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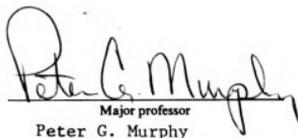
Growth Dynamics and Successional Trends in an Old
Growth, Cedar-Hardwood Dune Forest

presented by

Michael Lloyd Scott

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Botany and Plant Pathology


Major professor
Peter G. Murphy

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GROWTH DYNAMICS AND SUCCESSIONAL TRENDS IN AN
OLD GROWTH, CEDAR-HARDWOOD DUNE
FOREST

By

Michael Lloyd Scott

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

GROWTH DYNAMICS AND SUCCESSIONAL TRENDS IN AN OLD-GROWTH, CEDAR-HARDWOOD FOREST

By

Michael Lloyd Scott

A 20 hectare old-growth stand of northern white cedar (Thuja occidentalis L.) and associated hardwoods, including sugar maple (Acer saccharum Marsh.) and white ash (Fraxinus americana L.), exists on the southwestern corner of South Manitou Island, Michigan. Mature cedar within the stand were associated with a series of old-dune ridges and early growth rates for these trees were statistically equivalent to those for cedar currently establishing upon open dune slopes. It is suggested that the present forest association was initiated when cedar colonized the slopes of dunes which had advanced toward hardwood stands inland.

The present stand has a total aboveground biomass of 148.5 metric tonnes/hectare and a total aboveground annual net primary productivity (NPP) of 7.1 mt/ha/yr. The dominance of cedar in the stand results from a collection of massive individuals which together account for 61% of total stand biomass. These large cedar are rather unproductive, however, and account for only 26% of total stand production. In contrast, numerous small maple represent the largest percentage (42%) of stand NPP.

Despite the current importance of cedar, this species is not successfully replacing itself in smaller size-classes. Cedar seedling establishment has become increasingly restricted to log substrates and currently 99.7% of all first year seedling establishment occurs on logs. Logs in advanced stages of decay represent the best substrates for germination and early growth of seedlings. However, long-term survival on logs appears tenuous. Mortality for log-established cedar seedlings reaches 99.4% by year 12 and no cedar > 40 cm dbh showed evidence of having established on a log substrate.

Old-growth cedar were logged from a 3.4 ha portion of mature forest in 1896. The stems removed represented a basal area of 49 m²/ha. Post-logging trends in stand composition reveal that between 1920 and 1930 the basal area for second-growth sugar maple began to increase rapidly. Currently, maple accounts for 77% of total stand basal area (29 m²/ha). In the 85 years following logging, bole biomass and productivity in the second-growth stand have recovered to levels which exceed those found presently in the mature stand. Second-growth bole biomass (186.4 mt/ha) was 38% greater than mature bole biomass (allometrically estimated as 115.3 mt/ha) and bole NPP (3.9 mt/ha/yr) was nearly twice that of the mature stand (2.1 mt/ha/yr).

To my wife
Dr. Kathryn Vosburgh Scott
and my parents
Lloyd Allen Scott and Mary Margaret Scott

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INTRODUCTION

Cedar and Cedar Forests

Northern white cedar (Thuja occidentalis L.) is a component of boreal and northern-mixed-hardwoods forest associations (Braun 1950) and its range is limited to southeastern Canada and portions of the mid-western and northeastern U.S. (United States Forest Service 1965). The northern limit of the continuous range for cedar extends from southeastern Manitoba to the southern end of James Bay and eastward to the Gulf of St. Lawrence. The southern limit stretches from east-central Minnesota through central Wisconsin and extends around the southern tip of Lake Michigan. From the lake eastward the range includes southern-lower Michigan, southern New York state through central Vermont and New Hampshire. Outside of this range cedar occurs in disjunct, localized populations through southern Ohio, western Pennsylvania and into the Appalachian Mountains from Virginia and West Virginia south to North Carolina and Tennessee.

Cedar is common in areas characterized by low topography and high water tables such as sluggish streams and partially filled lake basins (Gates 1926). Most commercially harvested stands of cedar are from swampland, but the species is occasionally an old-field invader of moist,

well-drained soils of limestone origin. Old-field cedar typically show good form on these sites, and exhibit rates of growth up to three times greater than trees from swamps (Curtis 1944). The occurrence of cedar in both poorly drained lowland habitats and on well-drained upland sites has led to suggestions that there are distinct uplands and lowland ecotypes (Potzger 1941 and 1944). Several studies indicate that there may be some morphological (Habeck 1959) and physiological (Caulkins 1967, Musselmann et al. 1975) differences but the data are inconclusive.

On certain swamp sites cedar is able to perpetuate itself in dense, almost pure stands but more often it is associated with a number of other tree species. On moist sites common associates include black ash (Fraxinus nigra), tamarack (Larix laricina), and black spruce (Picea mariana), while on better drained sites they would include eastern white pine (Pinus strobus), basswood (Tilia americana) and occasionally sugar maple (Acer saccharum).

Cedar reproduces vegetatively by layering, and in some swamp stands this form of reproduction has been shown to account for as much as 73% of all new stems (Nelson 1951). In addition to layering, cedar reproduces effectively from seed. Germination and early growth of seedlings are reported to be best on moist, organic seedbeds including moss patches, rotting logs and burned-over soils (Johnston 1977). The seedlings are moisture sensitive and desiccation

in swamp sites appears to be a primary cause of mortality (Nelson 1951).

In Michigan, the majority of cedar habitat is lowland swamp (Johnston 1977), but the species has been reported from a limited number of upland sites as well, including the dunes of Lake Michigan (Cowles 1901, Wolfe 1932). Cedar is rare in protected ravines along the southern dunes (Moran 1978) but becomes increasingly common northward (Waterman 1922). Olson (1958) characterizes cedar as an early successional dune species colonizing damp depressions and lee dune slopes. The association of cedar with dune slopes may be related in part to soil conditions. Specifically, cedar has been reported to have a very high calcium content in its foliage and wood (Dyer 1967, Young and Carpenter 1969) and the return of this element (and others) through litterfall may help to explain the rapid soil improvement and high exchangeable base values observed in these locations (Olson 1958). Additional nutrient inputs may result from the importation of carbonate rich sands and organic material, such as leaves, from more exposed dune slopes. Aside from soil improvement, these sites may also receive additional moisture along inequalities in the bedding planes of sand, as water moves from high surrounding dunes. Thus, the occurrence of cedar in such locations may relate to the unique soil conditions which develop on lee slopes.

The South Manitou Forest

The finest known example of upland cedar forest is found on South Manitou Island in Lake Michigan. South Manitou is the southernmost island of an archipelago located in northeastern Lake Michigan (Figure 1), and is situated 11 km to the northwest of Sleeping Bear Point and 24 km due west of the town of Leland, Michigan. On the southwest corner of the island is an old-growth forest of approximately 20 ha (Figure 2), dominated by white cedar (Hatt 1948, Thompson 1963). Of particular note are the immense size and great age reported for cedar in the stand. Thompson reported tree heights in excess of 31 m (100 ft) and estimated the age of one tree to be more than 500 years. Because a portion of the forest is located between and on two large dune ridges, it was named "The Valley of the Giants".

As the result of logging activities on South Manitou at the turn of the century (Rogers 1966), much of the timber on the island was cut, including a portion of this old-growth cedar stand as described by Hatt (1948). Many large cedar were removed during logging and presently the second-growth stand adjoins 10.9 ha of mature forest which was the focus of this investigation (Figure 3). At the time work was initiated, a footpath roughly paralleled the east edge of the study area, extending from southeastern to northeastern corners. The defined eastern boundary of the stand follows the crest of an old dune ridge generally

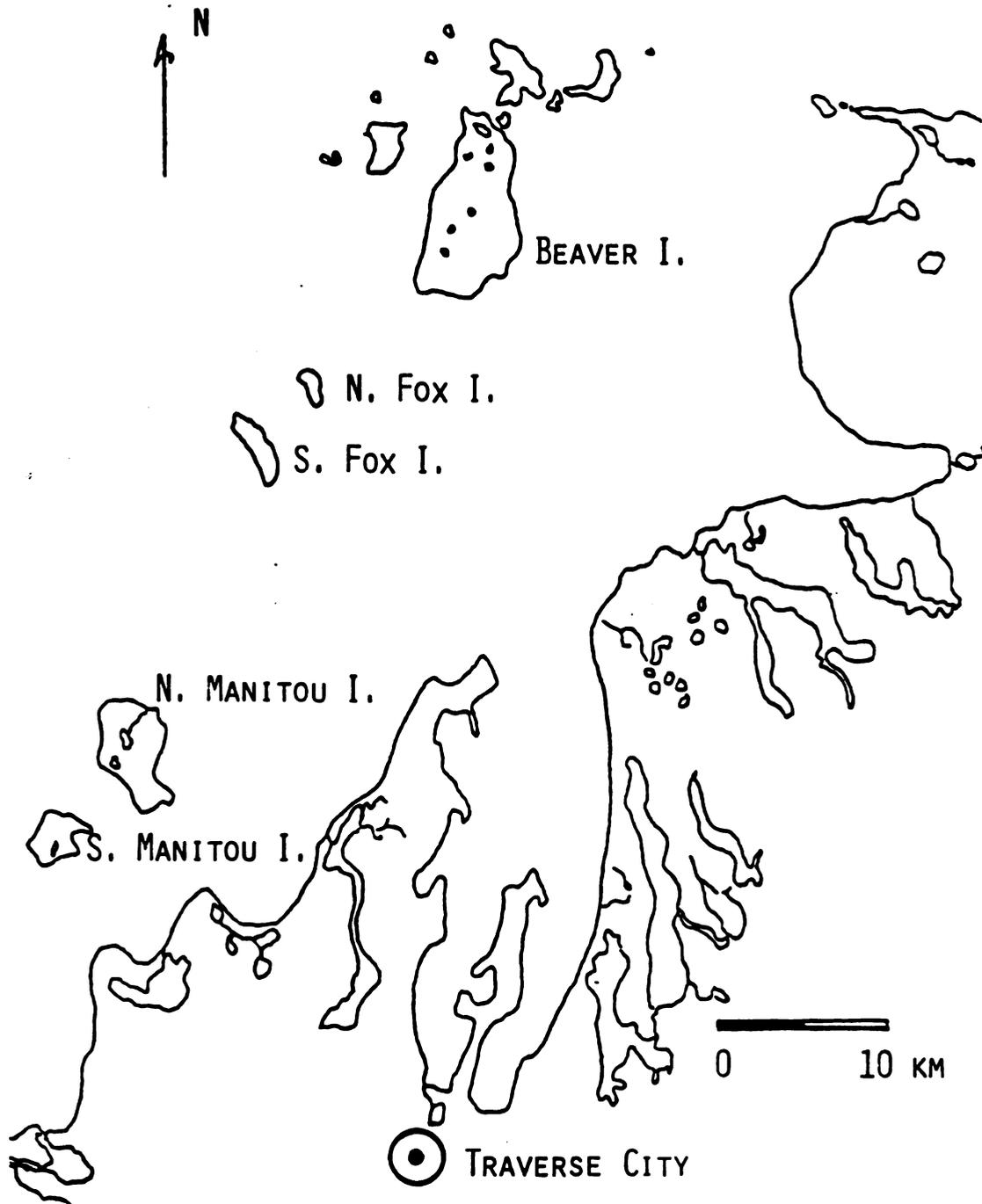


FIGURE 1. Island archipelago of northern Lake Michigan, including South Manitou Island, Michigan.

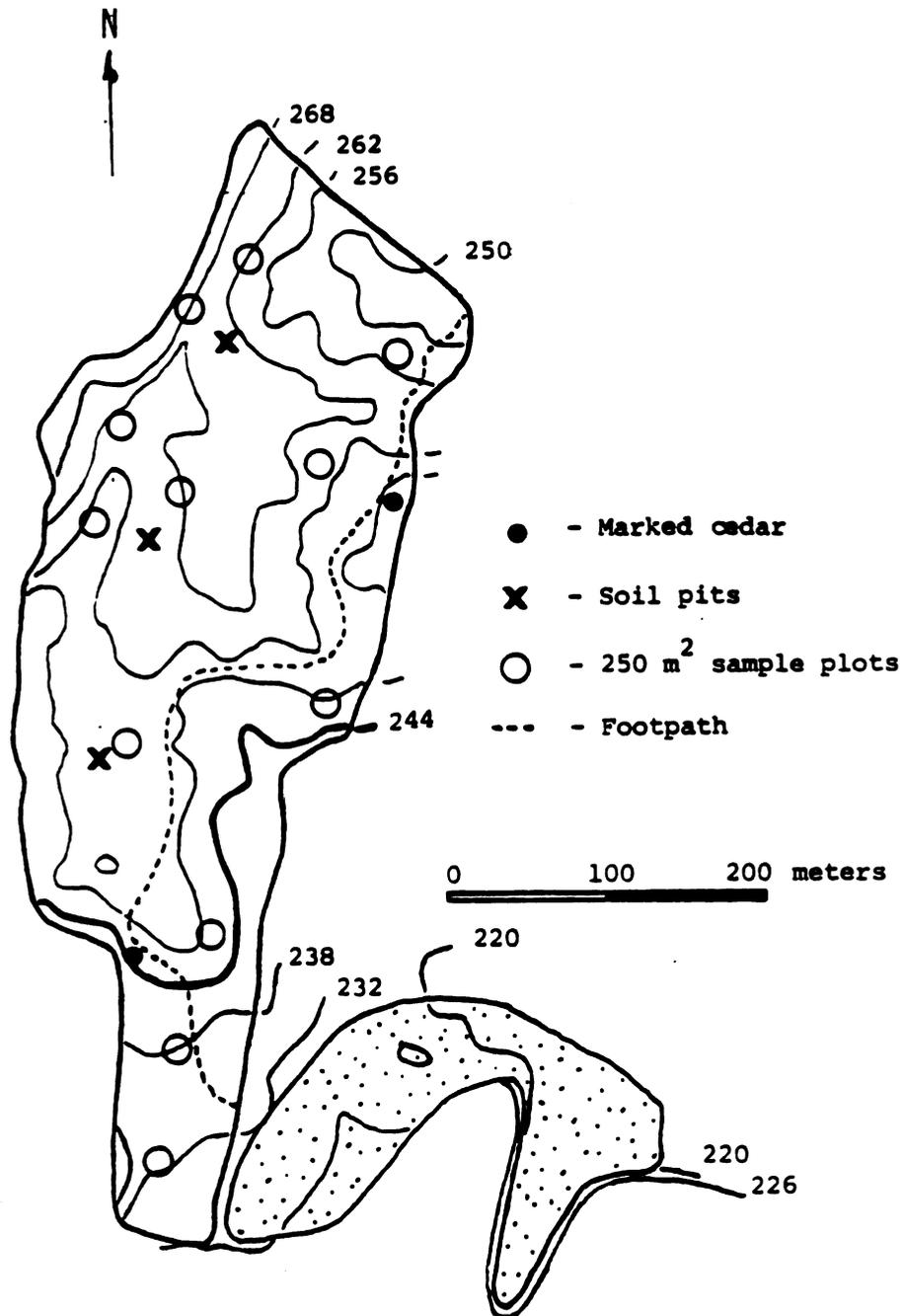


FIGURE 3. Map of study area indicating locations of soil pits, sample plots, walking path and large cedar marked by the Michigan Botanical Club. Size of sample plots are drawn to scale and all contour lines are in meters. The second-growth forest is indicated by stippling.

outlined by the 244 m contour line. The western boundary is defined by a steep dune ridge corresponding with the 274 m contour line. Aside from several stumps along the southeastern boundary, the study area appears to be free from human-induced disturbance and is representative of this upland cedar forest.

Research Hypotheses and Objectives

Existing descriptions of the old-growth cedar forest on South Manitou Island are somewhat contradictory; Hatt (1948) described this stand as cedar-hardwood dominated while Thompson (1963) considered it to be an essentially pure cedar stand. Because of this, a major objective of this study was to provide a detailed description of stand composition and structure.

Based upon the observed association of cedar with the lee slopes of dunes, it is hypothesized that this forest community originated with the encroachment of dune ridges into a hardwood forest, followed by establishment of cedar on the dune slopes. As a consequence, it is expected that old-growth cedar are associated with the old dune ridges and that early growth rates of these trees should be similar to those of cedar currently establishing on open dune slopes. Thus, another objective of this research was to examine the occurrence of cedar in relation to dune topography and compare rates of growth for old-growth and open-dune cedar.

Although large cedar presently dominate the South Manitou forest community, there is reason to question whether cedar will maintain dominance or eventually be replaced by associated hardwoods. The limited information on cedar growth and regeneration suggests that with present conditions, mortality may exceed recruitment. Further, establishment and survival of small seeded species such as cedar may be inhibited by a continuous cover of leaf litter (Grime 1977), and the fact that cedar is rarely associated with hardwoods (Curtis 1946) may be a function of the lack of adequate seedbeds and the effects of hardwood leaf litter. It is, therefore, hypothesized that cedar reproduction within the present old-growth stand is insufficient to maintain a stable age structure. Consequently, an evaluation of the reproductive success and mortality patterns for cedar within the old-growth stand are important objectives of this study.

Logging of a portion of the old-growth stand provided a unique opportunity to examine regeneration of cedar and other tree species following this disturbance. Further, it provided valuable insight into how this regeneration has influenced long-term trends in stand composition and structure, relative to the old-growth forest. A number of factors influence the path of forest recovery following logging; these include successional status of the pre-cut stand, amount of disturbance to the litter and topsoil, availability of suitable seedbeds, species removed in

logging, species left intact, as well as others (Bormann and Likens 1979; Boring, Monk and Swank 1981). The factors or conditions which have affected the course of forest recovery following logging and how these have influenced the structure and composition of the second-growth stand relative to the old-growth cedar stand are unknown. However, present composition of the old-growth stand suggests that it is a late successional forest, and at the time of logging likely had advanced regeneration of tolerant species such as sugar maple. In some late seral stands, removal of all or part of the canopy resulted in release of advance regeneration of tolerant or climax species, and thus accelerated the successional process in these stands (Spurr and Barnes 1973, Kapustka and Koch 1979). Removal of the overstory in the old-growth stand, without significant damage to the understory or topsoil, likely did not create seedbeds favorable for cedar reproduction. Therefore, given advance regeneration of tolerant tree species like sugar maple, it is hypothesized that such species will dominate the second-growth stand. An additional objective, then, was to gather information on compositional changes which have occurred in the second-growth stand as the result of logging.

There are few data available on the biomass and productivity of old-growth forest stands in the lake states (Crow 1978) and, therefore, a major objective was to document values of biomass and productivity in the mature cedar stand. Furthermore, the extent to which this old-growth

stand conformed to values presented for similar forest types (Whittaker and Likens 1975) was of interest. Closely linked to changes in structure and composition following logging are trends in energy relations. The recovery of biomass and productivity in the second-growth stand, in comparison with the old-growth stand, was examined in light of recent theories concerning patterns of forest regeneration following logging (Bormann and Likens 1979, Peet and Christensen 1980, Peet 1981). Thus, a final major objective was to determine current levels of biomass and productivity in the second-growth stand, and contrast this with the uncut stand.

METHODS

Forest Composition and Structure

From an initial survey of the southwest corner of South Manitou Island, a study area representative of the mature forest was selected and mapped (Figure 3). The site included a walking path and two exceptionally large white cedar which had been marked with aluminum plaques by the Michigan Botanical Club.

Descriptive information on the forest was collected from twelve 250 m² circular plots (Figure 3). A grid system was established for the site and plot selection was made with the use of a random numbers table (Steel and Torrie 1960). Within each plot the following data were collected on each tree \geq 2.5 cm diameter at breast height (dbh): 1) tree species; 2) tree dbh; 3) live or dead; 4) height to top of crown; 5) crown width in two perpendicular directions.

Importance values for all tree species were calculated based upon relative dominance, relative density and relative frequency (Mueller-Dombois and Ellenberg 1974). Additionally, at least two stems per plot of each of the four dominant canopy trees were cored (north and south side of tree) with an increment borer. All stems were chosen so

that cores were obtained over the observed size range for each species. Cores were placed in straws and returned to the lab where they were air dried and mounted on grooved wooden blocks. Ring widths for each core were then enumerated using a dendrochronometer. Sampling adequacy was determined by graphing cumulative means of basal area and species richness.

Finally, two 7 m wide belt transects (Figure 4) were extended in an east-west direction across the study area in order to construct profile diagrams of the forest. Information gathered within each transect included: 1) tree species and dbh; 2) height to top of crown; 3) length of crown along the transect; 4) crown depth (top to bottom of crown); and 5) tree position along the transect.

Forest Soils

Descriptions of soil within the study area was based on three randomly located soil pits (Figure 3) from which samples of the A₁, B, and C horizons were collected. All samples were placed in polyethylene soil bags, sealed and returned to the lab for analysis. Percent organic matter for the A₁ horizon was determined from ash-free dry weight measurements, and particle-size distribution for the profile was analyzed using the hydrometer method (Day 1965). Soil pH values were determined using a glass electrode pH meter

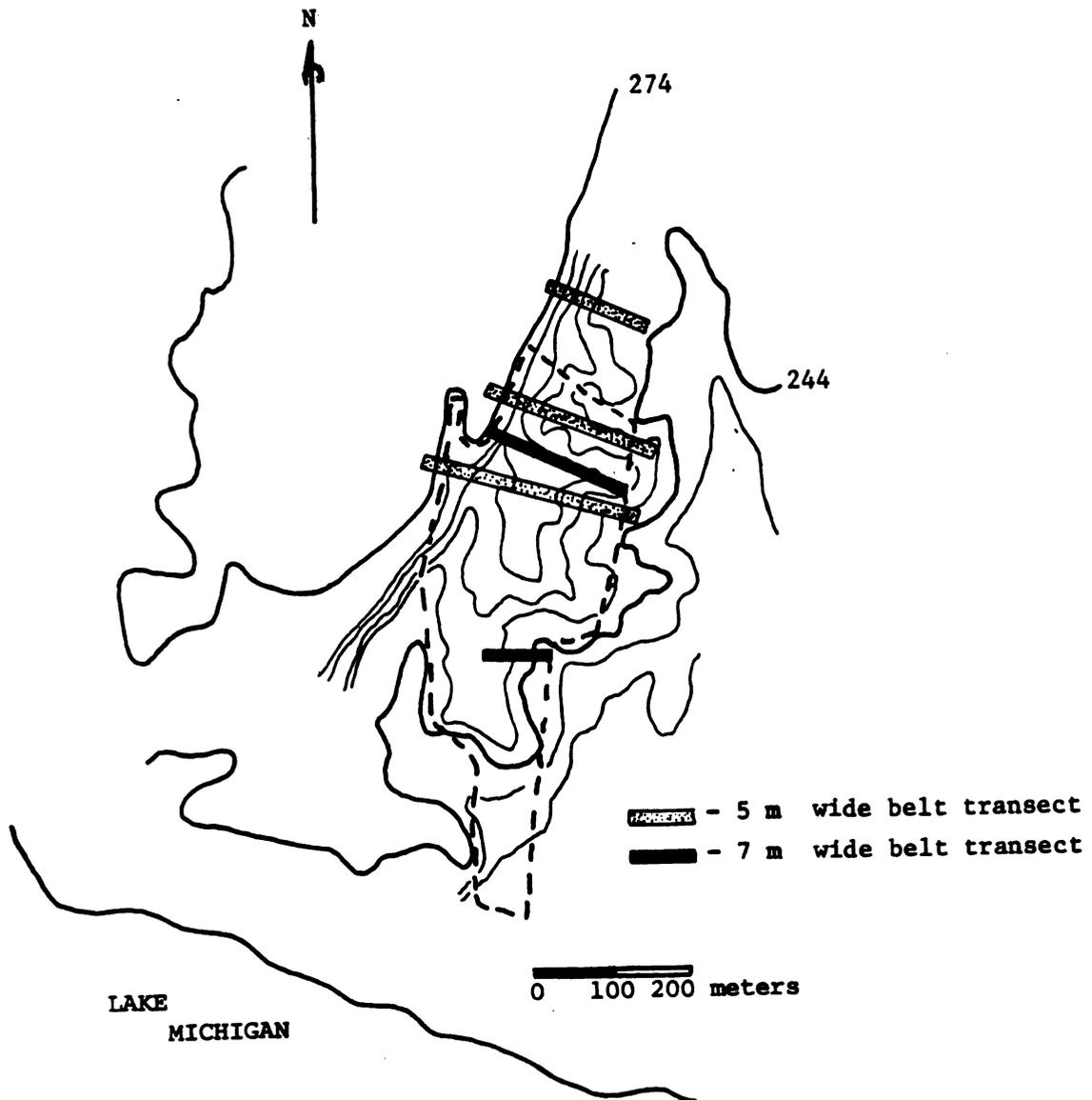


FIGURE 4. Location of profile diagram transects (solid bands) and transects assessing cedar density relative to dune topography (stippled bands). Study area delimited by dashed line. Contour lines in meters.

with individual 10 g samples of soil in a 50 ml solution of 0.01 M CaCl_2 .

