



Effects of retention harvests on structure of old-growth *Pinus strobus* L. stands in Ontario

D.P. Bebber^{a,1,*}, W.G. Cole^{b,2}, S.C. Thomas^{a,1}, D. Balsillie^{a,1}, P. Duinker^{c,3}

^aFaculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, Ont., Canada

^bOntario Forest Research Institute, 1235 Queen St. East, Sault Ste. Marie, Ont., Canada P6A E5

^cSchool for Resource and Environmental Studies, Dalhousie University, 1312 Robie St., Halifax, NS, Canada B3H 3J5

Received 12 June 2003; received in revised form 29 September 2004; accepted 12 October 2004

Abstract

Retention of structural elements, or legacies, of old-growth stands at harvest has been proposed as a means of maintaining wildlife habitat and ecosystem function in managed forests. However, little is known of the effects and consequences of such practices on the residual stand. A “structural retention harvest” of old-growth eastern white pine *Pinus strobus* L. was carried out in 1992 in the Algoma Forest of Central Ontario, Canada. In contrast to then-current guidelines, declining- and cavity-trees, snags and coarse woody debris (cwd) were retained at harvest. Cut and uncut stands were surveyed in 2001 to determine the effects of this harvest on forest structure. Basal area prism sweeps for trees and snags were taken at 100 m spacing in 12 logged and six unlogged stands in August 2001. Ground cover, regeneration, and cwd were recorded. White pine basal area before harvest varied among stands from 4.5 to 25.7 m² ha⁻¹, or 21–68% of stand total. No white pine trees below 18 cm dbh were found. Around half of white pine basal area was removed at harvest. Logging damage was found on 7% of residual white pines. Harvested stands had similar numbers of cavity trees, standing snags, and volume of natural-origin cwd, to unharvested stands. Inputs of logged white pines left in situ increased the total volume of cwd in harvested stands compared with unharvested stands. Harvested stands also contained more recently dead pines and tip-over trees than unharvested stands. White pine regeneration was scarce, though marginally greater in cut stands. Regeneration was correlated with increased canopy openness in cut stands. Herbaceous cover and sapling density was greater in harvested stands. The study shows that structural retention harvesting can maintain or exceed levels of habitat provision such as cavity trees and cwd, found in old stands, though increased tree mortality and wind-throw can result.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Variable retention; Legacy retention; Biological legacies; Stand structure; Snags; Coarse woody debris

* Corresponding author. Present address: Department of Plant Sciences, Oxford Forestry Institute, University of Oxford, South Parks Road, Oxford OX1 3RB, UK. Tel.: +44 1865 275000; fax: +44 1865 275074.

E-mail addresses: dan.bebber@plants.ox.ac.uk (D.P. Bebber), bill.cole@mnr.gov.on.ca (W.G. Cole), sc.thomas@utoronto.ca (S.C. Thomas), david.balsillie@utoronto.ca (D. Balsillie), pduinker@is.dal.ca (P. Duinker).

¹ Tel.: +1 416 978 1044; fax: +1 416 978 3834.

² Tel.: +1 705 946 2981; fax: +1 705 946 2030.

³ Tel.: +1 902 494 7100; fax: +1 902 494 3728.

1. Introduction

Though disturbance and succession are ubiquitous in forests, anthropogenic disturbances can differ substantially from natural ones. For example, clear-cutting, stand improvement cuts and slash burning tend to simplify habitat, while natural disturbances such as fire and storms leave heterogeneous patches of late-successional forest, standing trees, snags, and coarse woody debris (cwd) (Lindenmayer and McCarthy, 2002). These legacies of the original stand are utilized by a wide variety of forest-dwelling species and play an important role in ecosystem processes such as nutrient cycling, soil protection, and regeneration (Harmon et al., 1986; Hansen et al., 1991; Perry and Amaranthus, 1997; Spies, 1997, 1998).

Recognition of the importance of structural complexity has led to modification of silvicultural systems to mimic natural disturbance by retention of elements of the original stand at harvest (Franklin et al., 1997). To date, few data are available regarding the outcomes and consequences of these modified silvicultural practices. Such questions are now being addressed by studies such as the Demonstration of Ecosystem Management Options (DEMO) in old-growth Douglas-fir (*Pseudotsuga menziesii* Mirb.) in Oregon and Washington (Halpern et al., 1999), and the Montane Alternative Silvicultural Systems (MASS) in old-growth montane forests on Vancouver Island, British Columbia (Arnott and Beese, 1997).

Silvicultural guidelines for eastern white pine (*P. strobus* L.) in Ontario incorporate structural retention within the stand, and a diversity of habitat types across the landscape (OMNR, 1998, 2001). However, these guidelines are primarily based on knowledge of species habitat requirements obtained in forests outside Ontario with structures and compositions different from those in the guidelines (e.g. Bull and Meslow, 1977; Chapman and Feldhammer, 1982; Parker et al., 1983; Rogers, 1987), and there remains a lack of empirical appraisal of structural retention in white pine forests.

This study describes medium-term (9 years after harvest) effects of a structural retention harvest on trees, snags, cwd, and regeneration in a replicated set of control and harvested old-growth white pine stands in the Algoma Forest, Ontario, Canada. Conducted in

1992, this harvest represents an early attempt at the maintenance of structural complexity at harvest via the retention of old-growth legacies. The study addressed the questions: (a) did structural components differ between harvested and unharvested stands after harvest? (b) Did harvesting affect tree regeneration? (c) Did harvesting affect residual tree growth and survival? Question (c) has been addressed in Bebbler et al. (2004).

2. Study site

The study was conducted in the vicinity of Galloway Lake in the Algoma Forest of Central Ontario, 83°55'W–47°13'N. The topography is undulating, ranging from 450 to 600 m a.s.l., and the area contains many small lakes. Soils are variable in quality and depth, ranging from moist peaty bogs on sandy depressions to thin discontinuous organic mats on rocky outcrops. The parent material is granite of the Canadian Shield. White pine stands occur mainly on fresh, very fine silty and loamy sands. The forest is situated at the Boreal-Great Lakes St. Lawrence transition zone, with variable stand composition, size and age. Boreal species found include black spruce (*Picea mariana* (Mill.) BSP), white spruce (*P. glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and white birch (*B. papyrifera* Marsh). The Great Lakes St. Lawrence region is represented by sugar maple (*Acer saccharum* Marsh), red maple (*A. rubrum* L.), eastern white pine *P. strobus* (referred to as white pine from hereon), red pine (*P. resinosa* Ait.), eastern white cedar (*Thuja occidentalis* L.), and yellow birch (*B. alleghaniensis* Britt).

