

RESEARCH ARTICLE

•
Historical Changes
in White Pine (*Pinus
strobus* L.) Density
in Algonquin Park,
Ontario, During the
19th Century

Ian D. Thompson¹

Canadian Forest Service
1219 Queen Street East
Sault Ste. Marie, ON, Canada P6A 2E5

Julie H. Simard²

Rodger D. Titman

McGill University
Department of Natural Resource Sciences
Ste-Anne-de-Bellevue, QC,
Canada H9X 3V9

¹ Corresponding author:
ian.thompson@nrcan.gc.ca;
705-541-5644

² Current address:
Ontario Ministry of Natural Resources,
300 Water St., Peterborough, ON, Canada
K9J 8M5

ABSTRACT: Understanding historical forest condition is important as a basis for forest restoration and the development of forest management policies. White pine (*Pinus strobus* L.) historically has been an important commercial tree species, and significant post-settlement declines in its populations have been suggested in eastern North America since the 1600s. Logging of white pine in eastern Ontario, Canada, began in the late 1700s. We estimated the loss of white pine and changes in white pine diameter distribution in Algonquin Provincial Park by direct sampling of old stumps, censusing trees in an area that has never been harvested, assessing Crown Surveyor's records from the 1800s, using a GIS mapping technique to assess probabilistic change in pine-dominated stands, and comparing our data to other published information. Stump and tree densities since the 1800s suggested a mean reduction in the number of white pine trees of 88% from about 3 to >8 pines/ha to <1 pine/ha today in mixed and deciduous stands. GIS-based mapping predicted a maximum decline of pine-dominated stands of about 40% by area, from 539 km² that may have historically supported such forests. The diameter distribution of the current white pine trees was significantly smaller than in the historical forest (means, 44.5 cm vs. 73.4 cm, $P < 0.001$). Aside from early over logging, the continued low density of white pine in all forest types can be attributed in part to intense post-logging fires in the 1800s and to the past 60 years of fire suppression, which have eliminated seed sources and seedbeds. We suggest that a program using several silvicultural techniques will be necessary to restore the white pine in forest types that existed historically.

Index terms: forest policy, forest restoration, historic landcover, old-growth, Ontario, white pine

INTRODUCTION

As a result of early logging practices following European settlement (e.g., Frelich and Reich 1996), several eastern North American tree species have been substantially reduced in abundance over historical levels, including red spruce (*Picea rubra* Sarg.) (Mosseler et al. 2003), black oak (*Quercus velutina* Lam.) (Leverett 1996), eastern hemlock (*Tsuga canadensis* L.) (Mearns (1899), and white pine (*Pinus strobus* L.) (Aird 1985, Leverett 1996, Hannah 1999). Another explanation for reduced abundance of some species is the introduction of insects or diseases (Karnosky 1979), such as American elm (*Ulmus americana* L.). These changes to forest ecosystems have had implications for forest community structure and biodiversity, even within protected areas (Foster 1992, Foster and Motzlin 2003).

White pine has been a commercially valuable tree species in eastern North America since the 1600s, when it was originally harvested for ships' masts, and later for sawn timber (Wray 1986, Long and Whiteman 1998). At the peak of white pine logging in Ontario, Canada, in the late 1800s, >4 million m³ of pine was estimated to have been harvested in a single year (Aird 1985), as compared to present harvests of <0.5 million m³/yr (Ontario Ministry Natural Resources 2002). White pine is absent or

occurs at reduced density over much of its former range in Canada (e.g., Aird 1985, Rajora et al. 1998) and the United States (Howard 1986, Frelich 1995, Leverett 1996), although in some States, white pine forests have recovered as a result of proactive management (Abrams 2001).

Logging has been implicated as a major cause in the decline of white pine density (Aird 1985, Sharik et al. 1989, McRae et al. 1994, Zhang et al. 2000). This decline in white pine, especially of forest stands with large old white pines, has been a public concern for more than a century (e.g., Mearns 1899). Understanding the extent of decline in old growth white pine in forests relative to historical conditions can provide important information on which to base forest restoration projects and guidance to forest policies. While many studies have provided insights into historical occurrence of white pine in forests of the eastern United States, (e.g., Sharik et al. 1989, Foster 1992, Abrams and Ruffner 1995, Frelich 1995, Zhang et al. 2000, Abrams 2001), only limited quantitative information is available in Canada. In the U.S., reported changes in percentage of white pine in forest stands, compared to historical densities, ranges from an increase of 20% in Massachusetts to a 35% decline in some Wisconsin forests, with an average decline of about 14% among the Great Lakes States (Abrams 2001). Frelich and Reich (1996)

reported that <1% of the American primary white and red pine forests remain intact. Compounding the loss of white pines to early logging were the often subsequent hot fires in accumulated slash that eliminated many of the remaining seed trees and on-ground seeds (Heinselman 1981, Frelich 1995).

In Ontario, available information suggests either significant decline, no change, or slight increase in the amount of white pine forest, depending on the source of information and the location of the study area (e.g., Aird 1985, Guyette and Cole 1999, Jackson et al. 2000, Leadbitter et al. 2002, Suffling et al. 2003). The disparity among these studies is not surprising, as the distribution of white pine in Ontario is variable and dependent on soils, fire regimes (Carleton and Arnup 1993), and logging history (Burgess and Methven 1977). Further, some of the 'historical' information may actually refer to a period following the earliest logging. In no study has the decline in density of white pine trees been estimated.

Determination of North American pre-settlement forest types has been attempted using diverse techniques. In Ontario, several authors have relied on the original

notes of Crown Land Surveyors to assess historical relative tree abundance (e.g., Evans 1997, Jackson et al. 2000, Leadbitter et al. 2002). The value of the available information on pre-European white pine forests in Ontario is often diminished by the lack of distinction among red pine (*P. resinosa* Ait.), white pine, and jack pine (*P. banksiana* Lamb.) in some of the historical sources. This lack of distinction confounds the capability to compare species composition between the current and past forests. Non-random selection of witness trees has been cited as a bias from some of the survey records (Bourdo 1956, Black and Abrams 2001). Further, interpretation of the Crown Surveyors' notes to describe past forests requires several assumptions, including that the identification of tree species was correct, that the order of tree species recorded was in order of abundance, that no species was over- or under-represented or disregarded, and that those trees above the canopy were not missed.