Stand Origin

To examine the occurrence of old-growth cedar relative to dune topography, three 5 m wide belt transects were established on a dune crest defined by the 274 m contour line. These transects were extended west to east from the crest into old-growth forest (Figure 4). Each transect was marked at 10 m intervals along its length creating a series of 5 m X 10 m plots. Within each plot the number of cedar stems \geq 5.0 cm dbh were tallied. In addition, slope angle was measured within each plot with a clinometer to obtain a ground contour map along the length of each transect.

Further information on stand origin was obtained from a number of canopy ($n = 11$) and sub-canopy ($n = 10$) cedar from within the study area as well as individuals ($n = 5$) which had established on open dune slopes adjacent to the study area. All trees were measured for dbh and increment cores were extracted at breast height, placed in straws and returned to the lab. Cores were mounted on grooved wooden blocks and growth over the first 50 years was measured with a dendrochronometer and recorded. Because of the size of old-growth trees, it was difficult to consistently obtain cores which had passed through the center of these trees, however, a comparison of core length to tree diameter

indicated that all cores were within 8 cm of the center. The amount of wood missing from incomplete cores was determined from overall length of the core relative to stem radius. From this, the number of missing years was estimated by dividing the length of missing core by the mean annual increment from the five innermost rings. Lastly, average annual increments over the first 50 years of growth were estimated for old-growth, closed-forest and open dune cedar and were compared statistically using a F-test and Tukey's honestly significant difference (hsd) test (Sokal and Rohlf 1969).

Forest Succession

To examine possible successional trends within the mature stand, tree reproduction was examined within four canopy gaps (Figure 5). These gaps, each created from the fall of one to six trees, were of different sizes and generally elliptical in shape. As such, gaps were measured along major and minor axes to determine the area of each canopy gap. Gap boundaries were defined by the edges of surrounding canopy tree crowns. Within gaps, compositional features such as number of down trees were noted and all trees ≥ 2.5 cm dbh were identified to species and measured for dbh. From this information, importance values were calculated (Mueller-Dombois and Ellenberg 1974) for trees in each of the four gaps.

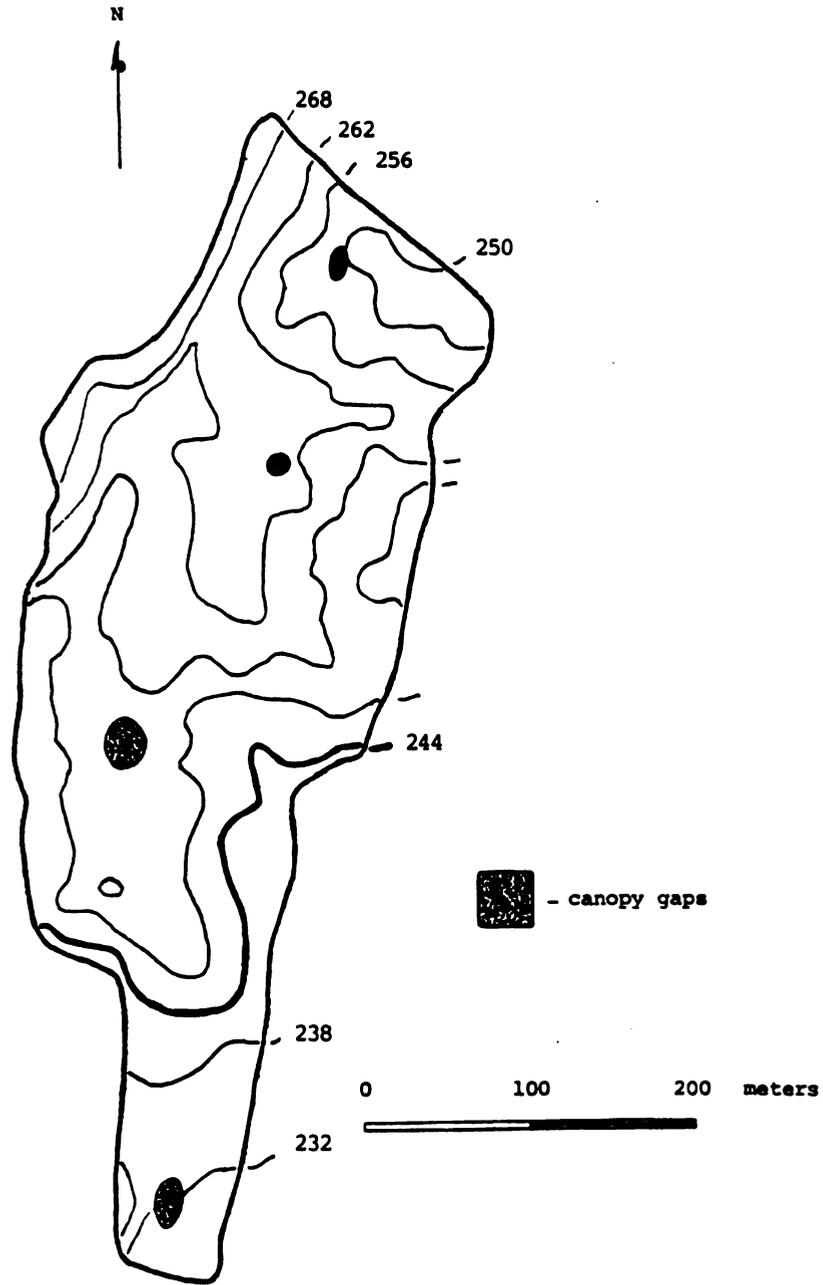


FIGURE 5. Location of canopy gaps within the study area. Contour lines in meters.

Additionally, replacement of old-growth cedar was examined by selecting standing dead cedar ($n = 10$) and measuring dbh as well as distance to the four nearest live trees (≥ 2.5 cm dbh). Neighboring trees were identified by species and measured for dbh. From these data, calculations similar to those for point-quarter sampling were used to establish importance values for trees nearest to standing dead cedar (Brower and Zar 1977).

To determine if establishment of cedar seedlings was associated with a particular seedbed or substrate type, all seedlings (≤ 1 m in height) in five, randomly located, 10 m X 10 m quadrats were identified and noted as to the type of substrate (log, stump, litter, other) upon which they had established. A chi-square goodness of fit test was used to examine whether seedling number was randomly associated with substrate type. From this information along with stand data on trees (forest structure and composition section), the number of cedar stems/ha which had established on logs or stumps was calculated for six size classes: 1) seedlings ≤ 1 cm tall (first year seedlings); 2) seedlings ≥ 1 cm tall and < 1 m tall; 3) stems 2.5 to 15 cm dbh; 4) 15.1 to 40 cm dbh; 5) 40.1 to 70 cm dbh; and 6) > 70 cm dbh. It was assumed that larger stems which had established on logs would appear to have aerial or stilt roots. Such roots result when seeds germinate on a substrate which eventually erodes away, exposing the roots (Kramer and Kozlowski 1979).

Preliminary observations on cedar seedlings within the study area suggested that recruitment was confined to emergent substrates such as logs and stumps. To evaluate the success of seedlings on such substrates three randomly located 10 m X 50 m transects were established in which the number of tree seedlings on logs and stumps was tallied. Seedling heights and surface area for all logs and stumps were also calculated. Cross-sectional stump area was measured as a circle and log area was approximated as a trapezoid:

$$A = \frac{1}{2} (a+b)h \quad (1)$$

where: A = area

a = diameter at one end of log

b = diameter at opposite end of log

h = overall length of log

State of decay for each log and stump sampled was also evaluated according to criteria presented in Appendix 1. As such, these different stages of decay represented a spectrum of substrate quality upon which seedlings may establish. Success of seedling establishment with regard to substrate was assessed in terms of the number of seedlings per unit area of substrate type. A cumulative mean of seedling number per plot was calculated to ensure sampling adequacy.

The population age structure of cedar seedlings was analyzed by harvesting seedlings (n = 65) throughout a height range (1 - 100 cm) from logs outside of the study

area. Harvested seedlings were placed in polyethylene bags, returned to lab, and measured for total height, foliage height (bottom to top of foliage), foliage width (in two directions) and stem width at ground level. All seedlings were then sectioned at ground level with a razor blade and with a dissecting scope each stem was aged. The above data were entered into a multiple regression program (Stat 4 Computer Program, Michigan State University) to determine which variable or variables were the best predictors of seedling age. From this, a population age structure was established. Survivorship was examined using the negative exponential and power function models as described by Hett (1971) and Hibbs (1979). Seedlings were grouped into two-year age classes and mid-points of each class were used in the regression analysis. From the survivorship data a life-table was also prepared.

Stand Mortality

Information on tree mortality was gathered from the sample quadrats on all fallen and standing dead stems. Where possible, dead stems were identified to species and measured for dbh. The direction of fall was recorded for all down stems and a chi-square goodness of fit test performed to determine if fallen trees were oriented randomly. Finally, the numbers of fallen and standing dead trees were tallied by species.

Biomass and Productivity

Biomass

Because of the unique status of this old-growth stand, non-destructive techniques were employed to estimate the biomass components of the tree strata. Bole wood biomass was estimated using the equation for parabolic volume (Whittaker and Woodwell 1968, Newbould 1967). Wood volumes were multiplied by oven-dried wood densities for each species (Forbs 1955), summed over all sample trees and expressed on a metric tonne per hectare (mt/ha) basis by species.

In addition to the parabolic estimate of bole wood biomass alternate estimates of cedar bole wood biomass were made from direct measurements of fallen cedar trees. Diameter measurements were taken at 2 m intervals along the boles of 23 down trees throughout the observed size range for cedar. From this information a regression of height on dbh was established (Figure 6), along with a regression of tree height on diameter ratios (or the diameter at height z divided by dbh) (Figure 7). The second distribution was best described by two separate curves: one for trees < 15.3 cm dbh and another for trees ≥ 15.3 cm dbh. These separate curves reflect a more rapid bole taper for the smaller trees.

Next, a computer program was written to calculate individual tree heights and diameters at 2 m intervals from

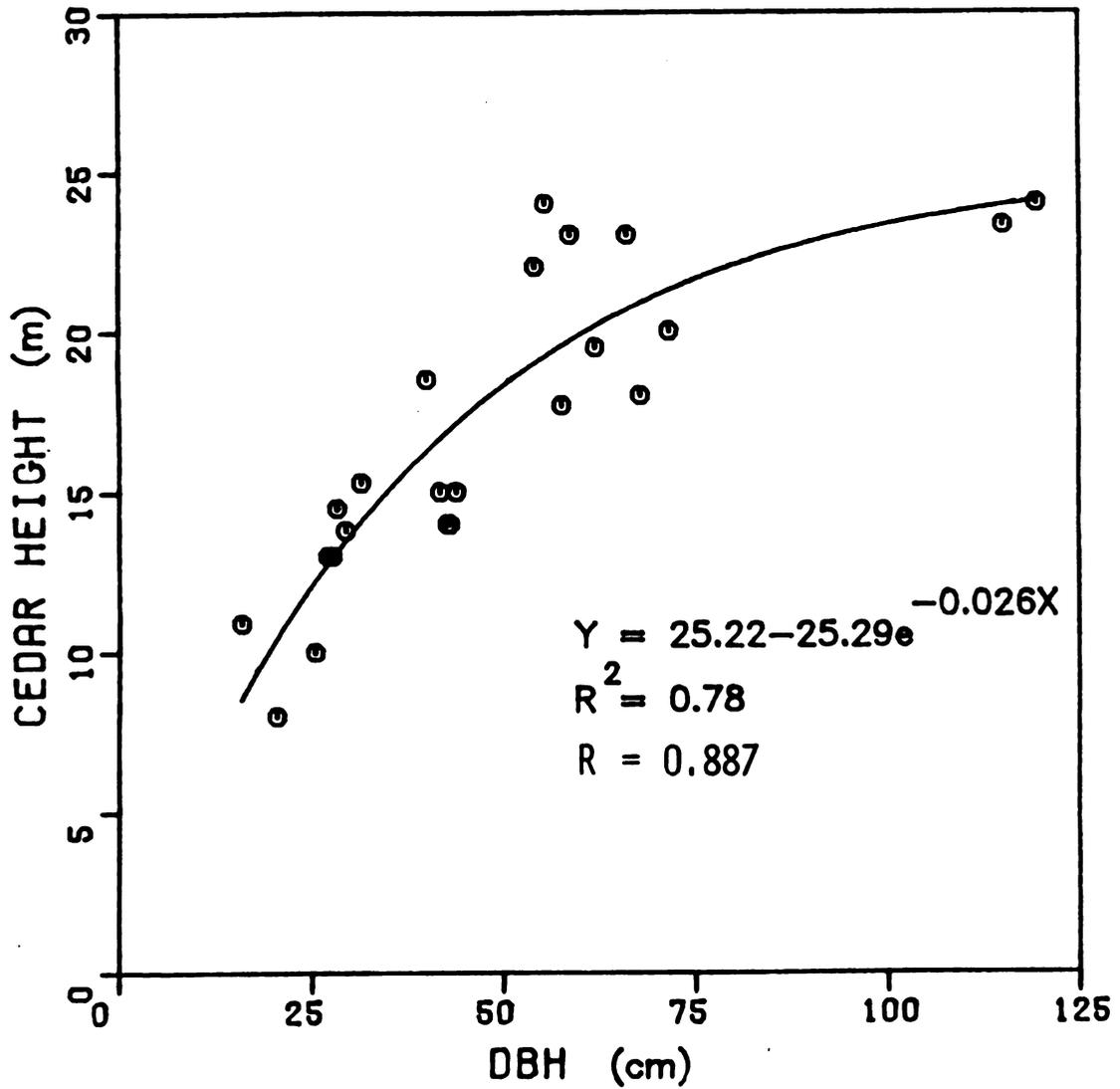


FIGURE 6. Regression of height on diameter for cedar.

Y (height in meters) = $25.22 - 25.29 e^{-0.026x}$ (dbh in cm).
 (n = 23, r = 0.887).

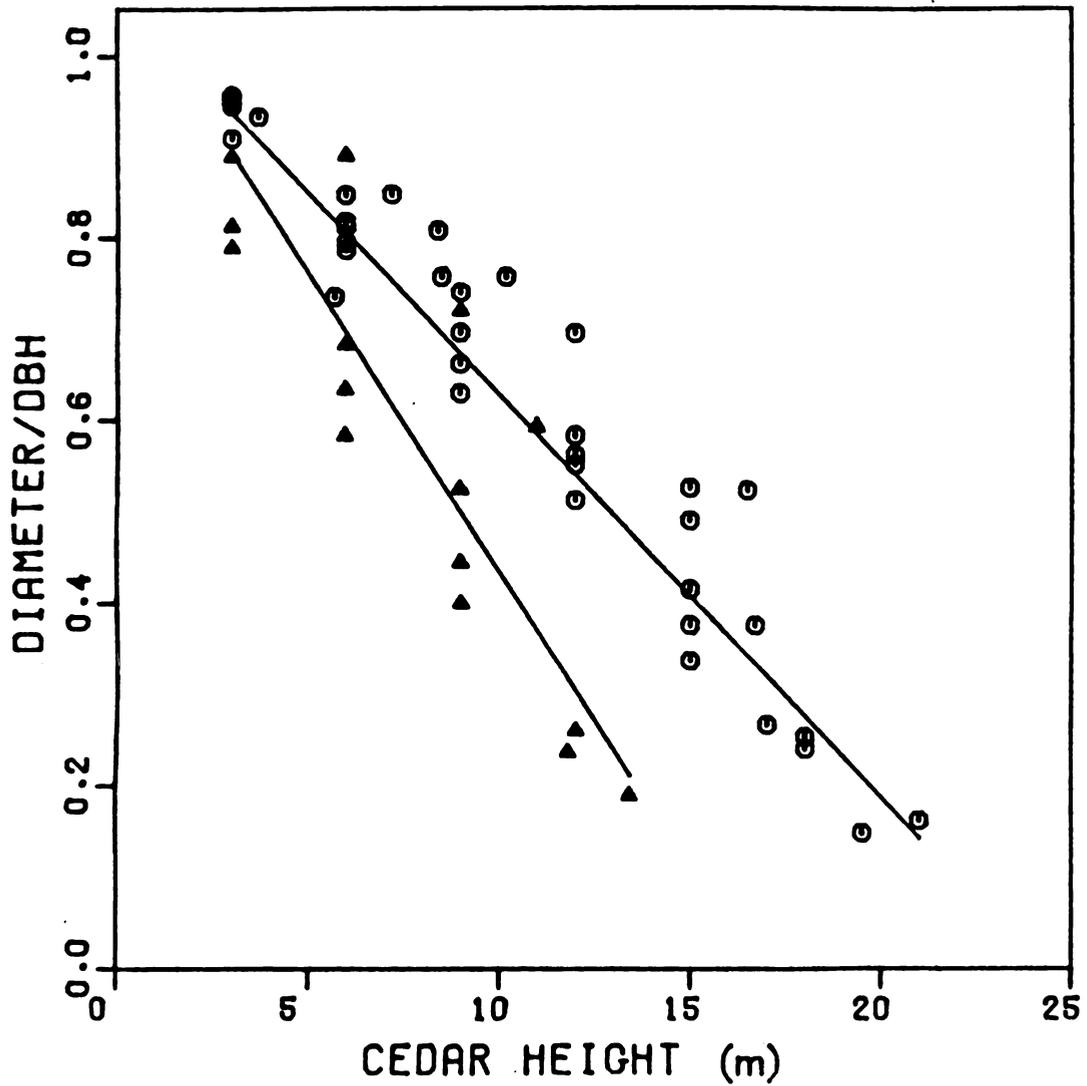


FIGURE 7. Regressions of height on diameter ratios for white cedar. Regressions for trees < 15.3 cm, dbh (\blacktriangle); X (height in meters) = $-0.0655 Y$ (diameter to dbh, ratios) + 1.09 ($R = 0.9344$, $n = 4$). For trees ≥ 15.3 cm, dbh (\odot); X (height in meters) = $-0.04414 Y$ (diameter to dbh, ratios) + 1.07 ($r = 0.9058$, $n = 7$).

the regression curves for a given dbh. Once diameters at each interval were calculated the program estimated volumes for each segment using the equation for the frustrum of a right circular cone, and the top-most segment was estimated as a right circular cone (Shelby 1967). Volumes of all stem segments were then summed to produce a value for total bole wood volume. Diameters (minus bark) of all standing cedar sampled were entered into the program and a second estimate of bole wood volume was obtained. Bole wood volumes were then converted to total bole wood biomass using oven-dried wood density and expressed on a mt/ha basis.

Bole bark biomass was calculated for the three dominant species (cedar, maple and ash) by subtracting bole wood volumes from total bole (wood and bark) volumes. Measurements of bark thickness from increment cores allowed for estimates of total bole volume (wood and bark) and bole wood alone for each tree. Once bark volume was estimated, dry weight biomass was determined by multiplying volumes by bark specific gravity (dry) for each species. Only specific gravity for sugar maple bark was available from the literature (Whittaker et al. 1974). Values for cedar and ash were estimated from 10 samples each, using the immersion technique (Forbs 1955). Bark biomass values were tallied and expressed as mt/ha for cedar, maple and ash. Estimates of bole bark biomass for minor species (importance values < 40) were not made. Branch biomass was not sampled directly but was estimated as a proportion of total bole biomass from the

literature. Cedar was estimated from Reiners (1972) while the remaining species were estimated from the data of Whittaker et al. (1974).

Leaf biomass values for all deciduous species were estimated as litterfall collected over two growing seasons from fourteen 1 m X 1 m quadrats. All collected leaves were returned to the laboratory, separated by species and air dried. Foliage biomass was estimated as leaf dry weight in mt/ha. Cedar foliage biomass was estimated as a proportion of bole biomass (wood and bark) from existing data on cedar (Reiners 1972).

Productivity

As with biomass, net annual primary productivity (NPP) was estimated nondestructively. Because of the usually infrequent and often dispersed occurrence of tree falls, stem productivity, based on litter fall, is likely to be underestimated in short term studies which assume steady state conditions (Newbould 1967, Reiners 1972). For this reason a direct evaluation of stem wood production for the most important canopy tree species (cedar, ash, maple and basswood) was made. This involved calculation of the estimated volume increment (EVI) described by Whittaker and Woodwell (1968). Mean annual radial wood increments were obtained for these species by coring sample trees (n = 36) over their observed size ranges and averaging wood growth rates over the previous ten years (Whittaker and Marks

1975). Average annual increments were calculated by species and applied on a size class basis in each sample plot. Estimated volumes were then summed across plots, and with specific gravity values (dry weight) for each species, annual stem wood production was calculated for the stand.

Since minor species (I.V. < 40) were not systematically cored, the ratio of bole wood productivity to bole wood biomass was determined for basswood (Tilia americana) and used to estimate bole wood production for all trees not cored ("other" category). Total bole wood biomass for "others" was multiplied by this ratio to obtain bole wood productivity for this category.

As with biomass, bark productivity was not estimated for minor tree species. For the dominant species, bole bark primary productivity was estimated as the ratio of bole wood productivity to bole wood biomass, multiplied by the biomass of bole bark (cf. Reiners 1972).

Production of branches (≥ 2.5 cm basal diameter) was estimated over two growing seasons from litterfall collected in a 2 m X 350 m transect located within the study area (Figure 8). This assumes that branch production and branch fall are in steady state on an annual basis. All branches were collected, separated by species and weighed in the field. Subsamples obtained from each species were placed in polyethylene bags and returned to the lab. These branches were weighed within 24 hours and then oven dried to a constant weight to determine percent moisture. This value was

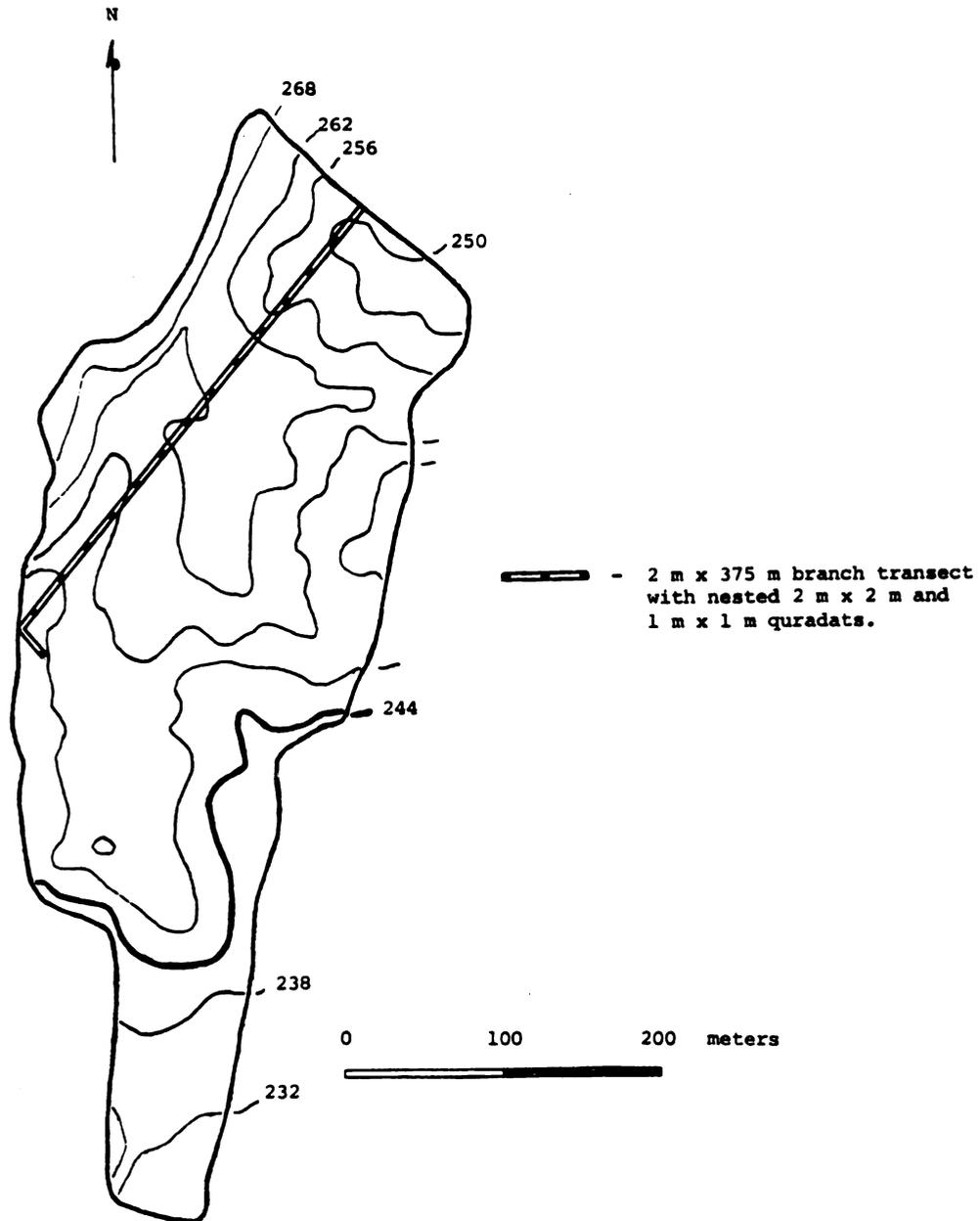


FIGURE 8. Location of litter plots (branches and leaves) within the study area. Contour lines in meters.

used to correct field weights to dry weight values. This method was also used for twigs (< 2.5 cm basal diameter) which were collected from fourteen 2 m X 2 m quadrats located at 25 m intervals along the branch transect.

