# Predicting forest growth and composition

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## Abstract

The study of forest succession has been hindered by the biological time scale at which change occurs relative to the time period and money usually devoted to ecological studies. A tool used to focus research questions and better understand the dynamics of the forest is computer simulation. To improve the function of computer models as heuristic tools, validation of their predictive power is essential. Botkin *et al.*(1972) created JABOWA, one of the first forest succession models to look at tree species interactions on a small spatial scale. Minimal validation to test JABOWA's forecasting accuracy has occurred because the data are often gathered over too short a time period, are in low supply and are of variable completeness. In 1952, Stephens clearcut a 0.36 ha plot at Harvard Forest in Petersham, MA to reconstruct the vegetative history of the plot for the preceding 100 years. Using the felled trees, he determined their growth and historic patterns of natural and anthropogenic disturbance. To test the predictive ability of JABOWA, I re-analyzed Stephens data, calibrated the model for the Harvard Forest site, and compared model predictions with empirical observations. Strengthening of models such as JABOWA is important not only for use in research and education, but also for their potential in testing the effect of forest resource management activities (i.e. clearcutting) on ecosystem integrity.

# Introduction

The significance of exogenous disturbance on species composition, hydrological cycles, biogeochemistry, and structural integrity of forest ecosystems has become a focus for the present development of succession theory. The Clementsian view of terrestrial ecosystems as super-organisms that develop towards a homeostatic climax state has been challenged as unrealistic considering the rate and scale of autogenic and exogenous disturbances (Shugart, 1984). Disturbance regimes vary by geography (Runkle, 1990), season and climate (*i.e.* fire probability during summer), proximity to a coast (Foster 1988a, 1988b) and other factors.

While perturbations vary from region to region, alteration of succession depends on the type of disturbance, the intensity, and the scale (temporal and spatial) at which it occurs. Types of disturbances range from windstorms, tornadoes, fire, ice storms, pathogens, insects, interactions with herbivores, hurricanes, landslides, floods, mudslides, and forest harvesting practices to local gap replacement effects. Gap replacement occurs when the death of an overstory tree creates a change in microclimate and soil conditions altering the species favored by such conditions (Runkle, 1990). In addition to certain areas being more vulnerable to disturbance than others, the effect of disturbance on stem replacement depends on its intensity. Oliver and Stephens (1977) distinguished between effects of disturbance intensity on species response, and their recovery. On a 0.36-ha plot at Harvard Forest they found that new age classes were created after large disturbances (removal of more than 40% basal area) but not after small disturbances.

As a result, smaller disturbances did not alter the autogenic process of succession.

Not only can disturbances have different effects on succession depending on their intensity, but each disturbance can alter differentially species composition depending on the slope and orientation of the site (*e.g.* for wind related disturbances; Foster, 1988b), the species-specificity of the disturbance (*i.e.* pathogens and insects), the structural integrity and size of individual trees (Foster, 1988b) and the degree of forest floor disturbance (*e.g.* various harvesting methods; Covington 1981; Bormann and Likens 1979). The hurricane of 1938 in central New England caused catastrophic damage to certain sites at the Harvard Forest in Petersham, MA while only minimally altering species mortality rates in other more protected sites. Differential tree mortality depended not only on site location and slope relative to the direction of the storm, but also on the resilience of a particular species to torsional stress (Foster 1988b). Other species affected by a particular disturbance were Chestnut (*Castanea dentata* ) killed on a wide-scale by the chestnut blight fungus (*Endothia parasitica* ) and spruce (*Picea* spp.) disrupted by the spruce-budworm epidemic. ? In a study of a chestnut-dominated forest on Salt Pond Mountain in Virginia, Stephenson (1985) found that the chestnut blight significantly altered the forest composition as it had for much of eastern North American forests. After a half-century of being damaged by the blight, *C. dentata* was replaced in dominance by red oaks (*Quercus rubra* ) on Salt Pond Mountain resulting in the complete disappearance of *C. dentata* in the study area.

Of a more anthropogenically controlled nature, various harvesting regimes (i.e. shelterwood, clearcut) can determine directly the species that are disturbed. However, the effect of soil erosion and nutrient run-off following cutting may affect all species by limiting the amount of nutrients available for growth (Hornbeck et al. 1986). Alterations in nutrient capital could also provide an advantage to the nitrogen tolerant trees.

While a region's susceptibility to a variety of disturbances may vary, disturbance continually alters the successional sequence making Clements' static view of seral development a useful heuristic concept from which to hypothesize the reasons a forest does not usually reach a stable state. The statement that

> ...most ecological studies are carried out in settled regions where disturbance is the ruling process. In all such instances it is exceedingly difficult or entirely impossible to strike a balance between stability and change, and it becomes imperative to turn to regions much less disturbed by man, where climatic control is still paramount (Clements, 1936).

depends on the assumption that humans are the main disturbance factor and that sites undisturbed by humans exist. Connell and Slatyer (1977) developed alternate models to the view that disturbance is only an exogenous process. They proposed that facilitation, tolerance and inhibition models may be more realistic approaches to viewing successional dynamics. Each of these models depend on continual perturbation opening space and modifying the survival, competitive and growth advantage of species with respect to each other. The perturbation that causes the initiation of succession can be natural or anthropogenic. In fact, humans have affected the landscape and its species composition for a long time, and those effects are not always obvious to the observer because of the spatial and temporal scale on which change occurs

(Sprugel, 1991).

The scale at which a forest is observed strongly affects the perception of dynamic change (Smith and Urban 1988). At a gap scale (the area disturbed by the death of a single full-grown tree), forest dynamics are dominated by the shade provided by a dominant tree inhibiting the available light necessary for growth by understory trees (Veblen 1992). However, as the spatial scale of observation increases, the rate of change occurs at an order of magnitude slower than was observed at smaller scales (Smith and Urban 1988). Thus, the process of forest dynamics can be viewed differently with respect to regeneration after catastrophic disturbances, gap-phase replacement, and continuous regeneration (Veblen 1992). Continuous regeneration involves the replacement (or competition) of shade-intolerant trees by shade-tolerant trees in areas free of disturbance (Veblen 1992). For each of these processes, scale is crucial for understanding the contribution of each kind of growth to the dynamics of the entire forest.

To investigate forest dynamics, computer simulation models have aided in assessing the importance of spatial scale and in overcoming the limits of the temporal scale at which forest growth occurs. The first computer model which focused on forest gap-phase dynamics was JABOWA (Botkin *et al.* 1972). More than two dozen gap models have evolved from JABOWA, including FORET (Shugart and West 1977), BRIND (Shugart *et al.* 1981), FORTNITE (Aber and Melillo 1982) and ZELIG (Smith and Urban 1988). Each of these models focus on different types of forests in various regions, often for the purpose of applying the model to some management-related problem such as the effects of fire or logging.

JABOWA's construction was based on the idea that one should choose the fewest forest variables that could accurately predict forest growth (Botkin 1993). The equations used to construct the model relate allometric relationships, tree diameter growth, environmental response, and mortality (Urban and Shugart 1992). The model incorporates all of these elements by beginning with a growth equation that determines the maximum amount of growth that can occur for a tree of a particular species without being limited by competition for resources and exogenous disturbance. In particular, in JABOWA-II, growth is affected by light, temperature, soil nitrogen, soil-water depletion, and soil-water saturation (Botkin 1993). In the original version of JABOWA, the growth equation determined an optimal growth curve whereby a tree would reach approximately two-thirds of its maximum diameter ($D_{max}$) in one-half of its maximum age (Botkin *et al.* 1972). In the present version, the growth equation depends on the maximum amount of growth possible for each species. In a general form, the growth equation (1.1) (Botkin 1993) states growth in terms of change in volume determined by the change in diameter times the height so that:

$$\partial(D^2H/\partial D)\partial D = R * LA \left(1 - \frac{DH}{D_{max(i)}\,H_{max(i)}}\right) * f(\text{environment}) \qquad (1.1)$$

where D = diameter at breast height

H = height of tree

R = a constant

LA = leaf area of tree

$D_{max(i)}$ = maximum known diameter for trees of species (i)

$H_{max(i)}$ = maximum known height for trees of species (i)

The process of developing a change in diameter from the equation for the change in volume involves the assumption that leaf area is proportional to leaf weight (Botkin *et al.* 1972):

$$W = C_i D^2 \quad (1.2)$$

where W = leaf weight

Ci = a constant.

Relating leaf weight to the square of the diameter is justified by the assumption that nonphotosynthetic tissue grows proportional to the amount of leaves added to the tree. So, the amount of leaves added to a tree could be deduced from taking a proportion of the cross-sectional area of the xylem (which is a constant times the square of the trunk's diameter) (Botkin 1993).

The relationship between height and diameter is determined by the function:

$$H = 137 + b_2 D - b_3 D^2 \quad (1.3)$$

where 137 is the height in centimeters at which diameter is measured. To determine the coefficients in equation 1.3 (b2 and b3), one assumes that a tree of species (i) reaches its maximum height and diameter at the same time; and, that, at the maximum height, there is no change in diameter. The diameter coefficients then can be determined by:

$$b_{2(i)} = \frac{2(H_{max(i)} - 137)}{D_{max(i)}} \quad (2.4)$$

$$b_{3(i)} = \frac{(H_{max(i)} - 137)}{D^2_{max(i)}} \quad (2.5)$$

From a combination of the above equations, the change in diameter is calculated by the equation $\partial(D^2H) = 2DH\partial D$ or :

$$\partial D \backslash \partial t = \frac{\{G_{(i)} D\ [1 - (DH/D_{max(i)} H_{max(i)}))\}\ *\ f(environment)}{274 + 3b_2 D - 4b_3 D^2} \qquad (2.6)$$

where G is a growth constant (Botkin 1993). The growth constant was determined separately for each species in the default values accompanying the model. Using the natural history of each species, the growth constants established the size of a tree at one-half its maximum age determining the point of inflection of the sigmoidal growth curve. The value G was chosen so that D/Dmax varied among species from 2:9 to 8:9. The growth equation (2.6) produces species-specific growth curves that are used in the model as the maximum levels of growth to be limited by environmental factors and competition for resources.

Competition among neighbors in a plot is determined by the different needs of a species with regards to light, temperature, soil nitrogen (kg/ha/yr), soil moisture, and precipitation (Botkin 1993). The effect of light on photosynthesis and growth is determined by equation 3.1, which forms three solution curves for shade tolerant, shade intolerant, and intermediately tolerant species. The light response function can be written as:

$$f(AL)_L = A_1 \{1 - e^{(A_2 AL - A_3)} \} \qquad (3.1)$$

where AL is the light available to the tree determined by the time of year, slope and latitude, $_L$ is the light tolerance class (1 = intolerant of low light, 2 = intermediate in tolerance of low light, and 3 = tolerant of low light), and $A_1$, $A_2$, and $A_3$ are empirically derived constants (Botkin 1993).

In JABOWA, temperature influences growth by determining when a species can grow. A minimum temperature, which is not species-specific, is considered to be needed for all North American temperate forests for a tree's photosynthetic rate to exceed their respiration rate (Botkin 1993). The model uses the minimum temperature of 4.4 degrees-C as the baseline for growth. To calculate how many days in a year that a particular species can grow, mean monthly temperatures for the lower (and upper) boundary of the species' range are determined. The integral under that mean monthly temperature curve, but above the minimum temperature required for growth, calculates the "growing degree-days" (Botkin 1993). The form of the growing degree-day equation is:

$$DEGD = \int_0^{365} T_t dt \tag{4.1}$$

where $T_t$ is the instantaneous temperature (Botkin 1993). The assumptions of the parabolic growth curves that result from applying such temperature functions are that the increase and decrease in growth in response to a change temperature is symmetric and that if the temperature falls below certain levels, zero growth occurs (Botkin 1993).

To calibrate the model for a particular site, JABOWA requires input for elevation, latitude, soil depth, precipitation and temperature, nitrogen available in the soil (kg/ha/yr), water available in the soil ($mmH_2O/m$ depth), and the percent of rock in the soil. Latitude is necessary for determining the light available on the plot, especially with respect to the snowmelt calculations. Precipitation and temperature are major driving components of tree growth in JABOWA. Mean monthly values for both variables are needed for calibration of the model for a particular site. If the weather data are collected at a site of a different elevation from the elevation of the study site, the model compensates for the change in temperature and precipitation due to elevation.

Soil fertility affects tree growth in three ways, depending on which of the three nitrogen tolerance classes a particular species belongs. First, the amount of nitrogen available for a tree's growth must be determined as a site-specific parameter. However, the measurement of nitrogen in the soil (kg/ha/yr) is not the amount of nitrogen available for use by a tree since most of the soil nitrogen has not been decomposed or converted to a usable form for uptake. As a result, JABOWA adjusts the nitrogen soil measurement to represent the amount of nitrogen available for growth by the equation:

$$v = -170 + 4.0*AVAILN \qquad (5.1)$$

where AVAILN is the amount of nitrogen measured in the soil (Botkin 1993). The next step towards determining the effect of nitrogen levels on tree growth is to calculate the nitrogen content of the leaves for each tolerance class, using the equation:

$$C_N = a_1[\ 1 - 10^{-a_2(AVAILN\ +\ a_3)}\ ] \qquad (5.2)$$

The response of the trees to various nitrogen levels is determined by the equation:

$$NF_i = \frac{(a_4 + a_5 * C_N)}{a_6} \qquad (5.3)$$

where C is the concentration of nitrogen in leaves for a particular tolerance class N, the coefficients $a_{1-6}$ are empirically derived values, and $NF_i$ is the nitrogen response function for species (i) (Botkin 1993).

Soil texture ($mmH_2O$/m depth) is another model input which is needed for calibration for a particular site. Soil texture affects site quality by affecting the amount of water stored on the site. Percent rock decreases the amount of moisture that the soil can hold.

To complete calculating the effect of site quality on tree growth, functions to determine the effect of drought on tree growth and the effect of the depth to the water table on a species' ability to grow are multiplied by the temperature and nitrogen functions.

While species grow and respond to various environmental factors in a deterministic manner in JABOWA, the stochastic processes that make forest dynamics continuous are mortality and regeneration. JABOWA models mortality with respect to the inherent risk of death and competition induced death (Botkin 1993). The inherent risk of death is expressed as:

$$M_i = 1(1 - \beta_i)^{AGEMX_i} \tag{6.1}$$

where $M_i$ is the probability that a tree of species (i) at age 1 will reach its maximum possible age, $AGEMX_i$ is the maximum possible age that the particular species can reach, and $\beta$ is the annual probability of death (Botkin 1993). In this version of the model, the determined aspect of mortality is that of all species, only 2% will reach their maximum possible age. The stochastic aspect is that a random number is selected for each tree in each year. If that value is less than $\beta$, then the tree dies. Another way that a tree can die is if it grows poorly (below a species-specific minimum value) for 10 successive years, then, that tree has only a 1% chance of surviving those ten years (Botkin 1993).

For regeneration, the input of seeds is considered to be a non-limiting factor to germination. JABOWA only begins to consider entry of new individuals into a plot after they have reached 1.37 m in height. Yet, the actual height of a sapling once it enters the plot is determined randomly as falling between 1.37 m and 1.67 m. From this height, dbh is calculated.

Sapling recruitment involves stochastic processes that are constrained within biologically determined limits. The decision as to whether or not shade-intolerant saplings are entered into a plot for a particular year is deterministic. However, the number of species that are added each year is a stochastic function. For saplings of intermediate shade-tolerance, the possibility of entering into a plot for a particular year is a stochastic function of the environmental conditions. Once those environmental conditions are met for shade-intermediate and shade-tolerant species, then, the number of saplings added is species-specific and independent of environmental conditions (Botkin 1993).

Because of the stochastic aspects of JABOWA, which reflect the stochasticity of the forest, when making predictions, one needs to run the model for multiple iterations and obtain a confidence interval averaging the output values. Values to determine the number of saplings to enter a plot, to predict mortality, and to determine the response of individual trees to environmental stresses are generated randomly within biological limits. Because of these stochastic inputs into the model, each simulation run that begins with the same initial plot will produce a different prediction. To obtain usable predictions, the model allows for multiple simulations to be run from the same initial conditions. The output from each simulation is then averaged and a confidence interval for the range of values determined by each run is created. For example, the final output for the frequency of red maple will be a mean value with a confidence interval showing the range of values predicted from each simulation iteration.

To be able to use a predictive model with some degree of confidence in its accuracy, validation is needed. Validation is a procedure that tests the agreement of the model's predictions with a dataset not used in the construction of the model's equations or parameters (Shugart 1984). Verification is a proceedure distinct from validation in that it determines whether the predictions can be made consistent with a set of observations. Alterations of parameters and constraints set on equations that drive the model are made with a dataset. Thus, the data used in the procedure is not independent of the construction of the model. While verification is used to improve the model, validation determines the reality of the model's predictions (Shugart 1984). The most prominent validation test of JABOWA was with Hubbard Brook data which, although limited, revealed some of the limitations of the model. Furthermore, testable hypotheses concerning the effect of different nitrogen concentrations on model results were discernible from this validation test (Botkin 1993). However, none of these tests were conclusive. Given the wide-spread adaptability and potential usefulness of a gap-succession model such as JABOWA, further tests and improvements will be needed to understand the situations for which JABOWA is best suited and to better understand its limitations.

The lack of validation tests usually stems from the absence of adequate data with which to compare the predictions. Long-term datasets often are of variable quality and completeness. However, even with data that contains their own limitations, valuable information concerning JABOWA's predictive power can be obtained. Since the lack of data is a result of the short-time period used to conduct experiments and monitoring, the method of reconstructing forest history developed by

Stephens (1955) can be valuable towards understanding succession trends and testing succession models.

The techniques which Stephens (1955) used to reconstruct forest history involved the removal of all live and dead tree stems in a 0.36 ha plot in Harvard Forest in Petersham, MA to analyze their birth, growth and mortality. Age was determined at incremental heights along the length of some of the cut trees and radial growth was determined by measuring annual tree-growth rings. A less destructive adaptation of Stephens' methods was used by Henry and Swan (1974) to perform a similar analysis of an old forest in New Hampshire.

