In situ regeneration of *Pinus strobus* and *P. resinosa* in the Great Lakes forest communities of Canada

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Abstract. Two extensive forest vegetation survey datasets are explored, using ordination and classification, for evidence of *in situ* regeneration by *Pinus strobus* (Eastern white pine) and *P. resinosa* (Red pine). Ordination of tree species contributions to total basal area in 320 upland northern hardwood-conifer stands produced distinct stand groups for *P. banksiana*, *P. resinosa*, *P. strobus* and mesic hardwoods in an ascending sequence along the first axis. *Quercus rubra* (red oak), *Q. alba* (white oak) and tolerant conifer groups formed segregates from the hardwood complex along the second axis. *P. strobus* mixes with all other forest types, but *P. resinosa* is restricted to its own group. Seedlings and trees of *P. strobus* are more abundant than saplings, which are restricted to the pine and oak forests. Therefore, seed production, dispersal and seedling establishment seem to be less of a barrier to *in situ* regeneration by *P. strobus* than subsequent survival and growth.

Canonical correspondence analysis of 170 pine-dominated stands from the Canadian Shield of Ontario, in which tree species variables are segmented into height-class pseudo-species, yielded no linear relationship between environmental features or stand structure and seedling densities of *P. strobus*. However, total tree basal area appears to impose an upper limit to seedling density on the forest floor. Strong correlations emerged between pine seedling density and understorey vegetation. Stand classification of the understorey vegetation, using constrained indicator species analysis, yielded distinct high and low seedling groups. Low pine seedling density was associated with abundant broadleaved shrubs, herbs and seedlings as well as feathermosses and tolerant conifers. High seedling density could not be ascribed to the presence of seedbed taxa, such as *Polytrichum*, but is ascribed to the absence of competition and other forms of inhibition in the understorey vegetation and down through the canopy profile. *In situ* regeneration of *P. strobus* does, therefore, occur but conditions over the forest landscape are largely restrictive.

Keywords: CCA; COINSPAN; Oak; Pine; Stand classification; Stand ordination.

Nomenclature: Gleason (1952) for vascular taxa, Crum et al. (1973) for mosses, Hale & Culberson (1970) for lichens.

Introduction

Pinus strobus (Eastern white pine) and *P. resinosa* (Red pine) each form monospecific stands and may also form a tall, emergent supercanopy in many mixed forests of the Great Lakes region, the Canadian Maritimes and throughout the Appalachian mountains (Burns & Honkala 1990). Forests dominated by these pines have received attention in eastern Canada in recent years because of a decline in the abundance of large trees through heavy harvesting in the past and probably also through forest fire suppression activities. One aspect of such concern is a debate over the extent to which *P. strobus* can establish and regenerate through gap-phase replacement on the forest floor of an uneven-aged forest of which it is a component species. The prevalent view is that catastrophic clearance or partial canopy removal by forest fire is essential for effective pine regeneration and that little occurs by other means (Ahlgren 1976; Ahlgren & Ahlgren 1981; Day & Carter 1991; Frehlich 1992; Heinselman 1981; Maissurow 1941; Methven 1973). Bergeron & Brisson (1990) demonstrate how recurrent forest fire leads to multiple cohorts of *P. resinosa* in a stand.

Similar situations have been demonstrated for mixed *P. strobus* and *P. resinosa* (Cwynar 1977) and for *Picea mariana* beneath a *Pinus banksiana* canopy (Carleton et al. 1996). Unlike *P. banksiana*, *P. rigida* and *Picea mariana*, neither *P. strobus* nor *P. resinosa* produce serotinous cones, the seed being dispersed at cone maturity. A countervailing view is that gap-phase replacement is possible in very old white pine forest (Gilbert 1978; Holla & Knowles 1988; Quinby 1991). Others have referred to the critical nature of the interaction between site factors, light levels and the nature of hardwood competition in determining the success or failure of such *in situ* white pine regeneration (Hibbs 1982).

Most of the conflicting evidence derives from intensive case studies which focus largely on the detailed

reconstruction of a few stands (Hibbs 1982; Day & Carter 1991). Little attempt has been made to integrate this intensive approach with more extensive studies, as has been done for *Picea mariana* (black spruce) (Payette 1992), and for tolerant northern hardwoods (Frehlich & Lorimer 1991), into an overall perspective of the way in which environmental variation over the regional landscape affects forest structure, composition and succession. In order to address such an objective it is necessary to examine stand structure on an extensive basis in relation to composition and site characteristics.

The purpose of this paper is to explore the evidence for *in situ* white and red pine regeneration in two, previously unreported, forest vegetation datasets from central eastern Canada. One survey encompasses the full range of forest canopy composition in the upland northern hardwood-conifer/Great Lakes-St. Lawrence lowlands region (Curtis 1959; Rowe 1972). The second dataset derives from a more detailed structural, compositional and forest site survey of *P. strobus* and *P. resinosa* dominated forests located solely on the Canadian Shield of Ontario. The aim is to use the first dataset to examine the compositional relations of pine dominated stands in the context of the upland northern hardwood-conifer forest as a whole. With the pine forest survey on the Canadian Shield, the aim is to explore environmental and temporal correlates of stand structure, composition and regeneration in order to provide a perspective on intensive studies. *P. strobus* and *P. resinosa* occur naturally throughout the full geographical extent of stands in both surveys.

To characterize the conditions under which white and red pine regeneration are likely to occur in the northern hardwood-conifer forest complex, in the absence of catastrophic disturbance, the following questions are posed: (1) Over what range of forest compositional variation do *P. strobus* and *P. resinosa* occur as trees, saplings and seedlings in central eastern Canada?; (2) is there a relationship between site condition, pine size and age structure?; (3) are differences in pine seedling and sapling abundance among stands linked to site conditions, are they linked to conditions of tree size and age structure or a combination of the two?; (4) Does the understorey vegetation appear to influence *in situ* pine regeneration?

Methods

The conifer-hardwood survey encompasses the full spectrum of upland forest composition in the Great Lakes-St. Lawrence Forest Region of eastern Ontario and western Quebec (Rowe 1972), traversing both the Paleozoic deposits of Southern Ontario and the Cana-

dian Shield. The geographical area encompasses all of southern Ontario north of a line from Grand Bend, on the Lake Huron shoreline, eastwards to Toronto (Fig. 1). The northern boundary corresponds to the line drawn by Rowe (1972) for the limit of the Great Lakes - St. Lawrence lowlands forest as far as the eastern limit of the Eastern Townships of Quebec. Data were collected during the period 1964 to 1972. 320 stands were included in the upland northern conifer-hardwood analysis. Stands on wet sites were omitted. Saplings are defined as any woody stem between 2.54 cm and 10 cm diameter at breast height (dbh) and a tree as any woody stem greater than 10 cm DBH. The data form part of the database of Dr. P.F. Maycock, Erindale College, University of Toronto, and derive from point-quarter, plotless sampling following methods of the Wisconsin school (Curtis 1959; Maycock 1963).