Net annual leaf production for deciduous trees was estimated from litter collections following leaf fall. The turnover of leaf biomass for cedar was not directly determined in this stand. For cedar, alternatively, leaf productivity was estimated as a percentage of total leaf biomass from a ratio presented by Reiners (1974) for cedar.

All fruits and seeds for cedar, maple and ash from the litter collections were assumed to represent annual production. These fractions were separated by species, air dried and weighed. Fruits and seeds of the other tree species were included with leaf litter.

Forest Recovery Following Logging

Stand Description

A logged-over area of 3.4 ha adjacent to the mature stand was selected to represent second-growth forest (Figure 9). The stand was characterized by a sugar maple canopy with many cut cedar stumps in evidence throughout. To describe this stand, ten 10 m X 10 m quadrats were randomly located within the selected area and the following information collected for each tree \geq 2.5 cm dbh: 1) tree species; 2) live or dead; 3) dbh; 4) tree height. Two increment

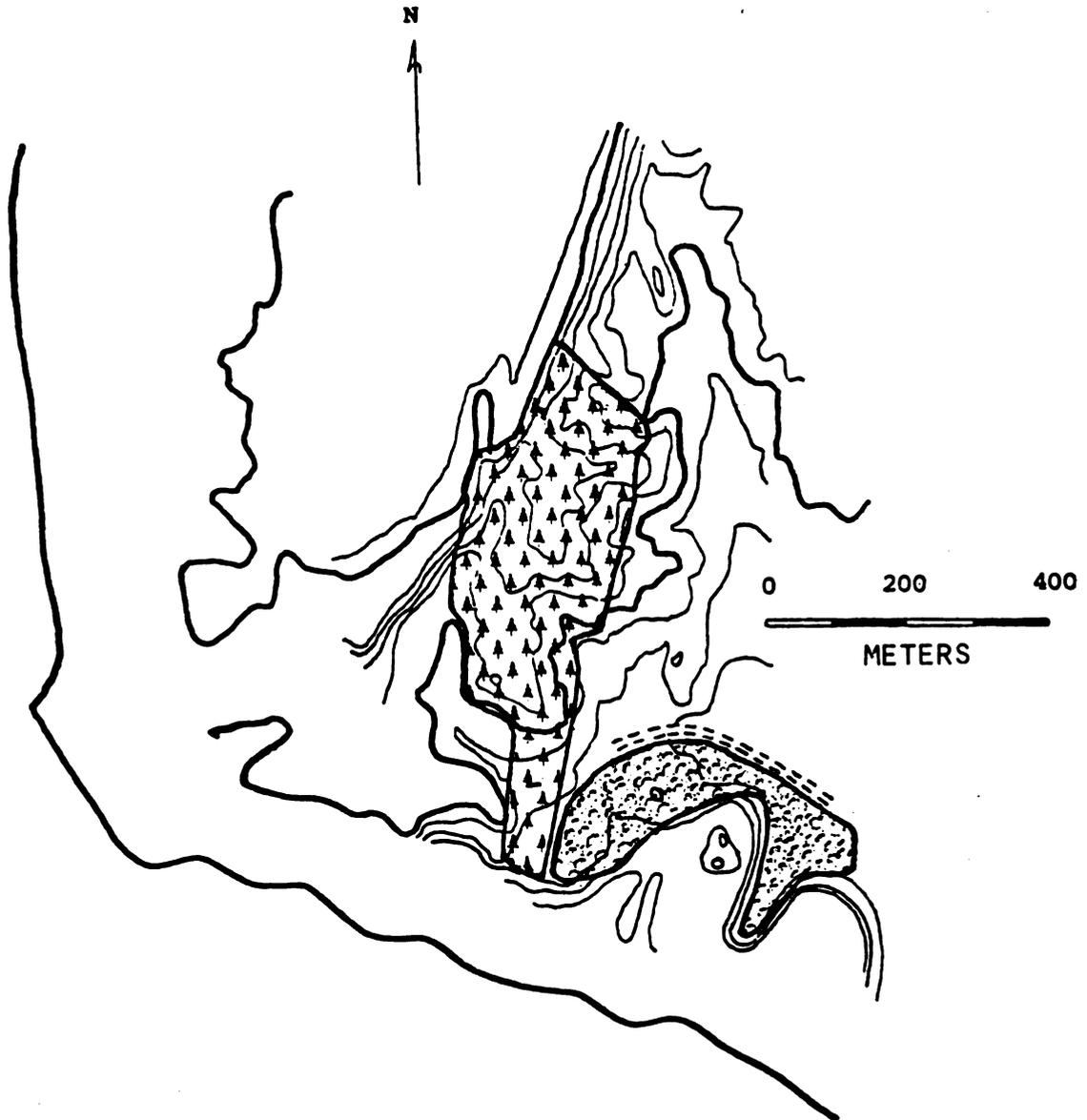


FIGURE 9. Location of old-growth and second-growth study areas on South Manitou Island, Michigan. Old-growth stand indicated by tree symbols and second-growth stand by heavy stippling.

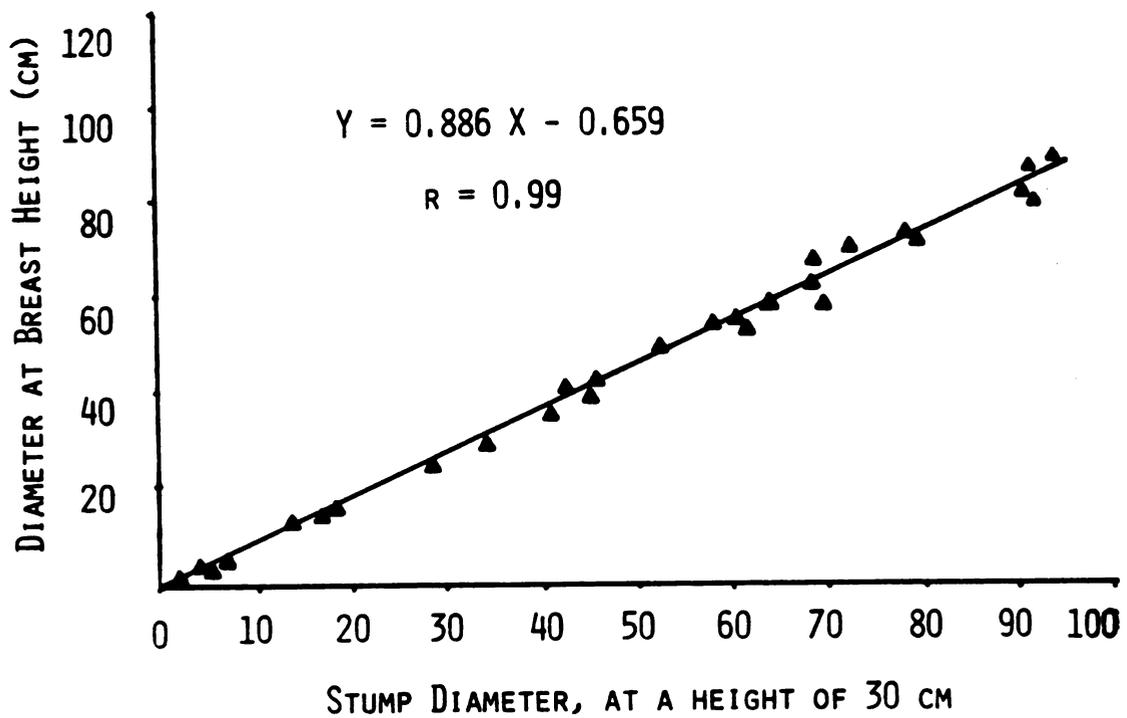


FIGURE 10. Regression of diameter at breast height on diameter at stump height (diameter at 30 cm above ground surface), for old-growth cedar. Y (diameter at breast height) = $0.886 X$ diameter at stump height - 0.659 . ($n = 29$, $r = 0.99$).

cores were also extracted from several live trees per plot over the observed size ranges for each species. Additionally, all identifiable cedar stumps were measured for diameter at 30 cm above the surface of the ground. This was defined as diameter at stump height (dsh). An estimate of dbh for these stumps was obtained from a regression of dsh on dbh using measurements from 29 live cedar in the mature stand (Figure 10). From this, cumulative means of basal area for logged cedar along with second-growth maple were used to assess sampling adequacy. Based upon the above information importance values and total basal area for the present second-growth stand were calculated as in the mature stand.

Estimated Date of Logging

An attempt was made to pinpoint as accurately as possible the date at which many large cedar were logged from the area adjacent to the mature stand. To do this the following approaches were taken: 1) old-growth cedar were examined for growth release; 2) trees which had established on cut cedar stumps were aged by ring count; 3) an age profile of second-growth maple was established.

Four large cedar from the mature forest adjacent to the logged area were selected and cored with an increment borer. Two cores per tree were extracted and placed in straws. All cores were returned to the lab and measured for annual rates of growth. Since cedar is reported to respond well to release (United States Forest Service 1965, Johnston 1977)

it was expected that a disturbance such as logging would result in distinct, identifiable changes in growth of these trees at the time of logging. To discriminate between changes in growth in response to logging as opposed to changes resulting from the effects of climate or small-scale disturbances (e.g. tree falls), criteria from Lorimer (1980) were applied to the data. The release criteria were: 1) the period of release had to occur abruptly and be sustained for at least 15 years; 2) release had to be preceded by at least 15 years of comparatively slow growth (< 1.0 mm/yr as measured in the laboratory); 3) average growth rates for the 15 years following release had to be at least 100% greater than previous average growth rates; and 4) for trees with moderate rates of growth prior to release (i.e. 1.0 mm/yr) a 50% increase in average growth following release was required. By way of comparison, average rates of growth 15 years before and after the estimated cutting date were examined in four cedar from within the mature stand.

Trees of various species which had established on cut cedar stumps were also cored as described above and aged by ring count. Further, age and diameter information gathered on second-growth maple were used to construct a linear regression of age on dbh (Figure 11) and from this an age profile for second-growth sugar maple was established.

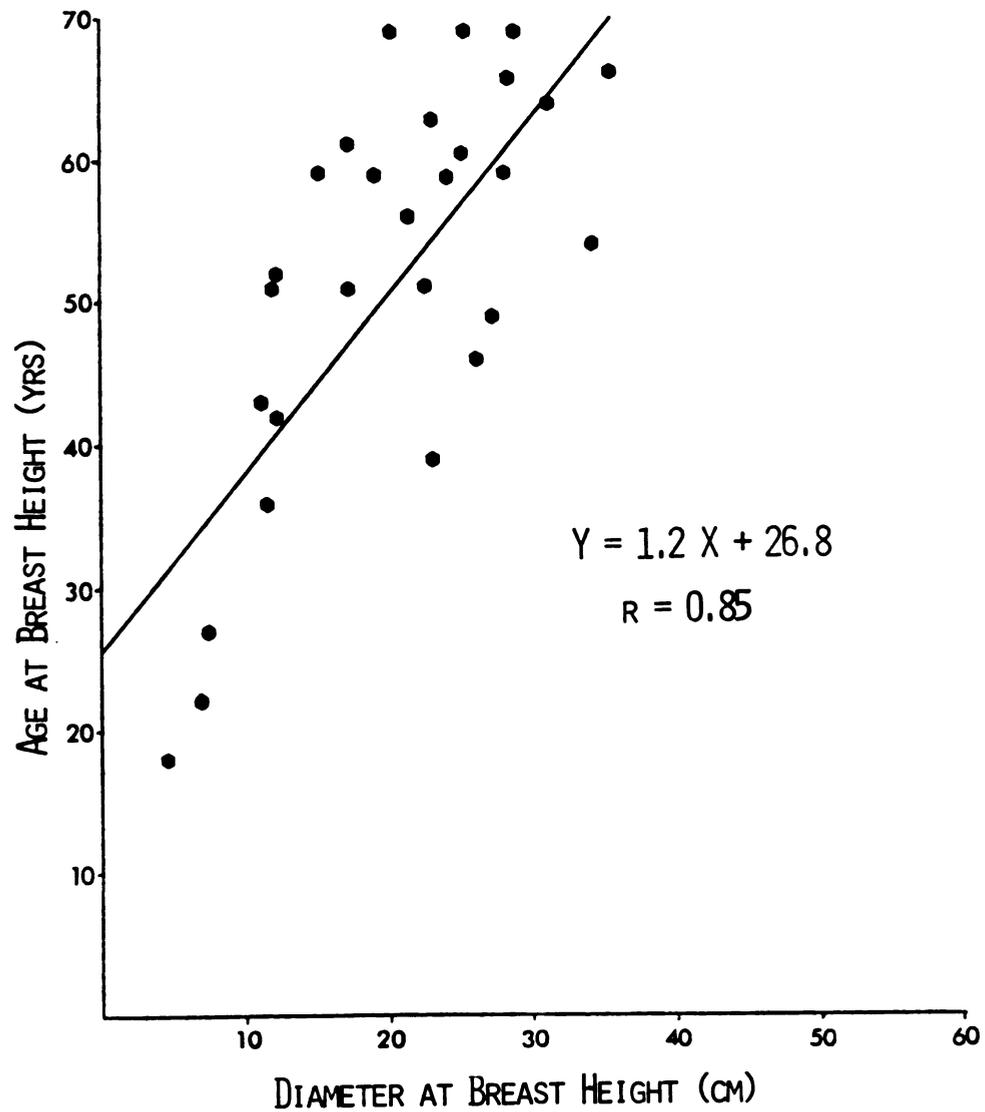


FIGURE 11. Regression of age on diameter for second-growth sugar maple. Y (age in years) = $1.2 X$ (dbh cm) + 26.8 ($n = 27$, $r = 0.85$).

Forest Recovery

To contrast structural and functional changes which have occurred in the second-growth and mature stands following logging, it was important to first document how similar the original (pre-logging) stands were. This was accomplished by comparing pre-logging estimates of density (stems/ha) and basal area (m^2/ha) for cedar in both stands. This information was reconstructed from stump data in the second-growth stand and compared with values from the mature stand, where mortality and growth were taken into account. Based upon the sound condition of cut cedar stumps in the second-growth stand, all sound, identifiable cedar stumps and fallen logs, as well as standing dead cedar, were assumed to be post-logging. All such mortality was included in estimates of density and basal area for cedar in both stands. Growth of cedar during this post-logging period was estimated from cored trees. Average annual increment over the last ten years was subtracted from all live trees, on a per plot basis over the years following logging. Finally, a standard t-test was performed to test for differences in basal area and stem density for cedar in the second-growth and mature stands at the time of logging.

To examine forest recovery, compositional shifts in basal area of the second-growth stand relative to the mature stand were evaluated. This parameter was chosen as it is a reflection of the dominance and physiological status of forest trees (Oliver and Stephens 1977). Basal area change

in ten-year intervals were calculated from stand data for cedar and maple for a period of 80 years. In each stand, maple and cedar were divided into 10 cm size classes and average growth increments over the last decade were estimated for both species, as above. The growth increments were subtracted from each tree in the appropriate size class on a per plot basis. Basal area was then calculated and summed across plots, providing an estimate of basal area (uncorrected for mortality) in each stand ten years earlier. This process was repeated for each successive decade from 1980 back to 1900. As discussed previously, a portion of cedar mortality was assumed to have occurred following logging. It was further assumed that mortality was constant over time and thus total basal area loss to mortality was factored out equally for each decade.

Changes in biomass and productivity which resulted from logging were evaluated by contrasting bole biomass and net primary productivity in the second-growth stand with values from the mature stand. In the second-growth stand bole biomass for all trees was determined per plot by estimating total volume which was approximated from the equation for a paraboloid of rotation (Newbould 1967). Volumes were converted to biomass values by multiplying each tree by the appropriate specific gravity (dry weight) value. Biomass was summed over all plots and expressed as mt/ha. Similarly, net annual bole production for all trees was approximated by calculating the estimated volume increment (EVI)

for the last ten year period (Whittaker and Marks 1975). These values were converted to dry weight values and expressed as in the mature stand (mt/ha/yr).

RESULTS

Composition and Structure of the Old-Growth Stand

Of the nine tree species encountered within the study area cedar was the stand dominant, accounting for 38% of the total importance value. Sugar maple and white ash were important co-dominant species, and together with cedar comprised 77% of total stand importance (Table 1). The importance of cedar in the stand derives primarily from the large basal area (dominance) of some individual cedar stems. One cedar tagged by the Michigan Botanical Club measured 162 cm dbh, and is listed as a national champion tree.

There were a total of 884 stems (≥ 2.5 cm dbh)/ha in the stand, 61% of which were between 2.5 and 10 cm dbh (Figure 12). This reflects the large number of maple and ash in this size range (Figure 13). By contrast, cedar is evenly distributed across a broad size range (Figure 13) and accounts for all stems ≥ 50 cm dbh. Despite the large diameters of some cedar within the stand, no trees measured were over 30 m in height and only 5% of all stems were between 20 and 25 m (Figure 14). For cedar specifically, 15% of all stems attain heights exceeding 20 meters.

TABLE 1. Importance values for the old-growth forest.^{1/}

| SPECIES | RELATIVE FREQUENCY | RELATIVE DOMINANCE | RELATIVE DENSITY | IMPORTANCE VALUES | PERCENT OF TOTAL IMPORTANCE |
|----------------------------|--------------------|--------------------|------------------|-------------------|-----------------------------|
| <u>Thuja occidentalis</u> | 24 | 72.5 | 17.4 | 113.9 | 38.0 |
| <u>Acer saccharum</u> | 24 | 15.7 | 37.7 | 77.4 | 25.8 |
| <u>Fraxinus americana</u> | 18 | 8.3 | 14.7 | 41.0 | 13.7 |
| <u>Acer spicatum</u> | 16 | 0.9 | 16.2 | 33.1 | 11.0 |
| <u>Prunus virginiana</u> | 4 | 0.3 | 4.5 | 8.8 | 2.9 |
| <u>Tilia americana</u> | 4 | 1.2 | 2.3 | 7.5 | 2.5 |
| <u>Cornus alternifolia</u> | 2 | 0.2 | 4.2 | 6.4 | 2.1 |
| <u>Ostrya virginiana</u> | 4 | 0.2 | 1.9 | 6.1 | 2.0 |
| <u>Abies balsamea</u> | 4 | 0.3 | 1.1 | 5.4 | 1.8 |
| TOTALS | | | | 299.6 | 100.0 |

^{1/} Importance Value = (relative frequency) + (relative dominance) + (relative density)
(Mueller-Dombois and Ellenberg 1974).

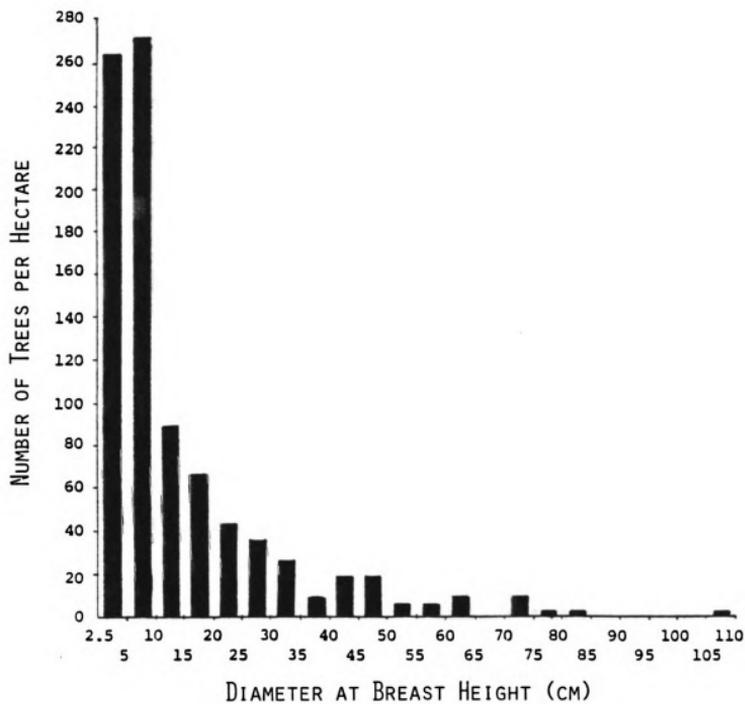


FIGURE 12. Size class distribution for all trees within the old-growth stand.

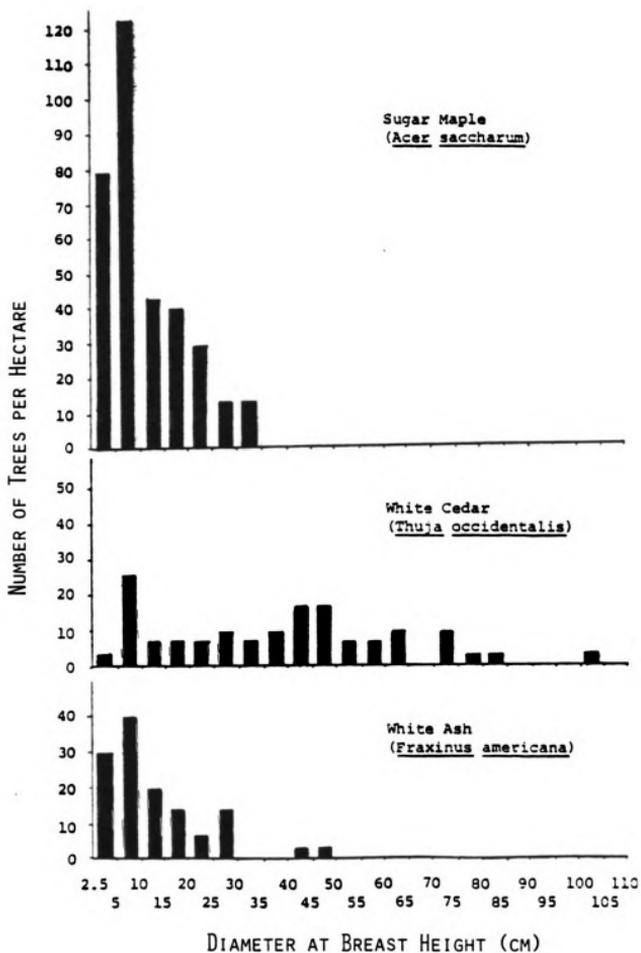


FIGURE 13. Size class distribution for maple, cedar and ash in the old-growth stand.

