White Pine Regeneration in the Obabika Lake Old-Growth Pine Stand: A Landscape Perspective

by

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ABSTRACT

Less than one percent of the world's old-growth white pine forest remains - of those stands that remain, few are regenerating white pine at replacement levels. If these ancient forests are to continue as old-growth white pine forests, active regeneration management for most of them will be required. The most effective management practices will be based on the mechanisms of natural white pine regeneration taking place in ancient forest ecosystems. For this study, 30 plots (20 m x 50 m) were sampled for understory trees, shrubs and herbaceous plants in the world's largest known stand of old-growth white pine forest - the Obabika Lake old-growth pine stand located in Temagami, Ontario. These data were used to characterize the spatial variability of white pine regeneration within the landscape particularly as it relates to wildfire. Influences on regeneration other than natural wildfire were addressed including environmental conditions, resource availability and competition. The results of the age-class analysis for the white pine population in the Obabika Lake stand showed a typical uneven-aged condition. It was also found that, for hilltops and ridgetops versus slopes and valleys, (a) white pine regeneration for the ages 1-65 years was three times more abundant, (b) white pine regeneration had twice the probability of survival, and (c) recruitment into the oldest age group (46-65) was much higher. Fire was most frequent on the upper most upland sites mainly because of wind patterns, lightning probability, drier soil conditions and more volatile litter. It is likely that non-catastrophic surface fires, as opposed to catastrophic fires, facilitated the vast majority of white pine reproduction by reducing competition, exposing mineral soil and leaving living pine trees as seed sources. White pine regeneration is most likely determined by a delicate balance among a variety of major factors including fire frequency and intensity, soil nutrient and moisture conditions, litter composition and thickness, seed production and dissemination, light and root competition, and seed and seedling predation. The interactions and combinations of these variables change mainly as a function of topography, season and forest development. At present, if the natural condition of the Obabika Lake old-growth pine stand is to be maximized, a natural wildfire regime must be facilitated.

INTRODUCTION

It has been estimated that only .2 percent of the original old-growth white pine (<u>Pinus strobus</u> L.) forests of Canada and the United States remain (Quinby 1991a). Of these, many are not regenerating white pine principally because of forest fragmentation and fire suppression (Hett and Loucks 1968, Conkling 1978, Gilbert 1978, Carmean and Clarke 1980, Sheehey 1980, Baird 1983, Whitney 1984, Quinby 1989, Day and Carter 1991). If these old-growth white pine stands are to be maintained, active management will be required to regenerate the pine (Quinby 1987a, Quinby 1988, Day and Carter 1991). At present for Ontario, however, only regeneration of white pine as a component of even-aged logging methods has been addressed (Chapeskie et al. 1989). Although proper application of these methods can result in white pine regeneration, removal of major portions of the forest overstory is necessary. This loss of overstory is not compatible with maintaining the natural character of old-growth forest. In contrast, the mechanisms of natural white pine regeneration that result in a natural, uneven-aged condition within the old-growth forest are poorly understood (Gilbert 1978, Holla and Knowles 1988, Quinby 1991b).

Natural mechanisms of white pine regeneration are best studied in large, relatively undisturbed forest stands (Lutz 1930, Whitney 1987, Mlinsek 1990). One such stand is located at the north end of Obabika Lake in the Temagami Region of Ontario (Sharpe 1989, White 1990) and has been identified as the largest known stand of old-growth white pine forest remaining in the world (Quinby 1991a). The white pine in this area has been self-replacing for at least two generations and, with an uneven-aged population structure and greatest density in the youngest age classes, there is potential for self-replacement in the future (Day and Carter 1991, Quinby 1991b).

Of all natural disturbances, white pine regeneration has been most highly associated with natural wildfire (Maissurow 1935, Heinselman 1973, Frissell 1973, Swain 1973, Fahey and Reiners 1981, Heinselman 1981, Whitney 1986), particularly non-catastrophic surface fires that reduce ground level competition and expose mineral soil (Logan and Brown 1956, Horton and Brown 1960, Quinby 1991b). In forested areas with high topographic diversity, such as the current study area, wide spatial variations in fire frequency are common (Clements 1910, Larsen 1925, Quirk and Sykes 1971, Loope and Gruell 1973, Romme and Knight 1981, Hemstrom and Franklin 1982). Variations in white pine regeneration with topography in central Ontario have also been observed (Logan and Brown 1956, Day and Carter 1991).

Recognizing the strong association between natural wildfire and white pine regeneration, and the variable nature of fire frequency with topography, the purpose of this study was to characterize the spatial variability of white pine regeneration within the Obabika Lake old-growth white pine stand particularly as it relates to wildfire. In addition, other factors influencing the variation in white pine regeneration were identified. Without a thorough understanding of white pine regeneration within the old-growth forest and application of this knowledge, we may lose these majestic ancient ecosystems forever.

STUDY AREA

The forest vegetation of the Temagami Region falls within the Temagami Section, Great Lakes-St. Lawrence Forest Region (Rowe 1972). These forests are typified by

> eastern white pine with scattered white birch and white spruce, although the spruce frequently rivals the pine in abundance. Another common though variable type is a mixture of the birch, pine and spruce, with balsam fir, trembling and largetooth aspens. Both red pine and jack pine are present, the former often prominent in bluffs along ridges and the latter generally restricted to the driest sandy or rocky sites. The tolerant hardwoods, yellow birch and sugar maple, have only a scattered occurrence. The prevalent forest cover on the uplands is clearly a reflection of periodic past fires, and the sandy soils have provided conditions especially favourable for the propagation of eastern white pine, red pine and jack pine. On the lowlands, in poorly-drained depressions and in swamps, black spruce with tamarack or eastern white cedar, form well-marked communities.

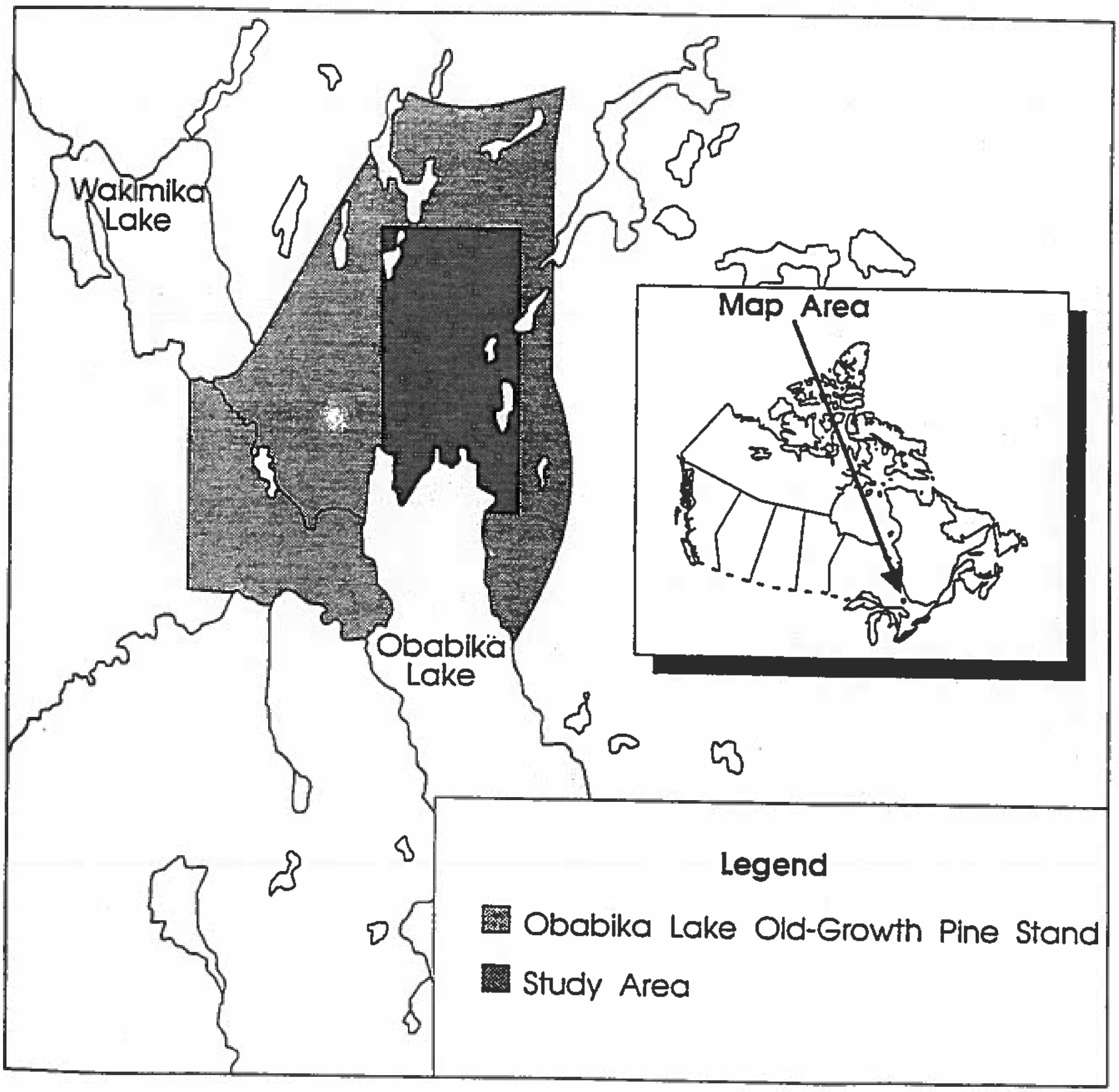
General climatic features of the Temagami Region were provided by Brown et al. (1980). Mean daily temperature varies from -13 degrees C for January to 19 degrees C for July. Mean annual precipitation is approximately 81 cm. The frost-free period is approximately 100 days and the mean annual length of the growing season is approximately 180 days.

