00	1	0.75	S5
Fagus grandifolia	<1	0.06							<1	0.50			2	0.50	S5
Picea glauca	<1	0.06											2	0.13	S5
Pinus banksiana			<1	0.38					<1	0.19	<1	1.00	2	0.50	S5
Populus tremuloides	<1	0.06	<1	0.44					<1	0.44	<1	1.00	2	0.25	S5
Prunus serotina	<1	0.06	<1	0.25			3	0.25	<1	0.38			1	0.50	S5

	Thinning treatment														
	CN		1R		SLT		2R		G1		G2		CN2		
	%	F	%	F	%	F	%	F	%	F	%	F	%	F	SR
Shrubs and vines															
Rhamnus cathartica	<1	0.50	<1	0.75	<1	0.75	<1	0.50	<1	0.50	<1	1.00	4	0.50	SE
Rubus idaeus	<1	0.50	1	0.56	<1	0.75			1	0.13	1	0.94	5	0.25	S5
Sambucus racemosa	<1	0.50	<1	0.56					<1	0.44	<1	1.00	2	0.31	S5
Lonicera hirsuta	<1	0.25													S5
Rhus radicans	<1	0.25											2	0.13	S5
Viburnum cassinoides	<1	0.25			<1	0.50									S5
Vitis riparia	<1	0.19	<1	0.94	<1	0.69			<1	0.38	<1	0.81			S5
Clematis virginiana	<1	0.06	<1	0.25					<1	0.13	<1	1.00			S5
Comptonia peregrina	<1	0.06			<1	0.06							<1	0.06	S5
Cornus alternifolia	<1	0.06	<1	0.06	<1	0.06	<1	0.06	<1	0.06	<1	0.06	1	0.25	S5
Corylus cornuta													2	0.25	S5
Cornus stolonifera													2	0.19	S5
Diervilla lonicera													1	0.25	S5
Epigaea repens													<1	0.44	S5
Linnea borealis													<1	0.13	S5
Lonicera canadensis													2	1.00	S5
Mitchella repens													<1	0.56	S5
Prunus pennsylvanica	<1	0.13	<1	0.56			<1	0.25	<1	0.31	<1	1.00	1	0.25	S5
Prunus virginiana	<1	0.06											1	0.75	S5
Rosa acicularis													<1	0.25	S5
Rubus alleghaniensis													4	0.25	S5
Sorbus americana	<1	0.06	<1	0.56					<1	0.31	<1	1.00			S5
Viburnum aceriform													<1	0.75	S5
Viburnum trilobum													<1	0.25	S5
Sedges and grasses															
Carex arctata			<1	0.25			<1	0.13	<1	0.38	<1	0.81	<1	0.63	S5
Carex communis	<1	0.06											<1	0.44	S5
Carex pedunculata													<1	0.13	S5
Carex sp.			<1	0.19			<1	0.13	<1	0.31	<1	0.63	<1	0.13	S5
Deschampsia flexuosa	<1	0.75	2	0.19	<1	0.69	2	0.06	2	0.25	2	0.88	2	0.13	S5
Danthonia spicata	<1	0.38	<1	0.25	<1	0.75	<1	0.06	<1	0.69	<1	0.75	<1	0.50	S5
Oryzopis asperifolia	<1	0.31	<1	0.19	<1	0.75	<1	0.06	<1	0.44	<1	1.00	1	0.31	S5
Deschampsia cespitosa	<1	0.25													S5
Agrostis gigantea	<1	0.06	<1	0.25	<1	0.06	<1	0.06	<1	0.06	<1	0.81	<1	0.25	SE
Bromus sp.	<1	0.06	<1	0.31	<1	0.06	<1	0.06	<1	0.44	<1	0.75	<1	0.13	
Agrostis scabra			<1	0.13	<1	0.44	<1	0.06	<1	0.44	<1	0.63	<1	0.31	S5
Brachyelytrum erectum													<1	0.13	S5
Cinna latifolia													<1	0.31	S5
Herbs															
Taraxacum officinale	<1	0.56	<1	0.19	<1	0.38	<1	0.13	<1	0.81	<1	0.75	<1	0.19	SE
Hypericum perforatum	<1	0.44	<1	0.25	<1	0.69	<1	0.06	<1	0.81	<1	0.63			SE
Trifolium hybridum	<1	0.38	<1	0.06	<1	0.31			<1	0.56	<1	0.31	<1	0.19	SE
Polygonatum pubescens	<1	0.31	<1	0.19			<1	0.06	<1	0.50	<1	0.50	<1	0.63	S5
Asclepias syriaca	<1	0.25	<1	0.25	<1	0.69	<1	0.06	<1	0.19	<1	0.38	<1	0.19	S5
Epilobium angustifolium	<1	0.25	<1	0.06	<1	0.75			<1	0.38	<1	0.19	<1	0.38	S5
Phlox paniculata	<1	0.25			<1	0.38			<1	0.38	<1	0.19			SE
Rumex acetosella	<1	0.25											<1	0.19	SE