The Harvard Forest site that contains Stephens' plot is a second-growth hemlock-mixed hardwood composition. After disturbances, the plot regenerated with a mixture of hardwoods tending towards an eventual dominance of eastern hemlock, red maple and black birch (Oliver and Stephens 1977).

In 1993, the regrowth of Stephens' transect when compared with the surrounding forest was striking. The overstory of Stephens' plot in 1993 predominantly appears to consist of red maple, paper birch (*Betula papyrifera*) and black birch, while the understory abounds with hemlock, amelanchier (*Amelanchier canadensis*) and white pine. The neighboring forest consists of a heavily closed overstory of hemlock with a scattering of beech and white pine. The more mature and relatively undisturbed forest adjacent to Stephens' plot favors the slower-growing hemlock.

To further understand the effect of disturbance on this tract of forest, to test the predictive ability of JABOWA , and to explore the limitations of the model and the data, I prepared Stephens' data for simulation runs through JABOWA and calibrated the model for the Harvard Forest plot.

## Site Description and Disturbance History

The study plot is part of the Tom Swamp tract (fig. 1; compartment VI) of Harvard Forest, located in Petersham, Massachusetts on the east side of the Quabbin Reservoir. The plot (0.36 ha) has a westerly aspect and is situated on an elevational gradient. The plot rises to 274 m westward from the swamp at 235 m. The soils of the study area are of granite and schist origin and were categorized in the late-1980's as belonging to three series, Charlton-Hollis-Chatfield (table 1; Soil Interpretation Record). Each of these series is well-drained loamy to coarse-loamy soil formed on glacial till. The soil is full of small boulders and stones with a depth to the bedrock 25 - 150 cm. The soil is fairly acidic with the pH ranging from 4.5-6.0.

As with most New England forests, the study plot has experienced a series of disturbances, both natural and anthropogenic, which have affected species composition over time (Foster 1988b). However, compared to other sites at Harvard Forest, the study site was relatively unaffected by the 1938 hurricane. The hurricane was a catastrophic disturbance for nearby stands causing a release of understory shade tolerant trees in some areas and the regeneration of pioneer species in others (Foster, 1988b). In the plot of study, the hurricane of 1938 removed 44 percent of the basal area (1.10 out of 2.48 $m^2$), mainly white pine (*Pinus strobus* ) and hemlock (*Tsuga canadensis* ) (Oliver and Stephens

1977). The plot is one of the few forests which had never been plowed for agriculture in the area (Oliver and Stephens 1977).

Besides the occurrence of a fire and two hurricanes at unknown dates prior to 1800, the first disturbance that Stephens noted in his reconstructed history of the experimental plot was an 1803 clearcut that removed mainly white pine and chestnut. Minor logging occurred in 1841, but its effects were obscured by the logging of 1854. White pine never significantly recovered from the 1854 logging (cut 75% of the basal area) that resulted in the removal of most of the large white pines. A series of small-scale logging and fuelwood cuts were performed from 1864 to 1889, mostly harvesting chestnut and a few white pine. In 1915, the chestnut trees were dying of chestnut blight which prompted a salvage cut in that year. In 1935, a fuelwood cutting removed some red oak, aspen (*Populus grandidentata*), and hemlock. The final natural disturbance before the 1952 research clearcut was gypsy moth damage occurring in the mid-1940's that damaged red oak, red maple (*Acer rubrum*) and black birch (*Betula lenta*). Since 1952, there has been no major known natural or anthropogenic disturbance of the study area.

## Methods

### *Model calibration*

To calibrate JABOWA for a specific site, information on climate, soil and site characteristics, and species-specific parameters must be collected. For the climatic input, the model requires mean monthly precipitation and mean monthly temperature. Botkin (1993) suggests using at least 30 years of climate data. If the model is used to project longer than 30 years, the original set of climate data can be used repeatedly for as long as the model is run. The climate data for the experimental plot were gathered at a site several kilometers from the test area at the Harvard Forest administration building (fig. 1). The data were compiled from maximum and minimum daily temperatures and daily precipitation for 30 years (1962 to 1992).

The soil and site characteristics required for calibration include maximum basal area of trees that can be supported on a plot ($cm^2$), elevation (m), latitude (degrees), soil depth (m), depth to the water table (m) , soil texture (mm $H_2O$ / m depth), percent rock in soil, available nitrogen (kg/ha/yr), and the initial seed input. Elevation is needed only if the elevation of the location where the climate data were collected is different from the elevation of the test site. The latitude is used to correct for the amount of sunlight available on the plot. An assumption of the model is that the leaves of a tree are arranged at the top and there is no vertical gradient of light attenuation caused by differential distribution of leaf area. The variables soil depth (depth to bedrock) and depth to the water table determine whether or not the site is considered "wet" or "dry". If the water table is higher than the soil depth then the site is considered wet. If the water table depth is greater than the soil depth then the site is considered dry. Soil texture measures the capacity of the soil to hold water, which is effected by the percent rock in the soil. Available nitrogen measurement represents the soil mineralization of nitrogen on a scale from -100 to +100. I used the value 70.0 kg/ha/yr because at Harvard Forest the available nitrogen range for soil is within the range of 60.0 to 90.0 kg/ha/yr, with 70.0 being a reasonable value for a plot in the Tom Swamp Tract (Richard Boone, pers. comm. 1993). Initial seed input was determined using a pseudo-random number generator.

Since the season of my study was winter, I gathered the site information from sources other than field sampling. The soil data were obtained from the Chatfield-Hollis-Charlton series (table 1; Soil Interpretation Record). Most of the variables required by the model were similar in each series. Soil depth varied between series, and soil texture varied not only between series but also between soil horizons. As a result of these discrepancies, I ran the model for each test plot separately for the three series. The model computes the average and confidence interval for species frequency and basal area over the multiple iterations (40).

Within the model package, Botkin (1993) includes default values for the characteristics of 40 common species. Species-specific parameters for any additional species found must be added. For the Harvard Forest plot, I determined species parameters for black birch (*Betula lenta* ) and amelanchier.

The maximum DBH (cm), maximum height (m), maximum age (yrs), shade type (shade intolerant, intermediate, or tolerant), and nitrogen type (intolerant, intermediate, and tolerant) for black birch and amelanchier are well documented in various texts, with the exception of maximum age for amelanchier (Harlow *et al.* 1979; Hightshoe 1988).

The growth constant (G) is a parameter in the fundamental growth equation used in the model (2.6). To calculate this value for black birch and amelanchier, I used their maximum diameter and height and the maximum annual diameter increment from yellow birch and beech, respectively.

For the leaf weight (C), minimum to water depth that the species requires (m), the wilt maximum value (a relative measurement), the maximum leaf weight (kg), the minimum light value which determines when a sapling can enter the plot, the minimum annual diameter growth (cm), and the maximum number of saplings that could be added to a plot in a year, I used yellow birch and beech values for black birch and beech, respectively. The wilt maximum value determines the tolerance of a species to soil dryness (low value implies low tolerance). When the minimum annual diameter growth is high, a higher probability of mortality was included in the model.

### *Height equation test*

To test the height equation (1.3) against the Harvard Forest data, I compared real heights of a number of trees per species with the heights predicted from DBH. I tested only those species for which more than ten tree heights were available. I conducted a matched pairs two-sample t-test to test the null hypothesis that the actual and predicted heights are from the same population and are, therefore, not significantly different.

### *Model validation*

To test JABOWA's predictive power against data derived independently of the model's construction, the test data must be prepared in a form that is acceptable and comparable with the model. First, initial plots must be created that include the species type, DBH and height for each tree. The plots in JABOWA are 100m$^2$ so that if a dominant tree grew to its full height, it would shade all the other trees until it died. After preparation of the initial plot data, the model output is in the form of number of individuals per species, basal area (cm$^2$/m) per species.

The data collected by Stephens that I used to create initial plots for JABOWA and to compare with the predictive output of the model were in the form of silvagrams and stem analyses. Information on the history of the plot was gathered as far back as 1635. However, logging in this century obscured much of the evidence of tree growth. The data are more accurate towards the mid-1850's, so I compiled growth data for the model beginning at this date. Stephens made a contour map of the 0.36-ha transect (25.6 m wide and 140 m long) on a 10-foot grid (3 m) recording the spatial arrangement of live stems, dead, stems, woody fragments, boulders, stones and mound and pit location. In 1952, all 444 live stems and dead stems, stumps and stump remnants (245 stems) were cut and removed for analysis. All live and dead trees were aged, and their heights, DBH inside the bark, and diameter inside bark at the root collar were measured. Three hundred and twenty-two of the felled trees were measured using a stem analysis technique where the age was recorded at the root collar and subsequent ages were recorded every 1.3 m along the tree's length. Stephens discovered patterns of disturbance using mound and pit information, direction of tree fall, the temporal occurrence of sprout initiation and growth and historical documents (Oliver and Stephens 1977).

Radial growth data were obtained when possible by making incremental tree ring marks from a polished stump section along a strip of paper. These marks were then transferred with pencil along a horizontal line, making the vertical distance from the line to the mark the incremental radial growth in inches per year. These data combined with the disturbance information described above were used to construct a silvagram placing the life span of the trees along a grid where one inch (2.54 cm) represents ten years of growth (fig. 2). For the live trees where radial growth rates were known, the life span is indicated with a bold line. For trees where radial growth rates were not available and information on life spans was compiled from multiple sources, the probable estimated life span is indicated as a dashed line with a standard error of estimated age. The cause of death of a tree prior to 1952, when known, is indicated as death due to felling, uprooting, bole or crown broken-off, pathogen (chestnut blight), or insect defoliation (gypsy moth).

To extract the data necessary for testing JABOWA from this forest history, I divided the transect map into 36 sections, each 100 $m^2$. Botkin notes that it is possible to change the plot size in the code; however, he suggests that the lack of spatial arrangement in the model is compensated for by the size of the plot not exceeding the size determined by the area shaded by a full-grown tree (Botkin 1993). For the 36 plots, I used Stephens' maps to locate the tree number and species contained on each plot. Because incomplete radial growth data existed for most trees, I determined which plots contained a complete segment of radial growth data for all trees represented. Once I established which plots had radial growth data for all trees on the plot, I discovered that the radial growth data often did not exist for the entire life span of the tree. So, I selected a time span up until 1952 where radial growth data were known for all trees for each plot. The number of years of growth data for plots ranged from 20 years to 108 years. For each plot that I ran through the model, a different span of time was projected.

To test the model's overall predictive accuracy, I used the longest time period determined by the availability of data for each plot. Because disturbance was a significant factor in the successional sequence in this plot (Oliver and Stephens 1977), I planned to test the model's windthrow component for the period 1936 to 1952 (hurricane) when mortality resulting from uprooting occurred. However, while over the entire transect mortality did occur from the hurricane, the plots that had sufficient growth data for testing the model were relatively undisturbed. For 1936 to 1952, I made projections using JABOWA for a short time period which was constant for all plots.

To obtain initial composition for the nine plots that fit all of the criteria listed above and composition of those plots in 1952 for comparison with the predictions, I needed DBH and height data. For DBH, I first digitized the incremental diameter growth lines (fig. 2). Using the scanned image projected on the screen, I was able to calibrate the grid such that one square represented one inch (2.54 cm). By measuring the incremental radial growth marks per year for the time period to be used in the model simulation, I obtained the diameter at stump height by summing the annual radii (x2) and subtracting them from the diameter at stump height gathered after the felling of the tree. Unfortunately, all of the summed diameters were significantly greater than the total diameter at stump height. To resolve this discrepancy, I enlarged the dendrograms so that one grid square equalled one inch (2.54 cm). I measured several trees using a ruler to approximately 0.8 mm accuracy. The accuracy of hand measurements differed from digitizer measurements. However, when the time period selected for model testing for a particular plot included the entire life span of a tree, the sum of the diameters measured by hand minus the diameter at stump height at the time of death equalled zero. So, for all of the trees on the test plots, I remeasured their annual radial growth by hand (fig. 2). To convert the diameter at stump height to diameter at breast height for each tree, I used Stephens' species-specific tables, which were based on an average of all of the trees on his plot for which he had both sets of data.

Since my criterion for choosing plots and time periods for testing the model was the presence of radial growth, height data were not always available. I calculated the height at the test year. For this calculation, I first determined the age at the test year for those trees that Stephens had determined age at incremental height by subtracting the difference between the test year and 1952 from the age recorded in 1952. Next, I located the two ages on the height growth curve that contained the age value at the test year. After calculating the percent difference between these two known ages, I subtracted that difference from the corresponding height values. For the trees where no height data existed, I used the same procedure except that I averaged all of the known heights for each species into average height growth curves (figs. 3 -8). The utility of this process is that it allowed me to change the time period for projection by the model for any plot. I was able to make predictions from disturbance to disturbance for as long a period as I had diameter growth data.

To analyze the percent difference between the model's predictions and the recorded observations, I calculated the fraction of the observed value that is the difference between the predicted and the observed values Botkin (1993) stated that the predicted values should be within +/-20% of the actual values. Prediction values within this range supposedly provide a level of accuracy adequate for most purposes of the model (Botkin 1993). The choice of adequate range values must be reevaluated for each model use. While the intention of the model is not to reconstruct the dynamics of the forest tree by tree because of the stochastic components (Botkin and Nisbet, pers. comm. 1993), the model output should reflect qualitative changes in species number and size over time. Validation tests of this type are important for showing how accurate model predictions are, for determining at what level the model can provide information on forest succession, and possible reasons for significant differences between model predictions and observations. I have used the +/-20% criterion of acceptability of model predictions so that I can compare my results with the Hubbard Brook validation test (Botkin 1993).

This acceptability criterion is not intended to determine the suitability of the model for predictive accuracy, but can be used as a guide to establish the strength of the predictions. Positive values indicate that the prediction is an overestimate while negative values indicate an underestimate of the actual value.

A different criterion for evaluating the acceptability of model predictions is to determine whether or not the observed value falls within the confidence interval of the predicted value. This criterion is also helpful for determining model accuracy.

Patterns in growth may be recognizable from model output by averaging over a large number of plots. However, the variation between plots may cause the averaging of model output to obscure actual successional trends.

Evaluation of the model results consisted of determining whether better predictions could be made with the Charlton, Chatfield or Hollis soil series (figs. 16 - 45). Results were analyzed to consider whether there was consistency among exclusion of species in the predictions when they were observed to have actually existed and inclusion of species in the predictions when they were not observed to have existed (figs. 16 - 45). Additionally, determination of predictive accuracy allowed for discernment of patterns among species. Concerning the stochastic quality of the model, I found that with 40 iterations the mean and confidence interval remain relatively constant and reduce the variability implicit in the design of the model.

## Results

### *Tree growth*

Although gypsy moth damage and natural death were the only causes of tree death in my plots, annual decreases in diameter growth at the dates of disturbance (Stephens 1955) were evident (figs. 9 - 15). In general the major disturbances caused an immediate decrease in growth of the less vigorously growing individuals and a delayed decrease in growth (1 or 2 years) for individuals with high growth rates. In plot 12 (fig. 9), a significant decrease in growth occurred in 1889 for the trees which had limited growth rates. For the rapidly growing hemlock and red oak, the 1889 logging scarcely slowed down their ascent to the period of most growth in the time interval 1885 to 1952. For all trees of this period in plot 12, the most significant period of growth occurred from 1889 to 1905, after the 1888 logging. The 1915 chestnut salvage had a similar effect, immediately decreasing the growth rate of the less vigorously growing trees and decreasing the growth of the more vigorous individuals one year later. In 1935 (fuelwood cutting), the vigorous individuals actually increased growth, only to decrease growth one or two years later. The less vigorous individuals had even growth during 1935 and a small decrease in 1936. During the 1938 hurricane, a switch in the general trend occurred such that the more vigorous trees were immediately effected while the less vigorous trees were effected in 1939. Decrease in growth for all trees occurred in 1944, while the gypsy moth damage was listed by Stephens to have occurred in 1945.

In plot 13 (fig. 10), the range of adequate growth data was available for 1915 to 1952. No response in growth patterns was evident during the 1935 fuelwood cutting. A significant decrease in growth occurred during the 1938 hurricane for all except the most stagnant individuals. Post-hurricane growth increase was gradual but evident from 1939 to 1945. Gypsy moth damage in 1945 did not cause a decrease in growth for any trees in this plot. In fact, a small general increase in growth occurred from 1943 to 1945.

In plot 14 (fig. 11), growth data were available from 1888 to 1952. One of the most significant periods of growth for this plot over this time interval occurred from 1891 to 1906. A decrease in growth was apparent for all trees, except for the most even growing individuals, during the 1915 chestnut salvage. From 1935 to 1938, all significantly growing individuals decreased their growth. Although the hurricane was in 1938, a decrease in growth for the most vigorous trees occurred during 1937, with an increase in growth from 1938 to 1939. For the trees which were in the intermediate range of growth, a decrease in growth occurred during and after the hurricane. From 1945 to 1946, the most vigorous individuals decreased their growth, while the other trees retained a constant growth rate. Post-hurricane growth increases were evident from 1938 to 1944.

Plot 20 (fig.12) contained few trees, yet, the period of available growth data was sizable (1855 to 1952). For the two hemlocks and the white pine which had the highest growth rates, a response to the 1864 and the 1872 logging resulted in a growth decrease. The 1872 logging affected growth in 1873, rather than the year of the disturbance. The 1878 logging scarcely decreased growth which is not surprising since that logging only resulted in a 13.5 percent decrease in basal area for the entire 0.36 ha. There was no consistent pattern of change during the 1889 logging. A decrease in growth resulted for most trees from 1914 to 1915. After the chestnut salvage a significant increase in growth resulted. A slight decrease in growth occurred in 1936 after the fuelwood cutting. The small magnitude of the response reflects the minimal loss of basal area (12.5%) for the entire transect. As in the other plots, an increase in growth is evident during the 1938 hurricane. After the hurricane, a gradual but significant decrease in growth occurs for all but the individuals with the most constant and minimal growth. No significant response is apparent to the gypsy damage during or after 1948. As in the previous plots, some of the most significant and constant growth occurs from 1888 to 1904, after the 1889 logging.