The second, more intensive survey of undisturbed pine forests was conducted during the summers of 1991 and 1992. It includes 170 stands with at least 10 % of the basal area composed of *Pinus strobus* and/or *P. resinosa*, located throughout eastern and north western Ontario on the Canadian Shield. The survey was stratified with a design of five age classes: 50-80 yr, 81-100 yr, 101-120 yr, 121-180 yr, and 180+ yr, in each of three main site quality categories, poor, medium and rich. In each stand a 20 m × 20 m (0.04 ha) plot was established within which the position of each woody stem >10 cm DBH was mapped and species identity, total height, height to the lowest live branch, dbh and crown radius were recorded. For stems <10 cm DBH, the species and numbers within a 5 m wide strip, along the centre line of the plot, were recorded in each of three height classes: 0.1-1.5 m, 1.5-3.0 m, 3.0-10.0 m. Pine seedlings only (i.e. <10 cm height) were counted in the same 5 m × 20 m strip. The cover of each understorey plant species was recorded in 20 contiguous 1 m × 1 m quadrats, forming a belt transect, along the centre line of the plot. In addition, the cover of various forest floor materials, including mineral soil, exposed rock, needle litter, broadleaved litter, tree bases, fine and coarse woody debris, were recorded.

Site features recorded for each stand include angle of slope (inclinometer), aspect (compass degrees from 0 azimuth), position on the slope, volume of standing dead timber, and volume of coarse woody debris on the forest floor. In addition, average cover among the quadrats for each of the forest floor materials was summarized per stand.

Two site-related indices were derived, a microclimatic index MICRO, and a white pine site index PWSI. For MICRO the compass direction of slope aspect was adjusted to within the range -90° to +90° at either side of a line from northwest (315° azimuth) to southeast (135° azimuth) as 0°. This follows the scheme

Fig. 1. Mapped locations of 320 northern hardwood-conifer stands (filled rectangles) and 170 *Pinus strobus* and *P. resinosa* dominated stands (filled circles) in Ontario; western longitude and northern latitude coordinates indicated.

of Hills (1959) for irradiance distribution with landscape in Ontario. The calculation:

$$\text{MICRO} = (\text{adjusted aspect} * \% \text{slope angle}) / 1000 \quad (1)$$

yields an index in the range + 8.1 for which positive values are progressively warmer than normal and negative values are colder than normal, where a normal site is one with no slope.

PWSI was based on the empirical construction of height/age curves in which the increment core ages and heights of five pine trees, representing the height class distribution in each stand, were fitted to harmonic normal yield tables for the region. Site index age was fixed at 120 yr. For stands with little or no white pine (*P. strobus*), an equivalent height/age relationship was derived for red pine (*P. resinosa*), with site index registered at 100y. Conversion from a red pine site index PRSI to a PWSI equivalent was done by regressing one set on the other in those stands containing both species

($n = 89$; $\text{PWSI} = 11.0 + 0.61 * \text{PRSI}$; $R^2 = 38\%$). The conversion was necessary for only 29 of the 170 stands in the dataset.

Data on soil horizon thickness, colour, texture, mottling were collected from a $1 \text{ m} \times 1 \text{ m} \times 1.2 \text{ m}$ deep soil pit and three point auger samples around the perimeter of each plot (Anon. 1985). Air-dried soil samples, collected from the upper B horizon of the pit, were analyzed for pH, P, K, Ca, Mg, and particle size distribution (Anon. 1985). Organic, F and H, soil layers were analyzed for total C and N using a Leco CHN-600 determinator.

For the northern hardwood-conifer data, one data table, comprising relative dominance (i.e. percentage contribution to total basal area) for each tree species in each stand, was produced. For the pine survey data, individual trees were assigned to height classes. The seven height classes were <5 m, 5.1-13.0 m, 13.1-21.0 m, 21.1-25 m, 25.1-29.0 m, 29.1-35.0 m, > 35 m.

Three variable $\times$ sample matrices were generated:

- (1) tree height class pseudospecies $\times$ stands;
- (2) understorey species (average cover) $\times$ stands; and
- (3) environmental variables $\times$ stands.

Data were analyzed with the ordination techniques, Detrended Correspondence Analysis (DCA: Hill & Gauch 1980) and Canonical Correspondence Analysis (CCA: ter Braak 1986), using the program CANOCO (ter Braak 1990). Stand classification was performed with the program COINSPAN (Constrained Indicator Species Analysis: Carleton et al. 1996). This method is an extension of the popular correspondence analysis (CA) based technique, two way indicator species analysis (TWINSPAN: Hill 1979). Whereas TWINSPAN involves the bisection of unconstrained CA axes, COINSPAN involves the constraint, or regression, of one or more external variables onto the axes such that they become canonical correspondence axes. The method is akin to a hybrid between canonical correlation analysis, in that external variables and vegetation ordination axes are first maximally correlated (rotated to congruence), and a polythetic-divisive cluster analysis, in that an hierarchic stand classification is created by successive axis bisections. Where the external variables are categorical, rather than continuous, there exists a close analogy with canonical discriminant analysis, such that indicator species which emerge, typify the various categories. Multiple regression was conducted using SAS (Anon. 1989).

Results

The location of 320 northern hardwood-conifer stands and 170 pine dominated stands from each of the two surveys in Ontario illustrate a discontinuity due to the northern shore of Lake Superior extending into the southern boreal forest zone. Neither *P. strobus* nor *P. resinosa* occurs here. Only 27 stands from the northern hardwood-conifer survey are located in northwestern Ontario whereas 60 stands from the pine forest survey occur in this region (Fig. 1).

Table 1 shows *Acer saccharum* (sugar maple) to be the most abundant species in both the tree and sapling strata in the hardwood-conifer survey and this species accounts for almost one quarter of total tree basal area in the data. *Acer rubrum* is also widespread but contributes far less to total basal area. However, *P. strobus* accounts for an equally high proportion of the total basal area even though it is a less frequent species. In contrast, *P. resinosa* contributes considerably less to the total basal area and is found in fewer than 10 % of the stands in the survey. In the case of neither pine species are saplings particularly frequent or abundant compared with shade tolerant species such as *A. saccharum*, *Fagus grandifolia*,

Table 1. Percentage of plots in which each tree species occurs (%P), average proportional basal area (%BA), sapling presence, and average proportional sapling density (%D) for species among 320 northern hardwood-conifer stands in Ontario.

