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dissertation entitled

STRUCTURE, BIOMASS AND NET PRIMARY PRODUCTIVITY

FOR AN AGE-SEQUENCE OF JACK PINE ECOSYSTEMS

presented by

William C. Larsen

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Botany and Plant Pathology

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Major professor

Date May 24, 1982

STRUCTURE, BIOMASS AND NET PRIMARY PRODUCTIVITY FOR AN AGE-SEQUENCE OF JACK PINE ECOSYSTEMS

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Botany and Plant Pathology

1982

ABSTRACT

STRUCTURE, BIOMASS AND NET PRIMARY PRODUCTIVITY
FOR AN AGE-SEQUENCE OF JACK PINE ECOSYSTEMS

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Three jack pine (Pinus banksiana) stands located in north-central lower Michigan were studied. The stands were of natural origin, occurred on the same soil type, and represented an age series of 37, 52 and 75 years. The three stands had site index values of less than 15 m (50 yrs) and occurred on poor quality sites. Tree density was greatest in the youngest stand (1611 stems/ha) and lowest in the oldest stand (448 stems/ha). Stand basal areas were 20.2, 22.0 and 16.2 m^2/ha for the youngest, intermediate and oldest stands, respectively. The lower density and basal area for the oldest stand is a result of high jack pine mortality. Diameter, height and age class profiles illustrated the lack of jack pine recruitment into the stands, and suggest that the jack pine overstories will eventually be succeeded by more tolerant species. Radial growth data showed that jack pine individuals in the smallest size classes were suppressed and at a greater risk of dying than larger and more dominant individuals.

Overstory biomass and net primary production were estimated using published regression equations for jack pine. Total aboveground live tree biomass estimates were 65.7, 75.8 and 71.0 mt/ha for the youngest, intermediate and oldest stands, respectively. Corresponding stem wood

biomass represented 67.4%, 65.4% and 78.3% of total aboveground jack pine biomass. Mean annual production of stem wood, estimated by non-harvest techniques, was 1.50, 1.45 and 0.95 mt/ha/yr for the youngest, intermediate and oldest stands, respectively.

Percent distribution of aboveground biomass and net primary production by stratum of vegetation was determined in the oldest stand for 1979. The distribution of aboveground biomass was as follows; jack pine - 94.7%, white pine saplings - 1.8%, blueberry shrubs - 1.3%, and ground cover species - 2.2%. Aboveground production in the stand was apportioned among the strata as follows; jack pine - 45.8%, white pine - 12.1%, blueberry - 12.5% and ground cover species - 29.6%. Bracken fern alone represented 18.2% of the total aboveground stand production for 1979.

Developmental trends in biomass and annual production for jack pine forests are examined and compared to other more advanced successional forest types.

ACKNOWLEDGMENTS

My sincere thanks are due to the members of my graduate committee, Professors Stephen Stephenson, Donald Dickmann and Jay Harman, for the time and effort expended in their thoughtful and constructive criticisms of the original draft.

A special thanks is given to chairman of the committee, Peter G. Murphy, for his personal and intellectual contributions to the study. His practical solutions to difficult problems were extremely valuable throughout this study. I am grateful for his constant willingness to advise me regarding all aspects of my doctoral training.

I also wish to thank Patti Perkins for typing the final draft of this dissertation.

This dissertation is dedicated to my wife, Deborah A. Allen, who supported me in love and provided the encouragement and understanding necessary for the completion of this study.

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INTRODUCTION

Biomass and productivity studies are fundamental to understanding the dynamics of ecological systems. The energy fixed by photosynthesis is used in part, as maintenance energy, while the remainder represents new plant biomass. Estimates of plant biomass and its annual accumulation are essential for determining the distribution and cycling of materials and flow of energy within ecosystems. Present and future demands placed on natural resources require continued and expanded research on ecosystem structure and functioning. Basic research on plant productivity is also a necessary prerequisite to understanding the problems associated with environmental deterioration.

Forest Biomass and Productivity

The increasing demand for forest products and the recent world energy crisis have acted as important catalysts to viewing forest biomass as a renewable source of raw materials and energy. Forest biomass and productivity data are essential for evaluating differing forest management systems and the impact of complete-tree utilization, tree nutrition and forest fire control programs (Hitchcock and McDonnell 1979). Biomass data are also useful for comparing differing forest stands and studying the biological and physical factors which influence productivity, nutrient cycling and energy flow within forest ecosystems (Stanek and State 1978). Additional biomass and productivity data will be needed to adequately design and analyze programs which view forest ecosystems as important and renewable energy sources (Grantham and Ellis 1974, Brown 1976, Adams and Boyle 1979, Boyce 1979).

The extensive logging operations within northern lower Michigan during the latter portion of the 19th century resulted in the removal of mature high-quality forest stands. Frequent fires which followed lumbering activities favored the spread of jack pine (*Pinus banksiana* Lamb.) onto the barren drier sites (Roth 1902). Zimmerman (1956) has reviewed the studies which describe the increase in jack pine acreage after logging and fires within the Great Lakes Region. Chase *et al.* (1970) estimated that the jack pine forest type represents one-half of the total pine cover type within the state of Michigan. Jack pine accounts for 15% of the state's annual pulpwood harvest (Blyth 1975). The significance of jack pine to the forest economy of Michigan is further enhanced by its ability to produce productive stands on the extensive dry outwash plains where red and white pine no longer exist (Sterrett 1920, Beaufait 1960a). Recent studies by Zavitkovski (1979) and Zavitkovski and Dawson (1978) have shown that production within jack pine plantations can be increased considerably by using intensive culture technology.

During the past two decades numerous studies have estimated the biomass, productivity and nutrient accumulation and cycling within a variety of forest ecosystems. Results from these studies have been summarized by Ovington (1962), Rodin and Bazilevich (1967), Art and Marks (1971), Duvigneud (1971), Whittaker and Marks (1975), and Pardé (1980).

Forest biomass and production is typically estimated from regression equations which relate the biomass and production of individual trees or parts of trees to an easily measured parameter such as tree height, diameter at breast height or a combination of parameters. The established regression equations are then applied to the remaining trees in the stand or sample plot (Kira and Shidei 1967, Newbould 1967, Whittaker and Marks 1975). The papers by Stanek and State (1978) and Hitchcock and McDonnell (1979) provide listings of regression equations for calculating biomass and production for several tree species. Where destructive tree sampling is not possible or feasible, Newbould (1967) and Whittaker and Marks (1975) recommend the use of previously established regression equations.

Within Michigan little information is readily available concerning the biomass and productivity of the state's forest resources. Parker and Schneider (1975) have estimated the aboveground biomass and net primary productivity of an alder swamp dominated by Alnus rugosa and Fraxinus nigra. Similar estimates for three largetooth aspen (Populus grandidentata) stands occurring on soils of differing quality are available by Koerper and Richardson (1980). At Michigan State University investigations are presently being completed which have estimated the biomass and annual production of several forest types. One of the major goals of this study is to estimate the biomass and net primary productivity of jack pine stands within the north-central portion of Michigan's southern peninsula.

Aboveground biomass of jack pine has been estimated for stands in Minnesota (Crow 1970, Schlagel 1975, Alban *et al*. 1978), Ontario (Hegyi 1972), New Brunswick (MacLean and Wein 1976) and Quebec (Doucet 1974, Doucet *et al*. 1976). Green and Grigal (1978) using original data from these studies have developed geographically generalized biomass regression equations for jack pine. These equations were used in this study to estimate the aboveground biomass of selected jack pine stands. Net primary productivity was estimated using the regression equations developed by Doucet (1974) and Doucet *et al*. (1976). In addition, the regression estimates of biomass and productivity for selected stand components were compared to estimates derived from tree ring analysis, stem volume and litter fall data.

Research Objectives

The overall goal of this research was to characterize the general ecology of selected jack pine dominated plant communities in northern lower Michigan. The specific research objectives were as follows:

1. Describe the structure and composition of selected jack pine forests in Michigan.

2. Estimate and contrast rates of jack pine growth and stem wood volume increment for different aged stands.

3. Estimate and contrast biomass and net primary productivity of the jack pine overstory for an age-sequence of forest stands.

4. Compare regression and alternate non-destructive methods of estimating forest biomass and net primary productivity.

5. Compare biomass and productivity of jack pine forests to other forest types in the Great Lakes region.

6. Estimate the aboveground biomass and net primary productivity of saplings and ground cover vegetation in a 75-year old stand.

7. Describe developmental trends in biomass accumulation and production for jack pine forests occurring on oligotrophic sites in northern lower Michigan.

DESCRIPTION OF SPECIES

The following information is primarily taken from publications by Sterrett (1920), Rudolf (1958), U.S. Forest Service (1965), Cayford (1970), Schoenike (1976), and Benzie (1978). Review and bibliographic studies on jack pine are available by Cayford (1957), Cayford *et al.* (1967) and Shoup and Nairn (1970).

Species Description

Jack pine (*Pinus banksiana* Lamb.) is a small, short-lived species with individuals seldom reaching an age of over 100 years. For its first 20-25 years, jack pine is one of the fastest growing conifers within its natural range. In dense stands jack pine is tall, has a slender trunk and a short crown.

Needles of jack pine are 2.0 - 4.0 cm long in fascicles of two, dark yellow-green and persist of 2-3 years. Bark on young trees is reddish brown to dark grey and slightly scaly, on older branches and stems it is grey to black with loose irregular scales. Cones are 4.0 to 5.0 cm long, oblong-conic, often strongly incurved and typically serotinous. Jack pine is a prolific seed producer and can produce female cones by age two. Because of the production of serotinous cones a large accumulation of seed may be stored within a mature stand. Non-serotinous jack pine populations have been described by several investigators (Rudolf 1959 *et al.*, Arend *et al.* 1961, Teich 1970).

Investigations on the root system of jack pine indicate that it is strongly influenced by soil conditions. Studies by Cheyney (1932), Bannan (1940) and Adams and Chapman (1941) found that on sandy soils the majority of roots are within the top 30 cm of soil with some vertical roots directly beneath the stump. Similar studies by Hansen (1937), Cheyney (1932), Stoeckler and Linstrom (1942) and Day (1945) reported that jack pine develops a long tap root on sandy soils.

Species Distribution

Range maps for jack pine are included in the publications by Rudolf (1958), Critchfield and Little (1966) and Schoenike (1976). The distribution of jack pine extends an east-west distance of approximately 4,200 kilometers, with a maximum north-south extension of 1,600 kilometers. Within its range, jack pine is abundant, but not continuously distributed. In the United States, jack pine is commercially valuable only in the Great Lake states. In Canada the greatest concentration of jack pine occurs in the western portion of Ontario where it also reaches its greatest size. The natural ranges of jack pine and lodgepole pine (*Pinus contorta*) overlap in northwest Alberta and natural hybridization occurs (Schoenike 1976). Yeatman (1967), Canavera (1969) and Schoenike (1976) have reviewed the available information which describes the geographic origin, pleistocene distribution and subsequent migration of jack pine into its present range.

General Ecology

Throughout its range, jack pine occurs within a wide diversity of habitat and forest types. Characteristically, jack pine is found growing on plains of dry, coarse to medium sands that have developed on glacial outwash, morainic, aeolian or beach deposits. Studies by Bedell *et al*. (1953), Jameson (1965) and Bella (1968) reported that the greatest production of jack pine occurs on moist loam to sandy-loam and clay-loam soils.

Silviculturally, jack pine is described as an intolerant pioneer species that occurs on burned-over areas (Benzie 1978). The significance of fire-dependent adaptations to the perpetuation of jack pine forests has been extensively documented (Maissurow 1941, Ahlgren 1959, 1974, Ahlgren and Ahlgren 1960, Beaufait 1960a, b, Cayford *et al*. 1967, Cayford 1970). Heinselman (1973) provides a detailed account on the importance of fire to the ecology of the Great Lakes conifer forests. From his studies of the Boundary Waters Canoe Area in northern Minnesota, Heinselman (1973) concluded that "the frequency of fire largely determined the species composition, age-structure and mosaic of successional forest types present in the area". He suggests that prior to implementation of fire suppression policies jack pine forests burned at intervals of 50-100 years.

If fire disturbance is reduced or eliminated jack pine will be naturally replaced by more tolerant species. Kilburn (1960), studying the xeric forests of Cheboygan County, Michigan, concluded that "the jack pine type will probably be reduced in area as oak (*Quercus ellipsoidalis*) replaces pine under fire protection". Heinselman (1973) reported that mature jack pine dominated communities in northern Minnesota exhibited succession to either fir-spruce-birch (*Abies balsamea-Picea glauca-Betula papyrifera*) or black spruce (*P. mariana*) - feather moss community types. However, he emphasized that "jack pine may persist as a scattered overstory element for at least 210-250 years without fire". Braun (1950) suggests that on loamy-sands and sandy-loams jack pine may be succeeded by red pine (*Pinus resinosa*) or white pine (*P. strobus*) or a mixture of these species. Coffman *et al*. (1980) indicate, in their habitat classification guide for the western upper peninsula of Michigan and northern Wisconsin, that on sandy soils, jack pine will be replaced by a great variety of successional forest types and be found associated with several tree species. On the most xeric sites, Benzie (1978) suggests that jack pine may represent an edaphic climax and remain indefinitely.

DESCRIPTION OF STUDY AREA

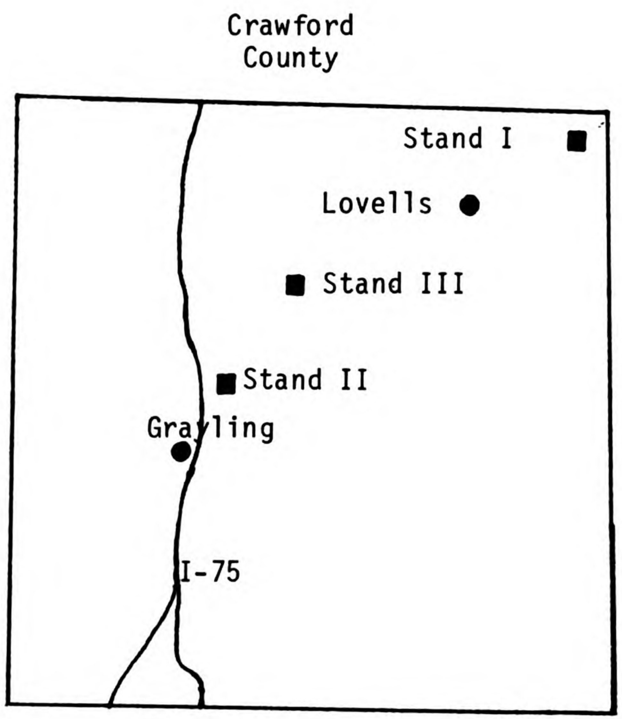
Location

In the southern peninsula of Michigan natural jack pine stands are primarily confined to the well and moderately well drained sandy soils (Shetron 1969). Figure 1 shows the distribution of major jack pine forested areas throughout the peninsula. Zimmerman (1956) provides a thorough description of jack pine dominated areas by county for Michigan's southern peninsula. Survey and sample stands for this study were located in the north-central portion of the peninsula.

Climate

North-central lower Michigan is described as having a humid, moderately continental climate with long, snowy winters and short mild summers (Niedringhaus 1966). The climate within the region is strongly influenced by the proximity of the Great Lakes. The lacustrine control of the climate varies slightly, with inland stations exhibiting greater daily, seasonal and annual temperature ranges (Sommers 1977). Climatological data from selected inland stations are provided in Table 1. The area has a mean annual temperature of 6.1°C (43°F). Mean annual precipitation varies from 67.7 cm (26.6 in) at Mio to a high 83.7 cm (33 in) at Gaylord. Within this region approximately 60% of the total precipitation falls during the period May-October. Evaporation from a class "A" pan at Lake City average 71.7 cm (28 in). Because potential moisture evaporation during the growing season exceeds the average

Figure 1. Distribution of major jack pine dominated forests in the southern peninsula of Michigan. Shaded areas include both pure and mixed stands of jack pine and associated species. No distinction is made between age and size of jack pine trees. (redrawn from Zimmerman 1956).


Crawford
County
Stand I
Lovells
Stand III
Stand II
Grayling
I-75


EMMET
CHEBOYGAN
PRESQUE ISLE
CHARLEVOIX
ANTRIM
OTSEGO
MONTMORENCY
ALPENA
LEELANAU
BENZIE
GRAND TRAVERSE
KALKASKA
CRAWFORD
OSCODA
ALCONA
MANISTEE
WEXFORD
MISSAUKEE
ROSCOMMON
OGEMAW
IOSCO
MASON
LAKE
OSCEOLA
CLARE
GLADWIN
ARENAC
HURON
BAY
OCEANA
NEWAYGO
MECOSTA
ISABELLA
MIDLAND
TUSCOLA
SANILAC
MONTCALM
GRATIOT
SAGINAW
MUSKEGON
KENT
OTTAWA
IONIA
CLINTON
SHIAWASSEE
GENESEE
LAPEER
SAINT CLAIR
ALLEGAN
BARRY
EATON
INGHAM
LIVINGSTON
OAKLAND
MACOMB
VAN BUREN
KALAMAZOO
CALHOUN
JACKSON
WASHTENAW
WAYNE
BERRIEN
CASS
ST JOSEPH
BRANCH
HILLSDALE
LENAWEE
MONROE

Table 1. Climatological data for selected locations in north-central lower Michigan. Values represent annual means for the period 1940-1979. (Michigan Department of Agriculture 1974).

Climate Parameter	Cadillac	Houghton Lake	Grayling	Gaylord	Mio
Temperature (°C)					
Annual Mean	5.8	6.5	6.2	6.3	6.2
Monthly Means					
May	11.3	12.4	11.9	12.1	11.6
June	16.9	17.6	17.4	17.4	17.2
July	18.9	19.7	19.6	19.6	19.5
August	18.1	18.7	18.6	18.7	18.5
September	13.7	14.6	14.3	14.3	14.1
Extremes					
High	37.2	37.2	37.8	37.2	37.8
Low	-41.7	-37.2	-38.9	-31.7	-39.4
Precipitation (cm)					
Annual Mean	80.7	71.2	83.2	83.7	67.7
Monthly Means					
May	7.2	7.1	8.4	7.4	6.4
June	8.1	7.9	9.3	7.7	7.0
July	8.1	6.9	9.7	8.6	8.2
August	7.5	7.0	8.6	8.2	7.7
September	9.0	7.7	9.5	10.0	7.4
Snowfall (cm)*					
Annual Mean	180.9	209.8	235.7	346.0	156.7
Frost-Free Days (No.)*					
Annual Mean	136	81	100	116	94

*Values represent means for the period 1940 - 1969.

precipitation by 34% at Grayling and more than 45% at the other stations, soil moisture replenishment during the fall and winter months is important for the growth of forests and agricultural crops (Michigan Department of Agriculture 1974). Despite the northern location and lake influence, this area has recorded the highest absolute maximum and lowest absolute minimum temperatures for the state (Niedringhaus 1966).

Physiology and Soils

Lower Michigan belongs to the Great Lakes Section of the Central Lowland physiographic province (Thornbury 1965). The topographic features within the study area are a result of the various glacial advances and retreats which occurred during the Wisconsin stage of Pleistocene glaciation. The various glacial events which occurred are described in detail by Flint (1957), Hough (1958, 1963) and Kelly and Farrand (1967). The last glacial ice sheet began retreating from northern lower Michigan approximately 11,000 years ago (Dorr and Eschman 1971).

The inorganic material deposited by the most recent glacial advances range widely in texture, composition and depth. Shetron (1969) describes the glacial drift as being composed of a "heterogenous mixture which changes in composition from coarse to fine textured material over short horizontal and vertical distances". The variability of glacial material has been a significant factor in determining soil conditions and vegetation in north-central lower Michigan.

Within the Great Lakes region, jack pine dominated forest communities occur almost exclusively on acidic sands which typically lack heavy accumulations of organic matter. For this study, forest surveys and intensive field sampling were restricted to jack pine stands occurring on Grayling and closely associated soil types. McCool and Weidman (1929) estimate that the Grayling soil type covers an area of approximately three million acres in northern lower Michigan. Approximately 35% of the soils of Crawford and Oscoda counties are mapped as the Grayling soil type (Veatch *et al*. 1931a, b.). These extensive and continuous areas of dry sandy soils are often referred to as the "Jack Pine Plains of Michigan" (Roth 1902, Veatch, 1953).

Within the revised soil taxonomic system, known as the Seventh Approximation, the Grayling series is classified among the sandy, mixed frigid family of *Typic Udipsamments* (USDA 1976). These soils have a sandy profile, developed under a humid, cool climate, and lack distinct differentiation of soil horizons (Buckman and Brady 1969). A detailed description of the Grayling series is included in the Appendix.

Vegetation

The forest vegetation within the northern half of the lower peninsula has been described and classified by numerous authors. Sargent (1884) originally described the area as belonging to the northern pine belt of the United States, characterized by the presence of white pine. The region has also been variously referred to as the Northern Hardwood Forest (Frothingham 1915), the Great Lakes Forest (Weaver and Clements

1929), the Hemlock - White Pine - Northern Hardwoods (Nichols 1935) and the Great Lakes Section of the Hemlock - White Pine - Northern Hardwoods (Braun 1950). Braun (1950) describes the region as being characterized by a "pronounced alternation of deciduous, coniferous and mixed forest communities". Because of the intermingling of northern coniferous and southern deciduous elements, the region is often described as representing a transitional or ecotone position between two forest formations (Maycock and Curtis 1960). From the above descriptions it seems apparent that the diversity of forest types within northern lower Michigan is a result of compositional modifications in response to microclimatic, physiographic, edaphic and disturbance factors.

Within Michigan, Beaufait (1960a) has estimated that jack pine dominated communities occupy approximately 400,000 hectares and rank third in area among forest types of the state. Disturbance factors have been of primary importance in determining the present distribution and abundance of jack pine. Logging operations and subsequent forest fires caused dramatic changes in the composition of the state's pine forest. Red pine and white pine were almost totally removed, while jack pine, because of its small size and inferior wood quality, was left uncut. As a result of its ability to colonize cut and burned areas, jack pine quickly dominated much of northern lower Michigan (Beal 1888, 1889, Darlington 1945). Zimmerman (1956) provides a comprehensive review of the literature describing the structure, composition and successional relationships of jack pine communities in lower Michigan.

Although jack pine was once regarded as a weed species, it is presently considered to be an important commercial species in the Great Lake States and Canada. The nearly pure stands, fast growth rate, low wood waste and high yield of long fiber which characterizes the species facilitates harvest operations and make it highly desirable as commercial pulpwood. The economic importance of jack pine is further enhanced by its ability to produce commercial stands on dry, barren sand plains which are unsuitable to other native species (Sterrett 1920, Beaufait 1960a, b). The greater demand for pulpwood products has led to an increasing interest in jack pine utilization. During the period 1960-1975 jack pine contributed approximately 15% of Michigan's annual pulpwood harvest, ranking second to aspen in total pulpwood production (Horn 1965, Blyth 1971, 1975, Blyth and Hahn 1977). In addition to the economic interest, jack pine stands in northern lower Michigan are being intensively managed to preserve the habitat of the Kirtland's Warbler (*Dendroica kirtlandii*). This endangered bird species nests almost exclusively in dense and extensive stands of 7-20 year-old jack pine (Beuch 1980, Harwood 1981).