For plot 22 (fig. 13), the interval of growth data is from 1900 to 1952. While growth before 1900 is not known for the entire plot, the most significant growth for the interval observed occurred from 1900 to 1906, repeating the pattern seen in the previous plots. The first major disturbance, the 1915 chestnut salvage, is corresponded with a gradual decrease in growth from 1915 to 1916. The response to the 1935 fuelwood cutting was almost identical in magnitude as the response to the chestnut salvage. A constancy of growth can be observed for 1937 to 1938. In fact, there was a slight increase in growth after 1938. The pattern of growth during and after 1945 was the same in plot 27 as most of the other plots. All trees had a spurt of growth after 1943 culminating in 1945, with a gradual decrease to 1950. In fact, for plot 27, the second most significant period of growth was from 1943 to 1945.

Plot 27 (fig. 14) showed its most significant period of growth from 1898 to 1902 (with a decrease in 1901). There were fewer trees in plot 27 and less overall growth. The changes in growth were of a more gradual nature; and, the catastrophic disturbances for the area had a minimal effect on the growth of each tree. The 1915 chestnut salvage did not significantly alter growth for any of the trees in this plot. The 1935 fuelwood cutting resulted in significant decrease in growth for all trees. There was no evidence of disturbance by the hurricane in 1935 or directly in the years immediately following the disturbance. A spurt of growth is evident from 1944 to 1945 followed by an overall decrease in 1946.

In plot 30 (fig. 15), which was located at an elevation higher than plots 12 -22, growth was much more constant than the erratic growth of the lower elevations. The growth pattern is similar to the other plots, except for the difference in magnitude. There was a subtle but noticeable decrease in growth during the 1935 fuelwood cutting. Any decrease in growth following the hurricane was not significant. In fact, there is a general trend of growth increase from 1937 to 1940. Similar to the previous plots, a growth increase is evident from 1941 to 1943 followed by a decrease from 1943 to 1945. However, after 1945, a gradual increase results indicating the lack of growth inhibition from the gypsy moth damage.

The major disturbances listed by Stephens (Stephens 1955) were not the only causes of growth rate change. All plots showed simultaneous (or slightly unaligned) periods of growth increase and decrease for years not included in the major list of disturbances. In fact, often the major disturbances did not result in the largest decreases in growth. Some of the additional growth changes not listed in Stephens' thesis were similar in magnitude and time from plot to plot, while other growth changes were unique.

### *Height equation test*

The matched pairs two-tail t-test showed that only the white pine did not reject the null hypothesis that the actual and predicted heights are from the same population, and, are therefore not significantly different (table 2). The other test values were close to zero and thus reject the null hypothesis.

### *Model Validation*

When the Charlton, Chatfield and Hollis soil series were used to calibrate the model for the site conditions of the study plot, the Chatfield and Hollis soil series produced identical results for every simulation. Thus, I have included only the Charlton and Chatfield series in the results (figs. 16-45). While the Charlton and Chatfield series occasionally predicted the same value, they typically produced different predictions with a similar confidence interval width. The two series were more similar than different in that the predicted value of one series was usually within the confidence interval of the other. A notable exception was the overestimation of white pine basal area by the Chatfield series in plots 12,14, and 20 (figs.17, 25 and 29). Also, when one series overestimated or underestimated, the other series did the same. Out of the 106 predictions made, the Charlton series produced 68 predictions that were more accurate than the predictions made by the Chatfield series. The Charlton series resulted in frequency predictions that were more accurate than the Chatfield series for 40 out of 51 trees. These differences were rarely significant since the mean values for predictions made by both soil series were usually within each other's confidence interval.

In the two longest run simulations (figs. 16-17 and 24-25), the prediction for hemlock frequency was considerably overestimated while the prediction for basal area was underestimated. In other words, there were a few large trees observed with more smaller trees predicted.

In every simulation, with the exception of plot 20 (figs. 30-33), amelanchier was introduced when none actually existed. In these cases, though, the frequency was high while the basal area was low. Beech was repeatedly included in both the Charlton and Chatfield predictions when none or few actually existed. The frequency of predicted beech was usually high relative to a low basal area.

In the long-term predictions (figs. 16-17 and 24-25), white pine was introduced when no white pines existed (except for one tree in plot 20). The overestimation of white pine frequency is different from the overestimation of amelanchier and beech frequency because the predicted basal area for white pine was high indicating larger trees.

The patterns for introduction of species by the model when those species were not observed was consistent among species. The lack of inclusion of a species by the model when that species was observed occurred only once with a single paper birch in plot 14 (figs. 24-27).

The most accurate and precise predictions were made for white oak (tables 2-16). The percent observed calculation was consistently within 40% of the actual value. In plot 20 and 27 (tables 9-10 and 14-15), the Charlton series indicated the presence of white oak when none existed. However, for both of those plots the basal area was negligible. The black birch predictions were repeatedly within 20 % of the observed values (tables 2-16). Red oak predictions were occasionally within 20% observed over a short time-span (1936 to 1952). However, long-term predictions caused an overestimation of frequency and an underestimation of basal area. An exception to this trend occurs where red oak is not present at a time when it is predicted (fig. 28-29). Red maple and hemlock are the only other species which were projected to be within 20 % at some time. No consistent trend of overestimation or underestimation was apparent for either species.

In each plot the predictions were better over the short time interval (1936 to 1952) than the longer time intervals.

## Discussion

The trend that each dominant tree on a plot, and often each subdominant and suppressed tree, increases and decreases in growth in a pattern similar to each other after major disturbances supports Oliver and Stephens' (1977) conclusion that the predominant cause for a change in growth is exogenous rather than endogenous influences. However, in addition to the noted major exogenous influences, synchronous change in growth occurs at other dates for each plot. Also, for most trees in each plot, with the exception of plot 30, periods of increase or decrease in growth occur at dates which are unique for each plot relative to the other plots. This phenomenon may be a consequence of the small number of plots; however, it may also be indicative of small-scale dynamics. The gap-size plots used by JABOWA may obscure some of the overall disturbance forces on the 0.36 ha transect by including the dynamics of the gap-phase regeneration mode.

On the other hand, responses in growth to the major disturbances are apparent on each plot even though they are not always the most pronounced change in growth. Yet, the plots for which I had growth data were the least disturbed. Disturbance as incorporated in the model affects only tree death and the subsequent availability of light. Response to disturbance was evident on my plots where no tree death from the major disturbances occurred. One possible explanation for this behavior is that branches were lopped off during the disturbances to the degree that mortality did not occur (at least within the tested time interval), yet, the availability of light to the forest floor increased thus affecting growth. If this hypothesis were true, then, the predictions would tend to underestimate growth of shade-intolerant species for the periods after major disturbances. This hypothesis is difficult to test since all of the species on the plots were intermediate to tolerant of shade. Another possible explanation is that disturbance-related mortality occurred in adjacent plots (which on the whole is true) where those tree deaths increased the light available for growth of individual trees on the edge of the relatively undisturbed plot.

Most of the model's predictions varied from the observed values to the degree that their utility would be limited. The only predictions that could be used with some degree of confidence would be the projection of white oak frequency and basal area. If the data and calibration are correct, then the level of accuracy in the predictions can be used to determine which aspects of the model input, if altered, might improve the predictive accuracy. However, incomplete data can also affect model output. Limitations of this dataset that might have affected the results consisted of height values which were obtained from average height curves, the exclusion of a small size class in Stephens' sampling (stems with DBH below 5 cm), the substitution of some species parameters for black birch and amelanchier from yellow birch and beech, the possibility of different available nitrogen values, and the generality of the soil series.

The average height curves would impede accuracy only when the confidence interval is large and the sample size of heights used to calculate each average point is small. This occurs for species for which little data on height / age relationships (figs. 3-8) were available. The consequence of high confidence intervals and small sample size is irregularity in the height growth curve (figs. 5,6, and 7). To determine heights within the distorted segment of the curve, I connected the height points which surrounded the aberration with a straight line. This method takes the most advantage of the known height values and limits the error.

The exclusion of stems below 5 cm DBH in Stephens' data would be a more serious limitation, except that the patterns where this limitation alters the predictive accuracy are generally apparent. For amelanchier (figs. 16-17, 20-31, and 34-45), beech (figs. 16-29, and 34-45), and red oak (figs. 24-25 and 28-29), the high frequency relative to the low basal area of predicted values when compared to the absence (or near absence) of those species in observations could be a result of the introduction of small stems of each of these species by the model. Addition of smaller trees will be obscured in the frequency predictions for other species. However, the smaller trees will not significantly affect basal area. Therefore, in plots where the frequency prediction is different from the observed value, but the basal area prediction is reasonably accurate, the explanation for the inaccuracy could be the absence of the small size class.

The reason for overestimation of the occurrence of amelanchier could be closely tied to the overestimation of beech, since some of the parameter values for amelanchier were the values used for beech. The black birch predicted values were frequently within 20 % of the observed values thus, the occassional use of yellow birch species parameters should not be a limitation to predictive accuracy for black birch.

Other aspects of model input that could decrease the model's predictive accuracy are that the default values included in the model for species parameters are too general or specific for a different site. Also, the emphasis on climate change and the ability to use projected climate warming in the model to test the effect of such increases in temperature on vegetation dynamics (Botkin 1993), leads one to suppose that complete climate data are necessary for the time interval of simulation. While the projections for climate change have emphasized the increasing rate of warming over the half-century (Botkin 1993), climate stability over each year can not be guaranteed. Unfortunately for validation tests, past data for more than thirty years are difficult to obtain and usually exist at increased distances from the study site.

Another possibility for model input error is the potential change in available nitrogen values after disturbances such as clearcutting. If the model is calibrated only once before harvesting practices begin, then the potential change in available nitrogen levels (Bormann and Likens 1979) could alter species growth and the competition for below-ground resources. Available nitrogen levels do significantly alter the predictive accuracy in the model as was demonstrated in the Hubbard Brook validation test (Botkin 1993). Attention to the change in levels over time would be of interest for use of the model in forestry practices.

The inaccuracy of the predictions made by JABOWA in this validation test are a result of insufficient data and the limitations of the model. Many of the problems with the data have been partially resolved such that the effects of the data limitations are obvious or are not significant. The average height curves were only a problem when there were insufficient trees to produce a realistic age at a particular height. This problem was resolved by smoothing over the abberation in the growth curve. The difficulty with the beech and amelanchier parameters have a minimal effect on the final result because neither species were major factors in the dynamics of any of the plots.

The exclusion of the small size class in the Harvard Forest data is one of the most serious limitations of the data. However, inclusion of the smallest size class in the data would only decrease the overestimation of frequency. In many plots, especially where the frequency was overestimated, the basal area was underestimated. In these cases the predictions were inaccurate beyond the exclusion of data because larger trees actually existed in the plot than were predicted. If the main problem with the predictions was the exclusion of the small size class in the data, then most of the frequency predictions would be overestimated and the basal area predictions would be underestimated. This was not the case.

Another problem with the data which does not heavily influence the results is the generality of the site condition calibration. The model results are not significantly sensitive to the difference in parameter values between the Charlton, Chatfield and Hollis soil series. Since the Chatfield and Hollis calibrations produced the same results, the model is not at all sensitive to the possible range of values for the variables soil texture and percent rock in soil. Since the depth to the water table is the same for each soil series, it can be considered reliable. The depth of the soil is the only difference between the Charlton and the Chatfield / Hollis series which could produce the prediction differences. However, as is evident, this factor does not usually cause the results to be significantly ferent from each other.

Since problems with the data do not account for all of the accuracies of the predicitons, the model must also be responsible for he over- and underestimation of observed values. One possible model alteration that could improve the predictions is better estimation of the growth parameter for each species. Botkin (1993) suggests a method preferable to the present method of estimation. The alternate method involves determining from field data the maximum observed diameter increment for each species. Once this value is determined, it could be required that each tree reaches that value at some time in its life cycle.

One indication of the need for a new method for determining growth parameter values was the reasonably consistent overestimation of hemlock frequency and the underestimation of hemlock basal area. I hypothesized that for plot 12 (from 1886 to 1952) the considerable overestimation of frequency for hemlock and the underestimation of basal area could be accounted for by a growth parameter value which is lower than would actually be observed. I tested this hypothesis by lengthening the period of prediction to 300 years rather than the actual 66 years. The mean predicted frequency over that interval of time was exactly the value observed. The actual basal area for hemlock was within the confidence interval of the prediction over 300 years. This test supports my hypothesis that hemlocks are grown too slowly in the model when compared with the actual growth in the plot. This hypothesis could be confirmed further by performing a regression on an average growth curve of hemlocks in the study plot with the growth curve calculated by the model.

Another aspect of the model which needs to be further evaluated is plot size. With the plot size set at $100m^2$, the ratio of edge length to interior area of the plot is high. As a result, trees in adjacent plots will influence the dynamics of many trees in the study plot. For example, one full grown tree on the edge of an adjacent plot could shade at least one third of the neighboring plot. Yet, larger plots are not necessarily preferable because JABOWA does not incorporate spatial effects.

Another feature of the model that could be improved is the accuracy of the height equation. The height equation, while in this plot was shown to be inaccurate in predicting heights from diameter at breast height, may not have a tremendous effect on the overall ability of the model to predict species composition and basal area. The equation is more important for outputs not included in this paper, but important to foresters, such as volume, biomass and merchantable timber. Botkin (1993) notes that predictions of species' frequency are the most accurate, while, predictions of biomass are the least accurate. This accuracy could probably be improved with a better height equation.

To further improve JABOWA with regard to the effect of disturbance on tree growth, an option which specifies which species are to be cut (and a size range specific to the species) should be included. Also, the model needs to have the flexibility of incorporating species-specific susceptibility to disturbances such as hurricanes (Foster, 1988b).

As in past experiments, the results of a validation test on JABOWA lead to insights about the data and the limitations of the data for use in validations. However, the patterns of inaccuracy of JABOWA's predictions were not solely the consequence of incomplete data. Determining why the predicted values are significantly different from the actual values can lead to more insight into the model's ability and suggests testing of hypotheses to reinforce the data.

Such hypotheses would include deducing whether or not the clearcut plot, if left undisturbed by humans, will ever converge to look like the neighboring hemlock-dominant stand. The best test, of course, would entail following the composition of both plots for twenty to one-hundred years. A smaller scale test would be to project the present composition of Stephens' plot into the future and compare it with the present composition of the adjacent plot. The strengthening of a model such as JABOWA could easily occupy a life-time, yet, the data collected for such tests would by invaluable for a multitude of studies concerning the understanding of forest dynamics.

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fig. 1: Map of the Harvard Forest area surrounding Stephens' plot and the weather site in Petersham, MA

