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Michigan State University PH.D. 1984

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BIOMASS, NET PRIMARY PRODUCTION AND SUCCESSIONAL DYNAMICS OF A VIRGIN WHITE PINE (PINUS STROBUS) STAND IN NORTHERN MICHIGAN

By

Willard M. Rose

A DISSERTATION

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Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

BIOMASS, NET PRIMARY PRODUCTION AND SUCCESSIONAL DYNAMICS OF A VIRGIN WHITE PINE (PINUS STROBUS) STAND IN NORTHERN MICHIGAN

By

Willard M. Rose

Eastern white pine (Pinus strobus L.), averaging 177 years in age, dominates the forest at Hartwick Pines State Park, Michigan, with a basal area of 48.4 m^2/ha, 66.7% of the total. Its mean diameter and height were 58 cm and 36 m, respectively.

Biomass and net primary production were estimated using standard nondestructive techniques. Total tree biomass for the stand was 681 mt/ha, using a measured white pine wood density of 0.29 g/cm^3, or 800 mt/ha using a density value of 0.37 g/cm^3 from the literature. With few exceptions, Hartwick's total biomass and basal area (72.6 m^2/ha) are among the highest reported in the literature for forests worldwide. Total net primary production of trees, on the other hand, was a relatively low 7.5 mt/ha/yr.

Diameter and height distributions of mature trees and seedling dynamics were investigated to determine the successional status of this stand. Diameter and height distributions suggest that red maple, sugar maple and beech are succeeding white pine. The large number of red maple seedlings and the large crowns of sugar maple seedlings may contribute to the eventual success by maples in dominating the stand. The large crowns of sugar maple seedlings may also account for their greater rate of shoot growth. White pine seedlings were as numerous as sugar maple but grew poorly. A study of different-aged gaps in the white pine canopy indicated that only maples survived past the seedling stage, filling in canopy gaps after approximately 50 years. Associated with closing of canopy gaps was a decrease in seedling average age, height, basal diameter, crown cover, shoot growth and percentage of seedlings browsed by deer. Further, it appears that maple seedlings do not do as well under a maple canopy as compared to a pine canopy or gap.

Seeding survivorship was greater in the gaps than under the canopy and greater during winter than summer. Sugar maple had the highest overall annual survival rate (90.2%) and red maple had the lowest (79.6%). Maple natality was 1.3/m^2/yr in the gap and 1.5/m^2/yr under the canopy. White pine and hemlock combined natality was 11.25/m^2/yr, but there was 100% mortality, possibly due to mechanical damage. In comparing seedling dynamics among three situations (within a canopy gap, under the forest canopy, and in an open area where white pine were regenerating), the white pine regeneration site had the lowest humidity and highest air temperature and solar insolation.

Deer are believed to retard succession by browsing a high percentage of seedlings. Results of a paired plot exclosure study revealed no significant differences in length of shoot growth between browsed and unbrowsed maples. There was a significant increase in height and crown cover of unbrowsed maple seedlings because shoot length had not been reduced by browsing. These increases could have resulted in increased competition which led to decreased survival of white pine in unbrowsed areas.

It was concluded that a possible successional series for this area, if uninterupted by fire or other disturbance, would be: jack pine for the first 80 years, white pine for 170 years, white pine-northern hardwoods for 200 years, hemlock-northern hardwoods for 200 years with

maple dominated hardwoods following as a long term stable community. It is hypothesized that biomass would increase to a maximum when white pine dominated and then decrease when hardwoods assumed dominance. Fire was the most obvious disturbance factor that helped maintain white pine as a dominant species in this area prior to lumbering.

TO LINDY

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INTRODUCTION

From 1840-1900 Michigan led the nation in lumber production, white pine (Pinus strobus L.) accounting for the majority of timber harvested. By the end of this era it was estimated that 160 billion board feet of pine had been cut (Maybee 1960), with as much as an additional 160 billion board feet lost to fire (Frothingham 1914). Prior to 1840, the dominant forest of the upper peninsula and the northern half of the lower peninsula of Michigan consisted of pure and mixed stands of white pine, red pine (Pinus resinosa), jack pine (Pinus banksiana), and hardwoods. The southern limit of white pine lumbering extended across the state from VanBuren County in the west, northeast to Gratiot County and east to St. Claire County (Wheeler 1898).

White pine's abundance and utility was an important factor in the development of Michigan. However, by 1914 virtually all large trees had been eliminated and today only a few small virgin tracts, those that are relatively undisturbed and have maintained a presettlement character, remain. The only stand in the lower peninsula larger than fifty acres is located at Interlochen State Park (Collins 1958), an open stand of white pine mixed with hardwoods (Kittredge and Chittenden 1929). Another, smaller, virgin stand where white pine clearly dominates is found at Hartwick Pines State Park.

Hartwick Pines is in Crawford County about 7 miles northeast of Grayling, Michigan. The area in and around Crawford County is a pine barrens or plains dominated by jack pine. This is the center of the northern highlands of Michigan's lower peninsula (Veatch et al. 1927). High rolling hills produced by glaciers overlook the virgin white pine stand at Hartwick, which occupies a low sandy ridge and part of a flat sandy plain.

Several factors, documented in the literature, have been shown to influence the presence of white pine and associated tree species. The litter layer affects white pine germination and survival (Frothingham 1914, Ahlgren 1976). Although they can germinate and grow in a litter layer or bare mineral soil with an adequate moisture supply (Maissurow 1935), quite often the litter becomes too dry for seedling survival (Smith 1940, Graham 1941). White pine are often outcompeted by hardwoods on better soils and are usually relegated to sandy soils (Frothingham 1914). For example, many of Michigan's early white pine forests, including Hartwick Pines, grew on moist sandy soil (Harlow and Harrar 1968). Generally, sandy soils throughout the state supported mixtures of white pine, red pine, hemlock (Tsuga canadensis), balsam fir (Abies balsamea) and hardwoods. On drier sites, red pine, jack pine or oak (Quercus spp.) dominated. Finer textured soils generally led to the development of hardwood stands. Outside of Michigan on better soils, hemlock, red spruce (Picea rubens), sugar maple (Acer saccharum), beech (Fagus grandifolia), basswood (Tilia americana), elm (Ulmus americana) and yellow birch (Betula lutea) associate with white pine, while red pine, jack pine, pitch pine (Pinus rigida), oak and chestnut (Castanea dentata) were associates of white pine on dry sandy soil.

It was estimated that in Michigan's Upper Peninsula alone, prior to lumbering, there were 1.6 million acres of white pine (Cunningham and

White 1941). By 1896-97 the total remaining white pine acreage in Michigan had been reduced to 775,208, with 13,000 in Crawford County (Wheeler 1898). When Hartwick Pines Park was given to the State of Michigan in 1927, it contained the last known 85 acres of pure virgin white pine in the lower peninsula. Wackerman (1924) estimated the board footage of the stand at 2,589,000, with white pine comprising 1,691,000 board feet.

There are several explanations for why Hartwick Pines was not lumbered. Hansen's lumbering operation in Grayling originally owned the property in this area and had cut the best timber to the present virgin forest boundary. Cutting stopped because many of the white pines had a lower value salmon-pink-color wood, similar to the old growth timber in New Hampshire described by Baldwin (1951). Concurrent with this was the economic panic of 1893 when lumber orders dropped dramatically (Maybee 1960). After recovering from the 1893 panic, lumber operations began to first cut the remaining few large virgin pine tracts and later used trees from the edge of Hartwick Pines as a source for special orders. At this time timber value had gone up but a new tax assessment made it more economical to sell the property. Karen B. Hartwick then purchased the stand and gave it to the state as a living memorial to her husband, a lumber baron.

A wind storm in the 1940's reduced the tract from 85 to 49 acres, possibly aided by a road through the forest that hampered natural soil drainage, weakening roots and soil structure and exposing the trees to the full force of the wind. Human impact on Hartwick has influenced the forest in another way. During the time of the Civilian Conservation Corps a decision was made to "clean up" the virgin forest by removing some downed trees and small maples. Even with this influence, Hartwick Pines remains one of the few examples of a white pine dominated virgin forest.

The economic importance of white pine stimulated research and inventories in the early 1900's. At that time, research centered on management and production of white pine for timber products (Frothingham 1914, Cunningham and White 1941, Cline and Spurr 1942). Several studies concerned white pine ecology and successional status (Grant 1934, Kittredge 1934, Morey 1936). More recently the volume of literature, particularly ecological studies of natural stands, has declined, probably due to a decrease in the importance of these stands for timber production and the limited potential of white pine because of insect and disease problems (Harlow and Harrar 1968). Some of the more recent studies concern growth, root grafting (Bormann and Graham 1959, Bormann 1965) and regeneration after fire (Ahlgren 1976, Barrett et al. 1976).

But there is a surprising lack of information about the structure and function, specificially the standing biomass and primary productivity, of large old growth stands such as Hartwick. Biomass and productivity are often difficult to measure, and destructive sampling is either prohibited, or physically difficult (Denison et al. 1972). Also, emphasis in past studies has been on economically important forests, which include plantations and forests composed of younger and smaller trees. Of the 291 biomass and productivity studies reported by Art and Marks (1971), 35.4 percent were of plantations with an average age of 29 years (S.D. = 26.7). The average age of the natural stands was 45.8 years (S.D. = 34.0).

Theoretical aspects of productivity have been discussed in the past and relate the need for more research concerning production (Lindeman 1942, Macfadyn 1948, Odum 1971). Primary productivity of a system can be used as an indicator of functional capacity. Not only is it an indication of the natural environment's ability to support life, but it also leads to a better understanding of potential human impact. Heterotrophic organisms account for only 0.1% of the living matter in the biosphere (Rodin and Bazilevich 1968); therefore, biomass and productivity studies of green plants can lead to rational use or non-use of most living matter.

The energy crisis has stimulated interest in use of biomass as an energy source. The most important issue during an international Man and the Biosphere workshop in 1979 on rational forest utilization was the use of forests as a source of fuel (Boyce 1979). It was recommended that each country assess forest productivity and potential for use as an energy source.

The early literature dealing with the question of whether eastern white pine is a part of the climax forest is contradictory. Based on available literature, Detwiler (1933) put forth a case in support of white pine as a member of the climax forest, but Hawley (1933) questioned this view and cited the same literature (Fernow 1899, Whitford 1901, Stallord 1929) to show that white pine is not a climax species. Graham (1941) attempted to settle the issue by defining a climax forest as having the ability to reproduce itself generation after generation. He concluded that white pine does not qualify because it lacks a high degree of shade tolerance and the ability to reproduce in a deep litter layer. Objective literature review and field observation reinforce this conclusion. Even with this apparent controversy resolved, there is a lack of information on the dynamics of white pine's successional role.

Climax and succession have been major points of study and controversy among ecologists. Various methods have been used to identify a climax system (Cooper 1913, 1923, Weaver and Clements 1938, Braun 1950, Whittaker 1953, 1974, Shimwell 1971). As Whittaker (1974) has pointed out the community population structure should be considered in order to understand succession, climax and the way in which species perpetuate themselves. In addition, the successional trends presented by Odum (1969) of increasing biomass and stature should be tested.

This research project investigated primary production and successional status of a virgin white pine forest at Hartwick Pines State Park. The specific objectives were:

1. to describe the structure and taxonomic composition of the woody populations;

2. to estimate the biomass and net primary production of the populations of trees in the white pine community;

3. to determine the successional dynamics of the white pine community by studying forest canopy gaps and by using the age of trees, structural considerations, and seedling survivorship; and

4. to develop a successional model for this area and relate it to changes in biomass.

METHODS AND MATERIALS

Community Description

The experimental area was marked off by stakes every 20 m forming a 220 m x 160 m sample grid. Sampling was avoided near trails and the outer margin of white pine. Twenty randomly selected circular plots, each 200 square meters in area, were used to describe woody plants 1.5 meters or more in height. Measurements included diameter at breast height (DBH, 1.5 m), total height, height to the bottom of the crown, and N-S and E-W crown diameter. Importance values were calculated for all tree species (Mueller-Dombois and Ellenberg 1974). Crown height and crown diameter were used to estimate photosynthetic area for correlation with tree growth. Identical measurements were taken of all trees along an East-West transect (7.6 x 60 m) which was located to include a gap in the forest canopy produced by a fallen tree.

Increment cores of randomly selected trees were taken in 1978 from 24 white pine, 10 hemlock, and 6 each of red pine, sugar maple, red maple (*Acer rubrum*) and beech, and processed following the methods of Stokes and Smiley (1968). These cores were used to determine tree ages, from which a linear regression relationship was established between diameter and age. Because the increment borer did not reach the center of the largest trees, estimates of the number of unsampled years were made by dividing the remaining distance by the average annual increment of the five years sampled nearest the center. Two cores were also taken from each of two trees that were fire scarred to determine the date of the most recent fire.

To establish the extent to which Hartwick Pines resembles the virgin pine forest that once covered parts of northern Michigan, a comparison of tree density (number of trees per unit area) and mean stump diameter (60 cm above the ground) was made with a pine stump field two miles north of Hartwick Pines. Fifteen randomly selected circular plots, each 200 m^2, were used to obtain stump diameter measurements and density. A regression equation was developed between stump diameter and DBH for living trees at Hartwick Pines for application to the stump field. Procedures described by Parde (1968) were used to estimate tree volumes from stump measurements.

The virgin white pine area that was destroyed by a storm in the 1940's was also described from fifteen randomly selected 100 m^2 circular plots. Importance values were calculated from measurements of trees greater than 1.5 m tall. This information was used to determine changes in the forest as a result of the storm.

Biomass and Productivity

Destructive sampling of vegetation was prohibited by the Michigan Department of Natural Resources. Methods presented here were developed with this constraint in mind.

Stem. Allometric techniques were used to develop an equation to calculate white pine stem volume (Newbould 1967). The equation was obtained by using accurately estimated volumes of fallen trees, calculated from diameters that were measured every meter for the full length of the fallen trees (Table 2). Total stem wood volume was estimated from the DBH minus bark thickness using this equation. Bark thickness was calculated using a regression equation developed for this stand (Table 2). Bark volume is the difference between stem volume including bark and wood volume calculated using DBH without bark; to account for bark taper and ridges, this value was multiplied by 0.5, a conservative figure that probably led to slight underestimates in bark volume. Seventy percent of the cross sectional area between the wood and the perimeter established by the tip of each bark ridge was actually bark. Wood density and bark density were determined from sample cores and used for converting volumes to dry weights.

Stem productivity was estimated in part by following methods outlined by Newbould (1967) and Whittaker and Marks (1975). Average production of white pine stem wood was calculated in the following manner using the equation developed in this study relating DBH and volume. Using cores taken in 1978 from trees of all size classes, average annual radial increment for the five years preceding the study was determined. Annual volume increment was calculated by finding the difference between the volume predicted from the most recent DBH and the volume predicted from the DBH after subtracting the average radial increment. The average volume increment was converted to dry weight using wood density, allowing an estimate to be made of average annual stem wood production. Once the annual growth increment had been determined for all size classes, a regression equation was established relating volume and biomass increment to DBH.

Stem biomass and production of the other five species in the stand were estimated using equations from Newbould (1967). An approximation of volume was obtained using the equation for a paraboloid of rotations:

$$Vp = \frac{\pi r^2 h}{2}$$

where r is the radius at breast height and h is the tree height. The calculation was completed for each of the 5 species and multiplied by the density of their wood given by Brown et al. (1949), resulting in an estimate of biomass. The basal area increment was calculated from

$$A_i = \pi[(r^2 - (r - i)^2)]$$

where i is the average annual radial increment based on the last five years and r the radius at breast height. Using basal area increment (A) and height (h) an estimate of the stem wood volume increment was computed from

$$V_i = 1/2\ (A_i \times h).$$

Volume increment was then converted to biomass increment by multiplying by wood density.

<u>Branch</u>. It is commonly assumed that mature ecosystems are in energetic steady state and that net annual primary production is equal to annual litter production (Kimura 1960, cited by Newbould 1967, Nye 1961, Kira and Shidei 1967, Odum 1971). Bray and Gorham (1964) maintain that litter fall measurement might, therefore, be used as an easily obtained estimator of net production. Newbould (1967) presents appropriate methods for such an analysis. Following these assumptions, branch production was estimated by measuring branch litter fall from late summer 1975 to late fall 1978.

Fifteen litter traps, each one square meter in area, were randomly placed within the sampling grid and used to measure the accumulation rate of branch litter less than one centimeter in diameter. The plots were circular and bordered by a metal strip to prevent lateral movement of litter into and out of the sample plots. Transect plots, two meters wide and a total of 650 meters long, were established to sample branch litter larger than one centimeter in diameter. Initially, all branches were removed from the sample plots. Each spring and fall all branches were collected and weighed. In both cases, subsamples were used to determine dry weight. As it was not possible to sort branches by species, data were classified as branch litter fall (branch production) for all species combined. Branch biomass and production were assumed to be proportional to the stem biomass and production for each species. An estimate of each species' branch production was obtained by multiplying its percentage of total stem production by total branch production. Branch biomass was determined from the ratio $B/b = S/s$ where B = species branch biomass, b = species branch production, S = species stem biomass, s = species stem production (Whittaker 1965, Whittaker and Marks 1975).

Foliage. Using the one meter square branch litter plots, leaf litter fall was measured from late summer 1975 to late fall 1978 to estimate leaf production. Litter fall was measured once a month for a year to establish seasonal variation. Fifteen elevated litter traps were used to catch falling litter while snow covered the ground. The traps consisted of a cloth and plastic sack suspended from a wooden frame. The wooden frame was 0.25 m^2 in area and was supported by a single metal pole. The majority of pine litter fell in October and November, similar to the deciduous species, which allowed sampling once in the spring and once in the fall. Samples were sorted by species, dried, and weighed.

White and red pine leaf biomass was estimated by multiplying total leaf fall for one year by the life span of a needle. The age of the oldest needles, two years for white pine and four years for red pine, was determined by observing the needle's position on the branch in relation to branch age at that point, and confirmed by Harlow and Harrar (1968). Because white pine bud scales are produced and lost in the same year, the estimate of their annual litter production was equal to their biomass. The bud scale biomass was included in white pine leaf biomass. Leaf biomass of deciduous species was directly measured following leaf drop in the fall.

Root. Root biomass and production were estimated from data for similar forests given in the literature (Young and Carpenter 1967, Johnstone 1971, Leaf 1971). In most cases root biomass was given as 15-16% of the total above ground biomass. Root productivity was derived from equating the proportion of stem biomass to stem production with the proportion of root biomass to root productivity. These methods are only rough approximations, but they allow estimation of total biomass and productivity.

Succession

Tree diameter, height and age distribution. Inferences concerning succession were made by analyzing survival within tree populations. Two survival aspects were considered: the ability to live to the next age class, and the ability to reach reproductive maturity. Forest analyses have used height and diameter distributions to draw conclusions about survival (Hough 1936, Meyer 1952, Hett and Loucks 1971). For example, a large ratio of mature to immature individuals of a particular species has often been interpreted to mean that this species is failing to reproduce and is not replacing itself (Braun 1950, Mueller-Dombois and Ellenburg 1974). Even though this may be an incorrect assumption for some species, a distributional diagram of height and diameter was established for each species as one possible indicator of survival. Also, comparisons of age were made between species to more accurately determine species regeneration or replacement.

Canopy gap description. Additionally, a study of forest canopy gaps was used to assess the successional status of the community. Gaps of various sizes containing saplings and seedlings indicate the forest is being replaced in a gap phase fashion (Bray 1956). Skeen (1976) pointed out the significance of studying naturally created openings in determining seedling regeneration and survival. To this end, all gaps were located and mapped within the sample area. Each gap was considered to consist of a structural area, the canopy area left open by the death of a tree, and a functional area, defined by the outer foliage perimeter of those species that are invading the area affected by the opening in the canopy.

The age of each gap was estimated in 1977 by coring trees at the perimeter of the gap and determining the year of their release from suppression. Hemlock was used in most cases because it has been documented as an understory species that prominently exhibits this release from suppression (Graham 1941). After aging the gaps, eight were selected, covering the full range of ages, and sampled to illustrate what changes might occur over time in a relatively stable forest. This analysis allowed for estimation of the forest turnover rate and gap occurrence frequency.