Species	Trees		Saplings	
	%P	%BA	%P	%D
<i>Abies balsamea</i>	34.2	2.0	45.7	6.6
<i>Acer nigrum</i>	6.0	0.3	2.6	0.2
<i>A. pennsylvanica</i>	10.0	0.1	14.5	1.1
<i>A. rubrum</i>	51.7	8.1	49.8	8.4
<i>A. saccharum</i>	65.8	24.9	70.1	34.8
<i>A. saccharinum</i>	5.3	1.1	4.8	0.9
<i>A. spicatum</i>	1.3	0.0	3.2	0.3
<i>Alnus rugosa</i>	-	-	0.6	0.1
<i>Amelanchier arborea</i>	4.7	0.1	10.9	0.3
<i>Betula lutea</i>	46.1	4.1	37.9	2.2
<i>B. papyrifera</i>	39.2	3.1	27.3	2.2
<i>B. populifolia</i>	9.7	1.7	10.0	2.1
<i>Carya cordiformis</i>	13.8	0.6	11.6	0.4
<i>C. ovata</i>	4.7	0.4	2.9	0.1
<i>Carpinus caroliniana</i>	2.2	0.1	8.7	0.8
<i>Celtis occidentalis</i>	0.9	0.1	0.3	0.1
<i>Crataegus</i> spp.	1.3	0.1	1.3	0.1
<i>Fagus grandifolia</i>	42.3	4.8	49.5	5.8
<i>Fraxinus americana</i>	37.6	1.8	39.5	2.7
<i>F. nigra</i>	11.9	0.4	12.2	0.9
<i>F. pennsylvanica</i>	5.0	0.5	4.8	0.4
<i>Juglans cinerea</i>	6.9	0.2	1.3	0.1
<i>J. nigra</i>	0.3	0.1	-	-
<i>Juniperus virginiana</i>	1.3	0.4	1.3	0.3
<i>Larix laricina</i>	2.2	0.2	0.3	0.1
<i>Ostrya virginiana</i>	35.7	0.8	44.1	6.0
<i>Picea glauca</i>	16.6	0.7	15.4	0.7
<i>P. mariana</i>	2.8	0.1	1.9	0.1
<i>P. rubens</i>	11.6	0.5	10.6	0.9
<i>Pinus banksiana</i>	3.4	1.4	1.9	0.4
<i>P. resinosa</i>	9.7	3.3	7.1	0.8
<i>P. rigida</i>	0.3	0.3	0.6	0.3
<i>P. strobus</i>	28.2	8.1	14.5	1.9
<i>Populus balsamifera</i>	3.8	0.4	2.6	0.1
<i>P. grandidentata</i>	19.1	1.6	10.0	0.5
<i>P. tremuloides</i>	21.6	4.3	14.5	2.0
<i>Prunus pensylvanica</i>	7.8	0.2	7.4	0.3
<i>P. serotina</i>	23.5	0.7	22.8	1.1
<i>P. virginiana</i>	1.9	0.1	2.3	0.3
<i>Quercus alba</i>	6.3	0.9	3.2	0.3
<i>Q. bicolor</i>	0.9	0.2	1.0	0.1
<i>Q. macrocarpa</i>	6.3	0.6	3.9	0.1
<i>Q. muhlenbergii</i>	0.3	0.1	0.3	0.1
<i>Q. rubra</i>	25.1	5.3	17.4	1.0
<i>Q. velutina</i>	0.3	0.1	0.3	0.1
<i>Sorbus decora</i>	2.5	0.1	2.6	0.1
<i>Thuja occidentalis</i>	18.2	4.0	19.0	4.0
<i>Tilia americana</i>	37.6	2.8	36.7	1.7
<i>Tsuga canadensis</i>	29.5	4.5	25.7	3.3
<i>Ulmus americana</i>	37.6	3.7	28.6	2.1
<i>U. rubra</i>	8.2	0.3	5.8	0.4
<i>U. thomasi</i>	4.4	0.2	2.3	0.1

In order to examine the compositional position of the pine species in relation to all other trees, the data for percentage contribution to total basal area (relative dominance) were ordinated using detrended correspondence analysis (DCA). Axes 1 and 2 respectively accounted for 8.3 % and 5.6 % of the total trace. The species ordination illustrates the pine species toward the lower (left) end of the first axis grading to the

higher scores for tolerant hardwoods at the extreme right (Fig. 2). The second axis grades from species of oak at the low end to tolerant conifers, including *A. balsamea*, *Thuja occidentalis* and *T. canadensis* at the high end. The third ordination axis (5.2%: not shown) is characterized by *Betula papyrifera* and *P. tremuloides* at the high end with shade tolerant species scoring at the low end. This is, therefore, best interpreted in terms of a hardwood disturbance/succession trend. On the ordination of axis 1 vs 2, *P. banksiana*, *P. resinosa* and *P. strobus* form a sequence from the extreme left toward the centre (Fig. 2).

Fig. 3. a. Relative dominance (1 = 1–5%; 2 = 6–20%; 3 = 21–50%; 4 = >50%) per stand for trees of *Pinus strobus* plotted on the stand ordination by DCA (Fig. 1). b. Ibid. for *P. resinosa*. c. Percentage frequency of occurrence for seedlings of *Pinus strobus* plotted in the same ordination diagram. d. Ibid. for *P. resinosa*.