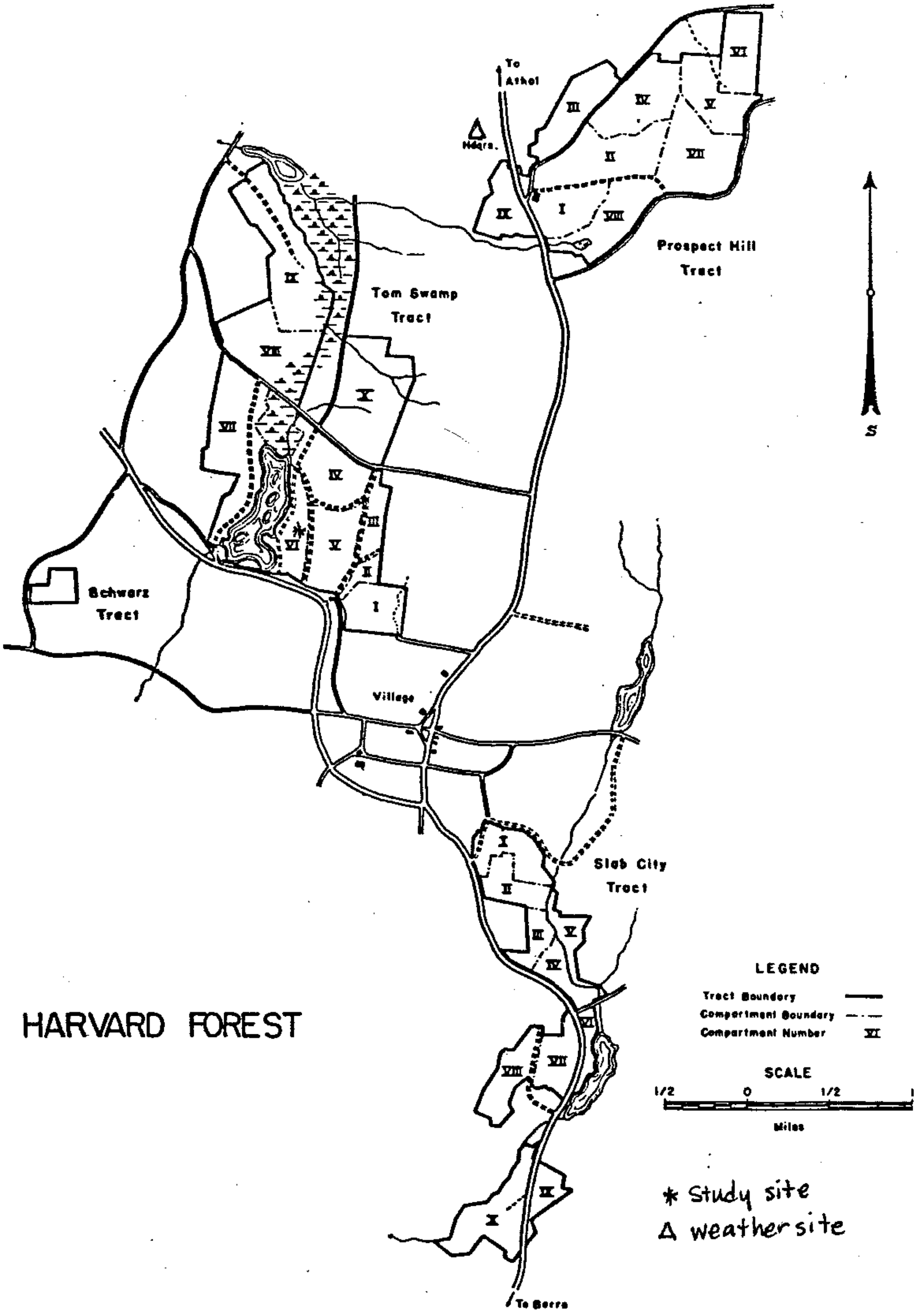
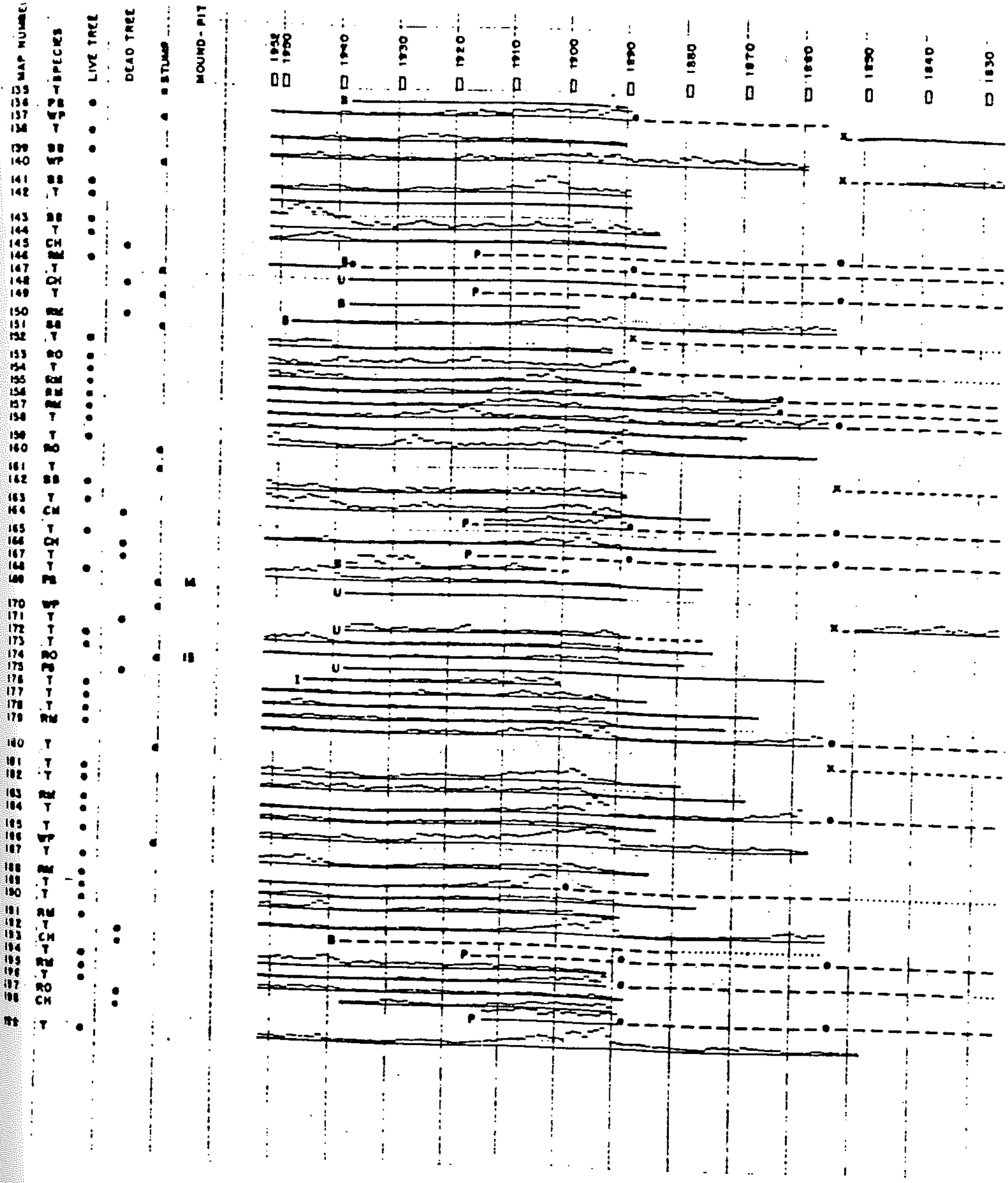


fig. 2: A sample of Stephens' annual incremental diameter growth data created by measuring tree-growth rings



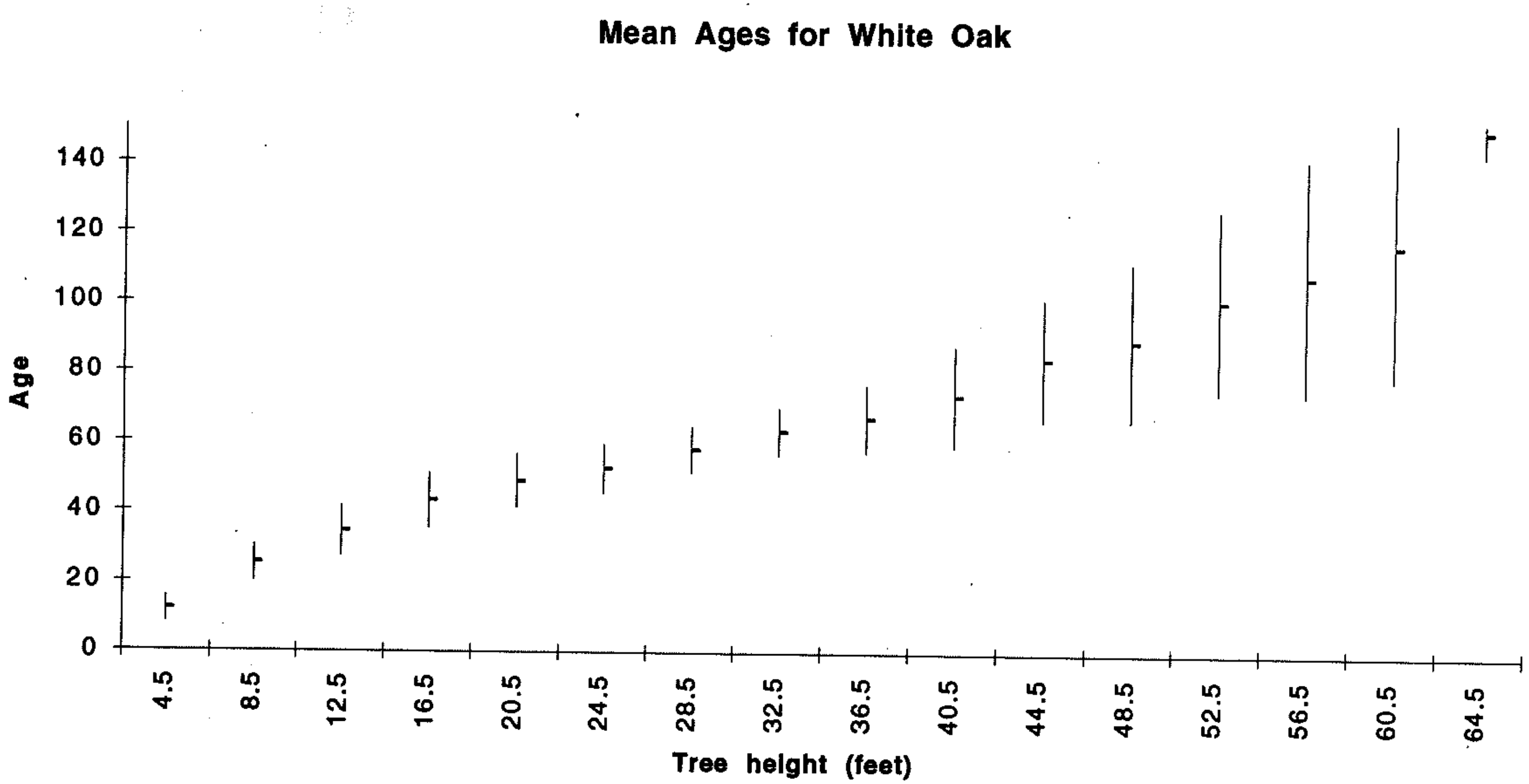


Fig. 3 - Mean ages calculated from tree-ring analysis at every four feet along felled tree's length

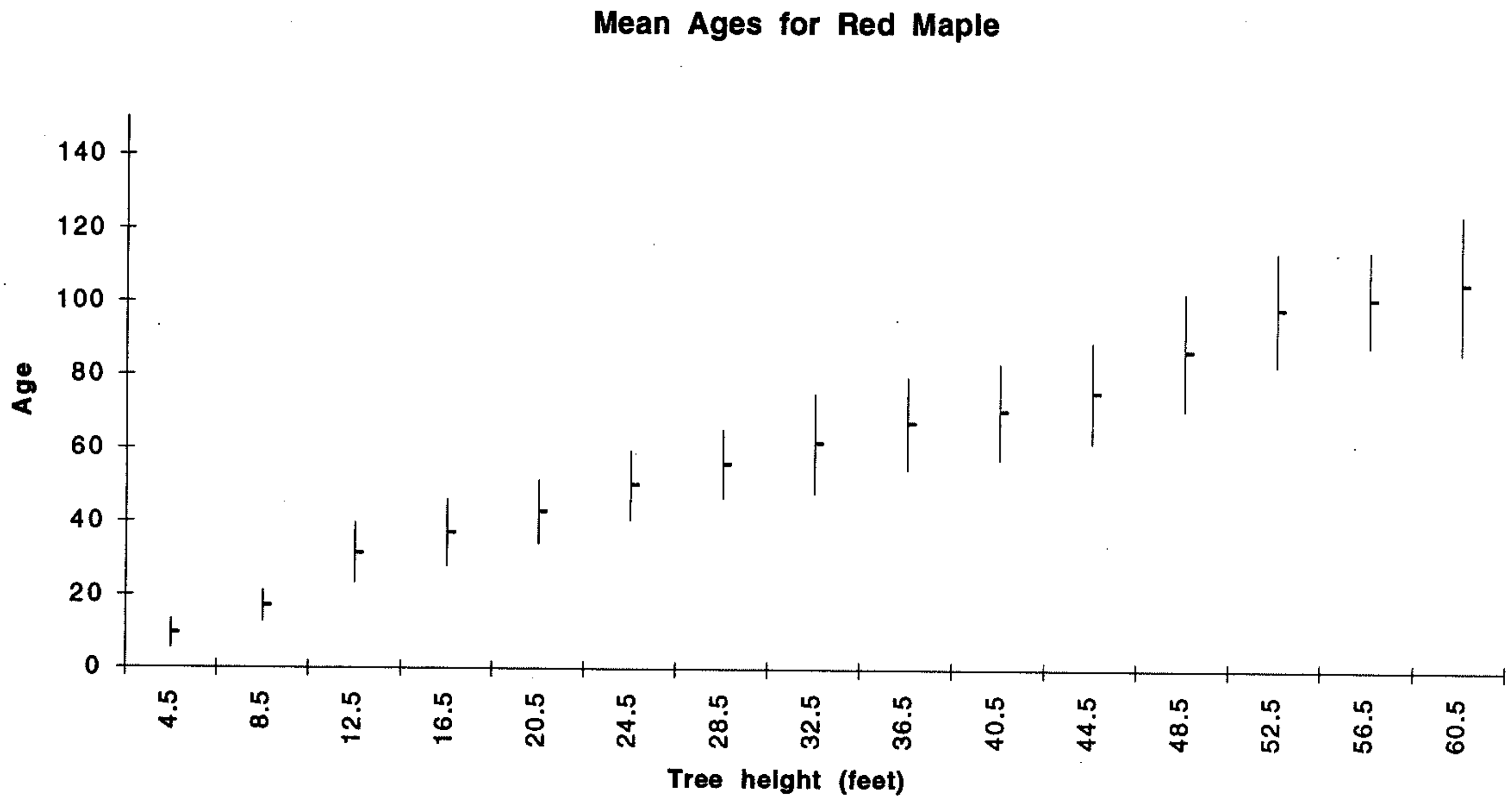


Fig. 4 - Mean ages calculated from tree-ring analysis at every four feet along felled trees' length

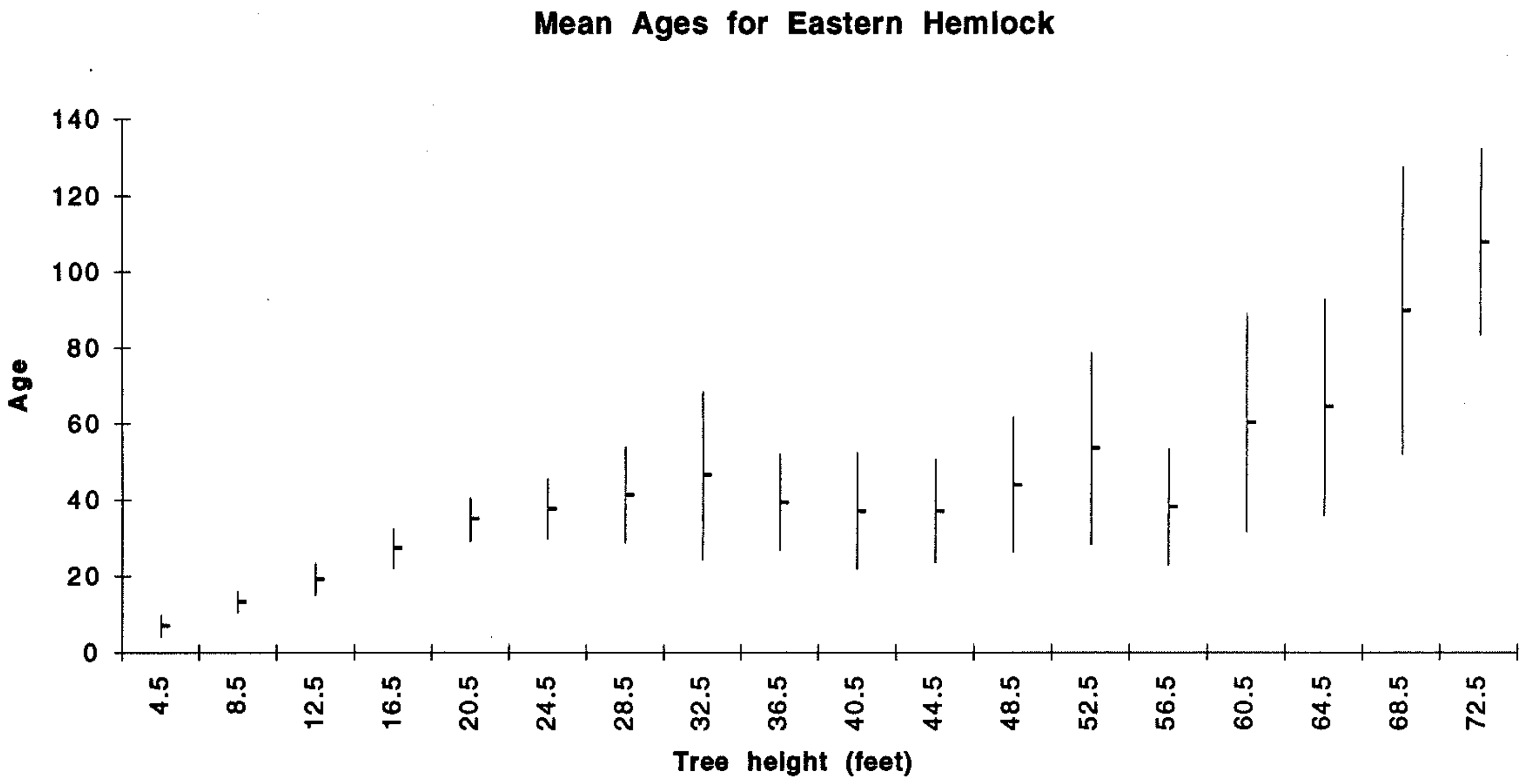


Fig. 5 - Mean ages calculated from tree-ring analysis at every four feet along felled trees' length