Seedling description, age and size distribution. Forest openings were the areas of most active turnover and the key to the successional status of this forest. Age and size distributions of all woody species found in the gaps were, therefore, constructed to provide information on gap colonizer survivorship. Four one meter square plots were established in each gap to sample seedlings. All woody individuals less than 1.5 m in height were to be included; however, none were larger than 100 cm. Seedling ages were recorded in the field by counting the number of bud scale scars or groups of needle leaf scars (Hett 1971). Other seedling parameters measured included diameter at root crown, height, crown cover, and stem growth. Stem growth was determined by measuring the length between the last bud scar and the terminal bud. Four one meter square plots were set up outside each gap to obtain the same information for seedlings of the same species on the undisturbed forest floor. The entire gap was sampled to obtain DBH for all larger individuals. This information was used for descriptive purposes and to establish age and/or size distributions.

Survivorship. Included among the relatively few studies of age distribution and survivorship of tree seedlings are those of Hett and Loucks (1968), Hett (1971), Hett and Loucks (1971) and Good and Good (1972). Their methods were applied to several seedling populations within the community to help in elucidating successional trends. Hett (1971) found in a study of sugar maple seedlings that seed crop or number of viable seeds had little influence on the number of seedlings established. For this reason, it was suggested that the study of age structural dynamics begin with germinated seedlings. Survivorship and natality were observed for seedlings in gaps and under the forest canopy. Percent survival was calculated as:

$$\frac{\text{number alive/unit area at } t_2}{\text{number alive/unit area at } t_1} \times 100,$$

(Hett and Loucks, 1971) and natality as number of new seedling/unit area from t_1 to t_2. The same plots that were used to sample seedling age distributions were used to collect data on survival and natality. Each seedling was identified and marked with an aluminum tag during fall 1977. Early the following spring and again the following fall, plots were examined to estimate winter and summer survival and natality.

Environmental parameters. Several environmental parameters were measured to obtain information that might suggest reasons for the observed seedling distribution and survival. When disturbance opens the forest canopy, air temperature, relative humidity and light intensity are all changed. All of these are correlated with light intensity and suggest that light intensity would be the single most important factor to correlate with forest growth (Shirley 1932). Light energy, temperature and humidity were recorded using a pyrheliometer and a hygrothermograph in each of the following areas: a site on the southeast edge of the virgin forest where white pine was regenerating, under the canopy gap, and under the forest canopy on July 23, 1977, August 1, 1977, April 29 and 30, 1978.

Deer browsing. Preliminary observation revealed that tree seedlings were being heavily browsed by white tailed deer (*Odocoileus virginianus*). Paired plots were established in both the gaps and forest to investigate the effect of deer browsing on seedling growth and survival. Exclosures covered half of the plots while the other half remained open for browsing. The following year height, length of new stem growth, crown cover area and survivorship were determined and comparisons made between browsed and unbrowsed seedlings.

White pine regeneration. To obtain a more complete picture of the overall successional status of white pine, two additional descriptive studies were undertaken in areas where young white pine were establishing. One study was in a virgin jack pine stand, near Hartwick Pines (T27N, R3W, S11) and the other was in a virgin white pine stand in Manistee County, Michigan (T21N, R13W, S26). Fifteen randomly selected one hundred square meter plots were used in the jack pine forest.

Height, crown cover, and age of each seedling was determined. Age was determined by the number of branch whorls. Woody species that were at least 1.5 m in height were measured for DBH, crown cover, total height, and number of dead and living stems. Cores were taken from thirty randomly selected trees and an age determination made. Age distributions were then plotted to make inferences concerning species regeneration. The virgin white pine forest in Manistee County was studied using ten randomly selected two hundred square meter plots. DBH and total height of woody species with DBH greater than 2.54 cm were measured. Importance values were calculated using density, basal area dominance, and frequency. A white pine tree with one of the largest diameters was aged.

RESULTS AND DISCUSSON

Description

Figure 1 illustrates the study area relative to the overall virgin forest. The total area of the virgin stand was 20 ha, reduced from the original 34 ha during a storm in the 1940's. A study area of 3.52 ha was chosen to keep the inclusion of edge areas (trails and unnatural disturbances) to a minimum. Small hills shown at the north end of the stand were included as part of the study area to incorporate any topographical variability. Species composition, however, was the same on the hills as on the sandy plain.

The virgin forest was composed of white pine, hemlock, red maple, sugar maple, American beech, and red pine. In the Great Lakes States and parts of northeastern North America, especially before the lumbering era, these species were commonly found together. Table 1, a review of thirteen different old growth stands, shows that twenty-five tree species occur with white pine in the central and eastern United States. Oaks are a common associate with white pine in the virgin forest at Interlochen State Park, Michigan (Kittredge and Chittenden 1929). In Canada, white pine occurs with yellow and paper birch (Betula papyrifera), balsam fir (Abies balsamea), aspen (Populus spp.), and spruces (Picea spp.) (Maissurow 1935). Hartwick's five associated species, as well as red oak (Quercus rubra) and yellow birch, are present in more than 50% of the stands.

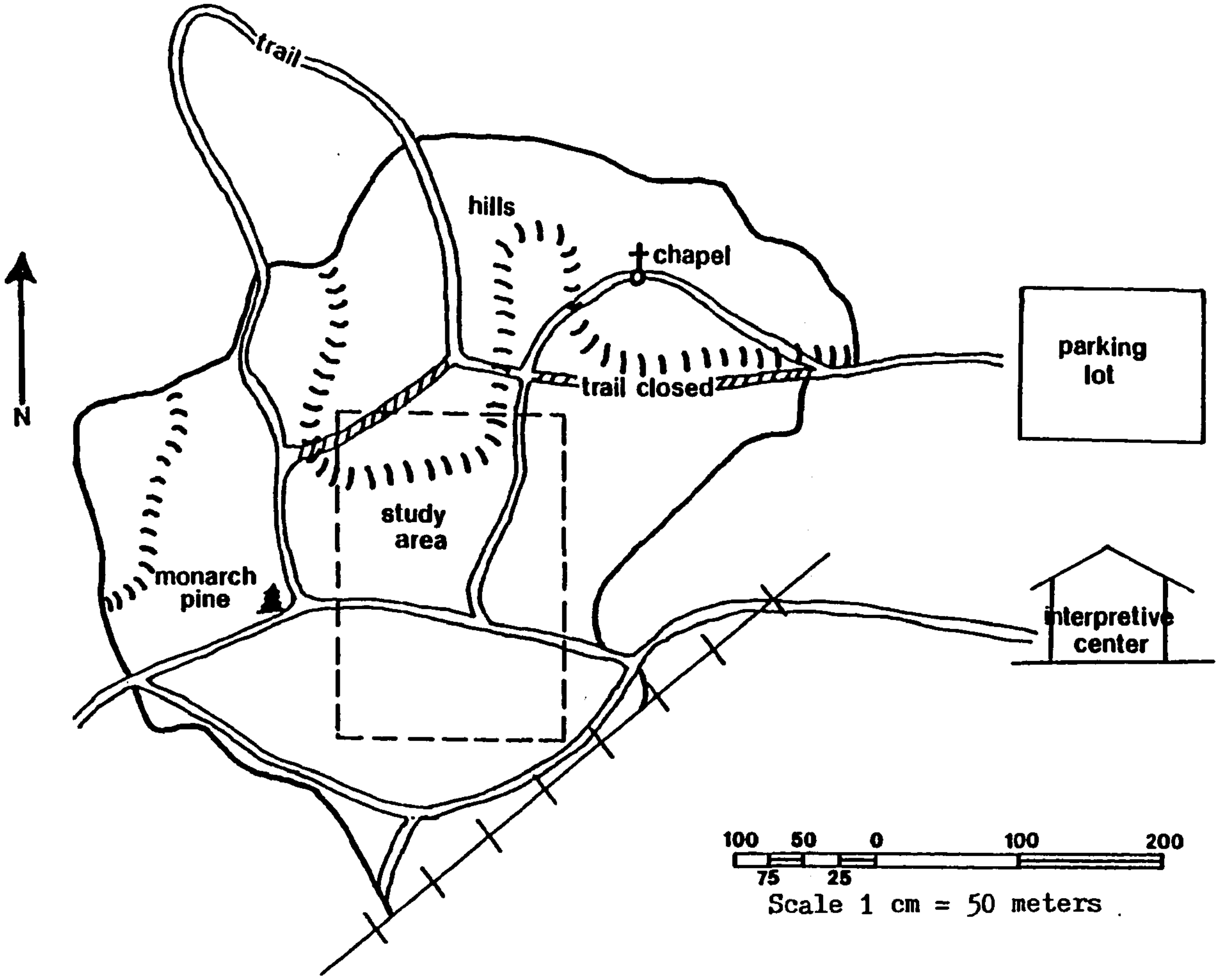

Fig. 1. Location of the study area within the virgin white pine forest at Hartwick Pines State Park.

Table 1. Tree species associated with old growth white pine in northeastern North America.

Species	Michigan I[1]	Michigan II[2]	Michigan III[3]	Michigan IV[4]	Mich.-Wisc.[5]	Minn. I[6]	Minn. II[7]	Minn. III[8]	N. Hamp. I[9]	N. Hamp. II[10]	Penn. I[11]	Penn. II[12]	Canada[13]	% Occurrence[14]
Pinus strobus	x	x	x	x	x	x	x	x	x	x	x	x	x	100
Pinus resinosa	x	x	x			x	x	x					x	54
Tsuga canadensis	x		x	x	x				x	x	x	x	x	69
Acer rubrum	x		x	x			x	x	x	x	x	x		69
Acer saccharum	x			x	x		x	x		x	x		x	62
Acer spp.		x												8
Fagus grandifolia	x	x	x						x	x	x	x		54
Quercus alba		x	x							x	x	x		38
Quercus rubra			x				x	x	x	x	x	x		54
Prunus serotina		x	x								x	x		31
Fraxinus americana			x							x	x			23
Fraxinus spp.		x												8
Pyrus malus		x												8
Betula lutea				x	x				x	x	x	x	x	54
Betula papyrifera					x		x	x		x			x	38
Betula lenta										x	x	x		23
Abies balsamea				x	x			x					x	31
Thuja occidentalis					x									8
Tilia americana							x	x		x				23
Populus grandidentata								x						8
Populus spp.													x	8
Ostrya virginiana								x						8
Picea rubens										x			x	15
Picea glauca													x	8
Magnolia acumenata											x			8
Castenea dentata											x	x		15
Hamamelis virginiana											x			8
Amalanchier arborea											x			8
Ilex opaca											x			8

[1] Hartwick Pines State Park, Grayling, Michigan.
[2] Manistee Co., Michigan, 4.4 miles east of Dublin.
[3] Interlochen State Park, Michigan (Kittredge & Chittenden 1929).
[4] Ottawa National Forest, the western end of the Upper Peninsula of Michigan (Graham 1941).
[5] Michigan-Wisconsin state line (Stearns 1950).
[6] Starr Island, Minnesota (Kittredge 1934).
[7] Starr Island, Minnesota (Kittredge 1934).
[8] Starr Island, Minnesota (Kittredge 1934).
[9] Bradford, New Hampshire (Baldwin 1951).
[10] Winchester, New Hampshire (Cline & Spurr 1942).
[11] Hearts Content Forest, Warren Co., Pennsylvania (Morey 1936).
[12] Cook State Forest Park, Clarion and Forest Co., Pennsylvania (Morey 1936).
[13] Pontiac Co., Quebec, Canada (Maissurow 1935).
[14] % occurrence = $\frac{\text{number of stands in which that species occurs}}{\text{total number of stands}} \times 100$

The profile diagram in Figure 2 illustrates the vertical structure of the forest and a canopy gap at Hartwick. The gap was 6 m wide and located at the center (30 m) of the transect. The profile on each side of the gap gave a qualitative indication of the high density and continuous crown cover of white and red pine. However, this site was unrepresentative of the forest, as it overemphasizes red pine density and underemphasizes white pine. Prevailing west winds have caused a crown structure resembling the flag form of trees at timberline (Spurr and Barnes 1980). Canopy stratification was apparent because the other four tree species only reach the bottom of the pine canopy. Hemlock was as abundant as white pine but much smaller in size, as are the less abundant deciduous species. Most of the dead stems and stumps were white pine. The presence of wind throws, old pits and mounds, and large tree size were indications of the forest's relatively undisturbed character.

Comparison of this forest to a white pine stump field suggested that its structure was very similar to at least one nearby forest cut in the late 1800s. White pine stump density (172.5 ind./ha) and frequency (1.0) were the same as found in Hartwick. A t-test comparison of the mean diameters at stump height showed no significant difference between the two areas at the 99% confidence level. An equation was developed from living pines at Hartwick to predict DBH from stump diameter. The stump forest was not reconstructed because the independent variables were the same and it was evident that by using equations developed from Hartwick Pines (Table 2), the stump forest would be similar to Hartwick. Reconstruction of stump fields using these equations should be approached with caution because of the variable growth forms of white pine under different conditions.

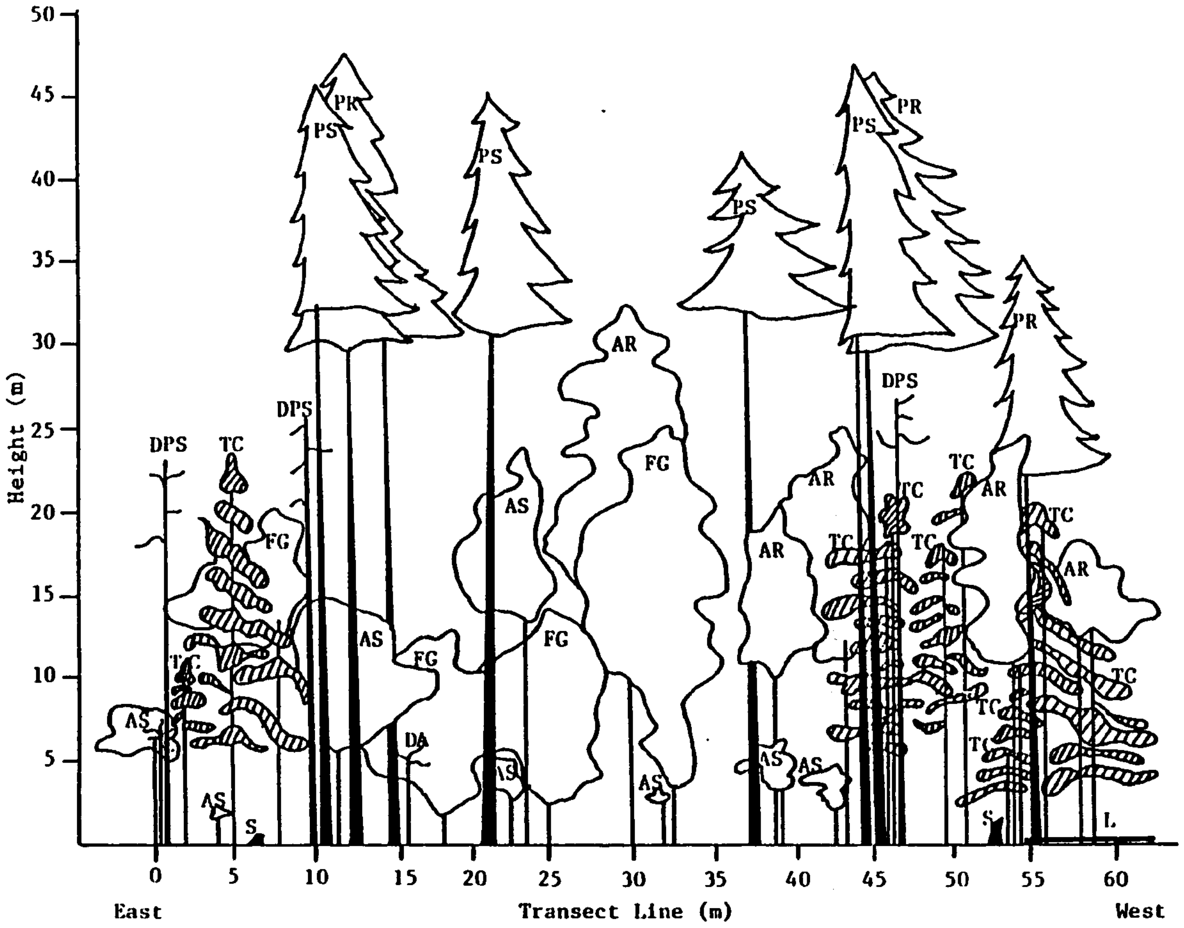

Fig. 2 . Profile diagram of the virgin white pine forest at Hartwick Pines State Park. This diagram represents a strip 7.6 m x 60 m through a 63-year-old gap extending from the 27 to 33 meter mark. Legend: PS=*Pinus strobus*, PR=*Pinus resinosa*, TC=*Tsuga canadensis*, AR=*Acer rubrum*, AS=*Acer saccharum*, FG=*Fagus grandifolia*, DPS=Dead *Pinus strobus*, DA=Dead *Acer* spp., S=Stump, L=Log.

Table 2. Linear regressions and coefficients of correlation with 95% confidence limits for allometric relationships developed from the study of Hartwick Pines virgin forest. Legend: * = significant at the 5% level, DBH = diameter at breast height, Bark Thick. = bark thickness, 60 cm Dia. = 60 cm diameter, Stem Vol. = stem volume, CC = crown cover, CV = crown volume, Stem Prod. = stem production, Stem Bio. = stem biomass.

Species	Dependent Variable (y)	Independent Variable (x)	Equation	n	r	Confidence Limits	
Pinus strobus	Stem Vol. (cm^3)	DBH (cm)	$y = -2847336.77 + 122401.06x$	15	0.95*	0.98	0.85
Pinus strobus	Bark Thick. (cm)	DBH (cm)	$y = 0.197 + 0.042x$	24	0.49*	0.75	0.11
Pinus strobus	DBH (cm)	60 cm Dia. (cm)	$y = -0.0284 + 0.9107x$	35	0.99*	0.99	0.98
Pinus strobus	Height(m)	DBH (cm)	$y = 27.98 + 0.16x$	70	0.47*	0.64	0.26
Pinus strobus	CC (m^2)	DBH (cm)	$y = -8.85 + 0.78x$	70	0.63*	0.75	0.46
Pinus strobus	Age (yr)	DBH (cm)	$y = 173.75 + 0.05x$	24	0.03		
Pinus strobus	Age (yr)	Height (m)	$y = 158.96 + 0.48x$	24	0.08		
Pinus strobus	Age (yr)	CC (m^2)	$y = 169.43 + 0.20x$	24	0.11		
Pinus strobus	Stem prod. (g/yr)	CV (m^3)	$y = 3387.0 + 5.25x$	24	0.04		
Pinus strobus	Stem bio. (mt)	CV (m^3)	$y = 0.97 + 0.01x$	24	0.45*	0.72	0.05
Pinus resinosa	Age (yr)	DBH (cm)	$y = 196.90 + 0.23x$	6	0.15		
Tsuga canadensis	Age (yr)	DBH (cm)	$y = 77.78 + 2.98x$	10	0.57		
Acer saccharum	Age (yr)	DBH (cm)	$y = 18.59 + 4.11x$	6	0.90*	0.99	0.33
Acer rubrum	Age (yr)	DBH (cm)	$y = 49.23 + 2.43x$	6	0.81*	0.98	0.02
Fagus grandifolia	Age (yr)	DBH (cm)	$y = 57.36 + 2.31x$	6	0.85*	0.98	0.13

At Hartwick, white pine represented 66.7% of the total stand basal area (72.6 m^2/ha), or four times that of any other species. In addition, white pine had the highest frequency value and a density equalled only by hemlock (Table 3). White pine's importance value was almost twice that of hemlock and four times as large as each of the remaining four species. Hemlock had the second highest importance value due to relatively higher density of small individuals. Individually, red pine were as large as white pine, but had the lowest importance value because of relatively low density.

White pine had the largest average diameter (58 cm) and second greatest height (36 m) after red pine (Figures 3 and 4). This is greater than the average 55 cm white pine DBH at Interlochen, Michigan (Kittredge and Chittenden 1929), but less than the 71 cm in Minnesota (Kittredge 1934) and 76 cm in New Hampshire (Baldwin 1951). Hartwick white pines had a wide distribution in size ranging from 26 to 110 cm in diameter and 22 to 48 m in height (Figures 3 and 4). Regression analysis indicated only very low correlations between diameter and height or crown cover. White pine in dense stands or those under suppression exhibit a decrease in secondary xylem production but height growth is relatively unaffected (Hysch and Lyford 1956, Bormann 1965). The less numerous red pine had a narrower height and diameter size range, although their mean height, 37.4 m, was greater than that of white pine. The four remaining species were considerably smaller in both diameter and height. There were no red maple, beech or sugar maple larger than 40 cm in diameter and 29 m in height. Hemlock was intermediate in size between the large pines and smaller deciduous species.