3. Harvest methodology

Harvesting of old-growth white pine stands was carried out in 1992. The aim of the harvest was to maintain selected old-growth forest characteristics such as structural and age diversity. Residual trees were to be a mix of healthy seed bearers and declining quality trees that would provide cavities, snags, and eventually cwd. This differed substantially from existing guidelines, which required that only "...good quality dominant and co-dominant white pine be

retained, . . .” (Chapeskie et al., 1989). As many large snags were to be retained as possible, with some limitations imposed by health and safety regulations (Ontario Occupational Health and Safety Act, 1990). Damage to residual pines, snags, den trees and stick nests was to be avoided. The number of roads, trails and landings was to be kept to a minimum.

4. Methods

A survey of six unharvested control stands and 12 harvested stands was conducted during August and September 2001. Stands that contained, or had contained prior to harvesting, high densities of mature white pine were selected using Ontario Forest Resource Inventory (FRI) maps. Harvested and control stands were interspersed over an area of approximately 1200 ha. Although treatments were not randomly assigned to stands, our data show that white pine basal area and total basal area were similar in both stand types prior to harvest (Table 1).

Sample points were placed within stand boundaries at the intersections of a 100 m × 100 m grid overlaid on FRI maps. Stand areas varied from 3 to 104 ha (mean 25.8 ± 7.0 ha S.E.), and the number of sample points varied with stand size. In total, 55 sample points were placed within control stands (range 3–20 points per stand), and 89 sample points within harvested

stands (range 3–14 points per stand). Sample point coordinates were entered into Garmin 12XL handheld GPS units (Garmin Corporation, Olathe, Kansas, USA) prior to sampling to allow accurate location of points in the field.

At each sample point, a prism sweep was conducted using a basal area factor (BAF) 2 m² ha⁻¹ prism for live trees and standing dead trees (snags) ≥ 10 cm diameter at breast height (dbh). Distances r from plot centre to trees and snags that were difficult to see or borderline for inclusion were measured using Forest Pro handheld laser units and reflectors (Laser Technology Inc., Englewood, Colorado, USA). Angle (in radians) subtended by the dbh from plot centre was calculated as dbh/r (Philip, 1994). If this angle was greater than the BAF prism critical angle θ , the tree or snag was included in the sample.

Species, dbh, crown class, condition, size and origin (excavated by animals or formed by decay) of cavities, and logging damage were recorded for sampled live trees. Crown class was recorded on a five-point scale referring to the position of the crown relative to surrounding trees: emergent, dominant, co-dominant, intermediate, and suppressed. Tree condition was recorded using the two-class system of Acceptable Growing Stock (AGS) or Unacceptable Growing Stock (UGS) to define silvicultural quality (Anderson and Rice, 1993). If trees were classified as UGS, the reason for this, e.g. poor form, forking, crown dieback, or fungal infection, was noted. Presence of cavities did not influence this classification, since cavities were recorded separately. Cavities were classified as small (diameter < 5 cm), medium (diameter 5–10 cm) or large (diameter > 10 cm), the largest dimension being used for non-circular cavities.

Species, dbh, decay class and presence of cavities were recorded for sampled snags. Snag class was recorded on a five-point scale (Carleton and Arnup, 1993): (1) tree recently dead, top intact, most fine branches present, bark intact; (2) top intact, most fine branches missing, more than half of coarse branches remain, bark loosening; (3) top intact, less than half of coarse branches remain, bark may be missing; (4) top broken, no coarse branches, bark may be missing, at least 6 m tall; (5) stub, repeatedly broken, bark likely missing, less than 6 m tall.

Table 1
Original stand basal area (mean of stand means ± S.E., m² ha⁻¹)

Species	Control	Harvested	<i>P</i>	<i>N</i>
White pine	16.5 ± 1.7	13.4 ± 0.9	0.32	1053
Red pine	1.4 ± 0.5	0.0 ± 0.0	0.99	38
White cedar	2.0 ± 0.5	3.6 ± 0.6	0.17	211
Sugar maple	0.8 ± 0.3	3.8 ± 0.7	0.01	191
Red maple	1.5 ± 0.3	1.5 ± 0.3	0.88	112
Yellow birch	0.4 ± 0.2	0.7 ± 0.2	0.80	42
White birch	3.5 ± 0.5	1.7 ± 0.3	0.14	177
Balsam fir	3.6 ± 0.5	1.9 ± 0.4	0.02	185
White spruce	0.9 ± 0.2	0.6 ± 0.1	0.18	51
Black spruce	0.4 ± 0.2	0.0 ± 0.0	0.04	11
Other hardwoods	0.1 ± 0.1	0.1 ± 0.1	0.99	9
Total	31.1 ± 1.6	27.4 ± 1.1	0.19	2080

Original harvested stand composition was reconstructed from stump diameters; tree dbh ≥ 10 cm; *P* = significance of Generalized Linear Mixed Model for effect of stand treatment on basal area, with error d.f. = 16; *N* = total number of trees sampled.

Stumps were sampled by measuring diameter and distance to plot centre. Estimated dbh of harvested trees was calculated using Eq. (1) ($r^2 = 0.97$, $P < 0.0001$) while in the field. Eq. (1) had been determined from measurements of stump diameter u and dbh of 432 white pines (unpublished data). If the angle subtended by reconstructed dbh from plot centre was greater than θ , the stump was included in the sample, i.e. it was assumed that the tree of which the stump remained would have been counted in a prism sweep. In this way, the pre-harvest composition of harvested stands could be estimated. Species and origin (cut or natural) was recorded for each sampled stump.

$$\text{dbh} = -2.68 + 0.92u \quad (1)$$

Cwd (≥ 10 cm diameter at the mid-point of the length) was sampled using Diameter Relascope Sampling (Bebber and Thomas, 2003) with a BAF 2 prism. In Diameter Relascope Sampling, pieces of cwd are included in a sample, if the angle subtended by the mid-point diameter from plot centre exceeds the critical relascope angle (Bebber and Thomas, 2003). Species, length, origin (logged or natural), and decay class were recorded. Decay classes (adapted from Carleton and Arnup, 1993) were: (1) recently dead, bark intact, twigs and branches present, wood solid; (2) more than half of bark present, twigs absent, branches present, wood solid; (3) less than half of bark present, branches absent, wood mostly solid; (4) no bark, wood mostly decayed and soft; (5) extremely decayed, collapsed, sinking into soil. Cwd, which had decayed to such an extent that less than half of the cross-section remained above ground, were not recorded.