White pine can be a minor to important component in shade-tolerant hardwood stands and mixedwood forests, but also occurs at high densities in pine-dominated stands. Our purpose was to examine the role that early logging (and subsequent fires) may have had on present tree community

composition in Algonquin Provincial Park, Ontario, Canada. Our focal question was at what density, did white pine historically occur in stands of mixed species, and what portion of pine-dominated stands might have been replaced by other forest types? We developed several lines of evidence to assess possible changes in white pine density and age-class structure in pre-settlement time compared to changes in the current forest, including direct assessments, predictive mapping, literature surveys, and an assessment of Crown Surveyors' notes.

METHODS

Study Area

We conducted our study in Algonquin Provincial Park (Figure 1), a 7653 km² forested area located in the Great Lakes-St. Lawrence Forest Region (Rowe 1972). The climate is temperate continental, and the eastern side of the Park receives about 50 mm less precipitation and has about 100 fewer growing-degree-days than the western side (Chambers et al. 1997). However, there were periods in history when the climate was more uniform across the entire area (Voigt et al. 2000). More area is over-

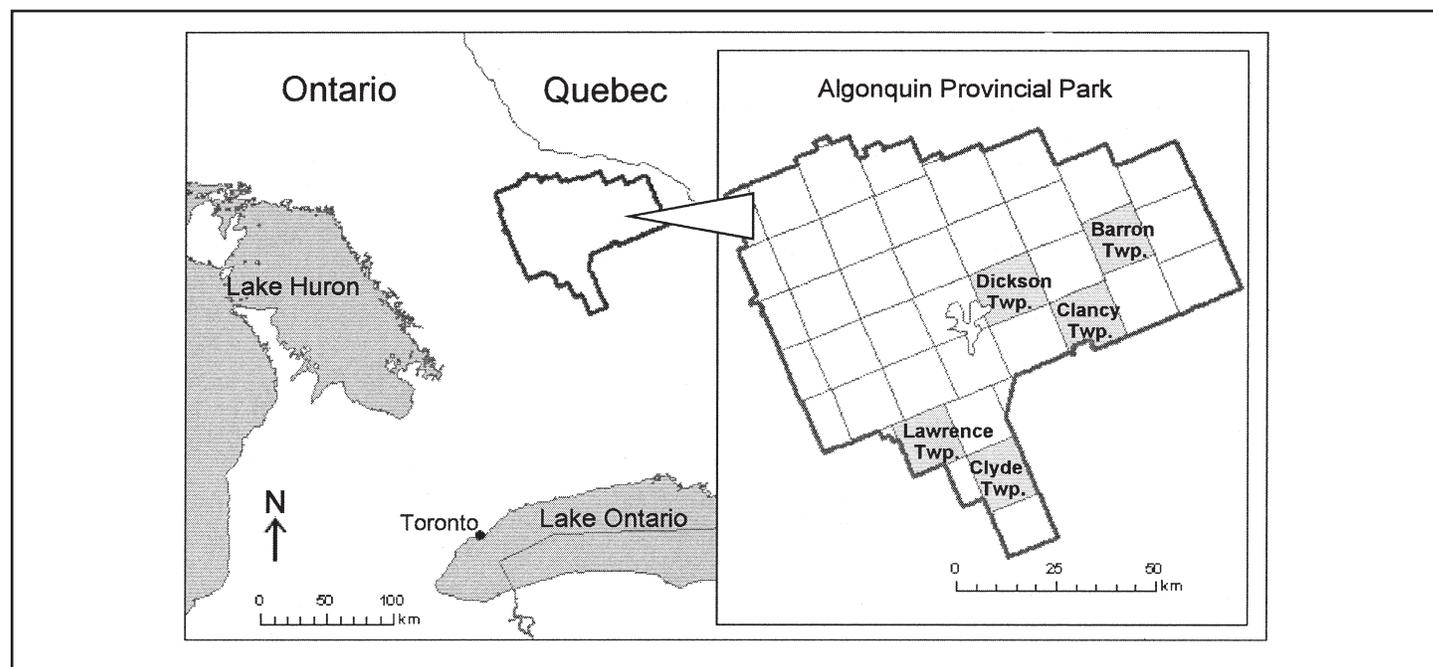


Figure 1. Location of Algonquin Provincial Park in eastern Ontario, Canada, showing townships surveyed for white pine stumps in grey.

lain by post-glacial and lacustrine silt and sand-dominated soils in the east, compared to less sorted glacial till soils in the west, but sandy outwash plains also occur over several large areas in the west (Geddes and McClenaghan 1983, 1984).

The earliest logging in Algonquin Park occurred in the eastern areas during the 1820s (MacKay, unpubl. data), but much of the logging in the southwest and central areas of the Park occurred in the 1890s (Long and Whiteman 1998). Most large pines had been taken from eastern Ontario by the early 1900's (Hughson and Courtney 1987, Strickland 1993, Long and Whiteman 1998). Selection logging for pine was succeeded by the selection harvesting of eastern hemlock in the early 1900s, and later for white spruce (*Picea glauca* Moench) (Macfie 1987). These harvests cumulatively contributed to the extensive shade-tolerant hardwood stands, where previously mixedwood forests had existed (Martin 1959, Leadbitter 2002), as has been caused by logging elsewhere in eastern North America (Frelich 1995, Frelich and Reich 1996). Nevertheless, even these former mixedwood forests were likely dominated historically by hardwoods (Nichols 1935, Lorimer and Frelich 1994). Human-caused fires were common during the late 1800s (Cwynar 1977, Heinselman 1981, Thompson 2000), but fire suppression has reduced the annual area burned since the 1920s and has had an additive negative effect on populations of pines that regenerate best on many site types following low-intensity ground fires (Frelich and Reich 1996, Carleton 2000).

Forests of Algonquin Park are typical of the Great Lakes-St. Lawrence biome in eastern North America. Dominant shade-tolerant hardwood tree species are sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton.), red maple (*A. rubrum* L.), white ash (*Fraxinus americana* L.), red oak (*Quercus rubra* L.), and ironwood (*Ostrya virginiana* (Mill.) K. Koch). Boreal-type mixedwoods are dominated by black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*B. papyrifera* Marsh.), trembling aspen

(*Populus tremuloides* Michx.), and large-toothed aspen (*P. grandidentata* Michx.). White pine-dominated stands occur mainly on shallow sandy soils, which have a low pH and low calcium content (Carleton and Arup 1993).