METHODS

Preliminary Survey and Selection of Study Stands

During the spring and summer of 1978 and 1979 jack pine stands were surveyed within the following six-county area of north-central lower Michigan; Roscommon, Ogemaw, Kalkaska, Crawford, Oscoda and Montmorency. This region is described and mapped by Zimmerman (1956) and Chase *et al*. (1970) as containing the greatest acreage of jack pine in the southern peninsula. Because of the variability in topography, disturbance and tree density, the following criteria were used to select stands for intensive field sampling. Study stands should:

1. occur on fairly level topography, be approximately 10 hectares in size and on soil that is mapped as Grayling sand;
2. be undisturbed within the lifetime of the stand;
3. represent an age sequence of naturally occurring jack pine stands of similar site quality; and
4. occur fairly close to one another to minimize climatic differences and travel.

Site quality is described as the "productive capacity of the habitat" (Gevorkiantz 1947). An easily estimated and widely accepted index of site quality is the average height attained by dominant and codominant trees in a specified period of time. This is referred to as "site index" and the period of time for jack pine is fifty years. The use and limitation of site index as a measure of site quality are discussed by Vincent (1961), Ovington (1965), Jones (1969) and Avery (1975).

Two approaches were used to select different aged stands of similar site quality. An initial approach was the use of stand summary tables that have been developed for jack pine in the Great Lake states by the U.S. Forest Service (1928, 1933, 1934), Wackerman et al. (1929) and Gevorkiantz (1947). These tables provide average height, diameter and density data for jack pine stands of different ages and classifications of site quality; good, medium and poor. Within each stand visited, height, diameter at 1.4 m (dbh) and age were determined for five randomly selected dominant trees. Each stand was then classified according to its degree of site quality.

A more quantitative approach was to estimate the site index for each stand. Height and age data were used to determine site index values from available site index curves (Gevorkiantz 1956) and the site index equation of Lundgren and Dolid (1970). Shetron (1978) provided the locations and site index values for several of the survey stands. The locations and site quality information for each stand surveyed is included in the Appendix (Table A-1). Three jack pine stands were selected which had similar site index values and represented a developmental sequence from young to mature jack pine forests.

Stand Sampling

Plot Establishment

A representative 2.0 ha (100 m x 100 m) area was located in each stand. Field sampling was based upon the establishment of a sampling grid system. Grid transects were spaced at 25 m intervals with each grid cell having an area of 625 m^2. The grid cells were further divided into four plots with each plot having an area of 156.25 m^2 (12.5 m X 12.5 m). Sample plots for data collection were randomly selected in each stand. The number of sample plots required in each stand was determined by graphing plot basal area against total area sampled (Greig-Smith 1957). A total of 12 plots were sampled in Stand III and 6 plots in Stands I and II.

Collection and Summarization of Plot Data

For each sample plot the following overstory data were recorded:

(1) Species, condition (living or dead) and dbh for all stems having a diameter greater than 5.0 cm.

(2) Total tree height and height to base of crown.

(3) Crown diameter along North-South and East-West transects.

(4) Bark thickness at dbh on the North and South facing sides of each tree bole in the sample plot.

All plot data were summarized in tables containing stand mean and standard error values.

An increment core was removed from each tree in all sample plots at a height of 50 cm. Cores were returned to the lab, glued in grooves along wooden blocks and sanded to reveal annual rings (Stokes and Smiley 1968, Maeglin 1979). Annual rings were counted and measured to the nearest 0.02 mm using an instrument designed for dendroclimatological work. Four years were added to the number of annual rings for total tree age estimates (Hansen 1946). Annual rings were averaged by year of formation for all trees in each stand. In addition, five year increments were calculated, converted to basal area increments and averaged by 2.5 cm dbh class intervals.

Understory vegetation was divided into tree saplings and ground cover vegetation. Tree saplings were stems having a dbh of less than 5.0 cm and a basal stem diameter greater than 1.0 cm. Basal diameter, sapling height and species were recorded for each sapling in the sample plots. For each sample plot, coverage values were recorded for each species of herbaceous plants, small shrubs and tree seedlings. The following coverage value scale of Mueller-Dombois and Ellenberg (1974) was used:

5 - Covering more than 75% of the sample plot

4 - Covering 50 - 75%

3 - Covering 25 - 49%

2 - Covering 5 - 24%

1 - Numerous but covering less than 5%

+ - Few individuals present in the sample plot.

Soils

A soil pit was excavated in each stand. Depth and thickness of the litter layer and A and B soil horizons were recorded for each stand. Duplicate soil samples were collected from each soil horizon, placed in plastic bags and returned to the lab. Soil texture was determined by the hydrometer method (Brower and Zar 1977). Analysis of nutrient concentrations was done by the Michigan State University Soil Testing Lab.

Litter Fall

Litter fall was sampled in the oldest stand from September 1978 to November 1980. Micro-litter (needles, bark, twigs, etc.) was collected in thirty-two traps which were distributed randomly throughout the stand. The traps were square, screen-bottomed boxes having an area of 0.25 m^2 and positioned approximately 25 cm above the forest floor. Litter was collected monthly in September, October and mid-November of 1978. Due to continuous snow cover, litter was next collected in mid-April of 1979 and monthly until November of 1979. A similar schedule was followed during 1980. Litter samples were returned to the lab, sorted into components, oven dried at 70°C for 48 hrs and weighed to the nearest 0.01 g.

Branch litter fall was estimated for each sample plot by collecting all fallen branches having a diameter greater than 1.0 cm and weighing them wet. A representative sample was returned to the lab for converting total wet weights to dry weights. Branch litter fall was estimated during the spring and fall of 1979 and 1980.

The volume and dry weight of fallen stem or bole litter was estimated during the fall of 1979 and 1980. Diameter measurements were recorded at one meter intervals and at dbh for all fallen stems in the sample plots. The volume was estimated for each meter segment and summed for the entire stem. Stem dry weights were calculated by multiplying stem volumes by the specific gravity of jack pine wood. For this study a specific gravity value of 0.411 from Maeglin (1973) was used for estimating stem dry weights. Similar measurements and calculations were done for several recently fallen trees in the stand. A linear regression equation was developed for estimating stem volume from dbh measurements for standing live stems.

Overstory Biomass and Production

Two approaches were used to estimate biomass and annual production of selected components of jack pine trees. Non-harvest or non-destructive techniques described by Newbould (1967), Kira and Shidei (1967), Whittaker and Woodwell (1969) and Whittaker and Marks (1975) were used to estimate stem wood biomass, bark biomass, stem wood production, bark production and foliage production. An alternate approach for obtaining estimates of biomass and production was the application of established regression equations obtained from the literature.

Non-Harvest Techniques

Volume of stem wood was determined for each tree within the sample plots by using the formula for parabolic volume (V_p) from Whittaker and Woodwell (1968):

$$V_p = 0.5\pi r^2 h \qquad (1)$$

where 'r' is tree radius (at dbh) and 'h' is tree height. Bark thickness was subtracted from diameter measurements. Figure 2 is a comparison of parabolic volume estimates and regression estimates for the measured fallen stems. Both equations provide similar accuracy for volume estimates (r^2 greater than 0.95). Parabolic volume was used for this

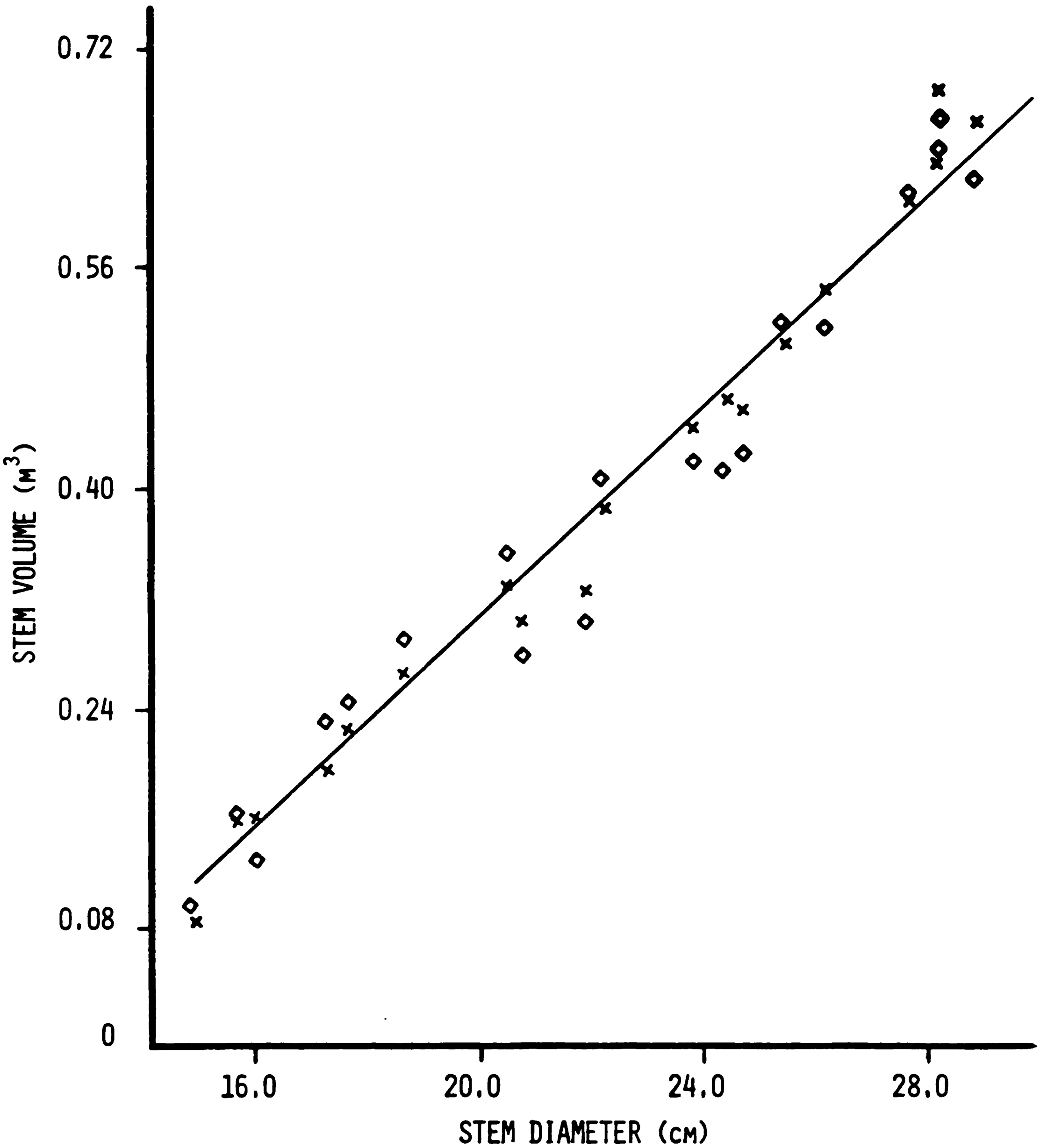


FIGURE 2. COMPARISON OF METHODS FOR ESTIMATING THE VOLUME OF TREE STEMS. SYMBOLS REPRESENT PARABOLIC STEM VOLUME (✖) AND STEM VOLUMES DERIVED FROM DIAMETER MEASUREMENTS OF FALLEN TREES (◆). THE LINE REPRESENTS THE LINEAR REGRESSION EQUATION: $Y = 0.0392\ X - 0.4648$, WHERE Y IS STEM VOLUME AND X IS STEM DIAMETER AT BREAST HEIGHT. $R^2 = 0.97$.

study to estimate standing stem volume because of its widespread use in the literature. Volume estimates were converted to stem wood biomass for each tree by multiplying by the specific gravity (0.411) for jack pine wood. Bark volume was estimated by subtracting stem wood volume from stem wood plus bark volume estimates. Bark biomass was estimated by multiplying bark volume for each tree by 0.340, the specific gravity of jack pine bark (Lamb and Marden 1968). Stem wood biomass, bark biomass and stem wood plus bark biomass was estimated for each tree, summed for each plot and mean and standard error values calculated for the stands.

Mean annual production of stem wood for each sample tree was determined by first calculating the mean annual volume increments from the equation of Whittaker and Marks (1975):

$$EVI = 0.5\pi h(r^2 - c^2) \qquad (2)$$

where EVI is estimated volume increments, 'r' is tree radius, 'h' is tree height and 'c' is tree radius minus the mean annual radial increment of stem wood as measured from increment cores. Volume increments were calculated using mean annual increments for five and ten year periods for each sample tree. For trees where a core was either not taken or damaged, the average increment for trees in the same 5.0 cm size class was used for estimating volume increments. Mean annual stem wood production for each tree was then estimated by multiplying EVI by the specific gravity of jack pine wood.

Stem bark production was assumed equal to the production rate of stem wood and was estimated as follows (Whittaker and Woodwell 1968):

$$\Delta W_b = W_b \cdot \frac{\Delta W_s}{W_s} \qquad (3)$$

where 'W_b' and 'W_s' are bark and stem wood biomass and 'ΔW_s' and 'ΔW_b' are stem wood production and bark production. Values for stem wood and bark production were summed for each plot and mean stand values calculated.

Foliage production was estimated only in Stand III from litter fall data recorded during the study period. Branch biomass, branch production, foliage biomass and belowground biomass were not estimated by non-harvest techniques.

Established Regression Equations

An alternate approach used to estimate overstory biomass and production for each stand was the application of established regression equations. Green and Grigal (1978) have derived generalized biomass equations for jack pine using data from several independent studies (Appendix Table A-2). The coefficients for the equations are included within Table 2 and are of the form:

$$Y = AD^BH^C \qquad (4)$$

where 'Y' is component biomass (kg), 'D' is stem diameter (cm) and 'A, B, C' are coefficients for the equations. All equations were applied to each sample tree, summed by plot and mean stand values computed.

Production values for aboveground stand components were estimated using the equations from Doucet *et al*. (1976). The equations are given in Table 3 and are of the form:

$$\text{Log } Y = A + B \text{ Log } D + C \text{ Log } H \qquad (5)$$

where the symbols are the same as in equation 4. The form of these equations represent a linear transformation of an exponential equation

Table 2. Coefficients for generalized regression equations used to estimate jack pine biomass. The equations are of the form; $Y = AD^B H^C$, where Y is oven-dry mass in kg, D is tree DBH in cm, and H is tree height in m. From Green and Grigal (1978)

Biomass Components	A	B	C	r^2	$S_{y \cdot x}$	$S_{y \cdot x/y}$	df
Stem Bark	0.0319	1.919	0.014	0.88	0.94	0.212	86
Stem Wood	0.0328	1.828	0.859	0.97	4.21	0.126	86
Total Stem	0.0230	1.722	1.136	0.98	8.02	0.149	163
Needles	0.1159	2.778	-1.498	0.84	1.38	0.348	163
Live Branches	0.0212	3.899	-1.884	0.83	4.62	0.542	163
Dead Branches	0.0663	1.791	-0.427	0.32	2.65	0.908	163
Total Live Mass	0.0601	2.090	0.490	0.98	7.88	0.118	163
Total Mass	0.0726	2.091	0.435	0.99	9.26	0.119	163

Table 3. Regression equations used to estimate jack pine production. Equations are in the form Log Y = A + B Log D + C Log H, where Y is oven-dry mass in kg, D is tree DBH in cm and H is tree height in m. From Doucet (1974).

Production Components	Regression Equations	n	r^2
Stem Wood	Log Y = -0.256004 + 2.011258 Log D + 1.013797 Log H	18	0.968
Stem Bark	Log Y = -0.203552 + 2.084478 Log D - 0.187252 Log H	18	0.925
Branch Wood + Bark	Log Y = 0.199059 + 4.383561 Log D - 2.266930 Log H	18	0.966
Needles	Log Y = -0.443545 + 4.005496 Log D - 0.914076 Log H	18	0.962
Cones	Log Y = -1.141223 + 4.018181 Log D - 1.870112 Log H	12	0.497
Total Mass	Log Y = 0.387944 + 2.950189 Log D - 0.203604 Log H	18	0.979

used by Green and Grigal (1978). Doucet _et al_. (1976) state that, since their sampling was not done at random, their equations may not be statistically applicable to other studies. The equations were used in this study to provide production estimates and for comparison to estimates derived by non-harvest techniques.

Belowground Biomass

The biomass of tree roots in the study stands were estimated as percentages of aboveground values (Newbould 1967, Whittaker and Woodwell 1971). In analyzing data on temperate coniferous forests, Ovington (1962) and Rodin and Bazilvich (1967) give a range of 20-30% for the proportion of total stand biomass contributed by roots. Herman (1974), in a more recent review, suggests that this range for root biomass is too high and may have to be revised as additional data become available. Recent studies by Crow (1970), Morrison (1974) and Alban _et al_. (1978) have shown that root biomass contributes 13-17% of total biomass in 30-50 year-old jack pine trees. For this study belowground biomass for each stand was estimated as 17% of total aboveground jack pine biomass. This proportion is similar to estimates reported for _Abies balsamea_ (Honer 1971), _Picea abies_ (Nihlgard 1972), _Pinus contorta_ (Johnstone 1971), _P. radiata_ (Ovington _et al_. 1967) and _P. taeda_ (Ralston 1973, Harris _et al_. 1973, 1977).

Understory Biomass and Production

Understory biomass and its annual production were estimated for the oldest study stand. Sapling biomass and production were estimated by dimension analysis methods similar to those described by Whittaker and Marks (1975). Biomass and production of ground vegetation was estimated by standard harvest techniques.

Sapling Biomass and Production

Because white pine represented approximately 90% of total sapling density, it was the only species sampled for estimates of biomass and production. Twenty-three saplings were harvested during September 1979. The harvested saplings represented the range and density of 1.0 cm size classes in the stand.

Saplings for harvesting were randomly selected from plot data, measured for basal diameter, height and felled at ground level. Saplings were separated into main stem and branches plus foliage, placed in plastic bags and taken to the lab. New twig and foliage production of the current year were separated from previous year's growth. A 2.5 cm disk was removed from the base of each stem for measurement of annual radial growth increments. All components were oven dried at 70°C to a constant weight. Following drying all foliage was removed from branches, twigs and stem material and redried for twenty-four hours. All samples were weighed to the nearest 0.1 g.

Annual stem wood plus bark production was estimated for each harvested sapling by using the methods outlined for trees. A specific gravity value of 0.319 from Maeglin (1973) was used to convert volume to production estimates. Branch wood production was calculated using the estimative ratio approach of Whittaker (1965) and Whittaker and Woodwell

(1968). This approach assumes that relative branch wood production can be estimated from stem wood production as follows:

$$\Delta B = B \frac{\Delta S}{S} + \text{New Twig Growth} \qquad (6)$$

Where 'ΔB' is branch wood production, 'B' is branch biomass and 'ΔS' is stem wood production and 'S' is stem wood biomass.

Biomass and production data from harvested saplings were used to develop regression equations. Basal stem diameter was used as the independent variable in all equations. The equations were used to estimate dry weights by component for all white pine saplings in the sample plots. Bark biomass and production were not estimated separately from stem wood biomass and production.

Ground Cover Vegetation

Biomass and production of herbs, tree seedlings and small woody shrubs were estimated during August of 1979 and monthly from May to August of 1980. All vegetation was clipped within twenty randomly located 0.25 m^2 quadrats, placed in plastic bags, returned to the lab and sorted to species. Aboveground production of the dominant shrub species, *Vaccinium spp.*, was estimated by separating current year's twig and leaf production from main shoots. Grazing losses were not determined during the sampling period. The annual increment of stem wood, stem bark and branch wood for *Vaccinium* was not directly measured but estimated from biomass and productivity ratios for *Vaccinium vacillans* included within the work of Whittaker and Woodwell (1968). The ratios were 0.031, 0.020 and 0.102 for stem wood, stem bark, and branch wood plus bark. Production estimates for herbaceous plants were considered to be equal to harvested biomass values. All harvested material was dried at 70°C to a constant weight and recorded to the nearest 0.01 g.

RESULTS

Description of Study Stands

Location

The three stands selected for intensive field sampling were located in Crawford County, Michigan (Figure 1). This and adjacent counties contain extensive level to gently rolling, dry sandy plains. Forest vegetation on the sandy soils is primarily jack pine alone or in association with oaks, aspen and an occasional red and white pine (Veatch et al. 1928, 1931a, b, 1936).

The sample sites are within 15 km of each other and all three stands occur on public lands. Site III (T27, R3W, sec. 11, nw¼nw¼) is located within Hartwick Pines State Park and has been protected from human disturbance since establishment of the park in 1927. Site I (T28N, R4W, sec. 1, nw¼nw¼) and Site II (T27N, R3W, sec. 32, nw¼nw¼) are younger in age than Site III but show no recent evidence of disturbance.

All three sites contain monodominant jack pine stands that became established following forest fires. Since stands were chosen to represent an age-sequence, they will also be referred to as youngest (Site I), intermediate (Site II) and oldest (Site III).

Soil Characteristics

Physical and chemical properties of major soil horizons for each site are presented in Table 4. The soil profiles are predominantly

Table 4. Physical and chemical properties of major soil horizons for each study site.

Site Number	Soil Horizon	Depth and Thickness (cm)	Soil Texture (%) Sand	Silt	Clay	Soil pH	Calcium (kg/hg)	Potassium (kg/hg)	Magnesium (kg/hg)	Nitrate Nitrogen (kg/hg)	Phosphorus (kg/hg)
	A	0 - 4	90.0	6.0	4.0	5.0	83.9	6.3	2.0	1.0	2.4
I	B	4 - 36	91.0	6.0	3.0	5.4	502.5	37.4	15.6	8.5	29.8
	C	36+	96.0	1.0	3.0	-	-	-	-	-	-
	A	0 - 7	91.0	5.0	4.0	5.0	183.1	17.1	6.9	1.5	1.8
II	B	7 - 35	93.0	4.0	3.0	5.2	762.1	21.9	13.7	6.0	33.0
	C	35+	98.0	0.0	2.0	-	-	-	-	-	-
	A	0 - 10	90.0	6.0	4.0	4.2	157.1	11.8	14.6	3.7	2.4
III	B	10 - 40	90.0	6.0	4.0	5.5	313.7	46.8	14.9	8.1	41.4
	C	40+	99.0	0.0	1.0	-	-	-	-	-	-

sandy in texture, acidic and low in nutrient availability. The A horizons are strongly leached with slight accumulations of nutrients occurring within B horizons.