The species and number of saplings greater than 1.3 m in height and less than 10 cm dbh were recorded in a 5 m radius plot around plot centre, as were percentage ground cover of fine woody debris, moss, and herbaceous vegetation. White pine seedlings were defined as plants less than 1.3 m in height. Seedlings were counted and aged by counting internodes of the stem.

Data on white pine regeneration, canopy openness, and ground cover were collected in four logged and four unlogged stands. A grid of sample points, separated by 10 m intervals, was set up. Grids were 20 m \times 240 m, giving 75 points per plot. One sample

grid was enumerated in each stand, though one of the unlogged stands contained three grids in different areas. Grids were placed 50 m into the stand from the point of access, and oriented to fit within the stand boundaries. At each point, the age of all white pine seedlings within a 2 m radius was noted, along with percentage vegetation cover below 1.3 m height. Canopy openness above 1.3 m was assigned on a seven-point scale at each sampling point (adapted from Clark and Clark, 1992): (0) no sky visible; (1) some sky visible below 45°; (2) <10% of sky visible above 45° of zenith, no overhead openings; (3) >10% of sky visible above 45° of zenith, no overhead openings; (4) >50% of sky visible above 45° of zenith, no overhead openings; (5) <50% of sky visible above 45° of zenith, sky visible overhead; (6) >50% of sky visible above 45° of zenith, sky visible overhead.

5. Analysis

The theory behind prism or relascope sampling is discussed in forest mensuration texts (e.g. Philip, 1994). Because a BAF 2 m² ha⁻¹ prism was used to sample trees, snags and (effectively) stumps, each sampled tree, etc. contributed 2 m² ha⁻¹ to the basal area at the sample point. Sampled trees, etc. also represented a certain frequency f ha⁻¹ at the sample point (Eq. (2)):

$$f = \frac{10^4 \theta^2}{\pi d^2} = \frac{4g}{\pi d^2} \quad (2)$$

where 10^4 represents 1 ha, θ is the critical prism angle in radians, g is the basal area factor of the prism in m² ha⁻¹, and d is the stem diameter at breast height in meters. Because this would lead to an inflated sample size for statistical analyses based on frequency, prior to analysis, the estimated frequencies were scaled by the number of trees or snags actually measured.

Cwd was treated as a cylinder with mean diameter d , the diameter at the middle of each piece (Bebber and Thomas, 2003). Sighting of the prism to d thus meant that sampled logs contributed the basal area factor times their length to the volume of dead woody debris per hectare (Huber's equation in Philip, 1994). Huber's equation gives good estimates of log volume in water-displacement tests (Martin, 1984; Figueiredo Filho et al., 2000).

Statistical analyses were conducted using R 1.9.1 (R Core Development Team, 2004). In the experimental design, several measurements were made in each stand, but inference was made at the stand level. For this reason, Generalized Linear Mixed Models (GLMMs) were used to compare control and harvested stands (Venables and Ripley, 2002). Fixed effects were stand treatment, and random effects were individual stands giving 16 error degrees of freedom (d.f.). The GLMM procedure employed allows a number of error distributions to be specified. In most cases, the data were over-dispersed, and a quasi-Poisson error distribution was specified that models over-dispersion. Binary data were modelled with binomial errors, and normally distributed data with Gaussian errors. Proportion data were arcsine transformed to reduce the dependence of the variance on the mean. Some analyses such as the relationship between snag and live-tree density, were conducted on stand means. Data for individual trees or snags were analysed using GLMMs with random intercepts for sample points within stands, weighted for the estimated frequency per hectare of each tree.

Spatial autocorrelation in errors was specified for GLMM analyses of white pine regeneration data. Empirical semivariograms (Isaaks and Srivastava, 1989) for residuals of an initial GLMM fit were calculated and modelled with the *geoR* package for R 1.9.1 (Ribeiro and Diggle, 2001). The error structure model was then specified in the updated GLMM.

6. Results

6.1. Stand composition

Stands consisted of a supercanopy of white pine (around 30 m height) over a mixed conifer–hardwood canopy (around 15 m height). White pine comprised the greatest proportion of total basal area, varying from 37 ± 8 to $80 \pm 7\%$ among stands (mean $50 \pm 2\%$). Basal area of white pine in control stands was similar to estimated pre-harvest basal area in harvested stands (Table 1). All species except white pine followed an ‘reverse-*J*’ diameter distribution. White pine had a unimodal distribution with mean dbh 54.9 ± 0.6 cm S.E. in harvested stands and 55.5 ± 0.7 cm S.E. in control stands. Minimum

diameter for sampled white pines ≥ 10 cm dbh was 18.0 cm.

6.2. Effects of harvesting on stand composition and structure

White pine frequency was reduced from 52.4 ± 4.5 to 28.3 ± 3.5 ha⁻¹ (mean of stand means \pm S.E.) in harvested stands, based on reconstructed frequencies of white pine from their stumps. As a rough estimate assuming a uniform distribution of trees, this is equivalent to an increase in tree-to-tree spacing from around 10 to 14 m. Around half of white pine basal area was removed (mean of stand means $52 \pm 4\%$), again based on reconstructed basal areas of harvested trees from their stumps. The canopy of harvested stands was more open than that of control stands, such that 46.7% of sample points were beneath open canopy in harvested stands versus 15.5% in control stands (GLMM, $P = 0.020$).

6.3. Tree quality

The proportion of residual white pines in acceptable (AGS) condition was slightly, but not significantly, lower in harvested stands (Table 2). Common reasons for designating white pines as unacceptable (UGS) were forking (31% of UGS white pines), crown dieback or dead tops (31%), and poor growth form (19%). The quality of other species varied considerably. Coniferous species had high proportions of AGS trees, e.g. balsam fir (84%), white spruce (90%), and red pine (95%), whilst broadleaved species were of poorer quality, e.g. sugar maple (32%), red maple (22%), white birch (33%), and yellow birch (38%). The lower quality of hardwoods was largely attributable to poor growth form. Logging damage was found on 7% of white pines and 6% of other species.

6.4. Snags

The distribution of snags was highly skewed. Balsam fir snags were most common (27% of the total), white pine, white birch, and balsam fir made up the largest proportion of snag basal area (around 20% each). The density of snags was correlated with the density of live trees for all species (GLMM, $P < 0.01$) except black spruce for which too few data were

Table 2
Comparisons between control and post-harvest stands (mean of stand means \pm S.E.)