Historical Forest Cover

We used two survey techniques to develop inferences about historical forest cover. In 1998, we conducted random surveys for stumps in four townships (16-18 km² each) in the central area of Algonquin Park (Lawrence, Dickson, Clancy, and Clyde), which were all logged for white pine prior to 1900 and are currently occupied by shade-tolerant hardwood and boreal mixedwood stands. These four areas were selected for ease of access and because other data existed for the areas (see below). The stump counting method was previously employed by Martin (1959) in several stands in Algonquin Park to examine changes in stand types. We classified stands into three broad forest types: (1) pine-dominated (>70% white pine and red pine), (2) shade-tolerant hardwoods (≥60% hardwood), and (3) boreal mixedwoods. We partitioned our samples among the types. Stumps from the earliest logging were still present and in most cases had sufficient definition to obtain diameters. White pine and eastern hemlock stumps were readily distinguished by the greater lattice structure of hemlock and often by the presence of some bark. The precise date that the trees were cut was not important, as we were only concerned with whether the trees would have been mature individuals during pre-settlement. We divided each township identified on forest inventory maps in quarters and, within each, 1 to 3 stands >8 ha were randomly chosen for surveys. Stumps of cut white pine were censused using the corrected point-distance technique (Batcheler 1975), with a search radius of 30 m at 15 points per stand, located systematically 50 m apart along 250 m transects. We surveyed 6-9 stands in each township resulting in 439 sample points among the three forest types. Points were pooled by township for two of our broad forest types: shade-tolerant hardwood (N = 223, range 50-73/township) and boreal mixedwoods

(N = 159, range 15-50 points/township). We measured the diameters of all stumps and if bark was missing we arbitrarily added 5 cm. We then calculated diameter at breast height (dbh) using a standard taper equation (Myers 1963).

We avoided sampling in stands that, based on historical fire records (Perera et al. 1998), had been burned since logging. We attempted sampling in former pine-dominated stands in Barron Township (Figure 1) in the eastern part of the Park, but found that these stands mostly had undergone post-harvest fires. Another broad forest type, dominated by shade-intolerant hardwoods, was not surveyed because these sites often had burned following logging (Cwynar 1977, Heinselman 1981) leaving few stumps.

As a second estimate of historical pine density, we studied a large area known as the 'Big Crow Wilderness Reserve,' a natural area reserve of primary forest in Algonquin Park that contains some 400-450 year-old pines (aged by Hosie [1953] at 350-400 years old). We used Batcheler's (1975) point distance technique to estimate tree density from 100 random points for all tree species (dbh >10 cm) on a 30 ha portion of the reserve of shade-tolerant hardwood dominated forests. We also counted all class 1 and 2 (Maser et al. 1979) fallen white pine logs and recently-dead standing pines as if they were still standing alive in order to obtain a more accurate assessment of the character of the stand at the turn of the century. We acknowledged that this method was conservative because some fallen trees may have already become class 3 or 4 logs.

Current Pine Density

We collected data on the current white pine size (dbh) distribution by sampling 418 randomly selected white pines from many accessible areas of the study area, including the unlogged Big Crow Wilderness Reserve. We determined tree density for four pine-dominated stands in Barron Township from 10 prism plots per stand. In 1995, D. Voigt (Ontario Ministry Natural Resources) independently col-

lected tree (> 10 cm dbh) density data with a prism on systematic transects in west-central Algonquin Park at 55 plots in boreal mixedwood stands and 56 plots in shade-tolerant hardwood stands. There is a significant correlation between tree density estimated from prism plots and Batcheler's (1975) modified point-distance technique (Thompson et al., in press).

Map-based Probability Determination of Historical Pine-dominated Stands

We used a geographic information system (GIS) to examine the relationship between present pine-dominated stands and soil types to predict the area of pine-dominated stands that may have been logged and converted to other forest types. The relationship was developed using current digital forest resource inventory and soil maps (Geddes and McClenaghan 1983, 1984, Algonquin Forest Authority, unpubl. data). We selected a ca. 2800 km² test area in the northeastern portion of Algonquin Park. Here pine has remained a common species possibly because of more fires there than elsewhere during the past 60 years (Cwynar 1977), as well as due to an abundance of soil types on which pine will regenerate in the absence of fire (Carleton and Arnup 1993). To minimize spatial auto-correlation of pine stands on different soil types, we only counted the majority soil type for each pine stand polygon from among the associated soil polygons. Counts of pine stands for soil types were analysed by chi-square contingency table. We then calculated a mean and standard error of probability of association between pine and the various soil types and extrapolated to the land area of the Park. The prediction was tested by field checking five stands in the west and central areas that were on soils having the highest probabilities of supporting pine. In these stands we censused pine stumps at 50 random points.

Data from Crown Land Surveyors' Notes

We compared our stump survey results to data derived from the 1890 Crown Land Surveyors' notes, based on Leadbitter (2000) and Leadbitter et al. (2002) who

had sampled the same four townships that we surveyed (plus six others). The land surveyors' notes can be used to describe white pine occurrence in two ways: by specific occurrence (frequency of pine as a percentage of all trees mentioned) and by what we now refer to as 'working group,' where pine was the first tree listed for a given point. In the surveyors' notes, 'pines' were not always distinguished by species, but when the species of pine was recorded, the ratio of white pine to red pine was 1.1:1.0. We used this ratio applied to all incidences of 'pine' to obtain an estimate of the proportion of white pine recorded by the surveyors. Jack pine also occurs in Algonquin Park but comprises <1.3% of the current forests (Algonquin Forest Authority, unpubl. data), so we considered it inconsequential.

RESULTS

Historical and Current Pine Density

Our estimated mean historical white pine density in shade-tolerant hardwood stands ranged from 0-11 pines/ha, and in boreal mixedwoods ranged from 5-7 pines/ha from stump surveys (Table 1). We encountered too few pine-dominated (or former pine-dominated) stands among our random samples to develop density estimates for this forest type from stump surveys.

The unlogged Big Crow Wilderness Reserve had a white pine density of 8.4 ± 2.8 pines/ha (3.3% of all stems) in what is a shade-tolerant mixedwood forest dominated by American beech, eastern hemlock, and sugar maple (33%, 29%, and 22% of stems, respectively). No young white pines (or red pines) were found with diameters <25 cm and only 3% of the pine stems were <30 cm. Present white pine densities in shade-tolerant hardwood and boreal mixedwood stands, which had been historically logged, were 0.2 ± 0.1 and 1.08 ± 2.4 pines/ha, respectively (D. Voigt, Ontario Ministry Natural Resources, unpubl. data). Comparing the current pine density to our stump data indicated white pine declines in shade-tolerant hardwood stands ranged from 0 to 98% (\bar{x} = 94%) and in what are now boreal-type mixedwood stands of from 80 to 86% (\bar{x} = 82%).