The terrain is very rugged featuring steep topography and many escarpments with elevations from 200 m to 700 m. Approximately one-quarter of the landscape is covered by lakes of various sizes with interconnecting systems of streams and rivers. In upland areas the surficial geological material is dominated by glacial tills. These tills are composed mainly of dry to moist silty loams (Johnson 1988). Some upland areas, usually knolls, are characterized by exposed bedrock and bedrock with very shallow loamy tills due to scouring during glacial advance. Valley bottoms are often dominated by medium to fine grained sands of glaciofluvial origin (Johnson 1988). A small percentage of the area is covered with organic soils where drainage is impaired.

The Obabika Lake old-growth forest (approximately 1700 ha) (see Figure 1) is dominated by white pine, however, there are pockets within the stand that are dominated by red ppine and areas where both white and red pine co-dominate. A general description of the vegetation in this stand is provided by White (1990) as follows.

> Red pine often dominates the forest in which it occurs, much to the exclusion of most other tree species. Such stands occur on knoll-tops, escarpment edges, and rocky shoreline bluffs where the site type is generally drier and warmer than normal. Because of the special site type parameters of moisture and temperature, fire plays a crucial role in the establishment and maintenance of the composition of these red pine-dominated stands. Evidence can be seen as charred stumps, basal fire

FIGURE 1 - LOCATION OF STUDY AREA



scars on living trees, and charcoal below the humus layer of the soil. The red pine usually occur in a number of age classes though often there are few individuals in the younger age classes. The understory is variable and consists of saplings of trees other than red pine with white pine and black spruce most common. The soils are mostly sandy loam.

The white pine-dominated and white and red pine co-dominant mixed forest stands occur on mesic sites with normal temperature and consist of a wide range of community structure and composition. Small stands of many large white pine are adjacent to openings where a few large trees have died or been blown over and the opening has created an area of rapid growth and competition with balsam fir and white birch often overtopping the white pine saplings present.

In general, the forest is dominated by white pine and sometimes red pine which together make up 60-70% of the canopy. The remainder is made up of balsam fir, black spruce, and white birch. The older white pine often form a 'super-canopy' towering above the rest of the forest canopy. These large trees are tall with occational individuals to 110 cm dbh and many in the 60-90 cm range. The understory is quite variable but

> generally somewhat sparse and made up of saplings of most tree species including a good complement of white pine saplings. The soils are generally humusy, sandy loam.

Logan and Brown (1956) provided a description of white and red pine regeneration in the Temagami Region as follows.

> One effect of an increase in nutrients appeared to be an increase in vigour of lesser vegetation and competing tree species. But there was also an increase in the vigour of red and white pine seedlings to a point where they seemed to be better able to compete with other plants. One district where this was particularly noticeable was Temagami in the north-central portion of the Forest Region. A luxurient undergrowth often developed on the rich soils in this district, but even so red and white pine were found successfully competing with vigourous shrubs, providing the shrubs and seedlings were established at the same time.

Less than 5% of the Obabika Lake old-growth white pine stand has been affected by logging including limited pulpwood extraction and some localized pine removal (Sharpe 1989). Since 1939, ten small fires, all less than 5 ha in size, have been observed and suppressed in the stand (Sharpe 1989). Evidence of fire throughout the stand indicates that natural wildfire has long been a part of the ecosystem (Quinby 1991b).

The study area is a 2 km x 4 km rectangular area including a portion of the north end of Obabika Lake comprising approximately 700 ha of the Obabika Lake old-growth forest (Figure 1). This portion of the stand is dominated mainly by white pine with some substantial pockets of red pine. Other common overstory species include black spruce, white birch, balsam fir, red maple, white cedar, trembling aspen and white spruce. Elevations range from a minimum of 285 m to a maximum of 388 m. A ridge with plateau-like features in places runs north-south along the eastern boundary of the study area bounded on its west side by a combination of very steep slopes and 50 m escarpments.

The central and western portions of the study area are both characterized by a series of hills of oblong shape also running north-south. Many of these hills have steep escarpments on their east and west sides. Because of the ridge and the predominance of hills, there are also many valleys distributed throughout the study area. In the wider and more level portions of the valley bottoms, soils are often very wet supporting wetland communities often populated with speckled alder, black ash and white cedar. There are also patches within the upland areas that are up to a few ha in size, where large, old white and red pine trees are absent. These areas are often dominated by black spruce, white birch, white cedar, red maple and trembling aspen.

METHODS

Most landscapes with relief can be divided into three major topographic positions including hilltops/ridgetops, slopes, and valleys (Whitney 1986). Slopes can be further stratified by aspect and by location relative to valleys and hilltops/ridgetops. For example, in the Obabika Lake old-growth stand, one can easily identify lower, middle and upper slopes both north- and south-facing. By sampling the range of topographic conditions, the probability is high that the range of environmental conditions and thus the range in biotic responses within the local landscape will be encountered (Gillison and Brewer 1985).

To represent the range of environmental conditions in the 700 ha study area, a total of thirty 20 m x 50 m sample plots were distributed among a variety of topographic positions including hilltops, ridgetops, interior valleys, shoreline valleys and north- and south-facing aspects for each of the upper slope, middle slope, and lower slope positions. Those sites most accessible along an existing trail system were chosen for sampling. Once off the trails, the plots were randomly chosen at each topographic position with the singular criterion that two white and/or red pine trees greater than 139 years old be present in the plot. One plot on the recently burned hilltop had only one live red pine tree greater than 139 years although it did also have one red pine snag of 115 cm dbh. At least four plots were sampled for each of the seven specific topographic positions. Within each plot all overstory trees >10 cm dbh were identified and measured. Increment cores were extracted from each white pine tree in each plot. The understory was sampled by systematically placing 18 1 m x 2 m quadrats along three 50 m lines such that six quadrats were located 10 m apart along each 50 m side perpendicular to the side and along a 50 m line bisecting the plot. Within each quadrat, saplings (trees and shrubs taller than .5 m and <10 cm dbh) were identified to species and assessed for % cover. The number of white pine saplings in each quadrat was determined and each one was aged by counting branch whorles. The herbaceous layer included all trees and shrubs <.5 m tall, herbaceous plants and mosses (Bryophyta spp.). The mosses were not identified to species. All species in the herbaceous layer in each quadrat were estimated for % cover, the number of white pine seedlings was determined and each white pine seedling was aged. Nomenclature follows Fernald (1950).

For data analysis, each tree dbh value was converted to a basal area value for use as an indicator of tree biomass and summarized for each species in each plot. All white pine increment cores were aged using a dissecting microscope. The number of years represented by missing portions of cores was estimated from an equivalent length of core representing the oldest portion of the tree. Because all cores were taken at 1.4 m high, 13 years was added to the age estimate. An age of 65 was chosen as the maximum age of white pine regeneration in this study because 65 years was identified by McCormack (1956) as the transition point between young and mature white pine trees.

The % cover for each understory species in each plot was determined by summing the values for each species in each of the 18 quadrats in the plot. Detrended correspondence analysis (DCA) was used to examine the variation in understory composition among the 30 sample plots. Only the common understory species were included in the DCA according to the following criteria: must occur in (1) 15 or more plots or (2) have at least 5% cover in at least one plot and presence in one or more additional plots. A total of 34 species were included in the DCA.

Also, for each sample plot, DCA scores, white pine density values and white pine cover values were correlated with 17 independent variables including overstory, understory and environmental factors to examine potential influences on white pine regeneration. Determination of the moisture index, one of the independent variables, was based on the fact that, in general, valley soils receive the greatest amount of moisture due to the accumulation of downslope water drainage, whereas hilltops, ridgetops and upper slopes generally have drier soil conditions due to exposure and lack of drainage accumulation. Thus, hilltop, ridgetop and upper slope samples were assigned a value of 1 (driest), middle slope samples were assigned a value of 2 (dry-mesic), lower slope samples were assigned a value of 3 (mesic) and valley samples were assigned a value of 4 (wet-mesic). To assess the role of fire, fire scars at the base of white and red pine trees were counted within each plot. The other independent variables were composed of tree species basal areas and sapling % cover estimates only for those species with at least 50% frequency.