Measure	Species	Control	Harvested	<i>P</i>
Basal area (m ² ha ⁻¹)	White pine	16.5 \pm 1.7	6.9 \pm 0.7	<0.01
–	Other conifers	8.3 \pm 0.9	6.0 \pm 0.7	0.10
–	Hardwoods	6.3 \pm 0.7	7.7 \pm 0.8	0.72
–	Total	31.1 \pm 1.6	20.5 \pm 1.1	<0.01
Trees (ha ⁻¹)	White pine	63.1 \pm 8.7	28.3 \pm 3.6	<0.01
Cavity trees (ha ⁻¹)	White pine	4.2 \pm 0.8	2.0 \pm 0.5	0.04
–	Other conifers	4.7 \pm 2.9	2.6 \pm 1.1	0.64
–	Hardwoods	13.9 \pm 5.3	8.8 \pm 2.0	0.94
–	Total	22.7 \pm 6.1	13.4 \pm 2.3	0.19
Snags (ha ⁻¹)	White pine	11.4 \pm 2.1	13.9 \pm 3.1	0.68
–	Other conifers	31.0 \pm 8.0	19.9 \pm 6.2	0.16
–	Hardwoods	17.4 \pm 4.6	29.2 \pm 5.6	0.14
–	Total	59.8 \pm 9.5	62.9 \pm 8.5	0.84
Snag basal area (m ² ha ⁻¹)	Total	4.1 \pm 0.4	4.3 \pm 0.4	0.50
AGS trees (%)	White pine	79.1 \pm 5.2	73.0 \pm 6.3	0.64
Cwd, natural (m ³ ha ⁻¹)	White pine	25.9 \pm 5.4	12.4 \pm 2.4	0.06
–	Other species	14.9 \pm 2.7	22.3 \pm 2.5	0.15
–	Total	40.8 \pm 6.2	34.6 \pm 3.6	0.70
Cwd, cull (m ³ ha ⁻¹)	White pine	0	20.9 \pm 3.6	–
–	Other	0	3.0 \pm 0.9	–
–	Total	0	24.0 \pm 3.8	–
Cwd (m ³ ha ⁻¹)	White pine	24.8 \pm 5.4	33.3 \pm 4.0	0.05
–	Other	16.0 \pm 2.7	25.3 \pm 2.6	0.05
–	Total	40.8 \pm 6.2	58.6 \pm 4.5	0.01
Fine woody debris cover (%)	–	12.2 \pm 1.5	13.9 \pm 1.6	0.71
Herbaceous cover (%)	–	26.7 \pm 3.0	42.5 \pm 2.7	<0.01
Saplings (ha ⁻¹)	White pine	30.9 \pm 14.0	64.4 \pm 35.1	0.84
–	Total	4317 \pm 508	5258 \pm 380	0.08
Seedlings (ha ⁻¹)	White pine	395 \pm 94	574 \pm 85	0.10

P = significance of Generalized Linear Mixed Model for effect of stand treatment, with error d.f. = 16.

collected. Total snag frequency, and white pine snag frequency alone, did not differ significantly between control and harvested stands (Table 2).

The proportion of snags in different classes was used to indicate the recruitment history of snags. Snag decay class distribution differed between stand treatments (GLMM, treatment–class interaction, *P* = 0.017). Snag density increased with decay class in control stands but there was a greater proportion of relatively recent (class 2) snags in harvested stands (Fig. 1).

6.5. Cavities

Cavities were more common in snags than in living trees (GLMM, *P* < 0.001). For example, 15 \pm 2% of white pine trees contained cavities versus 69 \pm 5% of white pine snags. The chance of a tree or snag having a cavity increased significantly with diameter (GLMM, *P* = 0.026). White pine snags had the highest incidence of cavities (69 \pm 5% versus 22 \pm 4% in other species combined). More white pines with cavities were found in control stands,

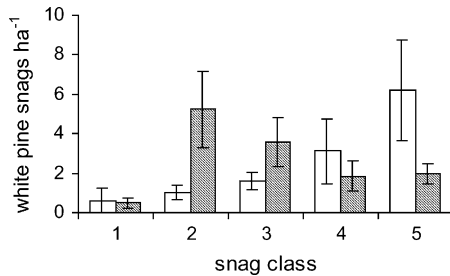


Fig. 1. White pine snag frequency per hectare per snag class for harvested (shaded bars) and control (open bars) stands, mean \pm S.E. Shaded bars are harvested stands, open bars control stands.

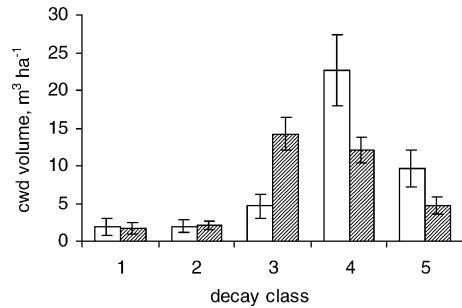


Fig. 2. Volume of natural-origin cwd by decay class for harvested (shaded bars) and control (open bars) stands, $m^3 ha^{-1}$, mean \pm S.E.

though the statistical significance of this difference was marginal (Table 2), and the percentage of white pine trees with cavities was similar between stand types ($10.8 \pm 2.1\%$ in control stands and $12.3 \pm 2.3\%$ in harvested stands, mean of stand means \pm S.E.). The percentage of trees with cavities that had been excavated by animals (as opposed to having been formed by decay processes) was greater in white pine than in other species combined (68.0% versus 9.8%, GLMM, $P < 0.001$). There was no significant difference for snags with cavities (86.5% excavated for white pine snags versus 70.9% for other species, GLMM, $P = 0.61$).

6.6. Woody debris

The distribution of cwd was skewed, with none being sampled in one-quarter of the sample points. The total volume of cwd was significantly larger in harvested stands (Table 2). This was due to cut trees that were unsuitable for timber being left on site, since there was no significant difference in the volume of natural (i.e. uncut) cwd between control and harvested stands, for white pine, other species, or in total (Table 2). The majority (59.6%) of white pine cull volume remained in sound condition (decay classes 1–3). In contrast, only 21.6% of naturally occurring white pine cwd volume was in sound condition.

6.7. Wind-throw

Of the 274 pieces of natural-origin cwd measured in the study (174 in logged stands, 100 in unlogged), 19 were whole trees that had fallen over, so exposing the root plate, rather than being pieces that had

snapped off a standing tree or snag. All of these were found in logged stands, and the difference between stand treatments was significant (log-likelihood ratio test, $P < 0.001$). Too few fallen trees were sampled to relate wind-throw to topographic or environmental factors, though there seemed to be evidence of a species effect in that seven of the trees were white cedar, and six white pine.

Since there was a possibility that wind-throw had been manifested in snapping as well as tipping of trees, the volume of natural-origin cwd in logged and unlogged stands was compared to determine differences in decay class distribution, as had been done for snags (Fig. 2). This revealed a similar pattern to that found in the snags, i.e. a relative increase in the proportion of newer (class 3) cwd in the logged stands compared with the unlogged stands (GLMM, treatment–class interaction, $P = 0.001$).