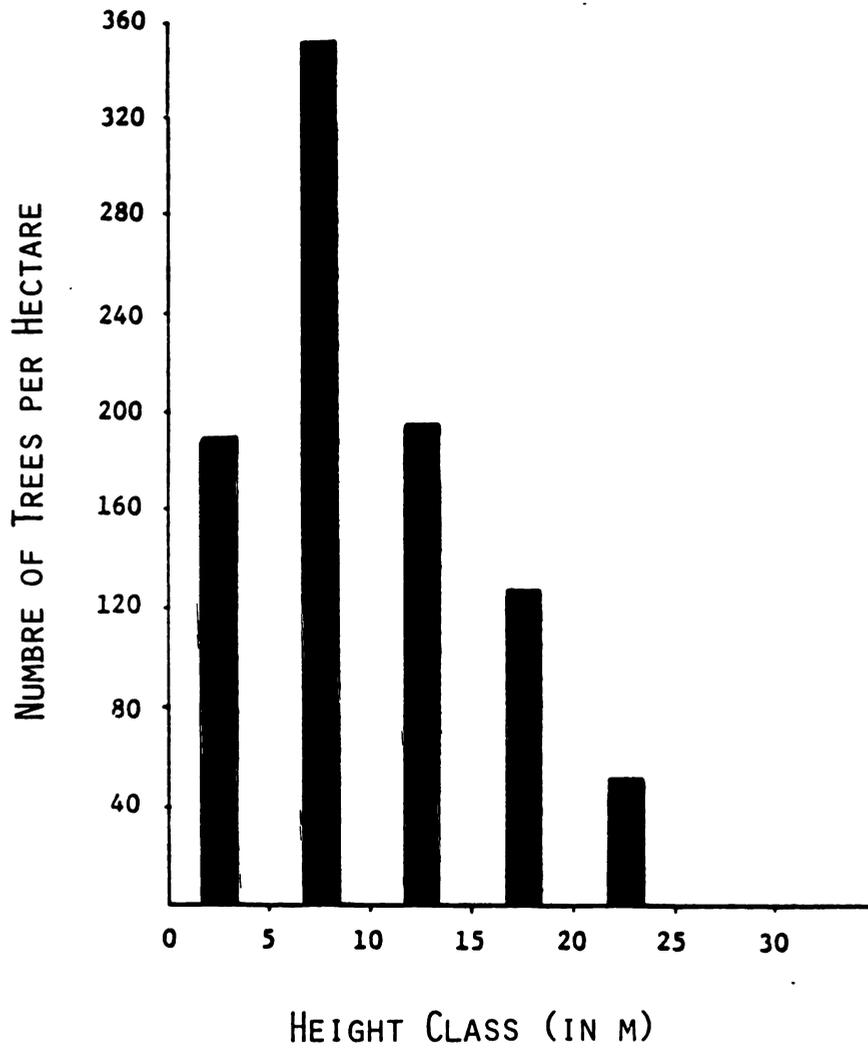


FIGURE 14. Height class distribution for all trees (> 2.54 cm dbh).

Forest Soil

Textural analysis from the soil profiles (A₁, B and C horizons) indicated that soil from three forest soil pits consisted of 89.5% (SD ± 3.7) sand, 5.8% (SD ± 2.3) silt and 4.7% (SD ± 1.2) clay (Table 2). This was consistent with the classification of this soil as a Deer Park sand (Weber 1973). The A₁ horizon was composed of 7.5% organic material. Soil pH within the study area averaged 6.4 and varied little throughout the profile.

Stand Origin

Mature cedar in this study were associated with a series of old dune ridges (Figure 15). The density of cedar stems on these ridges and slopes (2100 stems/ha, SD ± 99) was significantly greater ($\alpha < 0.01$) than in areas between the successive ridges (567 stems/ha, SD ± 981) based on a t-test comparison (Table 3).

Mean annual diameter increments, during the first 50 years of growth (Figure 16), indicate that mature cedar grew at rates statistically equal to cedar currently growing on open dune slopes. On the other hand, both old-growth and open-dune cedar had significantly greater rates of growth than cedar which had established within the mature stand (Table 4).

TABLE 2. Average soil characteristics for the study area.

| <u>SOIL FRACTION</u> | <u>MEAN (\pm SD)</u> |
|----------------------|-----------------------------------|
| sand | 89.5% \pm 3.7 |
| silt | 5.6% \pm 2.3 |
| clay | 4.7% \pm 1.2 |
| organic matter | 7.5% \pm 3.6 |

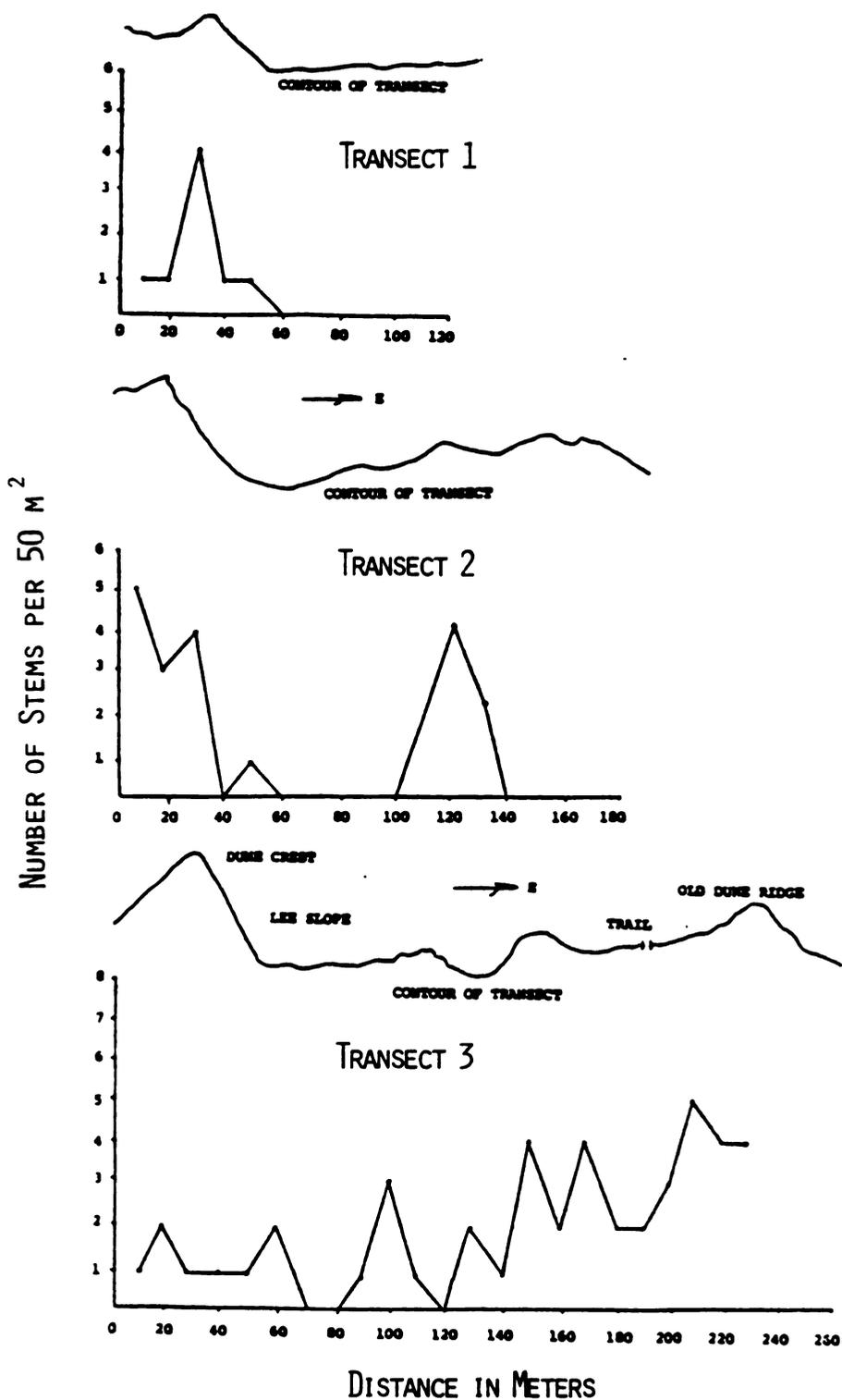


FIGURE 15. Distribution of cedar in relation to dune topography within the mature stand.

TABLE 3. At t-test comparison between the number of cedar stems per hectare on dune ridges and those in dune valleys.

| <u>Number of cedar stems/ha (\pm SD)</u> | |
|---|---------------------|
| <u>On Dune Ridges</u> | <u>Dune Valleys</u> |
| 2100 \pm 99.9 | 567 \pm 981.4 |
| $\alpha < 0.01^*$ | |
| n | n |
| 3 | 3 |

*(t = 89.9, $\alpha < 0.01$)

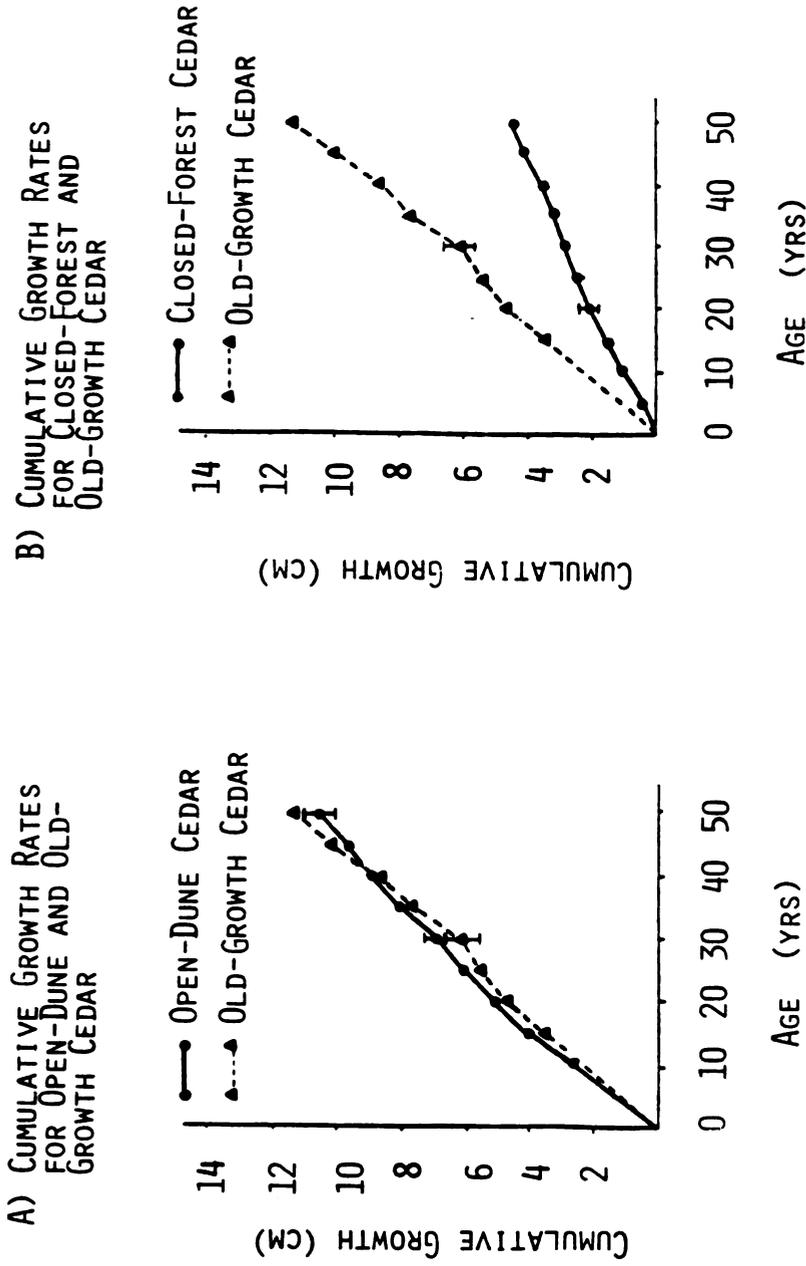


FIGURE 16. Comparison of cumulative growth for old-growth and open-dune cedar (A), and for old-growth and closed-forest cedar (B). Error bars reflect standard error of the mean.

TABLE 4. A F-test^{1/} and Tukey's honestly significant difference (HSD) test^{2/} comparison of mean annual growth rates for the first 50 years of growth for cedar in three locations.

| <u>Mean Annual Growth Rates (mm/yr)</u> | | |
|---|----------------------------|------------------------|
| <u>Old Growth Cedar</u> | <u>Closed Forest Cedar</u> | <u>Open Dune Cedar</u> |
| 2.19 | 0.89 | 2.15 |
| <hr style="width: 50%; margin: 0 auto;"/> | | |
| SD = 0.66 | 0.21 | 0.45 |
| n = 8 | 10 | 9 |

^{1/} F = 24.3, $\alpha < 0.001$

^{2/} Means underscored by same line were significantly different ($\alpha = 0.01$) according to Tukey's HSD test.

Successional Status of the Old-Growth Stand

Gap Reproduction

Canopy gaps which were sampled ranged in size from 157 to 589 m². White ash had the highest importance value in the three largest gaps (Figure 17a) but did not occur in the smallest gap where maple was the dominant. Both maple and cedar occurred in all gaps measured and maple was the most important species averaged over all gaps, representing 42% of total importance (Figure 17b). Ash was second in importance to maple in all gaps and together with maple accounted for 70% of total importance for all trees in the four canopy gaps. Maple was the most important tree species adjacent to standing dead cedar (Figure 18), representing 44% of total importance. These maple were more numerous and of a smaller average size than were cedar or ash (Table 5) which comprised 30% and 20% of the importance total.

Cedar Seedling Establishment

Ninety-eight percent of all cedar seedlings (≤ 1 m in height) sampled were found on logs or stumps while the remaining 1.7% has established within or on leaf litter. Moreover, all seedlings associated with leaf litter were determined to have germinated during the growing season in which sampling occurred. This association with emergent, woody substrates was found to be highly significant ($\alpha < 0.001$).

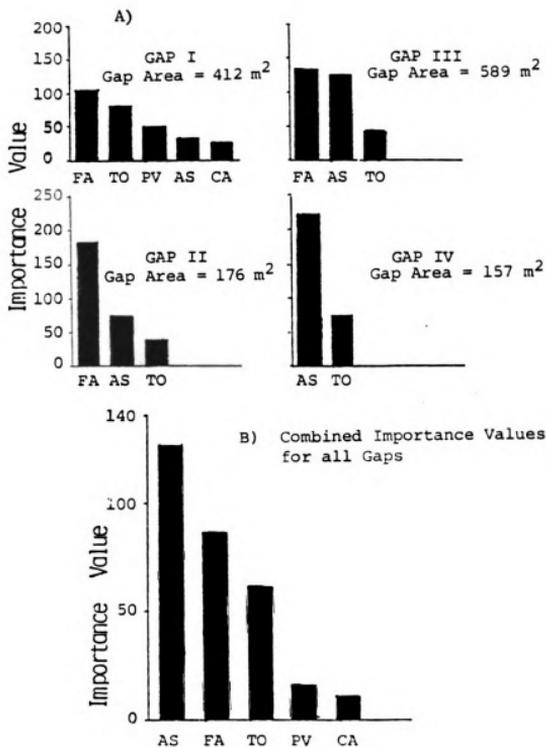


FIGURE 17. A) species importance values for trees within four canopy gaps, B) combined importance values from four canopy gaps. Tree species abbreviations: Acer saccharum (AS), Fraxinus americana (FA), Thuja occidentalis (TO), Prunus virginiana (PV), and Cornus alternifolia (CA). Importance values = (relative density) + (relative dominance) + (relative frequency).

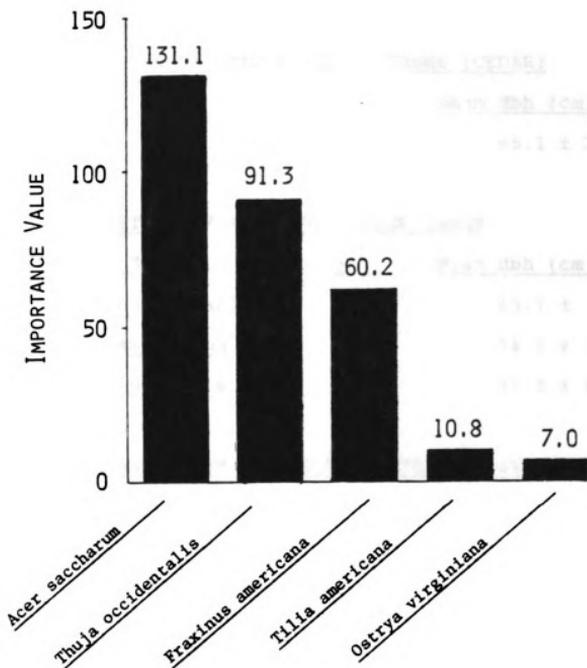


FIGURE 18. Importance values for four trees nearest standing dead cedar stems.

TABLE 5. Summary data for standing dead cedar stems and the four nearest live trees.

A) MEAN DIAMETER OF DEAD STANDING TREES (CEDAR)

| <u>n</u> | <u>Mean dbh (cm), ± SD</u> |
|----------|----------------------------|
| 10 | 85.1 ± 12.9 |

B) MEAN DIAMETERS OF ADJACENT LIVING TREES

| <u>Species</u> | <u>n</u> | <u>Mean dbh (cm), ± SD</u> |
|--------------------------------|----------|----------------------------|
| <u>Acer saccharum</u> (AS) | 27 | 13.7 ± 8.9 |
| <u>Fraxinus americana</u> (FA) | 6 | 34.2 ± 19.6 |
| <u>Thuja occidentalis</u> (TO) | 5 | 46.2 ± 40.6 |

C) MEAN DISTANCE FROM LIVING TREES TO DEAD STANDING CEDAR

| <u>Species</u> | <u>n</u> | <u>Mean distance (m), ± SD</u> |
|----------------|----------|--------------------------------|
| AS | 27 | 2.2 ± 1.1 |
| FA | 6 | 2.9 ± 1.2 |
| TO | 5 | 3.1 ± 1.6 |

With increasing size there was a marked change in the occurrence of cedar, from log to soil substrates (Figure 19). While 99.7% (2382 stems/ha) of first season seedlings are found on logs, only 8.3% (or 3.3 stems/ha) of cedar between 15 - 40 cm dbh were associated with logs. Although it may be difficult to accurately assess the original substrate of a large tree, no cedar > 40 cm dbh showed evidence of having established on a log substrate. Logs occupy an area of 680 m² per hectare of forest floor and represent various stages of decay. Based on an index of decay (Appendix 1) 70.4% of all logs were found to be well or very well decomposed. Additionally, the greatest seedling densities were found on logs in these more advanced states of decay (Table 6).

Seedling height was the best predictor of seedling age for cedar ($r = 0.84$) and was used to derive a population age structure for seedlings ≤ 1 m in height (Figure 20). Cedar seedling mortality was estimated to be 65% during the first growing season (Table 7). From years 4 through 12, mortality averaged 24% of the previous age-class and 99.4% of the initial cohort was lost by year 13. Regression analysis of the seedling age structure (years 4 - 12) indicated that the power function model represented age distribution more accurately ($r = -0.96$) than did the negative exponential model ($r = -0.92$)(Figure 21).

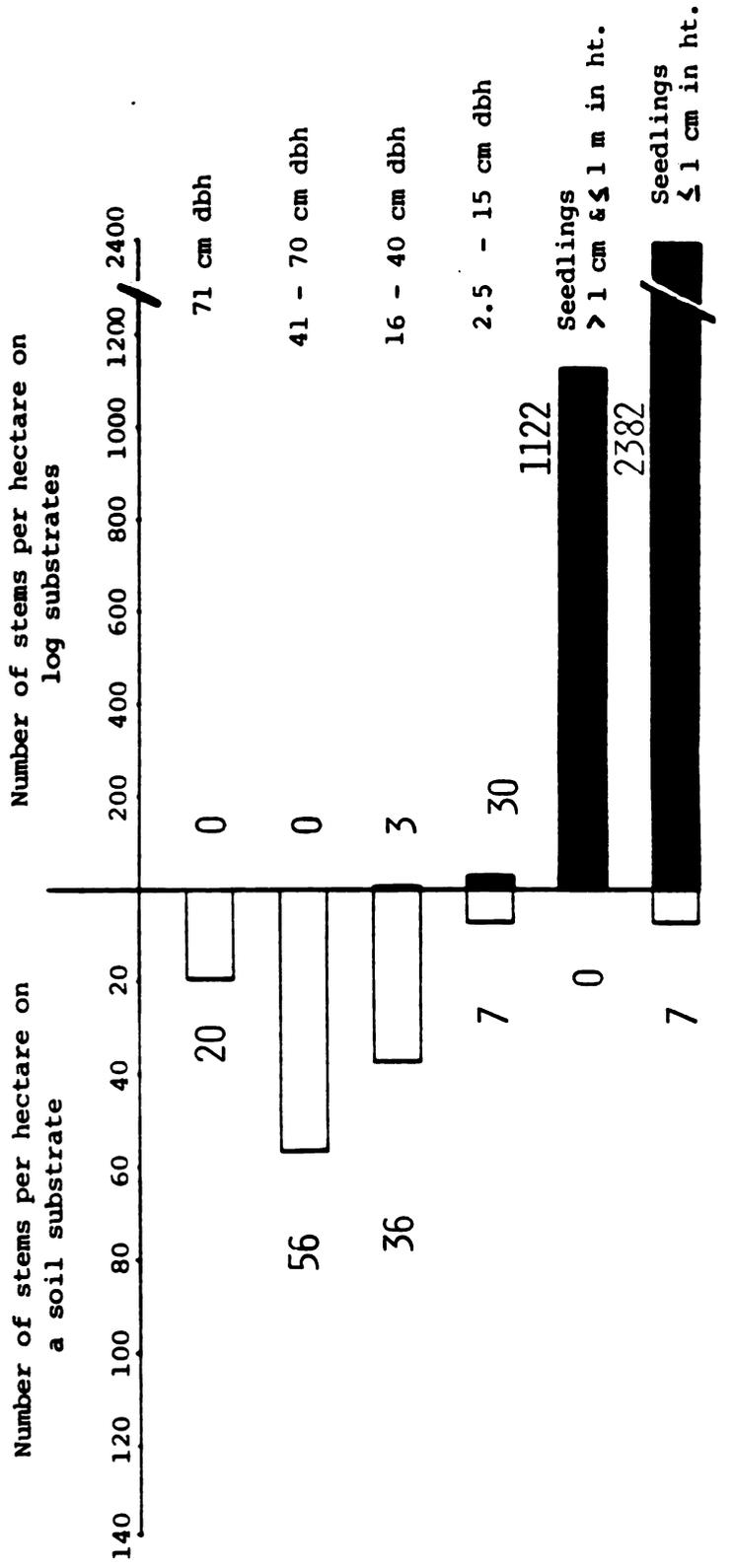


FIGURE 19. Occurrence of cedar stems by size classes, relative to log and soil substrates.

TABLE 6. Seedling density (seedlings/m²) for logs in four states of decay.

| DECAY STATES ^{1/} | SEEDLINGS/m ² OF LOG AREA (± SD) |
|----------------------------|---|
| 1. Relatively Undecomposed | 0.6 ± 0.5 |
| 2. Moderately Decomposed | 0.5 ± 0.4 |
| 3. Well Decomposed | 1.7 ± 0.3 |
| 4. Very Well Decomposed | 1.7 ± 0.9 |

^{1/} Descriptive criteria for decay states given in Appendix 1.

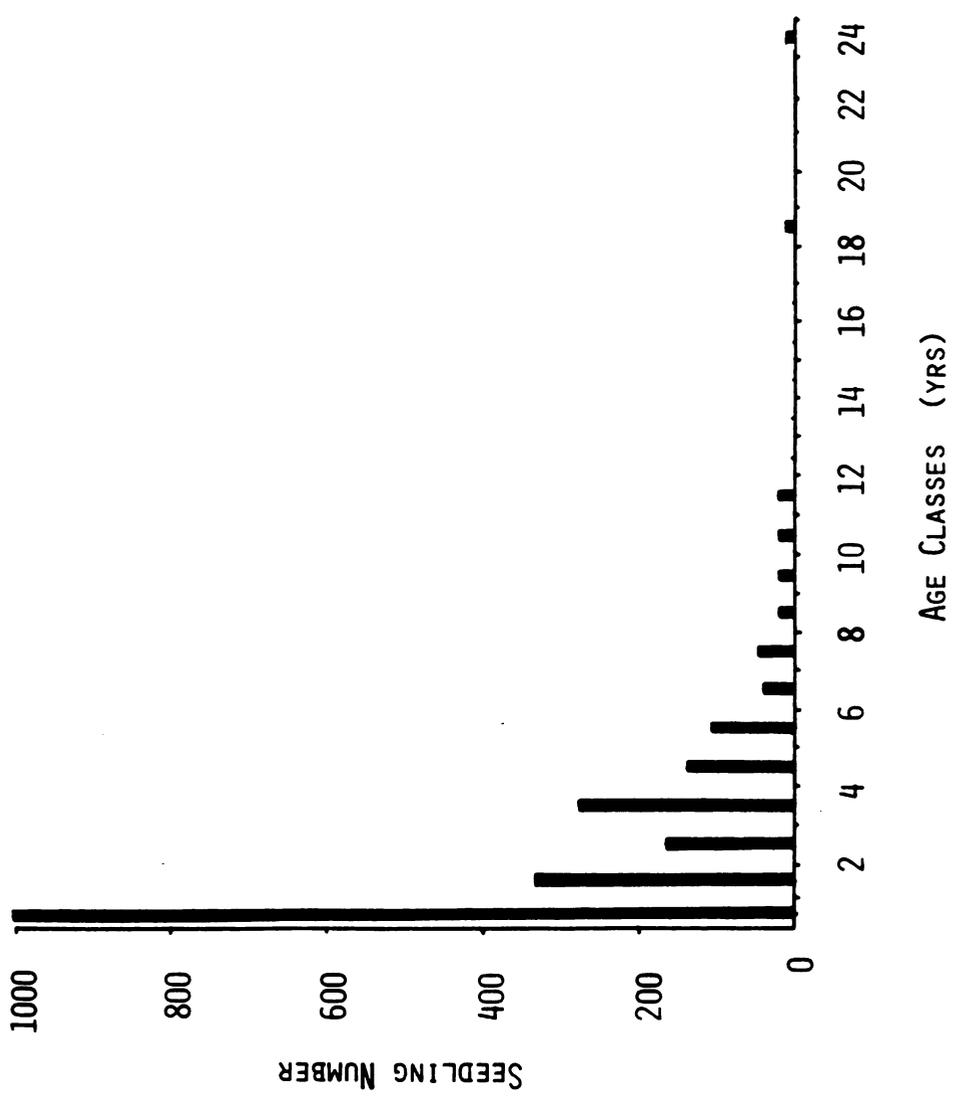


FIGURE 20. Population age structure for cedar seedlings (< 1 m in height). Seedling numbers adjusted to a first year cohort of 1000 individuals.