RESULTS

A total of 14 tree species, 15 shrub species, 27 herbaceous vascular plant species, 3 herbaceous vascular plant groups and the Bryophytes as a general group were found within the study plots (Table 1). From Table 2

TABLE 1 - SPECIES LIST

<u>Abies balsamea</u>
<u>Acer pennsylvanica</u>
<u>Acer rubrum</u>
<u>Acer spicatum</u>
<u>Alnus rugosa</u>
<u>Amelanchier sanguinea</u>
<u>Aster macrophyllus</u>
<u>Athyrium Felix-femina</u>
<u>Betula papyrifera</u>
<u>Betula lutea</u>
<u>Bryophyte</u> spp.
<u>Chimaphila umbellata</u>
<u>Clintonia borealis</u>
<u>Comptonia peregrina</u>
<u>Coptis groenlandica</u>
<u>Cornus canadensis</u>
<u>Corylus cornuta</u>
<u>Cypripedium acaule</u>
<u>Diervilla lonicera</u>
<u>Dryopteris spinulosa</u>
<u>Epigea repens</u>
<u>Equisetum fluviatile</u>
<u>Galium triflorum</u>
<u>Gaultheria hispidula</u>
<u>Gaultheria procumbens</u>
<u>Goodyera repens</u>
<u>Gramineae</u> spp.
<u>Gymnocarpium dryopteris</u>
<u>Kalmia angustifolia</u>
<u>Ledum groenlandicum</u>
<u>Linnaea borealis</u>
<u>Lonicera canadensis</u>
<u>Lycopodium complenatum</u>
<u>Lycopodium lucidulum</u>
<u>Lycopodium obscurum</u>
<u>Maianthemum canadense</u>
<u>Melampyrum lineare</u>
<u>Monotropa uniflora</u>
<u>Picea glauca</u>
<u>Picea mariana</u>
<u>Pinus resinosa</u>
<u>Pinus strobus</u>
<u>Pinus banksiana</u>
<u>Polypodium virginianum</u>
<u>Populus grandidentata</u>
<u>Populus tremuloides</u>
<u>Pteridium aquilinum</u>
<u>Pyrus americana</u>
<u>Ribes glandulosum</u>
<u>Salix lucida</u>
<u>Rubus pubescens</u>
<u>Carex</u> spp.
<u>Smilacina racemosa</u>
<u>Taxus canadensis</u>
<u>Thuja occidentalis</u>
<u>Trientalis borealis</u>
<u>Vaccinium angustifolium</u>
<u>Vaccinium myrtilloides</u>
<u>Viburnum cassinoides</u>
<u>Viola</u> spp.

TABLE 2 - WHITE PINE REGENERATION FOR TOPOGRAPHIC POSITIONS

Topographic Position	Plot	White Pine Cover (<10cm dbh)	White Pine Density (<66 yrs) (no./ha)	Mean Age	Age Range
HILLTOP/RIDGETOP					
Hilltop					
older/surface fire	24	33	8946	16.0	1-65
older/surface fire	42	29	5600	19.1	1-59
mean		31	7273	17.2	1-65
recent/crown fire	1	19	4448	8.2	2-15
recent/crown fire	2	18	1698	7.3	1-47
mean		19	3073	7.9	1-47
Mean Hilltop		25	5173	14.4	1-65
Ridgetop					
ridge plateau	10	5	8440	8.8	1-65
ridge plateau	9	9	5362	6.3	1-65
mean		7	6901	7.9	1-65
ridgeface (W-face)	27	10	6722	12.3	1-62
ridgeface (W-face)	28	7	4498	6.1	1-65
mean		9	5610	9.8	1-65
Mean Ridgetop		8	6256	8.7	1-65
Mean Hilltop/Ridgetop		17	5715	11.4	1-65
SLOPE					
Upper					
south-facing	7	37	10614	10.8	1-63
south-facing	3	7	3634	7.3	1-63
mean		22	7124	9.9	1-63
north-facing	13	5	6414	4.6	1-60
north-facing	44	4	6126	4.0	1-65
north-facing	23	2	2512	4.7	1-64
mean		4	5017	4.4	1-65
Mean Upper Slope		11	5860	7.0	1-65
Middle					
south-facing	34	3	2780	3.9	1-10
south-facing	35	3	2224	6.0	1-16
south-facing	6	5	2224	2.8	2-5
mean		4	2409	4.3	1-16
north-facing	19	8	9184	2.9	1-53
north-facing	12	9	5302	12.4	1-62
mean		9	7243	6.4	1-62
Mean Middle Slope		6	4343	5.6	1-62

TABLE 2 - WHITE PINE REGENERATION FOR TOPOGRAPHIC POSITIONS - CON'T

Lower					
south-facing	4	1	1390	1.4	1-2
south-facing	5	0	0	---	---
mean		.5	695	1.4	1-2
north-facing	14	4	2502	5.3	2-12
north-facing	16	4	4170	6.1	3-12
mean		4	2016	5.0	1-12
Mean Lower Slope		2	2016	5.0	1-12
Mean All Slopes		7	4220	6.1	1-65
VALLEY					
Interior					
central	11	7	7520	6.7	1-64
central	30	5	5560	2.5	1-4
mean		6	6540	4.9	1-64
perimeter	22	4	6672	3.0	1-6
perimeter	21	6	2860	12.0	2-64
mean		5	4766	5.7	1-64
Mean Interior Valley		6	5653	5.3	1-64
Shoreline					
south-facing	37	3	3614	2.5	1-4
south-facing	36	0	0	---	---
mean		2	1807	2.5	1-4
west-facing	38	1	278	13.0	13
west-facing	40	0	278	7.0	7
mean		.5	278	10.0	7-13
Mean Shoreline Valley		1	1043	3.6	1-13
Mean Valleys		4	3348	5.0	1-64

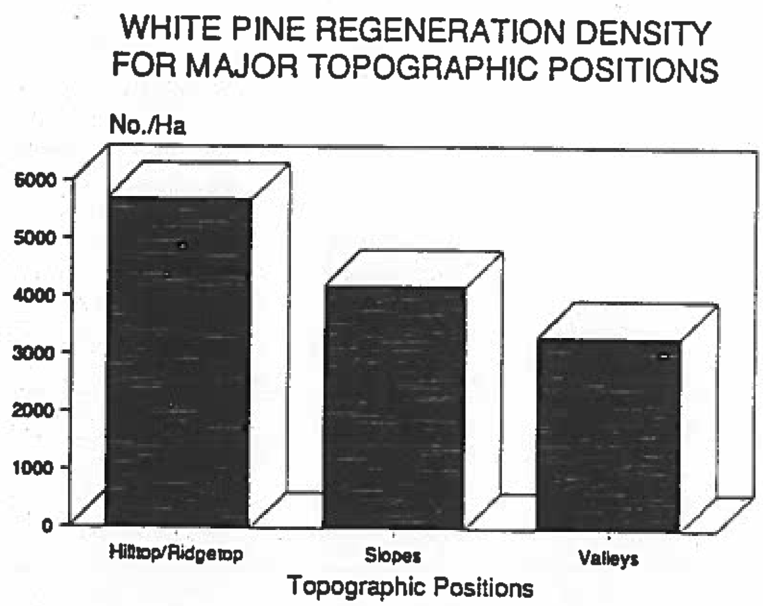
it is evident that white pine regeneration, in terms of % cover, density and mean age, was greater on the hilltops and ridgetops relative to the slopes which in turn was greater than in the valleys (see also Figure 2 for white pine regeneration density and mean age). Figure 3 shows that seedling production (ages 1-5) for hiltops/ridgetops (2534/ha), slopes (2798/ha) and valleys (2360/ha) did not differ substantially, but that recruitment into the age group 46-65 did show major differences among these topographic positions (hilltops/ridgetops - 36/ha, slopes - 29/ha, and valleys - 11/ha).

Considering topographic positions in more detail, white pine regeneration was most dense under the following conditions: the hilltop with the older, lighter fire (7273/ha); the middle, north-facing slope (7243/ha); the upper, south-facing slopes (7124/ha); and the ridgetop (6901/ha) (Table 2). Considering mean age, however, white pine regeneration on the hilltop with the older, lighter fire (17.2 yrs.) was three times greater than the mean age for the middle, north-facing slope (6.4 yrs.) (Table 2).

White pine regeneration was least dense in the west-facing shoreline valley (278/ha), on the lower, south-facing slope (695/ha) and in the south-facing shoreline valley (1807/ha). The mean age of the white pine regeneration in the west-facing shoreline valley (10.0) was, however, much higher than both mean ages for the lower, south-facing slope (1.4) and the west-facing shoreline valley (3.6). A very small range of ages was found on the lower, south-facing slope (1-2), in the south-facing shoreline valley (1-4), in the west-facing shoreline valley (7-13), on the lower, north-facing slope (1-12), and on the middle, south-facing slopes (1-16).