Table 3. Importance values[a] (I.V.) for tree species (> 1.5 m in height) in the virgin forest of Hartwick Pines State Park.

I.V. Rank	Species	Denisty Absolute (# of ind./ha)	Denisty Relative	Dominance Absolute (m^2/ha)	Dominance Relative	Frequency Absolute (# of pots/ total # of plots)	Frequency Relative	I.V.	I.V. %
1	*Pinus strobus*	172.5	27.38	48.43	66.71	1.00	22.73	116.82	38.94
2	*Tsuga canadensis*	172.5	27.38	11.91	16.40	0.90	20.45	64.23	21.41
3	*Acer rubrum*	90.0	14.29	2.92	4.03	0.70	15.91	34.23	11.41
4	*Acer saccharum*	90.0	14.29	0.96	1.33	0.70	15.91	31.53	10.51
5	*Fagus grandifolia*	70.0	11.11	1.22	1.69	0.65	14.77	27.56	9.19
6	*Pinus resinosa*	35.0	5.56	7.16	9.86	0.45	10.23	25.65	8.55
	Total	630.0	100.01	72.60	100.02	4.40	100.00	300.02	100.01

[a] Calculated following methods in Mueller-Dombois and Ellenburg (1974).

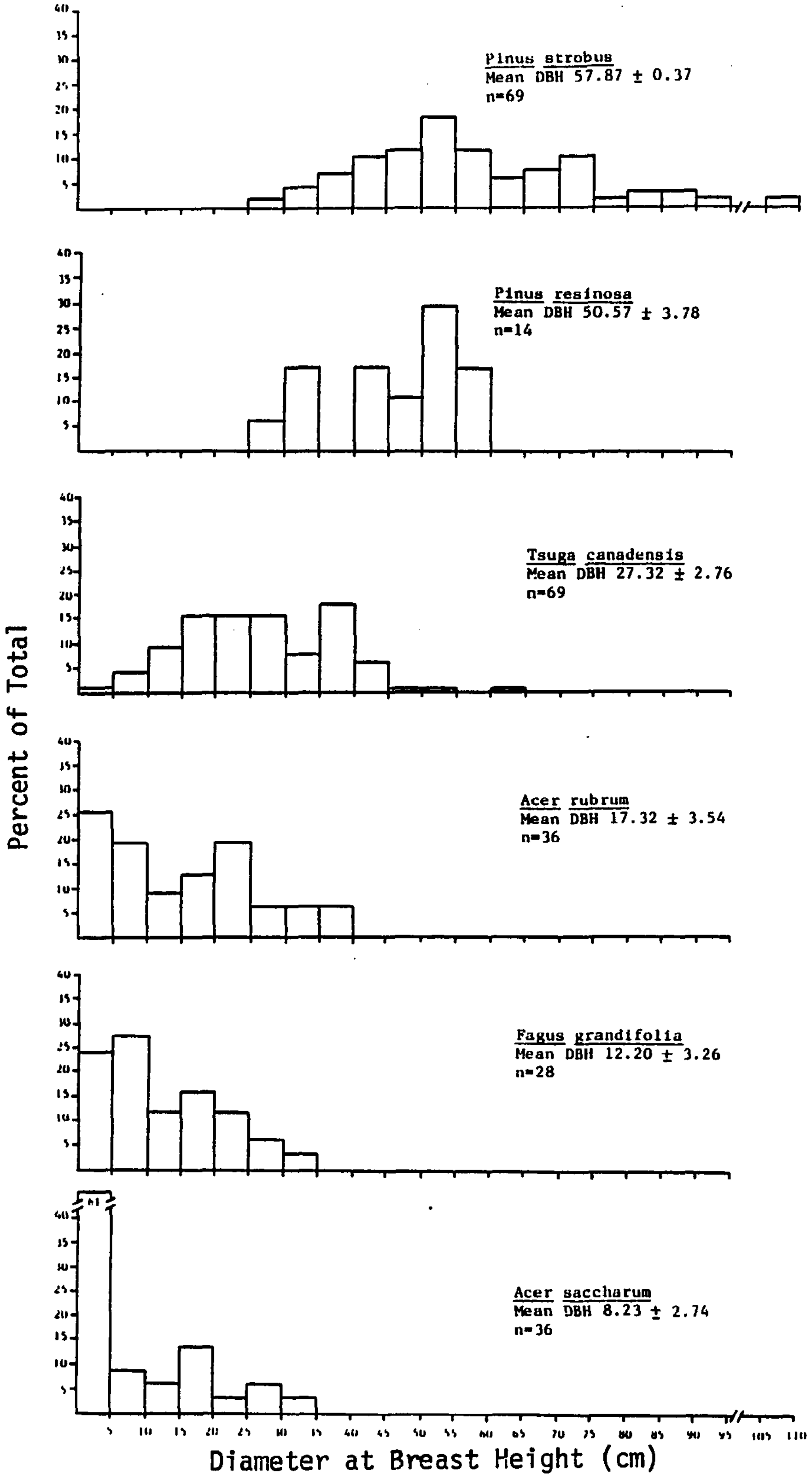

Fig. 3. Distribution of tree diameter by species. (mean ±2 S.D.).

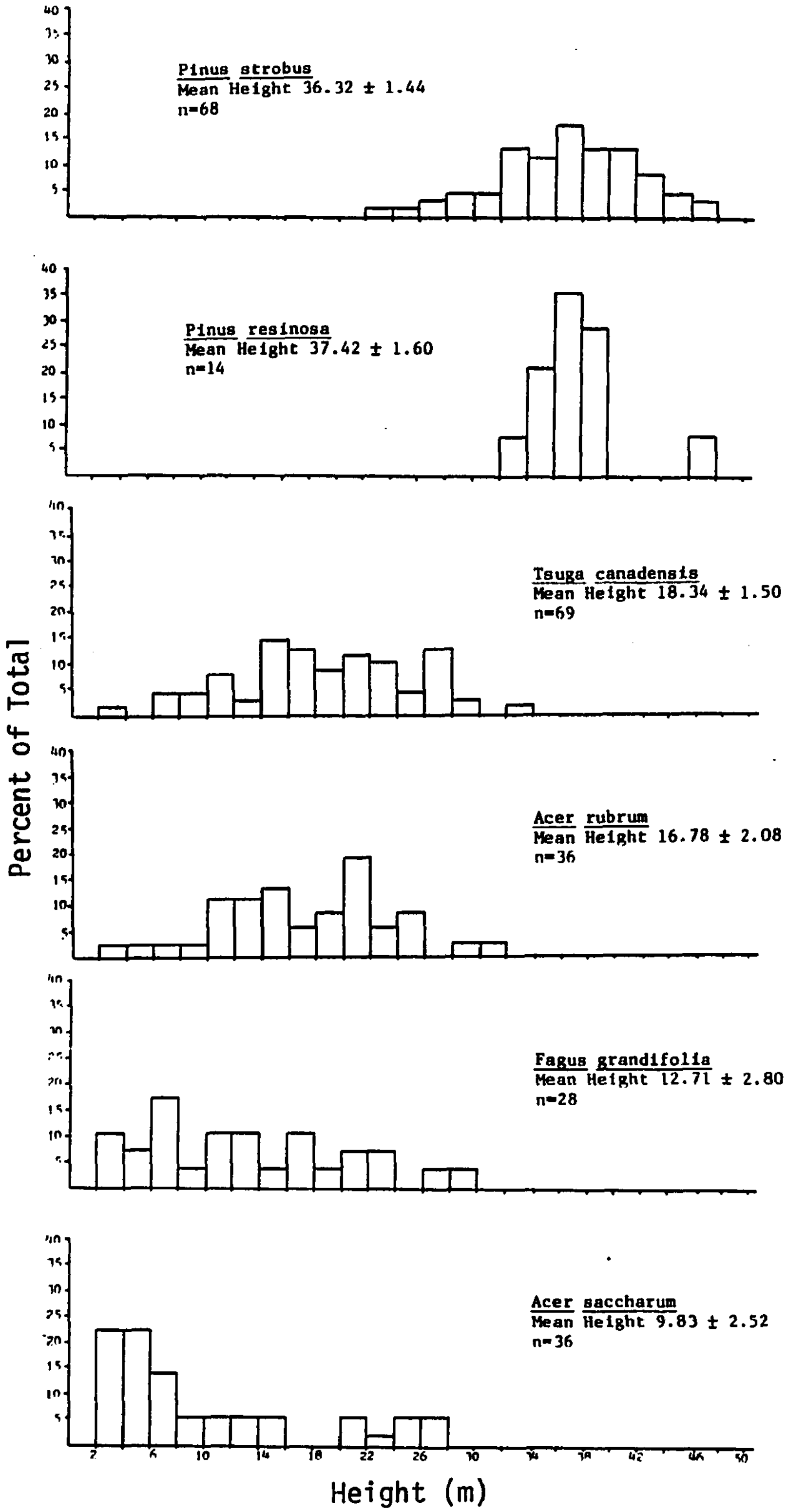

Fig. 4 Distribution of tree height by species. (mean ±2 S.D.).

The apparent discontinuity in diameter distributions of white pine between the 95 and 106 cm classes and hemlock between the 55 and 61 cm classes (Figure 3) suggested that several individuals of each species established well before the others. Wackerman (1924) hypothesized that a few white pine at Hartwick must be relics from a storm, and that they acted as seed trees. Assuming that a gap in size classes indicated a gap in age, the discontinuity appeared to be evidence to support the idea that some type of disturbance may have been responsible for the origin of the pines at Hartwick.

In contrast to the possible disturbance origin of Hartwick, there was no indication of white pine assuming dominance in most of the 14 ha section of the forest that was destroyed by wind in the 1940's. There were nine species in this area, six of which were the same as the six species in the undisturbed forest. The three others, black spruce (Picea mariana), speckled alder (Alnus incana), and paper birch, are commonly found in moist habitats. Shallow standing pools indicated poorly drained soil in the disturbed area. The loss of white pine and the introduction of new species may have been a result of natural soil drainage being interrupted by a road constructed through this part of the forest in the 1930's.

The average ages of the three deciduous species in the virgin forest were all in the 90's. Red pine and hemlock had average ages of 210 and 171 years, respectively. Linear regression analyses showed some correlation between diameter and age in the deciduous species (Table 2), but very low correlation in red pine and hemlock. The average estimated age of white pine was 177 years (Table 4), with the oldest tree sampled being 229 years. These trees are young, considering that white pine of

Table 4. Age distribution (as % of species total) and average age (±1 S.D.) of the five tree species (>1.5 m tall) found at Hartwick.

Species	Age (yr) 20-100	101-150	151-225	226+	n	Mean ± S.D.
Pinus strobus		12.5	83.3	4.2	24	177 ± 29.35
Pinus resinosa			100.0		6	210 ± 6.46
Tsuga canadensis		40.0	50.0	10.0	10	171 ± 49.36
Acer rubrum	50.0	50.0			6	91 ± 42.62
Acer saccharum	50.0	50.0			6	91 ± 37.79
Fagus grandifolia	50.0	50.0			6	96 ± 26.73

450 years and more in age have been recorded (Harlow and Harrar 1968). Many trees were 300 to 500 years old when cut in the Upper Peninsula of Michigan (Graham 1941); one such tree in the Estivant Pines near Copper Harbor was 400 years old when cut in the 1960's. Because of variable growing conditions of each individual, there was practically no correlation between age and diameter, height or crown cover at Hartwick (Table 2). Most of the old growth stands were cut when 200 to 300 years old and 4 to 7 feet (122-213 cm) in diameter (Frothingham 1914). In the forest reported by Stearns (1950) a tree 76.2 cm in diameter had 341 rings. A forest in Minnesota had trees with a mean diameter of 71 cm and mean age of 250 years (Kittredge 1934). In New Hampshire a stump 132 cm in diameter had a ring count of 153 (Baldwin 1951). Hartwick falls at the young end of the age range of old growth pine which suggested that the trees could potentially survive for several hundred more years. Windfall was a major cause of death and it appeared that many of these trees were structurally weakened by heart rot. The disease probably developed after sections of bark were destroyed during the last fire to burn through this area, 134 years ago.

Biomass and Productivity

Biomass. Total tree biomass for Hartwick Pines was 681.21 mt/ha when calculated using a white pine biomass figure based on a wood density of 0.29 g/cm^3. This density was determined from 24 increment cores taken at Hartwick. Total stand biomass, using 0.37 g/cm^3 for white pine (Brown et al. 1949), increased to 800.95 mt/ha, with a white pine biomass of 557.56 mt/ha. This demonstrates the outstanding and unusual character of this forest, especially in relation to second growth forests of today. It is well above average for most of the world's forest types (Table 5 and 6).

Table 5. Estimated biomass of standing trees (>1.5 m tall).

	Biomass (mt/ha)											
	Stem		Leaf		Branch[d]		Root		Reproductive			
Species	Absolute	% of spp. Total	Absolute	% of spp. Total	Absolute	% of spp. Total	Absolute	% of spp. Total	Absolute	% of spp. Total	Spp. Total	Spp. Total as % of Component Total
Pinus strobus	265.59	60.7	2.394[a]	0.5	107.23	24.5	62.44[e]	14.3	.077[i]	0.0	437.82	64
									.085[j]	0.0		
Tsuga canadensis	47.91	61.0	.897[b]	1.1	19.34	24.6	10.24[f]	13.0	.146[k]	0.2	78.53	12
Acer rubrum	16.37	61.1	.250	0.9	6.61	24.7	3.55[g]	13.3	.005[l]	0.0	26.78	4
Acer saccharum	5.92	60.8	.135	1.4	2.39	24.5	1.29[g]	13.2			9.74	1
Fagus grandifolia	8.47	60.5	.159	1.1	3.42	24.4	1.93[h]	13.8	.006	0.0	13.99	2
Pinus resinosa	69.09	60.4	1.049[c]	0.9	27.90	24.4	16.31[e]	14.3	.003[m]	0.0	114.35	17
Component Total	413.35	60.7	4.884	0.7	166.89	24.5	96.76	14.2	.322	0.0	681.21	100

[a] Based on the average needle life expectancy of 2 years and including the biomass of primary needles (Harlow and Harrar 1968).
[b] Based on the average needle life expectancy of 2.5 years (Harlow and Harrar 1968).
[c] Based on the average needle life expectancy of 4 years (Harlow and Harrar 1968).
[d] Individual species values were obtained by using the ratio B/b=S/s (Whittaker and Marks 1975).
[e] Based on the average value (16.63% of the total above ground biomass) for 100 year old *Pinus contorta* roots (Johnstone 1971).
[f] Based on the average value (15% of the total above ground biomass) for *Picea abies* (Lieth 1974).
[g] Based on the average value (15.3% of the total above ground biomass) for mature *Acer saccharum* (Whittaker and Marks 1975).
[h] Based on the average value (16% of the total above ground biomass) for *Fagus sylvatica* (Lieth 1974).
[i] Based on the average cone life expectancy of 1.5 years (Harlow and Harrar 1968).
[j] Staminate cones.
[k] Based on the average cone life expectancy of 1.5 years (Harlow and Harrar 1968, Fernald 1970).
[l] *Acer rubrum* and *Acer saccharum* combined.
[m] Based on the average cone life expectancy of 1.5 years (Harlow and Harrar 1968, Fernald 1970).

Table 6. Mean biomass and net primary producton for major forest types of the world.

Forest Type	Biomass (mt/ha)		Net Primary Productivity (mt/ha/yr)	
	Range	Mean	Range	Mean
Tropical Rain Forest	60-800	450	10-35	22
Tropical Seasonal Forest	60-600	350	10-25	16
Temperate Evergreen Forest	60-4000	350	6-25	13
Hartwick Pines (white pine)		681		7.5
Temperate Deciduous Forest	60-600	300	6-25	12
Boreal	60-400	200	4-20	8

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[1] Values are taken from Whittaker (1975) and a variety of sources including Art and Marks (1971), Lieth (1975), Rodin and Bazilevich (1967, 1968), Waring and Franklin (1979) and Woodwell and Whittaker (1968).

Only the coniferous stands of the Pacific Northwest with up to 4000 mt/ha and perhaps the eucalyptus forests of Australia far exceed the biomass of Hartwick (Waring and Franklin 1979). Several comparable stands have been recorded: a Tsuga canadensis stand with 610 mt/ha, and a Tsuga-Rhododendron stand with 511 mt/ha in the U.S.A. (Whittaker 1966); Abies, Tsuga, and Quercus in Nepal with 520 to 682 mt/ha (Yoda 1968, cited by Art and Marks 1971); Quercus in both the U.S.A. and U.S.S.R. with values over 400 mt/ha (Whittaker 1966, Rodin and Bazilevich 1967). White pine biomass from Hartwick alone is near or above (depending on wood density) the total biomass of 515 mt/ha for a Fagus-Acer forest in Michigan (Murphy, P. G. and G. K. Kroh, Biomass and Net Primary Productivity of a Virgin Beech-Maple Forest in Michigan, Michigan State University, in preparation). This was probably a result of the large white pine basal area of 48.4 m^2/ha compared to total basal area for the beech-maple stand of 42.6 m^2/ha.

White pine and red pine made up a disproportionate amount of the biomass in comparison to their importance value percentages. White pine was 64% of the biomass and red pine 17%, while their importance value percentages were 38.9 and 8.6, respectively. Biomass of the four other species was much less than their importance values might indicate. The lack of relationship between importance value and biomass indicates the limitation in using importance values to describe some forests. A better indicator of importance, in some instances, should include biomass and perhaps production as a modifier.

The allometric equation relating white pine DBH and stem volume, along with specific gravity, was used to estimate biomass (Table 2). The allometric equation proved to be a good predictor, with a coefficient of determination (r^2) of 0.91 (n=15). Even though white pine stems may vary to some degree in growth form between sites this equation should prove to be of value in similar studies of old growth white pine where restrictions prevent destructive sampling.

White pine wood density was 0.29 g/cm^3, 22% lower than .37 g/cm^3 listed by Brown et al. (1949). Bark density was 0.56 g/cm^3, within the range of 0.402-0.714 g/cm^3 given by Martin and Crist (1968) for Michigan and Virginia specimens. Bark comprised 8.7% of the total stem biomass.

Stem biomass was 60.7% and leaf biomass 0.7% of the total biomass. Stem biomass percentage appeared to be constant across species with different age and size classes, with single species values within 0.7% of each other. White pine leaf biomass of 0.5% of white pine total was low compared to the other species with leaf biomass percentages between 0.9 and 1.4. Kira and Shidei (1967) emphasize that leaf biomass of a tree in a closed stand will reach an upper limit, while stem biomass is still increasing. The amount of leaf biomass may be a limiting factor to growth and survival if this reduction in the percentage of leaf biomass continues. It would not be surprising to find this occurring with the white pine at Hartwick.

Productivity. Total net primary production (NPP) for Hartwick, 7.5 mt/ha/yr, is at the low end of the ranges reported in the literature for many of the world's forest types (Tables 6 and 7). It is comparable to a woodland, shrubland, or temperate grassland (Whittaker 1975) and falls within the range for temperate evergreen forests. This does not support the conclusions of Westlake (1963), Kira and Shidei (1967), and Rodin and Bazilevich (1968), that conifer forests have the highest NPP. These authors list figures for conifer forests of 10-28 mt/ha/yr in warm,

Table 7. Net primary productivity (kg/ha/yr) of the six tree species (>1.5 m tall) in the virgin *Pinus strobus* L. forest.

	Net Annual Productivity (kg/ha)											
	Stem		Leaf		Branch[c]		Root[d]		Reproductive			Spp. Total as % of Component Total
Species	Absolute	% of spp. Total	Absolute	% of spp. Total	Absolute	% of spp. Total	Absolute	% of spp. Total	Absolute	% of spp. Total	Spp. Total	
Pinus strobus	1239.9	36.2	113.5[a] 1140.2[b]	3.3 33.3	500.6	14.6	291.5	8.5	51.1[e] 85.4[f]	1.5 2.5	3422.2	45
Tsuga canadensis	695.3	44.0	358.9	22.7	280.7	17.8	148.6	9.4	97.3	6.2	1580.8	21
Acer rubrum	267.6	39.0	250.0	36.4	108.0	15.7	58.0	8.5			685.9	9
Acer saccharum	175.0	41.5	135.3	32.1	70.7	16.8	38.1	9.0	4.69	0.4	421.4	6
Fagus grandifolia	226.1	42.4	158.6	29.8	91.3	17.1	51.5	9.7	5.5	1.0	533.0	7
Pinus resinosa	384.8	43.0	262.2	29.3	155.4	17.4	90.8	10.1	2.1	0.2	895.3	12
Component Total	2988.7	39.6	2418.7	32.1	1206.7	16.0	678.5	9.0	246.0	3.3	7538.6	100

[a] *Pinus strobus* bud scales.