TABLE 7. Life-table for white cedar seedlings in the old-growth stand. ^{1/}

| Age (years) | Numbers per age class ^{2/} | Proportion of initial seedling population | Proportion lost before next age class |
|-------------|-------------------------------------|---|---------------------------------------|
| 0 - 1 | 1000 | 1.00 | 0.65 |
| 1.1 - 2 | 348 | 0.38 | 0.57 |
| 2.1 - 3 | 150 | 0.15 | 0.00 |
| 3.1 - 4 | 282 | 0.28 | 0.51 |
| 4.1 - 5 | 138 | 0.14 | 0.26 |
| 5.1 - 6 | 102 | 0.10 | 0.76 |
| 6.1 - 7 | 24 | 0.02 | 0.00 |
| 7.1 - 8 | 30 | 0.03 | 0.60 |
| 8.1 - 9 | 12 | 0.01 | 0.00 |
| 9.1 - 10 | 12 | 0.01 | 0.00 |
| 10.1 - 11 | 12 | 0.01 | 0.00 |
| 11.1 - 12 | 12 | 0.01 | 0.00 |
| 12.1 - 13 | 0 | 0.00 | |

^{1/} Life table extended to first unrepresented (no seedlings) age-class

^{2/} Numbers adjusted to an initial cohort of 1000.

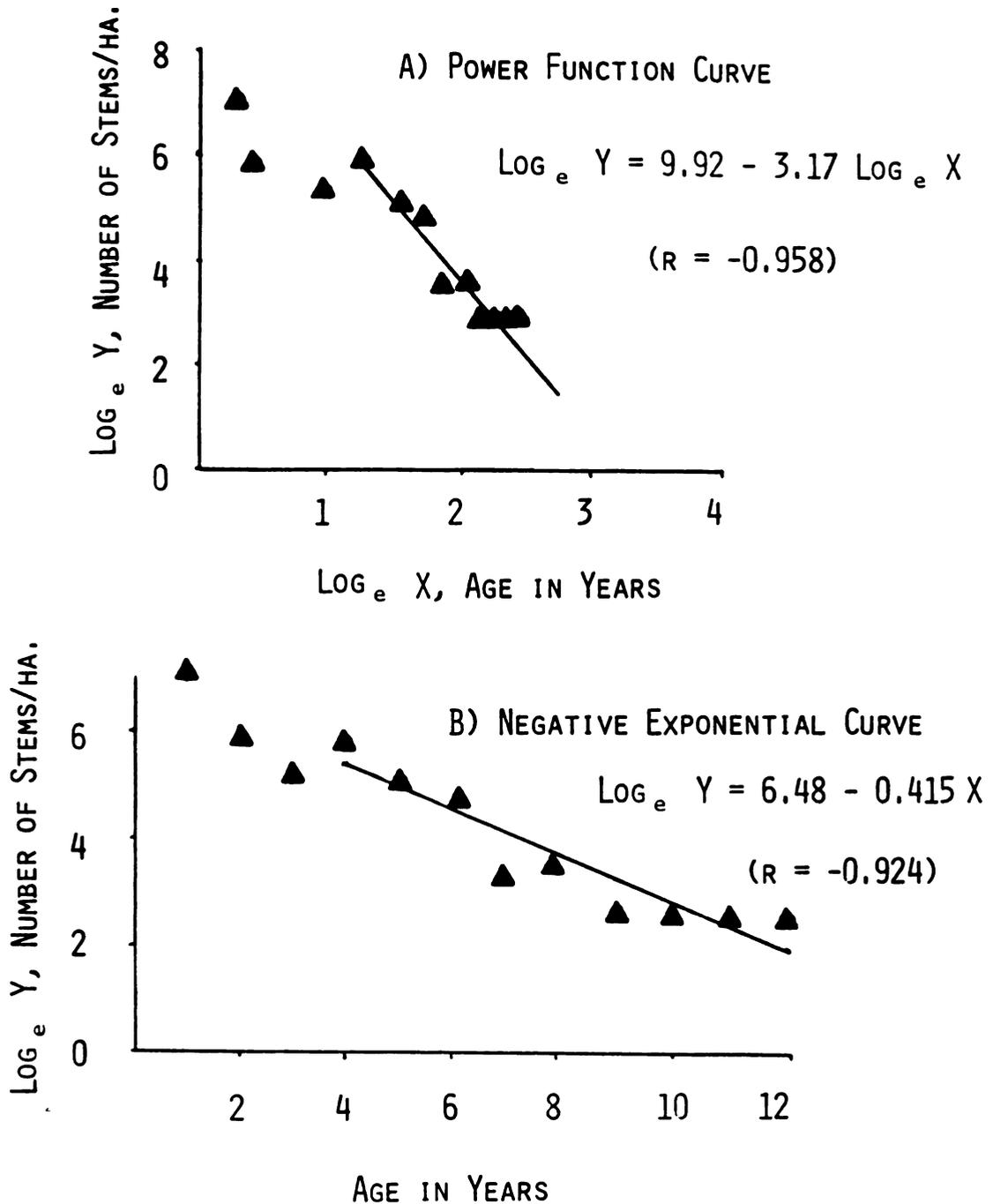


Figure 21. Regression analysis of cedar seedling survivorship. A) Power Function: $\text{Log}_e Y$ (number of stems/ha) = $9.92 - 3.17 \text{Log}_e X$ (age in years) ($n = 12$, $r = -0.958$). B) Negative Exponential: $\text{Log}_e Y$ (number of stems/ha) = $6.84 - 0.415 X$ (age in numbers) ($n = 12$, $r = -0.924$).

Stand Mortality

Total stand tree mortality (Table 8) was comprised primarily of cedar (68%). The senescent status of cedar was further suggested by the fact that 31% of all cedar stems sampled were dead, compared with 3% and 7% for maple and ash, respectively. Cedar mortality consisted of six standing dead stems (\bar{x} dbh = 49.6 cm) and 15 fallen stems (\bar{x} dbh = 46.9 cm). In contrast, sugar maple mortality was represented by two standing dead saplings (\bar{x} dbh = 6.9 cm) while mortality for white ash resulted from the death of two standing stems (\bar{x} dbh = 39.6 cm) and a single, large individual which appeared to have been wind thrown (\bar{x} dbh = 57.0 cm). Of particular note in this stand is balsam fir, a common associate of cedar on open dunes (Olson 1958). Mortality data indicate that 50% of all balsam fir stems in this stand were dead. An analysis of all down trees indicated that direction of fall was not statistically different from random (Figure 22).

Biomass and Productivity

Biomass

Distribution of aboveground biomass by component and species (Table 9) indicates the dominance of cedar in this stand. Cedar accounted for 61% of total bole biomass (wood and bark) in contrast to the codominants, maple and ash,

TABLE 6. Summary of mortality data from the mature stand for all trees (≥ 2.54 cm dbh) within twelve 250 m² sample plots.

| SPECIES | NUMBER OF LIVE STEMS | NUMBER OF DEAD STEMS | TOTAL NUMBER OF STEMS/HA (live/dead) | PERCENT DEAD FOR A SPECIES | PERCENT OF TOTAL STAND MORTALITY |
|----------------------------|-------------------------|-------------------------|---|-------------------------------|-------------------------------------|
| <u>Thuja occidentalis</u> | 46 | 21 | 67 | 31 | 68 |
| <u>Acer saccharum</u> | 103 | 3 | 106 | 3 | 10 |
| <u>Fraxinus americana</u> | 39 | 3 | 42 | 7 | 10 |
| <u>Tilia americana</u> | 6 | 1 | 7 | 14 | 3 |
| <u>Abies balsamea</u> | 3 | 3 | 6 | 50 | 10 |
| <u>Ostrya virginiana</u> | 5 | 0.0 | 5 | 0.0 | 0.0 |
| <u>Cornus alternifolia</u> | 12 | 0.0 | 12 | 0.0 | 0.0 |
| <u>Acer spicatum</u> | 43 | 0.0 | 43 | 0.0 | 0.0 |
| <u>Prunus virginiana</u> | 12 | 0.0 | 12 | 0.0 | 0.0 |
| TOTALS (n) | 269 | 31 | 300 | ----- | 99.8 |

TABLE 8. Summary of mortality data from the mature stand for all trees (≥ 2.54 cm dbh) within twelve 250 m² sample plots.

| SPECIES | NUMBER OF LIVE STEMS | NUMBER OF DEAD STEMS | TOTAL NUMBER OF STEMS/HA (live/dead) | PERCENT DEAD FOR A SPECIES | PERCENT OF TOTAL STAND MORTALITY |
|----------------------------|-------------------------|-------------------------|---|-------------------------------|-------------------------------------|
| <u>Thuja occidentalis</u> | 46 | 21 | 67 | 31 | 68 |
| <u>Acer saccharum</u> | 103 | 3 | 106 | 3 | 10 |
| <u>Fraxinus americana</u> | 39 | 3 | 42 | 7 | 10 |
| <u>Tilia americana</u> | 6 | 1 | 7 | 14 | 3 |
| <u>Abies balsamea</u> | 3 | 3 | 6 | 50 | 10 |
| <u>Ostrya virginiana</u> | 5 | 0.0 | 5 | 0.0 | 0.0 |
| <u>Cornus alternifolia</u> | 12 | 0.0 | 12 | 0.0 | 0.0 |
| <u>Acer spicatum</u> | 43 | 0.0 | 43 | 0.0 | 0.0 |
| <u>Prunus virginiana</u> | 12 | 0.0 | 12 | 0.0 | 0.0 |
| TOTALS (n) | 269 | 31 | 300 | ----- | 99.8 |

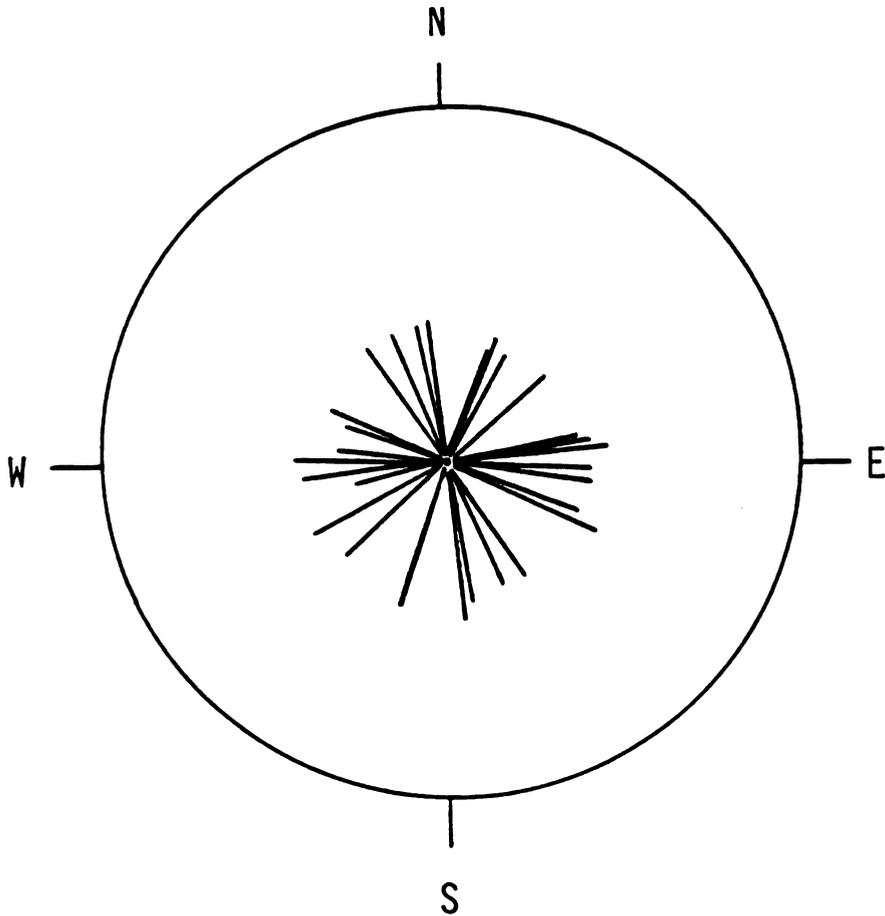


FIGURE 22. Direction of tree falls within the study area. Chi-square goodness of fit test for direction of fall was not significant ($\chi^2 = 3.75$; $\alpha > 0.05$), indicating tree fall was random.

TABLE 9. Estimated biomass values (mt/ha).

| SPECIES | BOLE WOOD | BOLE BARK | BRANCHES (wood + bark) | FOLIAGE | TOTAL ABOVEGROUND BIOMASS |
|-------------------------------|--------------|--------------|------------------------------|------------|---------------------------------|
| <u>Thuja occidentalis</u> | 66.8 | 3.6 | 15.0† | 5.5† | 90.9 |
| <u>Acer saccharum</u> | 25.9 | 1.7 | 6.2* | 1.2* | 35.1 |
| <u>Fraxinus americana</u> | 13.2 | 1.3 | 2.7* | 0.3* | 17.6 |
| Other species | 2.7 | --- | 1.6* | 0.6*° | 4.8 |
| TOTAL | 108.6 | 6.8 | 25.5 | 7.6 | 148.5 |

† Estimated from Reiners (1972)

* Estimated from annual litterfall

° Includes fruits which were not separated by species

which comprise 24% and 13% of bole biomass, respectively. Total bole biomass alone represented 78% of the aboveground total for the stand (148.5 mt/ha). This pattern of cedar dominance is also reflected in leaf and branch biomass values where cedar represents 73% and 59% of stand totals for these components, respectively.

A second, direct estimate of bole biomass for cedar, based on measurement of fallen stems, resulted in a value only 2% greater than the 69.8 mt/ha estimated from parabolic approximations of stem form. Both methods appeared to provide acceptable estimates of bole volume and biomass: however, for reasons discussed previously, all values reported here were based on parabolic estimates.

Productivity

Net annual production of bole wood and bark, by species, is presented in Table 10. Bole wood accounted for 94% of total bole production which equalled 2.1 mt/ha/yr. In contrast to the cedar-dominated pattern for biomass, maple and ash represented the greatest percentage of bole productivity (40% and 35%, respectively) while cedar accounted for 20% of the total.

A summary of mean annual litter production (Table 11) indicates that leaves comprise the majority (66%) of litter production while branches were 33% of the total. As with bole wood and bark, maple was most productive, representing 58% of branch production and 38% of leaf production.

TABLE 10. Estimated bole (wood and bark) annual net primary productivity.

| SPECIES | BOLE WOOD PRODUCTION (mt/ha/yr) | BOLE BARK PRODUCTION (mt/ha/yr) | TOTAL BOLE PRODUCTION | PERCENT OF BOLE PRODUCTION |
|-------------------------------------|---------------------------------------|---------------------------------------|--------------------------|----------------------------------|
| <u>Thuja</u> <u>occidentalis</u> | 0.4 | 0.02 | 0.43 | 20.1% |
| <u>Acer</u> <u>saccharum</u> | 0.8 | 0.05 | 0.84 | 39.6% |
| <u>Fraxinus</u> <u>americana</u> | 0.7 | 0.05 | 0.75 | 35.4% |
| Other species | 0.1 | 0.01 | 0.11 | 5.4% |
| TOTAL | 2.0 | 0.13 | 2.13 | 100.5% |

TABLE 11. Mean annual litter production.

| <u>LITTER COMPONENT</u> <u>SPECIES</u> | <u>ANNUAL LITTER PRODUCTION</u> (mt./ha./yr) | | <u>PERCENT OF TOTAL LITTERFALL</u> |
|---|---|--------------|------------------------------------|
| | <u>PARTIAL</u> | <u>TOTAL</u> | |
| Branches (wood and bark)..... | 1.6 | | 32.9% |
| <u>Thuja occidentalis</u> | 0.24 | | |
| <u>Acer saccharum</u> | 0.93 | | |
| <u>Fraxinus americana</u> | 0.16 | | |
| Other species | 0.28 | | |
| Leaves..... | | 3.2 | 65.8% |
| <u>Thuja occidentalis</u> | 1.2* | | |
| <u>Acer saccharum</u> | 1.2 | | |
| <u>Fraxinus americana</u> | 0.2 | | |
| Other species | 0.5 | | |
| Fruits | | 0.06 | 1.2% |
| <u>Thuja occidentalis</u> | 0.04 | | |
| <u>Acer saccharum</u> | 0.02 | | |
| <u>Fraxinus americana</u> | 0.01 | | |
| Other species | @ | | |
| TOTAL..... | 4.86 | | 99.9% |

* Estimated as a percentage of foliage biomass from Reiners (1972, 1974)

@ Value included with leaf litter

Fruit and seed production by cedar, maple and ash was 0.06 mt/ha/yr, and cedar accounted for the greatest share of this total (61%).

Total aboveground NPP was estimated to be 7.1 mt/ha/yr (Table 12). In contrast to biomass, overall cedar productivity was 26% of total aboveground NPP while maple accounted for 42%. Ash represented 18% of total aboveground NPP while the remaining 14% was divided among the other tree species.

Forest Recovery

Estimated Date of Logging

Growth release analysis for cedar located adjacent to the second-growth stand indicated abrupt growth increases in approximately 1896 (Figure 23). Patterns of annual growth (Table 13) show a 236% increase in average growth for cedar number 1 subsequent to 1890 and an increase of 117% for cedar number 2 after 1903. Cedar 3 increased 41% in average growth following release in 1895; however, this tree had an average growth rate of 2.7 mm/yr prior to release.¹ The growth record for cedar 4 began in 1882 and, therefore, did not provide the requisite 15 year growth period before

¹ Release for this study requires a 50% increase in average annual increment for trees with moderate rates of growth (≥ 1.0 mm/yr).

TABLE 12. Estimated annual net primary productivity (mt/ha/yr).

| SPECIES | BOLE WOOD | BOLE BARK | BRANCHES (wood/bark) | FOLIAGE | FRUITS | ABOVEGROUND TOTAL | PERCENTAGE OF TOTAL |
|-------------------------------|-----------|-----------|-------------------------|---------|--------|----------------------|------------------------|
| <u>Thuja occidentalis</u> | 0.4 | 0.02 | 0.24 | 1.2* | 0.04 | 1.9 | 26.7% |
| <u>Acer saccharum</u> | 0.8 | 0.05 | 0.93 | 1.2 | 0.02 | 3.0 | 42.3% |
| <u>Fraxinus americana</u> | 0.7 | 0.05 | 0.16 | 0.3 | 0.01 | 1.2 | 16.9% |
| Other species | 0.1 | ----- | 0.28 | 0.6 | ----- | 1.0 | 14.1% |
| TOTAL | 2.0 | 0.12 | 1.61 | 3.3 | 0.07 | 7.1 | 100% |

* Estimated as a percentage of foliage from Reiners (1972, 1974)

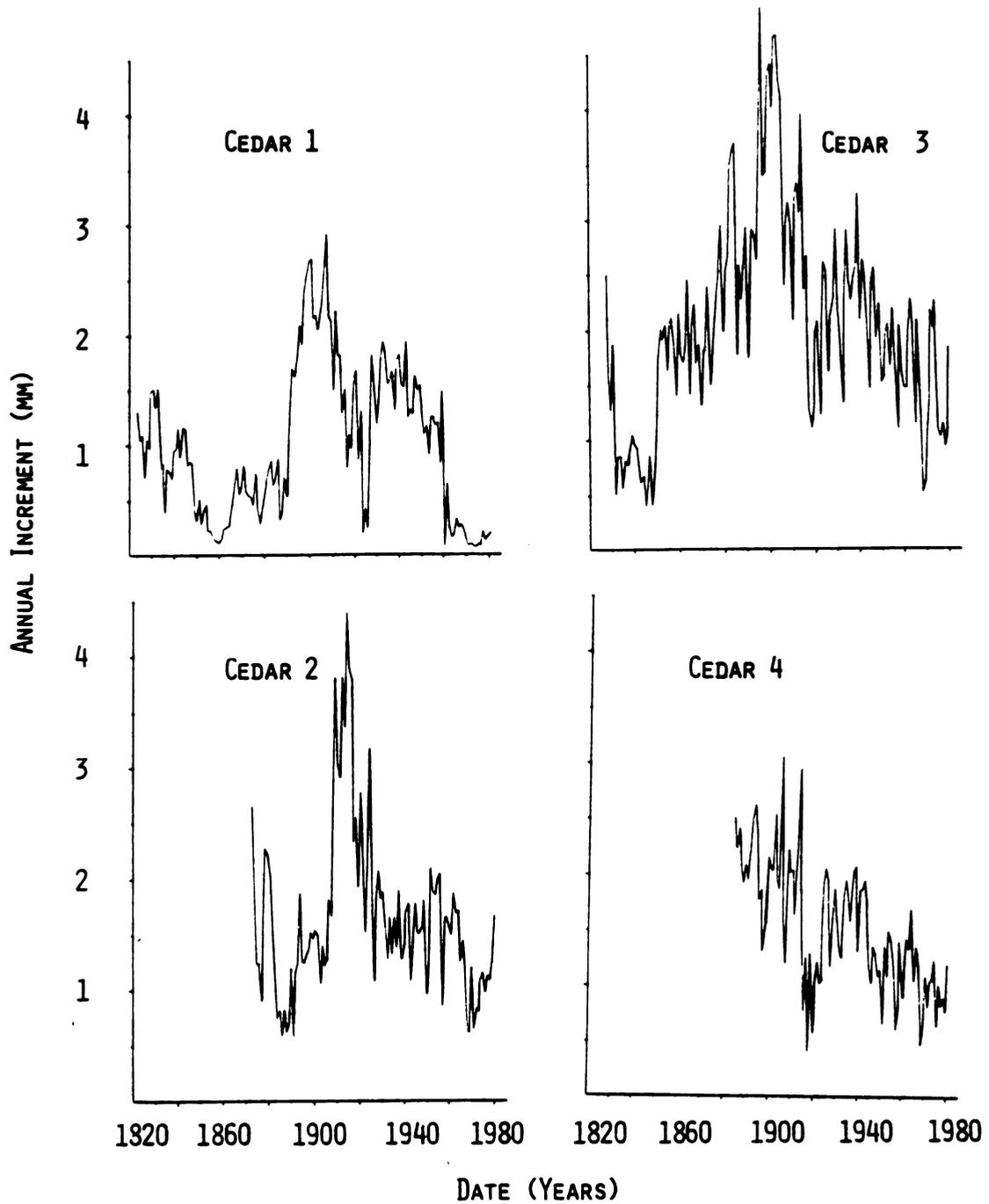


FIGURE 23. Patterns of average annual growth (in mm) for old-growth cedar adjacent to the logged stand. Dates indicate year of apparent growth release.

Table 13. Summary of growth release in cedar in response to logging.

| TREES EXAMINED | RELEASE (date of abrupt growth change) | AVERAGE GROWTH RATE (mm/YR) BEFORE RELEASE | AVERAGE GROWTH RATE (mm/YR) AFTER RELEASE | PERCENT CHANGE IN GROWTH AFTER RELEASE |
|----------------------|--|--|---|--|
| <u>EDGE REES</u> | | | | |
| Cedar 1 | 1890 | 0.6 | 2.02 | + 236% |
| Cedar 2 | 1903 | 1.26 | 2.74 | + 117% |
| Cedar 3 | 1895 [Ⓔ] | 2.72 [Ⓔ] | 3.83 [Ⓔ] | + 42% [Ⓔ] |
| Cedar 4 | no record | no record | 1.98 ^{*Ⓔ} | -- [Ⓔ] |
| | \bar{x} = 1896 | 0.93 | 2.38 | + 156% |
| <u>CLOSED FOREST</u> | | | | |
| Cedar 1 | Ⓔ | 1.90 [#] | 1.67 [*] | - 12% |
| Cedar 2 | Ⓔ | 1.63 [#] | 2.06 [*] | + 26% |
| Cedar 3 | Ⓔ | 0.64 [#] | 0.92 [*] | + 44% |
| Cedar 4 | Ⓔ | 1.52 [#] | 1.55 [*] | + 2% |
| | \bar{x} = ---- | 1.42 | 1.55 | + 9% |

Ⓔ Did not meet release criteria, and not included in average of release date, average growth rates or percent change in growth

Average growth rate (mm/yr), prior to estimated date of logging (1896)

* Average growth rate (mm/yr), following estimated date of logging (1896)

release. Based upon cedar 1 and 2 the average date of release was 1896 with an average growth increase of 156%.