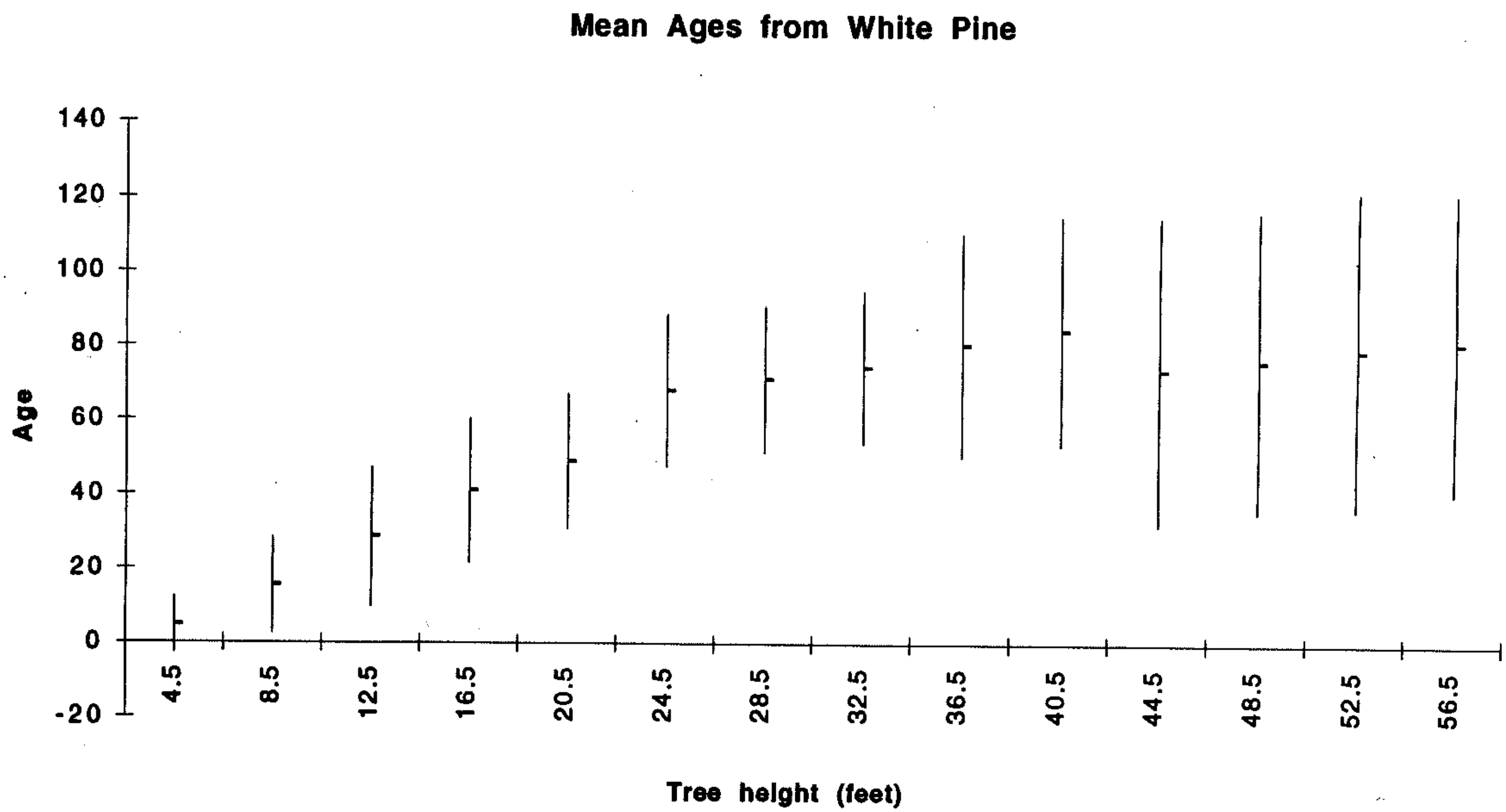


Fig. 6 - Mean ages calculated from tree-ring analysis at every four feet along felled trees' length

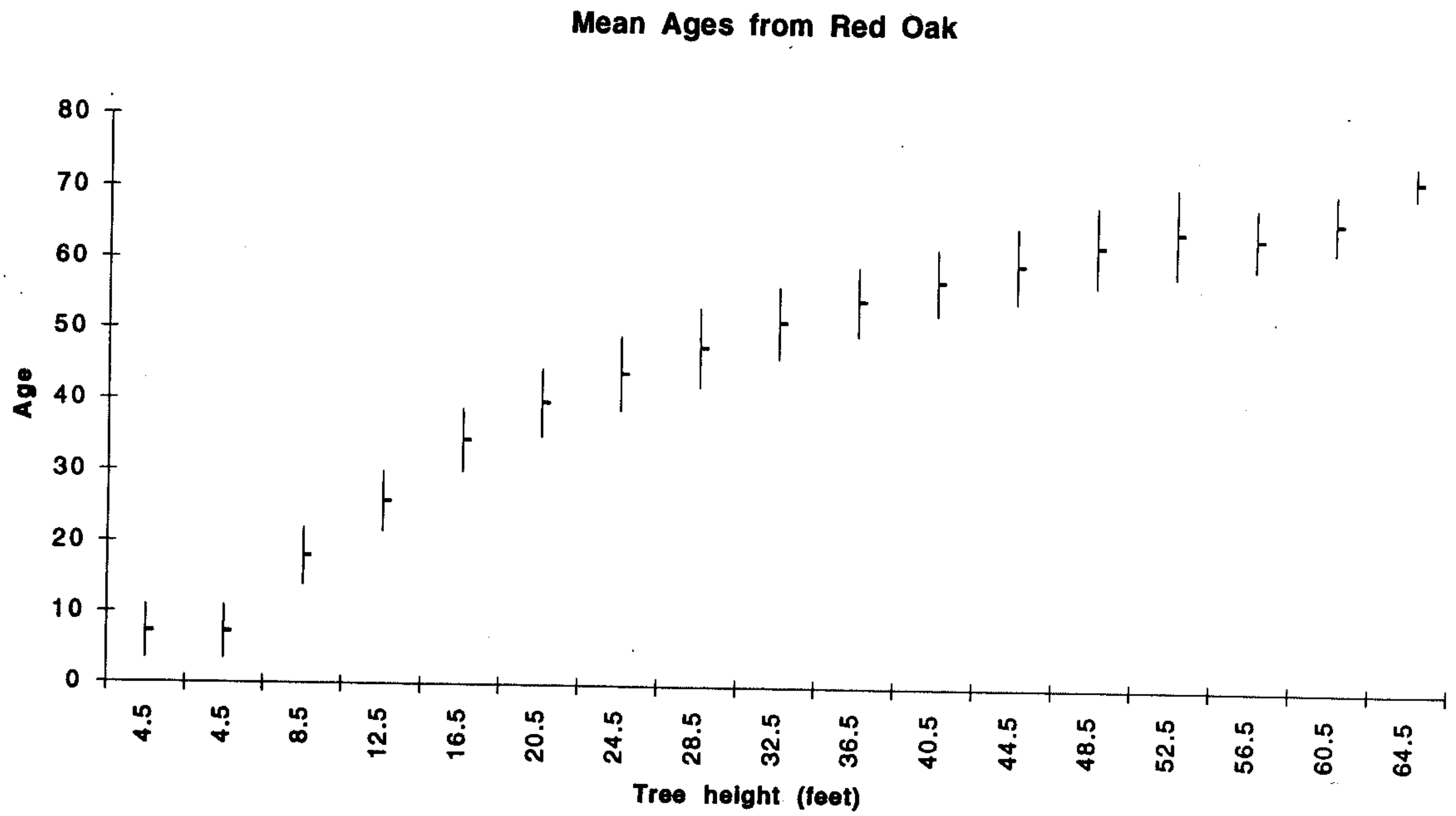


Fig. 7 - Mean ages calculated from tree-ring analysis at every four feet along felled trees' length

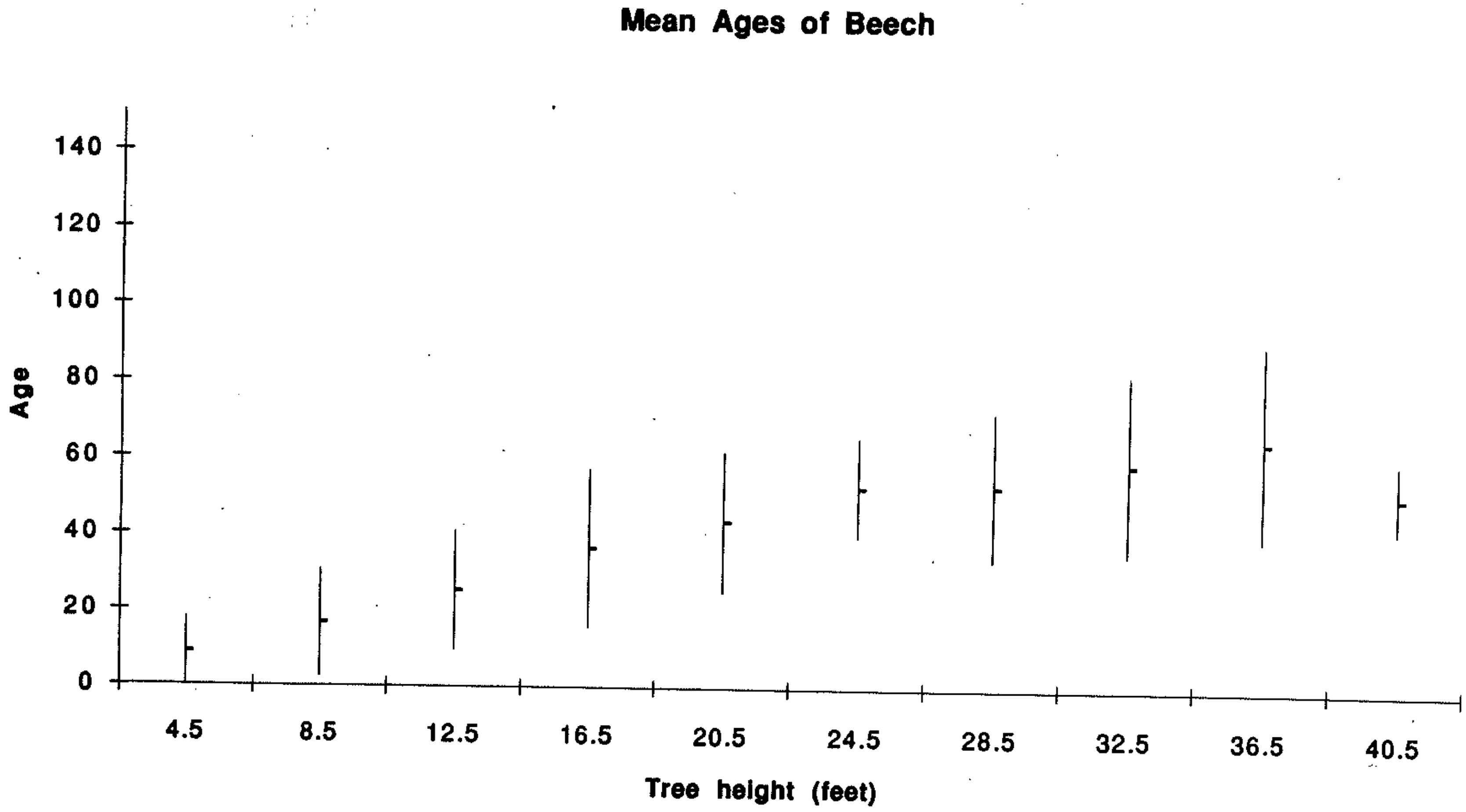


Fig. 8 - Mean ages calculated from tree-ring analysis at every four feet along felled tree's length

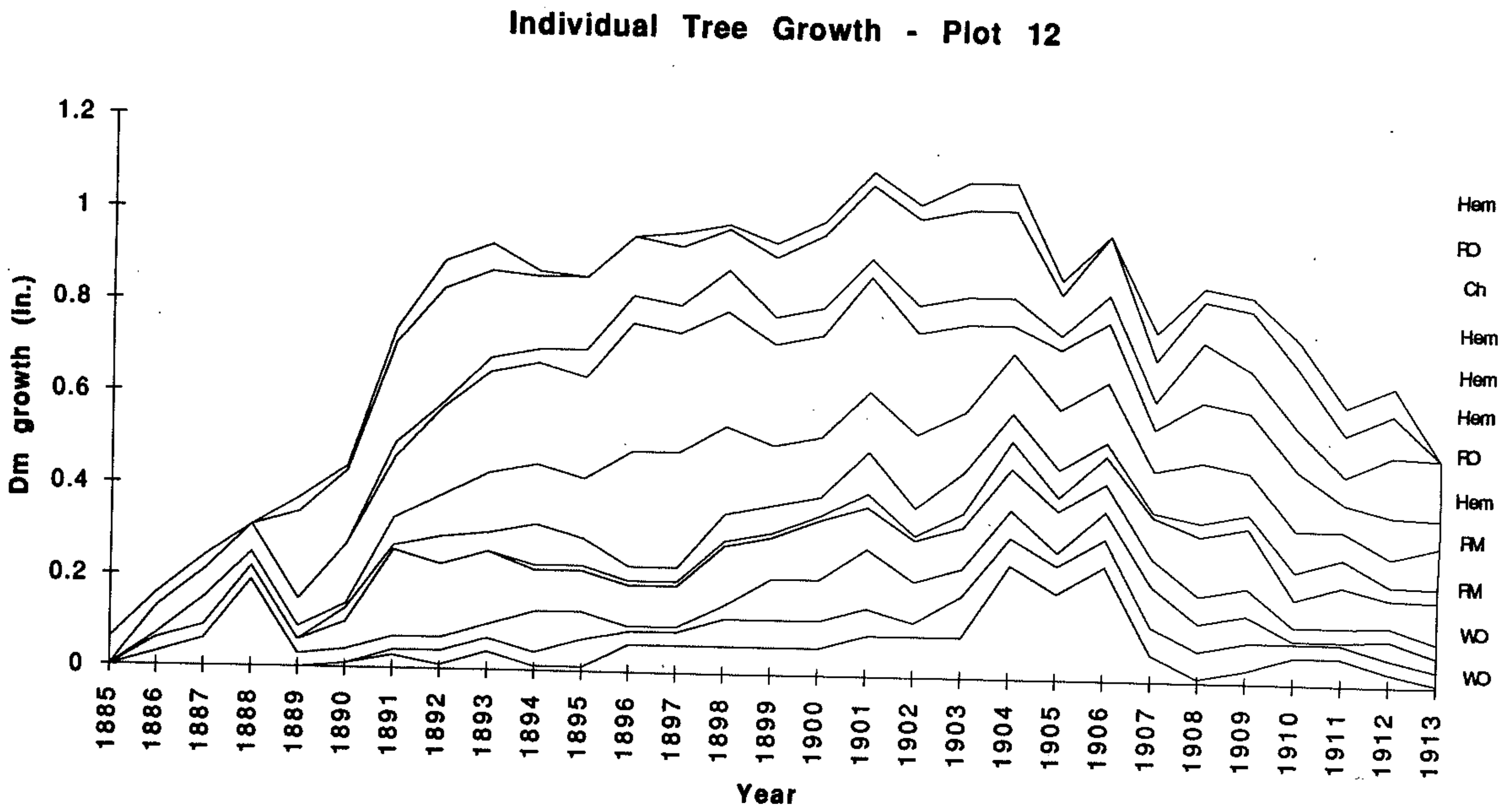


Fig. 9 - Annual incremental growth for all trees in plot 12 measured from tree-ring analysis

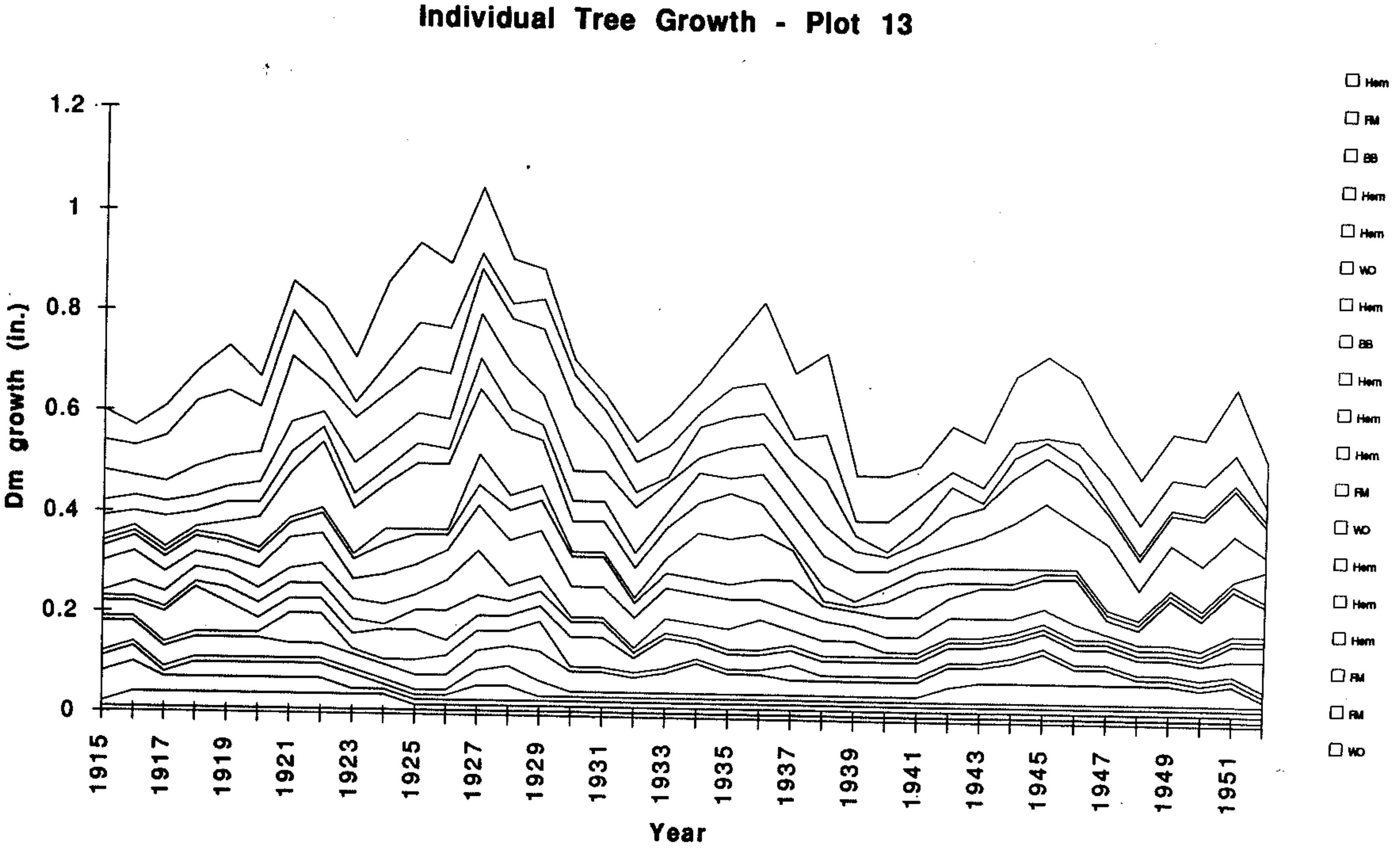


Fig. 10 - Annual incremental growth for all trees in plot 13 measured from tree-ring analysis