There was no significant difference in fine woody debris cover between control and harvested stands (Table 2).

6.8. Understorey vegetation

Herbaceous vegetation ground cover was significantly greater in harvested stands (Table 3). Raspberry (*Rubus idaeus* L.) was particularly abundant in harvested stands.

Altogether 25 species of saplings were identified in the sample plots. Several canopy tree species had greater sapling densities in the logged stands (Table 3), the exceptions being balsam fir (lower density in logged stands), white pine (no significant difference), and spruce species (no significant difference). Sapling density was positively correlated with basal area for

Table 3
Understorey vegetation cover in control and post-harvest stands
(mean of stand means \pm S.E.)

	Unlogged	Logged	<i>P</i>
Herbaceous vegetation cover (%)	26.4 \pm 6.0	40.3 \pm 3.9	0.03
Moss cover (%)	12.4 \pm 4.0	5.9 \pm 1.2	0.26
Total sapling density (ha ⁻¹)	4178 \pm 551	5109 \pm 708	0.08
Beaked hazel (<i>Corylus cornuta</i> Marsh.)	1822 \pm 679	1233 \pm 282	0.99
Mountain maple (<i>Acer spicatum</i> Lamb.)	506 \pm 201	763 \pm 215	0.39
Balsam fir	724 \pm 175	479 \pm 68	<0.01
Red maple	377 \pm 142	520 \pm 103	0.02
Sugar maple	135 \pm 85	490 \pm 147	<0.01
White birch	174 \pm 81	442 \pm 92	0.01
Mountain ash (<i>Sorbus americana</i> Marsh.)	144 \pm 43	215 \pm 50	0.49
Pin cherry (<i>Prunus pensylvanica</i> L. f.)	53 \pm 41	321 \pm 102	<0.01
Yellow birch	34 \pm 27	164 \pm 60	<0.01
White cedar	8 \pm 7	106 \pm 44	0.07
Other species	200 \pm 82	375 \pm 83	0.03

Sapling densities for the ten most abundant species are given individually, and the other species are lumped together. *P* = significance of Generalized Linear Mixed Model for effect of stand treatment, with error d.f. = 16.

most species (GLMM, *P* < 0.05), the exceptions being white pine and white birch (GLMM, *P* > 0.40).

6.9. Effect of harvesting on white pine regeneration

White pine regeneration sampled in the main survey was scarce in both logged and unlogged stands, though slightly more seedlings were found in logged stands (Table 2). The greatest difference in density was in seedlings aged between 4 and 8 years, i.e. 1–5 years post-harvest (Fig. 3). There was no relationship between regeneration and tree basal area, stump basal area, sapling density, vegetation cover, moss cover, or topographic variables (GLMM, *P* > 0.05).

In the regeneration survey, white pine regeneration distribution was highly skewed and was converted to presence/absence data prior to analysis. A GLMM was fit with binomial errors, with vegetation cover, canopy cover, and stand treatment as predictors. A spherical spatial autocorrelation structure was fitted to the empirical semivariogram of the GLMM residuals using

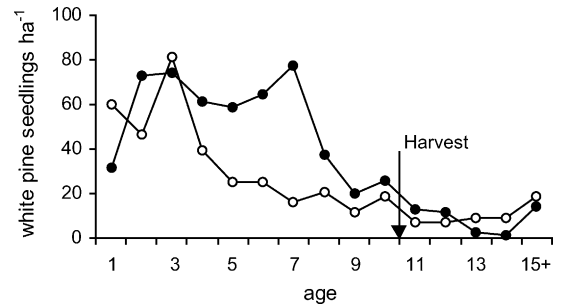


Fig. 3. Seedling age frequency distribution for harvested (filled circles) and control (open circles) stands, mean ha⁻¹. Year of harvest is shown by an arrow.

weighted least squares (Ribeiro and Diggle, 2001). The autocorrelation structure had a range of 34.9 m and relative partial sill (spatially structured component) of 25.3%. Presence of white pine regeneration increased with canopy openness (*P* = 0.018) and was greater in logged stands (*P* = 0.042), but there was no relationship with vegetation cover (*P* = 0.29) once these other factors had been taken into account. Vegetation cover was denser (logged stand mean 55.3 \pm 1.8% S.E. versus unlogged stand mean 37.3 \pm 1.3% S.E.) and canopy more open in logged stands (GLMM with spatially autocorrelated errors, *P* < 0.001).

7. Discussion

The data show that 9 years after harvest, many of the goals of structural retention harvesting were met, since cwd volume, snag frequencies, and cavity-tree frequencies were similar in logged and unlogged stands. Basal area of white pine in logged stands remained within the range of variation of natural stands, though there was an increase in wind-throw. Canopy cover was reduced in logged stands, while white pine and hardwood species regeneration and understorey vegetation increased. Though repeated measures of the same sampling points were not made and treatments were not randomly assigned, the results are supported by replication at the stand level and an absence of severe disturbances such as wind and fire between surveys, minimizing the possibility that differences between logged and unlogged stands are due to factors other than harvesting.

The results have implications for biodiversity conservation. Many species in the Great Lakes-St. Lawrence region utilize declining trees and the snags and cwd they form (Naylor, 1994), for example, the pileated woodpecker (*Dryocopus pileatus* L.) that forages on large-diameter snags and cwd (Naylor et al., 1996), and bats that roost in large snags (Jung et al., 1999). Increases in understorey density after logging can provide browse for ungulates such as white-tailed deer (*Odocoileus virginianus* Zimmerman) (Stiell et al., 1994), but can adversely affect animal species that require an open understorey for foraging such as bats (Jung et al., 1999).

The harvest resulted in a slightly increased proportion of trees with growth defects and decay in the residual stand. Retention of declining trees is desirable from a conservation perspective, but is anathema to the principal of selection harvesting, which seeks allow healthy, vigorous trees to develop with reduced competition and produce large quantities of seed for stand regeneration (OMNR, 1998). Studies in the same part of the Algoma Forest have shown that the structural retention harvest reduced a number of measures of genetic diversity in residual populations of adults, mainly through the loss of rarer alleles (Buchert et al., 1997; Rajora et al., 2000). Whether these losses will persist in future generations, or whether pollen from surrounding stands will replenish the gene pool, has yet to be determined. Natural white pine populations exhibit high outcrossing rates (Beaulieu and Simon, 1994, 1995), and even isolated populations maintain high genetic diversity (Rajora et al., 1998). This indicates that recovery of genetic diversity is possible in logged stands. Logging can break down related neighbourhoods in white pine (Epperson et al., 2001), and could, therefore, result in reduced inbreeding.