Composition and Structure of Overstory

Stand Age, Density and Basal Area

Mean structural data of the forest overstory for each study stand are presented in Table 5. Jack pine was the only overstory species sampled at each site. Mean stand ages were 36.7, 52.6, 75.5 years for the youngest, intermediate and oldest stands, respectively. Tree density was greatest in the youngest stand (1611 stems/ha) and least in the oldest stand (448 stems/ha). Mean tree diameter increased with stand age. Stand basal areas ranged from 16.2 m^2/ha for the oldest stand to 22.0 m^2/ha in the intermediate stand. Pairwise comparisons of stand basal areas were done using the Wilcoxon two sample test (Sokal and Rohlf 1981). The basal area for the oldest stand was significantly different ($P < 0.05$) from the basal areas of the two younger stands. The intermediate and youngest stands did not differ significantly in basal area.

Canopy Structure

Mean tree heights were 10.9 m, 15.2 m, and 19.9 m for the youngest, intermediate and oldest stands, respectively. Total range in tree heights were 9.0 m for the youngest stand and 11.0 m for the intermediate and oldest stands. Figure 3 shows the percent distribution of trees by

Table 5. Structural data for jack pine from the three study stands. Values are plot means ± one standard error. Plot data for each stand is included in the Appendix (Tables A3-5).

	Stand I	Stand II	Stand III
Stand Characteristics			
Age (years)*	35.7 ± 0.2	53.6 ± 1.0	75.5 ± 0.4
Site Index (meters at 50 years)**	13.8 ± 0.3	14.8 ± 0.4	14.5 ± 0.3
Tree Density (stems/ha)	1610.7 ± 95.3	960.0 ± 72.2	448.0 ± 40.9
Basal Area (m^2/ha)	20.2 ± 0.6	22.0 ± 1.5	16.2 ± 1.7
Canopy Coverage (m^2/ha)	4143.0 ± 301.0	4852.0 ± 382.0	3192.0 ± 409.0
Mean Tree Values			
Diameter (at dbh in cm)	12.1 ± 0.3	16.8 ± 0.5	21.0 ± 0.6
Total Tree Height (m)	10.9 ± 0.3	15.2 ± 0.5	19.1 ± 0.5
Height to Base of Canopy (m)	6.9 ± 0.1	8.0 ± 0.2	12.4 ± 0.2

* Number of increment cores analyzed for age estimates were 151, 90 and 67 for Stand I, II and III, respectively.

** Site index values are based on mean age and height measurements and using the equation of Lundgran and Dolid (1970). See Figure A-1 in Appendix.

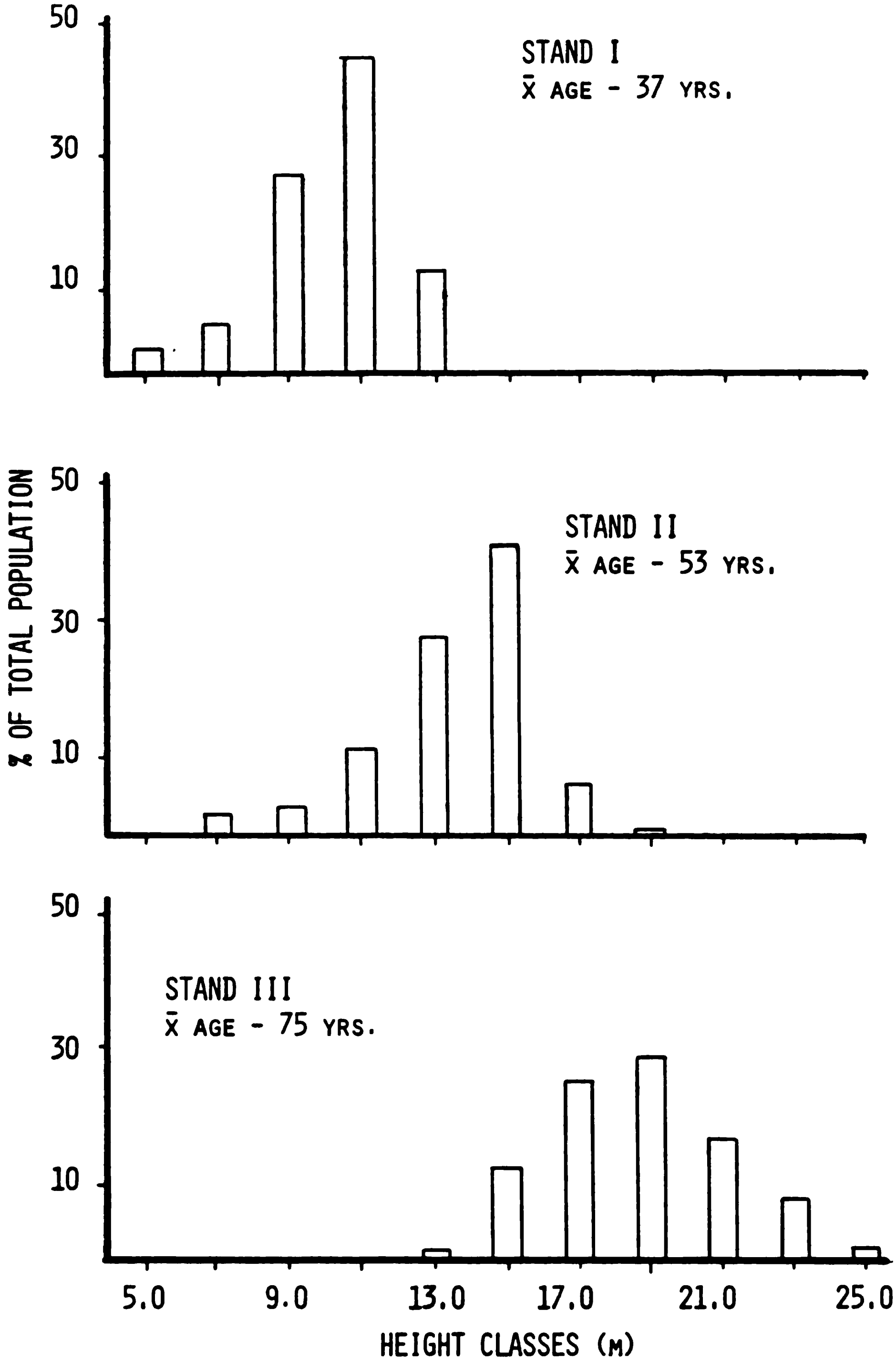


FIGURE 3. DISTRIBUTION OF TREES BY 2 M HEIGHT CLASSES FOR EACH STUDY STAND.

2.0 m height classes. Trees in the youngest stand were less evenly distributed into height classes than trees in either the intermediate or oldest stands. The oldest stand exhibited a more even distribution of trees by height class than the intermediate stand. Correlation coefficients (r) were calculated to determine tree height-diameter relationships. Positive and significant ($P < 0.05$) correlations were found between tree height and diameter for each stand.

Diameter Class Distribution

Tree distribution among 2.5 cm dbh classes were used to construct stand density histograms (Figure 4). The three stands exhibit a similar trend with the greatest density of trees occurring in the intermediate diameter classes. The histograms illustrate the influence of stand age on diameter distribution in jack pine forests. The greatest range in tree diameter (13.5-32.8 cm) and largest individuals occurred in the oldest stand. The intermediate stand had 65% of its trees in the 15.0-25.0 cm diameter range, with no trees greater than 25.0 cm or less than 7.5 cm in diameter. Seventy-five percent of the trees within the youngest stand had diameters of less than 15.0 cm. Recruitment of individuals into the smallest dbh class occurred only in the youngest stand. The lack of recruitment within the oldest and intermediate stands indicates that the populations are not self-replacing and will in time and barring disturbance be succeeded by more tolerant species. The youngest stand is expected to follow the same trend exhibited by the other two stands.

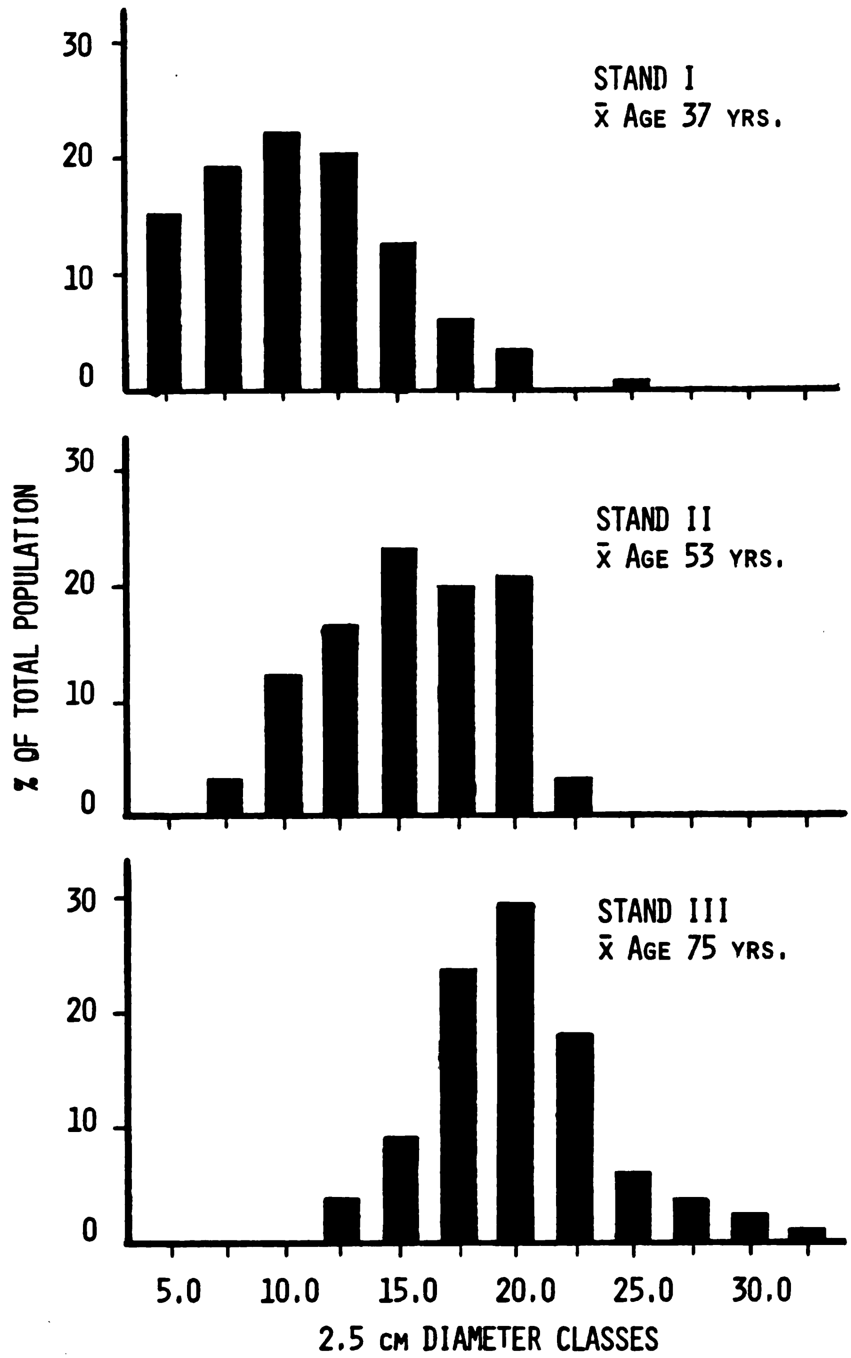


FIGURE 4. DISTRIBUTION OF JACK PINE BY 2.5 CM DBH CLASSES FOR EACH STUDY STAND.

Age Structure

Increment cores for age determination and annual ring width measurements were removed from all trees in each sample plot. Distribution of trees by five-year age classes was used to construct age class histograms. The age structure of each stand is presented in Figure 5. The histograms exhibit a trend similar to the height and diameter class histograms of Figures 3 and 4. The greatest density of stems is in the middle age classes. The youngest and oldest stands had a tree age range of twenty-five years. The intermediate stand had an age range of thirty-five years with few individuals in the youngest of oldest age classes.

Correlation coefficients (r) were calculated to determine both tree age-diameter and tree age-height relationships. Positive and significant ($P < 0.05$) correlations were found for both tree age-diameter and tree age-height comparisons for trees in the youngest and intermediate stands. Correlation coefficients ($r = 0.12$) were also positive for trees in the oldest stand but not significant. This analysis indicates that for youngest and intermediate stands tree age increases with both tree diameter and height. Tree age in the oldest stand is more variable and poorly associated with either tree diameter or height. Table 6 provides mean tree ages by diameter class for each stand.

Tree Mortality

The dbh of all dead standing tree stems was recorded for each sample plot. Table 7 compares density and diameter values for dead and live

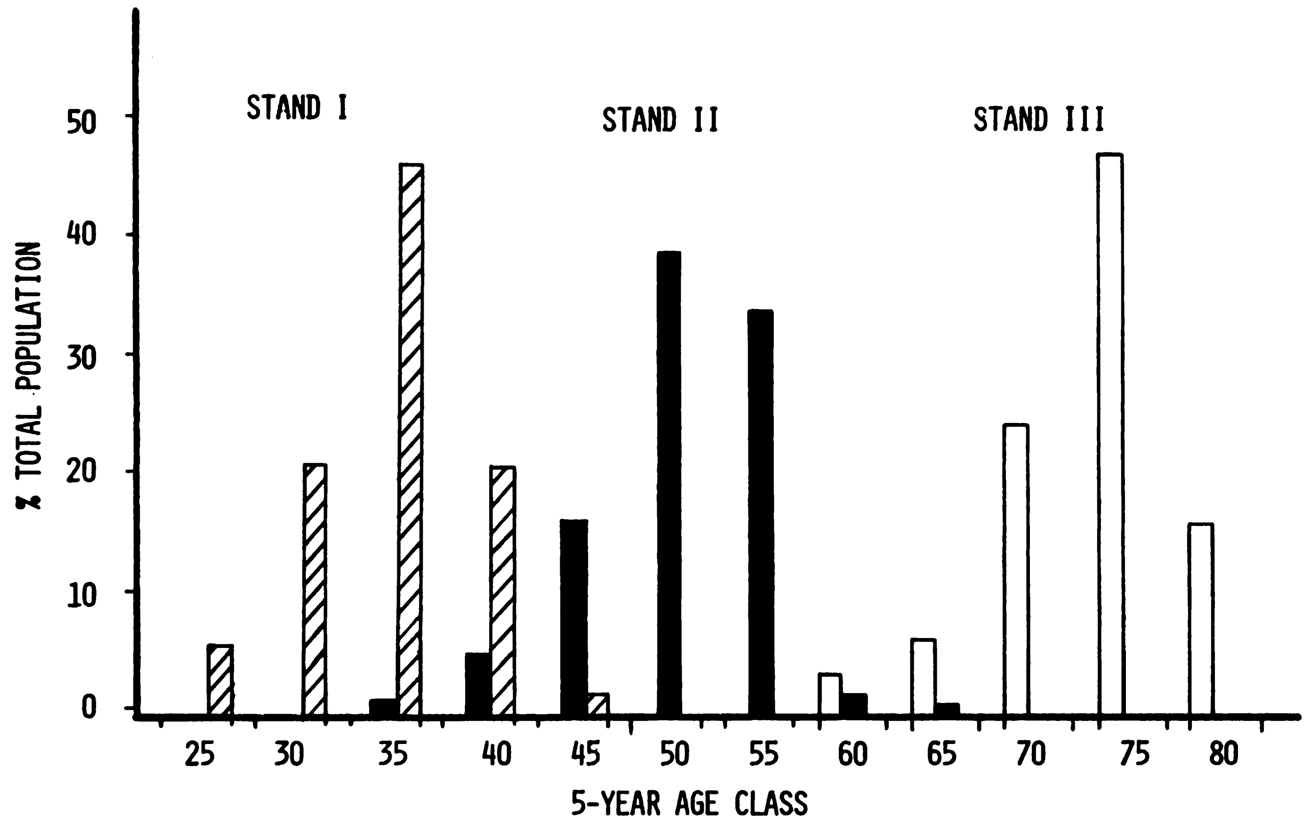


FIGURE 5. DISTRIBUTION OF JACK PINE BY 5-YEAR AGE CLASS INTERVALS FOR EACH STUDY STAND.

Table 6. Comparison of age estimates for jack pine trees by 2.5 cm diameter classes. Values represent mean tree ages ($\bar{x}$) ± one standard error in years.

Size Class Interval (cm)	Stand I $\bar{x}$ ± s.e.	Stand II $\bar{x}$ ± s.e.	Stand III $\bar{x}$ ± s.e.
5.0 - 7.4	31.4 ± 0.7	NS*	NS
7.5 - 9.9	34.0 ± 0.7	47.0 ± 3.8	NS
10.0 - 12.4	36.9 ± 0.5	49.1 ± 1.8	NS
12.5 - 14.9	38.5 ± 0.4	51.3 ± 1.1	71.5 ± 5.0
15.0 - 17.4	39.1 ± 0.6	50.4 ± 1.0	73.9 ± 1.6
17.5 - 19.9	41.7 ± 0.7	54.2 ± 0.8	75.8 ± 1.2
20.0 - 22.4	43.2 ± 1.0	55.8 ± 1.1	76.3 ± 1.1
22.5 - 24.9	NS	55.7 ± 0.3	74.4 ± 1.8
25.0 - 27.4	47.0	NS	76.5 ± 2.3
27.5 - 29.9	NS	NS	74.0 ± 2.0
30.0 - 32.4	NS	NS	78.0 ± 1.0
32.5 - 34.4	NS	NS	80.0

*No trees in size class

Table 7. Comparison of density, diameter and total basal area for live and dead standing jack pine stems. Values are plot means ($\bar{x}$) ± one standard error.

Stand Number	Tree Condition	Tree Density (stems/ha)	Mean Tree Diameter (cm)	Stand Basal Area (m^2/ha)
I	Live	1610.7 ± 95.5	12.1 ± 0.3	20.2 ± 0.6
	Dead	18.2 ± 0.9	8.3 ± 1.3	1.1 ± 0.4
II	Live	960.0 ± 72.9	16.8 ± 0.5	22.0 ± 1.5
	Dead	10.2 ± 1.8	11.0 ± 0.4	3.2 ± 0.5
III	Live	448.0 ± 40.9	21.0 ± 0.5	16.2 ± 1.7
	Dead	352.0 ± 36.9	18.2 ± 0.9	10.2 ± 1.8

trees. The oldest stand had the highest density, mean diameter and basal area for dead standing tree stems. In each stand mean dbh was greater for live trees than dead standing tree stems.

Density and diameter values for both live and dead trees were used to estimate total stand basal area and density (Table 7). Total stand basal area was found to increase with stand age when both live and dead trees are included in the analysis. Dead standing stems represented 5.2%, 12.7% and 38.6% of total stand basal area in the youngest, intermediate and oldest stands, respectively. Total stand density decreased with stand age with dead stems comprising 44% in the oldest stand and less than 20% in the other two stands.

Figure 6 compares diameter class distributions for live and dead stems occurring in the oldest study stand. Using the Kolomogorov-Smirnov test (Sokal and Rohlf 1981), the distributions are significantly different ($P < 0.01$) from one another. The dead standing stems are skewed towards the smaller size classes and the live trees are skewed to the right or larger size classes. Dead standing stems represent over 80% of all standing stems (dead + live) of dbh less than 15.0 cm. One-half of all dead standing stems, whereas only 15% of the live trees, have a dbh less than 17.5 cm. A portion of the difference in the distributions between live and dead standing stems may be accounted for in loss of stem bark and radial shrinkage of the dead stems. However, the greater number of dead stems in the smaller size classes suggest that smaller trees in the stand are at a greater risk of dying than larger and more dominant individuals.

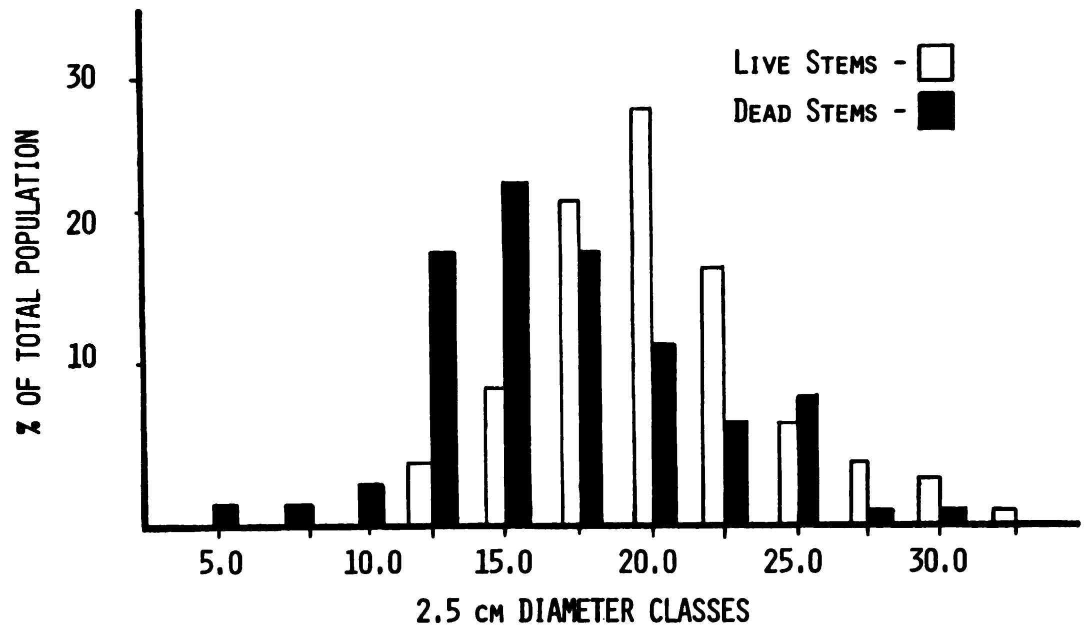


Figure 6. Comparison of diameter distributions for live and dead standing stems in Stand III.

Radial Growth of Jack Pine

Annual rings were measured for each tree and averaged by year of formation for all trees in each sample plot. Ring widths were also summed by five year periods and converted to basal area increments. Five-year increments were averaged by years for all trees in each 2.5 cm size class.