FIGURE 2 - WHITE PINE REGENERATION DENSITY AND

MEAN AGE FOR FOR MAJOR TOPOGRAPHIC POSITIONS



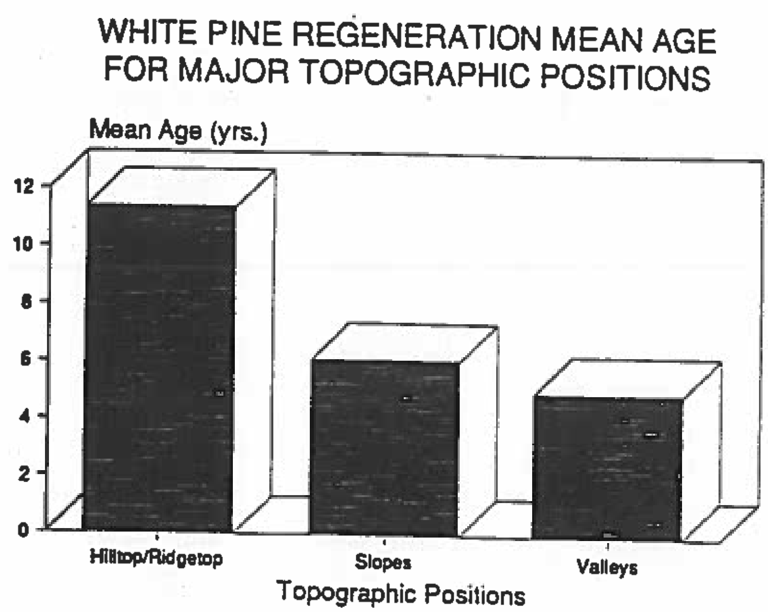
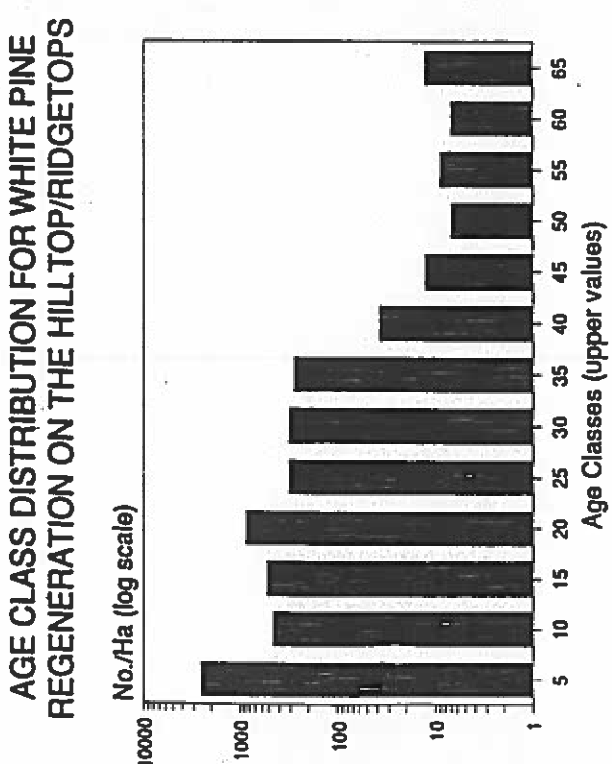
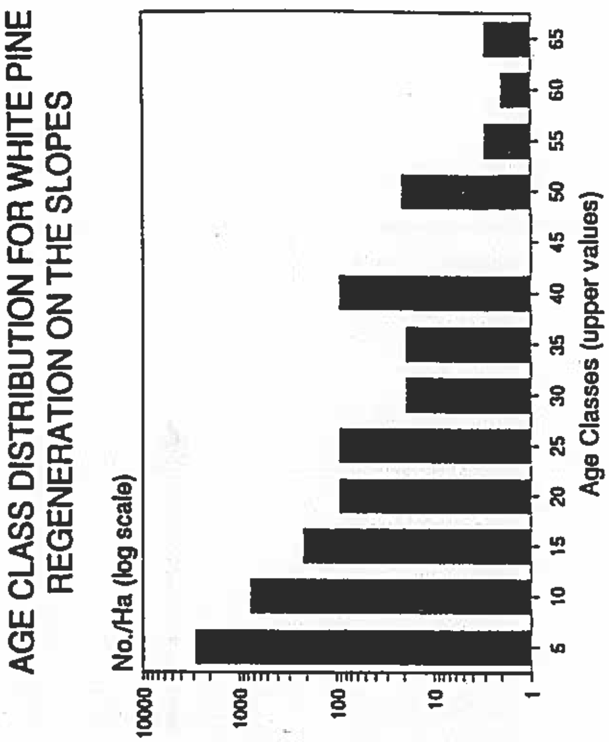
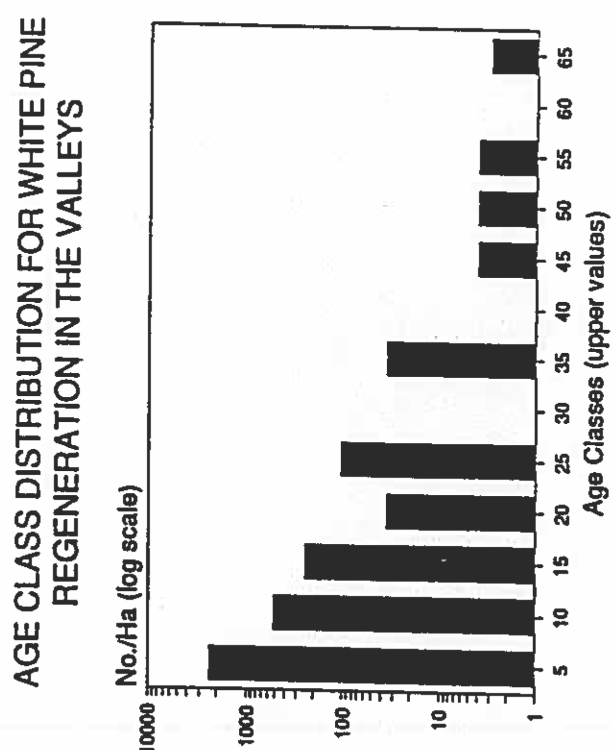


FIGURE 3 - AGE-CLASS DISTRIBUTION FOR WHITE PINE REGENERATION

ON HILLTOPS/RIDGETOPS, SLOPES AND VALLEYS







On both the middle and lower slopes compared to the upper slopes, north-facing aspects had both greater white pine regeneration density and greater white pine regeneration cover than on south-facing aspects.

The white pine age-class distribution for all 30 sample plots including all ages shows an inverse J-shaped curve which is typical of uneven-aged forests (Figure 5). White pine regeneration age-class distributions (ages 1-65) for the seven specific topographic positions are shown in Figure 4. Highest seedling production (ages 1-5) was on the upper slopes (3948/ha) and in the interior valleys (3817/ha). Lowest seedling production was in the shoreline valleys (902/ha) and on the lower slopes (1110/ha). A static age-class distribution has often been used to determine the probability of survival into older age classes (Krebs 1978, Holla and Knowles 1988). Applying this concept, it can be seen that highest recruitment of white pine into the four oldest regeneration-stage age classes (ages 46-65) occurred on the upper slopes (78/ha) and on the ridgetops (53/ha), whereas lowest recruitment into these older age classes occurred in shoreline valleys (0/ha) and on lower slopes (0/ha). This apparent absence of recruitment into the older age classes is, however, only a periodic event as white pine trees older than 65 years were observed in shoreline valleys and on lower slopes.

Eigenvalues for DCA axes 1, 2, 3 and 4 were .4126, .1237, .0528 and .0337, respectively. DCA axis 1 explains approximately 41% of the variation in the common understory species composition within the Obabika old-growth forest study area and DCA axis 2 explains approximately 12% of the variation. The eigenvalues for the last two axes are insignificaantly low. A scattergram of the 30 samples plotted with respect to DCA axes 1