Whether retention of declining quality trees adversely affects seed production in the residual stand is unknown. Seed production in *Pinus sylvestris* L. in Scandinavia increased with dbh and after thinning release, but there was no relationship with crown size, tree height, or age (Karlsson, 2000). An increase in cone production by residual trees is, therefore, likely, but the effects of tree condition are unknown. It is likely that site conditions, rather than seed production, are the limiting factors to regeneration in these stands.

Total cavity tree frequency was unaffected by harvesting, but white pine cavity tree frequency was somewhat lower in harvested stands. This was due to the reduced frequency of white pines in harvested stands. Naylor (1998) cites unpublished data from Algonquin Park, Ontario, showing that uncut pine stands have twice as many cavity trees (and twice as many snags) as stands that had received a shelterwood seeding cut within 10 years.

Snag frequencies were an order of magnitude higher (Jung et al., 1999), but snag basal area was lower (Carleton and Gordon, 1992b), than reported for other old-growth pine forests in Ontario. The data indicate a pulse of snag recruitment following harvest. Duvall and Grigal (1999) found that snag volume was lower in mature managed red pine stands than natural stands, and there were far fewer small and medium-sized snags, though the time since thinning varied in their study. Causes for the increase in snag recruitment after harvest might include soil compaction (Kozlowski, 1999) or sudden changes in the canopy microclimate due to thinning such as increased radiation and temperature, and decreased relative humidity due to thinning (Riegel et al., 1992). Persistent decreases in residual-tree growth have been found after green-tree retention harvests of Douglas-fir (North et al., 1996). Cores taken from residual trees in the Algoma Forest show a lag in tree response to harvesting, followed by an increase in diameter increment of up to 60% (Bebber et al., 2004).

Increased wind-throw has been reported in other variable retention studies. Three years after harvest, one-quarter of residual trees in dispersed retention cuts had been lost to wind-throw, while half of those lost in shelterwood cuts fell during a single severe storm (Beese and Arnott, 1999; Beese and Bryant, 1999). White pine is reported as being susceptible to snapping (Horton and Bedell, 1960), which may explain the increase in natural-origin cwd in logged stands.

Cwd volumes in control stands similar to those found by Carleton and Gordon (1992a) in other old-growth pine forests in northcentral Ontario. Total volume in that study was $52.0 \pm 7.7 \text{ m}^3 \text{ ha}^{-1}$, of which $11.75 \pm 3.9 \text{ m}^3 \text{ ha}^{-1}$ was white pine. The distribution of cwd in decay classes was identical to that in unlogged stands in the Algoma Forest, i.e. increased volume in class 4, with decreased volume in

class 5. This pattern has been found in other forest types, and agrees with the expectation of a constant rate of input and decay, and a geometric increase in residence time within decay classes (Harmon et al., 1986). Though, no decay rate data exist for terrestrial white pine cwd, and decay rates of cwd can be highly variable (Daniels et al., 1997), it is likely that the oldest logs predate the creation of the stands between 100 and 200 years ago. The sudden high input of cwd in logged stands is likely to be of benefit to wildlife, but may have unforeseen consequences, for example, as a habitat for pest insects (Hindmarch and Reid, 2001). A similar increase in new cwd in managed stands was found by Duvall and Grigal (1999) in red pine stands. A more natural rate of cwd input could have been achieved had some of these trees been left standing.

White pine regeneration was sparse in both unlogged and logged stands. Though some areas supported high seedling densities, most had far fewer seedlings than are considered adequate for stand regeneration, i.e. around 1500 ha^{-1} (Horton and Bedell, 1960). Further evidence of regeneration failure lies in the lack of small-diameter trees, and in the steep decline in the seedling age distribution. This is not surprising, since white pine has strict requirements for successful germination and growth. Natural regeneration is facilitated by moderate-intensity fire, which removes competition and reduces the thickness of organic material on the forest floor to allow germination (Maissurow, 1935; Heinselman, 1981; Kershaw, 1993). Self-replacement (i.e. gap-phase regeneration) occurs rarely, generally on poorer sites, where hardwood competition is reduced (Hibbs, 1982; Quinby, 1991). In the absence of fire, silvicultural treatments that expose mineral soil, reduce competition, and open the canopy are recommended (Stiell, 1985; OMNR, 1998). If site preparation and tending are not diligently pursued, as in the Algoma Forest, white pine regeneration will generally fail in this region (e.g. Stiell et al., 1994).

Soil disturbance could explain the increased level of regeneration in logged stands. Increases in sapling and understorey vegetation cover have been found in other old-growth stands after harvesting. Quinby (2000) found large increases in white birch, red maple and bracken in the understorey 8 months after shelterwood logging in Temagami, Ontario. However, most larger saplings, including white birch, declined.

The increases seen in the Algoma Forest 9 years after harvesting likely reflect the understorey increases seen by Quinby (2000). Though Jung et al. (1999) found no consistent differences in shrub density between old-growth white pine stands and those logged 3–7 years previously, their density estimates were similar to those in the Algoma Forest ($4000\text{--}8000 \text{ stems ha}^{-1}$). The density of small trees was lower in logged stands. Stiell et al. (1994) found that there was no significant difference in sapling density between logged and unlogged white pine stands in Ontario 20 years after an improvement cut, presumably because thinning and growth out of the sapling size class had occurred.

Despite attempts to limit residual tree damage, around 7% of white pine stems were found to have some logging damage, and there were signs of increased tree mortality in the snag and cwd decay class distributions. Brace (1978) reports 6% fatal damage and 14% non-fatal damage to understorey residual white pine after logging in Petawawa, Ontario, and that 30% of logging wounds were infected with decay organisms 5 years after logging. Since most of the damage found in the Algoma Forest was near the base of the tree (probably caused by skidding), there are long-term implications for tree stability and condition.

8. Conclusion

Structural retention is an increasingly important component of forest management guidelines in Ontario (OMNR, 1998, 2001) and elsewhere (Franklin et al., 1997). This study describes what may be the first attempt at a structural retention harvest of eastern white pine, information that is vital in the continuing development of forest management guidelines (MacDonald et al., 1997). The study indicated that structural retention can maintain levels of habitat elements such as snags, cavity trees, and cwd, but that factors such as wind-throw and changes in the frequency distribution of cwd decay class must be considered.