Annual Radial Growth

Figure 7 shows the mean annual radial growth of jack pine for each stand. First formed rings were wider than rings present in older and larger portions of a tree stem. Mean annual radial increment has decreased for each stand to a value of less than 1 mm per year. Trees in the oldest stand, on the average, had a radial growth of 1 mm per year for the past twenty years, whereas trees in the other two stands are approaching this level of annual growth. Year to year variation in radial growth is present for each stand with greater wood production occurring during certain years or period of years. All three stands exhibited an increase in mean annual increment during the period 1968-1973. The greatest mean radial growth for the intermediate stand occurred during the period of 1938 to 1942. Comparisons between mean radial growth for the oldest stand and annual and seasonal rainfall resulted in no significant correlations. Similar comparisons were not done for the other two stands. Radial growth is likely a response to a combination of several climatic and environmental parameters. The study of radial tree growth and its relationship to environmental or

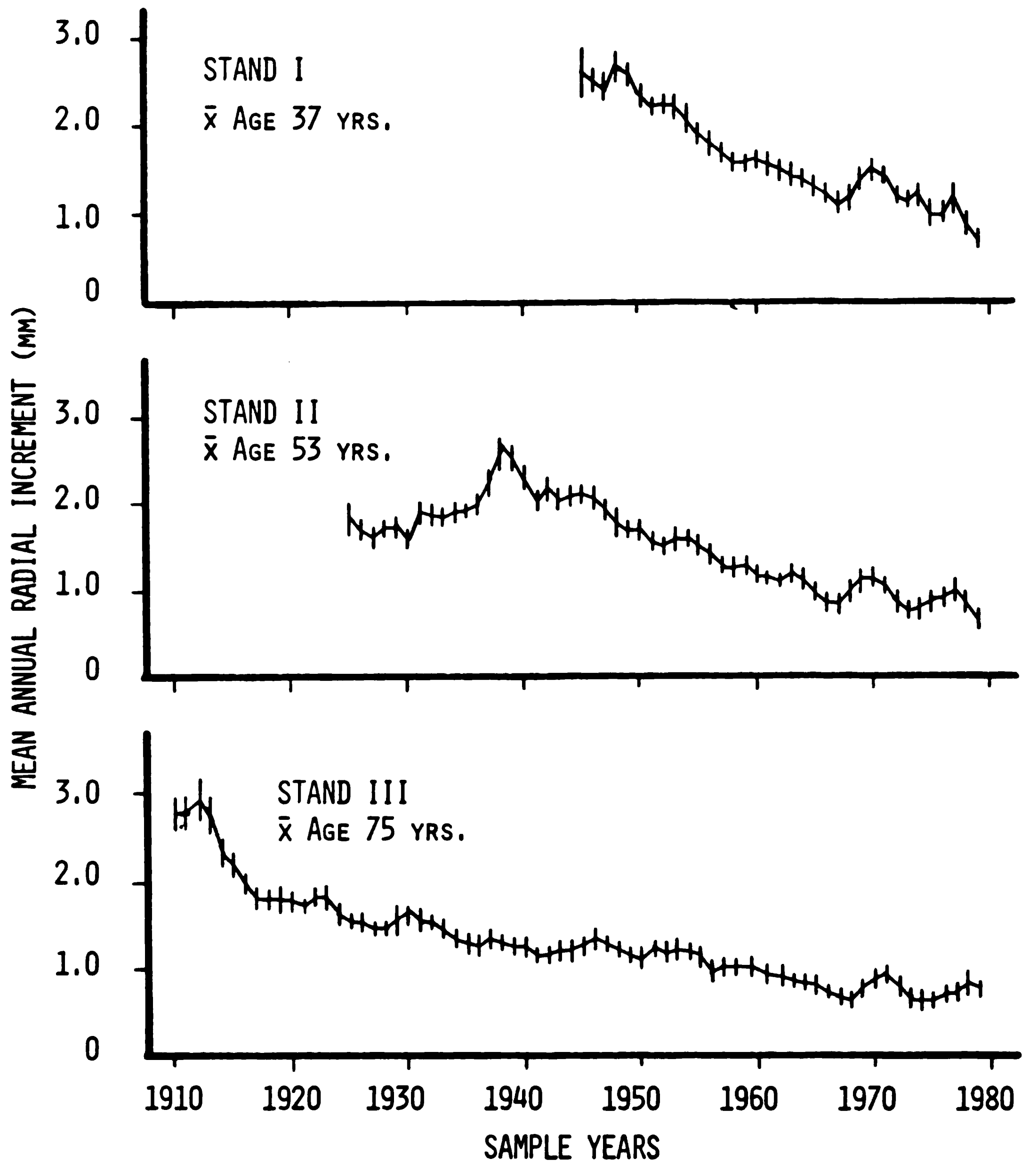


FIGURE 7. MEAN ANNUAL RADIAL INCREMENT FOR JACK PINE TREES IN EACH STUDY STAND. VALUES WERE AVERAGED BY YEAR OF FORMATION. VERTICAL LINES REPRESENT ± ONE STANDARD ERROR.

climatic change requires more intensive sampling and analysis than was undertaken in this study.

Basal Area Increment

Because younger trees often produce wider rings but less wood than larger diameter trees, actual radial growth and wood production may better be expressed as increments of basal area. The graphs in Figure 8 show the average five-year increments in tree basal area for diameter classes that contained ten or more sample trees. Comparison of age estimates (Table 6) to area increments (Figure 8) for each stand shows that the smaller trees are only slightly younger in age but produce considerable less wood than larger individuals.

Aboveground Biomass and Production of Overstory

Regression Estimates of Biomass and Production

Regression estimates of biomass components are provided in Table 8. The greatest total aboveground biomass occurred in the intermediate stand. The oldest stand contained 3.9% and 14.7% more biomass in stem wood than the intermediate and youngest stands, respectively. Stem bark, needle and live branch biomass were greatest for the intermediate aged stand. Root biomass, estimated as 17% of total aboveground biomass, ranged from 11.8 mt/ha (youngest stand) to 13.6 mt/ha (intermediate stand).

Regression biomass estimates (Table 8) were compared between stands using the Wilcoxon two sample test. Needle and dead branch biomass

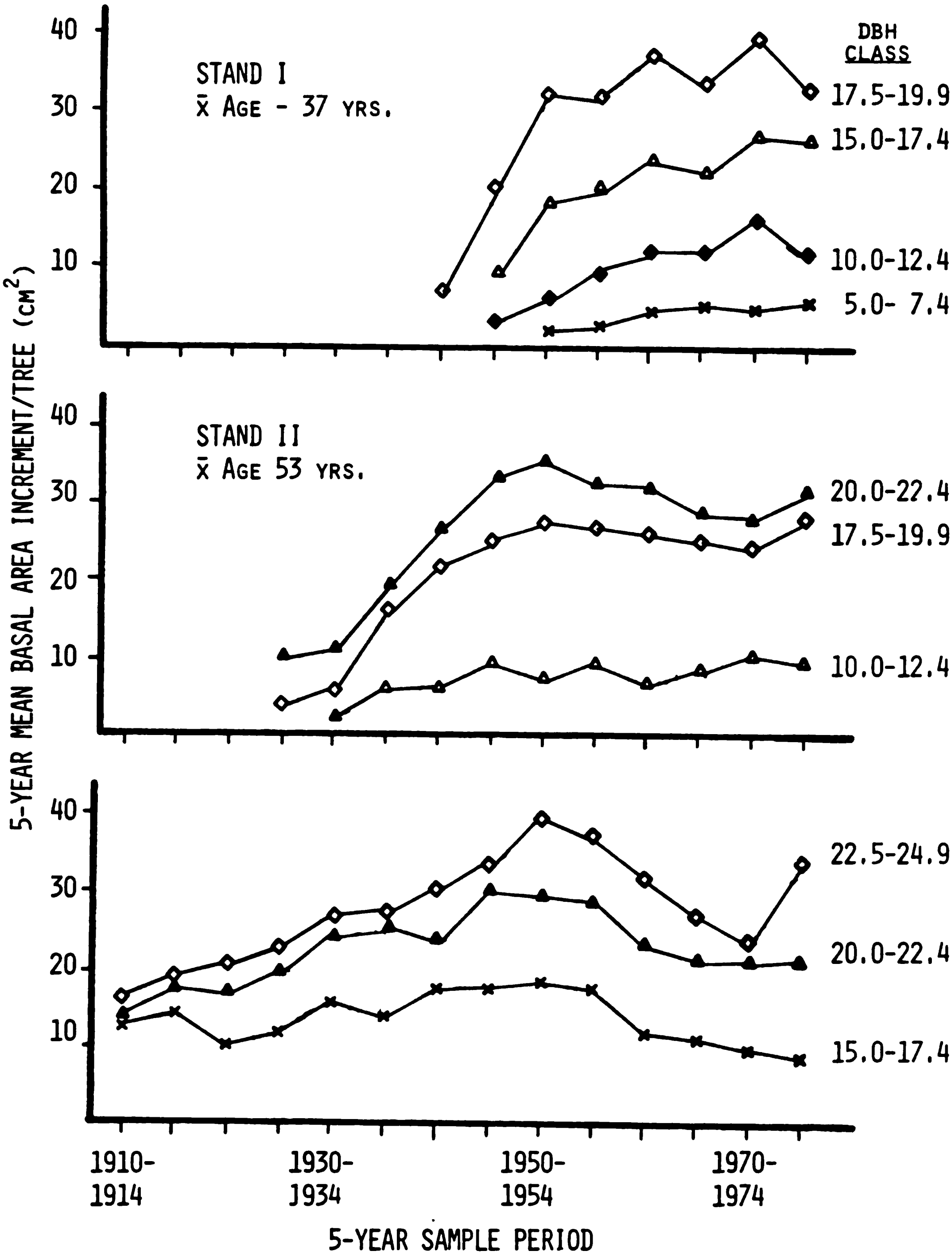


FIGURE 8. MEAN 5-YEAR INCREMENT IN TREE BASAL AREA BY DBH CLASSES FOR THE THREE STUDY STANDS.

Table 8. Live tree biomass estimates for jack pine components within the three study stands. Estimates were derived from regression equations of Green and Grigal (1978). Values are means ± one standard error in metric tons/ha. Plot estimates are included in the Appendix (Tables A9-11).

Biomass Component	Stand I $\bar{x}$ ± s.e.	Stand II $\bar{x}$ ± s.e.	Stand III $\bar{x}$ ± s.e.
Stem Wood	44.2 ± 1.3	49.8 ± 3.2	51.8 ± 6.1
Stem bark	6.9 ± 0.2	7.3 ± 0.5	5.4 ± 0.5
Total stem	46.7 ± 1.4	52.2 ± 3.3	59.8 ± 7.2
Needles	5.9 ± 0.4	6.9 ± 0.6	3.1 ± 0.3
Live Branches	8.6 ± 0.9	12.2 ± 1.3	5.9 ± 0.6
Total Aboveground Live Mass	65.7 ± 1.8	75.8 ± 5.1	71.0 ± 8.1
Dead Branches	3.5 ± 0.1	3.5 ± 0.3	2.0 ± 0.2
Total Aboveground Mass	69.5 ± 1.9	79.8 ± 5.3	73.0 ± 8.2
Roots	11.8 ± 0.3	13.6 ± 0.9	12.4 ± 2.0
Total Biomass	81.3 ± 2.2	93.4 ± 6.2	85.4 ± 10.2

estimates differed significantly ($P < 0.01$) between the oldest and two younger stands. Live branch biomass for the intermediate stand also differed significantly ($P < 0.05$) when compared to values for the other two stands. Total aboveground live biomass and the remaining stand components did not differ significantly between stands.

Figure 9 illustrates the distribution of aboveground biomass for each stand. Percent of total aboveground biomass in stem wood was approximately 10% greater for the oldest stand as compared to the other two stands. Canopy components (branch wood plus needles) represented 23.9% (intermediate), 21.0% (youngest), and 12.3% (oldest) of total aboveground biomass.

The regression equations (Table 3) of Doucet et al. (1976) were used to provide estimates of aboveground production for each stand component (Table 9). Total aboveground production by jack pine was greatest in the intermediate stand (3,526 kg/ha/yr) and least within the youngest stand (2,679 kg/ha/yr). Stem wood represented 47% of total aboveground production in the youngest and intermediate stands and 50% in the oldest stand. Needle production accounted for approximately one-third of total production for each stand.

Regression estimates of stand production (Table 9) were also compared using the Wilcoxon two sample test. Significant differences ($P < 0.05$) were found between the youngest and intermediate stands for stem wood, branch wood, needles and total production estimates. The oldest stand differed significantly ($P < 0.01$) from the other two stands in stem bark production.

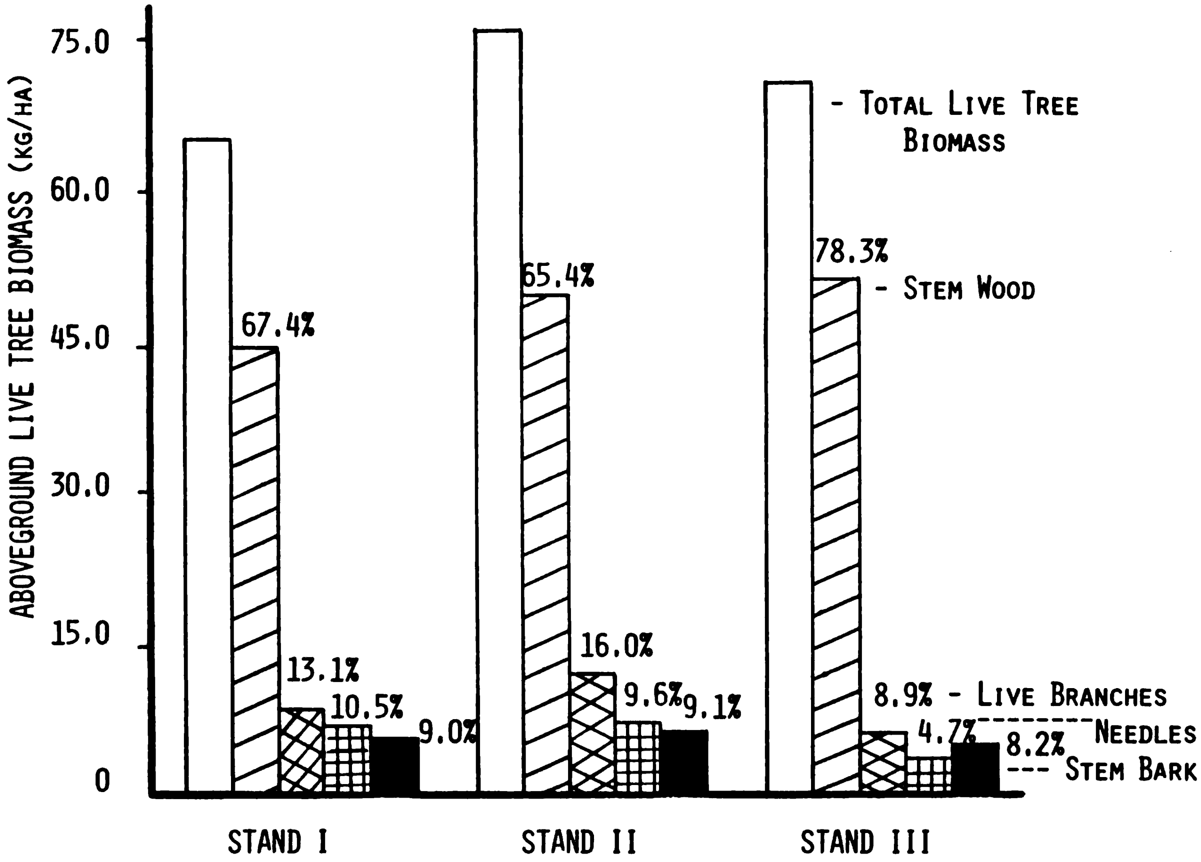


FIGURE 9. DISTRIBUTION OF ABOVEGROUND LIVE TREE BIOMASS FOR JACK PINE IN EACH STUDY STAND. BIOMASS WAS ESTIMATED USING THE EQUATIONS OF GREEN AND GRIGAL (1978). THE VALUE ABOVE EACH BAR IS THE PERCENT THAT COMPONENT REPRESENTS OF TOTAL ABOVEGROUND LIVE TREE BIOMASS.

Table 9. Estimates for net primary productivity for jack pine components in the three study stands. The estimates were derived from the regression equations of Doucet (1974). Values are annual means ± one standard error in kg/ha/yr.

Production Components	Stand I	% Total	Stand II	% Total	Stand III	% Total
Stem Wood	1252.5 ± 45.2	46.8	1647.4 ± 95.3	46.7	1695.7 ± 209.5	49.9
Stem bark	137.6 ± 6.8	5.1	132.5 ± 10.6	3.8	80.2 ± 7.3	2.3
Branch Wood	334.7 ± 9.8	12.5	465.9 ± 29.4	13.2	481.7 ± 60.8	14.2
Needles	852.5 ± 23.3	31.8	1163.5 ± 76.2	33.0	1147.3 ± 141.3	33.5
Total Production	2679.0 ± 72.3		3526.3 ± 222.7		3396.8 ± 409.3	

Non-destructive Estimates of Biomass and Production

For comparison to regression estimates, jack pine biomass and annual production were also estimated by non-destructive techniques. Stem wood and stem bark volumes and biomass estimates are provided in Table 10. Using non-destructive methods, the oldest stand contained 3.7%, and 29.1% more biomass in stem wood than the intermediate and youngest stands, respectively. Stem bark biomass was again greatest for the intermediate stand. Needle and live branch biomass were not estimated by non-destructive techniques.

Non-destructive estimates of mean annual stem wood volumes and dry weights are included in Table 10. Volume and dry weight estimates were greater when based upon the past ten year period for the youngest and intermediate stands. The oldest stand exhibited little variation between five and ten year annual means. Using non-destructive methods, annual stem wood production was 37% greater in the youngest stand as compared to the oldest stand but only 4.0% greater than the intermediate stand. The intermediate stand produced approximately 500 kg/ha more stem wood per year than the oldest stand and 50 kg/ha less than the youngest stand. Branch wood and stem bark production were not estimated by non-destructive methods.

Non-destructive estimates of overstory biomass and net primary production were compared by the Wilcoxon two sample test. Stem wood and stem bark biomass estimates differed significantly ($P < 0.05$) for the youngest and intermediate stands. Stem bark biomass was also

Table 10. Non-destructive estimates of volume and dry weight for jack pine stem wood and bark. Dry weights were calculated as volumes x specific gravities. Values are means ($\bar{x}$) $\pm$ one standard error.

Parameter Estimates	$\bar{x} \pm$ s.e.	$\bar{x} \pm$ s.e.	$\bar{x} \pm$ s.e.
Volume Estimates (m^3/ha)			
Stem Wood	101.2 $\pm$ 2.9	137.4 $\pm$ 8.5	142.8 $\pm$ 17.6
Stem Bark	18.2 $\pm$ 1.0	25.3 $\pm$ 2.1	18.8 $\pm$ 2.4
Annual Stem Volume Increment (m^3/ha)			
5-year mean	3.67 $\pm$ 0.16	3.52 $\pm$ 0.22	2.32 $\pm$ 0.28
10-year mean	4.32 $\pm$ 0.16	3.68 $\pm$ 0.20	2.27 $\pm$ 0.28
Biomass Estimates (mt/ha)			
Stem Wood[1]	41.5 $\pm$ 1.2	56.3 $\pm$ 3.5	58.5 $\pm$ 7.2
Stem Bark[2]	6.2 $\pm$ 0.3	8.6 $\pm$ 0.7	6.4 $\pm$ 0.8
Stem Wood + Bark[3]	47.7 $\pm$ 1.5	64.9 $\pm$ 4.2	64.9 $\pm$ 8.0
Production Estimates (mt/ha/yr)			
Stem Wood Production[1]			
5-year mean	1.50 $\pm$ 0.06	1.45 $\pm$ 0.09	0.95 $\pm$ 0.12
10-year mean	1.77 $\pm$ 0.06	1.51 $\pm$ 0.08	0.93 $\pm$ 0.11
Stem Bark Production[4]	0.22	0.22	0.10
Stem Wood + Bark Production[3]	1.72	1.67	1.05

1. Specific gravity of jack pine stem wood is 0.410 from Maeglin (1973)
2. Specific gravity of jack pine bark is 0.340 from Lamb and Mardin (1968)
3. Values obtained by summing stem wood and stem bark values
4. Values derived from the ratio of Bark Production/Bark Biomass = Stem Wood Production/Stem Wood Biomass

significantly different ($P < 0.05$) for the intermediate and oldest stands. Comparison of biomass estimates for the youngest and oldest stands resulted in no significant differences in stem wood, stem bark or stem wood plus bark values. Stem wood and stem bark production, estimated by non-destructive techniques, differed significantly ($P < 0.05$) between the oldest and two younger stands. The intermediate and youngest stands did not differ in their annual production of stem wood or stem bark. Sample plots for the oldest stand exhibited a greater range in estimates of jack pine biomass and production than plots in either the youngest or intermediate stands.

Litter Fall

Litter fall was sampled in the oldest stand. Table 11 presents dry weight estimates for litter fall components for the two sample years. Fallen tree stems represented the greatest portion of total litter weight. In the micro-litter component, jack pine needles represented over one-half of the dry weight for each year. Figure 10 describes the montly variation in micro-litter fall. Seventy-five percent (1979) and 80.0% (1980) of needle fall occurred during the period of mid-October to mid-April.

Annual needle production was estimated for the oldest stand from litter fall collections. Needle production was 710 kg/ha (1979) and 769 kg/ha (1980). An approximate needle production estimate of 740 kg/ha/yr was used to derive a ratio of 0.778 for needle to stem wood production. Using this ratio, I obtained estimates of 1,169 kg/ha/yr

Table 11. Litter fall data for Stand III. Values are plot means in kg/ha.

Litter Component	Sample year 1979	1980
Micro-litter		
Pinus banksiana		
Needles	710.1	768.5
Bark	262.0	197.8
Twigs	158.2	53.8
Male Cones	66.6	32.5
Female Cones	60.3	256.8
Total	1257.2	1309.4
Misc. Species	23.8	33.7
Sub-total	1281.0	1343.1
Macro-litter		
Branches	327.7	245.4
Stems	5996.0	4388.0
Sub-total	6327.7	4633.4
Total Litter Fall	7604.7	5976.0

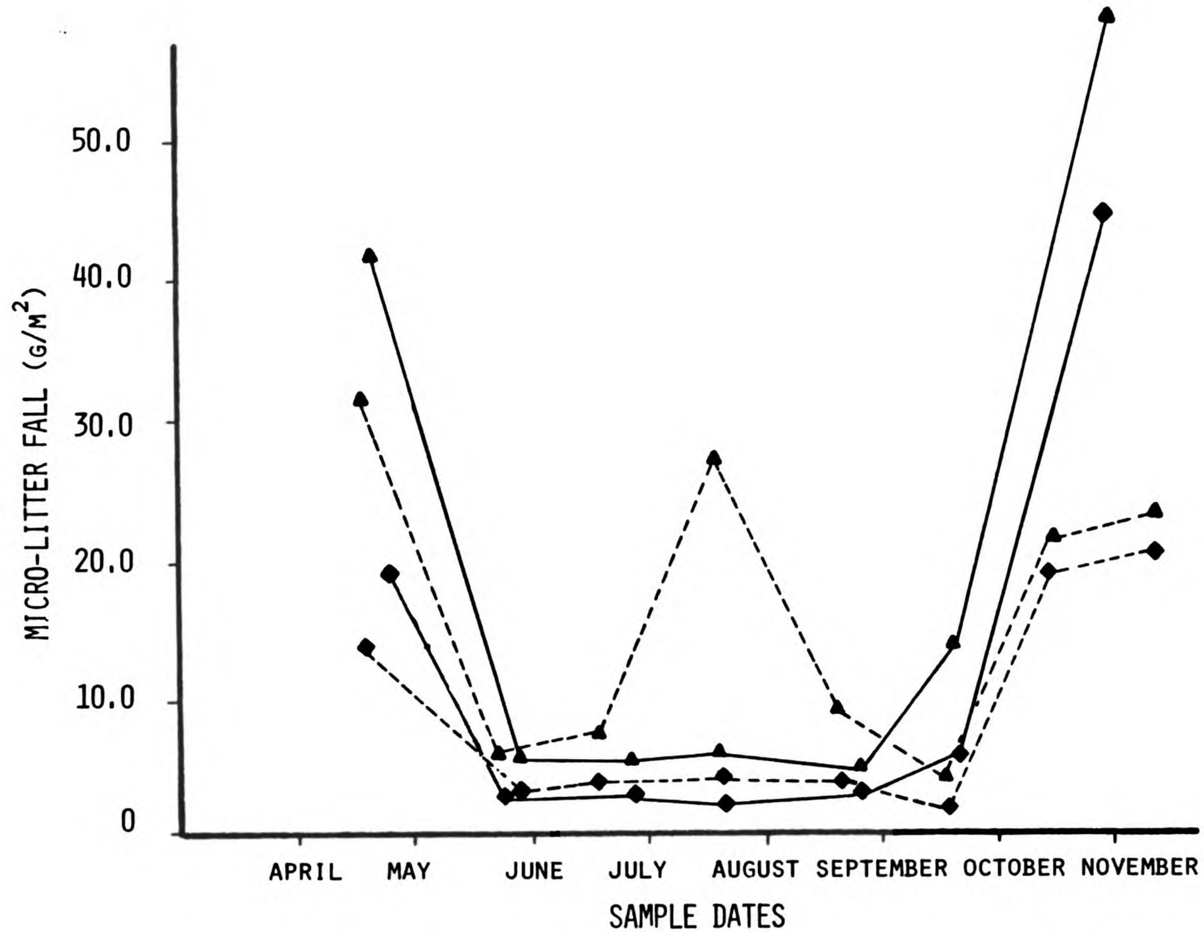


Figure 10. Monthly variation in needle (◆) and total micro-litter fall (▲) during 1979 (---) and 1980 (——). April values represent composite samples from November to April.

and 1,124 kg/ha/yr for needle production in the youngest and intermediate stands, respectively. These estimates represent only approximate values for these three stands.