Fig. 3a illustrates the relative dominance (in four classes) of *P. strobus*, on the corresponding stand ordination. While *P. strobus* attains maximum dominance in the centre of the ordination, the species clearly is associated with *P. resinosa* and *P. banksiana* further to the left, but also extends into the hardwood complex to the right. In addition, *P. strobus* is associated both with the oak complex toward the lower end of axis 2 and with the tolerant conifers at the upper end of axis 2. The spread of *P. resinosa* on the stand ordination, in contrast, is limited to the left side and does not extend into the (hardwood sections at all (Figs. 3 b). *P. banksiana* is even more limited to the extreme left hand cluster (not shown). The abundance of *P. strobus* saplings, as a percentage contribution to the total number of stems per stand (relative density), differs from that of the trees in being largely limited to pine-dominated forests with some

extension into the oak-dominated region of the ordination. There is a notable absence of pine saplings in the tolerant conifer and tolerant hardwood regions of the ordination (not shown). Seedlings of *P. strobus* in the understorey are more widespread in the ordination diagram than the saplings and shows something of a concentration in the tolerant hardwood region (Fig. 3c). Saplings of *P. resinosa* and *P. banksiana* were almost wholly restricted to the stand clusters dominated by their respective tree species. Seedlings of *P. resinosa* were somewhat more widespread than the trees and saplings but they appear sporadic in occurrence (Fig. 3d). The data summary by ordination, therefore, locates the optimum occurrence of each of the pine species as being rather distinct compared with most other tree species. *P. strobus* shows more intermingling with the hardwoods and tolerant conifers than *P. resinosa*. The

Table 2. Tree species presence (%P), average basal area (dm²/ha) among all stands (%BA all), and average basal area among those stands in which the species was recorded (%BA present) for a survey of 170 stands of *Pinus strobus* and *P. resinosa* on the Ontario Canadian Shield.

Species	%P	%BA all	%BA present
<i>Abies balsamea</i>	65.9	144	219
<i>Acer rubrum</i>	42.4	114	269
<i>A. saccharum</i>	4.7	19	409
<i>Betula lutea</i>	2.4	8	336
<i>B. papyrifera</i>	60.6	182	300
<i>Fagus grandifolia</i>	1.8	5	305
<i>Fraxinus nigra</i>	0.6	3	453
<i>Larix laricina</i>	0.6	1	217
<i>Ostrya virginiana</i>	2.4	1	50
<i>Picea glauca</i>	42.4	116	274
<i>P. mariana</i>	25.9	92	356
<i>P. rubens</i>	0.6	1	155
<i>Pinus banksiana</i>	14.7	115	783
<i>P. resinosa</i>	64.7	1691	2614
<i>P. strobus</i>	96.5	3659	3792
<i>Populus balsamifera</i>	0.6	1	30
<i>P. grandidentata</i>	21.8	133	612
<i>P. tremuloides</i>	32.9	159	484
<i>Prunus pensylvanica</i>	0.6	1	26
<i>Quercus alba</i>	1.2	2	141
<i>Q. rubra</i>	15.9	73	460
<i>Thuja occidentalis</i>	22.9	153	666
<i>Tilia americana</i>	1.2	1	120
<i>Tsuga canadensis</i>	8.8	88	996

comparatively restricted range of *P. strobus* sapling occurrence indicates that seedling establishment is less of a barrier to *in situ* regeneration than subsequent survival and growth.

The 170 stand dataset consisting of white and red pine dominated forests on the Canadian Shield contain higher total basal area, by an order of magnitude, for the pine species than any others. Other species that are prominent include *Thuja occidentalis*, *Abies balsamea*, *Populus tremuloides* and *Betula papyrifera* (Table 2). *P. strobus* is the most frequent throughout stands in the data but *P. resinosa* is comparable to *A. balsamea* and *B. papyrifera*. Compared with the 320 stand hardwood-conifer dataset, therefore, the shade-tolerant hardwood species, including *A. saccharum* and *Fagus grandifolia*, are poorly represented in the pine dataset.

The pine stand tree species basal area data were divided into pseudospecies, representing up to seven height classes for each true species. These pseudospecies data were then ordinated by DCA and CCA in order to explore the relations with postdisturbance stand age,

stand productivity, as assessed by site index, and by the more directly measured site related variables. The percentage of total compositional variance in the respective ordination axes drops more quickly in the CCA than the corresponding DCA. However, the first CCA axis accounts for approximately 90 % of the variance in the first DCA axis (Table 3). The species-environment biplot of CCA axes 1 and 2 indicates a strong primary trend in tree species composition linked to white pine site index (PWSI) and postdisturbance stand age (Fig. 4). The second axis appears, from the biplot diagram, to be linked with a soil depth gradient which is inversely related to slope angle. The third axis (not shown) corresponds best with the microclimate index. Because each tree species has been split into height classes *a* through *g*, the shift in associates and environmental features is evident with increasing size. Mid-height stems of *P. strobus* are abundant throughout the data under a wide range of conditions. Height classes *b*, *c*, *d* and *e* are, therefore, seen located at their average position near the centre of the ordination. Short *P. strobus* stems appear mostly associated with oak species and others on shallow sites and steep slopes. To a certain extent, these stands represent the youngest in the data and offer comparatively limited growth potential. However, the stands also include the most uneven size structures for pine in the 170-stand dataset. The tallest white pine, classes *f* and *g*, appear towards the right associated with *Acer saccharum*, short *Thuja occidentalis*, old stands and high PWSI (Fig. 4). Therefore, large white pine trees derive from a combination of stand longevity and productive soils but with a slight bias toward the latter. The bias is more apparent when ordinated in three dimensions on the first three axes (not shown). The pattern for *P. resinosa* is similar to that for *P. strobus* but with a general shift toward warmer and drier microclimates for small height classes and a stronger bias toward stands of advanced age, versus high productivity, for the tallest stem classes. Although comparable interpretations could be applied for all other species shown, the data do not necessarily include their full ecological range in the region. Therefore, these species are not considered. The stand ordination by CCA, corresponding to that for the species-environment biplot, of the height class data demonstrates a clear segregation along the second axis between *P. resinosa* dominated stands at the upper end and *P. strobus* dominated stands at the lower extreme (Fig. 5). The first axis places stands of increasing age and productivity from left to right. Plotting the seedling density for each species on this diagram illustrates that seedlings of *P. strobus* are abundant but those of *P. resinosa* are not. Significantly, the oldest stands, toward the bottom right of the ordination, support relatively few or no pine seedlings whereas

Fig. 4. Pseudospecies/environment biplot for the first two axes of a canonical correspondence analysis (CCA) on height class pseudospecies for trees in 170 pine dominated forest stands. Tree species: AB = *Abies balsamea*; AR = *Acer rubrum*; AS = *Acer saccharum*; BL = *Betula lutea*; BP = *Betula papyrifera*; FG = *Fagus grandifolia*; FN = *Fraxinus nigra*; LLR = *Larix laricina*; OV = *Ostrya virginiana*; PG = *Picea glauca*; PM = *Picea mariana*; PRU = *Picea rubens*; PB = *Pinus banksiana*; PR = *Pinus resinosa*; PS = *Pinus strobus*; POB = *Populus balsamifera*; POG = *Populus grandidentata*; POT = *Populus tremuloides*; QA = *Quercus alba*; QR = *Quercus rubra*; TO = *Thuja occidentalis*; TC = *Tsuga canadensis*. Height classes: a = < 5 m; b = 5.1 - 13.0 m; c = 13.1 - 21.0 m; d = 21.1 - 25 m; e = 25.1 - 29.0 m; f = 29.1 - 35.0 m; g = > 35 m. Codes for environmental data are as in Table 5. DRAIN = drainage class; AGE = estimated stand age (yr) since last disturbance.

younger and mid-aged stands support a wide range of pine seedling densities.