FIGURE 4 - WHITE PINE REGENERATION AGE-CLASS DISTRIBUTIONS FOR SEVEN TOPOGRAPHIC POSITIONS

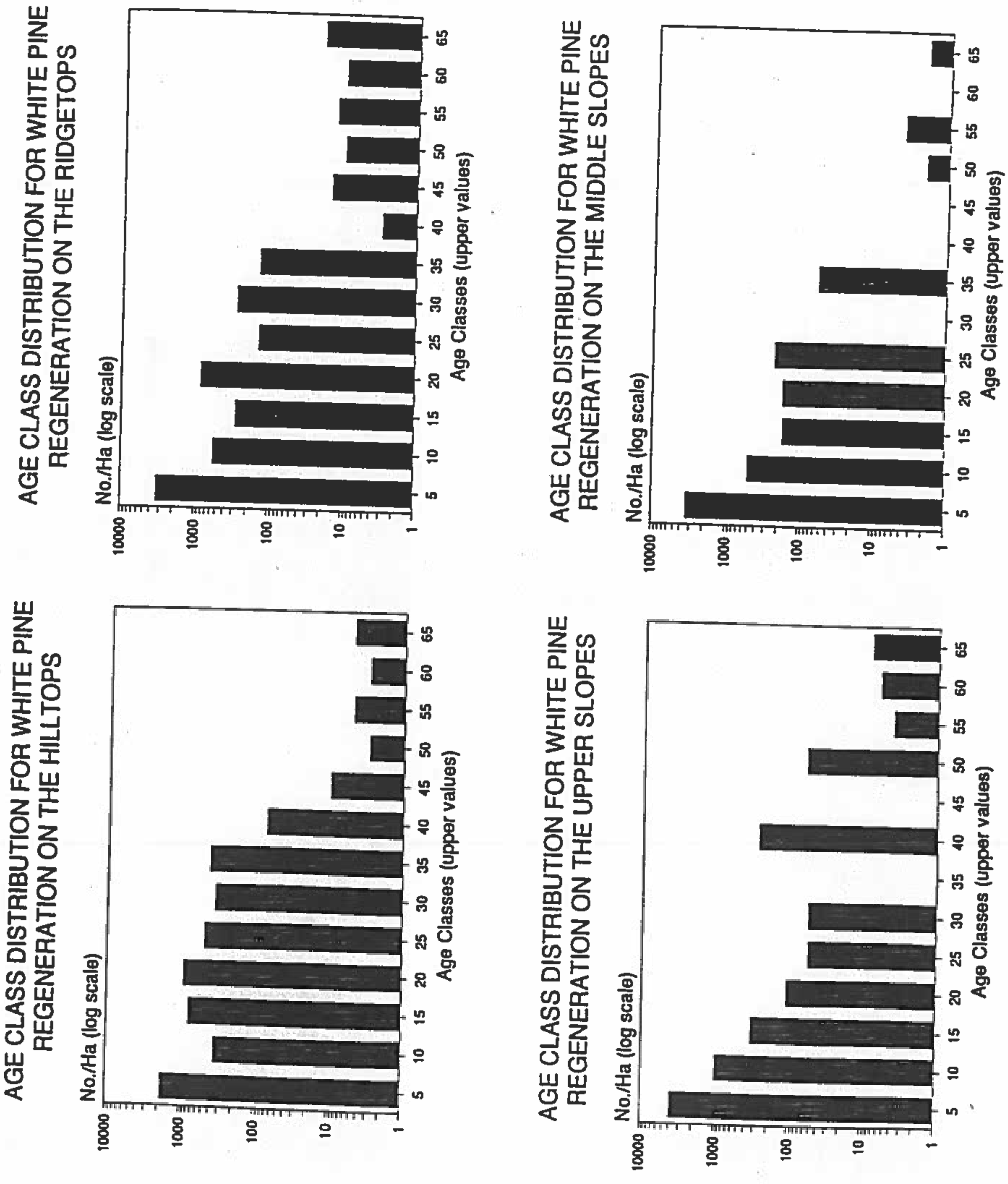
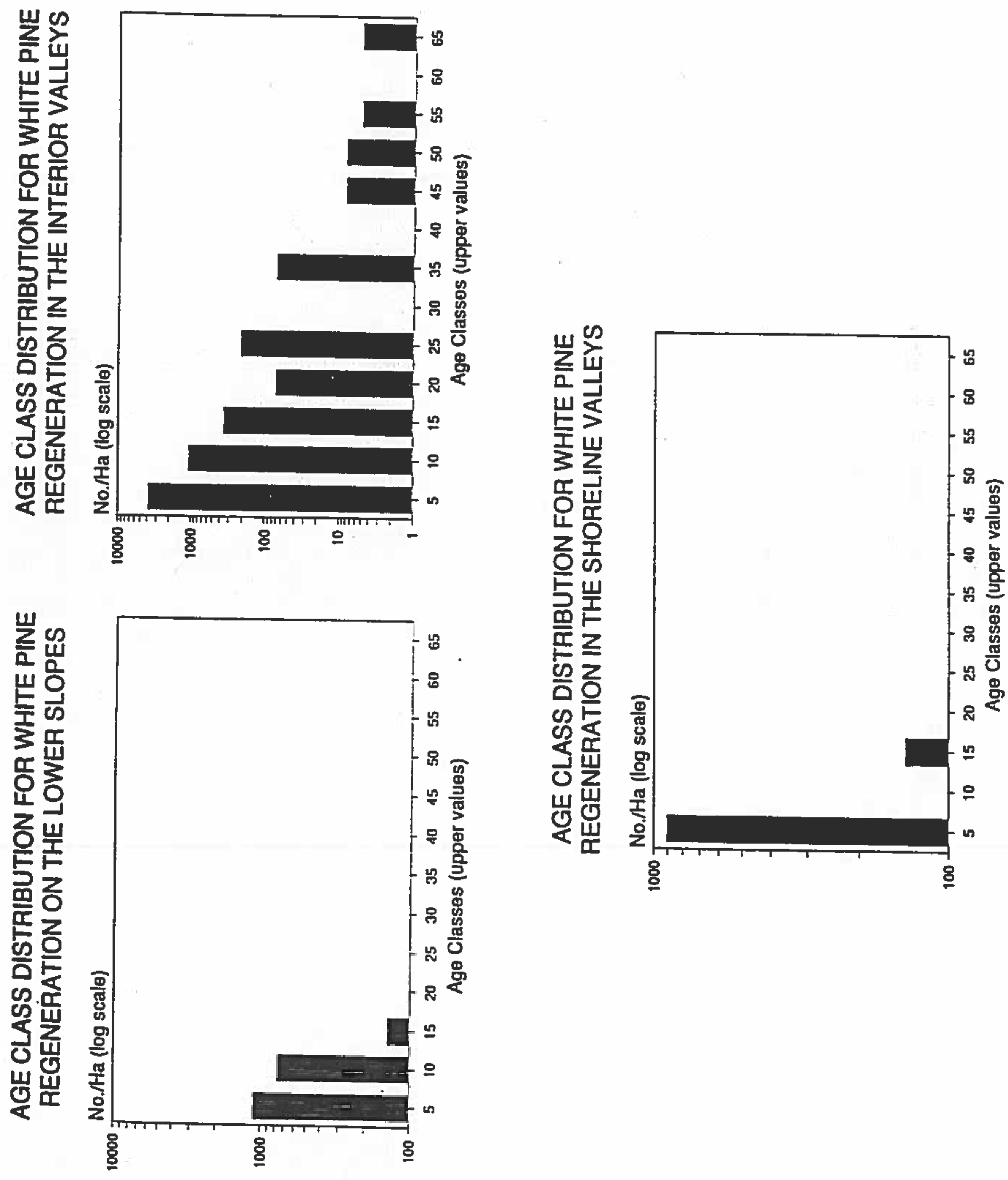


FIGURE 4 - WHITE PINE REGENERATION AGE-CLASS DISTRIBUTIONS

FOR SEVEN TOPOGRAPHIC POSITIONS - CON'T.



and 2 sample scores shows the ordination space for the hilltop/ridgetop, slope and valley topographic positions (Figure 6). The hilltop/ridgetop and valley ordination spaces do not overlap indicating that they have major differences in understory species composition.

For example, common understory species whose presence was most strongly associated with hilltops, ridges and upper slopes include late low blueberry (Vaccinium angustifolium), sheep laurel (Kalmia angustifolia), red pine (Pinus resinosa) and wintergreen (Gaultheria procumbens) (Table 3). In contrast, those common understory species whose presence was most strongly associated with lower slopes and valleys included mountain maple (Acer spicatum), large-leaf aster (Aster macrophyllus), yellow birch (Betula lutea), spinulose wood fern (Dryopteris spinulosa), violets (Viola spp.), tree clubmoss (Lycopodium obscurum) and oak fern (Gymnocarpium dryopteris) (Table 3). The most ubiquitous and abundant species (at least 90% frequency and at least 8% total cover) within the understory, in order of most to least abundant, were the mosses (Bryophyta spp.), balsam fir (Abies balsamea), black spruce (Picea mariana), Canada mayflower (Maianthemum canadense), braken fern (Pteridium aquilinum), clintonia (Clintonia borealis) and white pine (Pinus strobus) (Table 3).

The results of the correlation analysis (Table 4) show that the moisture index, balsam fir basal area, white cedar basal area, and deciduous tree species basal area are all significantly correlated with the three dependent variables. The highest correlations and the greatest number of correlations involve the DCA axis 1 sample scores. These scores are significantly correlated with all seven applicable independent variables presented in Table 4 and are most highly correlated with the

FIGURE 5 - AGE-CLASS DISTRIBUTION FOR THE WHITE PINE

POPULATION IN THE STUDY AREA

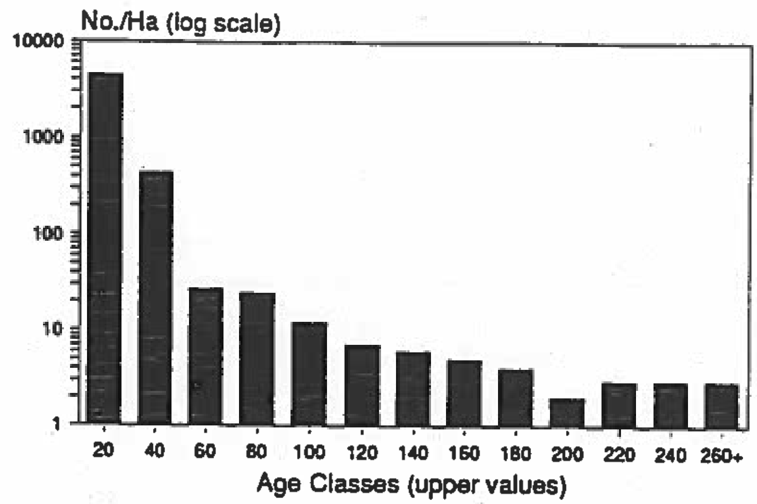


FIGURE 6 - DCA SCATTERGRAM OF THE 30 SAMPLES SHOWING

ORDINATION SPACE FOR THE HILLTOP/RIDGETOPS,

SLOPES AND VALLEYS

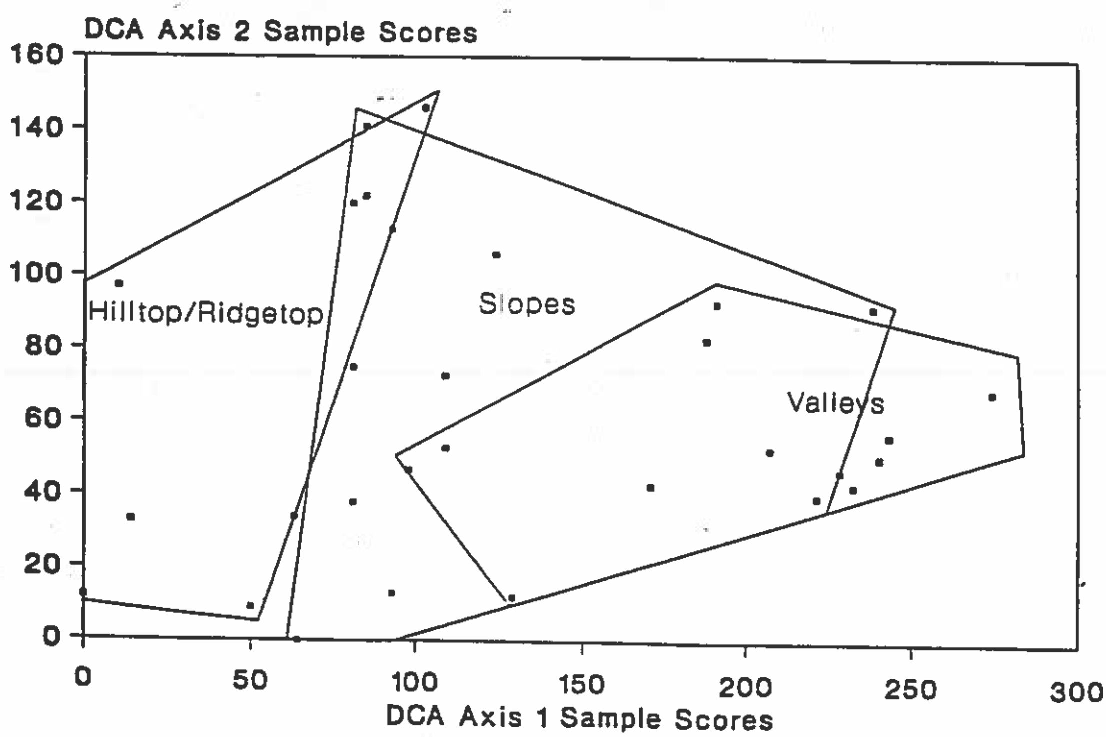


TABLE 3 - SPECIES COMPOSITION MATRIX FOR THE MOST COMMON UNDERSTORY PLANTS (criteria: (a) >4% cover in any one plot and present in at least one other plot, or (b) present in 15 or more plots; all values are in %cover; both species and plots are ordered according to DCA axis 1 scores; see species list for full species names; Tot=total)