The current mean white pine density (including 10% red pine) in four pine-dominated stands in Barron Township was 235 pines/ha (SE = 40.6). Few stumps remained in the current pine-dominated stands in Barron Township, and we found considerable charcoal on logs and in the soils, suggesting a history of post-logging fires in this area, as documented by Cwynar (1977) and Perera et al. (1998).

Table 1. Estimated historical density and 95% CL of white pine in two broad forest types, based on stump surveys in four townships in Algonquin Provincial Park conducted in 1998.

Township	Forest type	
	White pine/ha in shade-tolerant hardwood	White pine/ha in boreal mixedwood
Lawrence	0	5.3 (2.4)
Dickson	10.9 (8.1)	7.0 (3.9)
Clyde	0	6.3 (2.9)
Clancy	2.6 (2.3)	n.d. ¹
Combined	3.4 (4.2)	6.0 (3.4)

¹n.d. = no data as insufficient boreal-type mixedwood stands were encountered in Clancy Township.

Probability Mapping of Pine-dominated Stands

The probability of pine-dominated forest occurring on any of the 15 soil types in our test area was low (Table 2). There was a significant relationship between soil type and pine occurrence ($\chi^2 = 122.7$, $df = 13$, $P < 0.001$), with table cells for 'unsubdivided glacio-fluvial outwash' and 'loose to moderately compact silty-sand' contributing most of the chi-square value. Based on the probabilities by soil type, our GIS-based mapping suggested that a maximum of 674 km² (9%) of Algonquin Park may have historically supported high density white pine and/or red pine stands, as compared to the 321 km² that currently exists (Table 2). Ten percent was close to the 12% of our random points that fell in pine-dominated forests among the four townships that we surveyed for stumps. Based on the existing ratio of red pine

to white pine working groups (1:4) (Algonquin Forest Authority, pers. comm.), of that 674 km², 539 km² may have been occupied by white pine-dominated forest on the study area prior to original logging (a potential decline of 40%). For four of our five test stands, we recorded white pine stump densities of 52 ± 11 , 63 ± 10 , 6.7 ± 2.5 , and 5.2 ± 1.8 /ha. The fifth stand was occupied by a white pine-dominated forest, contained no old stumps, and was within an area burned by wildfire in 1922 (Perera et al. 1998).

Information from Surveyors' Notes

The data extracted from Leadbitter (2000) for our four central townships indicated declines in Lawrence and Clyde Townships for trees and working groups, and in Clancy Township for pine working group (Table 3). For Algonquin Park as a whole, based on his sample of ten townships, Leadbitter

(2000) reported a slight average decrease in white pine since the 1890s.

Tree Size Distribution

The shape of the distribution of current and historical white pine diameters was similar and approximated a normal distribution ($P > 0.1$). The mean diameter of present white pine trees in Algonquin Park was significantly smaller than the mean diameter of historical trees (44.5 ± 14.6 (SD) cm vs. 73.4 ± 19.1 cm; $t = 20.5$, $P < 0.001$) (Figure 2). Only 4.5% of the current white pines from logged areas were >70 cm dbh, compared to 50.0% of the historical pines. In the Big Crow Reserve, the 35 live or recently-dead white pines had an average diameter of 97 ± 21 (SD) cm. The largest historical pine (stump) that we found had a diameter of 117 cm, and the largest living white pine in the Big Crow Reserve was 92 cm.

Table 2. Estimated maximum portion of Algonquin Park in white pine-dominated forest (>70% pine) based on the relationship between percentage of various soil types with and without pine-dominated stands.

Soil type	Park area (km ²)	Test area (km ²)	Test area with pine (km ²)	P of pine	Estimated max. area historically dominated by pine (km ²)
Shallow drift soils over bedrock	1360	459	38	0.082	111.4
Thick sandy and gravel tills	904	442	35	0.08	72.3
Unsubdivided thick till	940	310	24	0.076	71.4
Thick sand and gravel	114	15	2	0.133	15.2
Unsubdivided silty-sand and sand	1120	618	42	0.068	76.2
Compact silty-sand	211	122	8	0.064	13.5
Loose to moderately compact silty-sand	95	4	1	0.250	23.7
Glacio-fluvial stratified sand and gravel boulders	68	16	2	0.125	8.5
Kames	255	74	9	0.122	31.1
Eskers	22	9	2	0.222	4.9
Unsubdivided glacio-fluvial outwash	836	452	106	0.235	196.5
Glacio-fluvial sandy outwash	77	20	3	0.166	12.8
Glacio-fluvial sand and gravel outwash	31	25	3	0.12	3.7
Alluvium: sand, silt, minor gravel	104	21	2	0.095	9.9
Organic	513	252	11	0.045	23.1
Total	6660	2848	288		674.2

Table 3. White pine occurrence based on Crown land surveyors' notes for four Townships in central Algonquin Park (Leadbitter 2000), and present percentage of a stand that was white pine compared to current forest resource inventory maps.

Township	% white pine		% white pine	
	of all trees recorded		by working group ¹	
	ca. 1890	1990	ca. 1890	1990
Lawrence	8.33	0.5	6.49	0
Dickson	5.49	6.01	5.75	9.98
Clyde	4.38	1.03	5.47	1.2
Clancy	7.4	6.78	14.14	6.53
Mean	6.4	3.58	7.96	5.9
Mean for Park ²	7.23	6.36	9.14	9.71

¹ assumed from the surveyors' notes as % points where pine was the first listed species.

² mean for ten townships for which the surveyors' notes were translated by Leadbitter (2000).

DISCUSSION

We can never know if our methods provided a true determination of historical forest conditions in Algonquin Park but our data, combined with various sources of information, enabled cross-checking among the methods that suggested consistency. Evidence from our surveys probably resulted in conservative estimates of historical pine density because some stumps may have rotted fully or burned, and some downed trees in the Big Crow Wilderness in decay classes >2 may have been living in the forest of 1800. Therefore, the decline that we have suggested is probably an under estimate of the true reduction in white pine.