Old-growth cedar from within the mature stand did not exhibit pronounced increases in growth following 1896 (Figure 24) and did not meet the established release criteria. These trees exhibited only a 9% increase in average growth in the period following 1896 (Table 13).

The average age for trees which had established on cut cedar stumps was 55.2 yrs, SD \pm 7.5 (Table 14) and the oldest stump-established tree was a cedar estimated to be 64 years of age. The population-age structure of second-growth sugar maple (Figure 25) conformed to a negative exponential model ($r = 0.985$) in a slightly irregular form. There was a distinct peak in the 60 year age class while the 30 and 40 year age classes had fewer stems than predicted by the model. Two sugar maple individuals per hectare were estimated to be between 135 - 144 years of age, indicating that maple existed in the stand prior to logging in 1896 (Table 15).

Forest Regeneration

The strong correlation between dsh (diameter at stump height) and dbh for cedar (Figure 10) allowed for a direct estimate of the basal area of trees removed by logging. A relatively narrow size range of trees (Figure 26) was cut, representing a basal area of 48.9 m²/ha and a density of 220 stems/ha. A small number of cedar (10 stems/ha) with an

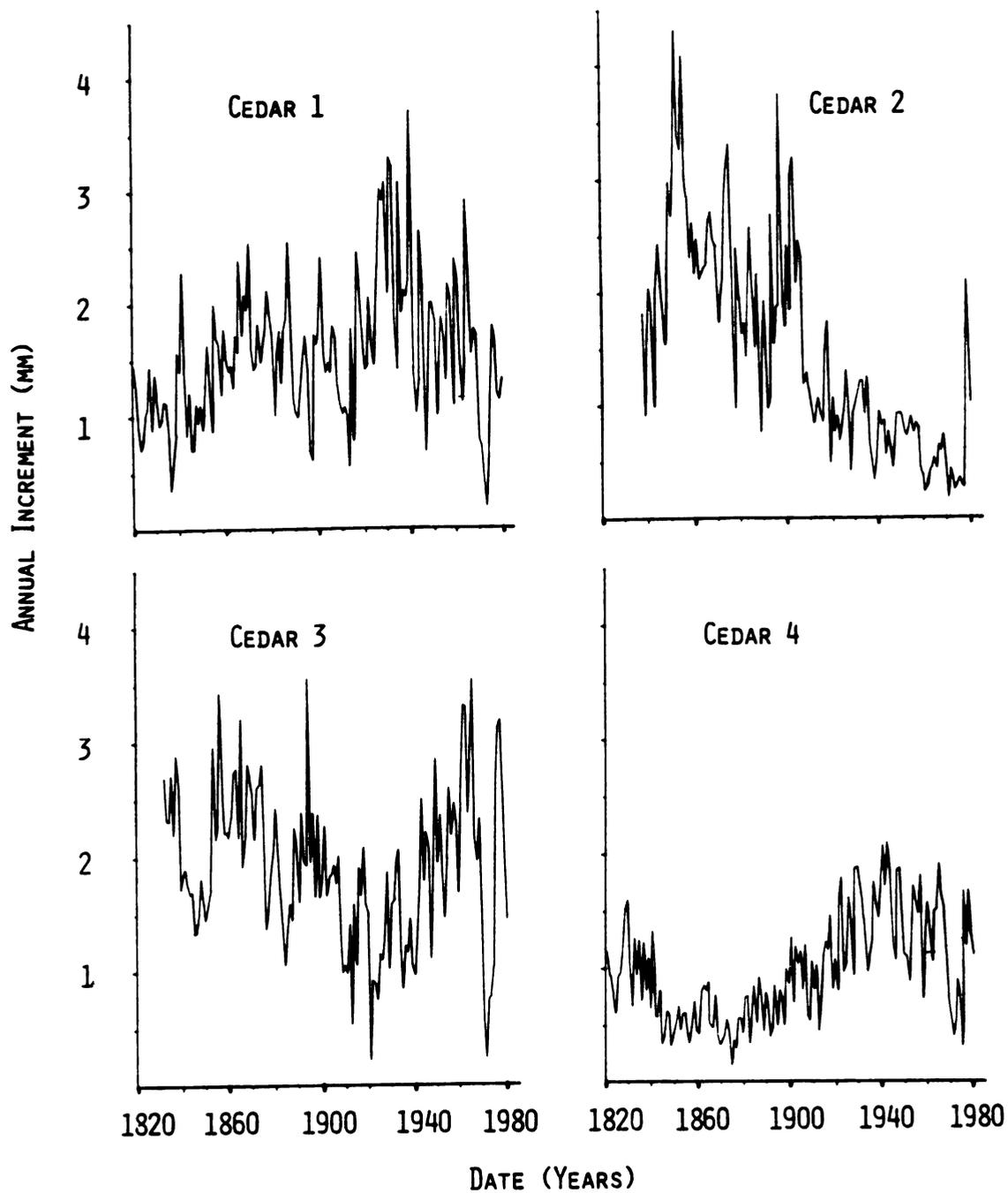


FIGURE 24. Patterns of average annual growth (in mm), for old-growth cedar from within the mature stand.



TABLE 14. Summary information on trees which had established on cut cedar stumps, within the second-growth stand.

| SPECIES | DIAMETER AT BREAST HEIGHT (in cm) | TYPE OF REPRODUCTION | ESTIMATED AGE (Years) |
|-------------|---|-------------------------|------------------------------|
| White Birch | 47.5 | Seed | 54 |
| White Birch | 43.0 | Seed | 49 |
| Basswood | 43.0 | Seed | 62 |
| White Cedar | 36.0 | Sprout ? | 64 |
| White Cedar | 36.8 | Seed | 47 |
| \bar{x} | 41.3 cm (SD \pm 4.8) | | 55.2 (SD \pm 7.5) years |

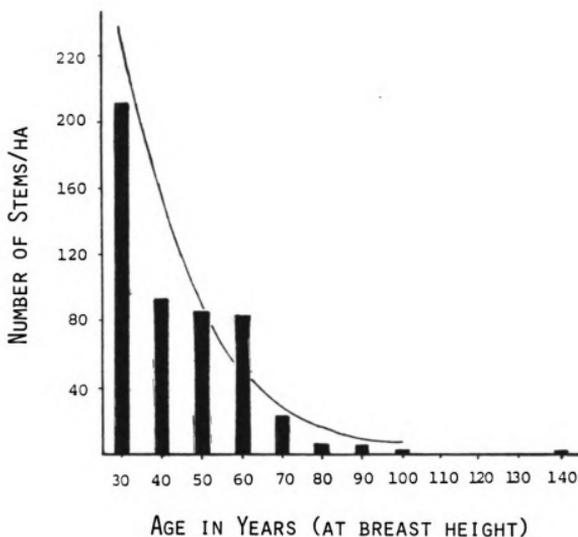


Figure 25. Age structure of second-growth sugar maple within logged study area. Negative exponential model: $\text{Log}_e Y(\text{stems/hectare}) = 7.5 - 0.06 X(\text{age in years at breast height})$ ($r = 0.967$), fitted to age class distribution.

Table 15. Population age structure of second-growth sugar maple^{1/}.

| AGE CLASS (years) | NUMBER OF TREES (in 4500 m ²) | PERCENT OF TOTAL | PROPORTION LOST BEFORE NEXT AGE CLASS |
|----------------------|---|---------------------|---|
| 25 - 34 | 95 | 41.3% | 55.8% |
| 35 - 44 | 42 | 18.3% | 9.5% |
| 45 - 54 | 38 | 16.5% | 2.6% |
| 55 - 64 | 37 | 16.1% | 73.0% |
| 65 - 74 | 10 | 4.3% | 70.0% |
| 75 - 84 | 3 | 1.3% | 0.0% |
| 85 - 94 | 3 | 1.3% | 33.3% |
| 95 | 2 | 0.9% | 100.0% |

^{1/} n = 230

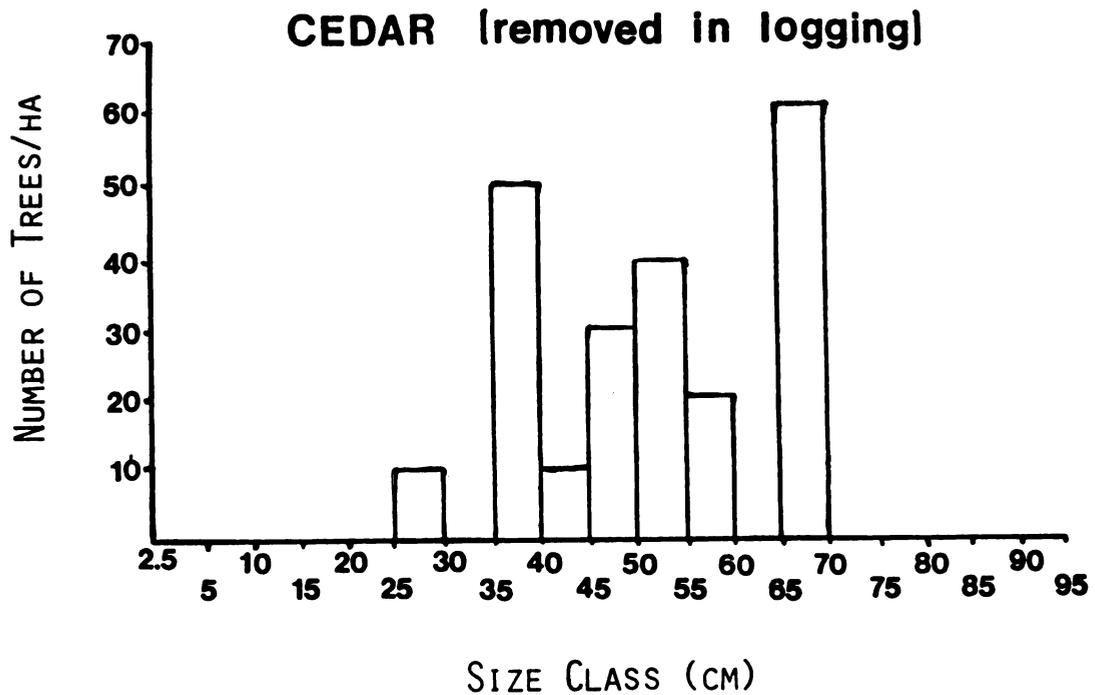


FIGURE 26. Size range of cedar removed by logging adjacent to the old-growth stand. Dbh estimated from stumps based on a regression of dbh on diameter at stump height (stump height: defined as being 30 cm above surface of the ground).

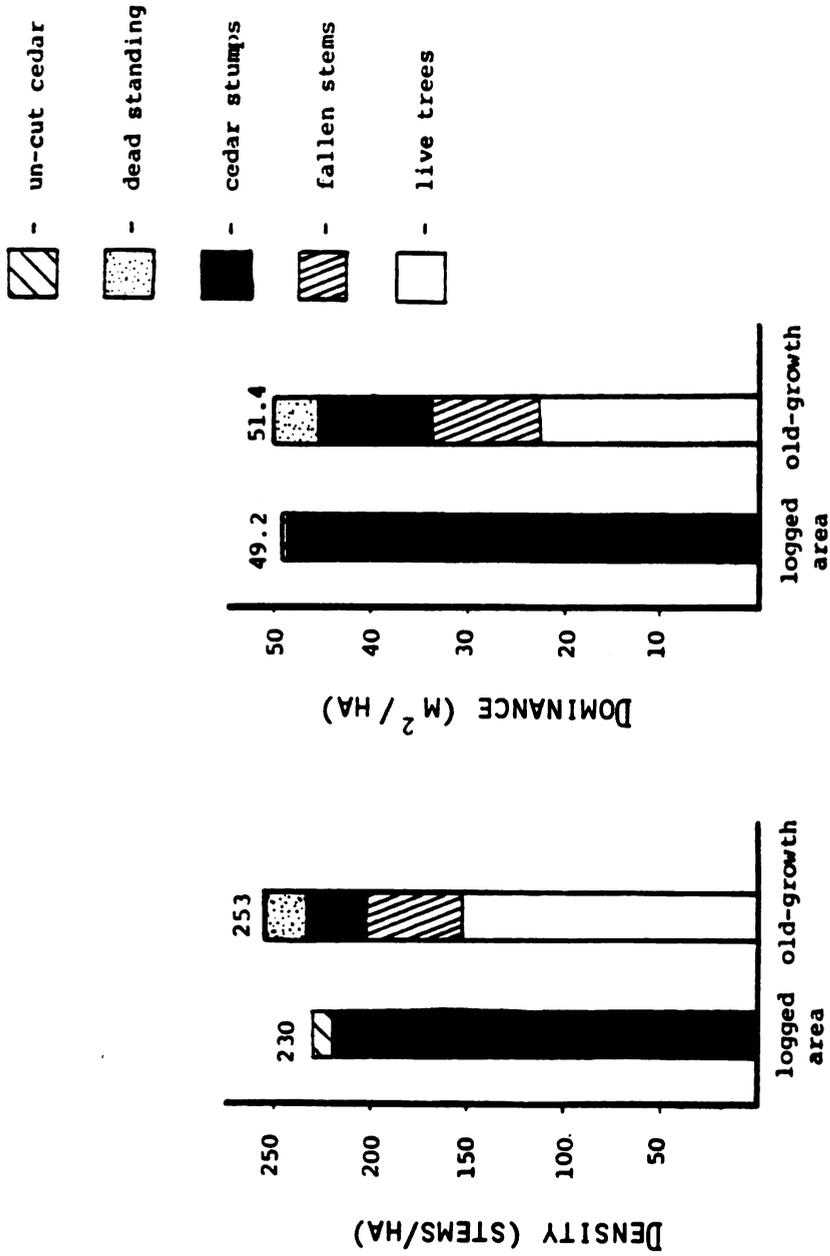


FIGURE 27. Comparisons of density and dominance for cedar in logged and old-growth locations. Density and dominance estimates reflect pre-logging values for both locations.

estimated basal area of 0.33 m²/ha were present at the time of logging but were not harvested (Figure 27).

In the old-growth stand basal area for live cedar was 23.8 m²/ha with a density of 152 stems/ha. Cedar mortality, which had presumably occurred since logging, contributed substantially to the decline in basal area and density (Figure 27). Regarding basal area, fallen stems accounted for 11.7 m²/ha while standing dead stems represented 4.5 m²/ha. Density values for logs and standing dead stems were 49.5 and 19.8 stems/ha, respectively. Stumps encountered within the study area had an estimated basal area of 11.8 m²/ha and a density of 29.7 stems/ha.

A comparison of estimated basal area, at the time of logging, indicates that total basal area for cedar in the old-growth stand was higher (51.4 m²/ha) than in the second-growth stand (49.2 m²/ha). These differences were also reflected in density values where, in the old-growth stand, there were 253 cedar stems/ha compared with 230 cedar stems/ha in the second-growth stand. These differences, however, were not significant (Table 16).

Relative to the mature (old-growth) stand, the logged stand is completely dominated by second-growth maple (Figure 28) which accounts for 72% of total importance, while cedar represented 12% of the total. Changes in species composition following logging are suggested by shifts in basal area (Figure 29). Total basal area in the second-growth stand increased slowly over the first two decades after cutting,

Table 16. Statistical comparison (t-test) between density (A), and dominance (B), for cedar in the second-growth stand, prior to logging.

| | <u>SECOND-GROWTH</u> <u>STAND</u> | <u>OLD-GROWTH</u> <u>STAND</u> |
|--|--------------------------------------|-----------------------------------|
| A) <u>DENSITY (stems/ha):</u> | | |
| \bar{x} | 230.0 | 253.2 |
| SD | 149.4 | 118.5 |
| n* | 10 | 12 |
| | n.s. ^{1/} | |
| B) <u>BASAL AREA (m²/ha):</u> | | |
| \bar{x} | 49.2 | 52.9 |
| SD | 36.9 | 35.4 |
| n* | 10 | 12 |
| | n.s. ^{2/} | |

* Values on a per plot basis

1/ t = -0.50, $\alpha > 0.50$

2/ t = -0.33, $\alpha > 0.50$

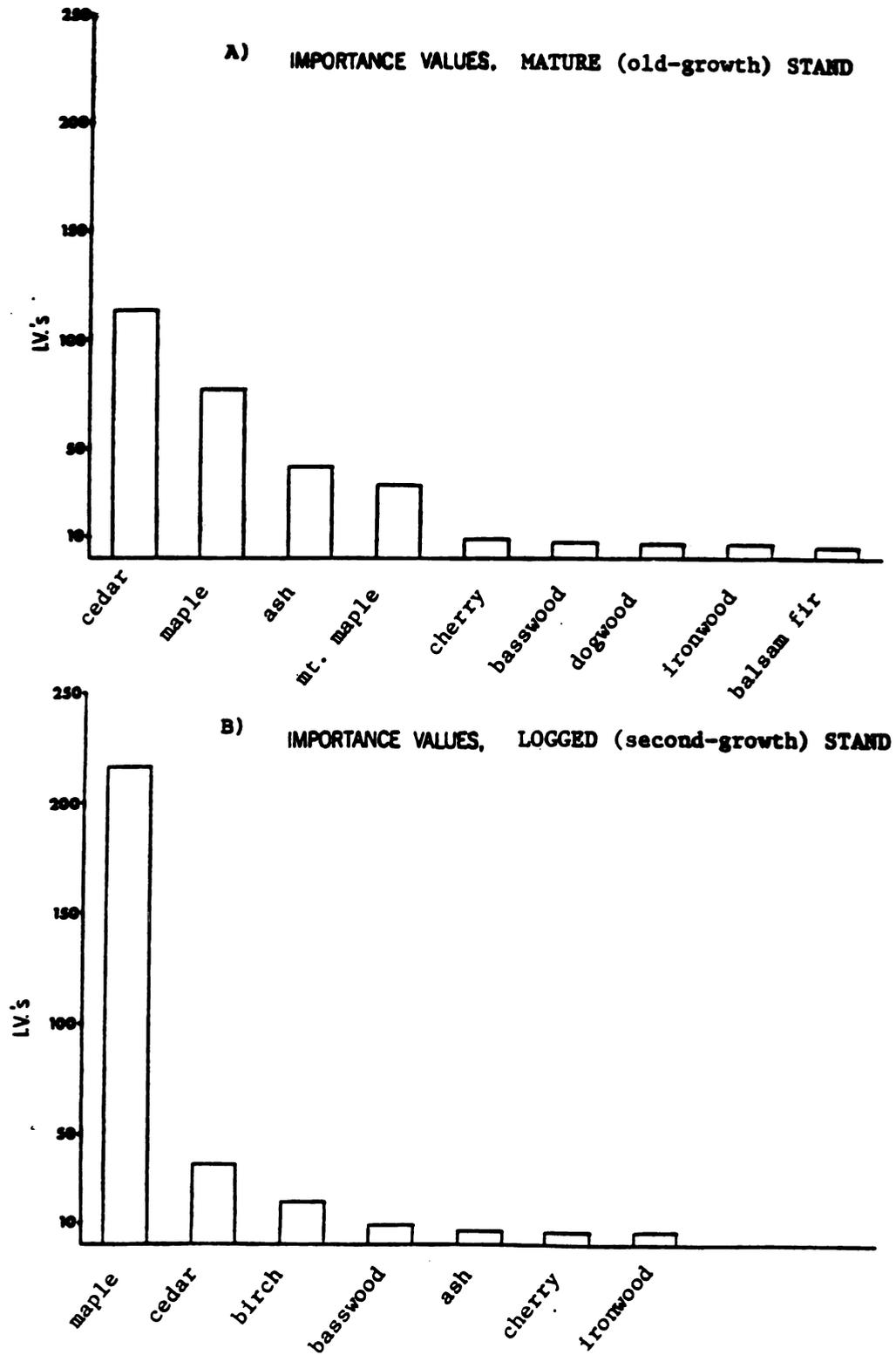


Figure 28. Importance values for the mature stand (A), and the logged stand (B).

but by 1920 began to increase exponentially because of the rapid increase in basal area for maple. There was a gradual recovery of basal area for cedar until 1960, after which little further increase was observed (Figure 29).

In contrast, the pattern of compositional change in the mature stand (Figure 30) was distinctly different. Since 1900 there has been a steady decline in cedar basal area. Overall stand basal area parallels the decline for cedar until 1940 and then increases coincidentally with maple until the present. Current basal area in the second-growth stand ($29 \text{ m}^2/\text{ha}$) is similar to that of the mature stand ($34 \text{ m}^2/\text{ha}$); however, there has been a dramatic reversal in the contribution of cedar and maple to total stand basal area (Figure 31). Whereas old-growth cedar comprises 71% of the basal area total in the mature stand, second-growth maple accounts for 77% of the basal area total in the logged stand.

Maple now represents 87% of total bole biomass and 94% of annual bole net primary productivity in the second-growth stand (Figure 32). The distribution of bole biomass and productivity is quite different in the old-growth stand (Figure 33), where mature cedar dominates bole biomass (61% of total) whereas maple accounts for 40% of total bole net primary productivity. Comparisons between second-growth and mature stands (Figure 34) indicate that overall bole biomass in the second-growth stand ($186.4 \text{ mt}/\text{ha}$) is currently 38% greater than that in the old-growth stand ($115.3 \text{ mt}/\text{ha}$).

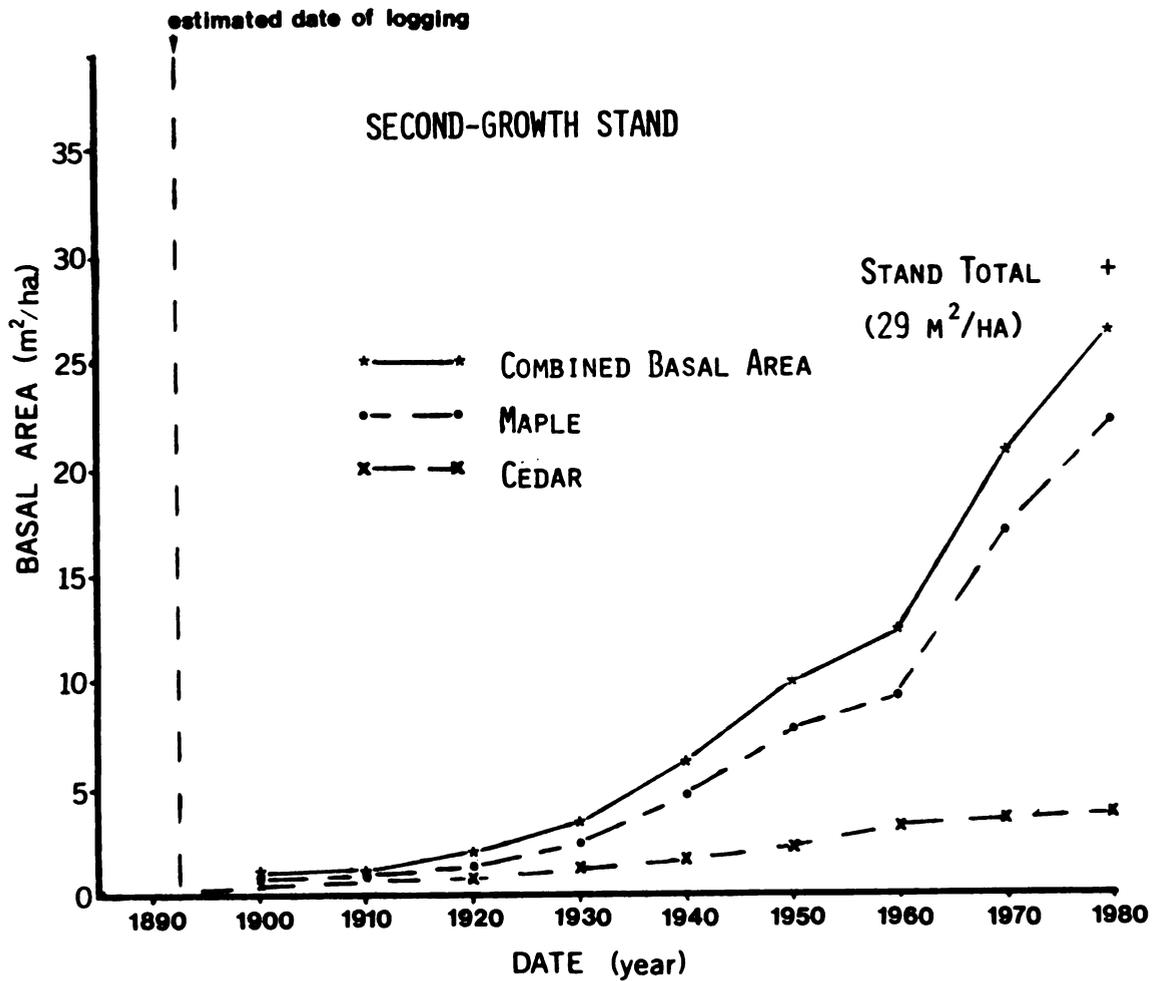


Figure 29. Basal area changes for cedar and maple in the second-growth stand, since 1900.