[b] *Pinus strobus* leaves.

[c] Individual species values were obtained by multiplying the total amount of branch production by the individual species percentage of the total stem production.

[d] Individual species values were obtained by using the ratio R/r=S/s. R=root biomass, r=root production, S=stem biomass, s=stem production.

[e] Pistilate cones.

[f] Staminate cones.

[g] *Acer rubrum* and *Acer saccharum* combined.

temperate and subarctic areas; however, Rodin and Bazilevich (1968) also cite a comparatively low value of 7.0 mt/ha/yr for the temperate zone.

These authors could have based their conclusion on a sample skewed toward young stands in which net primary production is higher. As previously mentioned, out of 291 biomass and productivity studies cited by Art and Marks (1971) the average age of natural stands was 45.8 years and plantations 29.0 years. White pine reaches its peak growth between the ages of 40 and 115 years according to Barrett et al. (1976) and at 26 years according to Cope (1932). Woodwell and Whittaker (1968) suggest that NPP of forests with a large biomass, such as the cove forests of the Great Smoky Mountains National Park (600 mt/ha) (Whittaker 1966), will be 2.0-2.5% of the biomass, twice that of Hartwick. The NPP values for Hartwick and the Fagus-Acer forest in Michigan mentioned previously, with an NPP value of 8.4 mt/ha/yr (Murphy, P. G. and G. K. Kroh, Biomass and Net Primary Production of a Virgin Beech-Maple Forest in Michigan, Michigan State University, in preparation), suggest a substantial decrease in NPP with stand age.

Total net stem production for Hartwick, 2,989 kg/ha/yr, is less than half the net stem production for a 15 year old white pine plantation in North Carolina (Swank and Schreuder 1973). The average radial increment of Hartwick white pine was 0.74 mm, only 29% of an old growth white pine forest in New Hampshire (Baldwin 1951), and less than the 1.22 to 4.05 mm measured from the first ten years of growth by white pine in northwestern Pennsylvania (Lutz and McComb 1935). Regression analysis between crown volume and white pine stem production or stem biomass indicated little correlation (Table 2). The main stem of white pine at Hartwick accounted for 36% of its total net production, while in the other species the stem comprised approximately 40%. These values fall within the range of 35-40% for forests in favorable environments (Woodwell and Whittaker 1968).

Leaf litter for all species combined represented 62% of total litter, not including input from the main stem; branch litter represented 31% and reproductive litter 6%. White pine leaf litter alone was 66% of its total litter, branch litter 26% and reproductive litter 7%. These values compare favorably with other Pinus forests ranging from 60-69% for leaf litter, 33-36% for branch litter and 2-17% for reproductive litter (Bray and Gorham 1964). The smaller value for Hartwick branch litter could have been a result of reduced lower branch pruning in larger pines.

Seasonal variation in the amount of leaf litter collected indicated that maples and beech dropped virtually all of their leaves in October and November (Figure 5). Similarly, the coniferous species dropped approximately 98% of their annual leaf litter in October and November; they retained their youngest needles, however, losing a few of those throughout the rest of the year. Large standard errors in these figures were a result of the limited number of samples that could be taken while keeping visual and human impact to a minimum.

Reproductive and photosynthetic structures were a relatively large part of the total production. Reproductive structures at Hartwick were only 0.05% of the total biomass but 3.3% of the total NPP. Leaf NPP was 22.7 to 36.4% of total individual species NPP, while leaves comprised less than 2% of the total biomass of each species. White pine had one of the higher values for leaf NPP as a percentage of species total at 33.3%, while hemlock was the lowest at 22.7%. The structurally small white pine bud scales alone made up 5% of the total leaf NPP (2.4 mt/ha/yr), which in turn was 32% of the total NPP. Hartwick's leaf production in comparison

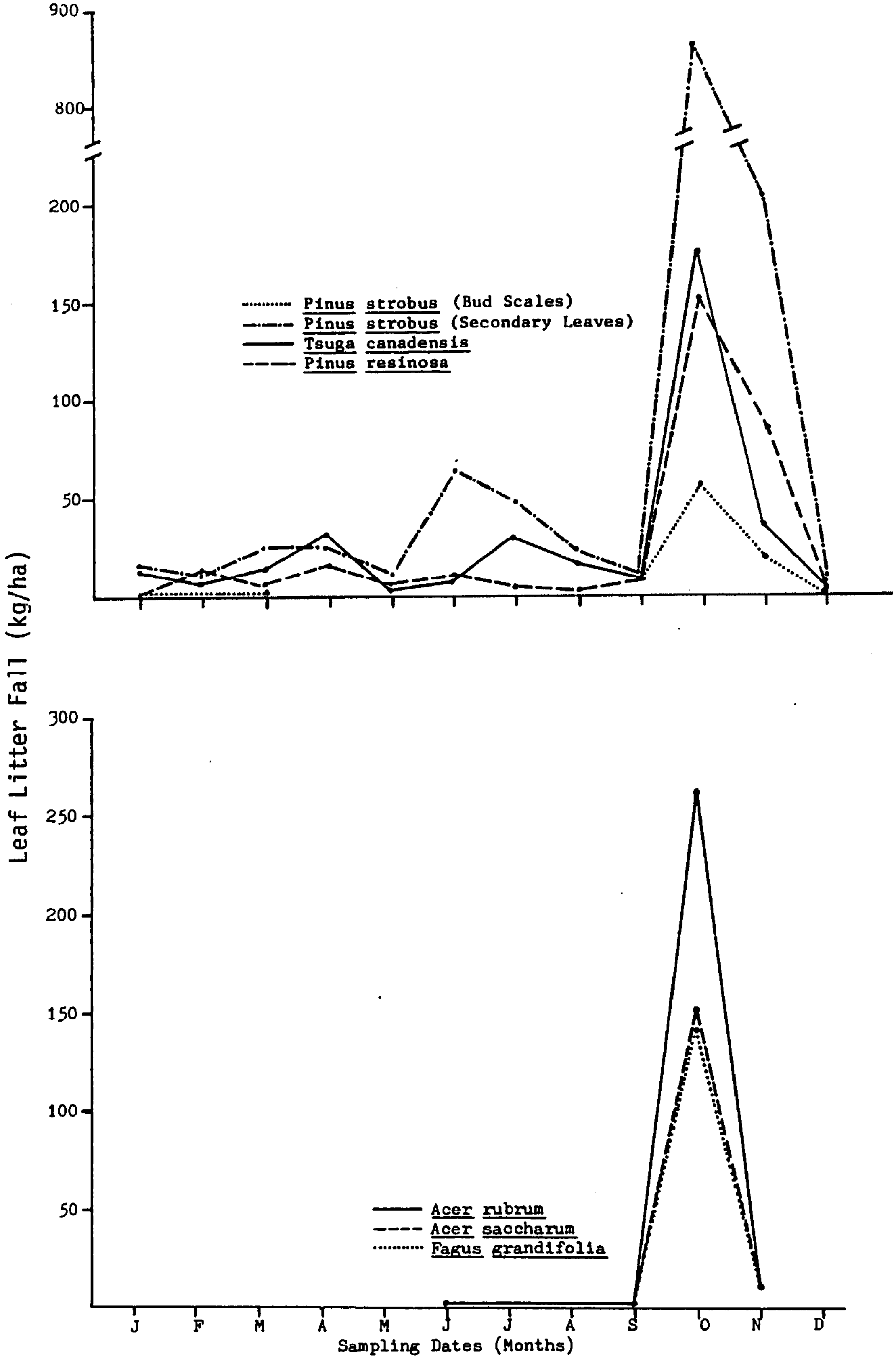

Fig. 5. Coniferous and deciduous leaf litter fall by month.

to the mean leaf production of 2.8 mt/ha/yr for five Pinus sites, 3-69 years old (Bray and Gorham 1964) suggests a slight decrease in leaf production with age.

Succession

Tree diameter, height and age distribution. Although white pine was once considered to be a component of climax forests (Detwiler 1933), it is today more commonly regarded as a successional species (Graham 1941). It is a pioneer on disturbed or open sites or is preceded by jack pine or oak and replaced by maples and beech (Grant 1934, Kittredge 1934, Morey 1936, Cline and Spurr 1942, Graham 1941, Stearns 1950). By comparing canopy to understory trees, Braun (1950) concluded that the successional series for Hartwick will be from white pine-red pine to white pine-hemlock with hardwoods to hemlock hardwoods or hardwoods alone. Successional trends can be infered from patterns of diameter and height distributions among the major tree species but with caution because the next successional stage is not always represented by the species with the largest proportion of smaller individuals. These data should be viewed as one piece of evidence that, when combined with other observations on succession, will lead to more confident conclusions. At Hartwick there were no white or red pine mature trees in size classes less than 26 cm in diameter or 22 m in height, possibly indicating their inability to regenerate (Figures 3 and 4). Red maple, beech, and sugar maple, present in the smaller size classes, can be expected, therefore, to have a competitive edge over pine seedlings in replacing the mature white and red pine. Hemlock was difficult to interpret because it is intermediate in size between the two groups and shows a decrease in the small size categories. It appeared to be an understory tolerant species and yet shows signs of not replacing itself.

The age of the three conifers averaged more than 170 years, while the three hardwood species were grouped near 90 years (Table 4). The date of establishment of the oldest hardwood species corresponded to the date of the last fire that burned through this area sometime between 1846-1856. It is likely that hardwoods established themselves prior to 1846 and that the fire eliminated them from competing with the surviving pines. Possibly because fire was no longer a factor, at the time of this study, hardwoods were once again able to compete for dominance in the canopy gaps caused by the death of large white pine. This supports the idea that fire is a major factor in perpetuating white pine forests (Frothingham 1914, Maissurow 1935, 1941).

Canopy gap description. Bergman (1923) considered white pine to be a climax species based on observations of a stand where white and red pine seedlings were the most numerous of all tree species in windfall openings. However, similar to the present observations at Hartwick, white pine were absent in the sapling category. Bergman had correctly suggested that study of canopy openings is important in understanding succession, but failed to account for the apparent lack of seedling survivorship. Since Bergman, the gap-phase concept has developed, stressing the importance of disturbance openings in replacement of canopy species (Watt 1947, Bray 1956, Oliver and Stephens 1977).

The size of the canopy opening is determined by the type of disturbance or destruction, which in turn influences species recruitment into the opened area. Sheet destruction caused by fire opens large areas, whereas the more common death of single trees opens small areas (Grubb 1977), such as those caused by windthrow at Hartwick. However, quite often when one tree is blown over several trees are taken down with it (Table 8).

Table 8. Comparison of the number of trees that died, creating the 21 gap formations, with the relative density of the living trees.

Species	Number Dead	Mean Number Dead Per Gap	Percent of Total Dead	Relative Density of Living
Pinus strobus	44	2.0	57.9	27.4
Pinus resinosa	11	0.5	14.5	5.6
Tsuga canadensis	5	0.2	6.6	27.4
Acer spp.	5	0.2	6.6	28.6
Conifer	3	0.1	3.9	
Unknown	8	0.4	10.5	
Total	76	3.4	100.0	

In the present study the total functional gap area constituted 15% of the total sample area while the total structural gap area constituted only 6% (Figure 6). Some windthrows at Hartwick may have been a result of heart rot that possibly began when the fire 130 years ago burned through sections of the bark exposing the wood, and making the trees more susceptible to disease and insect damage. During the past one hundred years, twenty-one gaps have formed in the study area, the most recent of which was five years old. Gap ages indicated that many of the gaps formed at the same time, probably during storms. Percent of total dead trees of white and red pine was more than twice their relative density among living trees. This was much higher than any of the other species, indicating a higher death rate. Size, age, and number of dead trees for each gap, including averages for these parameters, are listed in Table 9.

Seedling description, age and size distribution. Of the seedlings found in gaps, red maple, sugar maple and white pine had importance value percentages three to eight times greater than any other tree species (Table 10). These three were also most important under the forest canopy, where importance value percentages for red and sugar maple were 10-19% greater, and white pine 44% less, than under the canopy gap. This indicates the relative ability of red and sugar maple to establish and grow better than white pine under a canopy. However, the distinct drop in absolute values of all species, especially white pine, from the gap to the canopy understory indicates that those species do not do as well under the canopy. Red maple had four times the seedling density as sugar maple in the gap and under the canopy. In the gap, white pine density was 11% greater than sugar maple and under the canopy it was 42% less. However, sugar maple dominated crown cover area in the gap (2796 cm^2/m^2) and under

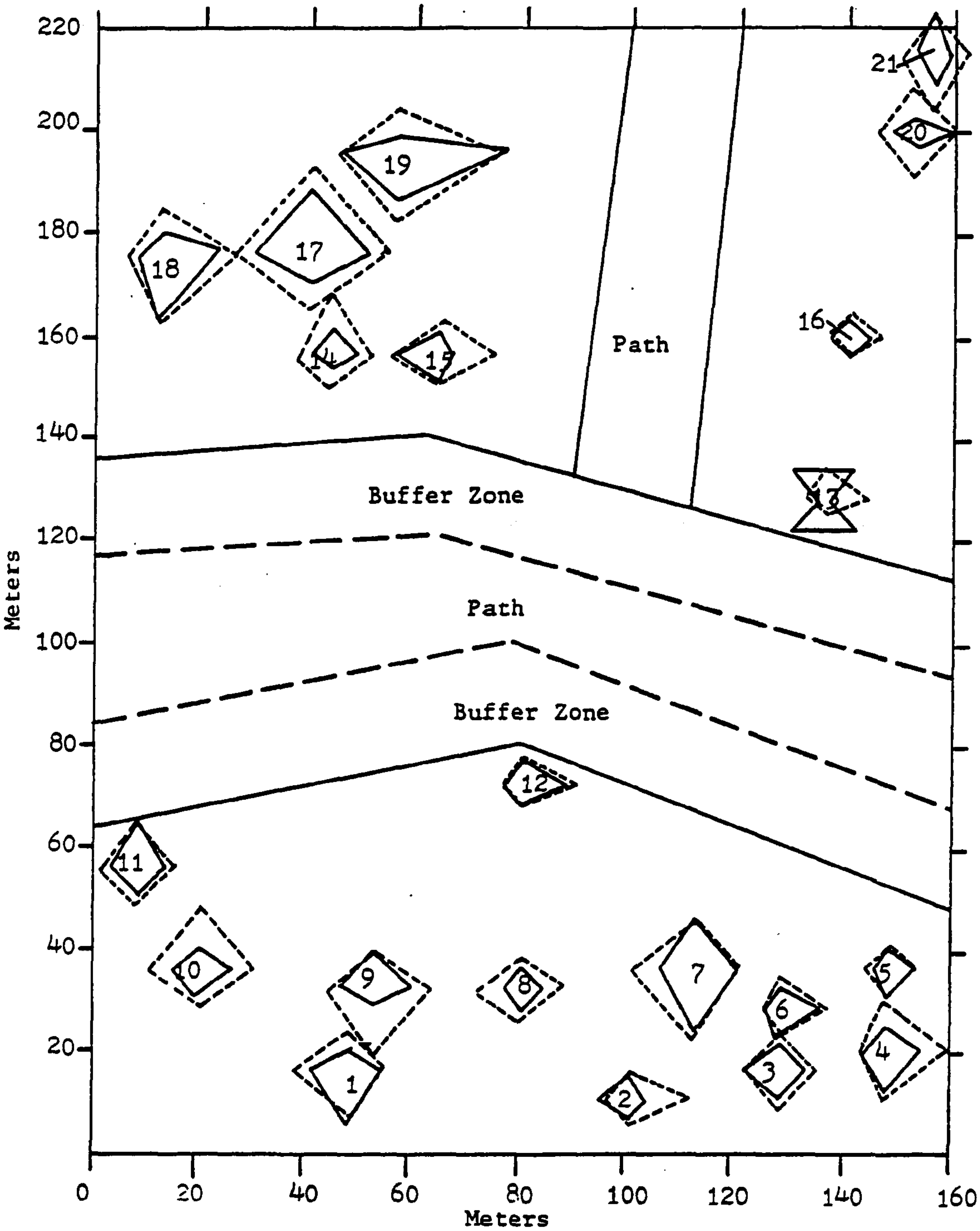

Fig. 6. Location and size of structural (-) and functional (--) gaps within the sample area. The path includes the area within the forest eliminated from the study to reduce the edge effect.

Table 9. The age, size and number of dead trees associated with each of the intensively studied gaps and the mean values for all gaps.

Gap	Functional (m^2)	Structural (m^2)	Age (year)	Number of dead trees
11	289	163	5	6
14	244	95	5	5
17	495	263	33	7
19	626	347	37	13
15	210	95	50	0[a]
1	242	121	63	4
8	168	84	90	3
10	274	121	100	5
Mean for all 21 gaps	251	113	40	3.6

[a] No downed trees were visible. They could have been decomposed or removed.

Table 10. Importance values[a] (I.V.) for the woody seedlings (<1.5 m in height) found in the gaps and closed forest.

	Density				Dominance[b]				Frequency					
	Absolute # of ind./m²		Relative		Absolute cm²/m²		Relative		Absolute # of plots/ total # of plots		Relative		I.V. %	
	Gap	Forest	Gap	Forest	Gap	Forest	Gap	Forest	Gap	Forest	Gap	Forest	Gap	Forest
Acer rubrum	11.4	6.3	55.6	65.9	2101.6	515.8	38.3	30.4	0.9	0.8	30.0	40.6	41.3	45.6
Acer saccharum	2.9	1.6	14.3	17.0	2796.3	995.9	51.0	58.8	0.7	0.6	22.0	28.1	29.1	34.6
Pinus strobus	4.2	0.9	20.7	9.8	218.6	25.2	4.0	1.5	0.6	0.2	18.0	12.5	14.2	7.9
Tsuga canadensis	0.7	0.2	3.4	2.0	27.4	5.9	0.5	0.3	0.4	0.2	12.0	9.4	5.3	3.9
Amelanchier sp.	0.8	0.1	3.6	1.4	202.1	11.5	3.7	0.7	0.4	0.1	12.0	6.2	6.4	2.8
Acer spicatum	0.0	0.4	0.0	4.0	0.0	139.8	0.0	8.3	0.0	0.1	0.0	3.1	0.0	5.1
Lonicera sp.	0.4	0.0	2.1	0.0	108.8	0.0	2.0	0.0	0.1	0.0	4.0	0.0	2.7	0.0
Fagus grandifolia	0.1	0.0	0.3	0.0	29.5	0.0	0.5	0.0	0.1	0.0	2.0	0.0	0.9	0.0
Total	20.5	9.5	100.0	100.1	5484.3	1694.1	100.0	100.0	3.2	2.0	100.0	99.9	99.9	99.9

[a] Calculated following methods in Mueller-Dombois and Ellenburg (1974).
[b] Based on crown cover.

the canopy (996 cm^2/m^2), while red maple was second (2102 and 516 cm^2/m^2) (Table 10). The crown cover area of white pine in the gap was only 8% and, under the canopy only 3% of sugar maple's respective values. The average individual crown cover for sugar maple seedlings in the forest and gap was five times larger than red maple, and 20 times larger than white pine. Sugar maple seedling shoot growth was three to six times greater than the other two species (Figure 7). Under the forest canopy, sugar maple seedlings grew an average 5 cm/yr while white pine grew less than 1 cm/yr; the difference was even greater in the gap, with sugar maple growing approximately 10 cm/yr and white pine less than 1 cm/yr. Hemlock and beech seedlings were rare, less than $1/m^2$, and red pine was absent, indicating a complete failure of this species to produce seedlings.

The averages of six seedling parameters measured in gaps of different ages are illustrated in Figure 8. Standard errors were not included because, in almost every case, they were nearly one half the mean value. Therefore, these figures only suggest changes that may occur as the gap ages. Most of the seedling parameters measured were at a maximum when gaps were between 5 and 40 years old. After several decades of growth, maples have partially closed the 33- to 63-year-old canopy gaps, and completely closed the 90-year-old gap, suppressing growth of new seedlings. The seedlings also showed reduced evidence of browsing. In the 100-year-old gap, several of the mature hardwoods died, creating a second gap in which seedlings were released (Figure 8). The data show that there was a rapid increase in seedling growth, with sugar maple displaying the greatest response, in the early years after gap formation. Red maple, because of its density, attained the largest importance value, which resulted in a sharing of canopy dominance by the two maple species.