Extent of the Decline in White Pine Density

We estimated that white pine density has declined by more than 80% in what are

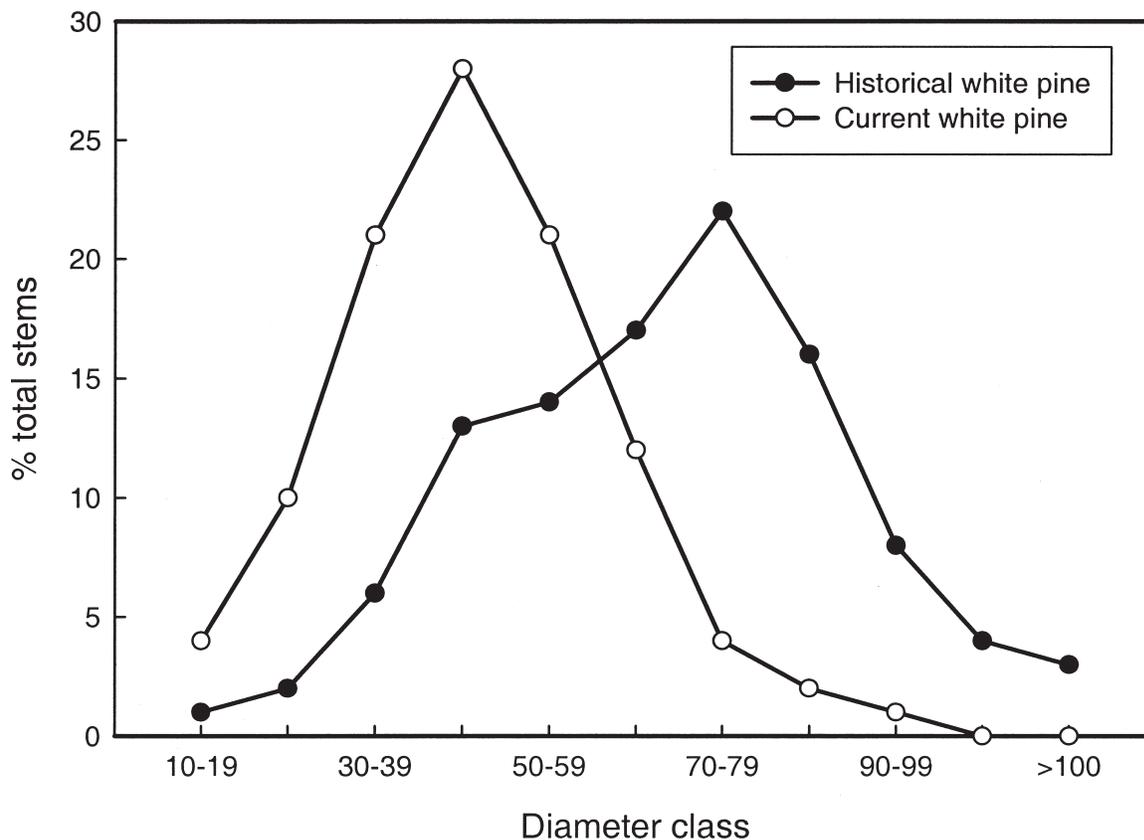


Figure 2. Diameters at breast height for current (n = 405) and historical (n = 196) white pines in mixedwood stands, in Algonquin Park.

currently mixedwood and deciduous forests throughout Algonquin Park, compared to density prior to logging in the 1800s. The white pine density from the Big Crow Reserve provided a control measure for our estimated historical density of pine from stump surveys in shade-tolerant hardwood stands and boreal mixedwoods stands. There, the white pine density (8.4/ha) was well within the estimated range of error of white pine density from our stump surveys. Our estimated decline in white pine density from current mixedwood and deciduous forests was also similar to values derived from Martin (1959). From that study, we calculated mean values for percentage change in white pine density in boreal-type mixedwood stands, shade-tolerant hardwood stands, and pine-dominated stands of 60.0% (n = 5), 91.6% (n = 10), and 0% (n = 1), respectively (Table 4). No change in the amount of white pine was recorded by Martin (1959) for two stands that had never been logged or for a pine-dominated stand that had been logged and subsequently burned. Martin (1959) provided no information on how his plots were selected but it appears that his survey was at least arbitrary based on stand types and locations.

The Crown surveyors' records for all of Algonquin Park (Leadbitter et al. 2002) indicated a small decline in white pine and red pine between 1890 and 1990. For that time period, this may be correct because most of the early logging had been completed before 1890, such as in Dickson and Clancy Townships (MacKay 1978, Macfie 1987, Leadbitter et al. 2002). Examination of township records for areas where logging had not yet occurred suggested there had been decline in white pine (Leadbitter 2000). For Lawrence and Clyde Townships, the Crown Land surveys were conducted prior to the first logging in the mid-late 1890s (Long and Whiteman 1998), and comparison of the surveyors' notes for these two townships to current density indicated declines in white pine that were similar to those recorded from our stump surveys.

Our data showed that there has been a widespread decline in the amount of primary forest with large white pines in

their oldest age classes. At Dividing Lake, another forest reserve in Algonquin Park, Guyette and Dey (1995a) reported ages of white pine trees from 267-486 years, with diameters ranging from 53-125 cm. Their mean diameter of 84.7 ± 19.8 cm was similar to our data from the Big Crow Reserve. Aside from the evidence that we presented from stumps and the Big Crow Reserve, the loss of very large trees is supported by many historical photographs showing trees much larger than any seen today (e.g., MacKay 1978, Hughson and Courtney 1987, Long and Whiteman 1998). Although photographs can present a distorted view of the true situation, it would now be impossible to duplicate such pictures of groves of huge pines in the Park. Guyette and Cole (1999) discussed the current lack of available large old pines with respect to normal debris loads in aquatic systems. Diameter and growth in white pine, as for all trees, depend on site conditions (e.g., Plonski 1974), but diameter is related to age until well past 130 years of age for white pine on all site types in Algonquin Park (Puttock and Bevilacqua 1995), but not necessarily past 250 years (Guyette and Dey 1995a).

Role of Fire in White Pine Regeneration

In Algonquin Park, while logging has been a major cause for the lack of white pine in hardwood and mixedwood ecosystems, it may not solely be responsible. Fire has played an important role in the ecology of white pine during the pre-settlement and post-settlement periods throughout eastern North America (Abrams 2001). The range in diameters and tree ages in the forest reserves at Dividing Lake (Guyette and Dey 1995a) and Big Crow Reserve suggested that multiple cohorts of pines within mixedwood stands resulted from various fire events between 1600 and 1900. On most site types favourable to white pine as a subdominant species, especially those sites with richer soils, mild to moderate fire is required for successful white pine regeneration (Ahlgren 1976, Holla and Knowles 1988, Sims et al. 1990). White pine regenerates best following ground fire that coincides with seed availability on the

trees (Van Wagner 1971), especially in mixedwood stands where shrubs and deciduous stems can out-compete white pine (Carleton 2000). Ongoing fire suppression in Ontario and elsewhere will continue to result in reduction of pines from remaining mixedwood stands, as was observed at Big Crow (our data) and Dividing Lake Forest Reserves (Guyette and Dey 1995a). Similar observations were reported by Zhang et al. (2000) in Michigan, where shade-tolerant species have become dominant in areas with a long history of logging and fire suppression.