Barbarea vulgaris	<1	0.19													SE
Cynanchum nigrum	<1	0.19	<1	0.25			<1	0.19	<1	0.44	<1	0.63			SE
Hieracium aurantiacum	<1	0.19													SE
Medicago lupulina	<1	0.19			<1	0.19			<1	0.38	<1	0.19	<1	0.13	SE
Silene vulgaris	<1	0.19			<1	0.31			<1	0.50	<1	0.31			SE
Solidago canadensis	<1	0.19	<1	0.25			<1	0.13	<1	0.25	<1	0.50			S5
Solidago sp.	<1	0.19	<1	0.44			<1	0.13	<1	0.50	<1	0.63			
Tragopogon pratensis	<1	0.19	<1	0.25	<1	0.06			<1	0.19	<1	0.44			SE
Verbascum thapsus	<1	0.19	<1	0.25			<1	0.13	<1	0.56	<1	0.69	<1	0.19	SE
Maianthemum canadense	<1	0.13	<1	0.19	<1	0.69	<1	0.44	<1	0.44	<1	0.56	3	0.25	S5
Pyrola elliptica	<1	0.13	<1	0.06	<1	0.13	<1	0.06	<1	0.19	<1	0.19	<1	0.38	S5
Solanum dulcamara	<1	0.13	1	0.13	1	0.06	1	0.06	1	0.31	1	0.50	1	0.19	SE
Solidago gigantea	<1	0.13													S5
Actaea pachypoda	<1	0.06	<1	0.44	<1	0.56					<1	0.06	<1	0.19	S5
Arctium minus	<1	0.06	<1	0.50	<1	0.50							<1	0.25	SE
Fragaria sp.	<1	0.06							<1	0.19	<1	0.13			
Leonurus cardiaca	<1	0.06													SE
Oenothera biennis	<1	0.06	<1	0.19					<1	0.25	<1	0.38	<1	0.19	S5
Phlox subulata	<1	0.06	<1	0.31			<1	0.06	<1	0.31	<1	0.56			SE
Urtica dioica	<1	0.06	<1	0.19			<1	0.06	<1	0.38	<1	0.31	<1	0.13	SE
Achillea millefolium													<1	0.13	S5

	Thinning treatment														
	CN		1R		SLT		2R		G1		G2		CN2		
	%	F	%	F	%	F	%	F	%	F	%	F	%	F	SR
Herbs (cont.)															
Actaea rubra													<1	0.19	S5
Amaranthus retroflexus													<1	0.25	SE
Anaphalus margaritacea													<1	0.19	S5
Anemone virginiana	<1	0.06	<1	0.25	<1	0.25									S5
Apocynum androsaemifolium													<1	0.13	S5
Aquilegia canadensis													<1	0.19	S5
Aralia nudicaulis													1	0.19	S5
Artemesia biennis													<1	0.19	SE
Capsella bursa-pastoris													<1	0.19	SE
Centaurea maculosa													<1	0.19	SE
Chenopodium album													<1	0.25	SE
Cirsium arvense	<1	0.06	<1	0.19	<1	0.44			<1	0.19	<1	0.75	<1	0.25	SE
Cirsium sp.			<1	0.25	<1	0.44							<1	0.06	
Clintonia borealis													<1	0.13	S5
Conyza canadensis													<1	0.19	S5
Cornus canadensis													<1	0.25	S5
Daucus carota	<1	0.06	<1	0.38			<1	0.06	<1	0.38	<1	0.38			SE
Echium vulgare									<1	0.19	<1	0.13			SE
Erigeron philadelphicus													<1	0.19	S5
Fragaria vesca													<1	0.19	S5
Fragaria virginiana					<1	0.50							<1	0.38	SE
Galium triflorum					<1	0.38							<1	0.25	S5
Geranium bicknelli													<1	0.19	S4
Heuchera americana													<1	0.19	S2
Hieracium praealtum	<1	0.06	<1	0.56	<1	0.25	<1	0.25	<1	0.19	<1	0.19	<1	0.13	SE
Matricaria matricarioides													<1	0.19	SE
Medicago sativa													<1	0.25	SE
Melilotus alba													<1	0.25	SE
Plantago major									<1	0.19	<1	0.19	<1	0.13	SE
Potentilla recta			<1	0.13	<1	0.19			<1	0.38	<1	0.31	<1	0.19	S5
Rudbeckia hirta			<1	0.25	<1	0.44	<1	0.13	<1	0.19	<1	0.50			S5
Sanicula marilandica													<1	0.19	S5
Sonchus arvensis													<1	0.19	SE
Stellaria media													<1	0.19	SE
Streptopus roseus													<1	0.50	S5
Tragopogon porrifolius													<1	0.19	SE
