

Self-replacement in old-growth white pine forests of Temagami, Ontario

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ABSTRACT

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Surveys of both live and dead vegetation were conducted to examine long-term successional trends in old-growth white pine forest. The forest successional trend, for a period of possibly up to seven centuries, shows that white pine has been the dominant species over this time period indicating that these old-growth white pine forests have been self-replacing. Size-class analysis was used as an indicator of age-class structure. Results of this analysis show that the old-growth white pine stands are at least partially uneven-aged. The uneven-aged condition, resulting from continuous recruitment, was most likely facilitated by local disturbances such as small surface fires, windthrown trees and the death of large individual trees through biological or other agents. These findings cast some doubt on the silvicultural theory that catastrophic fire is the only primary facilitator of natural white pine regeneration. Selection logging in white pine forest may make better use of the various non-catastrophic mechanisms of natural white pine regeneration. It is unlikely, however, that the old-growth condition can be maintained or enhanced under any cutting regime. In addition to the production of fibre, old-growth forests are valuable components of the landscape from both a functional ecological perspective and a scientific perspective.

INTRODUCTION

The view that fire creates even-aged eastern white pine (*Pinus strobus* L.) stands (Maissurow, 1935; Horton and Bedell, 1960; Stiell, 1978) has spawned the silvicultural theory that over-mature (also known as “old-growth”) white pine forests will simply fall apart in the absence of the catastrophic fires required to initiate even-aged stands. Thus, the theory follows that without catastrophic disturbance, fibre will be wasted unless the stand is actively managed. In Ontario, silvicultural guidelines for white pine harvesting state that white pine “...must be managed under some form of even-aged management system; uneven-aged management by the selection system is not acceptable” (Ontario Ministry of Natural Resources, 1983). As a result, the management strategy in many parts of Ontario, including the Temagami Region, has been

to clearcut old-growth white pine forest and maximize the number of rotations thereafter in order to obtain greatest fibre production (Ontario Ministry of Natural Resources, 1985; Stiell, 1985).

Recent studies, however, have shown that continuous white pine recruitment occurs within old-growth white pine dominated stands (Gilbert, 1978; Holla and Knowles, 1988; Quinby, 1989). This continuous recruitment of white pine may take place for centuries in response to non-catastrophic disturbance resulting in at least a partial uneven-aged stand structure. Non-catastrophic disturbances in the old-growth coniferous forests of the Pacific Northwestern USA are also critical to successful regeneration of shade tolerant as well as shade intolerant tree species (Spies and Franklin, 1989).

To date, studies of old-growth white pine forest dynamics in the northern portions of its range have focussed only on the living tree component resulting in descriptions of vegetation development limited to the number of years equivalent to the oldest trees in the stand, usually between 200 and 300 years (Gilbert, 1978; Holla and Knowles, 1988). By including dead vegetation as evidence of past forest composition, the successional sequence can be expanded by many years (Henry and Swan, 1974; Oliver and Stephens, 1977). The purpose of this study was to examine self-replacement and its general features in old-growth white pine forest. This was accomplished by reconstructing the composition and abundance of dead trees combined with sampling live overstory and understory trees in order to identify general successional trends. Implicit in the process of self-replacement in eastern North American forests unaffected by catastrophic disturbance is gap-phase regeneration hitherto only associated with deciduous dominated forests (Lorimer, 1980; Runkle, 1981, 1982).

STUDY AREA

The old-growth white pine forest in the Wakimika Triangle Area of Temagami, Ontario has been identified as the largest continuous stand of old-growth white pine forest remaining in the province (Pinto., 1989). The Wakimika Triangle Area is centrally located within the Temagami Region and lies adjacent to the southeast corner of Lady Evelyn-Smoothwater Provincial Park (Fig. 1). The study area included most of Shelburne Township, the northeastern portion of Delhi Township and the extreme western portion of Canton Township. It is centred approximately at latitude $47^{\circ}10'N$, longitude $80^{\circ}20'W$.