White pine is essentially a long-lived pioneer (sensu Webb et al., 1972) that is usually unable to regenerate in the absence of a disturbance that removes competition and reduces litter layer thickness. Several major forest industries depend upon large, long-lived pioneer species that have high conservation value, of which the Douglas-fir forests

of the Pacific Northwest and the mountain ash (*Eucalyptus regnans* F. Muell) forests of Southern Australia (reviewed in Lindenmayer and McCarthy, 2002) have been subject to the most research. In both these cases, traditional silvicultural techniques have focussed on promoting regeneration through clearcuts and prescribed burns. This level of disturbance has severely reduced habitat diversity, and structural retention has been advocated to lessen this impact (Franklin et al., 2002; Lindenmayer and McCarthy, 2002). However, increased retention can adversely affect subsequent regeneration (Birch and Johnson, 1992; Acker et al., 1998; Dignan et al., 1998; Zenner et al., 1998). Given the similarities between these species, consideration of the challenges faced in the management of each may be of mutual benefit in achieving the common goal of integrating conservation with silviculture.

Acknowledgments

The study was funded by the Ontario Ministry of Natural Resources. The authors would like to thank R. Ancelin, C. Bebber, D. Derbrowka, M. Kijazi, J. Kokes, E. Mallory, E. Orton and L. Zimmerman for assistance in the field.

References

- Acker, S.A., Zenner, E.K., Emmingham, W.H., 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: implications for green tree retention. *Can. J. For. Res.* 28, 749–758.
- Anderson, H.W., Rice, J.A., 1993. A Tree-Marking Guide for the Tolerant Hardwoods Working Group in Ontario. Ontario Ministry of Natural Resources, Queen's Printer for Ontario, Toronto.
- Arnott, J.T., Beese, W.J., 1997. Alternatives to clearcutting in BC Coastal Montane Forests. *For. Chron.* 73, 670–678.
- Beaulieu, J., Simon, J.-P., 1994. Genetic structure and variability in *Pinus strobus* in Quebec. *Can. J. For. Res.* 24, 1726–1733.
- Beaulieu, J., Simon, J.P., 1995. Mating system in natural populations of eastern white pine in Quebec. *Can. J. For. Res.* 25, 1697–1703.
- Bebber, D.P., Thomas, S.C., 2003. Prism sweeps for coarse woody debris. *Can. J. For. Res.* 33, 1737–1743.
- Bebber, D.P., Thomas, S.C., Cole, W.G., Balsillie, D., 2004. Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. *Trees: Struct. Funct.* 18, 29–34.
- Beese, W.J., Bryant, A.A., 1999. Effect of alternative silvicultural systems on vegetation and bird communities in coastal montane forests of British Columbia, Canada. *For. Ecol. Manage.* 115, 231–242.
- Beese, W.J., Arnott, J.T., 1999. Montane Alternative Silvicultural Systems (MASS): establishing and managing a multi-disciplinary, multi-partner research site. *For. Chron.* 75, 413–416.
- Birch, K., Johnson, K.N., 1992. Stand-level wood-production costs of leaving live, mature trees at regeneration harvest in coastal Douglas fir stands. *West. J. Appl. For.* 3, 65–68.
- Brace, L.G., 1978. An intermediate cutting in pine mixedwoods. In: Cameron, D.A. (Ed.), Proceedings of the White and Red Pine Symposium, Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario, Department of the Environment, Canadian Forest Service, pp. 131–138.
- Buchert, G.P., Rajora, O.P., Hood, J.V., Dancik, B.P., 1997. Effects of harvesting on genetic diversity in old-growth eastern white pine in Ontario, Canada. *Conserv. Biol.* 11, 747–758.
- Bull, E.L., Meslow, E.C., 1977. Habitat requirements of the pileated woodpecker in northeastern Oregon. *J. For.* 75, 335–337.
- Carleton, T.J., Gordon, A.M., 1992a. Understanding Old-Growth Red and White Pine Dominated Forests in Ontario. Report No. 2A. Ontario Ministry of Natural Resources, Sault Ste. Marie.
- Carleton, T.J., Gordon, A.M., 1992b. Understanding Old-Growth Red and White Pine Dominated Forests in Ontario. Report No. 2. Ontario Ministry of Natural Resources, Sault Ste. Marie.
- Carleton, T.J., Arnup, R.W., 1993. Vegetation Ecology of Eastern White Pine and Red Pine Forests in Ontario. Report No. 11. Ontario Ministry of Natural Resources, Sault Ste. Marie.
- Chapeskie, D.J., Galley, D.F., Mihell, J.R., Quinn, N.W., Struik, H.H., 1989. A Silvicultural Guide for the White Pine and Red Pine Working Groups in Ontario. Ontario Ministry of Natural Resources. Queen's Printer for Ontario, Toronto.
- Chapman, J.A., Feldhammer, G.A. (Eds.), 1982. Wild mammals of North America, Biology, Management, and Economics. John Hopkins University Press, Baltimore.
- Clark, D.A., Clark, D.B., 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol. Monogr.* 62, 315–344.
- Daniels, L.D., Dobry, J., Klinka, K., Feller, M.C., 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. *Can. J. For. Res.* 27, 1132–1141.
- Dignan, P., King, M., Saveneh, A., Walters, M., 1998. The regeneration of *Eucalyptus regnans* F. Muell. under retained overwood: seedling growth and density. *For. Ecol. Manage.* 102, 1–7.
- Duvall, M.D., Grigal, D.F., 1999. Effects of timber harvesting on coarse woody debris in red pine forests across the Great Lakes states, U.S.A.. *Can. J. For. Res.* 29, 1926–1934.
- Epperson, B.K., Chung, M., Chung, M.G., 2001. Spatial genetic structure of allozyme polymorphisms within populations of *Pinus strobus* (Pinaceae). *Am. J. Bot.* 88, 1006–1010.
- Figueiredo Filho, A., Machado, S.A., Carneiro, M.R.A., 2000. Testing accuracy of log volume calculation procedures against water displacement techniques (xylometer). *Can. J. For. Res.* 30, 990–997.
- Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: vari-