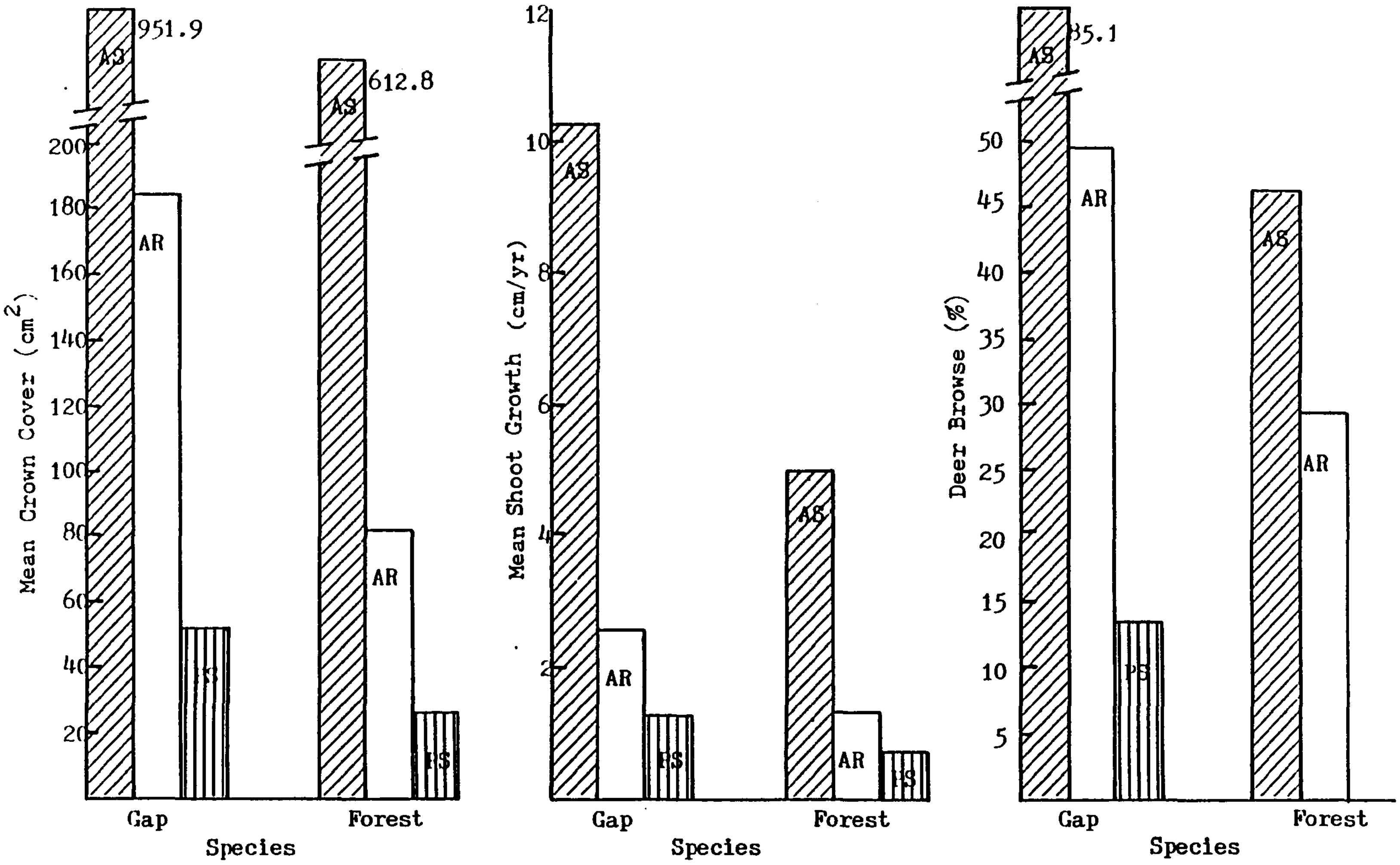

Fig. 7. Average seedling crown cover and shoot growth, and percentage of browsed seedlings in the gaps and forest. Legend: AS=*Acer saccharum*, AR=*Acer rubrum*, PS=*Pinus strobus*.

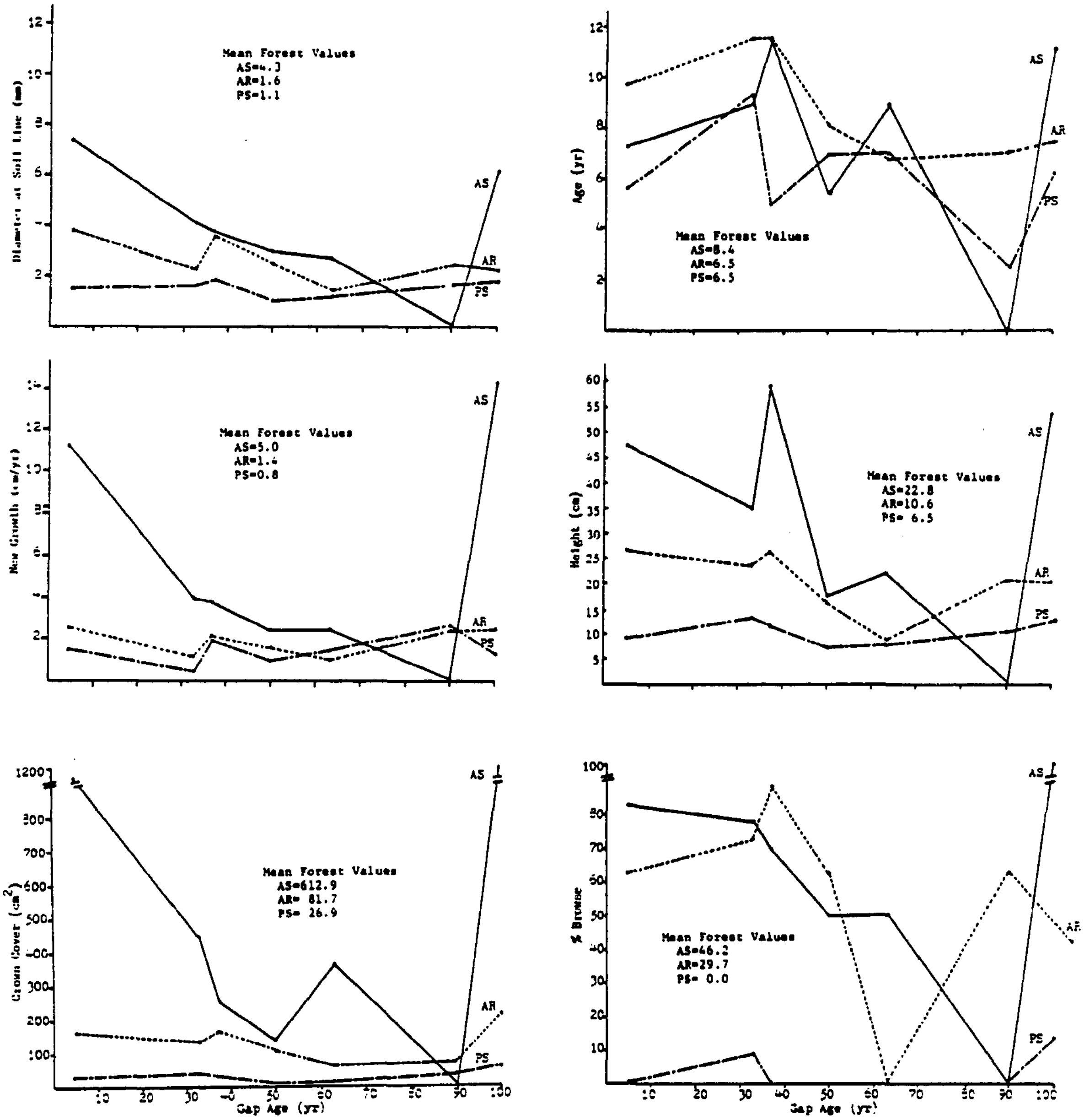

Fig. 8. Six seedling parameters measured in gaps of different ages, suggesting temporal changes. The mean values for seedlings under the forest canopy are also given. Legend: AS=*Acer saccharum*, AR=*Acer rubrum*, PS=*Pinus strobus*, % Browse = Percentage of Seedlings Browsed.

Red maple had a high probability of reaching the canopy because of the large number of its seedlings, and sugar maple because of its early vigorous growth. Comparisons of seedling values between the forest with a white pine-dominated overstory and the older gaps with a maple-dominated overstory seems to indicate that sugar maple does not do as well under its own canopy (Figure 8). White pine seedlings were produced in numbers equivalent to sugar maple, but they grew very poorly, both in the gap and under the canopy, and could not adequately compete for canopy dominance. There were too few beech seedlings to allow a study to explain its success in reaching the canopy. One possible explanation is that beech seedlings have a greater survivorship than sugar maple (Forcier 1975), perhaps as a result of establishing from root sprouts.

Age and size distributions of sugar maple, red maple, and white pine, within gaps of different ages, indicate the survival capabilities of these species (Figures 9-14). In the five-year-old gap, 67% of the white pine were in the youngest age category. Eight percent of white pine and over 50% of both red and sugar maple were older than six years. This reflects the ability of all three species to produce seedlings under the forest canopy before a gap forms, but seedlings survive only when a gap forms. In the five year old gap, sugar maple survived and dominated the older age categories, possibly by taking advantage of small gaps formed by the loss of branches from the original canopy tree.

In the 33- and 37-year-old gaps, the oldest white pine were in the 16 to 18 year class, indicating their inability to survive in a gap; in the same gaps, red maple survived to the estimated age of 66 and sugar maple to 56 (Figure 10). After 33 years, when the maples have partially filled the gap in the canopy, the age and size distribution changed abruptly, as

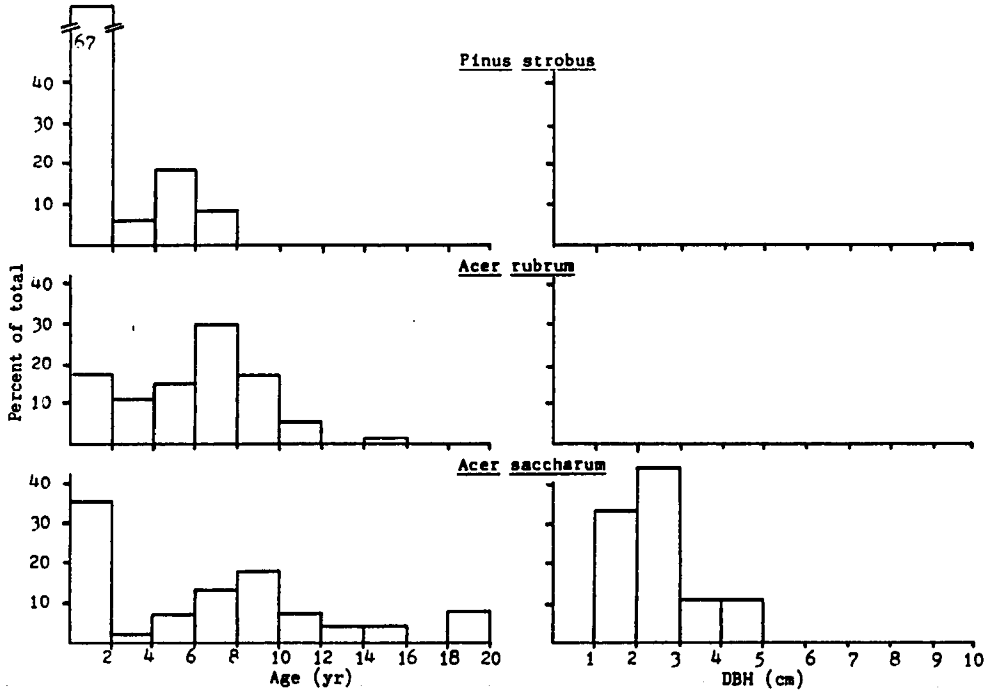

Fig. 9. Distribution of age (individuals <1.5 m in height) and DBH (individuals >1.5 m in height) of the three major species found in 5-year-old gaps.

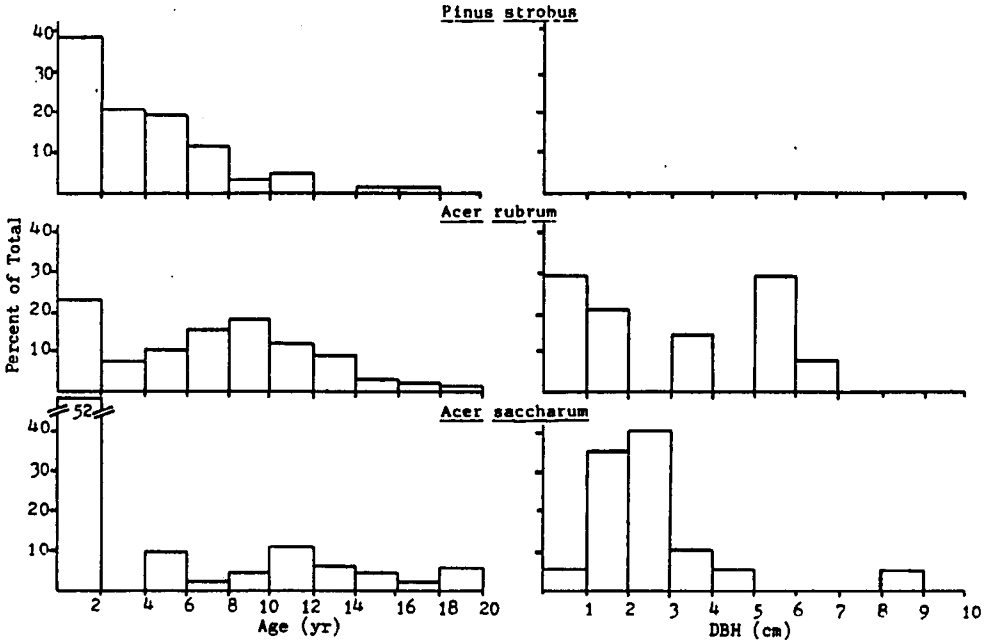

Fig. 10. Distribution of age (individuals <1.5 m in height) and DBH (individuals >1.5 m in height) of the three major species found in a 33- and 37-year-old gap.

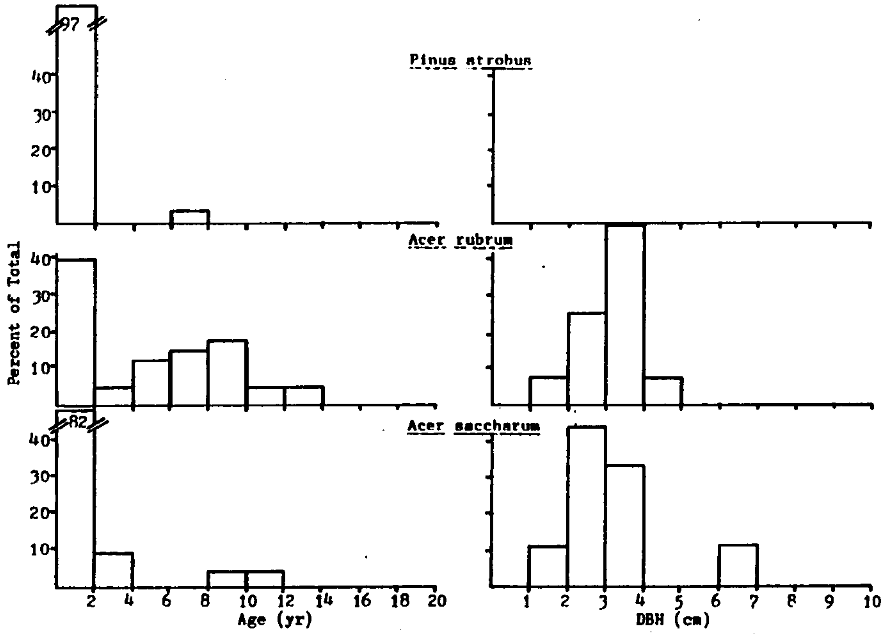

Fig. 11. Distribution of age (individuals <1.5 m in height) and DBH (individuals >1.5 m in height) of the three major species found in a 50-year-old gap.

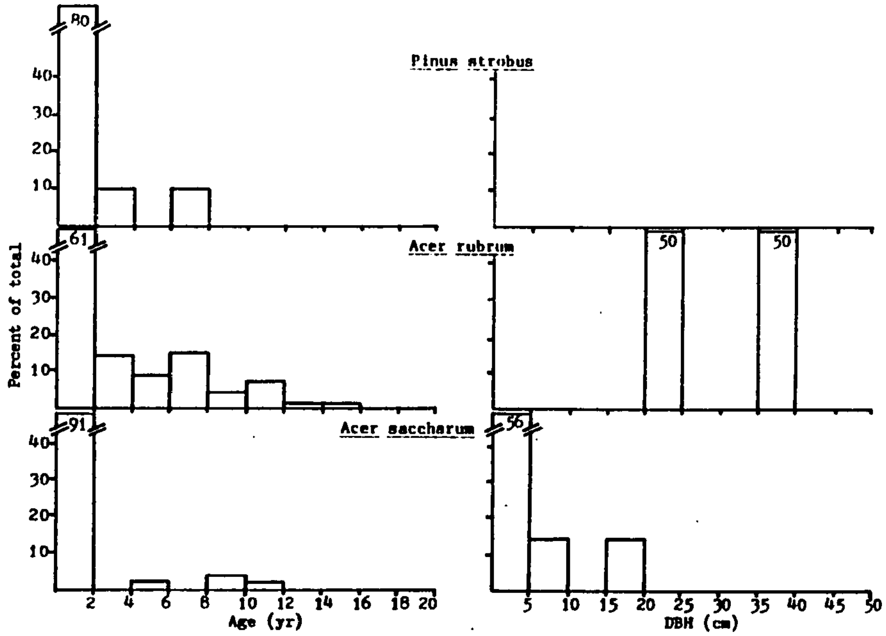

Fig. 12. Distribution of age (individuals <1.5 m in height) and DBH (individuals >1.5 m in height) of the three major species found in a 63-year-old gap.

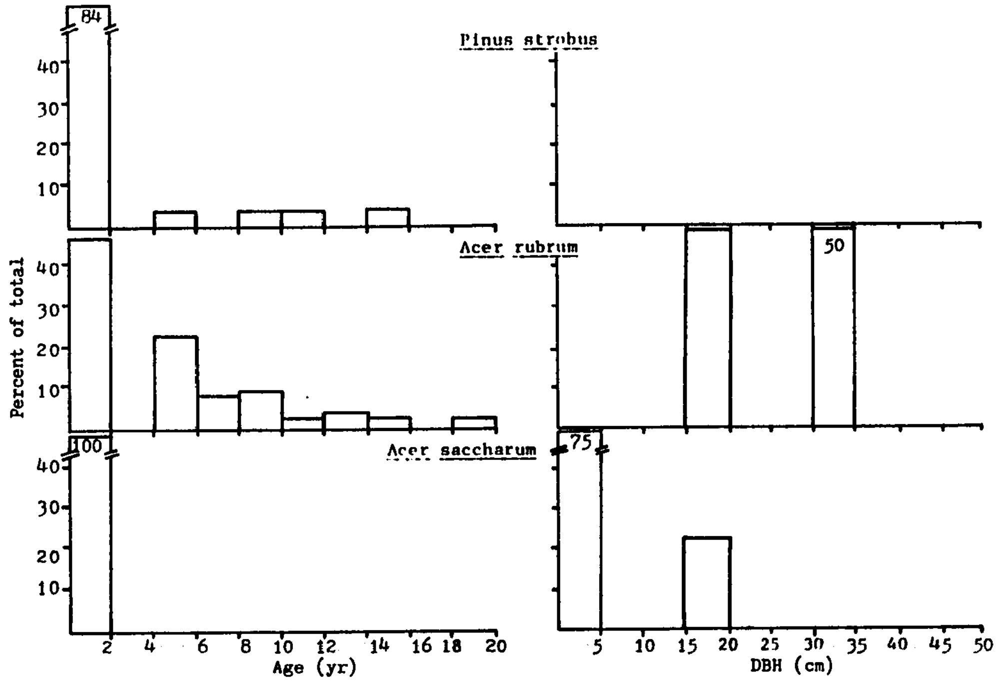

Fig. 13. Distribution of age (individuals <1.5 m in height) and DBH (individuals >1.5 m in height) of the three major species found in a 90-year-old gap.