General features of the climate in the Temagami Region were provided by Brown et al. (1980). Mean daily temperature varies from $-13^{\circ}C$ for January to $19^{\circ}C$ 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.

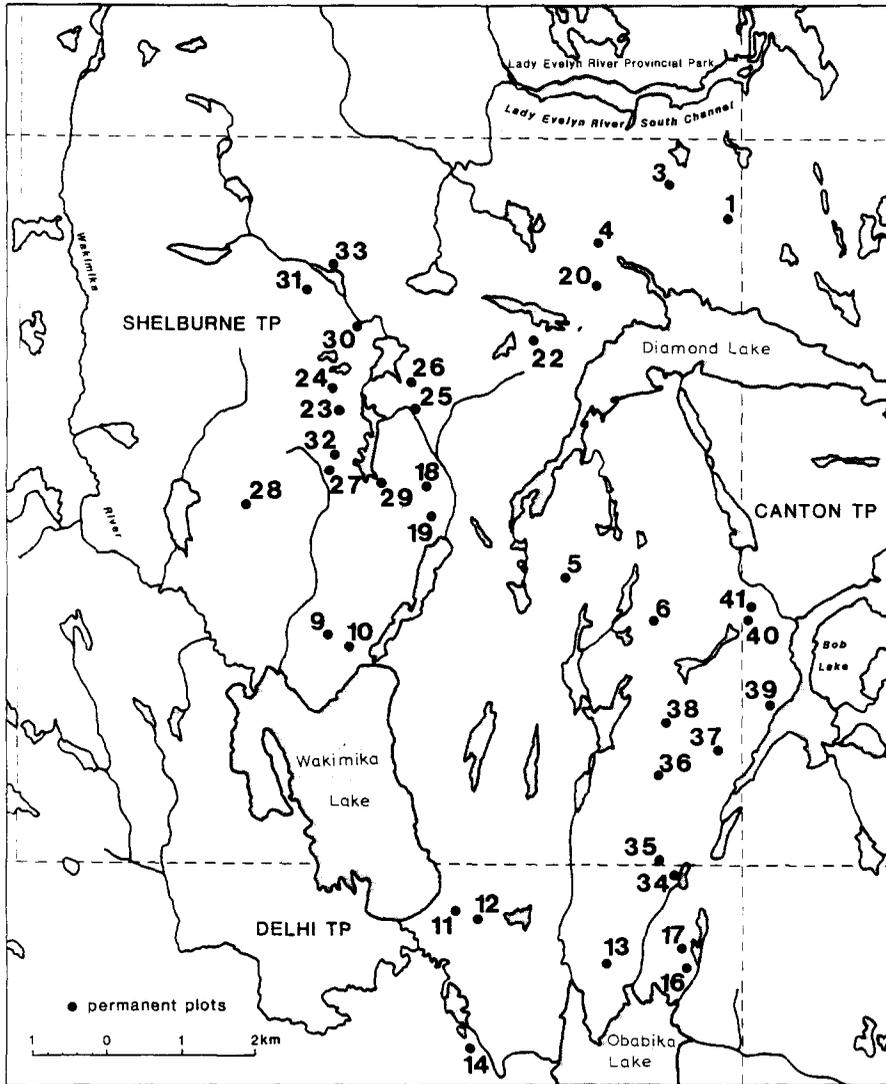


Fig. 1. Location of study area and plots.

The terrain throughout much of the Wakimika Triangle Area is very rugged featuring steep topography including many escarpments, with ever changing elevations that range from 275 to 460 m above sea level. The surficial geology is controlled mainly by the results of Wisconsin glacial activity and to a lesser extent by the underlying bedrock. There are many lakes both large and small 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 caused by 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 forest vegetation of the Temagami Region falls within the Laurentian Upland Section, Great Lakes–St. Lawrence Division, Hemlock–White Pine–Northern Hardwoods Forest Region (Braun, 1950). Rowe (1972) has described the forests of the area as 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.”