Comparison of Regression and Non-destructive Methods for Estimating Jack Pine Biomass and Net Primary Production

Regression and non-destructive biomass and production estimates of jack pine stem wood, stem bark and stem wood plus bark for the three stands are compared in Table 12. Non-destructive estimates for biomass components are consistently greater than regression estimates for both the oldest and intermediate stands. For the oldest stand, regression estimates are 8.0-16.0% less than non-destructive biomass values. Regression estimates of stem wood biomass and bark biomass are 6.5% and 11.0% greater than non-destructive estimates for the youngest stand.

To explain the observed differences in biomass estimates, stem wood biomass was estimated and compared for ten sample trees in each stand by both regression and non-destructive methods. Regression estimates were consistently lower than non-destructive estimates for trees having a dbh of 16.0 cm or greater in the oldest and intermediate stand and 18.0 cm in the youngest stand. Since the majority of trees in the intermediate and oldest stands have a diameter greater than 16.0 cm, the total stem wood biomass for the stands as estimated by regression analysis would be less than those estimates derived by non-destructive techniques. Similarly, the regression estimates of stem wood biomass

Table 12. Ratios for comparing regression and non-destructive biomass and production estimates for selected stand components. The ratios were calculated as: regression estimates/non-destructive estimates.

Stand Components	Stand Number I	II	III
Biomass Components[1]			
Stem Wood	1.07	0.88	0.89
Stem Bark	1.11	0.85	0.84
Stem Wood + Bark	0.98	0.80	0.92
Production Components[2]			
Stem Wood	0.84	1.14	1.78
Stem Bark	0.63	0.60	0.80
Stem Wood + Bark	0.81	1.07	1.69
Needles	1.37	1.04	0.65

1. Regression estimates for biomass components were taken from Table 8. Non-destructive estimates from Table 10.

2. Regression estimates for production components were taken from Table 9. Non-destructive estimates for stem wood and stem bark from Table 10. Needle production estimates from litter fall data.

for the youngest stand was greater than the estimates derived by non-destructive methods.

Regression and non-destructive estimates of biomass components included in Table 12 were also compared using t-tests for paired comparisons. Sample plots from each stand were treated as individuals with regression and non-destructive biomass estimates arranged as pairs. Regression and non-destructive estimates were signficantly different ($P < 0.05$) for all biomass components in each stand. Since jack pine trees were not harvested in this study it is not possible to state which technique, regression or non-destructive, provides the most accurate estimates of biomass. However, the use of published regression equations provide a more complete analysis of the distribution of jack pine biomass among stand components. In addition, the percent distribution of jack pine biomass among components, as estimated by regression analysis, is similar to that described for other jack pine (Crow 1970, Hegyi 1972, Doucet 1974, MacLean and Wein 1976) and coniferous forests (Ovington 1962, Rodin and Bazilevich 1967, Young 1976). Therefore, the regression estimates of jack pine biomass will be used throughout the rest of this dissertation.

Ratios of regression to non-destructive estimates for several production components are also included in Table 12. Stem wood production estimates derived by non-destructive methods ranged from 16% less to 78% more than regression estimates. The two methods for estimating mean annual production were compared using t-tests for paired comparisons.

Regression and non-destructive estimates were significantly different ($P < 0.05$) for all production components (Table 12).

In jack pine forests production of stem wood has been shown to increase up to an age of 20-30 years and is maintained at a high level before declining at a stand age of 50 years (Eyre and LeBarron 1944, Benzie 1978). In addition, jack pine stands on unproductive sites are under greater stress and exhibit slower growth than stands on more productive sites (Shetron 1969, Benzie 1978). The regression equations which were used to estimate net primary production were developed for 40-year old jack pine stands on medium to good quality sites (Doucet 1974). Since differences in stand characteristics (stand age, tree density) and soil physical properties influence tree growth, estimates of forest production should be based upon actual stand measurements and regressions that are as appropriate as possible, with care taken to include all possible sources of error (Whittaker and Woodwell 1971, Whittaker and Marks 1975). For this study, non-destructive methods which were based upon actual annual growth data provided more accurate estimates of jack pine production and will be used throughout the remainder of this study.

Understory Vegetation

Species Composition

Density of tree saplings and coverage values for ground cover species are given in Tables 13 and 14. The oldest stand contained the greatest variety of both sapling and ground cover species. White pine

Table 13. Sapling density within the three study stands. Values are number/hectare.

Species	STAND NUMBER I	II	III
Abies balsamea	NP	NP	122.7
Acer rubrum	NP	NP	58.9
Pinus banksiana	107.7	NP	NP
Pinus strobus	NP	NP	1484.8
Prunus spp.	NP	32.0	10.7
Quercus spp.	NP	149.3	37.3

A sapling was considered any woody plant having a diameter breast height of less than 5.0 cm and a height of greater than 1 m.

Table 14. Mean relative coverage values[1] for understory species within the three study stands

Understory Vegetation	STAND NUMBER I	II	III
Small and Prostrate Shrubs			
Arctostaphylos uva-ursi	1	1	+
Comptonia peregrina	1	1	+
Epigaea repens	NP	1	2
Gaultheria procumbens	+	+	2
Prunus sp.	NP	NP	+
Rubus sp.	NP	NP	+
Vaccinium angustifolium	1	3	3
Vaccinium mytilloides	NP	NP	3
Vaccinium vacillans	+	4	4
Herbaceous Plants			
Aster laevis	+	+	NP
Carex pensylvanica	2	3	3
Cornus canadensis	+	+	+
Danthonia spicata	2	3	+
Hieracium aurantiacum	1	1	+
Graminae aurantiacum	1	1	+
Graminae	+	+	+
Linnaea borealis	1	1	+
Maianthemum borealis	+	NP	2
Melampyrum lineare	1	+	+
Oryzopsis asperifolia	NP	NP	+
Polygala sp.	NP	NP	+
Pteridium aquilinum	NP	1	4
Spiranthes gracilis	+	NP	NP
Trientalis borealis	NP	NP	+
Viola adunca	+	NP	NP
Miscellaneous Vegetation			
Lichen	2	2	1
Moss	1	1	+
Lycopodium complanatum	NP	NP	+
Woody Seedlings			
Acer rubrum	+	NP	+
Betula papyrifera	NP	NP	+
Pinus banksiana	1	+	+
Pinus strobus	NP	NP	+
Quercus sp.	1	+	+

Table 14. continued

NP - Not present in sample plots

1 - Coverage Value Scale:

5 - Species coverage more than 75% of plot
4 - Species coverage 50 - 75%
3 - Species coverage 25 - 49%
2 - Species coverage 5 - 24%
1 - Species numerous but coverage less than 5%
\+ - Few individuals present in plot

represented approximately 90.0% of total sapling density in the oldest stand. Jack pine saplings were present only within the youngest stand and were the only sapling species sampled in the stand.

Ground cover vegetation may be divided into two distinct strata: a ground or lower stratum of less than one-half meter and an upper stratum (greater than 0.5 m) of low shrubs and bracken fern. The ground stratum consisted of herbaceous plants, prostrate shrubs, mosses and lichens. Blueberries (*Vaccinium* spp.) were the dominant shrubs, with *Carex pensylvanica*, *Danthonia spicata*, and *Maianthemum canadense* being abundant ground cover species in each stand. Prostrate or trailing shrubs, such as *Arctostaphylous uva-ursi*, *Epigea repens* and *Gaultheria procumbens* were present and often formed extensive patches in each stand. Bracken fern (*Pteridium aquilinum*) was extremely abundant within the oldest stand and not sampled within the youngest stand. Various mosses and lichens were present in all stands and often formed large patches within the youngest and intermediate stand.

Sapling Biomass and Production

Biomass and production were estimated for the white pine saplings in the oldest study stand. The other stands contained few saplings in comparison to the oldest stand. Biomass and production data for harvested saplings are included within the Appendix (Table A-12). Regression equations for calculating component biomass and production are provided in Table 15. The independent variable used in all equations was basal stem diameter.

Table 15. Regression equations for calculating white pine sapling biomass and net primary production within Stand III. Equations are of the form $\ln Y = A + B \ln X$, where Y is component dry weight in kg/ha, X is basal stem diameter in cm., and A and B are equation parameters. Estimate of relative error is presented as E.

Stand Parameters	Regression Equations	N	r^2	E
Biomass Components				
Stem Wood + Bark	$\ln Y = 2.523 + 2.449 \ln X$	23	0.985	1.0015
Branch Wood + Bark	$\ln Y = 1.485 + 3.009 \ln X$	23	0.973	1.0004
Needles	$\ln Y = 2.619 + 2.302 \ln X$	23	0.973	1.0018
Total Aboveground	$\ln Y = 3.454 + 2.535 \ln X$	23	0.993	1.0009
Production Components				
Stem Wood	$\ln Y = 0.293 + 2.907 \ln X$	23	0.980	1.0122
Branch Wood	$\ln Y = 0.745 + 2.881 \ln X$	23	0.970	1.0030
Twigs	$\ln Y = 0.646 + 2.411 \ln X$	23	0.960	1.0004
Needles	$\ln Y = 2.110 + 2.317 \ln X$	23	0.969	1.0018
Total Aboveground	$\ln Y = 2.441 + 2.559 \ln X$	23	0.984	1.0018

Coefficients of determination (r^2) are included in Table 15 for expressing the strength of the correlation between basal stem diameter and component biomass or production. Although all r^2 values exceed 0.95, indicating a strong correlation, they should be interpreted cautiously. Zar (1968), Baskerville (1972) and Beauchamp and Olson (1973) have shown that a bias is inherent within regression analyses which involve logarithmic transformations. The antilogarithmic conversion of the regression estimate into arithmetic units results in an underestimate of the dependent variable. Wiant and Harrer (1979) provide a method for estimating the percent bias for regression equations which involve logarithmic transformations. Calculations of percent bias for the equation used to estimate stem wood plus bark biomass gave a value of less than 2.0%. Thus, component biomass and production estimates were not corrected for logarithmic bias.

In addition to r^2 values, Whittaker and Woodwell (1968) and Whittaker *et al*. (1974) recommend calculating the relative error of estimate (E) for expressing the accuracy of a regression equation. The estimate of relative error for a logarithmic regression is the antilog of the standard error of estimation. A value for E of 1.20, for example, suggests an expected error range from Y/1.20 to 1.20·Y or $\pm$ 20.0% of the predicted Y value. The regression equations within Table 15 have E values of less than 1.002 for biomass components and 1.013 for productivity components. Therefore, the regression equations are accurate in predicting component weights for white pine saplings in the study stand and size range. Figure 11 shows the strong correlation which exists between basal stem diameter and total sapling dry weight for harvested saplings. All other sample data were plotted and exhibited a similar strong relationship.

Regression equations in Table 15 were used to estimate component biomass and production for all white pine saplings within the sample plots. Plot totals were then used to derive estimates of total stand biomass and production by sapling component (Table 16). Total aboveground biomass and net primary production was 1223.1 kg/ha and 516.5 kg/ha/yr, respectively. Stem wood plus bark contributed 35% of total aboveground sapling biomass and 17% of annual aboveground production. Branch wood plus bark represented 34% of total biomass and 26% of total production. Foliage contributed the remaining share of both total biomass (31%) and annual production (45%). Annual production by white pine represented 42% of the total white pine biomass during the 1979 sample year. The biomass accumulation ratio (aboveground biomass/net annual production) for white pine saplings was 2.40. Belowground biomass and annual production were not estimated for saplings.

Ground Cover Biomass and Production

Aboveground biomass values for ground cover species within the oldest stand are provided within Table 17. The values should be considered as minimum estimates because they represent samples harvested at peak biomass; supposedly late August. Total aboveground biomass was

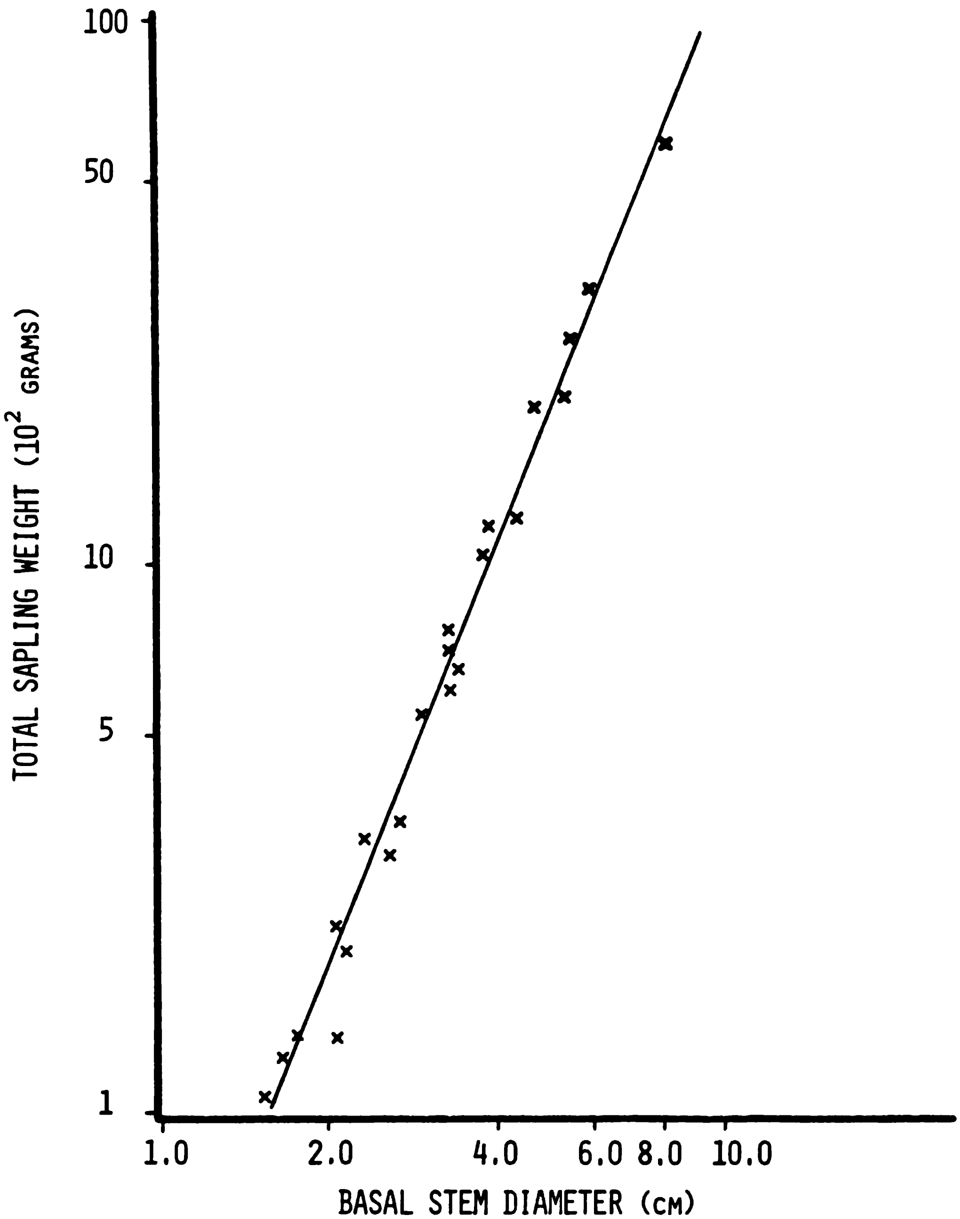


FIGURE 11. LOGARITHMIC REGRESSION FOR PREDICTING TOTAL WHITE PINE SAPLING WEIGHT (Y) IN GRAMS FROM BASAL SAPLING DIAMETER (X) IN CM. THE REGRESSION EQUATION IS; $\ln Y = 2.535 \ln X + \ln 31.62$, WITH AN R^2 OF 0.99. THE SYMBOLS REPRESENT ACTUAL SAPLING DATA FROM HARVESTED SAPLINGS.

Table 16. Component biomass, production and percent distribution for white pine saplings within Stand III. Dry weight values are plot means ± one standard error.

Sapling Component	Dry Weights	% Total Biomass	% Total Production
Biomass Estimates (kg/ha)			
Stem Wood + Bark	423.9 ± 111.1	34.7	
Branch Wood + Bark	420.1 ± 99.9	34.4	
Needles	379.1 ± 97.6	31.0	
Total Aboveground	1223.1 ± 321.7		
Production Estimates (kg/ha/yr)			
Stem Wood	88.1 ± 24.6	7.2	17.1
Branch Wood	133.3 ± 37.0	10.9	25.8
Twig Growth	61.4 ± 16.0	5.0	11.9
Needles	233.7 ± 60.3	19.1	45.3
Total Aboveground	516.5 ± 121.3	42.2	

Table 17. Aboveground biomass for selected understory species within Stand III during August of 1979 and 1980. Values are means ± one standard error in g/m^2.

Understory Strata and Species	Sample year 8-18-79 Dry Weight (g/m^2)	% Annual Total	8-29-80 Dry weight (g/m^2)	% Annual Total
Small Shrubs				
Vaccinium spp.[1]				
Foliage	32.9 ± 3.5	13.3	34.2 ± 3.4	12.5
Twig Growth	13.7 ± 1.3	5.6	15.1 ± 1.3	5.5
Stem	43.6 ± 5.1	17.7	52.8 ± 8.1	19.2
Total	90.2 ± 9.3	36.6	102.1 ± 11.2	37.2
Prostrate Shrubs				
Epigaea repens	29.7 ± 9.0	12.0	16.9 ± 4.8	6.1
Gaultheria procumbens	16.1 ± 3.2	6.5	12.2 ± 1.5	4.4
Herbaceous Plants				
Pteridium aquilinum	77.2 ± 9.8	31.4	123.1 ± 15.0	44.9
Carex pensylvanica	27.8 ± 4.2	11.3	17.2 ± 2.1	6.3
Maianthemum canadense	4.4 ± 1.0	1.8	1.5 ± 0.3	0.6
Miscellaneous Species	1.2 ± 0.4	0.5	1.6 ± 0.9	0.6
Annual Total	246.9 ± 14.6		274.4 ± 15.1	

1. Values represent the sum of *Vaccinium angustifolium*, *V. vacillans* and *V. mytilloides*.

9.0% greater during 1980 than it was in 1979. Blueberry shrubs and bracken fern accounted for 68% and 82% of total ground cover biomass during 1979 and 1980, respectively. Bracken fern exhibited a 59% increase in aboveground biomass during the 1980 growing season over 1979 levels. Blueberry species showed only minor increases (7.0%) in biomass estimates. The remaining species decreased in biomass levels from the 1979 to 1980 growing seasons.

Figure 12 shows the changes in aboveground biomass from May to August of 1980. Blueberry shrubs began growth during early May and continued increasing in weight through the month of June. By late July the blueberry species had reached their peak biomass. Bracken fern exhibited the greatest increase in biomass of any species during the period of mid-June to late-July. It represented the most productive ground cover species within the stand. The remaining species showed slight fluctuation during the spring and summer months.

Because of the predominance of blueberry shrubs within the stand, the harvested samples were separated into components. The distribution of monthly biomass by components is presented as Figure 13. Foliage biomass increased from 10 gms/m^2 during early May to 46 gms/m^2 by mid-July. Stem wood biomass showed little change through the growing season. New twig growth began after the May harvest and growth continued through August.

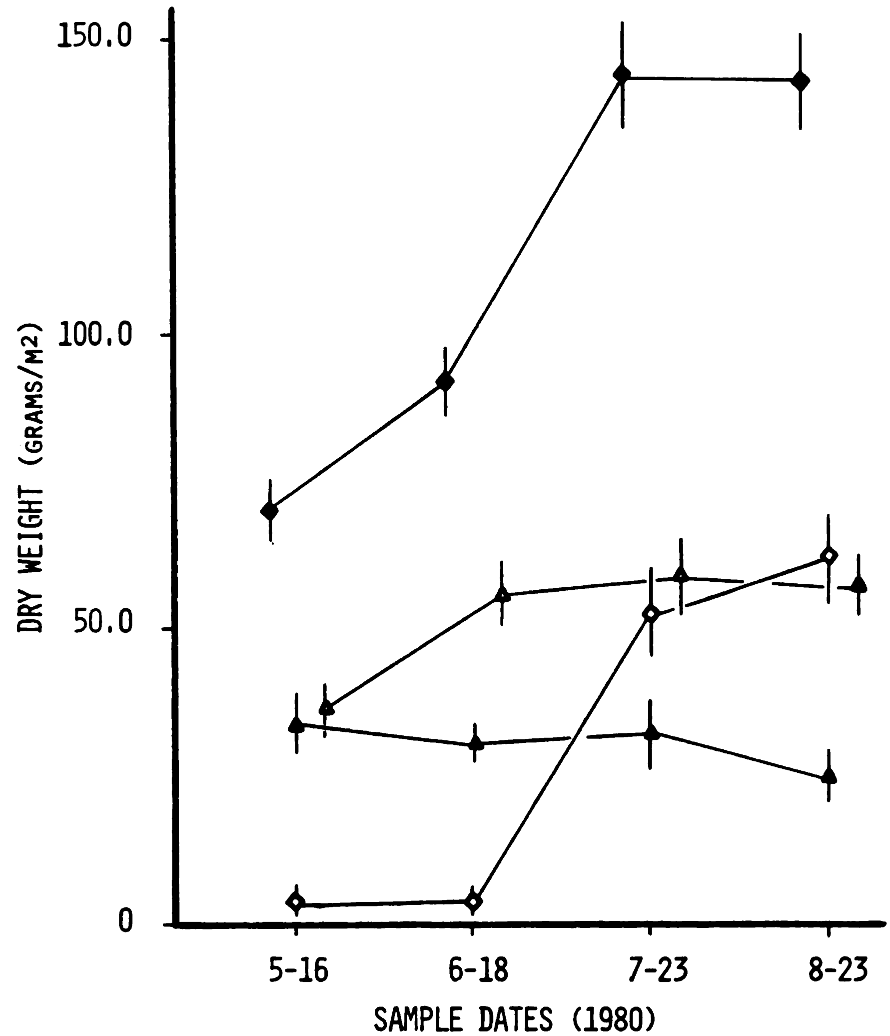


FIGURE 12. COMPARISON OF MONTHLY STANDING CROP FOR *Vaccinium spp.* (▲), *Pteridium aquilinum* (◇), MISC. SPECIES (▲) AND TOTAL GROUND COVER VEGETATION (◆) IN STAND III DURING THE 1980 GROWING SEASON. VERTICAL LINES REPRESENT ± ONE STANDARD ERROR.