The role of aboriginals in deliberate forest burning has been documented in many areas of eastern North America and related to the ensuing forest types (e.g., Clark and Royall 1995). In the Algonquin Park area, evidence is not conclusive, and little is known, about aboriginal use of fire. MacKay (unpubl. data) suggested few natives existed in the area and that there were no permanent settlements in the park during the 1600s. Guyette and Dey (1995a,b) presented dendrochronological evidence suggestive of some anthropogenic-origin fires, based on altered fire intervals during various periods, especially after 1780. Their data suggested that there were few human-caused fires during the period from 1636-1779, and no data exist prior to 1636, when many of the large pines whose stumps we censused would have originated. The role of aboriginals (and later by European settlers) in causing fires apparently had a smaller effect than natural fire on the forests occurring at the time of European settlement.

White pine can regenerate successfully in the absence of fire on certain low productivity forest sites, such as those with shallow and sandy soils that are calcium-limited, with a low pH (Burgess and Methven 1977, Chapeskie et al. 1989, Carleton and Arnup 1993). Unless seed sources are removed entirely from these sites, white pine can continue to be an important component in, or dominate, the stands (Burgess and Methven 1977, Heinselman 1981, Carleton and Arnup 1993). Somewhat surprisingly, therefore, our mapping suggested that even on sites where pine was capable of self-replacement in the absence of fire, the prob-

Table 4. Summary of stands surveyed by Martin (1959) for white pine stumps in Algonquin Park, and our calculated percent change in pine density.

Area description	Present forest type	Present white pine density trees/ha	Historical white pine density stumps/ha	Historical stand type	Percent change
Sunday Creek	Boreal mixedwood	0	0	Boreal mixed	no change
	Boreal wet	0	0	Boreal wet	no change
West side along highway corridor	Boreal conifer	0	12	Pine dominated	-100
	Boreal mixedwood	0	6.8	Mixedwood with white pine	-100
	Tolerant hardwood dominated mixedwood	14	261	White pine mixedwood	-44
Teepee Lake	Mixed deciduous	0.04	261	White pine mixedwood	-98.5
Joe Lake	Mixed deciduous	0.03	26	White pine mixedwood	-99.9
	Tolerant hardwood	0.4	12	White pine mixedwood	-96.7
Taylor Statten	Boreal mixedwood	0.04	26.4	White pine mixedwood	-99.9
Deer Lake	Boreal conifer	0	6.8	Mixedwood with white pine	-100
Achray	White pine	105	burned	White pine	no change
Reed Lake (never logged)	White pine	ca. 120	ca. 120	White pine	no change
Biggar Lake (never logged)	White pine/hemlock/tolerant hardwood	12.4	12.4	White pine/hemlock/tolerant hardwood	no change
Tea Lake	Tolerant hardwood/spruce	0	4.4	Mixedwood dominated by tolerant hardwood	-100
	Tolerant hardwood	0	3.2	Mixedwood dominated by tolerant hardwood	-100
Smoke Lake	Tolerant hardwood	0	0.4	Tolerant hardwood /hemlock/white pine	-100

¹ Martin (1959) did not indicate actual historical density of pine trees for this plot, but instead referred to the stand as “dominated by pine”. The value of 26 pines/ha is taken from two other stands (Taylor Statten and Joe Lake) where he provided the density and also referred the stand as to as “dominated” by white pine.

ability of pine occurrence was low. Sharik et al. (1989) suggested that white pine invasion of a given site is non-deterministic and specification of probability, such as we have done, is therefore an appropriate approach to identifying expectation occupancy by white pine. Among our five test stands, one was occupied by a pine-dominated stand and two stands historically had moderate densities of large white pines, indicating that pine was at least a co-dominant in some of the stands, indicating our predictions were robust. Therefore we believe that our predicted maximum decline of pine-dominated stands of about 40% was realistic.

Conclusions About the Extent of Decline in White Pine

The evidence for a decline in white pine in pine-dominated stands remains an open question, based on our mapped evidence (see Carleton 2000) and because of low probabilities of occurrence on all soil types and the lack of remaining stumps that would enable surveys. However, the evidence for a decline in white pine from mixedwood forests is robust. The scope of the decline of white pine from mixedwood ecosystems (mostly now deciduous ecosystems) in Algonquin Park since ca. 1800 has been immense. Tolerant hardwoods and boreal-type mixedwoods are the dominant types on the study area, comprising more than 90% of the forests. If these stands had 3-8 white pine trees per hectare on average, as we suspect they should, then this conservatively translates to more than a million fewer white pine trees in Algonquin Park now than occurred there historically. If the amount of pine-dominated forest has in fact declined by 40%, then at 235 trees/ha, an additional several million fewer white pines occur now compared to in the presettlement forests of Algonquin Park. The present low white pine density as a result of logging, coupled with fire suppression (since the 1940s) inside and outside of reserves, suggests that white pine cannot become a common species in deciduous or mixedwood forests without an active restoration program. Directed management would include the use of low- to moderate-intensity prescribed burning in the spring

(e.g., McRae et al. 1994) accompanied by under-planting in gaps because of the lost seed source, followed by tending as required to remove competing shrub to restore the original mixedwood and pine-dominated stand types.

ACKNOWLEDGMENTS

We thank Dan Strickland, Jack Myhill, Dennis Voigt, Bob Pick, Gordon Cumming, and Norm Quinn, of Ontario Ministry of Natural Resources and Algonquin Forest Authority for their help in locating field sites, providing data and maps, and for their willingness to share their intimate knowledge of local history. Funding for this project was provided by the Ontario Ministry of Natural Resources, and accommodations at the Harkness Fisheries Research Station by OMNR and by Natural Resources Canada, at the Lake Traverse Space Station. Darcy Ortiz, Martha Allen, and Peter Addison provided field assistance. Craig Robinson and Jason Bernard of Canadian Forest Service, Petawawa Research Forest, collected the data in pine stands in Barron Township. We appreciated comments by Mike Flannigan and Jim Baker on a draft of the paper.