In addition, McAndrews (1978) has shown that the center of white pine abundance in Ontario is located in the Temagami Region.

METHODS

Forest succession was reconstructed using both live and dead vegetation to examine the hypothesis that old-growth white pine forest is self-replacing. Logs were studied to determine the abundance and composition of the oldest forest. Snags (dead standing trees), which are generally younger than logs, were sampled to represent the more recent forest. The abundance and composition of the present forest was obtained by sampling the live trees, and the potential composition of the future forest was assessed by sampling tree regeneration in the understory.

The major weakness of this approach is that it does not incorporate the technique of cross-dating which provides for the determination of the year in which an individual tree died, allowing for a precise chronology of events. Thus, the approach used could not account for (1) the differential rate of decay between species, or (2) events in which a tree became a log without ever having been a snag. The state of decay (e.g. snag or log) is therefore, not always directly related to age. For example, a tree toppled by windthrow would be classified as a log and accordingly would be misinterpreted as being older than members of its cohort many of which may still be live trees. Recent windthrown trees were, however, seldom observed in the sample plots. Despite this weakness, this approach was useful for identifying general successional trends.

Old-growth forests are characterized by minimum amounts of old live trees, snags and logs (Old-Growth Definition Task Group, 1986). The major criterion used to select plots for this study was the presence of a minimum of two white or red pine trees each at least 140 years old within a 50×20 m plot. This minimum criterion was based on quantitative vegetation survey results from the Big Crow Nature Reserve in Algonquin Park, Ontario (Sheehey, 1980), which is considered by the Ontario Ministry of Natural Resources to be one of the finest examples of old-growth white pine forest in North America (Strickland and Ward, 1987). Through his survey work in Algonquin's old-growth white pine stands, Sheehey (1980) found that at most, two old white pine trees could be included within a circular plot of 1256 m².

A total of 36 plots within old-growth white pine stands of various sizes were established and permanently marked for future relocation within the Wakimika Triangle Area (Fig. 1) during July and August of 1988. To sample the overstory, all trees 10 cm diameter at breast height (dbh) and greater within the plot were identified, measured for dbh, and numbered using plastic tags. All snags greater than 10 cm dbh and taller than 2 m within the plot were identified to the species level when possible and measured for dbh. Logs occurring within the plot having a minimum diameter of 15 cm at the larger end and a minimum length of 1 m were also inventoried. Log measurements included diameter at each end and total length. In the case of genus level identification for both snags and logs, the proportion of species positively identified within that genus was used to allocate the unknown amount to the abundance of those species positively identified within that genus. Those logs that could not be identified to the genus level were excluded from the analysis.

Tree regeneration was defined as trees that were less than 10 cm dbh. A total of 11 2×1 m quadrats for estimating the percent cover of tree regeneration were located at 5 m intervals along the first 50 m side of the plot. The 2 m side of the quadrat was positioned perpendicular to the 50 m side such that the quadrat side ran 1 m either side of the plot line.

For each individual tree and snag sampled, dbh values were converted to

basal area values expressed as $\text{m}^2 \text{ha}^{-1}$. Log diameter and length measurements were used to produce log volume estimates. These basal area and volume estimates were then summed by species for each plot and for the study area as a whole. Tree regeneration cover for each species was estimated for each plot and for the study area as a whole.

A size-class analysis based on eight plots within the largest old-growth white pine stand in the study area was carried out. At each of the 36 plots, observations on fire and windthrow were also made. Nomenclature followed Fernald (1950).