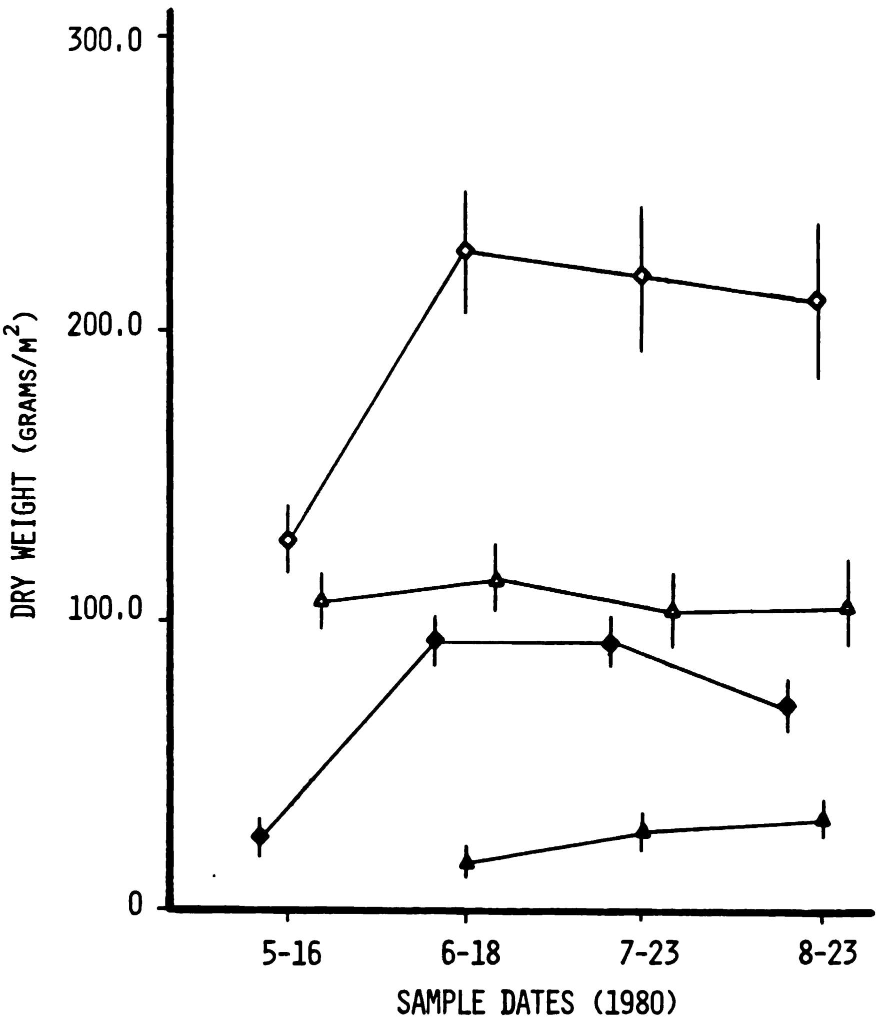


FIGURE 13. MONTHLY STANDING CROP IN VACCINIUM SPP. STEM WOOD (▲), FOLIAGE (◆), NEW TWIGS (▲) AND TOTAL SHRUB BIOMASS (◇) DURING THE 1980 GROWING SEASON. VERTICAL BARS INDICATE ± ONE STANDARD ERROR.

DISCUSSION

Growth and Development of Jack Pine Forests

Tree Growth, Mortality and Stand Structure

The sites selected for study contained forest stands of the jack pine type which occur on dry sandy plains throughout northern lower Michigan. The three stands had site index values of less than 15.0 m (50 yrs) which places them in the poor site class of Gevorkiantz (1947). Site index values were within the range of values estimated by Shetron (1969) for jack pine forests occurring on Grayling sand.

Mean overstory data for the three stands were compared to published values representing fully stocked jack pine stands occurring on poor sites in the Lake States (Wackerman et al. 1929, Eyre and LeBarron 1944, Gevorkiantz 1947). The study stands were only 40-50% as dense and had 30-40% as much basal area as fully stocked stands of the same age class as reported in the literature. Average tree heights and diameters (dbh) were greater for the study stands and approached values for stands on medium quality sites. Eyre and LeBarron (1944) state that, "trees occurring within understocked stands grow faster in diameter than trees in denser stands, and exhibit less mortality". Stocking in natural jack pine stands is highly variable and results from a combination of several factors during stand establishment and growth (Gevorkiantz 1947). Pawluk and Arneman (1961) and Shetron (1969), studying jack pine growth on several soil types, found a strong correlation between differences in soil physical properties and site index. Similarly, Zahner and Hedrich (1966) studying the influence of fine sand fractions, concluded that soils having a high percentage of fine to medium sands will retain substantially more moisture than coarser textured soils. They suggested that for the Grayling soil series differences in percentage of sand fractions may account for variation in stand structure, tree growth and site index. In addition to soil properties, temperature, light and moisture as well as seed characteristics, germination requirements, competition and insects have been intensively studied to determine their influence on jack pine regeneration, growth, and stand development (Eyre and LeBarron 1944, Cayford 1957, 1963, 1970, Rudolf 1958, Miller 1970).

In the present study, stands differed in mean tree age, diameter, height, tree density and basal area. Variation in mean tree height and diameter and stand density were related to mean stand age. Tree density was greatest in the youngest stand (1611 stems/ha) and lowest in the oldest stand (448 stems/ha). Stand basal area was not directly related to stand age, density or mean diameter but was determined by a combination of stand characteristics. The lower density and basal area for the oldest stand was a result of high jack pine mortality. Soil properties and site index varied slightly between sites. Because of differing stand ages, it is not possible to attribute present differences in stand structure solely to differences in soil factors.

Diameter and height profiles for trees in each stand were similar to those described for other jack pine forests occurring in the

Great Lakes region (Wackerman and Zon 1929, USFS 1933, 1934, Gevorkiantz 1947). The middle diameter and height classes contained the greatest number of trees in each stand. These size class distributions (Figure 3 and 4) illustrate that jack pine forests contain a range of tree sizes from small, suppressed individuals to large canopy dominants.

Age class profiles exhibited a distribution similar to the diameter and height class profiles. Individual tree age varied by 25 years in the youngest and oldest stands and 35 years in the intermediate stand. The age distributions for these stands indicate that jack pine regeneration may last for a considerable time following initial stand establishment. The ranges in tree age for these stands indicates that not all naturally occurring jack pine forests are even-aged stands in which the trees belong to a single age class that dates back to the most recent fire disturbance.

Rudolf (1958), Cayford (1970) and Benzie (1978) describe jack pine as an early colonizer which is normally replaced by more tolerant species. In the oldest stand, white pine saplings are rapidly invading, growing and replacing the deteriorating jack pine overstory. The other two stands are younger in age, denser and more productive than the oldest stand. Presently, they do not yet exhibit any trend toward replacement of the jack pine overstories by any other tree species.

Besides the differences in age, height and diameter class profiles, the three stands exhibited variation in tree mortality. Dead standing stems represented nearly one-half of the total number of standing trees in the oldest stand and less than 20% in the other two stands. The dead standing stems were smaller in diameter on the average than live trees in each stand. Major causes of tree death in jack pine forests include drought stress, insect damage and physical damage from storms (Rudolf 1958). The high number of fallen dead stems in the oldest stand plus the numerous standing dead stems (352 stems/ha) indicates a once more dense stand a high rate of tree mortality. Eyre and LeBarron (1944) state that jack pine forests which occur on poor sites begin to display a high rate of tree mortality after 60 years of age. Yarranton and Yarranton (1975) examined tree mortality for a 60-year old jack pine stand in northern Ontario. They reported that the jack pine survivorship curve was non-linear indicating that the rate of tree mortality was not constant during stand development. They also suggested that intraspecific competition is high during stand development and causes a high rate of tree mortality. Yarranton and Yarranton (1975) indicated that as individuals die the remaining trees appear to exhibit a more regular spatial distribution and be subject to reduced resource competition.

In the oldest stand, in the present study, tree mortality was greatest in the smallest size classes. Radial growth data from trees of all size classes also indicated that the smallest individuals were suppressed and less vigorous. The largest trees in each stand consistently had the widest annual tree rings. The smaller trees were suppressed, as evidenced by their narrow rings and slower growth rates. In the oldest stand it is these suppressed jack pine individuals that are dying. The smaller less vigorous trees in the other two stands are also being out competed for resources by larger trees and are dying at a greater rate. Over time, age and size class profiles for the youngest and intermediate stands are expected to follow a trend similar to those for the oldest stand, with eventual replacement of the jack pine by more tolerant species. It should be noted that death of larger trees by physical storm damage occurs in each stand.

High jack pine mortality and development of a suitable litter layer for seed germination have enabled white pine to become well established in the oldest stand. White pine saplings range up to 25 years in age, with a density of nearly 1,500 stems/ha. Replacement of jack pine by white pine or red pine has been described by several investigators (Sterret 1920, Brown and Petheram 1926, Kitteredge 1935, Rudolf 1958).

Composition of ground vegetation within study stands was similar to that described for other poor quality jack pine forests in the Lake States (Zimmerman 1956, Rudolf 1958). Darlington (1945) states that 95% of the plants associated with jack pine in lower Michigan are perennials which have deep root systems adapted to severe conditions of drought or surface burning. In this study there was an increase in diversity and coverage of ground cover species with increasing stand maturity. Eyre and LeBarron (1944) also reported an increase in understory coverage as stand age and tree mortality increased and overstory coverage decreased. Hansen (1937), studying environmental changes due to thinning jack pine stands, recorded increases in light, soil temperature, soil moisture and growth of understory plants in thinned stands. In the present study, bracken fern was absent in the youngest stand but had a mean coverage value of over 50% in the oldest stand. MacLean and Wein (1977a) also reported that bracken fern coverage was greatest in older jack pine stands throughout New Brunswick, Canada.

Biomass and Production of Jack Pine

Forest biomass and net primary production have been determined for several jack pine stands (Table 18). The aboveground biomass estimates for the three stands for this study are within the range of values reported for jack pine on poor sites. The aboveground biomass estimate of 75.8 mt/ha for the intermediate stand is 24% higher than the values reported for a similar-aged jack pine stand in Minnesota (Crow 1970, 1971) and northeastern New Brunswick (MacLean and Wein 1976). The biomass estimate of 65.7 mt/ha for the youngest stand is within the range of values reported by MacLean and Wein (1976) for similar-aged stands occurring on poor sites. No biomass values for jack pine stands on poor sites are available for comparing the estimate of 71.0 mt/ha for the oldest stand. Hegyi (1972) estimated the aboveground biomass on medium to good sites for 65-year old stands to range between 43.6 and 105.8 mt/ha. He suggests that the substantial range in stand biomass is a result of the variability in stand density.

Table 18. Comparison of mean stand data, aboveground biomass and percent distribution of biomass by components (in parentheses) for selected natural stands of jack pine.

Reference	Location	Stand Age (yrs)	Tree DBH (cm)	Tree Height (m)	Tree Density (stems/ha)	Basal Area (m^2/ha)	Site Index (ht/50yrs)
Crow (198)	Northern Minnesota	51	12.1	11.6	1482	18.1	12.4
Doucet *et al*. (1976)[1]	Southern Quebec	44	13.3	15.3	1828	23.6	16.5
		44	11.3	13.4	2034	21.7	14.5
Hegyi (1972)[1]	Northern Ontario	30	11.4	12.2	NA[2]	22.9	NA
		65	21.1	20.1	NA	16.1	NA
MacLean and Wein (1976)[1]	Northeastern New Brunswick	36	NA	NA	3040	17.9	NA
		48	NA	NA	3840	24.8	NA
Present Study	Northern Lower Michigan	37	12.1	10.9	1610	20.2	13.8
		52	16.8	15.2	960	22.3	14.8
		75	21.0	19.1	448	16.2	14.5

1. Values were averaged for three or more stands of similar age and site quality.

2. Data Not Available

Table 18. Continued

			ABOVEGROUND BIOMASS DATA (mt/ha)						
Reference	Location	Stand Age (yrs)	Stem Wood	Stem Wood + Bark	Bark	Live Branches	Live Branches+ Needles	Needles	Total Above-ground
Crow (1970)	Northern Minnesota	51	39.7 (68.6)	46.5 (80.4)	6.8 (11.8)	6.5 (11.2)	11.3 (19.6)	4.8 (8.4)	57.8
Doucet <u>et al</u>. (1976)	Southern Quebec	44	66.0 (76.6)	73.0 (84.7)	7.0 (8.1)	8.8 (10.2)	13.2 (15.3)	4.4 (5.1)	86.2
		44	51.7 (68.0)	57.9 (76.1)	6.2 (8.2	11.4 (15.0)	18.1 (23.9)	6.7 (8.9)	76.1
Hegyi (1972)	Northern Ontario	30	NA	NA	NA	NA	NA	NA	78.0
		65	NA	NA	NA	NA	NA	NA	69.9
MacLean and Wein (1976)	Northeastern New Brunswick	36	NA	NA	NA	NA	NA	NA	56.2
		48	NA	NA	NA	NA	NA	NA	76.6
Present Study[3]	Northern Lower Michigan	37	44.2 (67.4)	51.1 (77.8)	6.9 (10.5)	8.6 (13.1)	14.5 (22.1)	5.9 (9.0)	65.7
		52	49.8 (65.4)	57.1 (75.0)	7.3 (9.6)	12.1 (15.9)	19.0 (25.9)	6.9 (9.1)	75.8
		75	53.8 (75.9)	59.7 (84.2)	5.9 (8.3)	6.9 (9.7)	11.2 (15.8)	4.3 (6.1)	71.0

3. Biomass data for stem wood, stem bark, branches and needles from Table 8.

Doucet (1974) and Doucet et al. (1976) estimated the aboveground biomass and net primary production for several 40-year old jack pine stands on medium to good quality sites within Quebec. They reported that aboveground biomass increased with improved site quality and stand density. Maximum biomass values were for the densest stands on the best sites with the lowest values reported for stands on medium quality sites which also had the lowest tree density. However, total aboveground net primary production was found to be slightly greater within jack pine stands occurring on the medium quality sites. Stem wood production estimated for the youngest stand in the present study is within the range of values reported by Doucet (1974) for stands of low density.

The studies of Hegyi (1972) and MacLean and Wein (1976) have indicated that biomass of jack pine stands increases up to an age of 50-60 years, after which it begins to decline. Within the present study, the intermediate age stand of 52 years contained approximately 10% more total aboveground biomass than the 75-year old stand and 13% more than the 36-year old stand. Rates of mean annual stem wood production were found to be similar for the youngest and intermediate stands, which were approximately 35% greater than estimates for the oldest stand. The low rate of wood production within the oldest stand can be partially explained by the low stand density resulting from high tree mortality in the stand. In addition, comparison of basal area increments in stem wood between the three stands indicates that trees in the younger two stands are presently increasing or maintaining a steady rate of wood production. Trees within the oldest stand exhibit a constant or declining rate of annual stem growth. Therefore, the youngest and intermediate stands show a constant increase in aboveground biomass, while the oldest stand with high mortality exhibits a continual decrease in overstory biomass. Eyre and LeBarron (1944), Gevorkiantz (1947), Rudolf (1958) and Benzie (1978) recommend that for pulpwood harvest jack pine stands be harvested by age 50 to 55 years when mean annual growth is at its highest point and just prior to high tree mortality.

In addition to site quality and stand age, tree density within jack pine stands has been shown to be an important factor in determining individual stand biomass and annual production. Hegyi (1972) Doucet (1974) and MacLean and Wein (1976) have shown that variation in total aboveground biomass between jack pine stands of similar age and site quality can be partly explained in terms of stocking or stand density. Doucet (1974) reported that biomass increased linearly with stand density. He suggested that the denser stands achieved full occupancy of the site at a younger age than more open stands and as a result contained greater biomass. However, Rudolf (1951) warns that over-dense jack pine stands will exhibit high rates of tree mortality at a younger age and have reduced diameter growth.

Tree density within this study was greatest for the youngest stand and least in the oldest stand. Stem wood production was greatest for the two younger stands. The oldest stand exhibited both a high rate of tree mortality and a declining rate of mean radial growth for the remaining trees. Stem wood production for the oldest stand was significantly less than that estimated for the two younger stands. Peak annual production of the jack pine forests examined in this study occurred in dense young to intermediate aged (30-50 years) stands. Whereas, maximum biomass was attained in the intermediate to old aged stands (50-70 years) and just prior to increased rates of tree mortality. Zavitkovski et al. (1981) have shown that biomass production by jack pine can be increased through selection programs which match the seed source to the most suitable site.

Comparison to Regional Forest Types

The aboveground live tree biomass in the study stands as estimated by regression analysis (65.7-75.8 mt/ha) places them at the low end of the range for either temperate evergreen (60-2,000 mt/ha) or boreal (60-400 mt/ha) forest types (Whittaker and Likens 1975). Aboveground biomass of the overstory for all reported jack pine stands (30-100 yrs) ranges between 40-160 mt/ha. The lowest values are from stands of low density or those occurring on dry, sandy sites. Belowground biomass for jack pine has been found to range between 13-17% of total stand biomass within 35-51 year old stands (Crow 1970, Morrison 1974, Alban et al. 1978). Using a value of 17% for belowground biomass gives a range of 47-187 mt/ha for total overstory biomass within jack pine stands. This range of values still falls below the average values of

350 mt/ha and 200 mt/ha for temperate evergreen and boreal forest (Whittaker and Likens 1975). The range and average values of Whittaker and Likens (1975) were obtained from studies which included estimates from several old-growth forest types that had accumulated considerable biomass.

Crow (1978) has reviewed forest biomass and productivity data from the western Great Lakes region. He suggests that the aboveground biomass within second growth forest ranges between 100-200 mt/ha. Recent studies by Koerper and Richardson (1980) on largetooth aspen stands in Michigan gave a range of 38.5-171 mt/ha for aboveground biomass. The lowest stand biomass occurred within a 60-year old aspen stand on a sandy soil. A similar study by Pastor and Bockheim (1981) in a trembling aspen-mixed hardwood forest on a sandy loam soil in northern Wisconsin reported a value of 100.1 mt/ha for aboveground overstory biomass. The range of aboveground biomass within jack pine stands (40-160 mt/ha) for this region is within the range of values reported for other second growth forest types. However, the majority of jack pine forests occur on the most unproductive sites and could be expected to have aboveground biomass levels below or near the low end of the biomass range for the region (Crow 1978).

Maximum values for forest biomass within the Great Lakes region are from old-growth stands. Crow (1978), extrapolating from basal area data, obtained an estimate of 572 mt/ha for a white pine-hemlock-northern hardwood stand in northern Wisconsin. Murphy and Kroh (1982), using non-destructive techniques, estimated the total biomass of a American beech-sugar maple stand in southwestern Michigan at 515 mt/ha. In a similar study, Rose (1982) estimated the total biomass of an old-growth white pine stand in north-central lower Michigan at 681 mt/ha. The white pine stand investigated by Rose (1982) is within three kilometers of the 75-year old stand chosen for this study. These two stands exhibit considerable contrast in stature and total biomass. The white pine stand is three to four times older than the jack pine stand and has accumulated eight times the biomass. The soils within the main area of white pine studied by Rose (1982) are mapped as belonging to the Rubicon Series (Veatch _et al_. 1931a). Soils of the Grayling series, examined in this study, are described by Veatch _et al_. (1931a) and Shetron (1969) as being less developed and having slightly lower moisture content than soils of the Rubicon series. These studies on secondary and old-growth forest types within the Great Lakes region have shown that forest biomass varies considerably with species, stand age and site quality.

Within the Great Lakes region estimates of net primary productivity are available for several forest types. Crow (1978) reported aboveground production to range from 7.1 to 10.4 mt/ha for several forest types in Minnesota and Wisconsin. A recent study by Pastor and Bockheim (1981) estimated the production rate of an aspen-mixed hardwood stand to be 10.3 mt/ha/yr. Aboveground production in three largetooth aspen stands was 11.0, 7.3 and 2.9 mt/ha/yr on sites of good, medium and poor quality (Koerper and Richardson 1980). An old-growth beech-maple stand studied by Murphy and Kroh (1982) had an average annual aboveground production of 7.4 mt/ha. The mature white pine stand (Rose 1982) was estimated to have an annual production of 5.3 mt/ha. Doucet (1974) estimated aboveground productivities for jack pine stands in Quebec to range from 3.0 to 4.7 mt/ha/yr on good sites and 3.8 to 5.5 mt/ha/yr on medium quality sites.

In the present study, non-destructive techniques gave stem wood production estimates of 1.50, 1.45, and 0.95 mt/ha/yr for the youngest, intermediate and oldest stands, respectively. Applying a ratio of 0.479 for stem wood production to total production of jack pine (Doucet 1974) gives total aboveground estimates of 3.0, 3.1 and 2.0 mt/ha/yr for the youngest, intermediate and oldest stands, respectively. From the available date, net primary productivity of forests stands in the Great Lakes region ranges from 2.0 to 11.0 mt/ha/yr. Maximum values have been reported from aspen stands occurring on loamy sands and sandy loams with minimum values from jack pine stands on dry sandy soils.

Whittaker and Likens (1975) provide a range of 6.0-25.0 mt/ha for net primary productivity within temperate evergreen and temperate deciduous forests. For boreal forests they give an average value of 8.0 mt/ha/yr and a range of 4.0-20.0 mt/ha/yr. Their values include belowground production estimates which were not included in the studies from the Great Lakes forest types. Assuming a ratio of 0.15 (Herman 1974) for belowground production:aboveground production and applying it to the data from Great Lakes forests gives a range in total net primary productivity of 2.3 to 12.7 mt/ha/yr. These estimates suggest that the values of Whittaker and Likens (1975) may need to be revised as additional data become available.