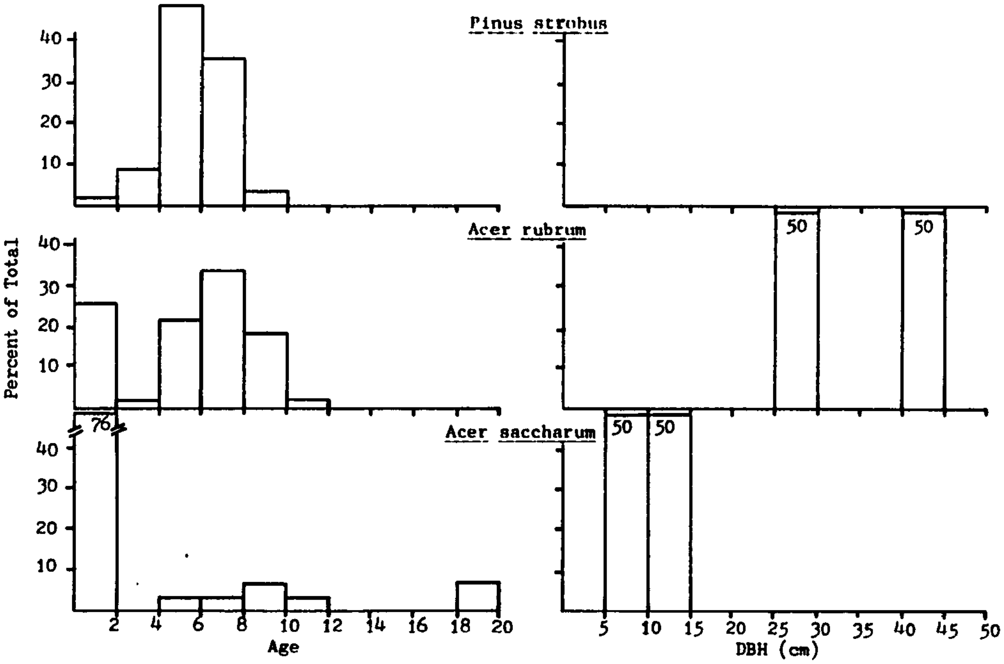

Fig. 14. Distribution of age (individuals <1.5 m in height) and DBH (individuals >1.5 m in height) of the three major species found in 100-year-old gap.

illustrated in the figures representing the 50-, 63-, and 90-year-old gaps (Figures 11-13). Greater than forty percent of the seedlings were 1 and 2 years old with very few older seedlings, indicating high mortality of young seedlings, especially among white pine. In addition, sugar maple seedlings in the 90-year-old gap were all in the youngest age category (Figure 13). The distribution for red and sugar maple shifts to larger size categories as a result of a few individuals surviving to fill in the canopy gap as illustrated in Figure 12. Similarly, Stearns (1950) described a virgin white pine forest and found sugar maple gradually gaining in importance. The 100-year-old gap had a greater percentage of seedlings surviving to the 6-8 and 10-year-old age categories because several large red and sugar maples blew over five years previous to the study. This resulted in a second generation gap and a second flush of seedling growth (Figure 14).

Survivorship. Overall mortality appeared to be greatest among youngest seedlings both in this study and others (Bormann and Buell 1964, Hett 1971, Good and Good 1972, Mulcahy 1975). A lack of white pine regeneration was evident from the 100% mortality after 18 years, similar to other old growth stands (Kittredge 1934, Maissurow 1935, 1941, Lutz 1930, Morey 1936, and Smith 1940). Second growth white pine occurs only where the old growth stand is open (Ahlgren 1976). This is supported by Frothingham's (1914) conclusions that only 5.5% of white pine seedlings survived to four years under dense crown cover, 60.8% survived under broken crown cover and 94.0% survived in the open. Hartwick Pines probably originated following a storm that left the area open with only a few seed trees (Wackerman 1924). Lutz and McComb (1935) also found that white pine of another virgin stand originated under a partial canopy. It was suggested by Bormann and Graham (1959) that root grafts with dominant trees may assist seedlings and saplings or may aid in resistance to windthrow. However, to be an effective aid in maintaining white pine dominance, seedlings must survive long enough to establish a root system with grafts. Several white pine seedlings of different ages were sampled at Hartwick and no root grafts were observed.

Sugar maple had the highest survivorship value among seedlings in gaps and under the forest canopy (Table 11), supporting the conclusions drawn from the age distributions. Contrary to what was concluded from the age distributions, red maple had the lowest survival rate in the gaps while white pine had the lowest value under the forest canopy. However, to attain Hartwick's age distributions, a few red maple presumably survived whereas all older white pine seedlings presumably died.

In addition, the survivorship study of the tagged seedlings shows that seedling mortality was at a minimum in the winter (Table 11), probably due to seedling dormancy. Extreme cold and desiccation were not problems for these seedlings because of the protection afforded by snow cover. Overall, survivorship was lower under the canopy while natality was similar for both the canopy and the gap, with sugar and red maple combined having a natality of $1.3/m^2/yr$ in the gaps and $1.5/m^2/yr$ under the canopy. During fall, 1979, overall natality for white pine and hemlock combined was $11.25/m^2$, in part a result of the prolific seed production of white pine that occurs every three to five years (Harlow and Harrar 1968). The large number of seeds produced may help compensate for the large loss of seed to red squirrels (Tamiasciurus hudsonicus). None of the new conifer seedlings survived to the following spring, but because they could not be identified to determine the proportion of white pine,

Table 11. Percent survivorship of different aged seedlings combined over one year (fall, 1977, to fall, 1978) in relation to season and browsing. n = number of seedlings at start of observation.

	Pinus strobus				*Acer saccharum*				*Acer rubrum*			
	Canopy Gap		Forest Canopy		Canopy Gap		Forest Canopy		Canopy Gap		Forest Canopy	
	n	%	n	%	n	%	n	%	n	%	n	%
Total	95	86.3	7	28.6	41	90.2	25	76.0	235	79.6	98	58.2
Winter		98.9		57.1		97.6		92.0	69	92.8		88.8
Summer		87.2		50.0		92.5		82.6	72	85.8		65.5
Browsed	25	80.0			26	96.2				76.8		
Unbrowsed	44	54.5			33	93.9				79.2		

they were not included in the survivorship calculations (Table 11). This would have decreased the survivorship values for white pine to a level less than that for red maple.

Mechanical damage is the suspected cause for the 100% mortality of recently-germinated conifer seedlings. Leaf fall from maple and beech trees covered the succulent white pine and hemlock seedlings and, with the additional weight of rain and snow, crushed them. Mortality would not have been as severe with only conifer needle litter which does not as readily blanket a seedling. Thus, white pine will establish best in open areas with less litter. This relationship between hemlock mortality and the deciduous litter fall is difficult to explain because it is often a common associate of hardwoods. Maples, on the other hand, germinate in the spring and by fall are single woody stems without branches, so leaves landing on them tend to slide off or are pierced, suggesting that growth form might be an adaptation for survival under a broadleaf canopy.

Environmental parameters. There appeared to be a relationship between the seedlings present and the temperature and humidity found in the three study areas. The open area where white pine were regenerating consistently had the highest daytime temperatures and the lowest humidity (Figures 15 and 16). However, the seedlings were partially shaded in the afternoon, protecting them from high temperatures that can produce seedling mortality (Smith 1940). White pine regenerating in partial shade were also observed in several other areas, including the virgin jack pine stand that was studied. If Hartwick was a result of a few seed trees that were left following a storm, as first proposed by Wackerman (1924), then Hartwick too originated in partial shade. In the gap, temperatures were between those found in the regeneration area and under the forest canopy.

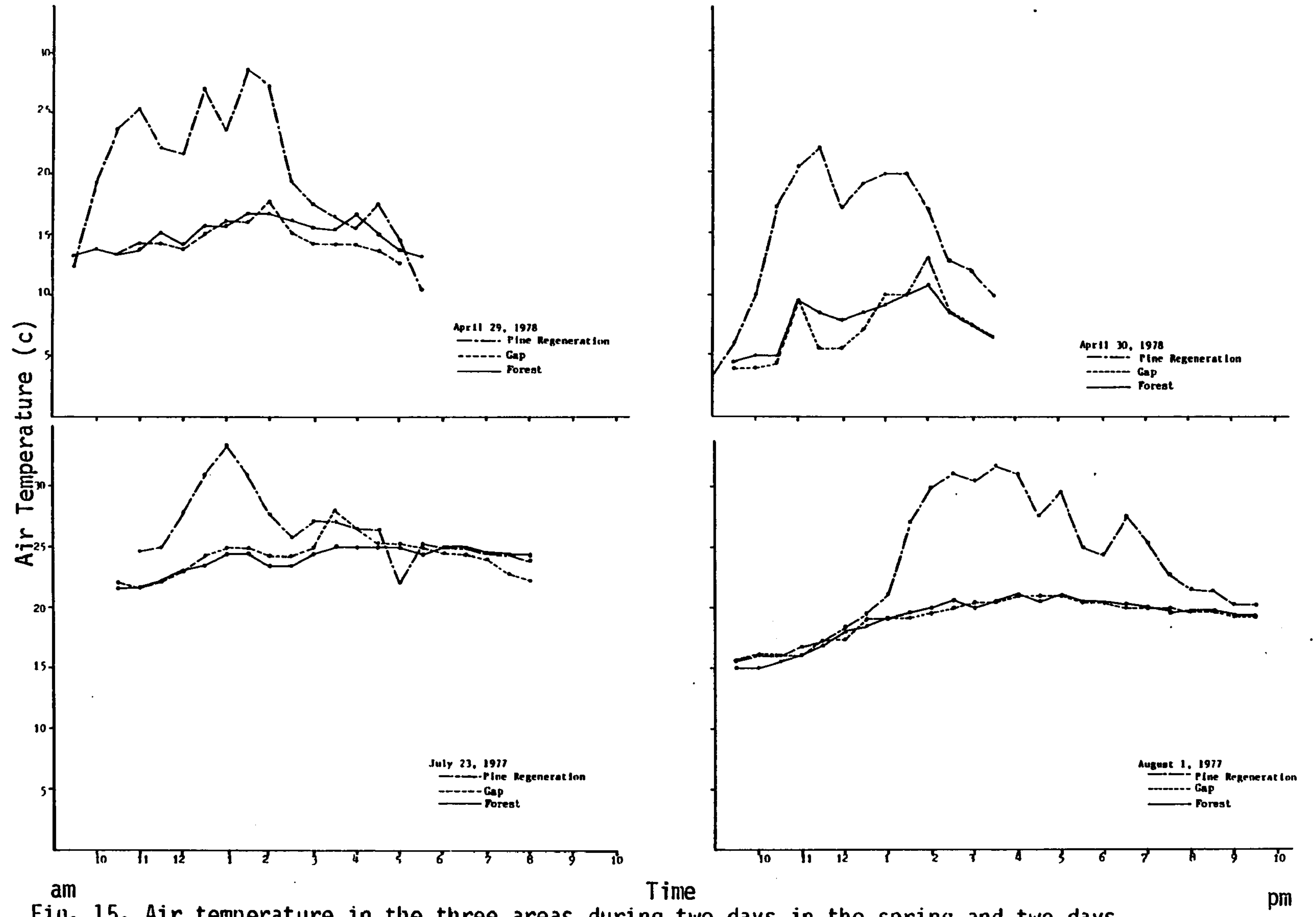

Fig. 15. Air temperature in the three areas during two days in the spring and two days in the summer. Legend: Pine Regeneration=open area where white pine are regenerating. Gap=area under the gap in the canopy, Forest=area under the forest canopy.

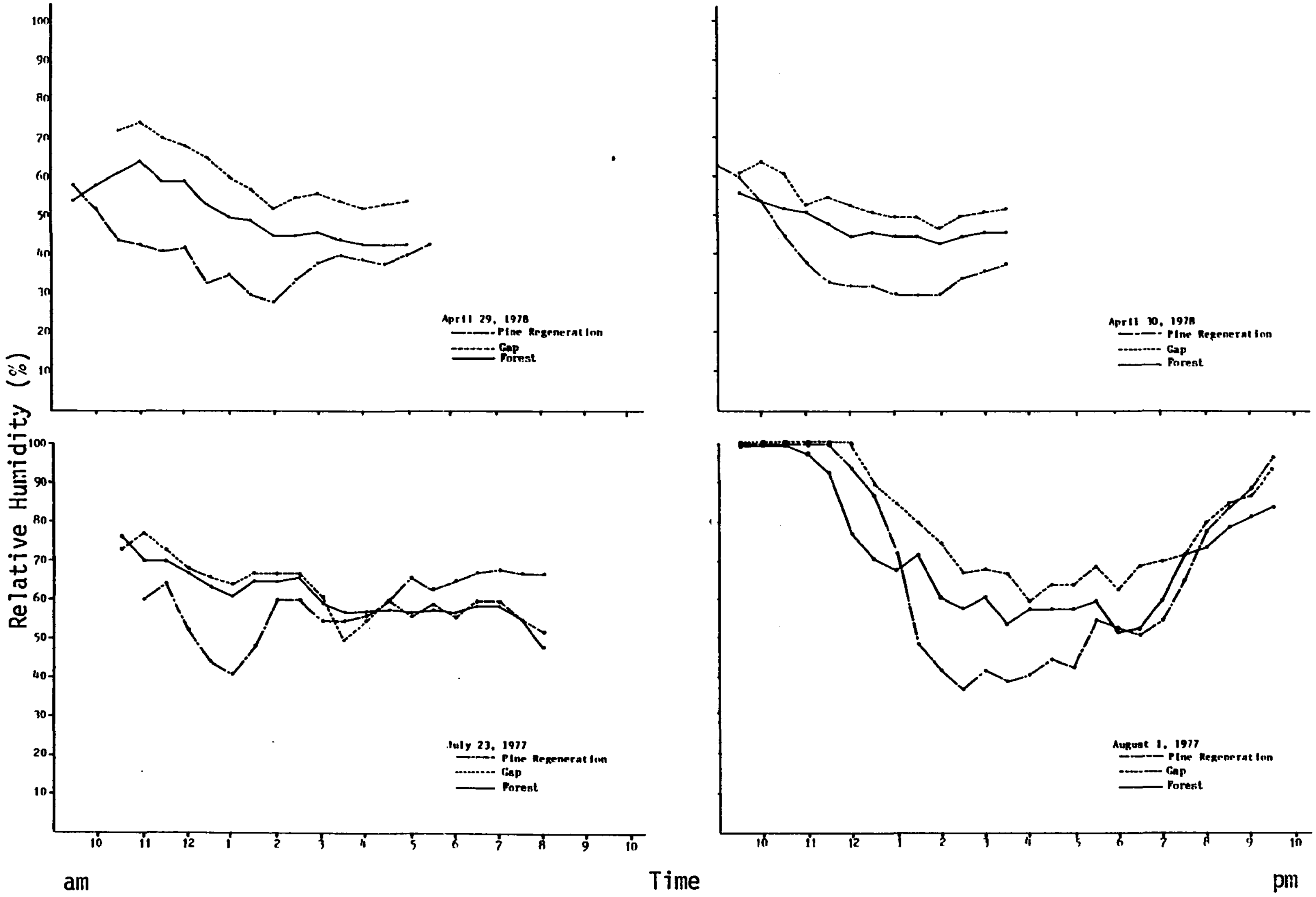

Fig. 16. Relative humidity in the three areas during two days in the spring and two days in the summer. Legend: Pine Regeneration=open area where white pine are regenerating, Gap=area under the gap in the canopy, Forest=area under the forest canopy.

Humidity was highest, probably due to the increased solar insolation which increased temperature and evapotranspiration, while the forest acted as a wind break.

The amount of solar insolation, by controlling temperature, humidity, and photosynthesis, and the species degree of shade tolerance are key factors in survival and succession of tree species (Burns 1920, Shirley 1943, 1945). Photosynthetic rates of intolerant species are higher than tolerant species at both high and low light intensity (Bohning and Burnside 1956, Grime 1965, Baker 1945, Shirley 1945). In general, however, light compensation points are higher for intolerant species because they have higher respiration rates (Baker 1945, Shirley 1945, Loach 1967). Eastern white pine is an intolerant species, as indicated by its compensation value of 5.8% of full light compared to sugar maple, 2.1% and eastern hemlock, 4.7% (Burns 1923). Smith (1940) found that at least 20% of full sunlight was required by white pine for survival in the field. The amount of light in the canopy gap of Hartwick Pines was approximately 12% of the average daily amount of light (488 g cal/cm^2) available in the Midwest during April and May (Reifsnyder and Lull 1965), not enough for the survival and perpetuation of white pine. Overall, the total amount of solar energy reaching the seedling layer on April 29 and 30, 1978, was 368.9 and 300.8 g cal/cm^2, respectively, in the white pine regeneration area, 64.2 and 57.8 g cal/cm^2 under the canopy gap, and 44.1 and 31.0 g cal/cm^2 under the forest canopy. It appeared that there was insufficient light energy under the forest canopy to support sustained growth of any seedlings. In the gaps, solar energy was adequate to insure growth and survival of the maples. In the larger open area there was enough solar input to maintain growth of white pine.

Deer browsing. White-tailed deer were having an important influence on the seedlings in the virgin stand by browsing the area during late fall and winter when tourist traffic was low. The greater percentage of sugar maples being browsed was probably related to their larger crown cover area (Figure 7), making them more visible and accessible. In addition, sugar and red maple are preferred by deer (Aldous 1939, Petrides 1941). White pine, on the other hand, was browsed least, reflecting the seedlings small size, low density and protection by a layer of snow during the winter. Seedlings within the gaps were browsed more than those under the canopy, possibly because deer were attracted by the larger stature and greater abundance of seedlings.

Unbrowsed seedlings had a significantly greater increase in height and crown cover area between 1977 and 1978 compared to browsed seedlings (Table 12). There was no significant difference in shoot growth between the two groups. Generally, the new leading shoot of the browsed seedlings grew more than the unbrowsed. However, because the browsed seedlings had to begin growth of a new lead shoot from an axillary bud, a height advantage was gained by the unbrowsed seedlings.

Survivorship of white pine in the unbrowsed plot was less than those that were in the browsed plot, probably because of increased competition from the unbrowsed maples (Table 11). Most of the seedlings under study were red and sugar maple and it appeared that their mortality was not affected by browsing. However, it is possible that long term seedling survival could be affected by the reduction in crown cover or photosynthetic area and, therefore, influence the successional status of the forest. In other studies, cattle grazing reduced the abundance of hemlock and beech, while almost eliminating red maple; and browsing by big game

Table 12. Student's t-test comparison of the effect of deer browsing over one year on the height, crown cover and shoot growth of *Acer saccharum* and *Acer rubrum* combined.

	Mean Increase in Height		Mean Increase in Crown Cover		Mean Shoot Growth	
	cm	n	cm^2	n	cm	n
Unbrowsed	5.7	86	186.0	77	3.44	174
Browsed	1.9	76	46.1	77	3.88	144
Significance	.005		.005		NS[a]	

[a] NS = Not significant.

animals on bitter brush in Idaho increased twig production and, at the same time, retarded succession (Lutz 1930, Peek et al. 1978). A long term study of this question would most likely show that the maples are being delayed from assuming dominance in the gaps and ultimately the forest by the reduced growth or possible reduced survivorship.

White pine regeneration. In the virgin jack pine forest near Hartwick Pines, white pine seedlings dominated the ground layer, suggesting that jack pine in this case is a seral stage preceding white pine. Jack pine dominated the open canopy with a crown cover area of approximately 2200 m^2/ha. In 1977 the jack pine, with an average age of 62 years and range of 39 to 85 years old, were senescing with only 65% of the 749 stems/ha living (Table 13). White pine and balsam fir were approximately the same age and size, and dominated the seedling stratum with densities of 1710 and 150/ha, respectively. There were also solitary individuals of black oak (*Quercus velutina*), black cherry (*Prunus serotina*) and red maple. Age distributions showed that there were no young jack pine, indicating its failure to reproduce. White pine started seeding-in about twenty years ago and was still coming in, but at a reduced rate (Figure 17).

Height and diameter distribution of the virgin white pine stand near Dublin, Michigan, shows that white pine has the ability to come in under its own canopy under certain conditions (Figure 18). White pine was the most dense canopy species, with 510 trees/ha, 60% of which were less than 10 cm in DBH and 10 m in height (Figure 18 and Table 14). Maples had the next greatest density, with 140 trees/ha whereas basal area was 4.85 m^2/ha, compared to 32.75 m^2/ha for white pine (Table 14). Maple and white oak individuals were scattered throughout the larger and smaller

Table 13. Mean (+2 S.D.) age, height, crown cover, and basal diameter of woody species found in the virgin *Pinus banksiana* Lamb. stand.