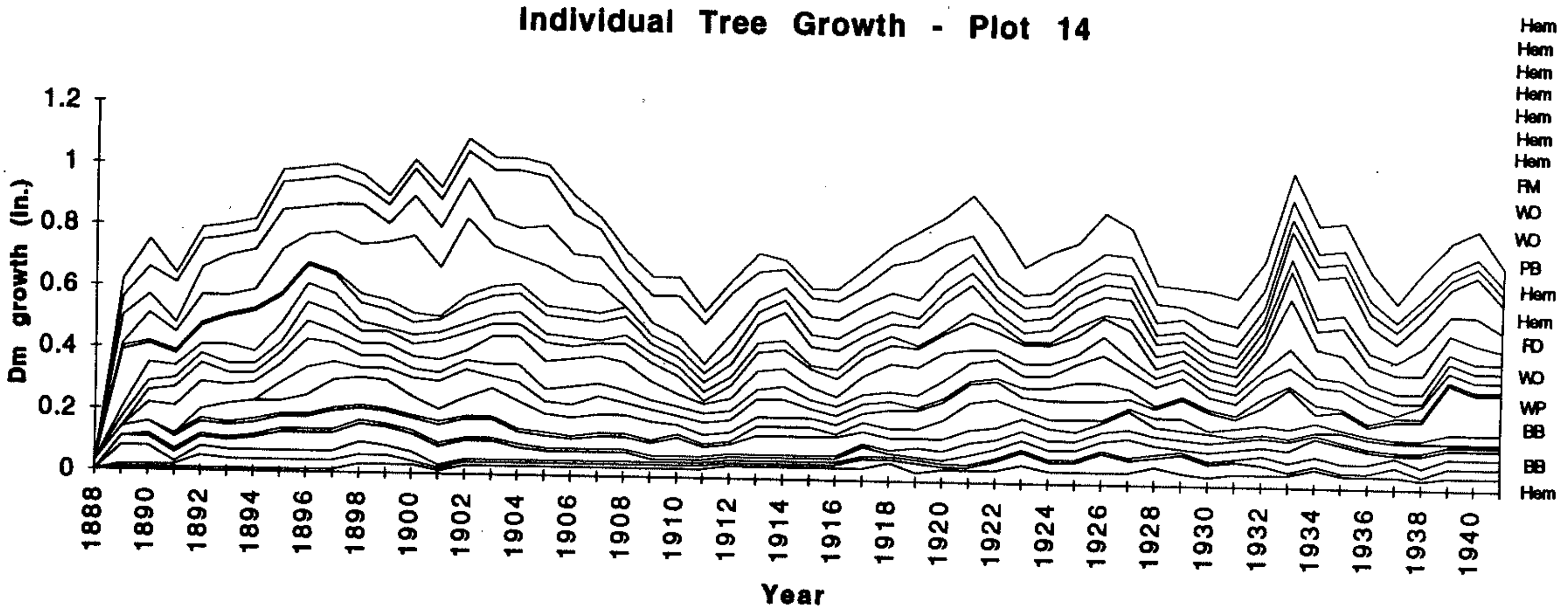


Fig. 11 - Annual incremental growth for all trees in plot 14 measured from tree-ring analysis

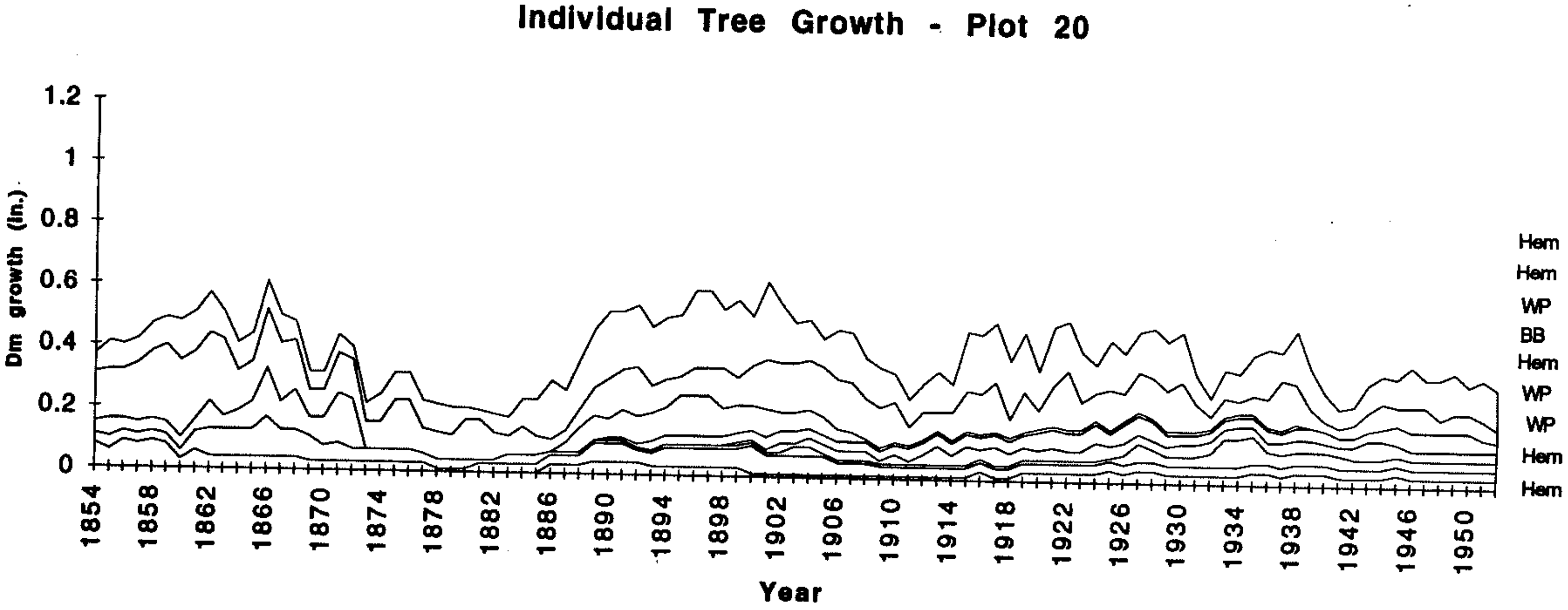


Fig. 12 - Annual incremental growth for all trees in plot 20 measured from tree-ring analysis

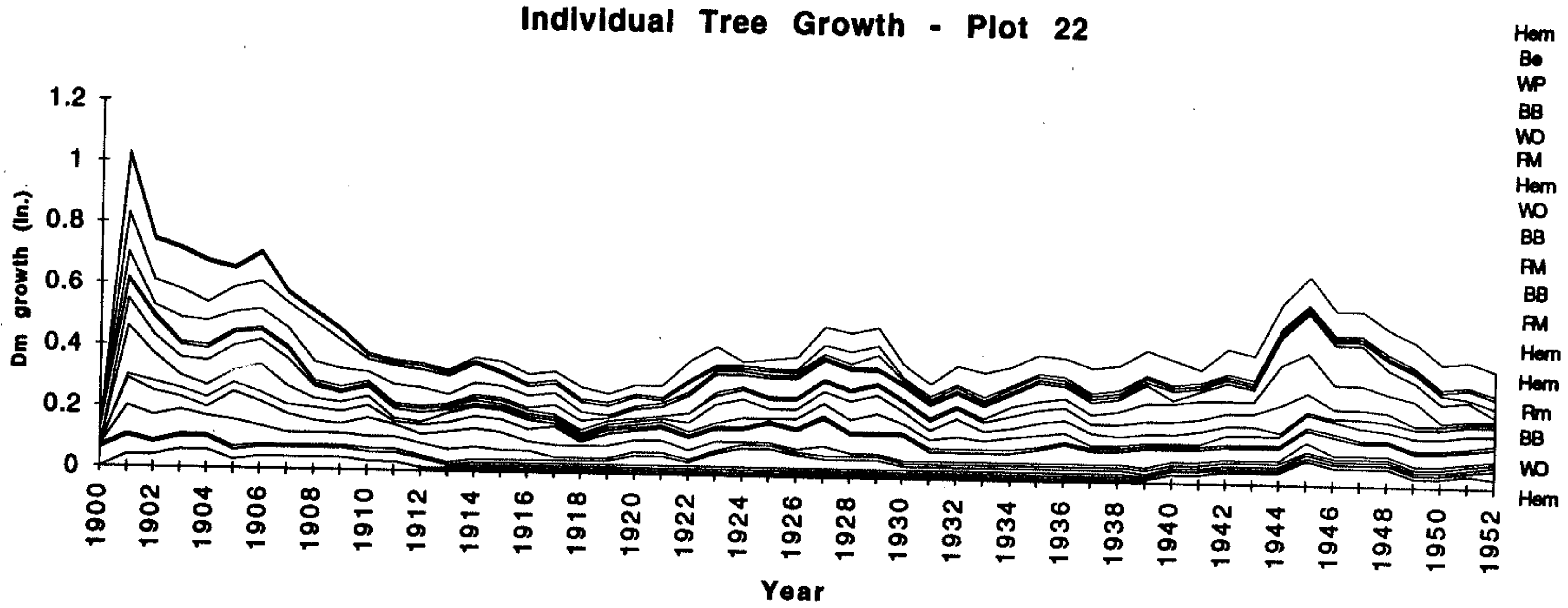


Fig. 13 - Annual incremental growth for all trees on plot 22 measured by tree-ring analysis

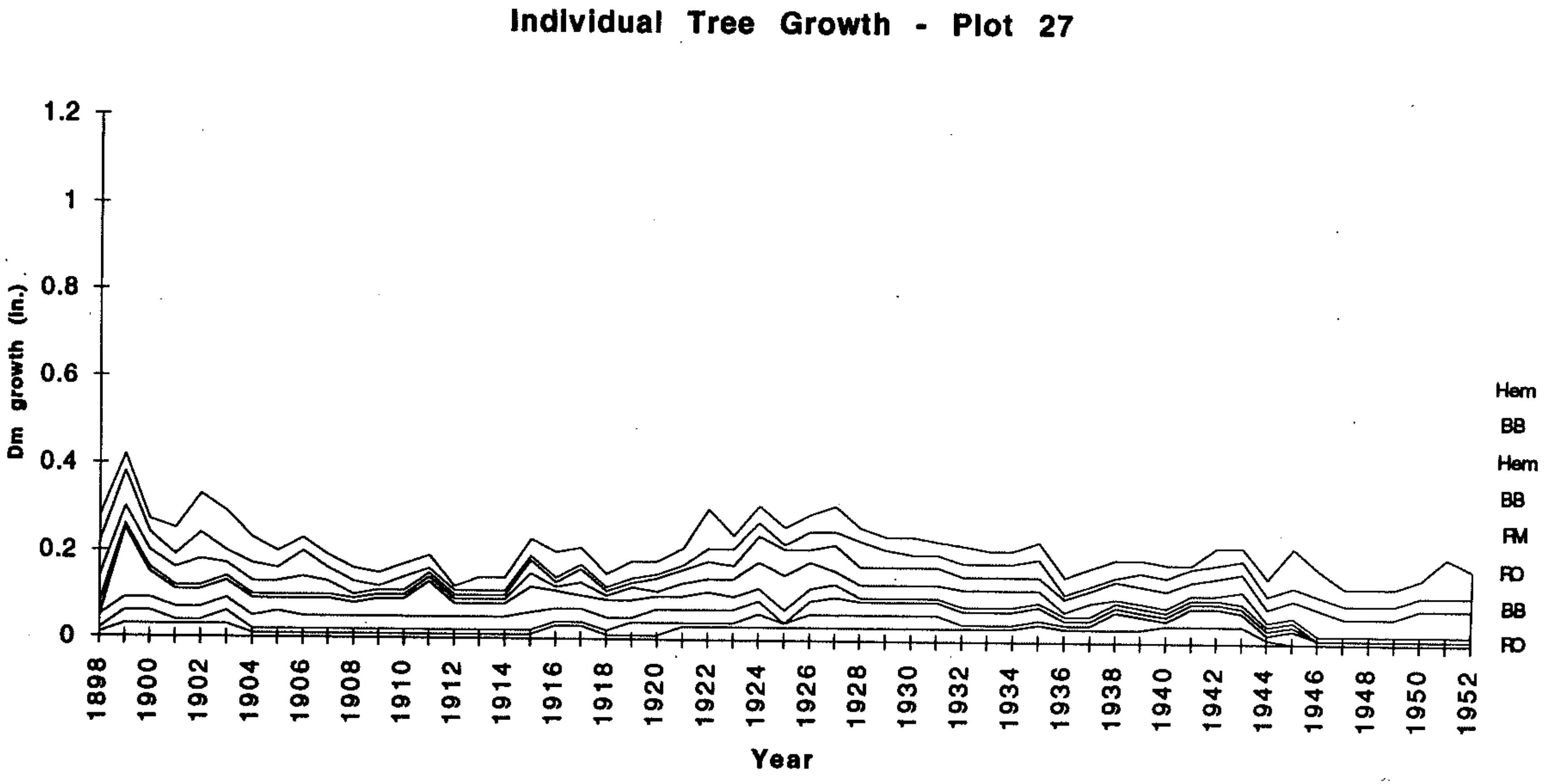


Fig. 14 - Annual incremental growth of all trees in plot 27 measured by tree-ring analysis

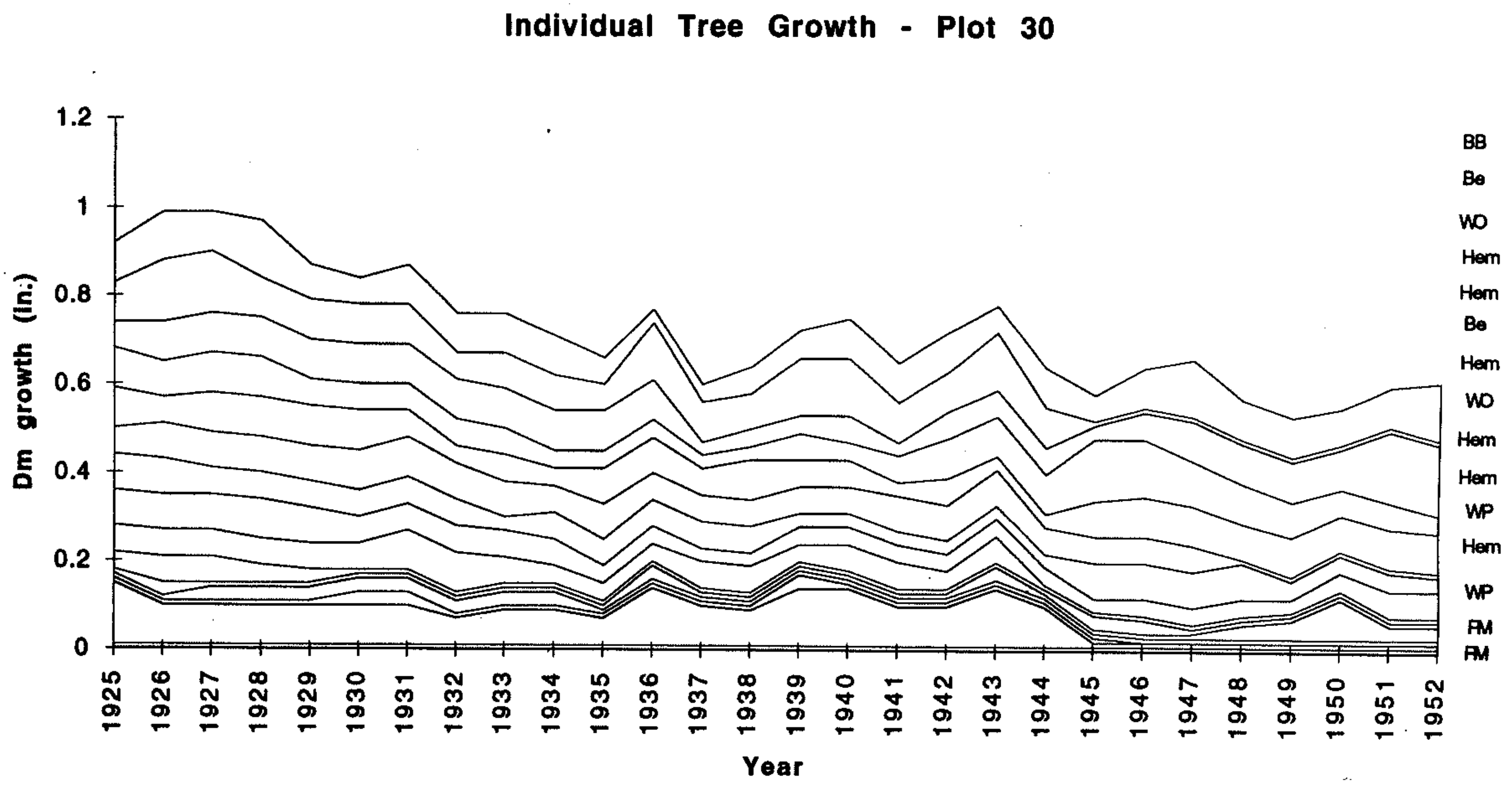


Fig. 15 - Annual incremental growth for all trees on plot 30 measured by tree-ring analysis