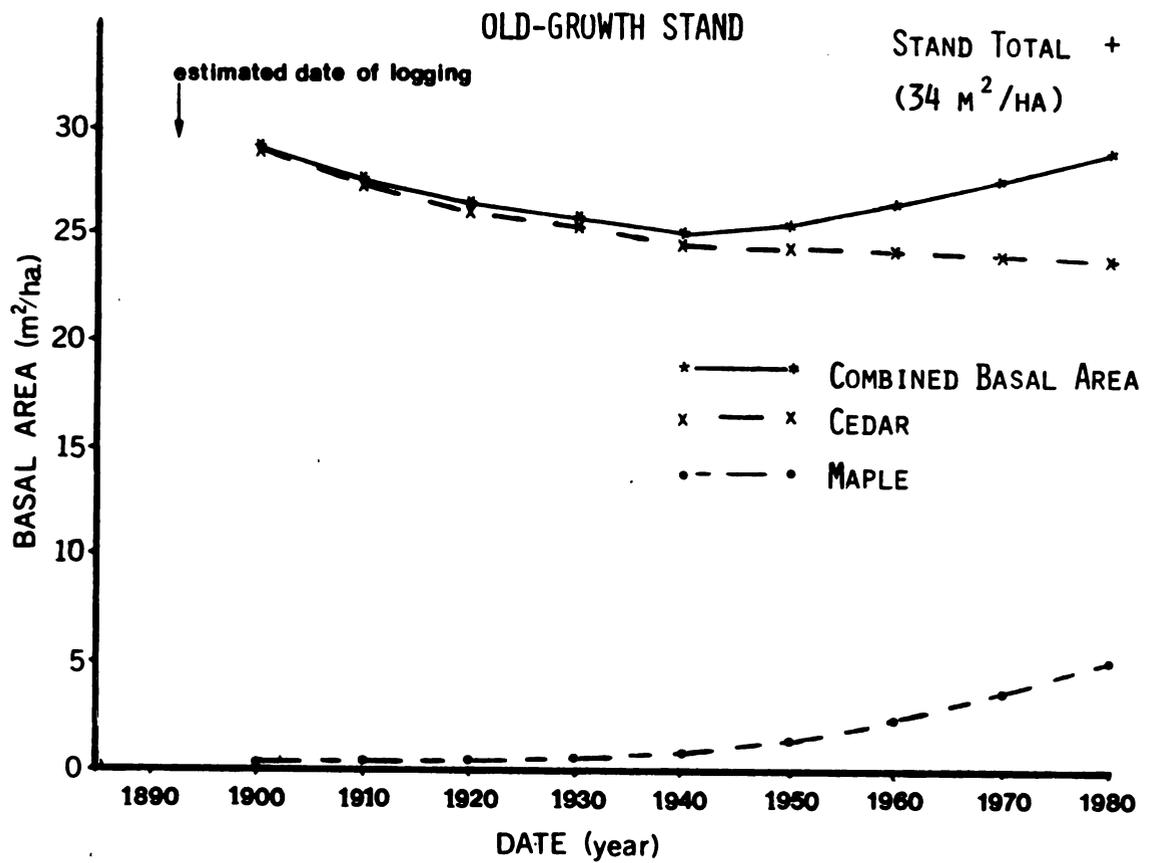


Figure 30. Basal area changes for cedar and maple in the old-growth stand, since 1900.

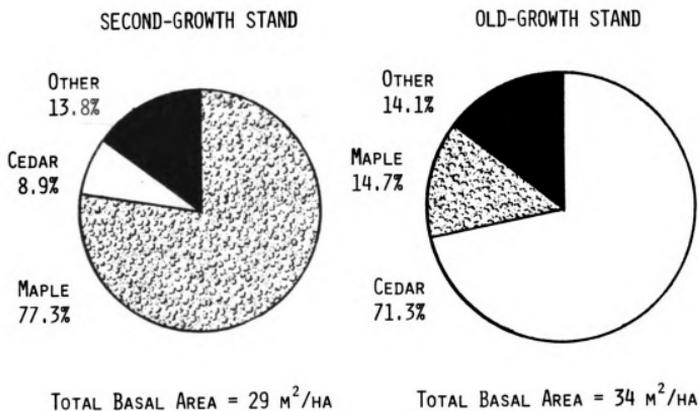


Figure 31. Shifts in the relative contribution of cedar, maple and other species, to basal area, between the old-growth and second-growth stands. Circle size reflects relative basal area.

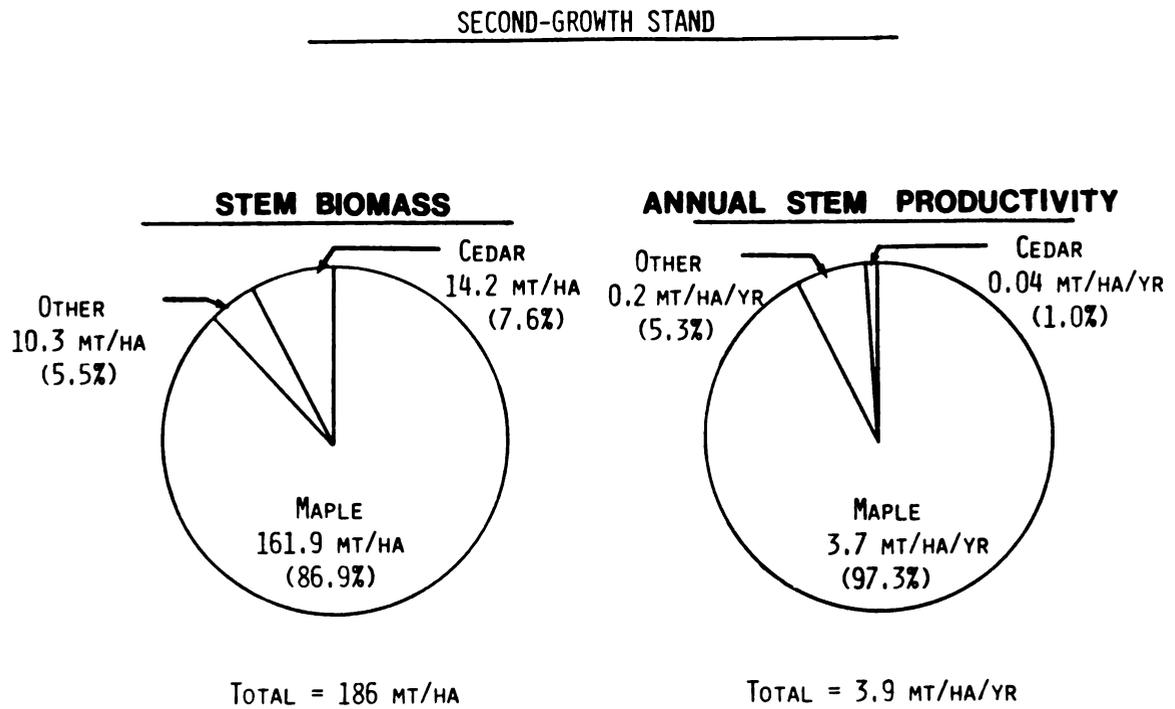


Figure 32. Stem biomass and net stem (bole) primary productivity for all trees in the second-growth stand.

OLD-GROWTH STAND

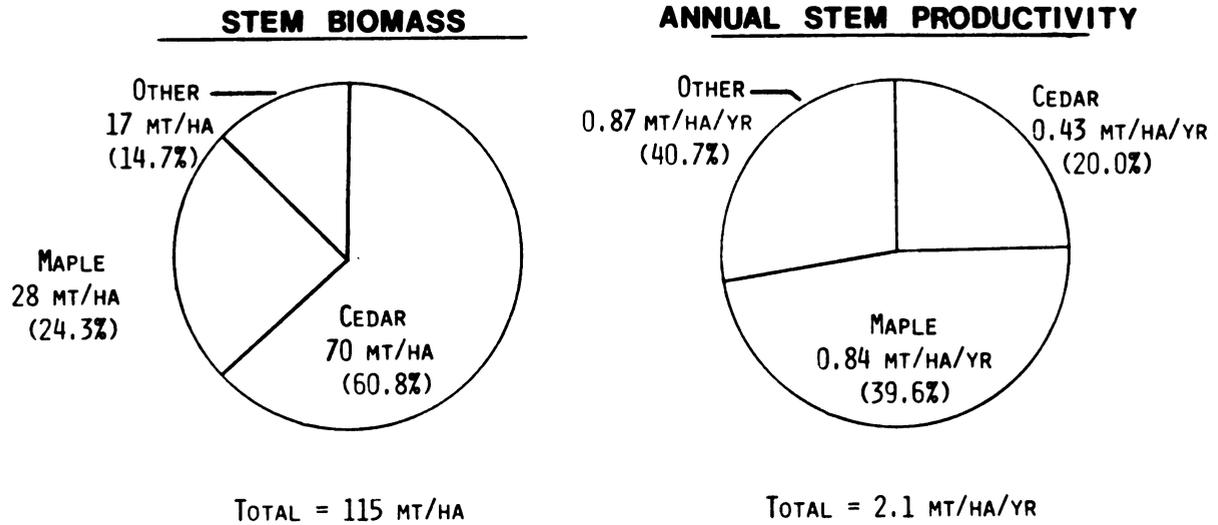


Figure 33. Stem biomass and net stem (bole) primary productivity for trees in the old-growth stand.

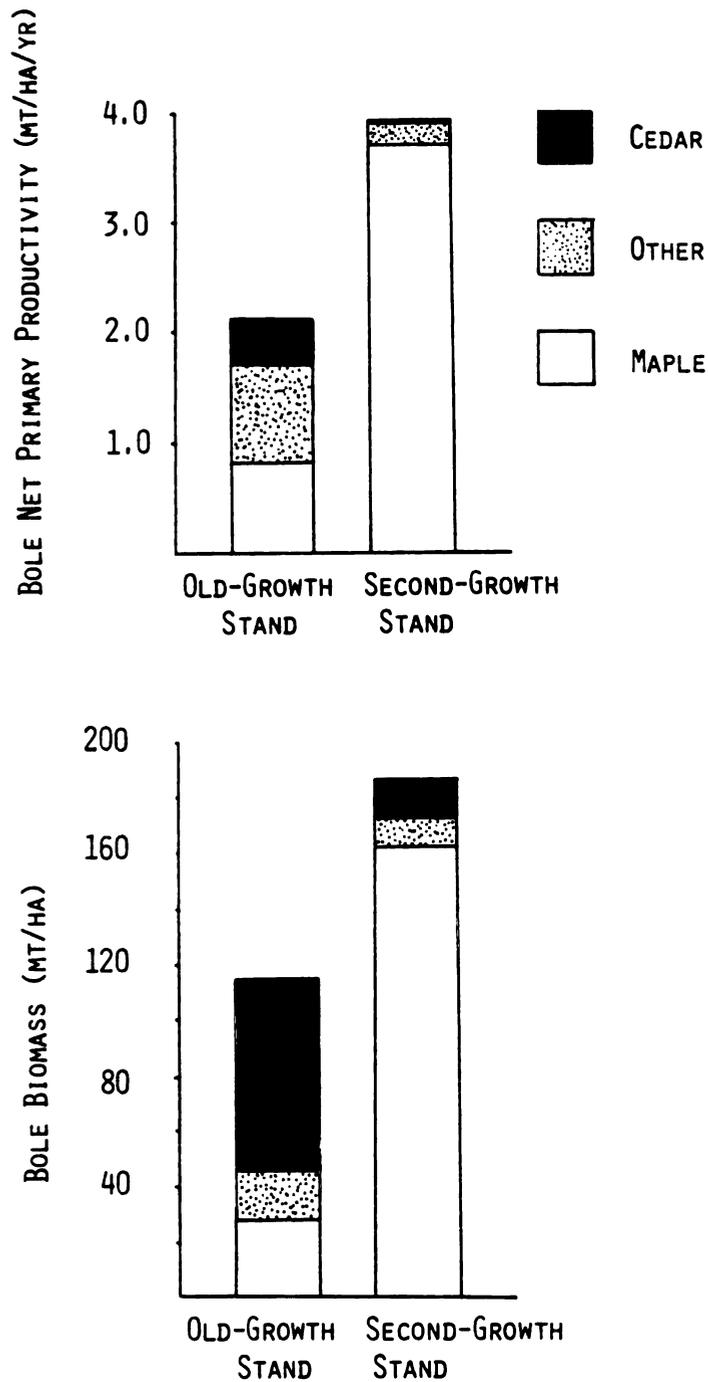


Figure 34. Comparisons of total bole net primary productivity (A) and total bole biomass (B) between old-growth and second-growth stands. Species categories include: cedar, maple and other.

Likewise, the second-growth stand is nearly twice as productive, with total bole production equalling 3.9 mt/ha/yr compared with 2.1 mt/ha/yr for the mature stand.

DISCUSSION

Composition, Structure and Origin of the Old-Growth Stand

The large contribution of maple and ash to stand structure, as described in this study, presents a different impression of stand composition than has been previously suggested by Thompson (1963) who described the stand as essentially pure cedar, based upon basal area values from two 25 m X 25 m quadrats. While specific locations were not given for these quadrats they may have been located in what is now the southern end of the study area and cannot be considered truly representative.

Reports of cedar in excess of 31 m (100 ft) in height (Thompson 1963) were unsubstantiated. The tallest live cedar measured for this stand was 24 m while the largest fallen cedar stem measured 26.1 m in length. These values agree closely with a reported height maximum of 25 m (80 ft) (United States Forest Service 1965). Growth curves for cedar presented by Gevorkiantz and Duerr (1939) suggest that cedar may have a species-specific height maximum near 23 m (75 ft) on good sites (site index = 40). Overall stature of this forest is smaller than other mature forest stands in

Michigan (Rose 1982, Murphy and Kroh unpub. data) and reflects the height maximum for cedar as well as the predominately small size (≤ 35 cm dbh) of the co-dominants.

Regarding the origin of this old-growth stand, a close association was found between the occurrence of mature cedar and old-dune ridges. The hypothesis that these cedar had originally established on open dune slopes is supported by early growth rates of mature cedar, which were not statistically different than growth of cedar currently colonizing the open lee slopes of dunes.

I conclude that stand composition and the observed distribution of cedar resulted from encroachment of a series of dune ridges toward hardwood forests of the island interior. Subsequent establishment of cedar on the dune ridges, along with hardwood regeneration, initiated development of the present old-growth stand. Such a process appears to be taking place in other island locations where cedar are currently establishing on arrested dune slopes adjacent to old-growth hardwood stands (Figure 35).

Thompson's (1964) report of trees in this stand exceeding 500 years of age was in accord with information obtained from dune soil profiles; textural analysis and pH values were similar to those reported by Olson (1958) for profiles between 500 and 1000 yr. It is suggested that this stand originated with dune migrations which occurred within the last several hundred years.



Figure 35. Photograph of cedar establishing on the open, lee slope of a dune which is encroaching upon hardwood forests of the island interior.

Successional Status of the Old-Growth Stand

A profile diagram (Figure 36) suggests that old-growth cedar are being replaced by more tolerant maple and ash. Specifically, small numbers of mature cedar were observed in association with abundant maple and ash, largely ≤ 35 cm dbh. Analysis of size-class distributions for the three dominants indicate that maple and ash are tolerant enough to maintain large numbers of stems in size classes ≤ 15 cm dbh while cedar shows correspondingly little recruitment. The negative exponential model provided a close fit (Figure 37) to distributions of maple and ash, which was in agreement with Lorimer (1980) who suggested that negative exponential distributions, in old-growth stands, should be expected for tolerant species only. In contrast, the negative exponential model provided a poor fit with the size-class data of cedar ($r = 0.37$). The uniform size distributions of cedar was similar to species described by Hough (1932) and Christensen (1977), for which high rates of mortality in small size classes occurred in conjunction with little population recruitment.

Negative exponential distributions such as those observed for maple and ash do not necessarily imply the future importance of a species within a stand. A similar size class distribution was observed for Nyssa sylvatica over the course of 20 years in an oak-dominated forest (Christensen 1977), yet this species did not increase in importance.

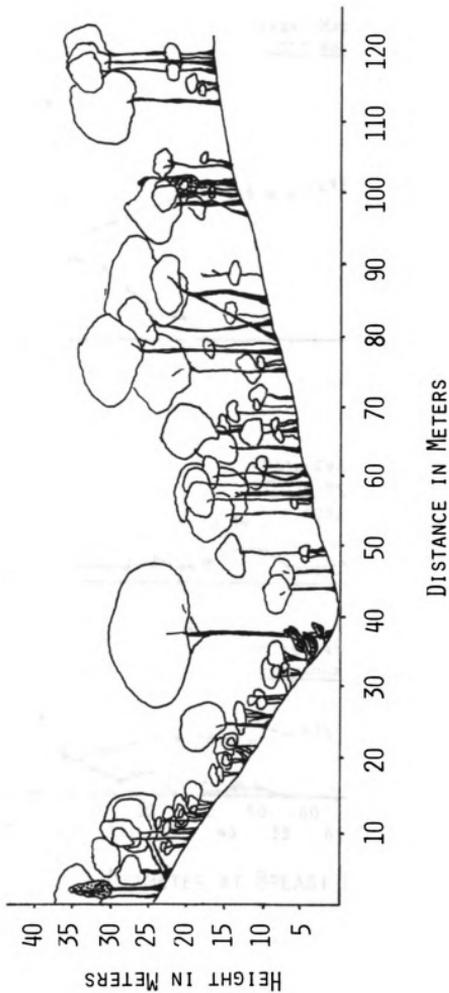


Figure 36. Profile diagram from within the mature forest. Cedar is indicated by heavy stippling.

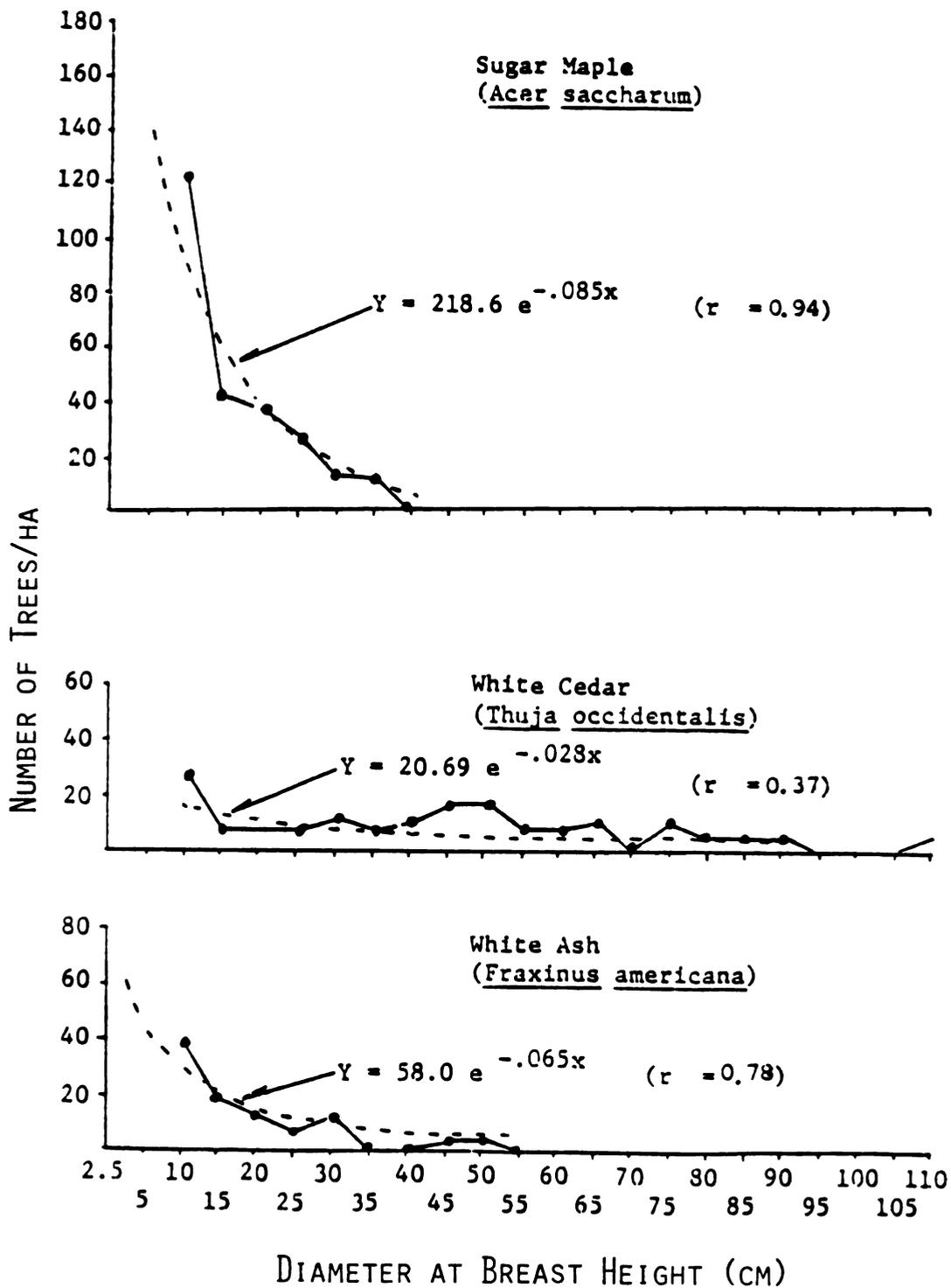


Figure 37. Negative exponential model analysis of size distribution for maple, cedar and ash in the old-growth forest.

Christensen attributed this to a rapid turnover among individuals in small size classes. Long-term patterns of recruitment and mortality for maple and ash were not examined but the dominance of mature individuals of these species in hardwood stands (Thompson 1974) adjacent to the study area suggests their future importance.

Also, the absence of cedar in smaller size classes does not preclude the recruitment of this species at some future time. Recruitment of trees in some forest stands is associated with large disturbances such as fire or hurricanes (Henry and Swan 1974, Oliver and Stephens 1977). Although it is possible that the recruitment of cedar may be episodic and disturbance-dependent, the timing and direction of tree fall, and the lack of fire scars on old-growth trees suggests that the stand has not recently been subjected to large-scale disturbances. Future catastrophic disturbances, like fire or reinvasion of the forest by migrating dunes may, however, permit the establishment of young age classes of cedar.

Gap Reproduction

Gap disturbance has been implicated in the maintenance of canopy diversity in old-growth or climax stands (Grubb 1977, White 1979 and Runkle 1981), and predictions of future canopy composition based upon species composition of saplings within forest gaps have been consistent with observed canopy importance values in several old-growth stands

(Runkle 1981). Canopy gaps in this study were similarly examined in an attempt to predict composition of the future canopy. Based upon relative density and dominance of tree seedlings (≥ 2.5 cm dbh), maple and ash are expected to be the major canopy dominants in this stand (Table 17). An analysis such as this is limited by the assumption that future canopy composition is accurately reflected in the densities and size of seedlings within gaps. However, factors such as tree position within the gap, tree life history strategies and gap size (Runkle 1982) are important determinants of successional change within gaps.