RESULTS

A total of 12 tree species were found within the old-growth white pine forest in the Wakimika Triangle Area (Table 1). All 12 occurred within the living overstory. Table 1 and Fig. 2 show the absolute and relative abundance of trees, snags, logs and regeneration. The most abundant species in the living overstory of these old-growth stands was white pine ($19.5 \text{ m}^2 \text{ha}^{-1}$) followed by red pine ($3.7 \text{ m}^2 \text{ha}^{-1}$) and white birch ($3.4 \text{ m}^2 \text{ha}^{-1}$). A total of 10 snag species were found in the study area. Of the 12 tree species found in the study area, yellow birch and red oak were missing from the snag component. White pine dominated the snag component with a basal area of $4.1 \text{ m}^2 \text{ha}^{-1}$, followed by white birch ($1.2 \text{ m}^2 \text{ha}^{-1}$) and balsam fir ($0.7 \text{ m}^2 \text{ha}^{-1}$). A total of nine log species were identified in the log component. Of the 12 tree species, yellow birch, red oak and red maple were absent from the log component. The most abundant species in the log component was white pine ($35.5 \text{ m}^3 \text{ha}^{-1}$) followed by white birch ($8.3 \text{ m}^3 \text{ha}^{-1}$) and red pine ($5.7 \text{ m}^3 \text{ha}^{-1}$).

TABLE 1

Summary of vegetation data for old-growth white pine stands

Species	Regeneration (% cover)	Trees (m^2 ha^{-1})	Snags (m^2 ha^{-1})	Logs (m^3 ha^{-1})
<i>Abies balsamifera</i>	19.4	0.6	0.7	1.6
<i>Picea mariana</i>	14.2	2.1	0.5	2.5
<i>Acer rubrum</i>	13.4	0.2	0.1	
<i>Pinus strobus</i>	6.3	19.5	4.1	35.5
<i>Betula papyrifera</i>	3.7	3.4	1.2	8.3
<i>Picea glauca</i>	2.6	0.6	0.1	0.1
<i>Thuja occidentalis</i>	1.1	1.9	0.1	0.8
<i>Betula lutea</i>	0.2	0.1		
<i>Populus</i> spp.	0.2	0.2	0.1	0.7
<i>Pinus resinosa</i>	0.1	3.7	0.3	5.7
<i>Pinus banksiana</i>		0.4	0.2	0.6
<i>Quercus rubra</i>		0.1		

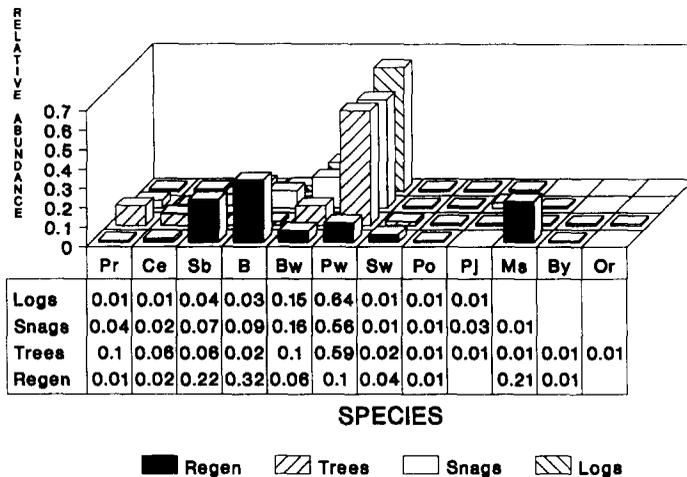


Fig. 2. Relative abundance of regeneration, trees, snags and logs in old-growth white pine stands. Key to species: Pr, red pine; Ce, white cedar; Sb, black spruce; B, balsam fir; Bw, white birch; Pw, white pine; Sw, white spruce; Po, poplar; Pj, jack pine; Ms, red maple; By, yellow birch; Or, red oak.

A total of 10 tree species were present in the understory of the old-growth white pine stands. Of the 12 tree species, both jack pine and red oak were absent. In contrast to the dominance of white pine in the overstory, snag and log components, white pine (6.3% cover) was only the fourth most abundant species within the understory behind balsam fir (19.4% cover), black spruce (14.2% cover) and red maple (13.4% cover). The success of tree regeneration, however, depends on more than species abundance. Also important to successful regeneration are species growth strategies and the availability of resources necessary for growth.