Annual productivity within jack pine forests on poor sites is below the estimates suggested for either temperate coniferous or boreal forest types. The average value for net primary production given by Whittaker and Likens (1975) was 13.0 mt/ha/yr for temperate evergreen forests. On better quality sites, net primary production by natural jack pine stands is at the low end of the range for temperate evergreen forest. The maximum reported biomass production by jack pine was 11.9 mt/ha/yr within intensively cultured and irrigated plantations (Zavitkovsky 1979, Zavitkovsky and Dawson 1978).

Distribution of Biomass and Production with a 75-year old Jack Pine Stand

Within the oldest stand biomass and net primary production were estimated for the jack pine overstory, white pine sapling, shrub and ground vegetation strata. The amount and percent distribution of biomass and production by strata and species is summarized within Table 19. The estimates for ground cover species should be considered as minimum values since the peak standing crop method does not account for losses before or production after the sample date (Odum 1960, Kelly *et al*. 1974, McLaughlin 1978). Also, other sapling species were present in minor amounts but were not sampled or included within the summary table.

Table 19. Distribution of living biomass and annual production by strata, species and components within Stand III for 1979. Jack pine production estimates are 5-year annual means. Biomass/Production ratios are also provided.

Species	BIOMASS DATA (kg/ha) Aboveground Biomass	% Stand Total	PRODUCTION DATA (kg/ha/yr) Aboveground Production	% Stand Total	Biomass / Production
Tree Overstory					
Pinus banksiana[1]					
Stem Wood	51,759	74.0	951	22.4	
Stem Bark	5,450	7.8	103	2.4	
Live Branches	5,925	8.5	123	2.9	
Needles	3,299	4.4	769	18.1	
Total[2]	66,232	94.7	1946	45.8	34.0
Sapling Layer					
Pinus strobus[3]					
Stem Wood + Bark	424	0.6	88	2.1	
Live Branches	359	0.5	133	3.1	
New twigs	61	0.1	61	1.4	
Needles	379	0.5	234	5.5	
Total	1223	1.8	516	12.1	2.4
Shrub Layer					
Vaccinium spp.					
Stem + Branches	436	0.6	67	1.6	
New Twigs	137	0.2	137	3.2	
Foliage	329	0.5	329	7.7	
Total	902	1.3	533	12.5	1.7
Ground Cover Layer					
Gaultheria procumbens	161	0.2	60	1.4	
Epigaea repens	297	0.4	90	2.1	
Maianthemum canadense	44	0.1	44	1.0	
Pteridium aquilinum	775	1.1	775	18.2	
Carex pensylvanica	278	0.4	278	6.5	
Misc. species	12	0.1	12	0.3	
Total	1567	2.2	1259	29.6	1.2
Stand Total	69,924		4254		16.4

Table 19. continued

1. Jack pine biomass values are from Table 8, production values for stem wood are from Table 10, needle production estimate is from litter fall data, bark and branch wood production estimated from ratio: stem wood biomass/stem wood production = component production/component biomass.

2. Total biomass for jack pine is the sum of the components rather than being estimated by a regression equation as in Table 8.

3. White pine values are from Table 16.

The total living aboveground biomass for the stand is estimated at 69.9 mt/ha with 95% contained within the jack pine overstory. White pine saplings, blueberry shrubs and bracken fern together contributed 5% of the total aboveground stand biomass. Crow (1970) reported a similar distribution for a 51-year old jack pine stand in Minnesota. MacLean and Wein (1977a) estimated that undergrowth species (shrubs + herbs) accounted for 71-88% of total aboveground biomass in 13- and 16-year old jack pine stands and only 1-6% within older stands. They attribute the initially high biomass contribution of understory species to their rapid regeneration following fire disturbance. Zavitkovski (1976) reported a mean aboveground understory biomass of 161 g/m^2 for early successional coniferous forests. The higher estimate for understory biomass (247 g/m^2) in the oldest stand, from this study, is a result of high overstory mortality and increased understory production. Bracken fern accounted for 31% of the total aboveground understory biomass.

Although the sapling, shrub and ground cover strata accounted for only 5% of the total stand biomass, they contributed approximately 54% of the stand's net primary productivity. The remaining 46% was produced by the jack pine overstory of which 22% and 18% was in the form of new stem wood and foliage. Bracken fern alone represented 18.2% of the total aboveground net primary production within the stand. These estimates are in contrast to Whittaker and Marks (1975) statement that, "in many woody communities, both successional and climax, the

the contribution of the undergrowth to community productivity is small (from several percent to less than 1%)". Their statement is based primarily on data taken from mature hardwood stands that have a well developed and dense canopy which suppresses the growth of understory vegetation. MacLean and Wein (1977a) also noted an increase in understory production within older (45-50 yrs) jack pine stands in New Brunswick. Ovington (1962) states that the contribution of ground vegetation to ecosystem production is greatest during juvenile and old stages of development. It is during these stages that the overstory does not form a complete canopy, thus allowing greater growth of understory vegetation. Recent studies by Foster (1974), Foster and Morrison (1976) and MacLean and Wein (1976, 1977a, b, 1978, 1980) have indicated that the understory vegetation within jack pine stands is important in cycling and accumulating nutrients on otherwise nutrient poor soils.

Biomass accumulation ratios (BAR) for the overall stand and dominant species for each stratum are included in Table 19. The BAR value of 16.4 for the entire stand is similar to values given by Whittaker (1966) for pine-heath forest types (13.8-15.9) in the Great Smoky Mountains. The relatively high BAR value for jack pine (34.0) reflects the low productivity and attainment of maturity for this successional tree species. In contrast, the low BAR for white pine (2.4) reflects the open grown appearance and high productivity of the saplings. The BAR value for the blueberry shrubs (1.7) is similar to values reported for

Vaccinium vacillans (1.6) and *V. angustifolium* (1.55) by Whittaker and Woodwell (1968).

Structural, biomass and productivity data from the oldest stand reinforces the visual appearance of the stand: an open canopy with well-developed sapling and understory layers. Presently, the physiognomy of the stand resembles more a woodland than a closed forest community. The data suggest that the jack pine overstory is gradually being replaced by the white pine saplings.

Jack Pine in Northern Lower Michigan

Forest Stand Growth and Development

Jack pine dominated forest communities represent an important cover type for northern lower Michigan. Species common to these forests are adapted to resprouting, reseeding and recolonization following fire. The post-settlement distribution and present composition of forest types in northern lower Michigan have been significantly influenced by the frequency and widespread occurrence of fire disturbance. Kittredge and Chittenden (1929) reported that fires burned on the average of every nine years in parts of the oak and oak-pine forests of northern lower Michigan. They indicate that frequent burning of oak forests prevents the natural conversion of oak stands to red pine or a mixture of red pine and white pine. Kilburn (1960) states that as fire disturbance is reduced or eliminated within the xeric jack pine forests of Cheboygan County, Michigan, northern pin oak (*Quercus ellipsoidalis*) will increase in abundance and replace the pine. Several investigators (Beal 1888, Roth 1902, Darlington 1945, Zimmerman 1956, Kilburn 1958, 1960) have described the increased importance and abundance of jack pine following the early lumbering activities (1870-1900) and subsequent slash fires in northern lower Michigan.

Presently, few natural jack pine or jack pine-oak communities exist in Michigan that are greater than 50 years in age. Frequent spring and summer fires occur throughout the region, often destroying large areas of mature jack pine and jack pine-oak communities. Heinselman (1973) has estimated that jack pine forests within the Boundary Waters Canoe Area of northern Minnesota, prior to implementation of fire suppression policies, burned at intervals of 50 to 100 years. His findings indicate that the extensive presettlement conifer forests of the Lake States were of fire origin. Maissurow (1941), Ahlgren and Ahlgren (1960), Frissell (1973), Swain (1973), Wright and Heinselman (1973) and Boerner (1982) strongly emphasize that random periodic fire disturbance should be considered a natural and common component of many temperate ecosystems.

In addition to influencing species composition and stand structure, periodic fire disturbance has been described as having a significant impact on such ecosystem properties as primary productivity, biomass, species diversity and nutrient cycling (Ahlgren and Ahlgren 1960, Heinselman 1973, 1981, Shafi and Yarranton 1973, Kozlowski and Ahlgren 1974, Ohmann and Grigal 1979). Loucks (1970) and Heinselman (1973) suggest that for some temperate forest ecosystems, periodic disturbance is essential to the maintenance of long-term species diversity, productivity and ecosystem stability. The availability of differing aged jack pine forests on similar sites in northern lower Michigan, provides an opportunity to investigate developmental trends in forest biomass and annual production. In addition the impact of periodic fire disturbance can be examined. However, as Peet (1981) emphasizes "this approach is subject to error resulting from stochastic variation in initial site conditions and stocking levels". But, owing to the length of time required for forest stand development this is the only approach readily available. It must also be emphasized that the conclusions from my study may be valid only for jack pine stands occurring on deep, dry sandy soils.

Results from my study indicate that for jack pine on oligotrophic sites in northern lower Michigan, stand development may be divided into four phases. The first stage of development is the initial post-fire establishment period which lasts from 10 to 20 years following fire disturbance. It is during this period that jack pine seedlings and associated species become established and gain dominance of the site. The second phase may be described as the period of stand development which last from age 20 to 50 and is characterized by dramatic increase in jack pine size. It is during this stage that canopy closure occurs. The third stage, from age 50 to 70, may be described as the mature stand stage in which tree growth rates slowly decline. The final stage, for stands greater than 70 years in age, is the senescent phase in which tree mortality progressively increases, the original stand structure is lost, and replacement of jack pine by more tolerant species occurs. This developmental sequence is based upon data from only three jack pine stands. Additional data is needed for all age classes to verify the accuracy of the sequence. However, Hegyi (1972) and MacLean and Wein (1976) have described similar developmental sequences for jack pine forests in Canada. Heinselman (1973, 1981) suggest, that for jack pine stands in northern Minnesota, the mature stage may last up to a stand age of 100 to 150 years with individual trees reaching ages of over 200 years. He also indicates that in presettlement times fires normally recycled the sequence during the mature stand stage of development.

Using data from the present study and similar studies (Hegyi 1972, MacLean and Wein 1976) developmental trends in biomass accumulation and net primary productivity can be presented for jack pine forests and compared to patterns described for other forest types. Because of the lack of sufficient data, the discussion will be limited to aboveground biomass and production of trees. Also, I assume that a dense stand of jack pine is established following a disturbance.

From the developmental sequence, jack pine biomass may be described as accumulating slowing during the initial post-fire establishment period, followed by a rapid accumulation up until canopy closure, then leveling off during the mature stand stage. Advanced mature and senescent stands would exhibit a continual decline in overstory biomass as a result of decreased growth rates and increased tree mortality. Overstory biomass would continue to decline until new trees fill in the canopy. Heinselman (1973, 1981) suggest that periodic fire disturbance functions to recycle jack pine forests at intervals of less than 50 to 100 years and in some situations less than 20 years.

For the present study, biomass accumulation may be described as following the asymptotic model of Odum (1969), at least up until the senescent stage. Peet (1981) has reviewed similar studies which provide additional evidence that biomass accumulation during stand development for several forest types follows "an asymptotic or logistic accretion model". This type of model has most often been used to describe biomass accumulation for tree species that occur in even-aged stands.

The pattern for net primary productivity during jack pine stand development is similar to that described for biomass accumulation. Annual production following disturbance steadily increases to a maximum level and then gradual declines as the original trees age and lose their productive capacity. In my study, aboveground production was greatest for the 37-year old stand and progressively less in the 52- and 75-year old stands. The actual rate of annual production and the age at which peak production is attained in jack pine stands has been shown to vary with site conditions and initial stand densities (Hegyi 1972, MacLean and Wein 1976, Doucet _et al_. 1976). For senescent stands with high tree mortality, annual production will decline until replacement of jack pine by more rapidly growing and younger trees or disturbance of the stand. In the present study, white pine saplings and seedlings were present and in time and barring disturbance are expected to replace the jack pine overstory.

SUMMARY

Jack pine dominated forest communities represent an important cover type for northern lower Michigan and account for a significant portion of the state's annual timber harvest. The primary objective of this study was to estimate the standing live tree biomass and net primary productivity of typical jack pine stands of north-central lower Michigan. These data are essential for evaluating forest management programs and as a first step toward understanding the structure and functioning of jack pine dominated ecosystems. A secondary objective of this study was to characterize developmental trends in biomass and productivity for jack pine dominated plant communities.

Three jack pine stands of natural origin and representing an age series of 37, 52 and 75 years were selected for study. Tree density ranged from 448 stems/ha in the oldest stand to 1611 stems/ha for the youngest stand. Stand basal areas were 20.2, 22.0 and 16.2 m^2/ha for the youngest, intermediate and oldest stands, respectively. Distribution of jack pine trees by diameter and age classes illustrated the narrow ranges in these stand characteristics that is typical for this forest type. Jack pine mortality was greatest in the oldest stand, but decreased with increasing tree diameter in the stand. Radial growth data indicated that smaller diameter trees in each stand exhibited slower growth rates than larger more dominant trees.

Estimates of tree biomass and net primary productivity were obtained by using published regression equations for jack pine. Values

for selected stand components were compared to estimates derived by alternate non-destructive techniques. Regression estimates of total aboveground live tree biomass were 65.7, 75.8 and 71.0 mt/ha (dry weight) for the youngest, intermediate and oldest stands, respectively. Stem wood represented 78.3% of total aboveground live tree biomass in the oldest stand and 67.4% and 65.4% for the youngest and intermediate stands, respectively. Canopy components (branches + needles) accounted for 23.9% (intermediate stand), 21.0% (youngest) and 12.3% (oldest) of total aboveground live biomass. Assuming that belowground biomass was 17% of aboveground live tree biomass (Crow 1970, Morrison 1970), total biomass of living trees was estimated to range from 81.3 mt/ha in the youngest stand to 93.4 mt/ha in the intermediate stand. Non-destructive biomass estimates for stem wood, stem bark and stem wood plus bark components were within 11.0%, 20.0% and 16.0% of regression estimates for the youngest, intermediate and oldest stands, respectively.

Non-destructive techniques for estimating the aboveground net primary productivity of stem wood ranged from 16.0% less than to 78.0% more than values derived from using available regression equations. Since non-destructive productivity estimates were based upon radial growth measurements of sampled trees they were accepted as being more reasonable estimates for net primary productivity. Stem wood plus bark production, estimated by non-destructive methods, was 1.72, 1.67, and 1.05 mt/ha/yr for the youngest, intermediate and oldest stand, respectively. Needle production estimated from litter fall collections was 710 kg/ha for 1979 and 769 kg/ha during 1980 in the oldest stand.

Species composition, sapling density and percent coverage were recorded for understory vegetation in each study stand. Jack pine was the only sapling species recorded in the youngest stand, whereas oak was the dominant sapling species in the intermediate stand and white pine in the oldest stand. A total of 21, 19 and 29 ground cover species were present in the youngest, intermediate and oldest stands, respectively. Blueberries (Vaccinium spp.) were the dominant shrub species in each stand. Abundant ground cover species in the three stands included Carex pensylvanica and Danthonia spicata. Prostrate shrubs, such as Arctostaphylous uva-ursi and Gaultheria procumbens were present in each stand and often formed extensive patches. Bracken fern (Pteridium aquilinum) was highly abundant in the oldest stand and not sampled in the youngest stand although it was present in the stand.

The distribution of aboveground biomass and net primary production between overstory and understory species was determined for the oldest stand. White pine sapling biomass and productivity were estimated by standard dimension analysis techniques. Regression equations for estimating aboveground sapling biomass and production had r^2 values which exceeded 0.95 and E (estimate of relative error) values of less than 1.013, indicating a strong correlation between component biomass or production and sapling basal diameter. Total aboveground biomass and net primary production were 1223.1 kg/ha and 516.5 kg/ha/yr, respectively. The distribution of biomass among sapling components was

35%, 34% and 31% for stem wood with bark, branch wood with bark, and needles, respectively. In white pine, annual aboveground production represented 42% of the total aboveground biomass during the 1979 sample year. Needle production contributed the largest share (45%) of total aboveground production, followed by branch wood plus bark (26%) and stem wood plus bark (17%) components.

The aboveground biomass and productivity for ground cover species in the oldest stand were estimated by harvesting 20 randomly located sample quadrats in August of 1979 and monthly from May to August of 1980. Total aboveground ground cover biomass ranged from 246.9 g/m^2 in August of 1979 to 274.4 g/m^2 in August of 1980. Blueberry shrubs and bracken fern together accounted for 68.0% and 82.1% of the total aboveground biomass for all ground cover species in 1979 and 1980.

The distribution of total aboveground live biomass and annual production among overstory and understory species was determined for the oldest stand during 1979. The stand had a total aboveground biomass of 69.9 mt/ha and an annual production of 4.3 mt/ha. Jack pine represented the greatest share of both stand biomass (94.7%) and annual production (45.8%). White pine saplings contributed 1.8% of the total stand biomass and 12.1% of the annual production. Blueberry shrubs and ground cover species accounted for 1.3% and 2.2% of the total biomass and 12.5% and 29.6% of the total stand production, respectively. Bracken fern alone contributed 18.2% to the total aboveground production of the stand.

The aboveground biomass and net primary productivity estimates for the study stands are within the range of values reported for similar jack pine dominated communities in Wisconsin, Minnesota and Ontario. Comparison of biomass and production estimates for jack pine forests indicates that biomass and annual production increases with increasing site quality and stand density (Hegyi 1972, Doucet 1974). In addition, this and similar studies have shown that stem wood production in jack pine stands on poor quality sites increases up to an age of 50 to 60 years after which it gradually declines.

Total (aboveground + belowground) overstory biomass estimates for the study stands plus those values available in the literature give a range of 47-187 mt/ha for jack pine forests. This range in stand biomass is below the average estimates reported for temperate evergreen (350 mt/ha) and boreal (200 mt/ha) forest types. However, biomass and productivity estimates for the study stands are within the range of values given by Crow (1978) for other second growth forest types occurring on sandy soils in the Great Lakes region.

Previous studies which describe forest succession in northern lower Michigan suggest that jack pine is either replaced by a red or white pine stage or an oak dominated community which in turn are succeeded by a climax northern hardwood forest. In the present study, replacement of jack pine by white pine was evident only in the oldest study stand. The two other sample stands did not clearly exhibit any successional trends. Other sites visited during this study did indicate replacement of jack pine by red oak and northern pin oak. Considerable data need to be collected to adequately determine species replacement patterns following jack pine dominance in northern lower Michigan.

CONCLUSIONS AND RECOMMENDATIONS

I will conclude with a listing of the more significant findings of this research and a discussion of recommended modifications to my research plan and suggestions for future research projects. This study was undertaken to obtain data on the structure, biomass and net primary productivity of jack pine forests occurring on Grayling sand in northern lower Michigan. A sequence of three jack pine stands, ranging in age from 37 to 75 years, were selected for study. The more important conclusions that can be drawn from this study are:

1. Tree height, diameters, and ages were found to exhibit unexpected ranges in each stand. These data indicate that jack pine regeneration may extend over a period of 25 or more years in some jack pine forests and result in considerable stratification of trees into size and age classes.

2. Radial growth and mortality data indicate that the smaller and younger trees in jack pine stands exhibit slower growth and higher mortality rates than the larger and more dominant individuals.

3. Results from this and similar studies suggest that for jack pine forests on oligotrophic sites overstory biomass increases continually during stand development up to an age of 50 years and remains near this level before declining at an age of approximately 70 years in senescent stands.

4. Similarly, net primary production is greatest for 30 to 50 year old stands and progressively declines in older stands as a result of

decreased growth rates and increased tree mortality. Biomass and net primary production of jack pine stands have been shown to be highly influenced by site conditions, initial stands densities and stand age (Hegyi 1972, Doucet 1974).

5. Biomass and annual production estimates for jack pine forests on oligotrophic sites in northern lower Michigan are below mean values reported for temperate evergreen and boreal forest types. These estimates may represent minimum values for second growth forests in the Great Lakes region.

6. Understory vegetation in senescent jack pine stands contributes a significant portion of the total production for the stand.

The results and conclusions summarized above must be interpreted in light of the limitations of this study. In addition to recommending changes to this research, I will conclude with suggestions for future research projects involving forest production and succession in northern lower Michigan.

1. One of the more serious limitations of this study is that only three jack pine stands were intensively sampled for estimates of growth rates, biomass and annual production. More data are needed on the structure, biomass and rates of production for all age and density classes. Information from additional stands will add to our knowledge on rates of jack pine mortality and survivorship, partitioning of biomass and production (e.g. aboveground and belowground) and successional patterns in community and ecosystem properties.

2. No trees were harvested during this study. Additional harvest data for jack pine are needed to verify the accuracy of published regression equations and specific gravity values used in the calculation of tree biomass and production. Such data will allow the derivation of more accurate relationships which will make possible the rapid estimation of forest biomass and production at additional sites.

3. A possible source of error in this study is in estimating radial growth and wood production from single increment cores for each sample tree. Radial wood increment varies with aspect and height in tree stems. Additional increment cores or stem cross-sections at differing locations along tree stems would provide more accurate measurements and estimates of radial growth.

4. In this study no data were collected for estimating organic matter content of litter and soil components. Such data would provide information on total stand biomass and rates of organic matter turnover for jack pine ecosystems.

5. An additional restriction of my research is that only jack pine forests occurring on Grayling sand were selected for study. Data for stands growing on other soil types are badly needed for evaluating the influence of site factors on forest growth.

6. Similarly, little information is presently available for the jack pine-oak forest association of northern lower Michigan. Data on this forest type are needed for analyzing successional patterns and for design of proper management programs.

Finally, there is a need for developing long term ecological studies of jack pine and associated forest types. These forest types represent an important natural resource for the state of Michigan. More detailed information on year to year variation in annual rates of production and how these forest types respond to environmental fluctuation is essential for understanding overall ecosystem dynamics and for developing long range management programs.

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APPENDIX

APPENDIX I

Description of Grayling Soil Series

The Grayling series is a mixed, frigid Typic Udipsamments. These soils are sand throughout. Typically they have black and grayish brown A horizons, dark brown and strong brown B horizons, and light brown C horizons.

Typical Pedon: Grayling sand - forested. (Colors are for moist soil unless otherwise stated).

A1 & A2: 0 to 3 inches; black (N 2/) (A1), and grayish brown (10YR 5/2) sand, (A2); coated and uncoated sand grains mixed throughout the horizon, giving a salt and pepper appearance; moderate organic matter content in upper part; weak medium granular structure; very fragile; very strongly acid; abrupt smooth boundary. (2 to 4 inches thick).

B21ir: 3 to 9 inches; dark brown (7.5YR 4/4) sand; weak coarse granular structure; very friable; medium acid; clear irregular boundary. (4 to 14 inches thick).