To examine links between pine regeneration potential and stand structure, a scatterplot of total woody stem density versus the density of well established *P. strobus* seedlings (i.e. 11-150 cm tall) illustrates that an upper bound of tree density appears to limit the number of seedlings (Fig. 6). However, many points lie below and to the left of this upper bound line indicating that other factors also operate to limit pine seedling density. A conclusion from this phase of the work is that the potential for *in situ* regeneration of *P. strobus*, as indicated by the abundance of seedlings, is quite strong but that the nature of stand structure and the phase of stand development only play a partial role in promoting or restricting seedling establishment and persistence.

To further explore correlations between pine seedling abundance and environmental factors, a multiple regression/correlation was performed between *P. strobus* seedling density as the dependent variable and 22 site related variables. These included moisture regime,

microclimate index, slope angle, soil texture class, depth of organic matter, depth to bedrock, mineral soil pH, available nutrients (P, K, Ca, and Mg), C/N ratio of the F-layer, average cover of unvegetated parts for forest floor substrata (logs, needle litter, exposed rock, broadleaf litter), white pine site index (PWSI), total basal area, percentage conifer basal area, percentage hardwood basal area, DCA on understorey vegetation (axes 1 and 2). Of these variables PWSI, broadleaf litter, pH and Ca

Table 3. Percentage of total compositional variance explained by the first four axes of Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) on the 170-stand dataset of tree height-class pseudospecies and associated environmental data.

	Ordination axes			
	1	2	3	4
DCA	6.9	5.1	3.8	3.6
CCA	6.2	1.7	1.5	1.2

Fig. 5. Number of seedlings (10 - 150 cm) in 20 m×20 m plot, for *Pinus strobus* and *P. resinosa*, plotted on the first two axes of stand coordinates for the CCA of tree pseudospecies in 170 stands (see Fig. 4). Large italics = *P. resinosa*; helvetic = *P. strobus*.

group 3. Although at considerably lower abundance, both seedling height classes of *P. resinosa* concentrate in group 4. The four stand groups are quite uneven in size, respectively accounting for 9 %, 58 %, 27 %, and 6 % of the total. Table 5, showing average basal area of tree species and site characteristics in each of the four stand groups, indicates that the small groups 1 and 4 support far less tree biomass than groups 2 and 3. Indeed, tree density in group four, comprising a few very old *P. resinosa* stands is exceedingly low. These

Fig. 6. Scatterplot of number of *Pinus strobus* seedlings (10 - 150 cm) per ha vs. total tree stem density in 170 pine stands. The dotted line is hand drawn and indicates a possible upper bound to the density of seedlings.

Table 4. Average density, $\pm$ standard error (s.e.) of *Pinus resinosa* and *P. strobus* seedlings in two height classes, among the four stand groups derived from a constrained indicator species analysis (COINSPAN) of understorey vegetation, using the pine seedling density data as constraining variables.

Group and No. of stands	<i>Pinus resinosa</i>		<i>P. resinosa</i>		<i>P. strobus</i>		<i>P. strobus</i>	
	< 10 cm	s.e.	10 - 150 cm	s.e.	< 10 cm	s.e.	10 - 150 cm	s.e.
1 (16)	3000 $\pm$ 890		1600 $\pm$ 700		50 $\pm$ 30		-	-
2 (100)	1750 $\pm$ 365		8250 $\pm$ 1415		150 $\pm$ 55		300 $\pm$ 240	
3 (47)	9800 $\pm$ 1780		42350 $\pm$ 5805		150 $\pm$ 100		500 $\pm$ 250	
4 (11)	9650 $\pm$ 3815		5800 $\pm$ 1640		3850 $\pm$ 1755		1650 $\pm$ 780	

stands are also the least productive, on the criteria of PWSI and total basal area. In contrast, the most productive stands in the data belong to group 2 and support, on average, over twice the biomass of the next most productive group (3: Table 5). The distinctive feature of Group 1 is that *Picea mariana* is prominent and, on examining the stand structure profiles (not shown), has clearly invaded the understorey. Group 1 stands are the northernmost in the data and here white pine regeneration may be influenced by climate. Group 2 stands only include hardwoods, *Thuja occidentalis* (eastern white cedar) and *Tsuga canadensis* (eastern hemlock) in any number. In addition, *Abies balsamea* is prominent in this group as an invasive understorey tree. Few distinguishing features emerge for stands in group 3, except that they lack the hardwoods and competitive understorey conifers and support a moderate to low density of pine stems.

Table 6 summarizes the mean cover of the dominant understorey species in each of the four stand groups. Species dominant in stand group 3, in which *P. strobus* seedlings are abundant, include *Pteridium aquilinum*, *Pleurozium schreberi*, *Dicranum polysetum*, *Vaccinium angustifolium* and *Maianthemum canadense*. Group 1, that with the minimum number of *P. strobus* seedlings, is typified by abundant *Pleurozium schreberi*, *Corylus cornuta*, *Abies balsamea*, *Acer spicatum*, *Ptilium crista-castrensis* and *Diervilla lonicera*. The very large group 2 is typified by *Corylus cornuta*, *Abies balsamea*, *Aralia nudicaulis*, *Maianthemum canadense*, *Aster macrophyllus*, and *Acer spicatum*. The small group 4 is characterised by abundant *Vaccinium angustifolium*, *Picea mariana*, and *Pteridium aquilinum*. The recurrence of the same dominants among these groups reflects the broad range of the main understorey species throughout all such pine stands. However, the shifts in peak abundance for each species among the four groups indicates more telling differences (Table 5). On this criterion, species which show such optima in group 1 include *Hylocomium splendens*, *Ptilium crista-castrensis*, *Coptis trifolia*, *Pleurozium schreberi* and *Clintonia borealis*. This assemblage typifies a feathermoss carpeted boreal

Table 5. Average basal area (dm²/ha) and average site-related variables in each of the four understorey stand groups. Moisture score runs from 1 (dry) to 5 (wet); Family particle size class runs from 1 (coarse) to 8 (fine).