	Sample Plots																														
Species	1	42	24	2	3	12	10	23	7	20	44	27	6	11	9	19	14	13	21	16	35	30	34	4	40	37	5	22	38	36	Tot
Lede groe		8																		1											.3
Kalm angu	21	30	16	1	18	8	11	1	5	5	3			2	2	2	2	1	3	1											4.4
Vacc angu	38	7	36	28	21	9	3	18	6	4	5	1	1	1	4	3	3	4	2		2	3	1	2				1			6.8
Vibu cass		3				1					6										1										.4
Gaul proc	7	1	7	2	6	4	11	2	4	3	2	4	7	1	8	1	1		1	2		1									2.5
Pinu stro	19	29	33	18	7	9	5	2	37	7	4	10	5	7	9	8	4	5	6	4	3	5	3	1		3		4	1		8.4
Pice mari	31	30	1	31	42	48		17	48	19	10	6	35	22	1	20	23	18	23	4	3	2	3	2	2		4		1		14.6
Pinu resi	12	1	3	5	42	4	1		7				22	1					1				1	10			5				3.9
Pter aqui	16	21	8	4	22	18	34	7	17	31	23	12	7	4	30	10	12	18	1	4	8	4	6	2			2		2	2	10.5
Betu papy	14		6	17	3	3	2	3	22	8	13	3	4	14	3		7	1	3		6		2	3	1			1	3	2	4.8
Vacc mert	1	11	1	3	2	10	11	6	13	16	17	13	2	5	20	11	7	3	6	4	4	1	1					2			5.6
Acer rubr	1	20	3	4	12	3	12	18	12	39	51	15	10	7	50	11	11	14	2	1		17		2			8	2		1	10.8
Gaul hisp		1		4	1	1		1	6		1					2	9	2	5	8	1	1									1.4
Pyru amer		1		1		1		7	3		7			3		2		1				4			3	2		1			1.2
Corn cana	4			2	1	1	5	3	4	2	7	4	7	3	2	4	6	1	4	13	1	7		3	6	1					3.0
Dier loni							1		1	1	2	1		1	1	1	2			1	1								1	1	.5
Bryo spp.	15	24	33	24	35	53	26	23	40	14	25	7	15	22	18	33	49	14	39	16	17	24	32	43	46	44	16	21	34	23	27.4
Maia cana	2		6	1	7	18	19	9	15	21	9	19	20	6	14	8	11	14	6	15	6	16	4	17	10	5	21	12	14	8	11.1
Copt groe							1		1		3				1	1	3			8		8		1	2	1					1.0
Abie bals	5	4	1	24	16	15	3	19	36	24	9	14	20	24	23	21	17	16	17	37	28	17	36	25	29	30	36	46	17	22	21.0
Trie bore			1		1	2	2	1	3	3	3	1	1	3	8	4	1	6	2	3	3	4	3	9	3	4	5	6	2	3	2.9
Clin bore	1	5	1	3	3	3	12	5	10	13	11	4	5	4	15	11	8	20	6	13	8	23	10	15	18	4	31	13	14	16	10.2
Linn bore										1		1		1	1		1		1	1	5	4		3		1		1	1		0.7
Thuj occi					19				13				11	2		3	7	2	25	19		11	12	38	10	6	1	14	14	9	7.2
Pice glau									3							1			3	11	3		3		5	2		6	2	1	1.3
Aral nudi							3	2	1	4	4	1	3		7	2	1	8	1	3	10	7	6	19	5	3	26	9	13	18	4.9
Gymn dryo																						7		1		2	1				0.4
Cory corn											3			1	4					3	13	13	14	14	3	5	21	1	8	4	3.2
Betu lute																				3		5				12			4		0.8
Dryo Spin											1								2					1	9	1		2	2	2	0.7
Aste macr							1								2			1		1	6	2	6	2		1	7	2	1	12	1.5
Viol spp.				1																				3		3	4	1	6	2	0.7
Lyco obsc												1													1	1		9	2	1	0.5
Acer spic											1				1		1			1	7	14	15	41	39	29	41	46	39	78	21.7

TABLE 4 - CORRELATION COEFFICIENTS FOR WHITE PINE REGENERATION PARAMETERS AND INDEPENDENT VARIABLES *

Independent Variables	Dependent Variables: White Pine Density (<66 yrs)	White Pine Cover (<10 cm dbh)	Understory DCA Axis 1 Sample Scores
Moisture Index	-.41	-.49	.78
Fire Scar Density	NS	NS	-.36
Ab Basal Area	-.40	-.37	.55
Bp Basal Area	NS	NS	.57
To Basal Area	-.39	-.40	.73
Deciduous Basal Area	-.36	-.40	.67
Total Basal Area	NS	-.55	.62
Bp Sapling Cover	.36	.52	NA
Pm Sapling Cover	NS	.44	NA
Ps Density (<66 yrs)	NA	.58	-.53

* All values significant at p<.05; independent variables that were not significantly correlated with any dependent variable included white pine basal area, red pine basal area, black spruce basal area, total understory cover, total sapling cover, balsam fir sapling cover, red maple sapling cover, black spruce sapling cover, white cedar sapling cover, and total herbaceous layer (< .5 m high) cover

Definitions: Ab-*Abies balsamea*, Bp-*Betula papyrifera*, Pm-*Picea mariana*, Ps-*Pinus strobus*, To-*Thuja occidentalis*

NS - not significant at p<.05

NA - not applicable

moisture index (.78) (Figure 7), white cedar basal area (.73) and deciduous trees basal area (.73). Of the three dependent variables, the DCA sample scores are the only ones that are significantly correlated with fire scar density (Figure 8). The DCA scores are also significantly correlated with white pine density (Figure 9).

White pine regeneration cover is significantly correlated with seven independent variables whereas white pine regeneration density is significantly correlated with only five independent variables. White pine regeneration cover is most highly correlated with total basal area (-.55), white birch sapling cover (.52) and the moisture index (-.49). One of the most abundant and ubiquitous species in the understory, black spruce sapling, is also significantly correlated with white pine regeneration cover. White pine regeneration density and white pine regeneration cover are also significantly correlated.

White pine regeneration density is most highly correlated with the moisture index (-.41), balsam fir basal area (-.40) and total basal area (-.39), however, the other two significant correlation coefficients are only slightly lower. Although the moisture index was based on only four ordinal values, its high correlation with white pine regeneration density and cover, and with community composition indicates its importance as one of the more influential site variables.

FIGURE 7 - VARIATION OF MOISTURE INDEX VALUES
ACCORDING TO DCA AXES 1 AND 2 SCORES
(x axis=DCA axis 1; y axis=DCA axis 2)

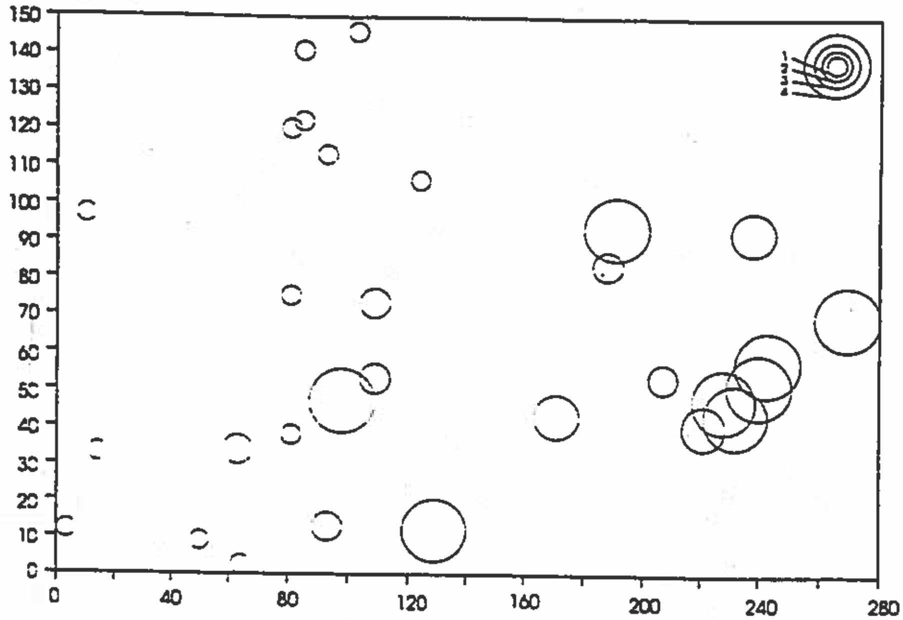


FIGURE 8 - VARIATION OF FIRE SCAR VALUES
ACCORDING TO DCA AXES 1 AND 2 SCORES
(x axis=DCA axis 1; y axis=DCA axis 2)