Fig. 16

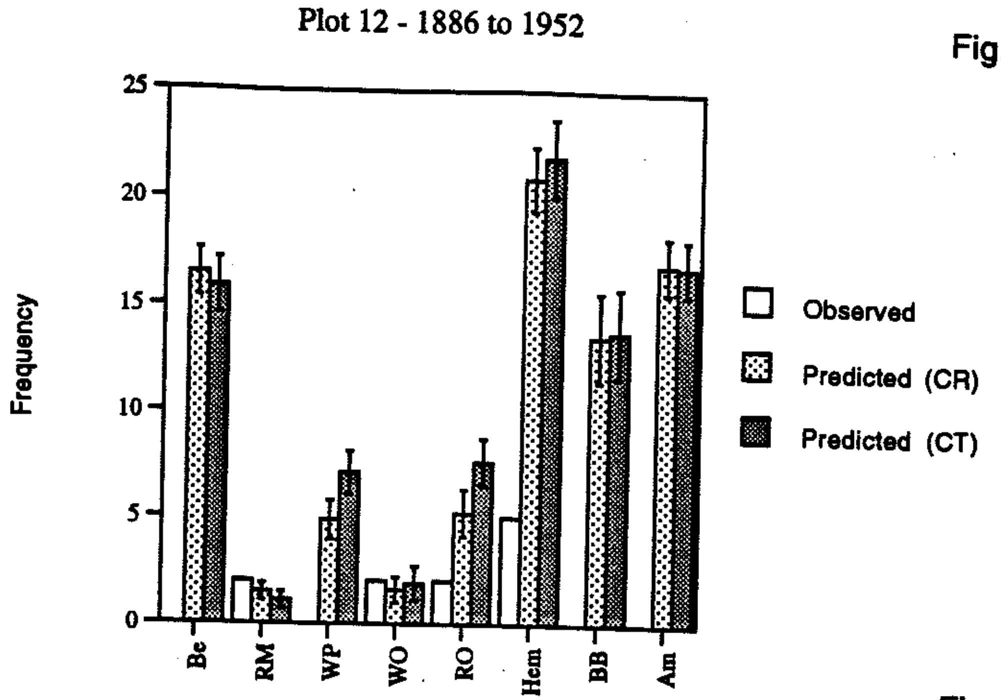


Fig. 17

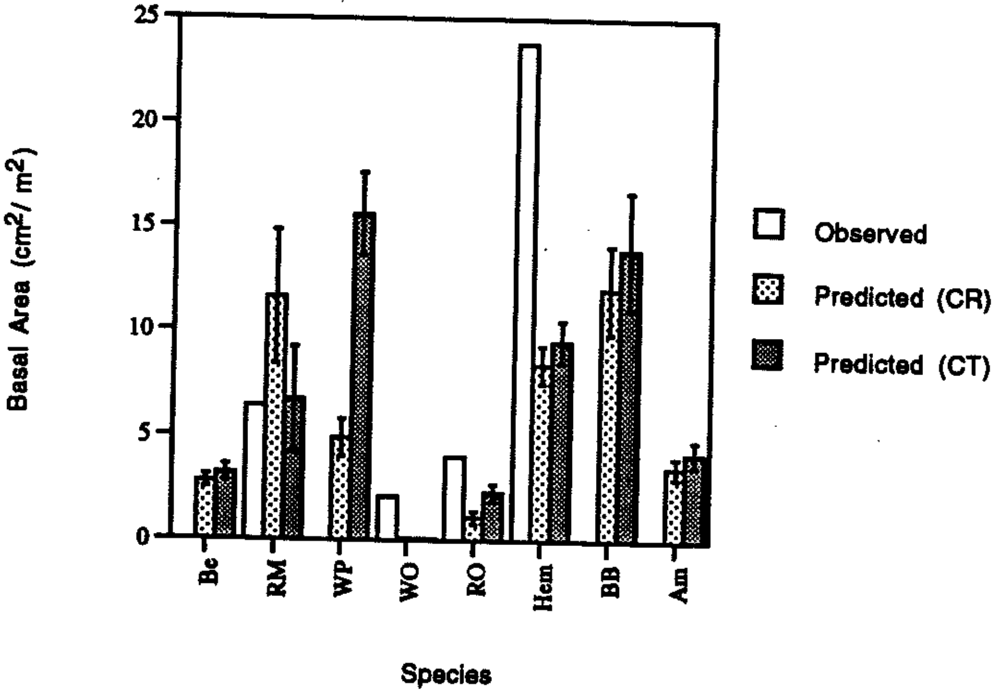


Fig. 16 and 17

JABOWA was run from 1886 to 1952 for plot 12 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (16) and basal area (17) of the species beech (Be), red maple (RM), white pine (WP), white oak (WO), red oak (RO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observ. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 12 - 1936 to 1952

Fig. 18

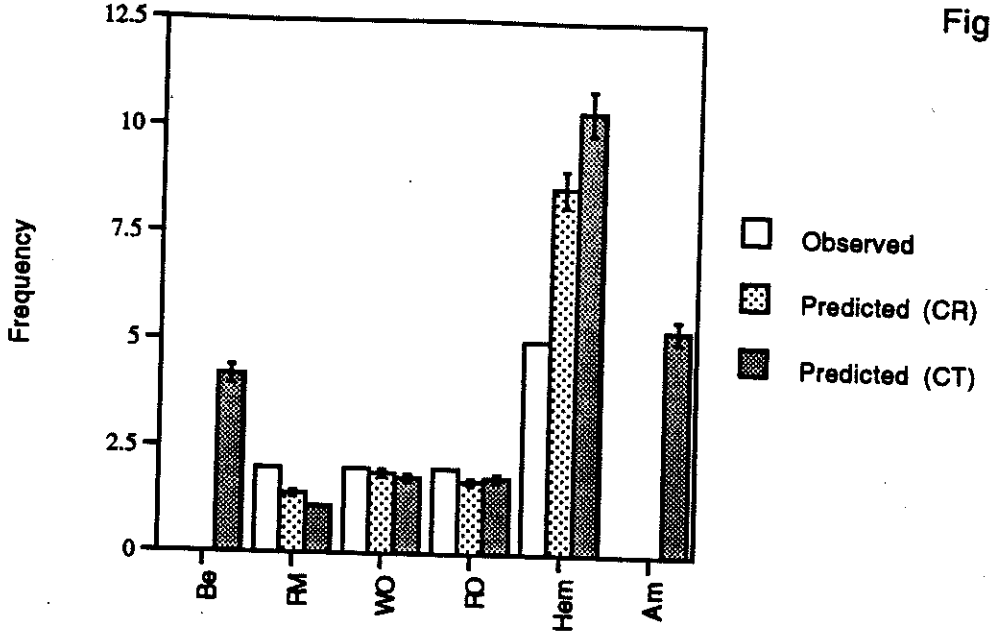


Fig. 19

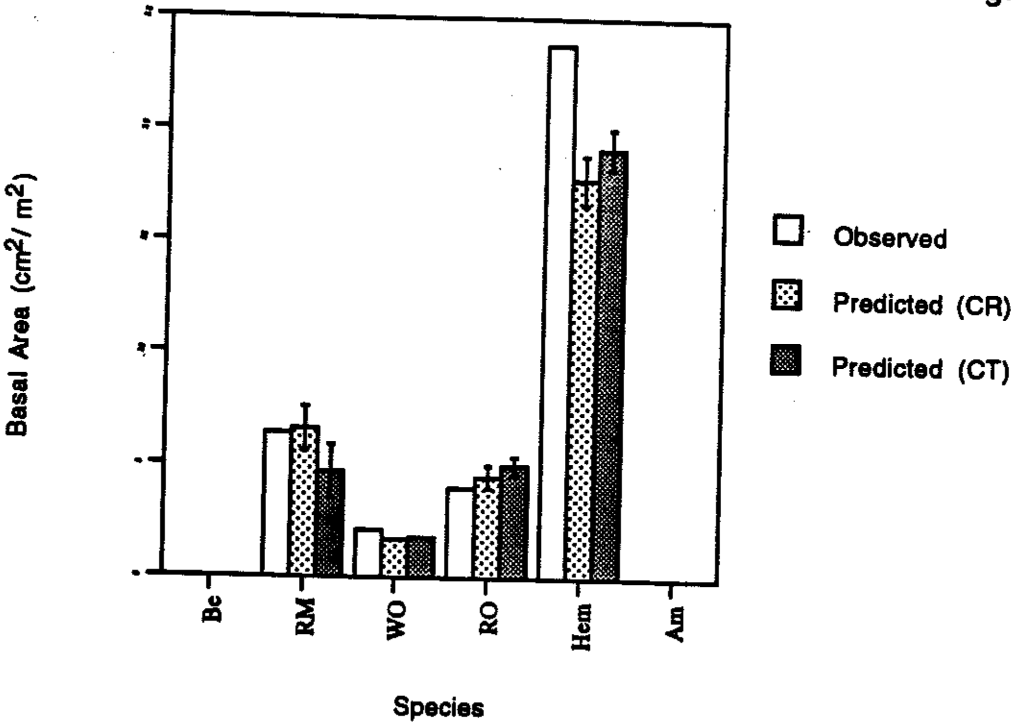


Fig. 18 and 19

JABOWA was run from 1936 to 1952 for plot 12 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (18) and basal area (19) of the species beech (Be), red maple (RM), white oak (WO), red oak (RO),hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 13 - 1915 to 1952

Fig. 20

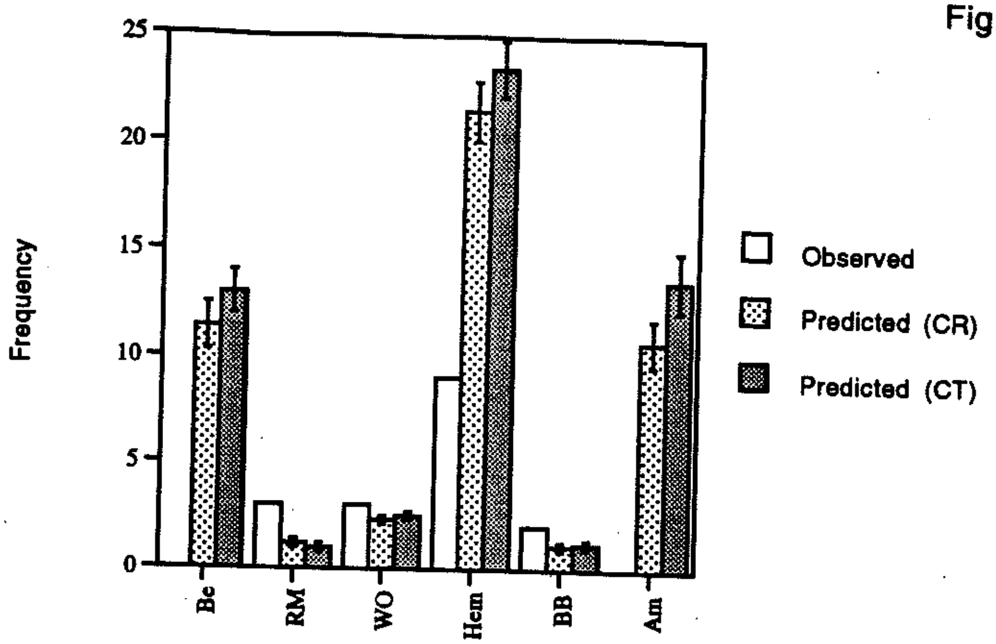


Fig. 21

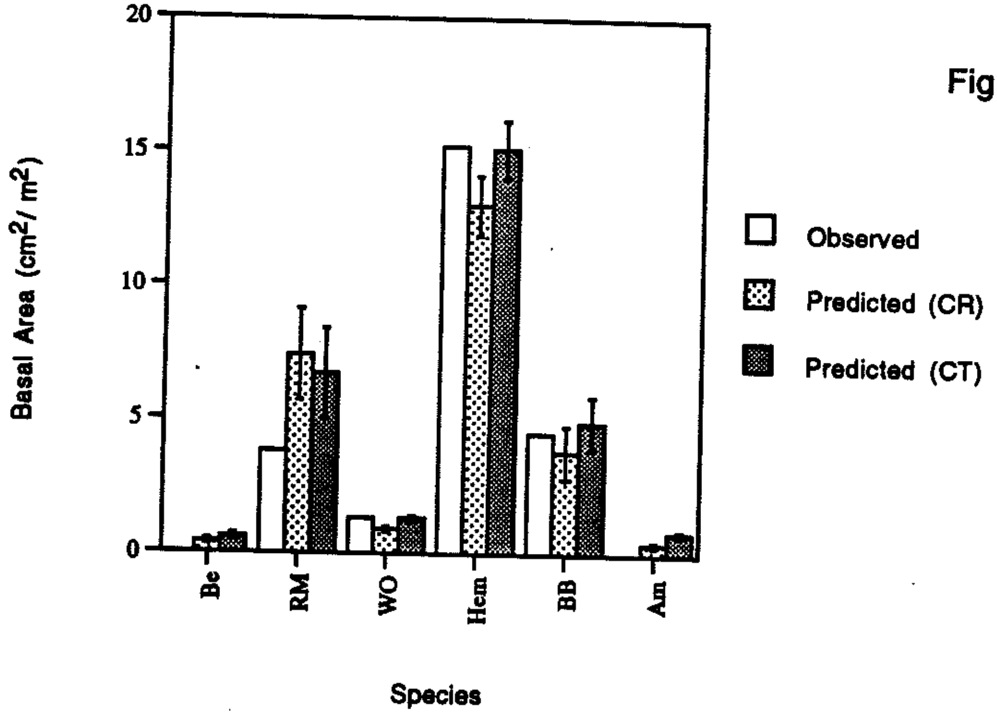


Fig. 20 and 21

JABOWA was run from 1915 to 1952 for plot 13 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (20) and basal area (21) of the species beech (Be), red maple (RM), white oak (WO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations.Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 13 - 1936 to 1952

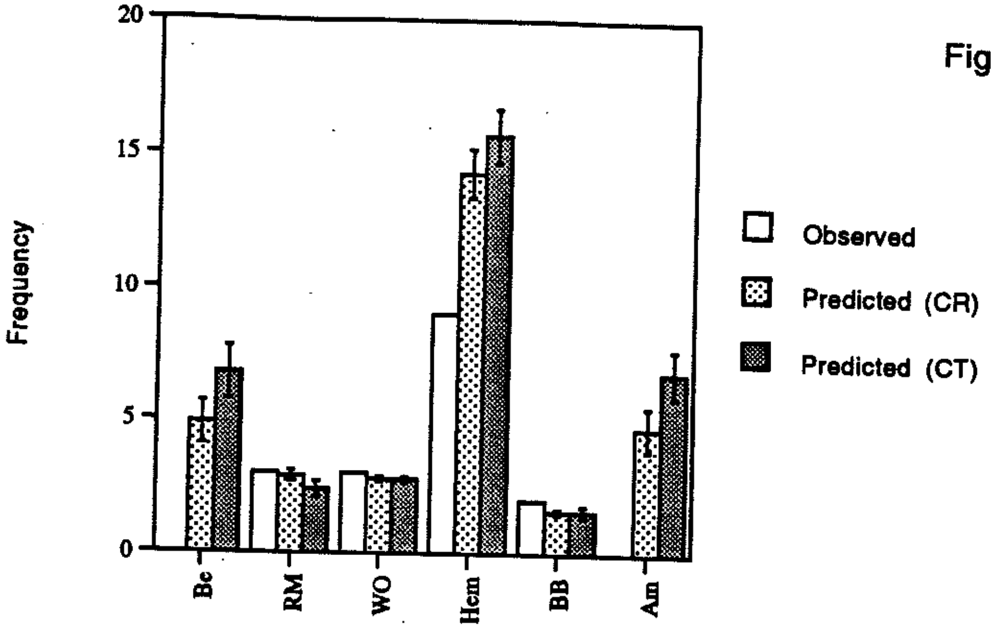


Fig. 22

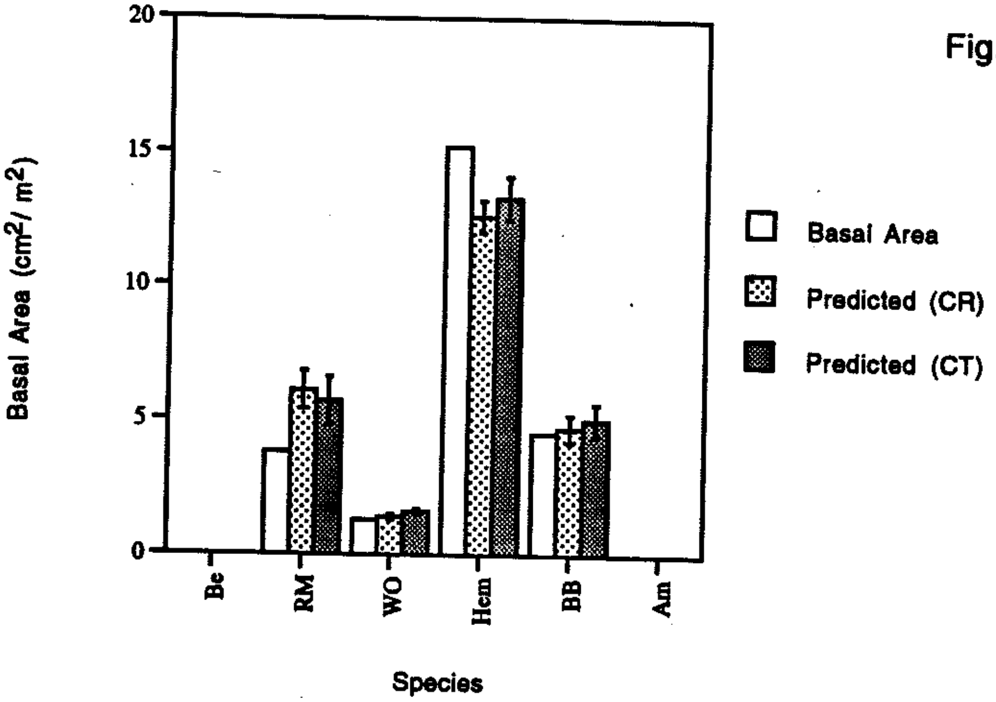


Fig. 23

**Fig. 22 and 23**

JABOWA was run from 1936 to 1952 for plot 13 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (22) and basal area (23) of the species beech (Be), red maple (RM), white oak (WO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations.Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 14 - 1890 to 1952