	Understorey stand group			
	1	2	3	4
Total basal area	6509	43751	18978	1372
<i>Abies balsamea</i>	252	1119	156	4
<i>Acer rubrum</i>	12	1028	172	0
<i>A. saccharum</i>	0	186	18	0
<i>Betula lutea</i>	0	84	0	0
<i>B. papyrifera</i>	543	1251	126	11
<i>Fagus grandifolia</i>	0	57	0	0
<i>Fraxinus nigra</i>	0	28	0	0
<i>Larix laricina</i>	0	0	14	0
<i>Ostrya virginiana</i>	0	12	0	0
<i>Picea glauca</i>	144	879	197	14
<i>P. mariana</i>	510	183	265	21
<i>P. rubens</i>	0	0	10	0
<i>Pinus banksiana</i>	548	354	281	40
<i>P. resinosa</i>	1034	8747	7127	1063
<i>P. strobus</i>	3280	24866	9377	118
<i>Populus balsamifera</i>	0	2	0	0
<i>P. grandidentata</i>	0	862	555	0
<i>P. tremuloides</i>	171	1334	188	0
<i>Prunus pensylvanica</i>	0	2	0	0
<i>Quercus alba</i>	0	10	8	0
<i>Q. rubra</i>	0	411	360	6
<i>Thuja occidentalis</i>	14	1443	70	97
<i>Tilia americana</i>	0	15	0	0
<i>Tsuga canadensis</i>	0	878	55	0
Depth of Solum (DSOLUM; cm)	57	61	59	25
Depth to bedrock (DBR; cm)	147	124	101	41
Moisture score (MOIST)	1.88	1.89	1.51	1.18
Slope angle (SLOPE, °)	13	14	16	11
Depth of organic (DORG; cm)	5.5	7.1	7.0	8.9
Family particle size class (FPSC)	3.1	2.2	1.8	1.6
pH	5.1	4.8	4.0	3.5
P (micro g/g)	4.4	6.0	3.2	2.9
K (mg/g)	0.12	0.17	0.13	0.25
Ca (mg/g)	0.84	1.29	0.36	0.22
Mg (mg/g)	0.21	0.19	0.10	0.11
Site Index (PWSI; m)	24.8	25.8	23.1	13.1

Table 6. Percentage presence (%P), average cover among all 170 stands (%C all), and average cover (%C) in each of the four understorey stand groups derived by COINSPAN (see Table 4), for those understorey plant species occurring in 10 or more of the 170 stands.

Species	%P	%C All	1	%C 2	3	4	Species	%P	%C All	1	%C 2	3	4
<i>Hylocomium splendens</i>	8.2	0.20	2.0				<i>Abies balsamea</i>	80.6	4.48	4.5	4.8	4.1	2.7
<i>Hypnum curvifolium</i>	14.7	0.05	0.1				<i>Deschampsia flexuosa</i>	10.6	0.13		0.1	0.4	
<i>Salix bebbiana</i>	5.9	0.03	0.1				<i>Polypodium virginianum</i>	11.2	0.32	0.1	0.1	0.2	0.2
<i>Ptilium crista-castrensis</i>	95.9	1.15	4.1	0.1			<i>Amelanchier laevis</i>	7.1	0.03			0.1	
<i>Coptis trifolia</i>	10.0	0.14	1.0	0.1			<i>Polytrichum juniperinum</i>	26.5	0.09			1.1	
<i>Rubus pubescens</i>	15.3	0.08	0.3	0.1			<i>Populus grandidentata</i>	5.9	0.03			0.1	
<i>Acer spicatum</i>	32.4	1.55	4.1	2.0			<i>Prunus virginiana</i>	5.9	0.05			0.1	
<i>Brachythecium reflexum</i>	18.8	0.05	0.2	0.1			<i>Gaultheria procumbens</i>	42.9	0.72		0.5	1.5	0.5
<i>Jamesoniella autumnalis</i>	41.2	0.13	0.3	0.2			<i>Cladina rangiferina</i>	80.0	0.34			0.7	0.1
<i>Clintonia borealis</i>	46.5	0.91	2.9	1.0	0.2	0.3	<i>Juniperus communis</i>	6.5	0.63		0.2	1.8	0.6
<i>Lycopodium obscurum</i>	17.6	0.20	0.4	0.2	0.1		<i>Quercus rubra</i>	25.9	0.31		0.2	0.7	0.4
<i>Pleurozium schreberi</i>	74.1	3.26	11.5	1.3	5.0	0.6	<i>Pinus strobus</i>	61.8	1.53	0.2	0.2	4.6	2.4
<i>Linnaea borealis</i>	45.9	0.75	2.0	0.5	1.0		<i>Acer rubrum</i>	59.4	1.25		1.2	1.7	2.2
<i>Diervilla lonicera</i>	53.5	1.67	3.4	1.7	1.3	0.1	<i>Pteridium aquilinum</i>	57.1	2.71	0.2	1.5	5.6	6.5
<i>Corylus cornuta</i>	52.4	4.11	6.4	4.9	2.3	0.1	<i>Picea glauca</i>	16.5	0.24	0.1	0.2	0.2	1.0
<i>Vaccinium myrtilloides</i>	28.8	0.45	1.1	0.3	0.6	0.1	<i>Melampyrum lineare</i>	12.9	0.03			0.1	0.1
<i>Ptilidium pulcherrimum</i>	17.1	0.42	1.7	1.2	0.8	0.8	<i>Thuja occidentalis</i>	7.6	0.50	1.1	0.6		1.6
<i>Cornus canadensis</i>	58.2	1.09	2.8	0.8	1.1	1.4	<i>Vaccinium angustifolium</i>	68.8	1.63	0.8	0.5	3.4	8.3
<i>Trientalis borealis</i>	47.6	0.34	0.6	0.4	0.1	0.1	<i>Epigaea repens</i>	7.6	0.08			0.2	0.4
<i>Brachythecium salebrosum</i>	38.2	0.22	0.3	0.3	0.1		<i>Ptilidium ciliare</i>	18.2	0.07			0.1	0.2
<i>Geocalyx graveolens</i>	30.6	0.07	0.1	0.1			<i>Dicranum ontariense</i>	28.2	0.14		0.1	0.1	0.9
<i>Lophocolea heterophylla</i>	38.8	0.09	0.1	0.1			<i>Picea mariana</i>	14.7	0.66	0.3	0.2	0.8	6.9
<i>Drepanocladus uncinatus</i>	11.8	0.04	0.1	0.1			<i>Viburnum cassinoides</i>	5.9	0.06			0.1	0.5
<i>Streptopus roseus</i>	22.4	0.15	0.2	0.2			<i>Barbilophozia attenuata</i>	5.9	0.01				0.1
<i>Dryopteris spinulosa</i>	14.7	0.13	0.1	0.2			<i>Cetraria pinastri</i>	5.9	0.01				0.1
<i>Populus tremuloides</i>	18.8	0.12	0.1	0.2			<i>Leucobryum glaucum</i>	6.5	0.02				0.1
<i>Aralia nudicaulis</i>	78.8	2.26	2.0	3.3	0.5		<i>Pohlia nutans</i>	15.3	0.04				0.2
<i>Lonicera canadensis</i>	42.4	0.49	0.3	0.7	0.1		<i>Polypodium virginianum</i>	12.4	0.01				0.1
<i>Plagiothecium laetum</i>	73.5	0.27	0.4	0.3	0.1	0.1	<i>Maianthemum canadense</i>	95.9	2.89	1.8	3.3	2.5	2.6
<i>Sorbus decora</i>	15.3	0.06	0.4			0.2	<i>Brachythecium curtum</i>	11.8	0.12		0.2	0.1	
<i>Polytrichum ohioense</i>	7.1	0.02		0.1	0.1		<i>Acer pennsylvanica</i>	7.6	0.18		0.3	0.1	
<i>Rosa acicularis</i>	17.1	0.15	0.1	0.2	0.1		<i>Actaea rubra</i>	61.2	0.16	0.1	0.1	0.3	
<i>Dicranum flagellare</i>	92.4	0.69	1.2	0.7	0.5	0.4	<i>Oryzopsis asperifolia</i>	27.6	0.62	0.3	0.5	1.0	
<i>Cladonia coniocraea</i>	24.7	0.23	0.8	0.7	0.6	0.5	<i>Hypnum pallescens</i>	37.1	0.18	0.1	0.2	0.1	0.1
<i>Dicranum scoparium</i>	42.4	0.23	0.3	0.3	0.2	0.1	<i>Tetraphis pellucida</i>	50.0	0.17	0.1	0.2	0.1	0.1
<i>Acer saccharum</i>	13.5	0.47		0.8			<i>Betula papyrifera</i>	32.4	0.16	0.2	0.2	0.1	0.2
<i>Crocynia membranacea</i>	20.6	0.04		0.1			<i>Bazzania trilobata</i>	12.4	0.04	0.1			0.1
<i>Dryopteris intermedia</i>	6.5	0.30		0.5			<i>Hypogymnia physodes</i>	9.4	0.02	0.1			0.1
<i>Fragaria virginiana</i>	10.0	0.07		0.1			<i>Chimaphila umbellata</i>	15.3	0.09		0.1	0.1	
<i>Mitella nuda</i>	6.5	0.06		0.1			<i>Fagus grandifolia</i>	5.9	0.05		0.1	0.1	
<i>Mnium medium</i>	18.2	0.05		0.1			<i>Cladonia chlorophaea</i>	95.3	0.65	0.4	0.3	0.4	0.4
<i>Rubus idaeus</i>	9.4	0.06		0.1			<i>Waldsteinia fragaroides</i>	12.4	0.23		0.2	0.3	
<i>Trillium grandiflorum</i>	5.9	0.05		0.1			<i>Carex communis</i>	18.8	0.25	0.1	0.2	0.5	
<i>Viola renifolia</i>	10.6	0.04		0.1			<i>Dicranum polysetum</i>	61.8	1.57	2.1	0.4	3.8	2.1
<i>Dicranum montanum</i>	59.4	0.20	0.2	0.2	0.1	0.1	<i>Amelanchier sanguinea</i>	13.5	0.12		0.1	0.3	
<i>Aster macrophyllus</i>	64.1	2.13	0.5	2.8	1.6								