Species	Age		Height		Crown Cover		Basal Diameter	
	years	n	m	n	m^2	n	cm	n
Pinus banksiana	62±10	26	21±5	73	4.5±2.4	73	21.6±7.4	73
Pinus strobus	11±5	223	1.22±0.73	223	.56±1.17	223	--------	
Abies balsamea	11±6	20	1.36±1.39	20	.48±0.15	20	--------	

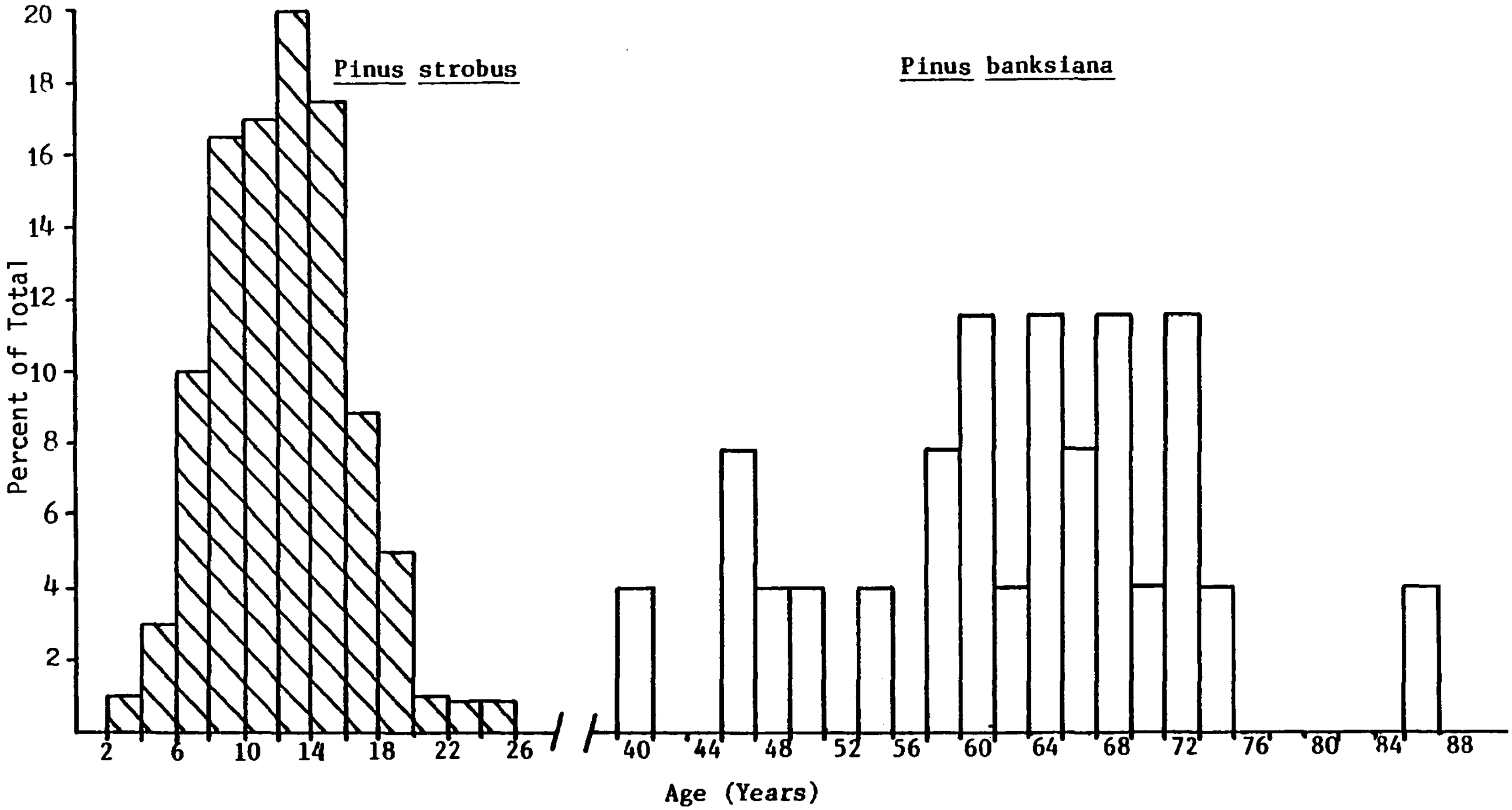

Fig. 17. Age distribution of *Pinus banksiana* and *Pinus strobus* in a virgin *Pinus banksiana* stand.

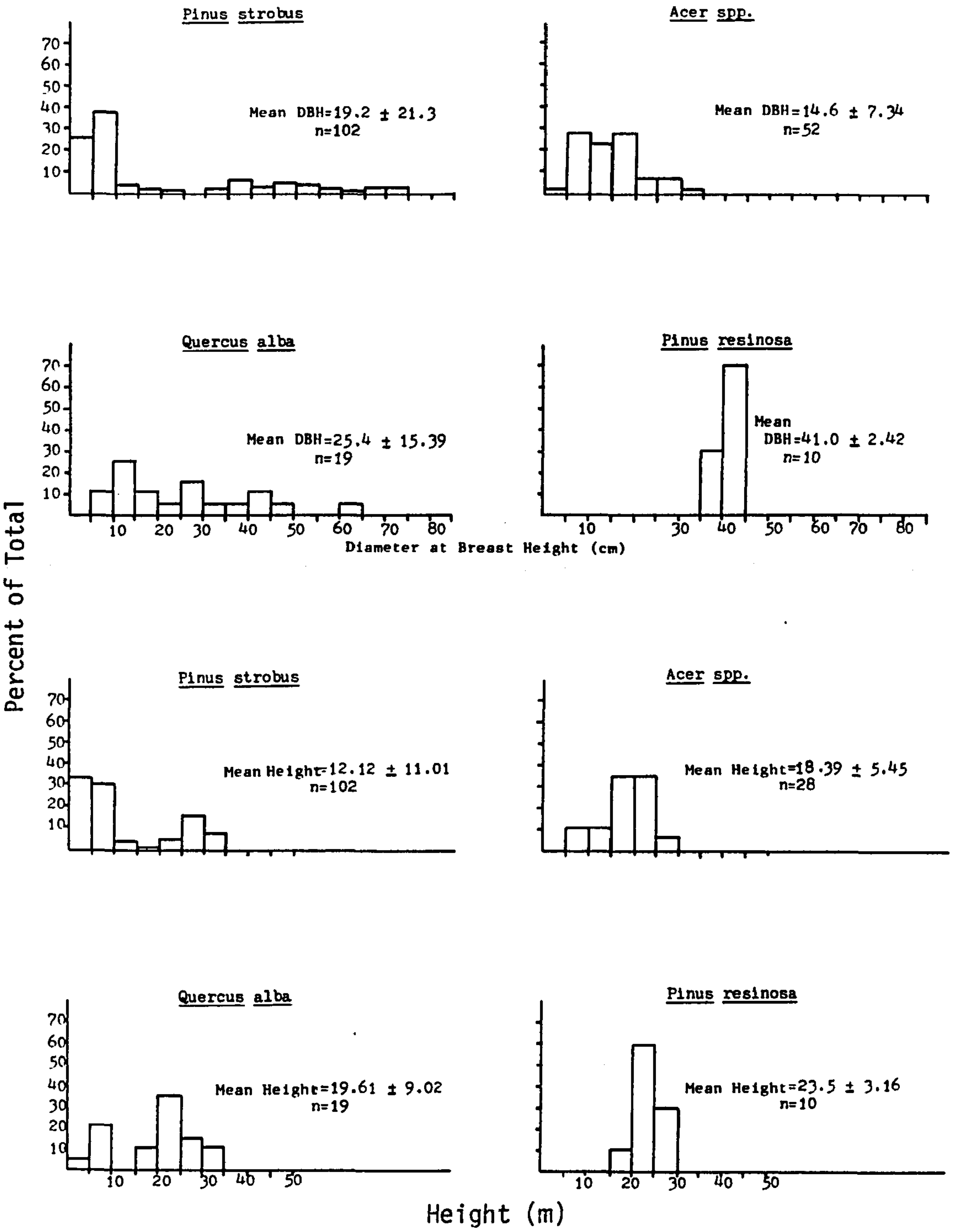

Fig. 13. Distribution of tree diameter and height by species in the virgin stand near Dublin, Michigan.

Table 14. Importance values[a] (I.V.) for tree species found in a 2 hectare virgin *Pinus strobus* L. stand in Manistee Co., Michigan.

I.V. Rank	Species	Denisty		Dominance		Frequency		I.V.	I.V. %
		Absolute	Relative	Absolute	Relative	Absolute	Relative		
1	*Pinus strobus*	510	60.0	32.75	64.1	1.0	25.6	149.7	49.9
2	*Acer* spp.	140	16.5	4.85	9.5	0.6	15.4	41.4	13.8
3	*Quercus alba*	95	11.2	6.40	12.5	0.8	20.5	44.2	14.7
4	*Pinus resinosa*	50	5.9	6.62	13.0	0.8	20.5	39.4	13.1
5	*Prunus serotina*	25	2.9	0.35	0.7	0.4	10.3	13.9	4.6
6	*Fraxinus sp.*	10	1.2	0.10	0.2	0.1	2.6	4.0	1.3
7	*Fagus grandifolia*	15	1.8	0.02	0.0	0.1	2.6	4.4	1.5
8	*Pyrus malus*	5	0.6	0.01	0.0	0.1	2.6	3.2	1.1
	Total	850	100.1	51.10	100.0	3.9	100.1	300.2	100.0

[a] Calculated following methods in Mueller-Dombois and Ellenburg (1974).

size classes, an indication that they are reproducing and surviving. Similar to Hartwick, there was no sign of red pine reproduction.

Although one of the larger white pine trees at the Manistee County site was only 97 years old, there is no indication of lumbering activity; and mounds indicate that trees have fallen in place. This supports the assertion that this area was relatively undisturbed by humans. Unlike Hartwick, this stand had an open canopy which produced white pine with large diameters between 70 and 75 cm, heights ranging to 30 and 35 m, and branches within 2 m of the ground (Figure 18). The largest maples were 30 to 35 cm in DBH, suggesting that they establish early in virgin white pine stands. These trees can then act as seed trees for future gaps. The surrounding area was dry sandy upland, dominated by relatively small second-growth oaks, which increased the openness of the small pine stand because of edge affect, and aided the regeneration of white pine under its own canopy. Observations of similar stands by some early researchers could have lead to the conclusion that white pine was a climax community type.

Kittredge and Chittenden (1929) also observed white and red pine reproduction in Michigan in old growth pine forest openings but they specified neither size nor cause of the openings. In a virgin red pine stand scattered with large white pine, Shirley (1932) found white pine regenerating in a 2929 m^2 opening, twenty-six times the size of the mean structural gap opening at Hartwick. White pine regeneration did not occur at Hartwick in openings as small as 89 m^2 or 135 m^2, as observed for loblolly and shortleaf pine (Pinus taeda and Pinus echinata) (Wahlenburg 1948, Jackson 1959).

Succession and Biomass Model

Hartwick exhibited succession as a result of related changes in vegetation, soils and microclimate (autogenic), and as induced by changes in the extrinsic environment (allogenic). Apparently white pine canopy development prevented some species from surviving, while gaps, caused by external factors, were insuring the survival of others. More studies are concluding that development of forest composition and structure is a result of large and small scale disturbances, and small gaps and dominant trees modifying the environment (Fox 1977, Oliver and Stephens 1977), as observed at Hartwick Pines.

Evidence from this study suggests that, given an appropriate seed source, one successional sequence for the Hartwick area starts with jack pine following a relatively large scale disturbance. Jack pine will possibly dominate the forest until they senesce at about 60-80 years of age (Figure 19). In the absence of any further relatively large scale disturbance, white pine and then hardwoods may dominate the forest. White pine may invade and hold dominance as a pure stand for approximately 170 years. A transition to a hardwood forest dominated by maples is likely to follow, as is presently occurring in Hartwick Pines. During this period white pine may remain a conspicuous part of the forest for as long as 200 years. The amount of time for this transition was determined, not by the present rate of death and canopy replacement at Hartwick (only 6% of the total sample area in the last 10 years), but was based on the reported maximum ages of white pine. This suggests an increase in the rate of replacement at Hartwick over the next century. After this, hemlocks and hardwoods would probably share dominance for 200 years with perhaps a gradual shift to maple-beech dominance. This forest would have the

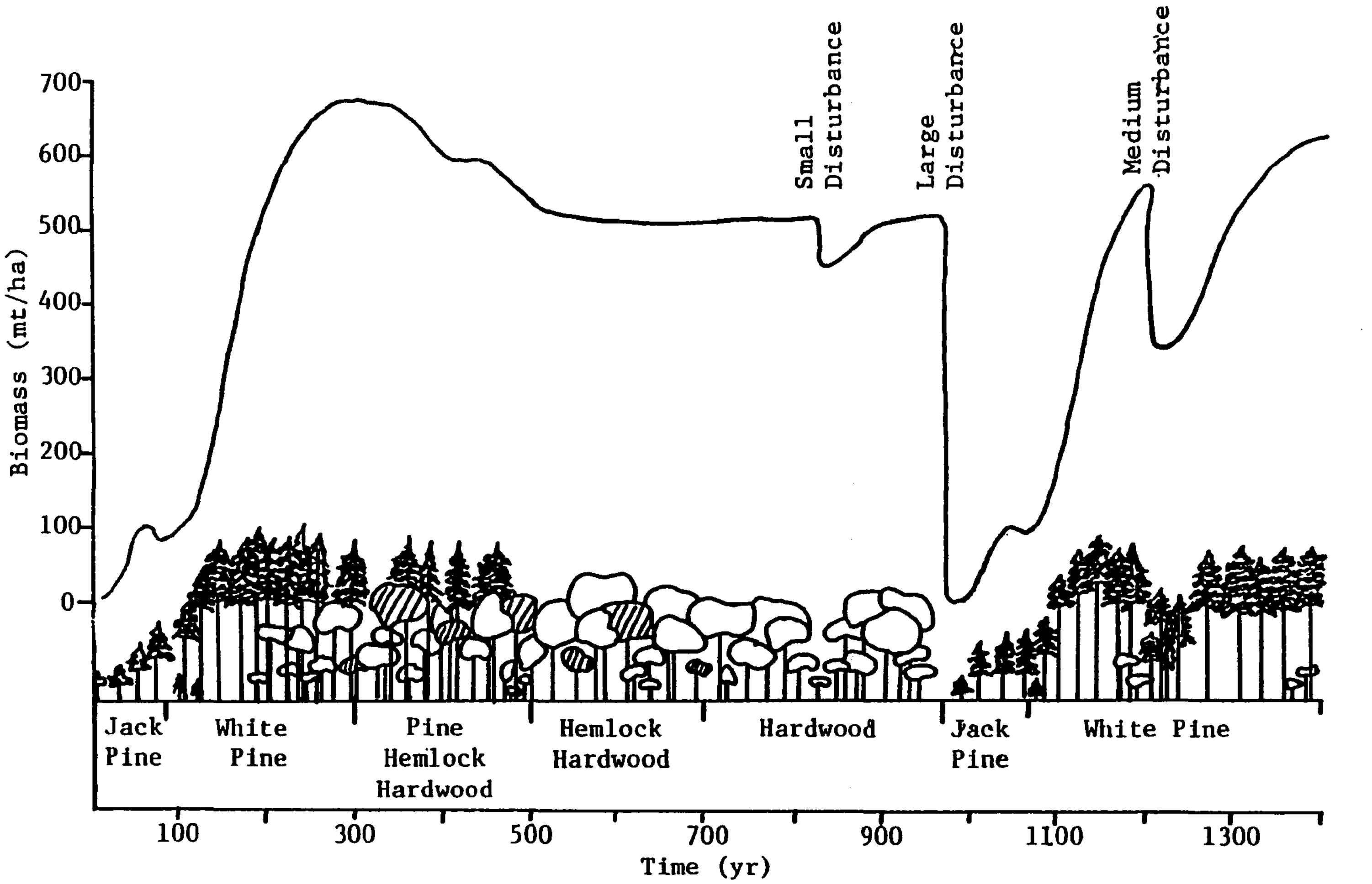

Fig. 19. Hypothetical seral stages in an area of central northern lower Michigan indicating changes in biomass and the influence of disturbance.

ability to reproduce and maintain itself as an old growth virgin forest, and in the case of Hartwick Pines, more appropriately be named Hartwick Hardwood State Park.

Recognizing the limitations of making comparisons between stands in different climatic regions, growing on different substrate and consisting perhaps of different genetic stock there is reason to believe that during this successional sequence biomass peaks and then actually decreases in the late stages. Biomass increases from the maximum jack pine biomass (85.4 mt/ha, Larsen 1982) to a peak when white pine dominates (681 mt/ha) and as the hardwoods assume dominance, biomass probably decreases (515 mt/ha, Murphy, P.G., and G. Kroh, Biomass and Net Primary Production of a Virgin Beech-Maple Forest in Michigan, in preparation) (Figure 19). This indicates that biomass may not always increase to a maximum at the climax stage as Odum (1969) had suggested.

The basal area of the beech-maple stand is 41% less than the white pine stand, which probably accounts for the decrease in biomass. The decreases may be a result of the way each type of stand is established and maintained.

Self-regenerating beech-maple forests naturally consist of small disturbance openings with young small trees that contribute little to the total living biomass. Taking into account these small disturbance openings, long term biomass equilibrium in tolerant beech-maple forests can still be established in relatively small areas. White pine establishes as a relatively even age stand that grows until the site is fully occupied by a near maximum sustainable biomass. During this phase litter production is balanced by new growth, creating a relatively short term biomass equilibrium. Tree deaths causing small canopy openings result in a decrease in biomass with beech-maple establishing in gaps. Long term biomass for white pine forests can be established if there is enough area to include the relatively large disturbance openings that are necessary for the regeneration of white pine. This situation results in white pines' long term biomass equilibrium being less than the short term equilibrium. As the size of the disturbance that is necessary to perpetuate the forest type increases, proportionately more area is needed to establish biomass equilibrium (Shugart and West 1981). Further study is required to determine the maximum biomass of an area large enough to support white pine as a regenerating dominant.

In a primitive setting, less influenced by humans, several different stable communities could exist adjacent to each other as a result of only differences in size, frequency and type of disturbance in an otherwise uniform environment (Horn 1976). Fire and wind are the two predominant natural disturbances, with fire being the most common large-scale disturbance that would allow pine to regenerate. Based on the hypothesized succession time scale, a very destructive fire with a frequency of 300-400 years could result in white pine continually regenerating itself, possibly preceded by jack pine or a light seeded hardwood depending on the available seed source (Figure 19). Forcier (1975) documented a microsuccessional pattern following a minor disturbance in a climax forest helping to insure continued co-occurrence of yellow birch, sugar maple and beech. On the other hand, Brewer and Merritt (1978) concluded that windthrow of single trees would only perpetuate beech in a beech-maple forest and that the diversity would have to be maintained through larger disturbances. Depending on the type of community, diversity can also be maintained by a certain frequency of disturbance. Smaller ground fires could also aid in perpetuating white pine by removing litter and hardwood seedling competition. If, in addition, a fire had opened a large enough area in the canopy and the remaining pine trees had a good seed year, white pine would regenerate. If this cycle were continually repeated, white pine could maintain itself as the dominant tree indefinitely. Possibly for these reasons, white pine was a major dominant or end point of succession in large areas prior to lumbering, even though it may now be viewed as a mid-successional species.

SUMMARY AND CONCLUSIONS

Eastern white pine at Hartwick Pines State Park, which averaged 177 years in age, was the canopy dominant with a basal area of 48.4 m^2/ha, 66.7% of the total. Its average diameter and total height were 58 cm and 36 m, respectively. White pine and hemlock diameter distributions indicate that the largest trees may be relics from a disturbance, and that these trees possibly acted as a seed source for most of the present individuals in the forest. At the present time the primary cause of death of white pine appears to be windfall. Heart rot that initiated from 134 year-old fire scars was a contributing factor to the death of some of the trees.

This stand had a total tree biomass of 681 mt/ha, above average for many of the worlds forest types. Total net primary production of the stand was low, 7.5 mt/ha/yr, but within the range of figures reported for temperate evergreen forests. Additional nondestructive studies of white pine biomass and production will be aided by the allometric equation relating white pine diameter and stem volume ($r^2 = 0.91$).