Ian D. Thompson has been a biodiversity scientist with Canadian Forest Service for the past 20 years and is currently working in Ontario. His focal interests are changes to forest systems through management and impacts on associated wildlife.

Julie H. Simard is currently a habitat conservation biologist for the Ontario Ministry of Natural Resources in Peterborough Ontario, where her main focus is on bird conservation planning and implementation.

Rodger D. Titman is a professor of wildlife ecology at the Faculty of Resource Management of McGill University in Montreal. His interests are wide-ranging with a focus on human-induced environmental changes.

LITERATURE CITED

- Abrams, M.D. 2001. Eastern white pine versatility in the presettlement forest. *BioScience* 51:967-979.
- Abrams, M.D., and C.M. Ruffner. 1995. Physiographic analysis of witness-tree distribution (1765-1798) and present forest cover through south-central Pennsylvania. *Canadian Journal of Forest Research* 25:659-668.
- Ahlgren, C.E. 1976. Regeneration of red pine and white pine following wildfire and logging in northeastern Minnesota. *Journal of Forestry* 74:135-140.
- Aird, P.L. 1985. In praise of pine: the eastern white pine and red pine timber harvest from Ontario's Crown forest. Report No. PI-X-52, Canadian Forest Service, Petawawa National Forest Research Institute, Chalk River, Ont.
- Batcheler, C.L. 1975. Probable limit of error of the point-distance neighbour estimate of density. *Proceedings of the New Zealand Ecological Society* 22:28-33.
- Black, B.B., and M.D. Abrams. 2001. Influence of native Americans and survey biases on metes and bounds witness-tree distribution. *Ecology* 82:2574-2586.
- Bourdo, E.A. 1956. A review of the General Land Office Survey and of its use in quantitative studies of former forests. *Ecology* 37:754-768.
- Burgess, D.M., and I.R. Methven. 1977. The historical interaction of fire, logging and pine: a case study at Chalk River, Ontario. Report No. PS-X-66, Canadian Forest Service, Petawawa National Forest Research Institute, Chalk River, Ont.
- Carleton, T.J. 2000. Vegetation responses to the managed forest landscape of central and northern Ontario. Pp. 179-197 in A.H. Perera, D.L. Euler, and I.D. Thompson, eds., *Ecology of a Managed Terrestrial Landscape: Pattern and Processes of Forest Landscapes in Ontario*. UBC Press, Vancouver, B.C.
- Carleton, T.J., and R.W. Arnup. 1993. Vegetation ecology of eastern white pine and red pine forests of Ontario. Report No. 11, Forest Landscape and Ecology Program, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont.
- Chambers, B.A., B.J. Naylor, J. Niepolla, B. Merchant, and P. Uhlig. 1997. Field guide to forest ecosystems of central Ontario. SCSS FG-01, Ontario Ministry Natural Resources, North Bay, Ont.
- Chapeskie, D.J., D.F. Galley, J.R. Mihell, N.W. Quinn, and H.H. Struik. 1989. A silvicultural