forest floor beneath a *P. mariana* canopy. Distinctive group 2 species include *Aster macrophyllus*, *Acer saccharum* and *Dryopteris intermedia*. In addition there are many minor species which typify a herb-rich, deciduous forest floor. Group 3 species include *Polytrichum juniperinum*, *Carex communis*, *Dicranum polysetum*, *Gaultheria procumbens*, *Juniperus communis*, *Deschampsia flexuosa* and *Cladina rangiferina*. These species indicate a heterogeneous forest floor of illuminated gaps, shallow soil, rocky outcrops interspersed with deeper soil pockets. Distinctive group 4 species are: *Vaccinium angustifolium*, *Dicranum ontariense*, *Picea mariana* seedlings and *Viburnum cassinoides*.

Discussion

The comparatively widespread occurrence of *Pinus strobus* throughout the northern hardwood-conifer forest complex indicates that the species is generally successful in achieving a significant presence notably on well-drained and somewhat, but not extremely, nutrient poor sites. In contrast, *Pinus resinosa* is quite restricted to dry, shallow soil outcrops and to well-drained sand plains. Trees and seedlings of *P. strobus* are more widespread than saplings, which occur only in pine and oak dominated stands. One interpretation would be that an episodic wave of pine recruitment is occurring through-

out the northern hardwood complex. However, the northern hardwood - conifer data were accumulated between two and three decades ago and no corresponding waves of pine recruitment to the sapling and canopy strata are evident in the more recent pine forest survey data. Another interpretation is that white pine trees in mixed forests, on relatively productive soils, produce seed which germinate and establish but which tend not to survive into larger seedlings and small saplings. Faster growth and associated competitive suppression by the hardwoods is the most likely mechanism (Hibbs 1982). Some of the oak dominated stands in the data support the lowest density of trees and are more akin to savannas than closed forests. Such stands include moderate white pine seedling frequencies and a notable pine sapling component. In these habitats it seems probable that a proportion of establishing pine seedlings will survive and eventually form an upper, discontinuous canopy or emergent supercanopy (Whitney 1986).

The distribution of trees and saplings of *P. resinosa*, with a very limited presence of seedlings throughout the northern hardwood-conifer complex, indicates that no continuous regeneration is occurring for this species. Indeed, saplings, as recorded here may simply represent small, suppressed trees of the same age as those stems recorded as trees in a stand. Some stands may support several cohorts, including saplings, because of surface fire recurrence and the stimulating effect this has on red pine seedling establishment (Burns & Honkala 1990; Ahlgren 1976; Cwynar 1977). The restricted number of seedlings also implies that *P. resinosa* is not particularly adventive into new habitats as seedlings, in contrast with *P. strobus*.