Trientalis borealis													2	0.63	S5
Veronica officinalis			<1	0.06	<1	0.44	<1	0.06	<1	0.13	<1	0.38	<1	0.25	SE
Viola sp.					<1	0.50									
Waldsteinia fragarioides													<1	0.06	S5
Pteridophytes															
Equisetum hyemale	<1	0.25	<1	0.19	<1	0.50	<1	0.19	<1	0.50	<1	0.63	<1	0.25	S5
Equisetum sylvaticum	<1	0.25	<1	0.13			<1	0.19	<1	0.38	<1	0.56	<1	0.13	S5
Athyrium filix-femina	<1	0.13	<1	0.31			<1	0.19	<1	0.44	<1	0.63	<1	0.13	S5
Dryopteris carthusiana	<1	0.13	<1	0.25			<1	0.13	<1	0.25	<1	0.50	1	0.63	S5
Dryopteris intermedia													<1	0.81	S5
Dryopteris marginalis													<1	0.63	S5
Onoclea sensibilis			<1	0.31			<1	0.19	<1	0.31	<1	0.44			S5
Pteridium aquilinum	<1	0.13	<1	0.19			<1	0.19	<1	0.25	<1	0.81	2	0.13	S5
Bryophytes															
Brachythecium salebrosum	<1	0.94	<1	0.31	<1	0.50	<1	0.25	<1	1.00	<1	1.00	<1	0.75	S5
Polytrichum commune	<1	0.50	<1	0.31					<1	0.75	<1	0.63	<1	0.50	S5
Ceratodon purpureus	<1	0.38	<1	0.19	<1	0.50	<1	0.06	<1	0.63	<1	0.81			S5
Pleurozium schreberi	<1	0.38	<1	0.25	<1	0.50	<1	0.06	<1	0.63	<1	0.69	2	0.19	S5
Pohlia nutans	<1	0.25							<1	0.31	<1	0.25	<1	0.63	S5
Plagiothecium laetum	<1	0.19											<1	0.19	S5
Polytrichum juniperinum	<1	0.19	<1	0.13					<1	0.56	<1	0.63	<1	0.50	S5
Brachythecium oedipodium	<1	0.06	<1	0.38			<1	0.38	<1	0.81	<1	0.94	<1	0.56	S5
Brachythecium reflexum	<1	0.06											<1	0.56	S4
Callicladium haldanianum	<1	0.06	<1	0.19					<1	0.81	<1	0.63	<1	0.69	S5
Climacium dendroides	<1	0.06											<1	0.19	S5
Dicranum flagellare	<1	0.06											<1	0.56	S5
Dicranum fuscescens	<1	0.06											<1	0.31	S5
Dicranum montanum	<1	0.06											<1	0.69	S5
Dicranum polysetum	<1	0.06			<1	0.50							4	0.13	S5
Dicranum scoparium	<1	0.06					<1	0.44					<1	0.19	S5
Euryhchium pulchellum	<1	0.06											<1	0.31	S5
Hedwigia ciliata							<1	0.06							S5

	Thinning treatment														
	CN		1R		SLT		2R		G1		G2		CN2		
	%	F	%	F	%	F	%	F	%	F	%	F	%	F	SR
Bryophytes (cont.)															
Hyclomium splendens	<1	0.06											<1	0.06	S5
Hypnum pallescens							<1	0.31					<1	0.31	S4
Leucobryum glaucum													<1	0.13	S5
Mnium spinulosum													<1	0.63	S5
Plagiomnium medium	<1	0.06											<1	0.19	S5
Polytrichum formosum													<1	0.13	S3
Ptilidium ciliare													<1	0.13	S5
Ptilium crista-castrensis													<1	0.50	S5
Ptilidium pulcherrimum			<1	0.19	<1	0.06			<1	0.56	<1	0.56	<1	0.94	S5
Rhytidiadelphus triquetrus			<1	0.19	<1	0.31	<1	0.06	<1	0.50	<1	0.56	<1	0.25	S5
Sanionia uncinata			<1	0.06	<1	0.50			<1	0.63	<1	0.63	<1	0.69	S5
Tetraphis pellucida			<1	0.19	<1	0.06	<1	0.06	<1	0.38	<1	0.63	<1	0.50	S5
Thuidium delicatulum			<1	0.19	<1	0.06	<1	0.06	<1	0.50	<1	0.88	<1	0.13	S5
Lichens															
Cladonia coniocraea	<1	0.06	<1	0.13			<1	0.13	<1	0.50	<1	0.75	<1	0.81	S5
Cladonia cristatella	<1	0.06											<1	0.31	S5
Peltigera canina	<1	0.06											<1	0.19	S5
Hypogymnia physodes													<1	0.13	S5
Parmelia sulcata													<1	0.13	S5
Icmadophila sp.													<1	0.06	S4