B22ir: 9 to 15 inches; strong brown (7.5YR 5/6) sand; very weak coarse granular structure; very friable; medium acid; clear irregular boundary. (4 to 14 inches thick).

B3: 15 to 23 inches; brown (7.5YR 5/4) sand; single grained; loose; medium acid; gradual smooth boundary. (3 to 10 inches thick).

C: 23 to 60 inches; light brown (7.5YR 6/4) sand; single grained; loose; medium acid.

Range in Characteristics: Thickness of the solum ranges from about 15 to 30 inches. The upper eight inches of the solum is sand or loamy sand and the rest of the solum is sand; medium sand is dominant. The upper part of the soil is very strongly acid or strongly acid and the lower part is medium acid or slightly acid. Mean annual soil temperature is estimated to range from about 38 to 43°F. Some pedons have an 01 horizon, ½ to 1½ inches thick. It is dark grayish brown (10YR 4/2) to black (10YR 2/1) and is composed of oak leaves or jack pine needles, some twigs and roots in various stages of decomposition. The A1 and A2 horizons are normally intermixed in a single layer, but some pedons have a separate A2 horizon. In the latter pedons the A1 horizon ranges from 1 to 3 inches in thickness and the A2 horizon from 1 to 3 inches in thickness, but the A2 horizon is intermittent within the pedon.

Setting: Grayling soils are on outwash plains and lake plains of Wisconsin age. Slope gradients are dominantly less than 8% but range from 0 to 15%. These soils formed in sandy glaciofluvial sediments. The climate is continental. Average annual precipitation ranges from 26 to 33 inches; mean to to 68°F.

Drainage and Permeability: Well drained. Runoff is slow or very slow. Permeability is very rapid.

Principal Associated Soils: These are the competing Rubicon and Croswell series and the Au Gres and Roscommon series. Au Gres and Roscommon soils are wetter.

Use and Vegetation: Used for woodland. Jack pine is the principal tree species in the Upper Peninsula of Michigan, whereas jack pine and scrub oak are principal tree species in the northern part of the Lower Peninsula. Ground cover includes lichens, mosses, wintergreen, sweetfern, and blueberries.

Distribution and Extent: Northern part of the Lower Peninsula and the Upper Peninsula of Michigan and Northern Wisconsin. The series is moderately extensive.

Series Established: Alger County, Michigan, 1929.

Remarks: Grayling soils were formerly classified as Brown Podzolic soils.

Reference: United States Department of Agriculture, Soil Conservation Service. 1976. Grayling Soil Series. 4 pp.

Table A-1. Location and site quality information for jack pine sites within north-central Lower Michigan. Data collected during the period 1977-1979.

Stand Number	County	Location	Mean Stand Age (years)	Site Index (m/50yr)	Site Quality Class	Soil Type
1	Crawford	T28N, R1W, Sec.1, nw¼nw¼	36	13.8	Poor	Grayling
2	Crawford	T27N, R3W, Sec.32,nw¼sw¼	52	14.8	Poor	Grayling
3	Crawford	T27N, R3W, Sec.11,ne¼ne¼	76	14.5	Poor	Grayling
4	Crawford	T28N, R1W, Sec.10,se¼se¼	48	15.1	Medium	Grayling
5*	Crawford	T27N, R3W, Sec.12,sw¼sw¼	62	14.8	Poor	Roselawn
6*	Crawford	T25N, R1W, Sec.22,sw¼	46	15.4	Medium	Grayling
7*	Crawford	T25N, R4W, Sec.30,ne¼	45	14.6	Poor	Grayling
8	Crawford	T27N, R1W, Sec.29,sw¼sw¼	48	14.1	Poor	Grayling
9	Crawford	T26N, R3W, Sec.11,sw¼sw¼	58	15.2	Medium	Grayling
10*	Roscommon	T24N, R1W, Sec. 2,ne¼se¼	64	16.5	Medium	Graycalm
11	Roscommon	T21N, R4E, Sec.20,nw¼ne¼	52	14.8	Poor	Grayling
12	Oscoda	T27N, R1E, Sec.15,ne¼ne¼	54	15.3	Medium	Grayling
13	Ogemaw	T24N, R2E, Sec.29,nw¼nw¼	43	13.2	Poor	Grayling
14*	Kalkaska	T27N, R7W, Sec.18,ne¼nw¼	56	13.7	Poor	Rubicon
15	Montmorency	T29N, R2E, Sec.32,nw¼ne¼	47	15.6	Medium	Grayling
16	Oscoda	T25N, R1W, Sec.32,ne¼nw¼	57	15.1	Medium	Grayling

*Site locations and soil descriptions were provided by Shetron (1978). Soil information for remaining sites was taken from county soil survey maps.

Table A-2. Sources of data used by Green and Grigal (1978) to develop generalized regression equations for estimating jack pine biomass

Source	Location	Number of Trees	Range of Data Diameter(cm)	Height(m)
Alban *et al*. (1978)	Central Minnesota	10	10.2-20.1	13.4-20.1
Crow (1970)	Central Minnesota	40	5.8-17.8	6.7-14.1
Doucet *et al*. (1976)	Southern Quebec	36	5.7-19.4	4.7-17.4
Hegyi (1972)	Northern Ontario	77	2.8-32.3	3.2-24.8
Totals		163	2.8-32.3	3.2-24.8

Table A3. Structural plot data for Stand I.

Plot Number	Tree Density (trees/ha)	Mean Tree DBH (cm)	Mean Tree Height (m)	Basal Area (m^2/ha)	Parabolic Stem Volume (m^2/ha)	Estimated Volume Increment (m^2/ha)	Tree Age (yrs)
1	1408	13.3	9.7	21.9	103.0	3.51	36.7 ± 1.0
2	1792	11.5	10.9	20.2	100.5	3.72	37.0 ± 0.9
3	1408	12.6	11.1	20.3	107.0	3.16	36.9 ± 0.9
4	1472	11.8	10.9	18.5	96.5	3.58	36.3 ± 1.0
5	1600	11.9	11.7	18.6	90.7	3.71	37.5 ± 0.6
6	1984	11.3	11.2	21.8	109.7	4.32	35.8 ± 0.7
Stand Values	1610 ± 93.3	12.1 ± 0.3	10.9 ± 0.3	20.2 ± 0.6	101.2 ± 2.9	3.67 ± 0.16	36.7 ± 0.2

Table A4. Structural plot data for Stand II

Plot Number	Tree Density (trees/ha)	Mean Tree DBH (cm)	Mean Tree Height (m)	Basal Area (m^2/ha)	Parabolic Stem Volume (m^2/ha)	Estimated Volume Increment (m^2/ha)	Tree Age (yrs)
1	832	17.5± 0.9	16.5	20.7	141.8	2.80	54.2±1.0
2	960	17.1± 0.7	16.1	22.5	144.8	3.69	52.3±0.9
3	768	17.0±1.2	15.9	18.5	120.9	3.12	56.5±0.8
4	1280	15.9±0.7	14.4	26.4	151.3	4.20	51.0±1.2
5	960	18.2±1.0	15.0	25.9	160.8	3.99	50.7±1.2
6	960	14.8±1.0	13.5	17.8	104.7	3.33	50.9±1.8
Totals	960.0 ± 72.0	16.8±0.5	15.2 ± 0.5	22.0 ± 1.5	137.4 ± 8.5	3.52 ± 0.22	52.6±1.0

Table A5. Structural plot data for Stand III

Plot Number	Tree Density (trees/ha)	Mean Tree DBH (cm)	Mean Tree Height (m)	Basal Area (m^2/ha)	Parabolic Stem Volume (m^2/ha)	Estimated Volume Increment (m^2/ha)	Tree Age (yrs)
1	768	19.3	17.8	23.1	188.8	2.70	73.5±2.4
2	448	22.3	18.4	17.8	148.6	2.11	75.6±2.3
3	256	20.9	17.6	9.0	70.9	1.13	76.0±1.5
4	384	18.8	18.2	10.9	91.3	1.36	76.3±2.6
5	576	23.3	22.1	25.6	253.2	4.12	75.1±1.8
6	448	19.2	17.6	13.1	104.0	1.77	75.5±1.4
7	320	21.0	18.8	11.4	95.8	1.48	75.3±1.4
8	512	18.7	18.6	14.6	123.0	2.65	77.7±1.9
9	512	24.4	22.1	24.2	240.1	3.97	72.8±2.8
10	320	20.4	18.0	10.7	86.1	1.62	73.0±1.3
11	512	19.4	20.6	19.8	183.0	2.97	77.4±1.8
12	320	23.8	19.7	14.5	128.2	1.95	76.2±2.2
Stand Values	448.0 ± 40.9	21.0 ± 0.6	19.1 ± 0.5	16.2 ± 1.7	142.8 ± 17.6	2.32 ± 0.28	75.5±0.4

Table A6. Five-year mean radial increments by 2.5 cm diameter size class for Stand I. Values are means ± one standard error in mm.

Sample period	Diameter Size Class (cm)					
	5.0 - 7.4	7.5 - 9.9	10.0 - 12.4	12.5 - 14.9	15.0 - 17.4	17.5 - 19.9
1945 - 1949	2.42 ± 0.1	1.57 ± 0.2	1.90 ± 0.2	2.65 ± 0.2	2.96 ± 0.4	3.46 ± 0.4
1950 - 1954	1.30 ± 0.1	1.71 ± 0.1	1.89 ± 0.1	2.24 ± 0.1	2.90 ± 0.2	3.25 ± 0.4
1955 - 1959	1.39 ± 0.1	1.53 ± 0.1	1.63 ± 0.1	1.69 ± 0.1	2.10 ± 0.1	2.17 ± 0.1
1960 - 1964	1.28 ± 0.1	1.27 ± 0.1	1.39 ± 0.1	1.55 ± 0.1	1.85 ± 0.1	2.08 ± 0.1
1965 - 1969	1.04 ± 0.1	1.00 ± 0.1	1.22 ± 0.1	1.40 ± 0.1	1.44 ± 0.1	1.61 ± 0.1
1970 - 1974	0.83 ± 0.1	1.11 ± 0.1	1.31 ± 0.1	1.44 ± 0.1	1.54 ± 0.1	1.69 ± 0.1
1975 - 1979	0.56 ± 0.1	0.83 ± 0.1	0.83 ± 0.1	1.07 ± 0.1	1.28 ± 0.1	1.26 ± 0.1
Number of Sample Trees	23	29	34	31	19	10

Table A7. Five-year mean radial increment by 2.5 cm diameter class for Stand II. Radial increment values are means ± one standard error in mm.

Sample Period	Diameter Size Class (cm)				
	10.0 - 12.4	12.5 - 14.9	15.0 - 17.4	17.5 - 19.9	20.0 - 22.4
1925 - 1929	2.22 ± 0.1	1.92 ± 0.1	1.63 ± 0.3	1.52 ± 0.1	1.50 ± 0.1
1930 - 1934	1.39 ± 0.1	1.66 ± 0.2	1.74 ± 0.2	2.03 ± 0.2	2.00 ± 0.1
1935 - 1939	1.86 ± 0.3	1.79 ± 0.2	2.26 ± 0.2	2.68 ± 0.3	2.63 ± 0.1
1940 - 1944	1.69 ± 0.3	1.86 ± 0.2	2.08 ± 0.1	2.14 ± 0.2	2.59 ± 0.1
1945 - 1949	1.35 ± 0.2	1.71 ± 0.1	1.92 ± 0.1	1.94 ± 0.2	2.32 ± 0.1
1950 - 1954	0.91 ± 0.1	1.36 ± 0.1	1.59 ± 0.2	1.72 ± 0.1	1.96 ± 0.1
1955 - 1959	0.86 ± 0.1	0.97 ± 0.1	1.36 ± 0.1	1.47 ± 0.1	1.59 ± 0.1
1960 - 1964	0.65 ± 0.1	0.96 ± 0.1	1.16 ± 0.1	1.25 ± 0.1	1.40 ± 0.1
1965 - 1969	0.67 ± 0.1	0.77 ± 0.1	0.88 ± 0.1	1.13 ± 0.1	1.16 ± 0.1
1970 - 1974	0.80 ± 0.1	0.80 ± 0.1	0.90 ± 0.1	1.09 ± 0.1	1.00 ± 0.2
1975 - 1979	0.61 ± 0.1	0.54 ± 0.1	0.71 ± 0.1	1.09 ± 0.1	1.12 ± 0.2
Number Sample Trees	10	14	21	18	19

Table A8. Five-year mean radial increment by 2.5 cm diameter class for Stand III. Values are means ± one standard error in MM.

Sample Period	Diameter Size Class (cm) 15.0 - 17.4	17.5 - 19.9	20.0 - 22.4	22.5 - 24.9
1905 - 1909	1.99 ± 0.3	3.07 ± 0.5	3.44 ± 0.2	3.69 ± 1.3
1910 - 1914	2.78 ± 0.6	1.94 ± 0.2	2.68 ± 0.2	3.07 ± 0.5
1915 - 1919	1.93 ± 0.3	1.55 ± 0.2	1.77 ± 0.1	2.47 ± 0.4
1920 - 1924	1.39 ± 0.3	1.57 ± 0.2	1.71 ± 0.1	2.42 ± 0.4
1925 - 1929	1.31 ± 0.4	1.34 ± 0.1	1.57 ± 0.1	1.78 ± 0.2
1930 - 1934	1.27 ± 0.2	1.26 ± 0.1	1.55 ± 0.1	1.67 ± 0.2
1935 - 1939	0.96 ± 0.1	1.11 ± 0.1	1.36 ± 0.1	1.53 ± 0.1
1940 - 1944	1.07 ± 0.2	0.96 ± 0.1	1.23 ± 0.1	1.50 ± 0.2
1945 - 1949	1.02 ± 0.2	1.01 ± 0.1	1.36 ± 0.1	1.48 ± 0.1
1950 - 1954	0.97 ± 0.1	1.04 ± 0.1	1.18 ± 0.1	1.53 ± 0.2
1955 - 1959	0.88 ± 0.1	0.87 ± 0.1	1.09 ± 0.1	1.34 ± 0.2
1960 - 1964	0.61 ± 0.1	0.88 ± 0.1	0.86 ± 0.1	1.06 ± 0.1
1965 - 1969	0.52 ± 0.1	0.74 ± 0.1	0.75 ± 0.1	0.88 ± 0.1
1970 - 1974	0.47 ± 0.1	0.83 ± 0.1	0.71 ± 0.1	0.71 ± 0.1
1975 - 1979	0.39 ± 0.1	0.82 ± 0.1	0.64 ± 0.1	0.98 ± 0.1
Number Sample Trees	10	17	20	10

Table A9. Regression estimates of jack pine biomass by sample plot for Stand I. Aboveground Biomass Components (mt/ha).

Plot Number	Stem Wood	Stem Bark	Total Stem	Needles	Live Branches	Total Live Mass	Dead Branches	Total Mass
1	42.1	7.2	44.8	7.9	12.7	68.9	3.8	73.2
2	44.5	6.9	46.8	5.7	7.7	64.8	3.5	68.6
3	45.8	6.9	48.1	6.0	9.5	68.1	3.4	72.1
4	41.1	6.3	43.3	5.4	8.5	61.0	3.1	64.4
5	42.2	6.4	44.9	4.9	6.2	60.3	3.2	63.8
6	49.5	7.5	52.7	5.8	7.5	71.1	3.8	74.9
Stand Totals	44.2 ± 1.3	6.9 ± 0.2	46.7 ± 1.4	5.9 ± 0.4	8.6 ± 0.9	65.7 ± 1.8	3.5 ± 0.1	69.5 ± 1.9

Table A10. Regression estimates of jack pine biomass by sample plot for Stand II. Aboveground Biomass Components (mt/ha).

Plot Number	Stem Wood	Stem Bark	Total Stem	Needles	Live Branches	Total Live Mass	Dead Branches	Total Mass
1	50.9	6.9	54.7	5.7	9.8	75.2	3.1	78.8
2	52.9	7.5	56.1	6.6	11.4	79.3	3.5	83.3
3	43.5	6.2	46.0	5.4	9.9	65.8	2.8	69.1
4	56.3	8.9	58.0	9.0	15.3	87.2	4.4	92.2
5	57.4	8.6	59.5	8.8	16.8	89.7	4.0	94.5
6	37.5	5.9	38.9	6.1	9.8	57.6	3.0	60.9
Stand Totals	49.8 ± 3.2	7.3 ± 0.5	52.2 ± 3.3	6.9 ± 0.6	12.2 ± 1.3	75.8 ± 5.1	3.5 ± 0.3	79.8 ± 5.3

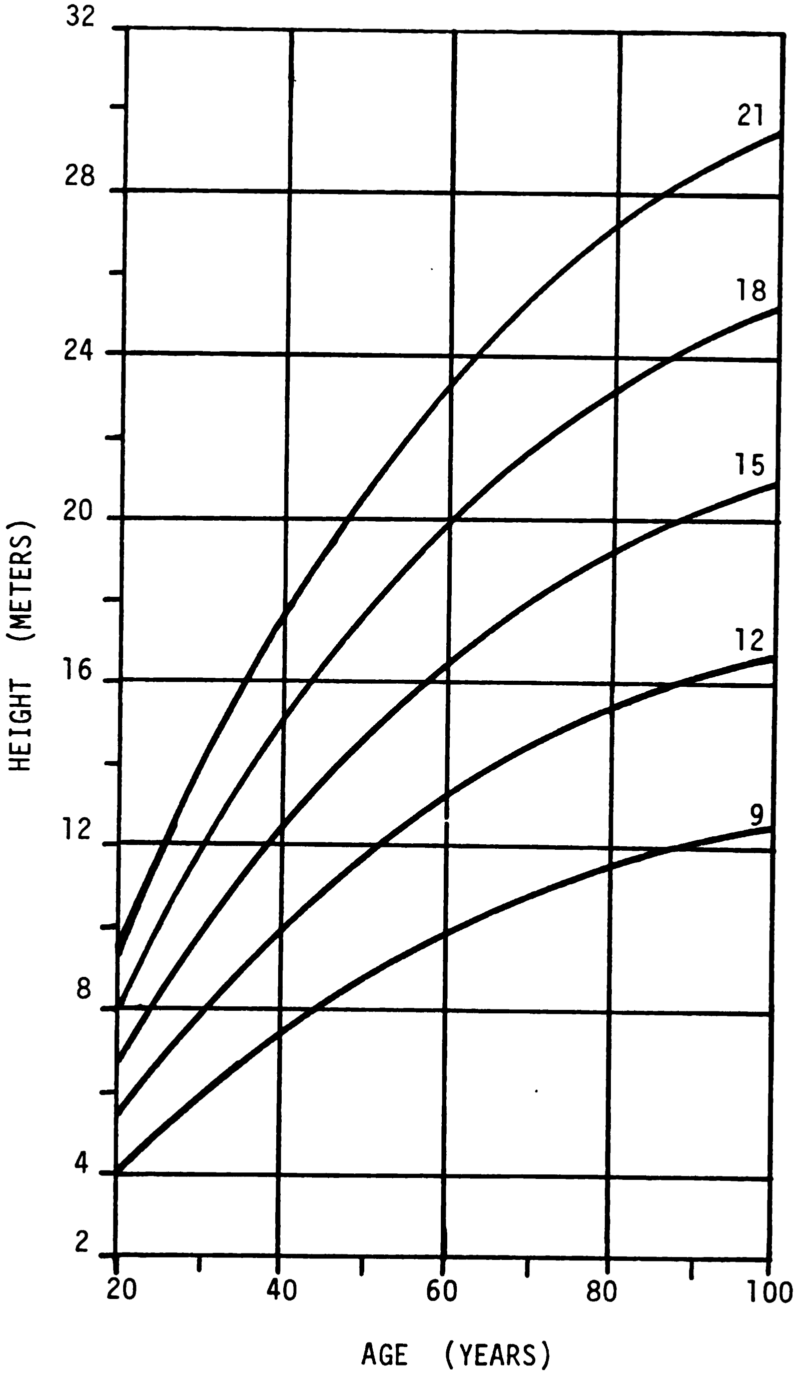
Table A11. Regression estimates of jack pine biomass by sample plot for Stand III. Aboveground Biomass Components (mt/ha).

Plot Number	Stem Wood	Stem Bark	Total Stem	Needles	Live Branches	Total Live Mass	Dead Branches	Total Mass
1	70.1	7.7	80.1	4.6	8.2	96.7	3.0	99.8
2	53.9	5.9	61.2	3.8	7.7	76.1	2.2	78.5
3	26.6	3.0	30.0	1.9	3.7	37.5	1.2	38.8
4	33.8	3.6	39.1	2.1	3.4	45.8	1.4	47.2
5	90.0	8.4	106.6	4.3	9.0	121.1	2.9	123.6
6	39.3	4.4	44.7	2.7	4.6	54.3	1.8	56.1
7	35.8	3.8	41.3	2.2	4.2	49.4	1.4	50.8
8	45.7	4.9	52.8	2.7	4.6	61.8	1.9	63.7
9	83.5	7.9	98.3	4.2	8.8	113.0	2.8	115.5
10	31.7	3.5	36.0	2.2	4.1	44.3	1.4	45.8
11	65.2	6.5	76.1	3.5	6.5	88.2	2.4	90.5
12	45.4	4.8	51.9	3.0	6.4	64.0	1.8	65.9
Stand Totals	51.8 ± 6.1	5.4 ± 0.5	59.8 ± 7.2	3.1 ± 0.3	5.9 ± 0.6	71.0 ± 8.1	2.0 ± 0.2	73.0 ± 8.2

Table A12. Mean biomass and production data for harvested white pine saplings within Stand I.

		BIOMASS COMPONENTS (gms)				PRODUCTION COMPONENTS (gms)				
Basal Stem Diameter (cm)	Number Harvested	Stem Wood + Bark	Branch Wood + Bark	Needles	Total Above-ground	Stem Wood	Branch Wood	Needles	Twigs	Total Above-ground
1.0 - 1.9	4	42.4	20.2	45.4	114.6	5.1	8.8	28.3	6.5	42.1
2.0 - 2.9	7	117.8	67.0	101.1	302.3	19.7	27.6	62.0	16.4	109.4
3.0 - 3.9	6	280.6	206.9	268.2	796.8	55.3	82.2	164.5	41.2	302.1
4.0 - 4.9	2	471.7	443.0	527.9	1533.9	137.7	220.7	268.2	91.3	626.5
5.0 - 5.9	2	721.2	736.5	652.4	1974.1	160.2	270.7	454.8	106.6	885.7
6.0 - 6.9	1	1107.2	1000.8	899.7	3169.5	271.0	406.7	569.5	161.8	1247.2
7.0 - 7.9	1	1956.6	1849.6	1280.4	5402.9	371.1	562.9	835.7	212.1	1769.7

Figure A-1. Site index curve for jack pine within the Lake States. Redrawn from Laidly (1979).


32
28
24
20
16
12
8
4
2
HEIGHT (METERS)
21
18
15
12
9
20
40
60
80
100
AGE (YEARS)