- guide for the white pine and red pine working groups of Ontario. Ontario Ministry Natural Resources, Toronto, Ont.
- Clark, J.S., and P.S. Royall. 1995. Transformation of a northern hardwood forest by aboriginal (Iroquois) fire: charcoal evidence from Crawford Lake, Ontario, Canada. *Holocene* 5:1-9.
- Cwynar, L.C. 1977. The recent fire history of Barron Township, Algonquin Park. *Canadian Journal of Botany* 55:1524-1538.
- Evans, M. 1997. Incorporating historical ecology into forest management planning. M.A. thesis, University of Waterloo, Waterloo, Ont.
- Foster, D.R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. *Journal of Ecology* 80:753-772.
- Foster, D.R., and G. Motzlin. 2003. Interpreting and censusing the openland habitats of coastal New England: insights from landscape history. *Forest Ecology and Management* 185:127-150.
- Frelich, L.E. 1995. Old forest in the Lake States today and before European settlement. *Natural Areas Journal* 15:157-167.
- Frelich, L.E., and P.B. Reich. 1996. Old growth in the Great Lakes region. Pp. 144-160 in M.B. Davis, ed., *Eastern Old-growth Forests: Prospects for Rediscovery and Recovery*. Island Press, Washington, D.C.
- Geddes, R.S., and M.B. McClenaghan. 1983. Geological series-preliminary maps, Quaternary geology (map). Map numbers: P.2608, P.2609, and P.2705. Ontario Ministry Natural Resources, Geological Surveys Branch, Queen's Park, Toronto, Ont.
- Geddes, R.S., and M.B. McClenaghan. 1984. Geological series-preliminary maps, Quaternary geology (map). Map numbers: P.2698, P.2703, P.2704, and P.2706. Ontario Ministry Natural Resources, Geological Surveys Branch, Queen's Park, Toronto, Ont.
- Guyette, R.P., and D.C. Dey. 1995a. Age, size and regeneration of old growth white pine at Dividing Lake Nature Reserve Algonquin Park, Ontario. Forest Research Report No. 131, Ontario Forest Research Institute, Sault Ste. Marie, Ont.
- Guyette, R.P., and D.C. Dey. 1995b. A dendroecological fire history of Opeongo Lookout in Algonquin Park, Ontario. Forest Research Report No. 134, Ontario Forest Research Institute, Sault Ste. Marie, Ont.
- Guyette, R.P., and W.G. Cole. 1999. Age characteristics of coarse woody debris (*Pinus strobus*) in a lake littoral zone. *Canadian Journal of Fisheries and Aquatic Sciences* 56:496-505.
- Hannah, P.R. 1999. Species composition and dynamics in two hardwood stands in Vermont: a disturbance history. *Forest Ecology and Management* 120:105-116.
- Heinselman, M.L. 1981. Fire and succession in the conifer forests of northern North America. Pp. 374-405 in D.C. West, H.H. Shugart, and D.B. Botkin, eds., *Forest Succession: Concepts and Application*. Springer Verlag, New York.
- Holla, T.A., and P. Knowles. 1988. Age structure analysis of a virgin pine stand. *Canadian Field Naturalist* 102:221-226.
- Hosie, R.C. 1953. Forest regeneration in Ontario. University of Toronto Forestry Bulletin 2:1-134
- Howard, T.E. 1986. The lure and lore of eastern white pine. Pp. 10-15 in D.T. Funk, ed., *Eastern white pine: today and tomorrow*, symposium proceedings. General Technical Report WO-51, U.S. Department of Agriculture, Forest Service, Durham, N.H.
- Hughson, J.W., and C.J. Courtney. 1987. Hurling down the pine. Historical Society of the Gatineau, Chelsea, Que.
- Jackson, S.M., F. Pinto, J.R. Malcolm, and E.R. Wilson. 2000. A comparison of pre-European settlement (1857) and current (1981-1995) forest composition in central Ontario. *Canadian Journal of Forest Research* 30:605-612.
- Karnosky, D.F. 1979. Dutch elm disease: a review of the history, environmental implication control, and research needs. *Environmental Conservation* 6:311-322.
- Leadbitter, P. 2000. A comparison of the pre-settlement and present diversity of the forests of central Ontario. M.Sc.F. Thesis, Lakehead University, Thunder Bay, Ont.
- Leadbitter, P., D. Euler, and B. Naylor. 2002. A comparison of historical and current forest cover in selected areas of the Great Lakes-St. Lawrence forest of central Ontario. *Forestry Chronicle* 78:522-529.
- Leverett, R. 1996. Definitions and history. Pp. 3-17 in M.B. Davis, ed., *Eastern Old-growth Forests: Prospects for Rediscovery and Recovery*. Island Press, Washington, D.C.
- Long, G., and R. Whiteman. 1998. When Giants Fall: the Gilmore Quest for Algonquin Pine. Fox Meadow Creations, Huntsville, Ont.
- Lorimer, C.G., and L.E. Frelich. 1994. Natural disturbance regimes in old-growth northern hardwoods: implications for restoration efforts. *Journal of Forestry* 92:33-38.
- Macfie, J. 1987. Parry Sound Logging Days. The Boston Mills Press, Erin, Ont.
- MacKay, D. 1978. The Lumberjacks. McGraw-Hill Ryerson, Toronto, Ont.
- Martin, N.D. 1959. An analysis of forest succession in Algonquin Park, Ontario. *Ecological Monographs* 29:187-218.
- Maser, C., R.G. Anderson, K. Cromack, J.T. Williams, and R.E. Martin. 1979. Dead and down woody material. Pp. 78-95 in J.W. Thomas, ed., *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*. Forest Service Handbook 553, U.S. Department of Agriculture, Washington, D.C.
- McRae, D.J., T.J. Lynham, and R.J. Frech. 1994. Understory prescribed burning in red pine and white pine. *Forestry Chronicle* 70:395-401.
- Mearns, E.A. 1899. Notes on the mammals of the Catskill Mountains, New York, with general remarks on the fauna and flora of the region. *Proceedings of the US National Museum* 21:341-360.
- Mosseler, A., J.A. Lynds, and J.E. Major. 2003. Old-growth forests of the Acadian Forest region. *Environmental Reviews* 11, Suppl. 1:47-77
- Myers, C.A. 1963. Estimating volumes and diameters at breast height from stump diameters, southwest Ponderosa pine. Research Note RM-9, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colo.
- Nichols, G.E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. *Ecology* 16:403-422.
- Ontario Ministry Natural Resources. 2002. State of the forest report. Queen's Printer, Toronto, Ont.
- Perera, A.H., D.J.B. Baldwin, F. Schneckeburger, J.E. Osborne, and R.E. Bae. 1998. Forest fires in Ontario: a spatio-temporal perspective. Forest Research Report 147, Ontario Ministry Natural Resources, Ontario Forest Research Institute, Sault Ste. Marie, Ont
- Plonski, W.L. 1974. Normal yield tables. Ontario Ministry Natural Resources, Queen's Printer, Toronto, Ont.
- Puttock, G.D., and E. Bevilacqua. 1995. White pine and red pine volume growth under uniform shelterwood management in Algonquin Provincial Park. NODA/NFP Technical Report TR-14, Canadian Forest Service, Sault Ste. Marie, Ont.
- Rajora, O.P., L. DeVerno, A. Mosseler, and D.J. Innes. 1998. Genetic diversity and population structure of disjunct Newfoundland and central Ontario populations of eastern white pine. *Canadian Journal of Botany* 76:500-508.
- Rowe, J.S. 1972. The forest regions of Canada. Publication 1300, Canadian Forest Service,

-
- Ottawa, Ont.
- Sharik, T.L., R.H. Ford, and M.L. Davis. 1989. Repeatability of the invasion of eastern white pine on dry sites in northern lower Michigan. *American Midland Naturalist* 122:133-141.
- Sims, R.A., H.M. Kershaw, and G.M. Wickware. 1990. The autecology of major tree species in the North Central Region of Ontario. Publication 5310, Ontario Ministry Natural Resources, Thunder Bay, Ont.
- Strickland, D. 1993. The trees of Algonquin Provincial Park. The Friends of Algonquin Park and Ontario Ministry Natural Resources, Whitney, Ont.
- Suffling, R., M. Evans, and A. Perera. 2003. Presettlement forest in southern Ontario: ecosystems measured through a cultural prism. *Forestry Chronicle* 74:385-501.
- Thompson, I.D. 2000. Forest vegetation of Ontario: factors influencing landscape change. Pp. 30-53 in A.H. Perera, D.L. Euler, and I.D. Thompson, eds., *Ecology of a Managed Terrestrial Landscape: Pattern and Processes of Forest Landscapes in Ontario*. UBC Press, Vancouver, B.C.
- Thompson, I.D., D.A. Ortiz, C.J. Jastrebski, and D. Corbett. 2005. A comparison of prism plots and modified point-distance sampling to calculate stem density and basal area. *Northern Journal of Applied Forestry*: in press.
- Van Wagner, C.E. 1971. Fire and red pine. *Proceedings of the Tall Timbers Fire Ecology Conference* 10:221-224.
- Voigt, D.R., J.A. Baker, R.S. Rempel, and I.D. Thompson. 2000. Forest vertebrate responses to landscape-level changes in Ontario. Pp. 198-233 in A.H. Perera, D.L. Euler, and I.D. Thompson, eds., *Ecology of a Managed Terrestrial Landscape: Pattern and Processes of Forest Landscapes in Ontario*. UBC Press, Vancouver, B.C.
- Wray, D. 1986. Managing white pine in Ontario. Pp. 67-69 in D.T. Funk, ed., *Eastern white pine: today and tomorrow*. General Technical Report WO-51, U.S. Department of Agriculture, Forest Service, Durham, N.H.
- Zhang, Q., K.S. Pregitzer, and D.D. Reed. 2000. Historical changes in the forests of the Luce District of the Upper Peninsula of Michigan. *American Midland Naturalist* 143:94-110.