Figure 3 shows the size-class distribution for all overstory species sampled within the largest old-growth white pine stand. The inverse “J” shaped curve is typical of an uneven-aged forest where many stems are present in the smaller size classes and where there is a rapid decrease in stem number through the progression to the largest size classes. When the size-class distribution for white pine alone is plotted for this stand, a more variable curve emerges (Fig. 4). The combination of some size classes (1, 2, 3, 7, 8, 14, 17, 18) fits the standard uneven-aged curve, whereas the peaks expressed by two other groups of size classes (4, 5, 6 and 9, 10, 11, 12, 13) are more characteristic of an even-aged size-class structure.

The species consistently of greatest abundance within the log, snag and overstory tree component included white pine, white birch, black spruce, red pine and balsam fir. Figure 5 shows the relative change in abundance over time for these five species. From this figure it can be seen that coincident with

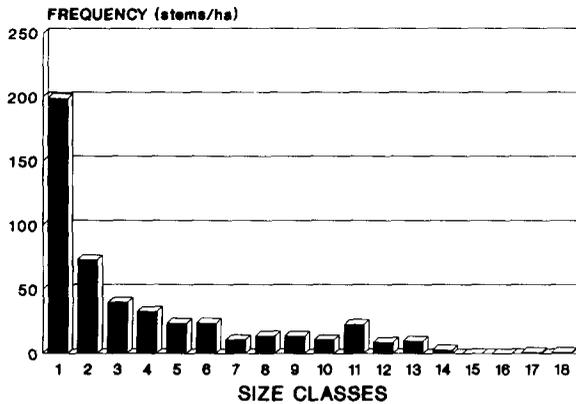


Fig. 3. DBH size-class distribution for all species in old-growth white pine stands, Size-class key (in cm): 1 (10.0–14.9), 2 (15.0–19.9), 3 (20.0–24.9), 4 (25.0–29.9), 5 (30.0–34.9), 6 (35.0–39.9), 7 (40.0–44.9), 8 (45.0–49.9), 9 (50.0–54.9), 10 (55.0–59.9), 11 (60.0–64.9), 12 (65.0–69.9), 13 (70.0–74.9), 14 (75.0–79.9), 15 (80.0–84.9), 16 (85.0–89.9), 17 (90.0–94.5), 18 (95.0–100.0).

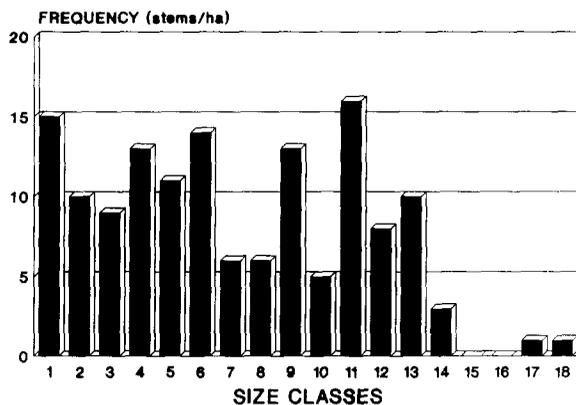


Fig. 4. DBH size-class distribution for white pine in old-growth white pine stands. Size-class key (in cm): 1 (10.0–14.9), 2 (15.0–19.9), 3 (20.0–24.9), 4 (25.0–29.9), 5 (30.0–34.9), 6 (35.0–39.9), 7 (40.0–44.9), 8 (45.0–49.9), 9 (50.0–54.9), 10 (55.0–59.9), 11 (60.0–64.9), 12 (65.0–69.9), 13 (70.0–74.9), 14 (75.0–79.9), 15 (80.0–84.9), 16 (85.0–89.9), 17 (90.0–94.5), 18 (95.0–100.0).

a decrease in white and red pine from the log component to the snag component was an increase in balsam fir, black spruce and white birch. With an increase in white and red pine abundance from the snag to the tree component there was a corresponding decrease in the other three species. This inverse relationship between changes in species abundance may reflect species growth strategy responses to both disturbance and stand aging.