The species composition of gaps in this investigation appears to be a function of gap size. Whereas ash was found to have higher stem densities (282 stems/ha) in gaps > 170 m², maple had higher stem densities (1050 stems/ha) in gaps < 170 m². These findings are consistent with Bormann and Likens (1979) who concluded that white ash is more likely to achieve importance in recently formed gaps of large size while maple appears to establish dominance more successfully in smaller gaps. Such patterns of reproduction and growth are attributed to differences in the reproductive strategies of these species and, more specifically, tolerance. Maple is considered tolerant by Bormann and Likens (1979) and as such is expected to respond to small gap openings (> 50 m²) by establishment of seedlings or upgrowth of advance regeneration. Ash, of intermediate tolerance, requires larger openings (> 100 m²) to attain dominance with

Table 17. Anticipated canopy composition estimated from relative density, relative dominance and an average of these values for trees from four canopy gaps of various sizes.

| SPECIES | PREDICTED CANOPY COMPOSITION | | |
|---------------------------|------------------------------|------------------|-----------------------|
| | RELATIVE DOMINANCE | RELATIVE DENSITY | AVERAGE ^{1/} |
| <u>Fraxinus americana</u> | 45 | 40 | 42 |
| <u>Acer saccharum</u> | 34 | 45 | 40 |
| <u>Thuja occidentalis</u> | 16 | 9 | 13 |
| TOTAL | | | 95 |

^{1/} Most accurate predictor of canopy composition
(Runkle 1981)

regeneration of seedlings and young, advance regeneration (generally < 10 years of age). Both species are considered able to respond to a spectrum of larger openings.

Importance values for trees adjacent to or beneath the crowns of standing dead cedar were similar to those from gaps and suggest that maple and ash are most likely to succeed cedar in these locations. Together, these data imply an increasing importance of hardwoods in this stand and suggest that cedar is not successfully replacing itself.

Regeneration and Growth of Cedar Under a Closed Canopy

Following the original establishment of cedar in this stand, conditions for cedar reproduction and growth deteriorated. This is made clear by the significantly slower growth rates of cedar establishing under closed-forest conditions relative to trees in the old-growth stand and on open-dunes, at comparable growth stages (Table 4). Additionally, based upon published information on cedar regeneration and growth, it was hypothesized that recruitment of cedar in this stand would be limited by hardwood leaf litter and the lack of adequate seedbeds. Presently, 99.7% of 1-yr cedar seedlings are restricted to log substrates and it is suggested that this results from the inhibitory effects of leaf litter, primarily from maple and ash (Table 11). Such a pattern of seedling establishment was described for hemlock in an old-growth, mixed-mesophytic forest in Pennsylvania. Keever (1973) observed that because of the annual

flush of leaf litter, small hemlock seedlings not on emergent substrates (stumps or logs) were physically destroyed by the litter cover.

Successful cedar seedling establishment appears limited to logs and is greater on those logs in more advanced stages of decay (Table 6). Log substrates represented an area of 680 m²/ha in the stand, with average seedling densities of 0.2 individuals/m², compared to 0.006 individuals/m² on leaf litter. This implies that logs serve as suitable seedbeds for cedar seedling establishment. For cedar seedlings in northern Michigan swamps, Nelson (1951) found that 87% had established on logs, and of these he noted that the highest root/shoot ratios were from seedlings growing on rotted wood. He speculated that intact (undecomposed) logs are less desirable growth sites because of resistance to root penetration. Similarly, in a spruce-fir forest, McCullough (1948) observed that the majority of seedlings were associated with well-decayed logs.

Initial establishment of cedar on logs was followed by high rates of mortality. The life-table and survivorship curve for cedar, based upon population age structure, demonstrate that there were two age-specific periods of mortality: 1) an initial period of high mortality (years 0 - 3) followed by; 2) a longer period of decreasing mortality (years 4 - 12). Causes of mortality at each phase in the life cycle were not specifically identified but results from similar studies allow for speculation. High seedling

mortality, in some cases exceeding 95%, has been described for first year seedlings of other tree species (Hermann and Chricote 1965, Van Valen 1975, Hibbs 1979). Hibbs (1979) found that mortality of first year striped maple seedlings resulted from predation and unsuitability of the seedbed. Nelson (1951) found that the majority of young cedar seedlings in a lowland swamp died from desiccation as a result of having germinated on moss patches or logs with little decay; these sites tended to dry out as the growing season progressed, creating unfavorable moisture conditions. Other cause of mortality identified by Nelson (1951) included spring frosts, leaf-litter burial and competition from other plant species.

Following an initial period of mortality (years 0 - 1) Hibbs (1979) noted a period (years 2 - 15) of no mortality for striped maple (Acer pennsylvanicum). This survival was thought to represent the ability of striped maple to persist in a suppressed state. In the present study, cedar exhibited continuous mortality through year nine, followed by no apparent mortality through year 12 (Table 7). Survivorship during years 4 - 12 was analyzed using the negative exponential and power function models. A power function curve more accurately described survivorship in this phase of establishment (Figure 21), and such a model implies decreasing mortality with age (Hett 1971, Hibbs 1979).

In this regard, Hett and Loucks (1968) related early differences in survivorship among white pine, balsam fir and

red maple to differences in shade tolerance for these three species. Cedar can survive in dense shade for several years and responds well to release at almost all ages (Johnston 1977). Thus, decreasing mortality for cedar in this stand may reflect increased shade tolerance with age. Nevertheless, cedar seedlings in this investigation exhibited 99.4% mortality by age 12, suggesting that although logs serve as adequate seedbeds for establishment of cedar seedlings, long-term survival on these substrates is low. This is consistent with the observation that while seedlings are restricted to log substrates, larger stems (> 15 cm dbh) are associated with soil substrates (Figure 19). Aerial or stilt roots on mature cedar may become obscured with increasing stem size; however, Hough and Forbes (1943) found distinct aerial roots on white pine (Pinus strobus) in Pennsylvania, which had established on the root-plates of trees exposed by a wind storm in 1811. I assume, therefore, that the lack of aerial roots on mature cedar in this study reflects their establishment on a soil substrate.

Patterns of mortality and survivorship data for seedlings support the hypothesis that cedar is not replacing itself in smaller size classes in this stand. Furthermore, although logs in advanced stages of decay are adequate seedbeds for early cedar establishment, they may limit the long-term survival of these seedlings.

Patterns of Mortality for Canopy and Sub-canopy Trees

Cedar in the old-growth stand appeared to represent a senescent population which accounted for 68% of total stand mortality (for all trees ≥ 2.5 cm dbh). Additionally, 28% of all cedar mortality was represented by standing dead stems, and it is likely that many of these individuals died as the result of physiological senescence or disease associated with reduced vigor. Such factors, along with lightning strikes and insects, have been cited as probable causes for the death of standing, old-growth trees in other mature stands (Lorimer 1980). In contrast to cedar, mortality for maple and ash represented a small percentage of stand mortality (9.6% each) and resulted from the death of small sub-canopy trees in the case of maple, along with wind-throw and death while standing for canopy-sized ash.

Biomass and Productivity in the Old-Growth Stand

Total aboveground biomass in the mature stand (176 mt/ha) is at the low end of the range for temperate deciduous forests (60 to 600 mt/ha; Whittaker and Likens 1975) and was less than the values reported for two old-growth Michigan stands. Murphy and Kroh (unpub. data) estimated total stand biomass for a mature stand of beech-maple to be 515 mt/ha, while Rose (1982) reported a value of 681 mt/ha for a relict stand of white pine. Biomass in this study was

comparable to regional second-growth forests and aboveground biomass (148 mt/ha) was bracketed by values presented by Crow (1978) for second-growth stands throughout the lake states. Because of the high stand mortality for massive, old-growth cedar and their apparent replacement by small maple and ash, biomass may be currently decreasing. Such a drop in stand biomass was noted by Larsen (1982) with canopy breakup in late successional jack-pine stands in Michigan. Presently, biomass is less than the 156.6 mt/ha reported for a 70 - 100 year-old stand of cedar in Minnesota (Reiners 1972).

Maple and ash account for the majority of stand NPP (61%) which equalled 7.0 mt/ha/yr. This value was similar to second-growth stands in northern Wisconsin reported by Crow (1978) where aboveground NPP ranged between 7.1 and 10.4 mt/ha/yr, and was less than the second-growth stand of cedar in Minnesota which had a NPP of 10.1 mt/ha/yr (Reiners 1972).

Old-growth stands are characterized by high standing biomass and low rates of net primary productivity (Odum 1969). Correspondingly, biomass accumulation ratios (BARs, the aboveground biomass divided by aboveground net primary productivity) are high. Such a relationship is seen in the old-growth stands of white pine and beech-maple in Michigan (Table 18). In contrast, BARs in second-growth stands are lower because the trees are generally of smaller size and are more productive. The BAR in this study (22.2) was lower

Table 18. Comparison of biomass, production and biomass accumulation ratios for old-growth Michigan stands.

| Forest Type | Total Biomass (mt/ha) | Total Net Annual Primary Productivity (NPP) (mt/ha/yr) | Biomass Accumulation Ratio (Biomass/NPP) | Source |
|----------------------|-----------------------|--|--|-------------------------------|
| White Pine | 681 | 5.3 | 128.4 | Rose (1982) |
| Beech-Maple | 515 | 8.4 | 61.3 | Murphy and Kroh (unpub. data) |
| White Cedar-Hardwood | 172 | 7.7 | 22.2 | This study |

than other reported old-growth stands and was, in fact, comparable to second-growth stands in the northeastern U.S. (Whittaker et al. 1974). Additionally, Reiners (1972) presented a BAR value of 15.4 for a second-growth stand of cedar in Minnesota. That the BAR for this old-growth stand was similar to less massive, more productive second-growth stands appears to be a consequence of the shift in stand composition. With replacement of mature cedar by smaller, more vigorous maple and ash, a decrease in biomass is expected to accompany an increase in productivity. Such a trend is suggested by Figure 38 where, compared to other old-growth stands, the present stand falls below the trend line for climax biomass relative to NPP. Stands below this line include immature and climax or near-climax stands which have been affected by disturbance (Whittaker et al. 1974). Thus, with the apparent successional replacement of cedar, levels of biomass and productivity were not characteristic of an old-growth stand but were instead comparable to regional second-growth stands.

Forest Recovery Following Logging of the Old-Growth Stand

Date of Logging

Changes in the annual growth rings of forest tree stems have provided accurate information for the reconstruction of disturbance history of various stands throughout the

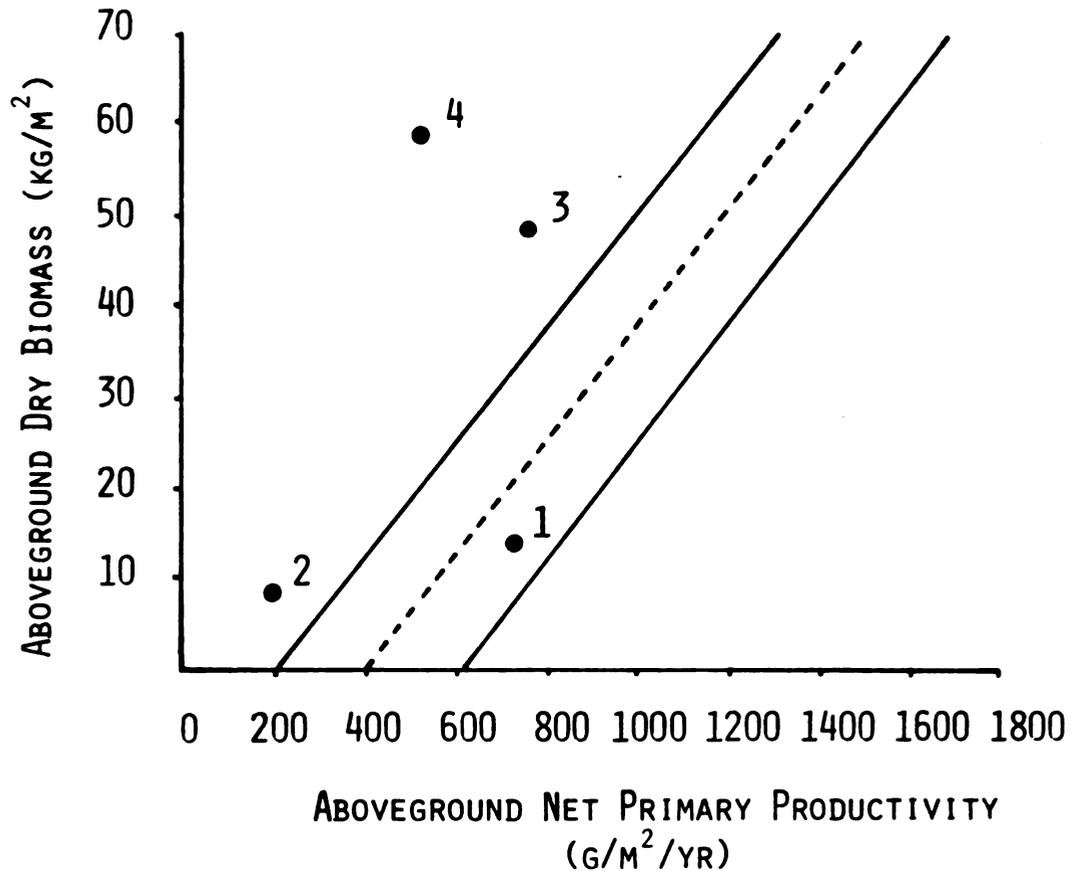


Figure 38. Aboveground biomass relative to net primary productivity (NPP). Closed circles represent old-growth Michigan stands; 1 (this study), 2 (Larsen 1982), 3 (Murphy and Kroh unpub. data) and 4 (Rose 1982). Dashed line is trend for climax biomass versus NPP. Solid lines include climax stands from woodlands through temperate-zone forests. Forest stands above biomass trend line were reported to be stable climax associations, while some climax or near-climax stands below this line had been affected by disturbance (Whittaker, Bormann, Likens and Siccama 1974). Graph modified from Whittaker et al. (1974).

northeast (Henry and Swan 1974, Oliver and Stephens 1977, Lorimer 1980). In this study, old-growth cedar directly adjacent to the present second-growth stand displayed dramatic and sustained increases in growth in approximately 1896. This growth release was thought to result from the catastrophic disturbance created by the removal of many large cedar during logging. Additionally, age data for trees which had established on cut cedar stumps and age-structure data for second-growth maple were used to corroborate growth release information in this investigation.

The oldest stump-established tree examined (64 years) indicated that successful establishment occurred approximately 20 years following the estimated logging date. Since seedling establishment for some tree species appears to be favored on logs in more advanced stages of decay (McCullough 1948, Nelson 1951) it may have taken up to 20 years for cut cedar stumps to decay sufficiently for successful seedling establishment to occur. This seems reasonable because even after 85 years these stumps were still recognizable (Figure 39).

Age-structure analysis of maple in the second-growth stand indicates that although this species was present prior to logging the majority of stems are second-growth. A fit of the negative exponential model to these data showed a peak in the 60 year age-class followed by smaller than predicted numbers of individuals in the 30 to 40 year age-classes (Figure 25). Such a distribution suggests that



Figure 39. Establishment of a second-growth birch on a cut cedar stump within the logged study area.

although sugar maple existed in the stand as advance regeneration, abundant recruitment occurred 20 - 25 years following logging. Bormann and Likens (1979) indicate that tolerant species such as sugar maple are much less responsive to major disturbances such as logging than are intolerant, rapidly-growing species like pin cherry, trembling aspen and white birch. With a decline in the importance of these intolerant species they suggest that species such as maple may begin to increase in importance 20 to 30 years after logging. Following the eventual development of a second-growth maple canopy further recruitment may have been suppressed, accounting for lower than expected numbers of individuals in the 30 to 40 year age classes. Suppression of regeneration under dense, even-aged canopies has been previously described (Peet and Christensen 1980, Peet 1981). The population age structure of second-growth maple and age analysis of stump-established trees support growth release information, which suggests that old-growth cedar were removed from a portion of the stand at the turn of the century.

Trends in Forest Structure and Function Following Logging

Pre-logging values of dominance and density were reconstructed for cedar in the old-growth and adjacent second-growth stand. Originally, stands were not significantly

different (Table 16), and thus the second-growth stand is assumed to represent structural and functional changes which resulted from logging of the old-growth cedar stand.

The harvesting of cedar from a portion of the old-growth stand at the turn of the century has given rise to a second-growth stand completely dominated by sugar maple. It was hypothesized that removal of old-growth cedar, without damage to the understory, would favor advance-regeneration of more tolerant species such as maple and, in effect, promote succession. Basal area changes subsequent to 1900 demonstrate the suggested replacement of cedar by maple in both old-growth and second-growth stands. However, in contrast to the rapid recovery of second-growth maple following logging is the gradual, tree-by-tree replacement of cedar by maple in the old-growth stand. Basal area of the mature stand declined over the period 1900 to 1930, then gradually increased to a current stand total of 34 m²/ha, as basal area increase for maple out-paced the loss for cedar (Figure 30). This successional process has been abbreviated in the second-growth stand, where a rather even-aged stand, dominated by maple, has recovered a total basal area of 29 m²/ha in the 85 years following logging. It is evident from this information that the logging of mature cedar accelerated a process which is presently occurring in the old-growth stand, that is, the successional replacement of cedar by maple and ash.

The cutting of cedar also altered energy relations within the stand and as a consequence current levels of biomass and productivity in the second-growth stand exceed those of the mature forest (Figure 34). Based upon basal area change, bole biomass in the second-growth stand is assumed to have increased sharply since 1930 (Figure 29) and presently equals 186 mt/ha. This increase is expected to continue to an undetermined site maximum as the even-aged canopy of maple reaches maturity. Peak biomass values following logging were observed within 70 years for Populus grandidentata stands in northern Michigan (Cooper 1981) and a subsequent biomass decline was anticipated with the mortality of mature aspen. Additionally, in disturbed Pinus contorta stands of Colorado, Peet (1981) noted coincident increases in basal area and biomass to maxima, followed by pronounced decreases. These decreases resulted from mortality of mature canopy trees coupled with a subsequent lack of regeneration.

In the old-growth stand, by comparison, a slow decline in basal area, and presumably biomass, occurred from 1900 until 1940 with the progressive loss of cedar (Figure 30). However, replacement of basal area and biomass through growth and reproduction of maple appears to have reversed this decline. Total bole biomass for the stand is 115 mt/ha and despite the apparent current increase, it is theoretically unlikely that this stand will ever approach a biomass maximum equal to that expected for the second-growth stand.

This follows from the fact that as cedar in the mature stand are replaced on a tree-by-tree basis by maple (or associated hardwoods), the resulting forest will have an all-aged population structure. Such a forest represents a spectrum of tree sizes which may not equal the biomass of an even-aged stand of mature trees (Peet 1981). In this regard, computer simulation of forest recovery following clear cuts of northeastern deciduous forest stands at Hubbard Brook, New Hampshire, indicate that biomass reaches a maximum in approximately 200 years with maturation of the even-aged canopy. After 350 years, biomass drops to an asymptote as the stand becomes more all-aged (Bormann and Likens 1979).

Total bole productivity for the present second-growth stand is 3.9 mt/ha/yr with maple accounting for 94% of this total (Figure 32). Although trends for productivity in this stand are not easily discerned, it is suggested that productivity in early successional communities may quickly reach levels approaching that for mature stands on the same or similar sites (Marks 1974, Bormann and Likens 1979). Boring et al. (1981) noted that first-year net production on a clear-cut site equalled 22% that of adjacent, undisturbed hardwood forest in the southern Appalachians, suggesting very rapid recovery of NPP. Further, Bormann and Likens (1979) indicate that within the first one to two decades after logging, net primary productivity may initially peak and then decline. Cooper (1981) observed that trunk or bole productivity for aspen in northern Michigan reached a

maximum between 40 and 45 years after cutting while overall productivity for aspen peaked between years 45 - 50, and thereafter declined. Such declines in long-term net production for post-disturbance stands may be attributed to changes in stand density, nutrient availability and species composition (Peet 1981). Additionally, Kira and Shidei (1967) suggest that increased respiration associated with stand size and age may further limit net production. Whether productivity in this second-growth stand is currently increasing, has reached a maximum, or is in decline is not known. However, with increasing tree size and decreasing density for this even-aged stand, an eventual drop in productivity from present levels is anticipated.

Total bole productivity in the mature stand was 2.1 mt/ha/yr (Figure 33). Future trends in productivity for this stand will be strongly dependent upon tree population dynamics. For example, if the gradual attrition of old-growth cedar continues as indicated by basal area change (Figure 30) and replacement by maple is correspondingly gradual, net productivity may show little overall increase with time. If, on the other hand, loss of mature, unproductive cedar occurs more rapidly than at present, rapid replacement of these trees by smaller, more productive maple and ash could result in a temporary production increase.

Current levels of biomass and productivity in the second-growth stand, relative to the old-growth stand, are summarized in Figure 34. The second-growth stand is nearly

twice as productive as is the mature stand, and has a higher total biomass. With synchronous growth and maturation of second-growth maple, biomass is predicted to reach an undetermined site maximum. The more gradual replacement of cedar by maple and ash in the old-growth stand has resulted in a more all-aged stand structure and as a consequence stand biomass, although increasing, is not anticipated to equal the peak biomass value expected for the second-growth stand. Barring future catastrophic disturbances, biomass and productivity in these two stands should converge with increased importance of maple in the mature stand, and development of a more all-aged population structure for the second-growth stand.

SUMMARY AND CONCLUSIONS

Results of this study provided interesting and surprising insights into the origin, structure and function of this unusual forest stand. Growth patterns exhibited by mature cedar on S. Manitou Island indicate that the trees established under open dune conditions. The present distribution of cedar on dune ridges apparently resulted from the advancement of dunes toward hardwood forests inland, followed by colonization of the open dune slopes by cedar.

Contrary to a report suggesting that the stand was essentially pure cedar, a total of nine dominant tree species were encountered within the study area, including cedar, maple and ash. Furthermore, diameter distributions suggest that while maple and ash are tolerant enough to maintain large numbers of individuals in smaller size classes (2.5 to 15 cm dbh), cedar is distributed throughout a broad size range with little population recruitment of stems ≤ 15 cm dbh. Prediction of future canopy composition implies the eventual dominance of maple and ash. White ash was more important in large canopy gaps (> 170 m²) while maple was more important in gaps < 170 m².

Presently, 99.7% of first year cedar seedlings are restricted to log substrates, which appear to provide safe sites for establishment. Seedlings which establish on the

forest floor may, in large part, be destroyed by the annual flush of hardwood leaf litter. Logs in advanced stages of decay provide seedbeds suitable for germination and establishment of cedar seedlings; however, long-term survival on these sites may be limited. Population age-structure information indicates that following germination 99.4% of all seedlings are lost by year 13. Further, no cedar stems > 40 cm dbh show evidence of having established on logs.

Cedar stems represent 68% of total stand mortality for trees ≥ 2.5 cm dbh, and 31% of all cedar sampled were dead. In contrast, maple and ash together accounted for only 19% of total mortality and a much smaller percentage (3% and 7%, respectively) of stems for these species were dead. Despite the current dominance of cedar, patterns of tree mortality, in conjunction with diameter distributions, provide evidence that maple and ash are replacing mature cedar in this stand.

The distribution of biomass and productivity in the mature stand was similar to second-growth stands throughout the lake states. Aboveground biomass was 148 mt/ha, with large, old-growth cedar comprising 61% of the aboveground total. Total annual aboveground net primary productivity (NPP) was 7.1 mt/ha/yr. While cedar represent 27% of aboveground NPP, small vigorous maple and ash account for 59% of the total. With the replacement of large, mature cedar by smaller, more productive maple and ash the biomass accumulation ratio (biomass/NPP) for the stand was lower than for

other old-growth Michigan stands, and comparable to a 70 - 100 year old stand of white cedar in Minnesota.

A portion of the mature stand was logged of cedar in approximately 1896. By 1930, basal area for second-growth maple began to increase exponentially and presently accounts for 77% of total stand basal area. As a consequence of the removal of mature cedar 85 years previously, the second-growth stand has recovered levels of bole biomass and NPP which now exceed those found in the mature stand. Bole biomass for the logged stand (186.4 mt/ha) is 38% greater than that of the mature stand (115.3 mt/ha), while bole NPP (3.9 mt/ha/yr) is almost double (2.1 mt/ha/yr). Biomass and NPP in the two stands are expected to converge as the second-growth stand becomes more all-aged while maple and ash continue to replace cedar in the mature stand.

APPENDIX

Appendix 1. Criteria used in assessing decay states of logs.

| <u>DECAY STATE</u> | <u>DESCRIPTION</u> | <u>SUBJECTIVE CRITERIA</u> |
|--------------------|-------------------------|---|
| 1. | Relatively undecomposed | Little or no moss; bark mostly intact |
| 2. | Moderately decomposed | Scattered moss patches; little or no bark |
| 3. | Well decomposed | Wood soft but not falling apart; at least $\frac{1}{2}$ moss or herb covered; no bark |
| 4. | Very well decomposed | Wood falling apart; outline of log not distinct |

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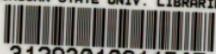
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