Analysis of the 170-stand, pine-dominated dataset is largely consistent with conclusions drawn from the broader stand base of upland northern hardwood-conifer forest data. Comparable separations between *P. resinosa* and *P. strobus* dominated stands are evident in the ordination results. Similarly, the comparative abundance of *P. strobus* seedlings is consistent between the two surveys. The environmental features, emphasized by the CCA ordination (Fig. 4), lend more detail to the site related factors linked to the distribution of each species. Nevertheless, none of those environmental features recorded were strongly linked to abundant pine seedling densities, although some were significantly associated (PWSI, broadleaved litter, pH, Ca).

An unexpected finding from the stand structure data is the comparatively poor regeneration of *P. strobus* in old-growth pine stands with the largest trees (Fig. 5). Shade tolerant conifers, notably *Abies balsamea* and *Thuja occidentalis*, cast heavy shade, deposit abundant litter and greatly reduce throughfall in many such stands in our data. Seedling establishment and mortality may

be short-lived events under such conditions. The strongest finding is the tight relationship between established pine seedling abundance and the understorey vegetation composition. Alternative explanations for a certain understorey vegetation type being associated with high white pine seedling density are threefold: (1) the understorey species are more sensitive indicators of appropriate site conditions than the single point-in-time measures and estimates of site and microsite that were made in the course of the vegetation surveys; (2) certain species, most abundant in understorey group 3, act as a favourable seedbed for pine; (3) species in the other three understorey groups directly inhibit pine seedling establishment.

Stands on sites with comparatively shallow soil overlying cracked but otherwise impervious bedrock, promote the survival and persistence of *P. strobus* seedlings (cf. Ahlgren 1976). Associated with such forest floor conditions, the tree canopy cover must be discontinuous or there must exist abundant lateral illumination, as on hill slope sites. However, the site related measures do effectively capture many such features. Furthermore, the understorey vegetation may differ considerably on otherwise comparable sites (Table 5) and this may relate to past opportunities for establishment and spread. Consequently, it seems unlikely that the vegetation is acting as an indicator of appropriate contemporary site conditions for pine seedling establishment, which cannot otherwise be detected, to any significant degree, by survey measurements.

Moss species of the genus *Polytrichum* offer favourable seedbed conditions for shade intolerant conifers (Burns & Honkala 1990) and these show a peak in understorey stand group 3. However, there was no simple correlation in our data between pine seedling abundance and *Polytrichum* cover, nor for any other understorey species or life-form group. One explanation may be that it is the combined seedbed effect of all plants in a certain understorey community which promotes pine establishment. This seems unlikely among a suite of species in understorey group 3 with growth forms which vary from moss mats to coniferous shrubs and which are not necessarily unique to that stand group.

Inhibitory conditions correspond, on one hand, to those stands in which a herb-rich and deciduous shrub understorey dominates, as in understorey group 2. On the other hand a feathermoss dominated forest floor appears equally inhibitory, as in understorey group 1. Herb rich stands characterize sites of relatively high site index (PWSI: Table 5). Competitive suppression of pine seedlings by a comparatively fast growing, broadleaved flora and by tolerant conifers, down through the attenuated canopy profile to the forest floor, is probable. At the other extreme, stands with abundant feathermoss cover

offer a very poor seedbed for conifer seedlings. Feathermosses dry out completely near the surface of the moss mat during dry spells (Jessee 1990). Whereas the poikilohydric mosses tolerate such episodes of moderate local drought, vascular plant seedlings, with shallow rooting in the moss carpet, cannot avoid permanent wilting. Alternatively, where frequent wetting occurs, the aerial growth rate of feathermosses can outstrip that of pine, smothering the seedlings.

Competitive and inhibitory processes, therefore, appear to primarily govern *in situ* pine seedling establishment. Where conditions cannot sustain the productive broadleaved species and tolerant conifers, yet also where the moss carpet is poorly developed, then white pine seedling establishment seems probable given sufficient seed rain and acceptably low levels of predation and parasitism (Abbott & Quink 1970). The two stand surveys reported here were conducted on well established, closed canopy forest vegetation. Sites of recent episodic disturbances by extensive blow-down and fire were not included, largely because of the non-availability of such stands under prevailing forest landscape management regimes. The cohort origin of most stands indicates that such episodic disturbances determine most *P. strobus* regeneration and nearly all of that by *P. resinosa*. Most of the pineries of the Great Lakes region established following extensive surface fires associated with both fire usage by hunting tribes (Curtis 1959) and slash burning following land clearance (Heinselman 1973). Pine seed for colonizing such disturbed areas appears to have originated from surviving individual trees, from those on adjacent ridges and from along the margins of wetlands. Such widespread fires promoted pine establishment over a broad range of soil, site and climatic conditions by delaying competition from broadleaved species on the relatively productive sites (Kershaw 1993; Maissurow 1935, 1941; van Wagner 1971). However, it appears from our results that it was not only broadleaved tree species that acted as potential competitors but also other components of the forest ecosystem including tolerant conifers, broadleaved shrubs, herbs and feathermosses.

Little evidence emerges in our data for the scenario in which a cluster of pine trees establish in a large forest gap on a productive site, followed by encroaching competitive exclusion by hardwood species from the exterior of the cluster to finally leave a single surviving pine tree at the centre (Hibbs 1982). Our results indicate that the understorey vegetation is likely to outcompete pine seedlings under such circumstances. However, mono-specific tree clusters or patches do appear to govern the dynamics of early, postfire succession between white pine and aspen (Squiers & Klosterman 1981). More in evidence here is the situation where hardwoods have

invaded the understorey of a thinning white pine stand on such productive sites and have subsequently grown to produce the main canopy. White pine survives in these stands as large, very old emergent trees at low density. Thus, at the landscape level, large gaps on productive sites appear to be readily colonised by the shade tolerant tree species which dominate the forest complex (Frehlich & Lorimer 1991).

Heinselman (1981) identified two classes of fire origin pine forest in the pre-settlement era: (1) pure *P. resinosa* and *P. strobus* needle mat stands growing on fire prone sites with light surface fire cycles of 5 to 50 yr and severe fires at longer intervals; (2) mixed pine with hardwoods and/or shade tolerant conifers on relatively productive sites which experience only very severe fires in the frequency range of 150 to 300 yr. Both types are evident in the pine survey reported here. Whereas recruitment of pine to the upper canopy is unlikely in the mixed type (2) forests, it is probable that some limited second and even third generation establishment will occur in type (1) stands under an active fire prevention regime. Where canopy cover is incomplete, subcanopy tolerant conifers are at low density, broadleaved tree, shrub and herb species are limited, and feathermosses are relatively low in abundance, then white pine seedling establishment and subsequent growth seem probable.

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