Evidence of windthrow was observed in or immediately adjacent to 26 of

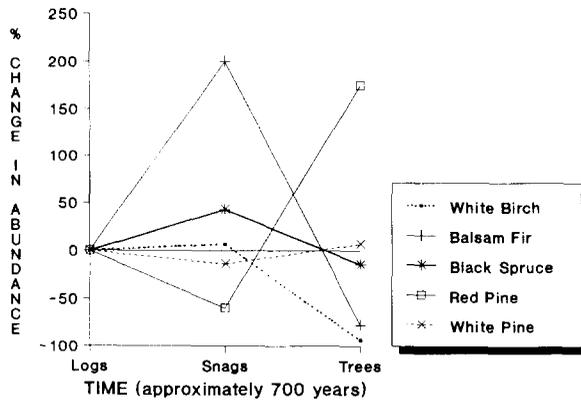


Fig. 5. Relative change in abundance for the five major tree species in a reconstructed old-growth white pine successional sequence.

the 36 plots or at approximately 72% of the plots. Evidence of fire in the form of fire scars on trees was observed in 22 of the 36 plots or at approximately 61% of the plots.

DISCUSSION

General successional trends for old-growth white pine forests in Temagami were examined by sampling both live and dead vegetation. Because data were not available for the rate of log decay of large white pine trees it was necessary to estimate the time period represented in these reconstructed successional trends using data available for Douglas-fir log decay. Douglas-fir logs between 40 and 60 cm dbh require up to 350 years to decompose (Harmon et al., 1986) and decomposition rates for Douglas-fir biomass may be more than twice that of white pine (data from Alway and Zon, 1930; NOAA, 1980; Cole and Rapp, 1981; Vogt et al., 1986). Extrapolating from these data, it is possible that large white pine may require up to 700 years to decompose completely. Accounting for the fact that many logs in their final stages of decomposition were excluded from the data set, it is likely that the successional trends represented by the dead wood component in this study represent up to 500 years of vegetation development. By adding 200 years to represent the live tree component, successional trends in this study may represent up to 700 years of vegetation development.

The reconstructed successional trend for this period shows that white pine has been the dominant species within these old-growth forests. Results of the size-class analysis show that this dominance of white pine over the past several centuries has been maintained by continuous recruitment of white pine which resulted in an uneven-aged condition. This condition has also been ob-

served in old-growth white pine forests in other parts of Temagami (Gilbert, 1978) and in northeastern Ontario (Holla and Knowles, 1988). In contrast, if these old-growth white pine forests were solely dependent on catastrophic fire for regeneration, even-aged stands with little or no continuous recruitment would dominate.

Over the time period examined, the abundance of white pine fluctuated less than any other species of major importance including red pine, black spruce, balsam fir and white birch. This suggests that white pine is most highly suited for the habitat conditions of the sites studied. When white and red pine reached their lowest abundance midway through the succession sequence, the three other species of major importance peaked in abundance. Declines in white and red pine abundance accompanied by increases in white birch, balsam fir and black spruce have also been shown from pollen analysis for a site only a few kilometres from the study area (Gordon, 1991). This cyclical or alternating species co-dominance (Fox, 1977) is a reflection of differing life history patterns of the resident tree species as they relate to conditions created by continuously occurring non-catastrophic, small-scale disturbances that shift throughout the landscape over time (Bormann and Likens, 1979; Barbour et al., 1987).