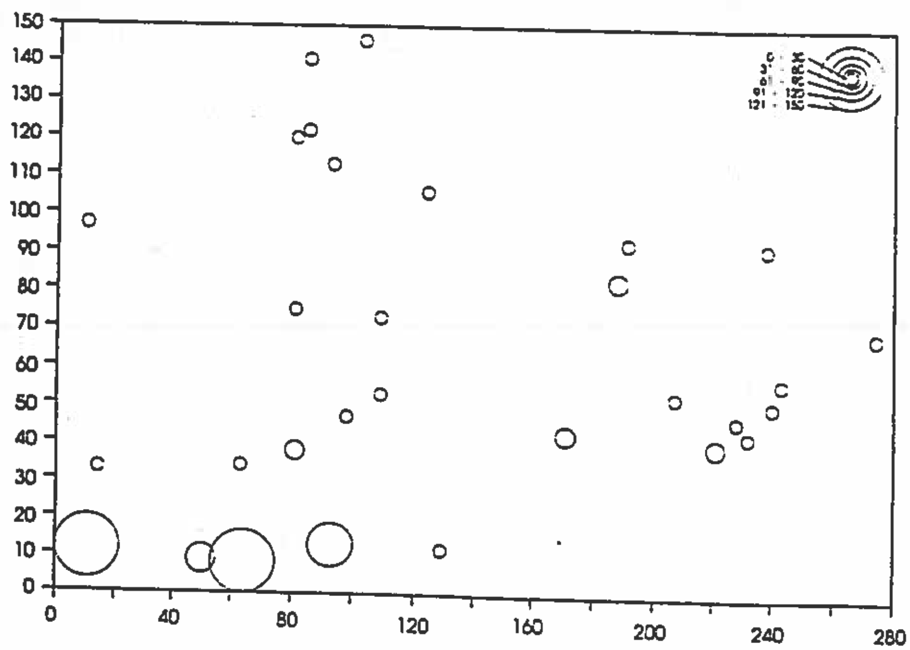
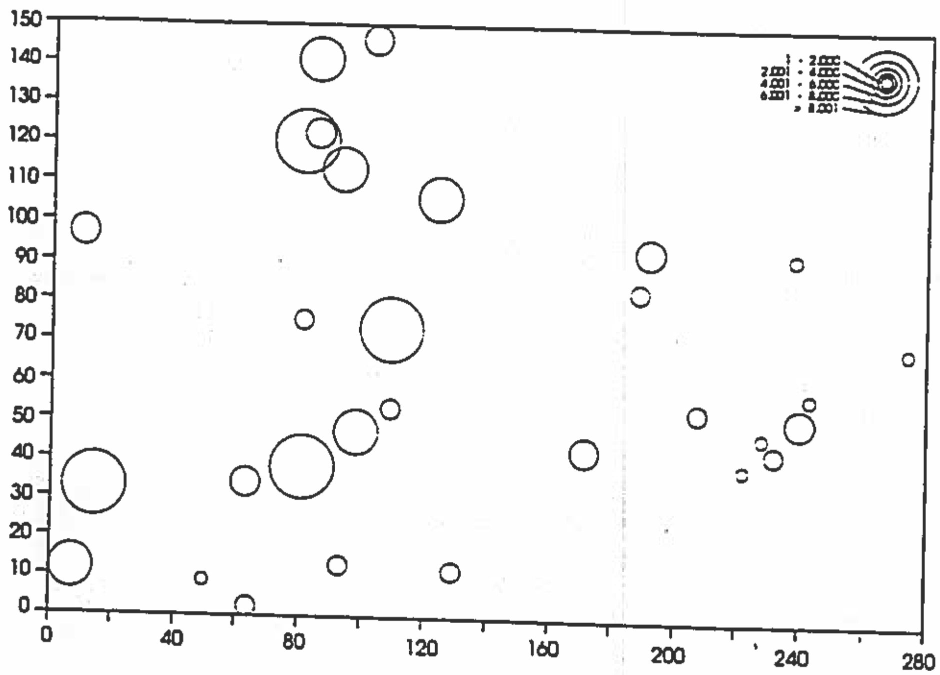


FIGURE 9 - VARIATION OF WHITE PINE REGENERATION DENSITY ACCORDING TO DCA AXES 1 AND 2 SCORES
(x axis=DCA axis 1; y axis=DCA axis 2)



DISCUSSION

White Pine Regeneration

The complete age-class distribution for the white pine population in the Obabika Lake old-growth pine stand displayed an uneven-aged condition similar to that obtained for white pine by Holla and Knowles (1988), Day and Carter (1991) and Quinby (1991b). For this regeneration study, only the portion of this complete age-class distribution between the ages of 1 and 65 years was analyzed relative to topographic variation.

Although white pine seedling (ages 1-5) production was similar for all three major topographic positions, and although white pine was one of the most ubiquitous and abundant species throughout the study area, overall white pine regeneration (ages 1 to 65) on hilltops/ridgetops in the Obabika Lake stand was three times more abundant relative to slopes and valleys. This is due to the fact that white pine regeneration on hilltops/ridgetops had over twice the probability of survival (mean age) relative to slopes and valleys and that its recruitment into the age group 46-65 on hilltops/ridgetops was much higher.

These patterns of white pine regeneration are influenced by a variety of factors that can be broadly categorized as disturbance, environmental conditions, resource availability and competition (Barbour et al. 1987). Although white pine regeneration and fire frequency are not directly correlated in this study, they are linked indirectly through their mutual correlation with DCA sample scores. In addition, visual analysis of Figure

8 shows a general trend of decreasing fire frequency moving from hilltops and ridgetops into valleys. The higher frequency of fire in upland areas relative to valleys has been observed by many researchers (Clements 1910, Larsen 1925, Barney 1968, Quirk and Sykes 1971, Loope and Gruell 1973, Tande 1979, Romme and Knight 1981, Hemstrom and Franklin 1982). This is due in part to the tendency for fire to burn upslope facilitated by upslope wind acceleration (Romme and Knight 1981, Hemstrom and Franklin 1982) and because upland areas have a higher probability of lightning strike (Brown and Davis 1973).

Higher fire frequency on upland sites is also facilitated by drier soil conditions due to drainage characteristics, exposure and forest floor composition (Horton and Brown 1960). Greater accumulations of water on the lower slopes and in the valleys results in more mesic conditions due to downslope drainage in contrast with the hilltops, ridgetops and upper slopes that have little or no drainage accumulation. Exposure to wind creating greater rates of evapotranspiration (Smith 1940, Stahelin 1943), especially on south- and west-facing slopes, also facilitates drier conditions on upland sites (Romme and Knight 1981).

Differences between understory vegetation composition on the hilltops/ridgetops versus the valleys were also found indicating a difference in habitat conditions between these two topographic positions. For example, both _Vaccinium angustifolium_ and red pine (saplings), which are common on hilltops and ridgetops, are known for their adaptations to post-fire conditions (Trevett 1962, Smith and Sparling 1966, Boerner 1981, Quinby 1988). Other species such as _Dryopteris spinulosa_ and yellow birch (saplings), which are common in valleys, are known for their adaptations to shaded, mesic conditions with low fire frequency (Maycock and Curtis 1960,Pregitzer and Barnes 1984, Quinby 1988).

Once white pine becomes established on dry sites, its superior root penetrating ability and deep tap roots (Brown and Lacate 1959, Spurr and Barnes 1980) enable it to outcompete most of its associates (Smith 1940, Fowells 1965). The higher mature pine density on the upland sites produces greater amounts of volatile pine litter resulting in greater forest floor flammability relative to the mesic litter on the lower slope and valley sites which has a higher, less flammable deciduous content (Horton and Brown 1960, Quinby 1987b).

It was on the sites of highest fire frequency, the hilltops, ridgetops and upper south-facing slopes in the Obabika Lake old-growth pine stand, that white pine regeneration was most abundant and had the greatest probability of survival. This higher frequency of non-catastrophic wildfire in upland areas, which leaves an intact canopy in most instances, facilitates white pine regeneration mainly through the reduction of ground level vegetation and exposure of mineral soil. Both of these events, when combined with adequate seed production, can result in efficient seed germination, rapid seedling establishment and rapid early growth of white pine (Maissurow 1935, Smith 1940, Shirley 1945, Logan and Brown 1956, Horton and Brown 1960, Heinselman 1973, Frissell 1973, Fahey and Reiners 1981). One old-growth stand dominated by white pine in the Temagami Region was analysed for fire frequency by Day and Carter (1991). The results of their analysis showed that white pine regeneration was over six times more abundant following surface fire than that following a more destructive crown fire.

Both Smith (1940) and Shirley (1945) determined that light was the resource most limiting to white pine regeneration. More precisely, however, tolerance to shade is the ability to be more competitive in obtaining nutrients and moisture under low light levels (Kimmins 1987, Keddy and MacLellan 1990). This is due primarily to the fact that root development depends on an adequate supply of light (Kurmis 1969). Thus, species that are adapted to extreme site conditions, such as white pine on xeric sites, may dominate for many generations irrespective of relatively low light levels at the forest floor (Spurr and Barnes 1980). White pine regeneration in the Obabika Lake old-growth stand did, in fact, have a much higher survival probability on the xeric sites such as hilltops, ridgetops and upper slopes.