- able retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), *Creating a Forestry for the 21st Century: the Science of Ecosystem Management*. Island Press, Washington DC, pp. 67–98.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155, 399–423.
- Halpern, C.B., Evans, S.A., Nelson, C.R., McKenzie, D., Liguori, D.A., Hibbs, D.E., Halaj, M.G., Raphael, M.G., 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. *Northwest Sci.* 73, 27–44.
- Hansen, A.J., Spies, T.A., Swanson, F.J., Ohman, J.L., 1991. Conserving biodiversity in managed forests. *Bioscience* 41, 382–392.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–302.
- Heinselman, M.L., 1981. Fire and succession in the conifer forests of northern North America. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), *Forest Succession: Concepts and Applications*. Springer Verlag, New York, pp. 374–405.
- Hibbs, D.E., 1982. White pine in the transition hardwood forest. *Can. J. Bot.* 60, 2046–2053.
- Hindmarch, T.D., Reid, M.L., 2001. Thinning of mature lodgepole pine stands increases scolytid bark beetle abundance and diversity. *Can. J. For. Res.* 31, 1502–1512.
- Horton, K.W., Bedell, G.H.D., 1960. White and Red Pine Ecology, Silviculture and Management. Report No. Bulletin 124. Canada Department of Northern Affairs and National Resources, Forestry Branch, Ottawa.
- Isaaks, E.H., Srivastava, R.M., 1989. *An Introduction to Applied Geostatistics*. Oxford University Press, New York.
- Jung, T.S., Thompson, I.D., Titman, R.D., Applejohn, A.P., 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *J. Wildl. Manage.* 63, 1306–1319.
- Karlsson, C., 2000. Seed production of *Pinus sylvestris* after release cutting. *Can. J. For. Res.* 30, 982–989.
- Kershaw, H.M.H., 1993. Early successional processes of eastern white pine and red pine in the Great Lakes-St. Lawrence forest. Ontario Ministry of Natural Resources, Sault Ste. Marie.
- Kozłowski, T.T., 1999. Soil compaction and growth of woody plants. *Scand. J. For. Res.* 14, 596–619.
- Lindenmayer, D., McCarthy, M.A., 2002. Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. *For. Ecol. Manage.* 155, 319–335.
- MacDonald, G.B., Arnup, R., Jones, R.K., 1997. *Adaptive Forest Management: a Literature Review and Strategic Analysis*. Ontario Ministry of Natural Resources, Sault Ste. Marie.
- Maissuraw, D.K., 1935. Fire as a necessary factor in the perpetuation of white pine. *J. For.* 33, 373–378.
- Martin, A.J., 1984. Testing volume equation accuracy with water displacement techniques. *For. Sci.* 30, 41–50.
- Naylor, B.J., 1994. Managing wildlife habitat in red pine and white pine forests of central Ontario. *For. Chron.* 70, 411–419.
- Naylor, B.J., 1998. *Integrating timber and wildlife management. A Silvicultural Guide for the Great-Lakes St. Lawrence Conifer Forest in Ontario*, Ontario Ministry for Natural Resources, Toronto, pp. 273–310.
- Naylor, B.J., Baker, J.A., Hagg, D.M., McNicol, J.G., Watt, W.R., 1996. *Forest Management Guidelines for the Provision of Pileated Woodpecker Habitat. V.1.0*. Ontario Ministry of Natural Resources. Queen's Printer for Ontario, Toronto.
- North, R., Chen, J.Q., Smith, G., Krakowiak, L., Franklin, J., 1996. Initial response of understorey plant diversity and overstorey tree diameter growth to a green tree retention harvest. *Northwest Sci.* 70, 24–35.
- OMNR, 1998. *A Silvicultural Guide for the Great Lakes-St. Lawrence Conifer Forest in Ontario*. Ontario Ministry for Natural Resources. Queen's Printer for Ontario, Toronto.
- OMNR, 2001. *Forest Management Guide for Natural Disturbance Pattern Emulation, version 3*, Ontario Ministry of Natural Resources. Queen's Printer for Ontario, Toronto.
- Parker, G.R., Maxwell, J.W., Morton, L.D., Smith, J.E.G., 1983. The ecology of lynx on Cape Breton Island. *Can. J. Zool.* 61, 770–786.
- Perry, D.A., Amaranthus, M.P., 1997. Disturbance, recovery, and stability. In: Kohm, K.A., Franklin, J.F. (Eds.), *Creating a Forestry for the 21st Century: the Science of Ecosystem Management*. Island Press, Washington DC, pp. 31–56.
- Philip, M.S., 1994. *Measuring Trees and Forests*, second ed. CABI, Oxford.
- Quinby, P.A., 1991. Self-replacement in old growth white pine forests of Temagami, Ontario. *For. Ecol. Manage.* 41, 95–109.
- Quinby, P.A., 2000. First-year impacts of shelterwood logging on understorey vegetation in an old-growth pine stand in central Ontario, Canada. *Environ. Conserv.* 27, 229–241.
- R Core Development Team, 2004. *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rajora, O.P., DeVerno, L., Mosseler, A., Innes, D.J., 1998. Genetic diversity and population structure of disjunct Newfoundland and central Ontario populations of eastern white pine (*Pinus strobus*). *Can. J. Bot.* 76, 500–508.
- Rajora, O.P., Rahman, M.H., Buchert, G.P., Dancik, B.P., 2000. Microsatellite DNA analysis of genetic effects of harvesting in old-growth eastern white pine (*Pinus strobus*) in Ontario, Canada. *Mol. Ecol.* 9, 339–348.
- Ribeiro Jr., P.J., Diggle, P.J., 2001. *geoR: a package for geostatistical analysis*. *R-News* 1, 15–18.
- Riegel, G.M., Miller, R.F., Krueger, W.C., 1992. Competition for resources between understorey vegetation and overstorey *Pinus ponderosa* in Northeastern Oregon. *Ecol. Appl.* 2, 71–85.
- Rogers, L.L., 1987. Effects of food supply and kinship on social behaviour, movements and population growth of black bears in northeastern Minnesota. *Wildl. Monogr.* 97, 1–72.
- Spies, T.A., 1997. Forest stand structure, composition, and function. In: Kohm, K.A., Franklin, J.F. (Eds.), *Creating a Forestry for the*

- 21st Century: the Science of Ecosystem Management. Island Press, Washington DC, pp. 11–30.
- Spies, T.A., 1998. Forest structure: a key to the ecosystem. *Northwest Sci.* 72, 34–39.
- Stiell, W.M., 1985. Silviculture of eastern white pine. *Proc. Entomol. Soc. Ont.* 116, 95–107.
- Stiell, W.M., Robinson, C.F., Burgess, D., 1994. 20-year growth of white pine following commercial improvement cut in pine mixedwoods. *For. Chron.* 70, 385–394.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth ed. Springer-Verlag, New York.
- Webb, L.J., Tracey, J.G., Williams, W.T., 1972. Regeneration and pattern in the subtropical rainforest. *J. Ecol.* 60, 675–695.
- Zenner, E.K., Acker, S.A., Emmingham, W.H., 1998. Growth reduction in harvest-age, coniferous forests with residual trees in the western central Cascade Range of Oregon. *For. Ecol. Manage.* 102, 75–88.