In contrast to shade-tolerant species, such as balsam fir and black spruce, and in contrast to shade-intolerant species such as red pine and white birch, white pine is intermediate in shade tolerance (Baker, 1949; Logan, 1966). In addition, it can exploit a range of light conditions at the forest floor ranging from full light or open canopy to as low as 25% full light beneath closed, multilayered canopies (Stiell, 1978). Thus, the success of white pine regeneration would not seem to be limited by its ability to grow in various light intensities, but rather by the potential for its relatively large production of seed (Fowells, 1965) to disseminate to and germinate on exposed mineral soil or on a thin litter layer. Throughout the mixed deciduous forests of eastern North America these forest floor conditions are created to a large extent by surface fire (Horton and Brown, 1960; Methven, 1973; Ahlgren, 1976) and windthrow (Cline and Spurr, 1942; Goodlett, 1954). Following white pine establishment, the death of large individual trees near the regeneration provides additional light which may facilitate rapid early growth of the young trees.

Although white pine regeneration in the study area was only fourth most abundant, observations indicated that it was often most successful when associated with small disturbance patches. These regenerating pine were sometimes observed in clusters of multiple stems where the peripheral saplings may act as buffers against competition maximizing the potential for the central or most competitive individual in the cluster to survive to maturity (Cline and Lockard, 1925; Goodlett, 1960; Hibbs, 1982).

The size of individual disturbed patches created by windthrow, small surface fires and tree death are not large relative to those areas affected by cata-

strophic fire. However, they are more numerous and more widely distributed across the landscape (Chandler et al., 1983; Runkle, 1985). Observations of natural disturbance in the study area indicated that windthrow occurred more frequently than surface fire, although the aerial extent of both disturbances is unknown and may not necessarily reflect this same relationship.

It is clear that old-growth white pine forest in Temagami has been self-replacing over the last 700 years or so, however, it is not evident whether this process will continue in the future, especially in the light of the current policy of fire suppression. It is also clear that catastrophic fire is not the primary stimulus for natural white pine regeneration in old-growth white pine forests in Temagami. In fact, according to Hunter (1989) it is the exclusion of catastrophic natural disturbance that permits the development of the old-growth conditions. More specific studies focusing on the nature and extent of these local disturbances and their associated tree regeneration are needed.

The findings that this forest is self-replacing owing to the successful response of white pine regeneration to non-catastrophic, local disturbances implies that the application of some form of uneven-aged silvicultural system may, in some cases, be suitable for management of white pine forest. Selection logging, particularly group selection, as opposed to clearcutting may make better use of the variety of mechanisms of natural white pine regeneration (United States Forest Service, 1983; Benson et al., 1989). Also, because the selection system is less disruptive to the health of the ecosystem than is clearcutting, its application would provide greater assurance for long-term sustainable forest productivity. It is unlikely, however, that the old-growth condition can be maintained or enhanced under any cutting regime (Society of American Foresters, 1984).

As a natural, unharvested component of the landscape, old-growth forests are valuable from a functional ecological perspective and from a scientific perspective. They maintain soil stability and water quality, retain large amounts of limiting nutrients, provide a reservoir of genetic diversity and provide a unique wildlife habitat (Franklin et al., 1981; Heinricks, 1983; Maser and Trappe, 1984; Brown, 1985; Whitney, 1987; Maser, 1988). Scientifically, "Old-growth forests have played a prominent role in the development of ecological thought and theory" (Whitney, 1987). Lutz (1930) was one of the first forest ecologists to point out that old-growth forests provide the best opportunity to determine "the cumulative effect of the factors of site on vegetational development". More recent studies have relied on the study of old-growth forests as the end-point of ecosystem development in order to construct ecosystem models (Odum, 1969; Vitousek and Reiners, 1975; Borrmann and Likens, 1979).

In addition to ecosystem studies of old-growth forests, tree ring analysis of old trees in natural areas has helped us to understand hydrologic processes better (Cook and Jacoby, 1983), forest decline (Cook et al., 1987) and trace

metals in the environment (Brownbridge, 1984). In the future, old-growth forest dendrochronology will play a key role in reconstructing historical climate conditions (Sheppard and Cook, 1988) which in turn can be used for evaluating the potential effects of environmental change, such as global warming, on forested ecosystems (Solomon, 1986).

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