In addition, within the Obabika Lake stand, white pine regeneration biomass increased with decreasing overstory biomass indicating a positive response to increased light penetration and reduced root competition from valleys to hilltops/ridgetops. For white pine seedlings growing in central New England, Smith (1940) found an increase in growth rate in direct proportion to the amount of radiation available. Even where light levels are very low beneath the forest canopy, white pine can survive with minimal growth for up to 60 years and can respond to release with vigorous growth within two to three years (Horton and Brown 1960, Brown 1984). Satisfactory first year seedling growth can occur with as little as 20 percent full sunlight (Smith 1940).

In particular, within the Obabika Lake stand, white pine regeneration decreased with increasing balsam fir and white cedar overstory abundance, both of which wer· most common on the lower slopes and in the valleys.

Both balsam fir and white cedar are more shade tolerant and less drought tolerant than white pine (Fowells 1965) and thus regenerate more successfully in the shaded mesic conditions of lower slopes and valleys. Of all the tree sapling species, white pine regeneration was positively correlated with white birch and black spruce abundance. Whether competition with these species results in reduced white pine regeneration is unclear from these results. It is more likely that the positive correlation with white birch saplings is due to its tendency to colonize recently burned sites and its relative shade intolerance (Fowells 1965). The positive correlation with black spruce saplings is more likely a relection of its ability to colonize and grow under dry and nutrient poor conditions (Fowells 1965).

White pine regeneration was not correlated with total herbaceous cover, total sapling cover or total understory cover as would be expected from results obtained by Shirley (1945), Horton and Brown (1960) and Kurnis (1969). More rigorous analysis using more than 30 samples will be required to adequately examine the effects of competition on white pine regeneration.

At a finer topographic scale, some contradictions to these general findings on white pine regeneration were discovered. First, white pine regeneration on north-facing lower and middle slopes was more abundant and had a higher survival probability than that on south-facing lower and middle slopes. This may be due to the drier conditions on south-facing slopes which, during drought periods, would put greater stress on pine seedlings due to competition. In addition, mosses are over 50 percent more abundant on the middle and lower north-facing slopes relative to the middle and lower south-facing slopes. Mosses can be favourable seedbeds for white pine as they protect the mineral soil from rapid evaporation, thus ameliorating the stress of drought (Kurmis 1969).

Second, white pine regeneration on north-facing middle slopes was more abundant than that on hilltops with recent crown fire, ridge plateaus and ridgefaces. In this case, the abundance of mosses may again be important. Mosses were, on average, two times more abundant on the middle north-facing slopes compared with the hilltops and ridgetops. Although the probability of survival is not as high on the middle, north-facing slopes due most likely to more intense competition (Logan and Brown 1956), the greater abundance of moss facilitates higher seedling production compared to hilltops and ridgetops which are more subject to drought conditions.

And third, white pine regeneration in the interior valleys was more abundant than that on lower and middle slopes while regeneration survival probability was roughly the same. Being positioned vertically below slopes, hilltops and ridgetops, valleys most likely receive the greatest amount of seed during dispersal thus increasing potential seedling numbers. In addition, it is possible that the floors of these interior valleys are lined with well-drained fluvial material which tends to be drier than adjacent till soils on the hillslopes thus supporting less competing vegetation for white pine regeneration (Logan and Brown 1956).

The findings of this study show that an uneven-aged white pine population in the Obabika Lake old-growth pine stand has been regenerating under a non-catastrophic disturbance regime contrary to the findings of Chapeskie et al. (1989). Although white pine regeneration beyond the age of 15 is absent on some lower slope and valley sites, the presence of mature and old white pine trees in these areas attests to the success of white pine regeneration on these sites. Aside from the influence of fire, white pine regeneration, particularly on the lower slopes and in the valleys, may also be facilitated by the death of individual trees which creates canopy gaps (Hibbs 1982), windthrow which creates canopy gaps and exposes mineral soil (Cline and Spurr 1942, Goodlet 1954, Kurmis 1969), mammals that cache and distribute pine seeds (Abbott and Quink 1970, Miiyaki 1987, Hayashida 1989), and by suitable germination substrate provided by decomposing coarse woody debris (Harvey et al. 1987).

Management practices designed to regenerate white pine within non-regenerating intact old-growth white pine stands must recognize the delicate balance among a variety of factors that facilitate white pine regeneration. These factors include, but may not be limited to, fire frequency and intensity, soil nutrient and moisture conditions, litter composition and thickness, seed production and dissemination, light and root competition, and seed and seedling predation. Not only do these factors and their interactions vary with topography but they vary also with season and forest development.

Value as a Protected Area

It was "...the harvest of eastern white pine [that] generated the capital and jobs needed to nourish the settlement of Ontario, and ultimately led to the confederation of the provinces" (Aird 1985). However, only approximately .2 percent of the original old-growth white pine (*Pinus strobus* L.) forests of Canada and the United States remain

(Quinby 1991a). Of all the remaining stands of old-growth white pine, the stand at the north end of Obabika Lake is the largest known in the world (Quinby 1991a). And, of all the old-growth white pine stands surveyed to date in the Temagami Region, the Obabika Lake stand is the most healthy with respect to white pine regeneration and stand size (Day and Carter 1991, Quinby 1991b, Quinby 1991c).

Thus, this stand represents one of the best opportunities in the world to study the natural ecology of white pine forest development. The results of such studies will provide the knowledge necessary to develop management plans for ensuring the survival of the Obabika Lake stand as well as many other old-growth white pine stands throughout its natural range. In addition, the results of such studies will be useful for developing sustainable management practices for white pine fibre production.

Old-growth forests are also valuable for the ecological services they provide. They maintain soil stability and water quality, retain large amounts of limiting nutrients, provide a reservoir of genetic diversity, provide unique wildlife habitat and act as carbon sinks which can help to ameliorate global warming.

Management Problems

Many problems must be overcome if the Obabika Lake old-growth pine stand is to be managed successfully as a protected area. To date, this stand has yet to receive legal protection and thus, could still be logged. Its future rests with the newly created Wendabon Stewardship Authority. A stand of such global significance should receive the highest form of legal protection either as a provincial wilderness park or nature reserve.

Once the stand is legally protected, a management plan that addresses both internal and external pressures must be developed. The most effective type of nature reserve management is based the continuous refinement of management practices according to the periodic findings of a well-established research program. At present, the most important management objective for the Obabika Lake old-growth stand will be to facilitate a natural wildfire regime to ensure the regeneration of white and red pine. Although our current understanding of pine silvics and fire ecology will allow us to start identifying certain techniques, a few key studies will be required to fine tune such practices to ensure success. In addition, a number of practices should be experimented with on a small scale within the stand so that those which are most successful can be used. As particular techniques are focussed on, permanent plots should be established so that long-term monitoring studies of these techniques can be conducted. With the results of these long-term studies, management practices can be continually refined and improved.

As the public becomes increasingly more interested in wilderness, forests and natural heritage, more recreational pressures will threaten certain portions of the Obabika Lake old-growth forest. Specific guidelines to control recreational activities within the stand should be developed in order to minimize vegetation trampling, erosion and waste accumulation.

External pressures emanating from outside of the protected area must also be addressed. Protection from adjacent land-use activities can be partially accomplished through the use of a buffer zone, perhaps up to

500 m in width. The more subtle effects of influences such as acid deposition and global warming are much more difficult to address and must be pursued through a variety of regional planning and political mechanisms.

SUMMARY

1. The age-class distribution for the white pine population in the Obabika Lake old-growth pine stand displayed a typical uneven-aged condition.

2. For hilltops and ridgetops versus slopes and valleys, (a) white pine regeneration for the ages 1-65 years was three times more abundant, (b) white pine regeneration had twice the probability of survival, and (c) recruitment into the oldest age group (46-65) was much higher.

3. Fire was most frequent on the upper most upland sites mainly because of wind patterns, lightning probability, drier soil conditions and more volatile litter.

4. It was on these upland sites of highest fire frequency that white pine regeneration was most dense and had the greatest probability of survival.

5. It is likely that non-catastrophic surface fires, relative to catastrophic fires, facilitated greater white pine reproduction by reducing competition, exposing mineral soil and leaving living pine as seed sources.

6. Light is likely the most limiting growth resource for white pine especially in terms of its influence on root development and absorbtion of water and nutrients.

7. Correlations between white pine regeneration and the abundance of other species are most likely a reflection of habitat preferences rather than the result of competition.

8. More detailed and rigorous studies will be required to elucidate relationships between competition and white pine regeneration.

9. Mosses may play a role in facilitating white pine regeneration by reducing evaporation of moisture from mineral soil.

10. White pine regeneration is most likely determined by a delicate balance among a variety of major factors including fire frequency and intensity, soil nutrient and moisture conditions, litter composition and thickness, seed production and dissemination, light and root competition, and seed and seedling predation. The interactions and combinations of these variables change mainly as a function of topography, season and forest development.

11. The Obabika Lake old-growth pine stand is the largest known stand of its type remaining in the world, yet it remains legally unprotected at this time. Although it will have many values as a protected area, perhaps it is most valuable as a site for scientific study and

education focussing on the sustainability of natural ecosystems.

12. At present, if the natural condition of the Obabika Lake old-growth pine stand is to be maximized, a natural wildfire regime must be facilitated.

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