Diameter and height class distributions indicate that sugar maple, red maple and beech are gradually assuming dominance. Among seedlings, red maple, because of its large numbers, had the highest importance value. Individual sugar maple seedlings had the largest crowns, reflected by their greater shoot growth. These factors contributed to eventual dominance by maples. White pine seedlings were as numerous as sugar maple, but grew poorly. Beech seedlings were not present in the study plots and only a few were observed in the forest. Only maples survived past the seedling stage and after approximately 50 years filled in canopy gaps. Associated with the closing of canopy gaps was a decrease in seedling average age, height, basal diameter, crown cover, shoot growth and percentage of seedlings browsed by deer. Sugar maple was least affected by gap closure; however, these seedlings did not do as well under a maple canopy as compared to a pine canopy or gap.

Survivorship was greatest for seedlings in gaps, as compared to the forest, and during winter as compared to the growing season. Sugar maple in gaps had the largest annual survivorship, 90.2%, whereas red maple was lowest at 79.6%. Natality for maples was 1.3/m^2/yr in the gap and 1.5/m^2/yr under the canopy. White pine and hemlock combined natality was 11.25/m^2/yr during a year of high seed production, but with 100% mortality possibly due to mechanical damage from leaf litter and snow. A comparison was made of seedling dynamics in three situations: within a canopy gap, under the forest canopy, and in an open area of white pine regeneration. The white pine regeneration site had the lowest humidity and highest air temperature and solar insolation, the latter factor being one of the most influential factors in the survival of white pine. Under some circumstances where the canopy was sufficiently open, white pine were able to regenerate under both virgin jack and white pine stands.

Deer appear to have retarded the hypothesized successional change at Hartwick by having browsed a high percentage of seedlings. Even though no differences were found in yearly shoot growth length between browsed and unbrowsed maples, only maple seedlings in exclosures had a significant net increase in height because their initial height had not been reduced by browsing. There was also a significant increase in crown cover among the unbrowsed maple seedlings which, along with the increase in average height, could have resulted in increased competition leading to decreased survival of white pine.

A possible successional series for this general area, if uninterrupted by fire, is jack pine for the first 80 years, white pine for 170 years, white pine and northern hardwoods for 200 years, hemlock northern hardwoods for 200 years with maple dominated northern hardwoods as a long term stable community. Biomass increases to a maximum when white pine are dominating and decreases as the forest succeeds to hardwoods. Fire has the ability to prevent hardwoods from assuming dominance; for example, at Hartwick the age of the oldest deciduous species corresponds to the time since the last ground fire. Large fires every 300-400 years would cycle the successional series through jack pine or a light seeded hardwood, depending on the available seed source, to white pine. Fires of a medium severity every 200 years would eliminate the hardwoods and open large enough gaps for regeneration of white pine indefinitely.

FOR FURTHER STUDY

Certain issues regarding the ecology of white pine forests remain unclear. I propose that the following questions are among the most deserving of further attention.

1. What is the significance of the relatively low white pine leaf biomass? Does the change in proportion of leaf biomass to total tree biomass as the tree ages affect its survival?

2. Is total forest organic matter (including detritus) greater for successional stages following white pine? What are the long term biomass equilibrium values for the seral stages described in this study? What are the differences in seral biomass changes between communities with and without naturally occurring fire?

3. What effect would the results of a long term study of survivorship and deer browsing have on the conclusion made in this study?

4. What accounts for the presence of beech and hemlock given the small number of seedlings observed?

5. Is mechanical damage responsible for 100% mortality of newly germinated pine and hemlock?

6. Why does sugar maple appear to exhibit poor growth under a maple canopy? How will this answer influence our understanding of regeneration and gap phase replacement as related to succession?

LITERATURE CITED

LITERATURE CITED

1. Ahlgren, C. E. 1976. Regeneration of red pine and white pine following wildfire and logging in northeastern Minnesota. Journal of Forestry 74:135-140.

2. Aldous, S. E. 1939. Pine in the diet of white-tailed deer. Journal of Forestry 37:265-267.

3. Art, H. W., and P. L. Marks. 1971. A summary table of biomass and net annual primary production in forest ecosystems of the world. Pages 3-32 In International Union of Forest Research Organizations, Working Group on Forest Biomass Studies, Section 25, Growth and Yield. Forest biomass studies. University of Maine, Orono.

4. Baker, F. S. 1945. Effects of shade upon coniferous seedlings grown in nutrient solutions. Journal of Forestry 43:428-435.

5. Baldwin, H. I. 1951. A remnant of old white pine-hemlock forest in New Hampshire. Ecology 32:750-752.

6. Barrett, J. P., R. J. Alimi, and K. T. McCarthy. 1976. Growth of white pine in New Hampshire. Journal of Forestry 74:450-452.

7. Bergman, H. F. 1923. The Composition of climax plant formations in Minnesota. papers of the Michigan Academy of Science, Arts and Letters 3:51-60.

8. Bohning, R. H., and C. A. Burnside. 1956. The effect of light intensity on rate of apparent photosynthesis in leaves of sun and shade plants. American Journal of Botany 43:557-561.

9. Bormann, F. H., and M. F. Buell. 1964. Old-age stand of hemlock-northern hardwood forest in central Vermont. Bulletin of the Torrey Botanical Club 91:451-465.

10. Bormann, F. H. 1965. Changes in growth pattern of white pine trees undergoing suppression. Ecology 46:269.

11. Bormann, F. H., and B. F. Graham, Jr. 1959. The occurrence of natural root grafting in eastern white pine, *Pinus strobus* L., and its ecological implications. Ecology 40:677-691.

12. Boyce, S. G. ed. 1979. Biological and sociological basis for a rational use of forest resources for energy and organics, An International Workshop, sponsored by the Man and the Biosphere Committees of Canada, Mexico and the United States. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina. 193 pp.

13. Braun, E. L. 1950. Deciduous forests of Eastern North America. Hafner Press, Division of Macmillan Publ. Co., New York. 596 pp and map.

14. Bray, R. J. 1956. Gap phase replacement in a maple-basswood forest. Ecology 37:598-600.

15. Bray, J. R., and E. Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101-157.

16. Brewer, R., and P. G. Merritt. 1978. Wind throw and tree replacement in a climax beech-maple forest. Oikos 30:149-152.

17. Brown, H. P., A. J. Panshin, and C. C. Forsaith. 1949. Textbook of wood technology, volume I, structure, identification, defects, and uses of the commercial woods of the United States. McGraw-Hill book Company, Inc., New York. 652 pp.

18. Burns, G. P. 1920. Tolerance of forest trees and its relation to forest succession. Journal of Forestry 18:610-615.

19. Burns, G. P. 1923. Studies in tolerance of New England forest trees. IV. Minimum light requirement referred to a definite standard. Vermont Agricultural Experiment Station Bulletin 235. 32 pp.

20. Cline, A. C., and S. H. Spurr. 1942. The virgin upland forest of Central New England. A study of the old growth stands in the Pisgah Mountain Section of southwestern New Hampshire. Harvard Forest Bulletin No. 21. 58 pp.

21. Collins, R. A. 1958. Old growth red pine in Lower Michigan. Ph.D. Thesis, University of Michigan, Ann Arbor. 106 pp.

22. Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. Botanical Gazette 55:1-44, 115-140, 189-235.

23. Cooper, W. S. 1923. The recent ecological history of Glacier Bay, Alaska. Ecology 4:93-128, 223-246, 355-365.

24. Cope, J. A. 1932. Northern white pine in the Southern Appalachians. Journal of Forestry 30:821-828.

25. Cunningham, R. N., and H. G. White. 1941. Forest resources of the Upper Peninsula of Michigan. United States Department of Agriculture Miscellaneous Publication Number 429. 32 pp.

26. Denison, W. C., D. M. Tracy, F. M. Rhoades, and M. Sherwood. 1972. Direct nondestructive measurement of biomass and structure in living old-growth Douglas-fir. Pages 147-158 In J. F. Franklin, L. J. Dempster, and R. H. Warind, eds. Research On Coniferous Forest Ecosystems: First Year Progress In The Coniferous Forest Biome, US/IBP. Pacific Northwest Forest and Range Experiment Station, Forest Service, US Department of Agriculture, Portland.

27. Detwiler, S. B. 1933. General aspects of the white pine situation. Journal of Forestry 31:514-521.

28. Fernald, M. L. 1970. Gray's manual of botany. 8th ed. D. Van Nostrand Company, New York. 1632 pp.

29. Fernow, B. E. 1899. The white pine. USDA Division of Forestry Bulletin 22. 19 pp.

30. Forcier, L. K. 1975. Reproductive Strategies and the co-occurrence of climax tree species. Science 189:808-810.

31. Fox, J. F. 1977. Alternation and coexistence of tree species. The American Naturalist 3:69-89.

32. Frothingham, E. H. 1914. White pine under forest management. United States Department of Agriculture Bulletin Number 13. 70 pp.

33. Good, N. F., and R. E. Good. 1972. Population dynamics of tree seedlings and saplings in a mature eastern hardwood forest. Bulletin of the Torrey Botanical Club 99:172-178.

34. Grahan, S. A. 1941. Climax forests of the Upper Peninsula of Michigan. Ecology 22:355-362.

35. Grant, M. L. 1934. The climax forest community in Itasca County, Minnesota, and its bearing upon the successional status of the pine community. Ecology 15:243-257.

36. Grime, J. P. 1965. Shade tolerance in flowering plants. Nature 208:161-163.

37. Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52:107-145.

38. Harlow, W. M., and E. S. Harrar. 1968. Textbook of Dendrology. McGraw-Hill Book Co., New York. 512 pp.

39. Hawley, R. C. 1933. Does northern white pine form a climax type? Journal of Forestry 31L866-868.

40. Hett, J. M. 1971. A dynamic analysis of age in sugar maple seedlings. Ecology 52:1071-1074.

41. Hett, J. M., and O. L. Loucks. 1968. Application of life-table analyses to tree seedlings in Quetico Provincial Park, Ontario. The Forestry Chronicle 44:29-32.

42. Hett, J. M., and O. L. Loucks. 1971. Sugar maple (Acer saccharum Marsh.) seedling mortality. Journal of Ecology 59:507-520.

43. Horn, H. S. 1976. Succession. Pages 187-204 In R. M. May, ed. Theoretical Ecology: Principles and Applications. W. B. Saunders Co., Philadelphia.

44. Hough, A. F. 1936. A climax forest community on east Tionesta Creek in Northwest Pennsylvania. Ecology 17:9-28.

45. Hysch, B., and W. H. Lyford. 1956. White pine growth and soil relationship in southeastern New Hampshire. New Hampshire Agricultural Experiment Station Technical Bulletin 95. 29 pp.

46. Jackson, L. W. R. 1959. Relation of pine forest overstory opening diameter to growth of pine reproduction. Ecology 40:478-480.

47. Johnstone, W. D. 1971. Total standing crop and tree component distributions in three stands of 100-year-old lodgepole pine. Pages 79-89 In International Union of Forest Research Organizations Working Group on Forest Biomass Studies, Section 25, Growth and Yield. Forest Biomass Studies. University of Maine Press, Orono.

48. Kimura, M. 1960. Primary production of the warm temperate laurel forest in the southern part of Osumi Peninsula, Kyushu, Japan. Miscellaneous Reports of the Resarch Institute for Natural Resources 52:36-47 (cited by Newbould 1967).

49. Kira, T., and T. Shidei. 1967. Primary production and turnover rate of organic matter in different forest ecosystems of the Western Pacific. Japanese Journal of Ecology 17:70-87.

50. Kittredge, J., and A. K. Chittenden. 1929. Oak forest of northern Michigan. Michigan State College Agriculture Experiment Station Research Bulletin 190. 47 pp.

51. Kittredge, J. 1934. Evidence of the rate of forest succession on Star Island Minnesota. Ecology 15:24-35.

52. Larsen, W. C. 1982. Structure, biomass and net primary productivity for an even age sequence of jack pine ecosystems. Ph.D. Thesis. Michigan State University, East Lansing.

53. Leaf, A. L. 1971. Root distribution of a plantation grown pine in an outwash soil. Ecology 52:153-158.

54. Lieth, H. 1974. Primary productivity of successional stages. Pages 187-193 In R. Tuxen, ed. Handbook of Vegetation Science. Part VIII Vegetation Dynamics. Dr. W. Junk, B.V. The Hague. 364 pp.

55. Lieth, H. 1975. Primary production of the major vegetation units of the world. Pages 201-213 In H. Lieth and R. H. Whittaker, eds. Primary Productivity of the Biosphere. Springer-Verlag New York Inc., New York.

56. Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399-418.

57. Loach, K. 1967. Shade tolerance in tree seedlings. I. Leaf photosyntheses and respiration in plants raised under artificial shade. New Phytology 66:607-621.

58. Lutz, H. J. 1930. Effect of cattle grazing on vegetation of a virgin forest in Northwestern Pennsylvania. Journal of Agricultural Research 41:561-570.

59. Lutz, H. J., and A. L. McComb. 1935. Origin of white pine in virgin forest stands of Northwestern Pennsylvania as indicated by stem and basal branch features. Ecology 16:252-256.

60. Macfadyen, A. 1948. The meanining of productivity in biological systems. Journal of Animal Ecology 17:75-80.

61. Maissurow, D. K. 1935. Fire as a necessary factor in the perpetuation of white pine. Journal of Forestry 33:373-378.

62. Maissurow, D. K. 1941. The role of fire in the perpetuation of virgin forests of Northern Wisconsin. Journal of Forestry 39:201-207.

63. Martin, R. E., and J. B. Crist. 1968. Selected physical-mechanical properties of eastern tree barks. Forest Products Journal 18(11):54-60.

64. Maybee, R. H. 1960. Michigan's white pine era. 1840-1900. John M. Munson Michigan History Fund Publication Pamphlet number 1. Michigan Historical Commission. 55 pp.

65. Meyer, W. H. 1952. Structure, growth and drain in balanced uneven-aged forests. Journal of Forestry 50:85-92.

66. Morey, H. F. 1936. Age-size relationships of Hearts Content, a Virgin forest in Northwestern Pennsylvania. Ecology 17:251-257.

67. Mueller-Dombois, D., and H. Ellenburg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.

68. Mulcahy, D. L. 1975. Differential mortality among cohorts in a population of Acer saccharum (Aceraceae) seedlings. American Journal of Botany 62:422-426.

69. Newbould, P. J. 1967. Methods for estimating the primary production of forests, IBP Handbook No. 2. Blackwell Scientific Publications, Oxford and Edinburgh. 62 pp.

70. Nye, P. H. 1961. Organic matter and nutrient cycles under moist tropical forests. Plant and Soil 8:333-346.

71. Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-270.

72. Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders Co., Philadelphia. 574 pp.

73. Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in Central New England. Ecology 58:562-572.

74. Parde, J. 1968. Bases and methods of assessing the productivity of timber stands not involving tree felling [in French, English summary]. pages 203-209 In F. E. Eckardt, ed. Functioning of Terrestrial Ecosystems at the Primary Production Level. United Nations Educational, Scienfitic and Cultural Organization, Paris.

75. Peek, J. M., F. D. Johnson, and N. N. Pence. 1978. Successional trends in a Ponderosa Pine/Bitterbrush community related to grazing by livestock, wildlife, and to fire. Journal of Range Management 31:49-53.

76. Petrides, G. A. 1941. Observations on the relative importance of winter deer browse species in Central New York. Journal of Wildlife Management 5:416-422.

77. Reifsnyder, W. E., and H. W. Lull. 1965. Radiant energy in relation to forests. Technical Bulletin No. 1344. U.S. Department of Agriculture, Forest Service. 111 pp.

78. Rodin, L. E., and N. I. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation [translated from Russian by Scripta Technica Ltd., English translation edited by G. E. Fogg]. Oliver & Boyd, Edinburgh, London. 288 pp.

79. Rodin, L. E., and N. I. Bazilevich. 1968. World distribution of plant biomass. Pages 45-52 In F. E. Echardt ed. Functioning of Terrestrial Ecosystems at the Primary Production Level. United Nations Educational, Scientific and Cultural Organization, Paris.

80. Shimwell, D. W. 1971. Description and classification of vegetation. Sidgwick & Jackson, London. 322 pp.

81. Shirley, H. L. 1932. Light intensity in relation to plant growth in a virgin Norway Pine forest. Journal of Agricultural Research 44:227-244.

82. Shirley, H. L. 1943. Is tolerance the capacity to endure shade? Journal of Forestry 41:339-345.

83. Shirley, H. L. 1945. Reproduction of upland conifers in the lake states as affected by root competition and light. American Midland Naturalist 33:537-612.

84. Shugart, H. H., and D. C. West. 1981. Long-term dynamics of forest ecosystems. American Scientist 69:647-652.

85. Skeen, J. N. 1976. Regeneration and survival of woody species in a naturally-created forest opening. Bulletin of the Torrey Botanical Club 103:259-265.

86. Smith, L. F. 1940. Factors controlling the early development and survival of eastern white pine (Pinus strobus L.) in Central New England. Ecological Monographs 10:373-420.

87. Spurr, S. H., and B. V. Barnes. 1980. Forest ecology 3rd ed. John Wiley & Sons, New York. 687 pp.

88. Stallord, H. 1929. Secondary succession in the climax formations of northern Minnesota. Ecology 10:476.

89. Stearns, F. W. 1950. The composition of a remnant of white pine forest in the lake states. Ecology 31:290.

90. Stokes, M. A., and T. L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago. 73 pp.

91. Swank, W. T., and H. T. Schreuder. 1973. Temporal changes in biomass, surface area, and net production for a Pinus strobus L. forest. Pages 171-182 In International Union of Forest Research Organizations, Working Party on the Mensuration of the Forest Biomass, 54.01 Mensuration, Growth and Yield, H. E. Young, chairman. IUFRO biomass studies. University of Maine, Orono.

92. Veatch, J. O., L. R. Schoenmann, Z. C. Foster, and F. R. Lesh. 1927. Soil survey of Crawford County, Michigan. United States Department of Agriculture, Bureau of Chemistry and Soils. Series 1927. Number 29. 39 pp.

93. Wackerman, A. E. 1924. Growth of the "Grayling Pine". Journal of Forestry 22:796-797.

94. Wahlenberg, W. G. 1948. Effect of forest shade and openings on Loblolly Pine seedlings. Journal of Forestry 46:832-834.

95. Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204:1380-1385.

96. Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

97. Weaver, J. E., and F. E. Clements. 1938. Plant ecology. 2nd ed. McGraw-Hill, New York. 610 pp.

98. Westlake, D. F. 1963. Comparisons of plant productivity. Biological Reviews of the Cambridge Philosophical Society 38:385-425.

99. Wheeler,C. F. 1898. A sketch of the original distribution of white pine in the lower peninsula of Michigan. Michigan Agricultural Experiment Station Bulletin 162:5-6.

100. Whitford, H. N. 1901. The genetic development of the forests of northern Michigan: A study in physiographic ecology. Botanical Gazette 31:289-321.

101. Whittaker, R. H. 1953. A comparison of climax theory: the climax as a population and pattern. Ecological Monographs 23:41-78.

102. Whittaker, R. H. 1965. Branch dimensions and estimation of branch production. Ecology 46:365-370.

103. Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103-121.

104. Whittaker, R. H. 1974. Climax concepts and recognition. Pages 139-154 In R. Tuxen, Ed. handbook of Vegetation Science: Part VIII Vegetation Dynamics. Dr. W. Junk v.b. Publ., The Hague.

105. Whittaker, R. H. 1975. Communities and ecosystems. 2nd ed. Macmillan Publ. Co., Inc., New York. 385 pp.

106. Whittaker, R. H., and P. L. Marks. 1975. Methods of assessing terrestrial productivity. Pages 55-118 In H. Leith and R. H. Whittaker, eds. Primary Productivity of the Biosphere. Springer-Verlag New York Inc., New York.

107. Woodwell, G. M., and R. H. Whittaker. 1968. Primary production in terrestrial ecosystems. American Zoologist 8:19-30.

108. Yoda, K. 1968. A preliminary survey of forest vegetation of eastern Nepal. II. Plant biomass in the sample plots chosen from different vegetation zones. J. Coll. Arts & Sci. Chiba (Nat. Sci. Ser.) 5:277-302. (cited by Art and Marks 1971).

109. Young, H. E., and P. M. Carpenter. 1967. Weight nutrient element and productivity studies of seedlings and saplings of 8 tree species in natural ecosystems. Maine Agricultural Experiment Station Technical Bulletin 28. 39 pp.