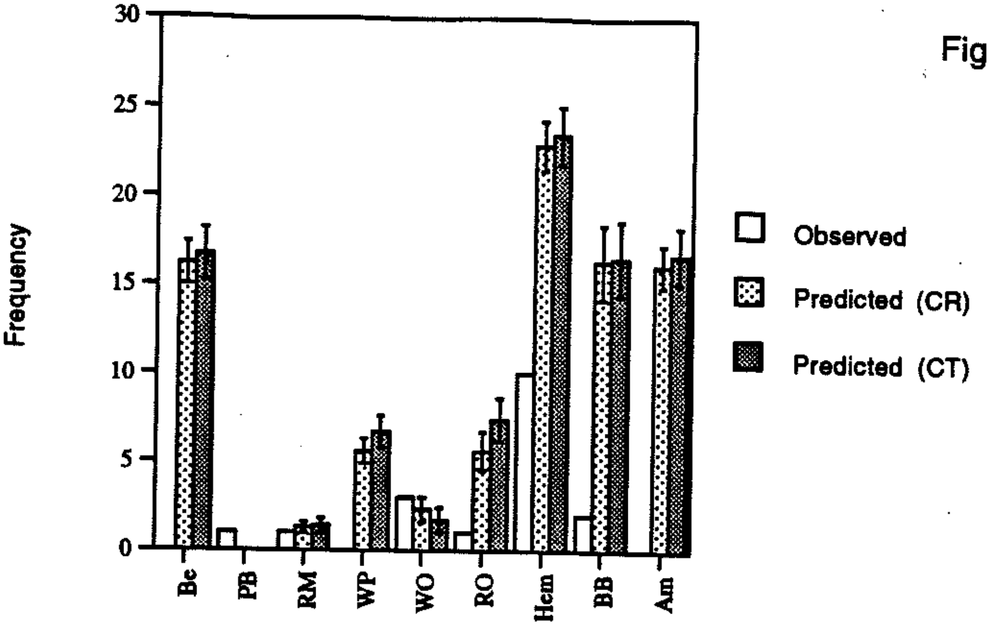


Fig. 24

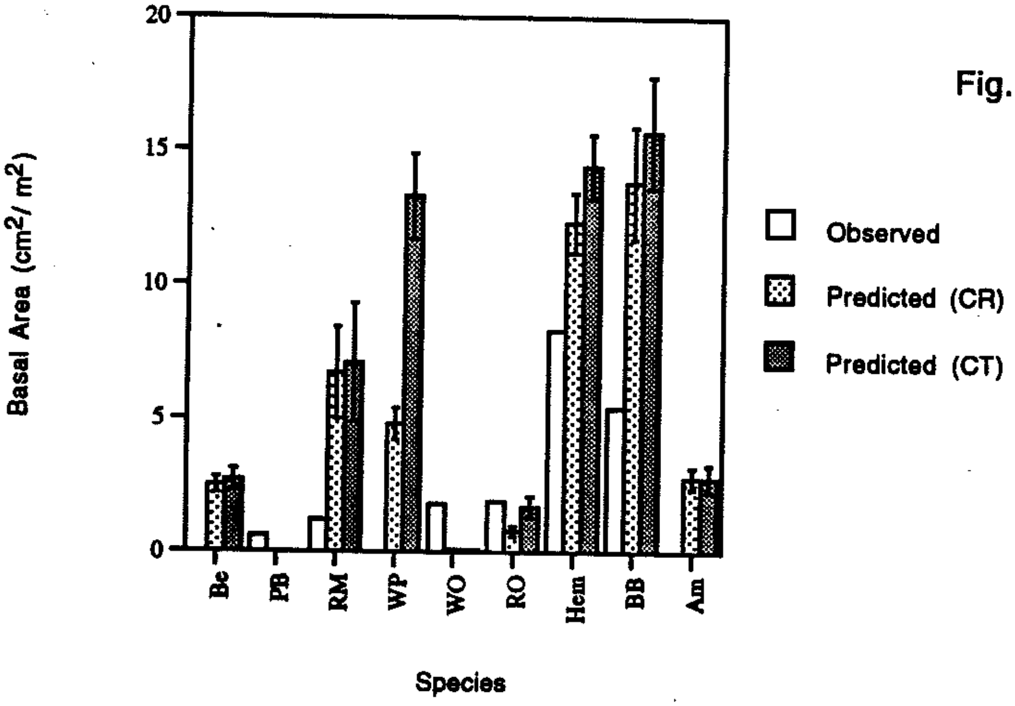


Fig. 25

Fig. 24 and 25

JABOWA was run from 1890 to 1952 for plot 14 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (24) and basal area (25) of the species beech (Be), paper birch (PB), red maple (RM), white pine (WP), white oak (WO), red oak (RO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations.Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 14 - 1936 to 1952

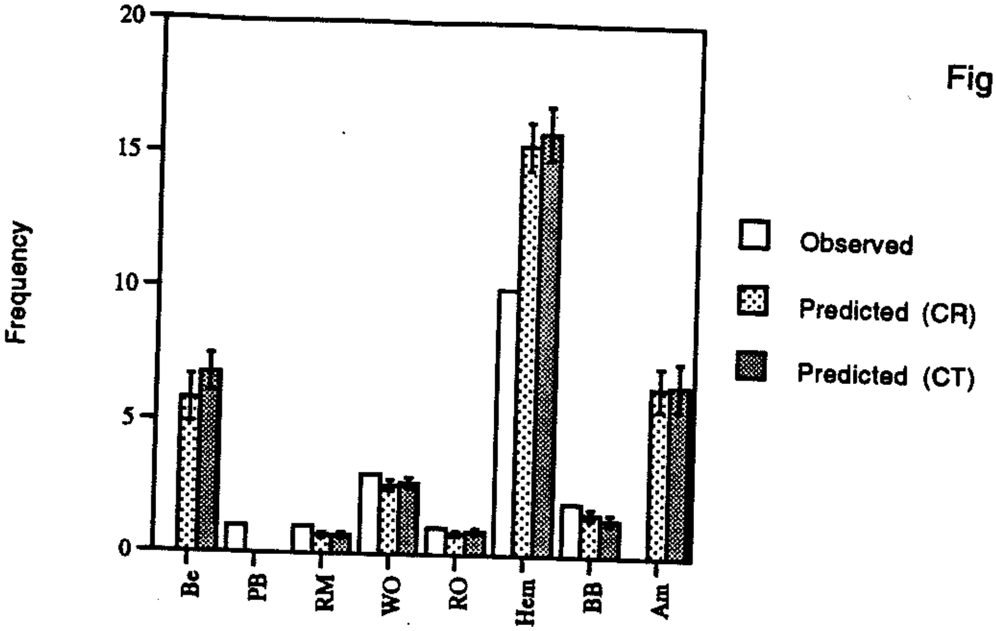


Fig. 26

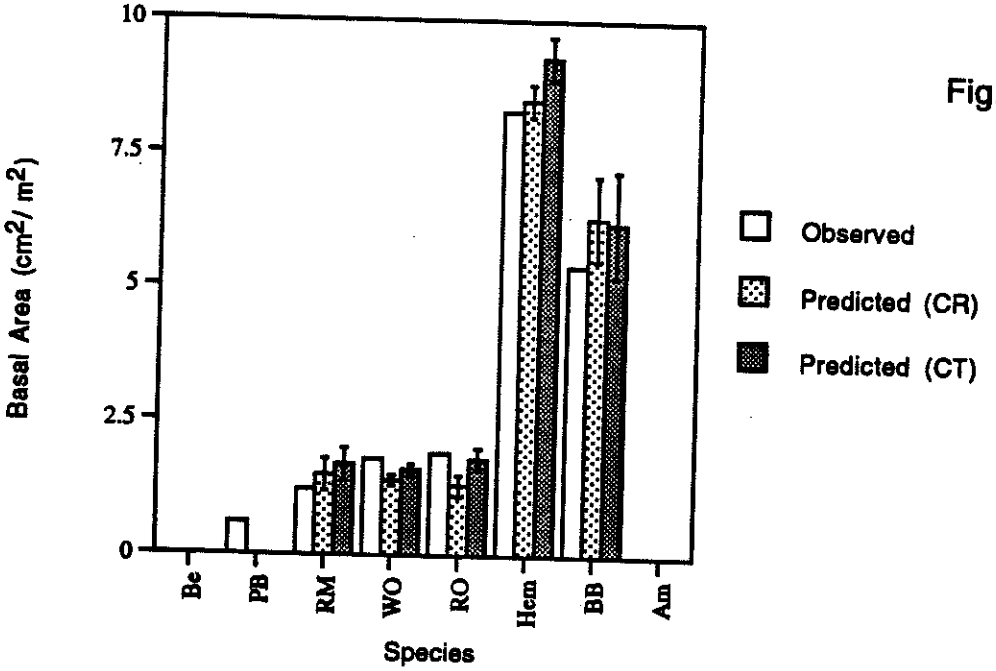


Fig. 27

**Fig. 26 and 27**

JABOWA was run from 1936 to 1952 for plot 14 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (26) and basal area (27) of the species beech (Be), paper birch (PB), red maple (RM), white oak (WO), red oak (RO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observ. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 20 - 1855 to 1952

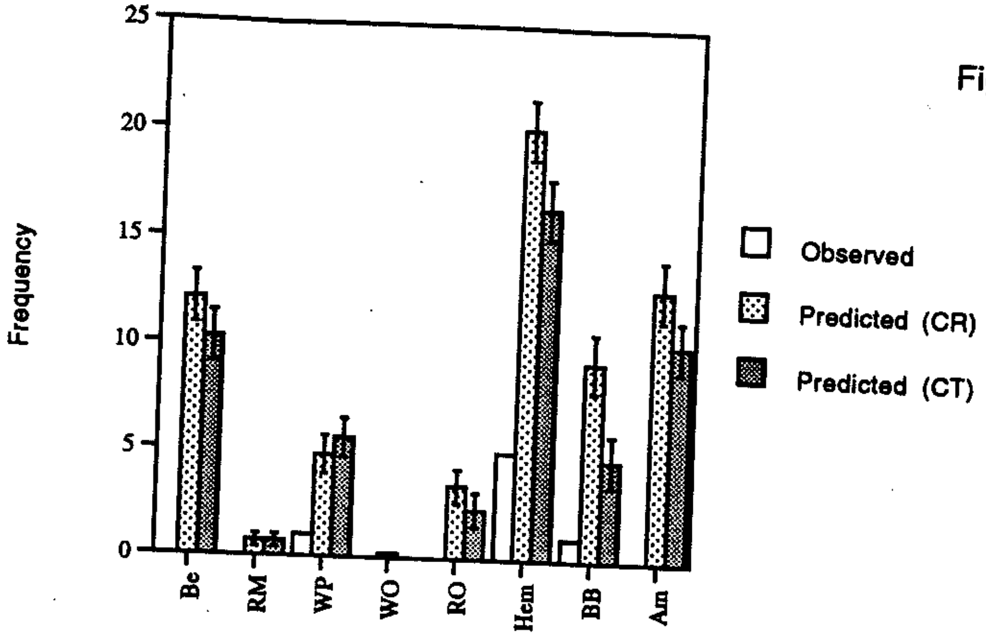


Fig. 28

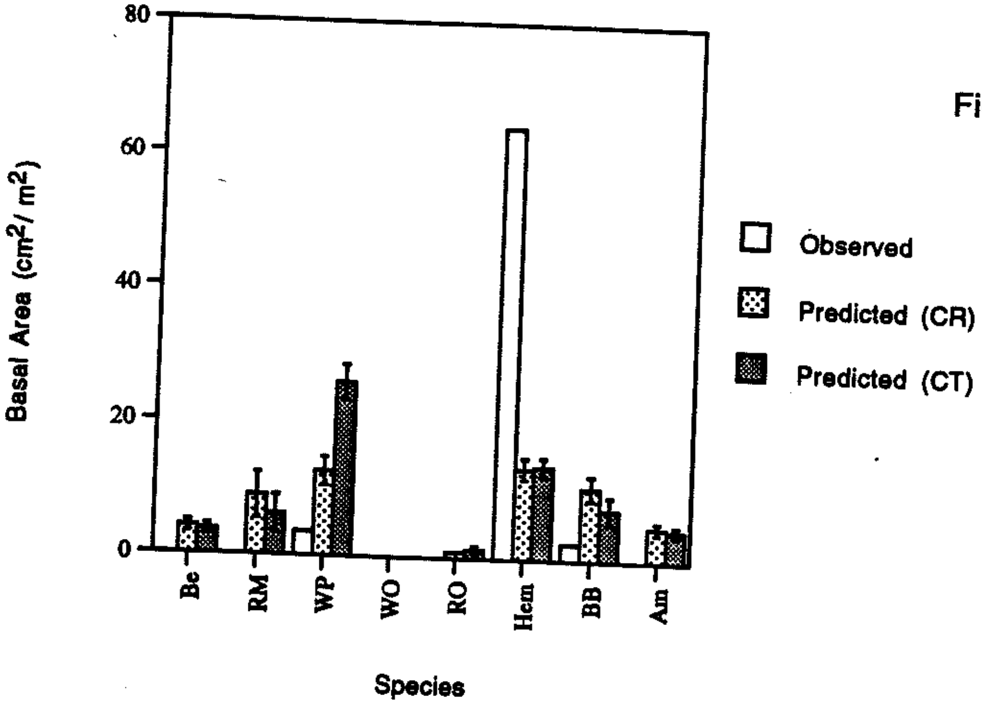


Fig. 29

Fig. 28 and 29

JABOWA was run from 1855 to 1952 for plot 20 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (28) and basal area (29) of the species beech (Be), red maple (RM), white pine (WP), white oak (WO), red oak (RO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observ. Confidence intervals for the predicted values were obtained from 40 iterations of the run

## Plot 20 - 1879 to 1888

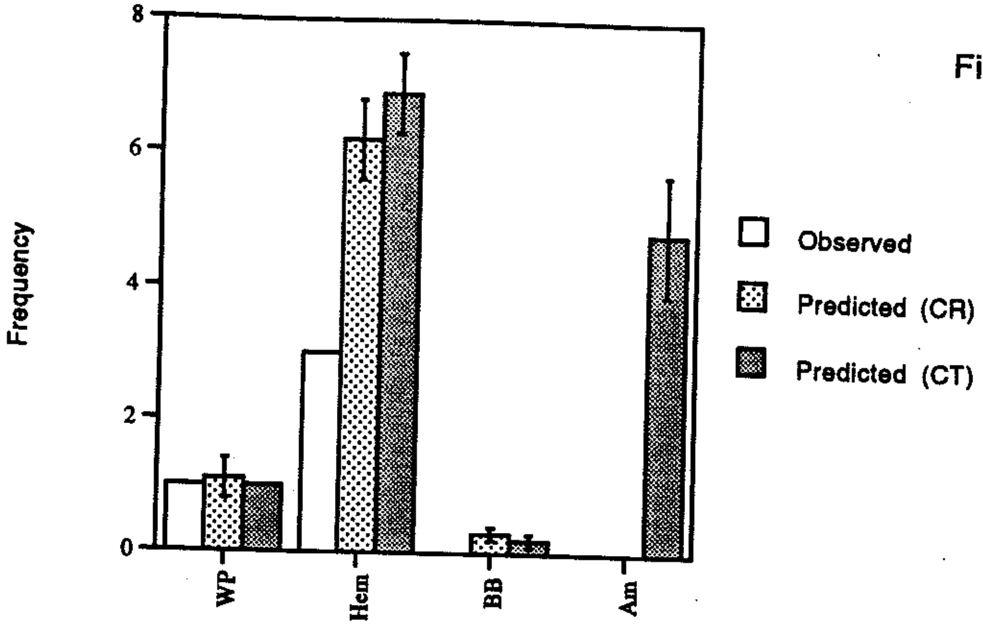


Fig. 30

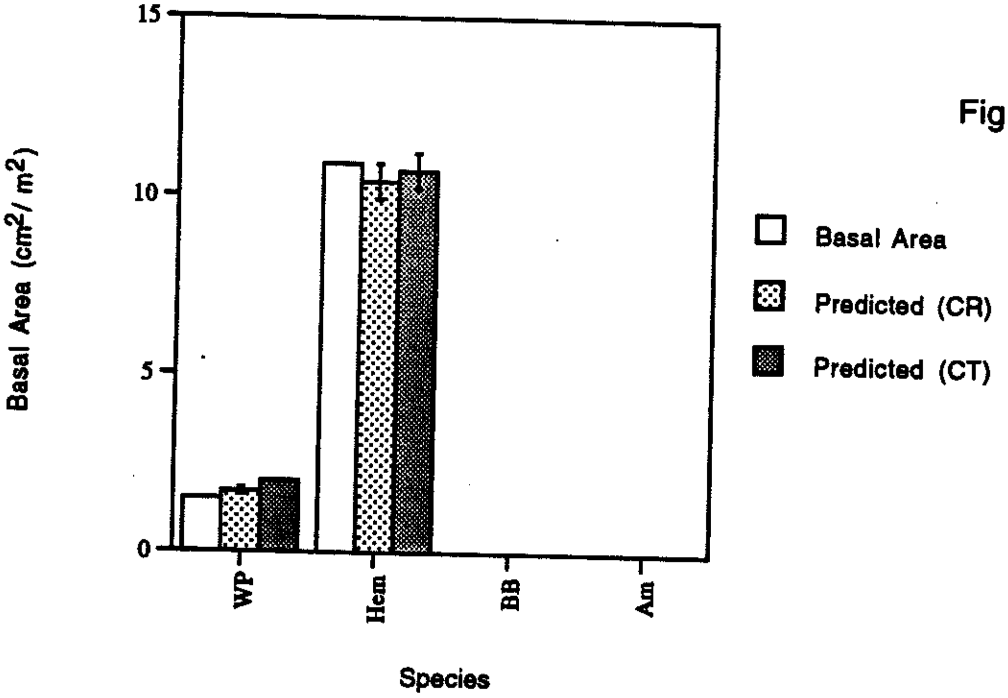


Fig. 31

Fig. 30 and 31
JABOWA was run from 1879 to 1952 for plot 20 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (30) and basal area (31) of the species white pine (WP), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observervations. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 20 - 1936 to 1952

Fig. 32

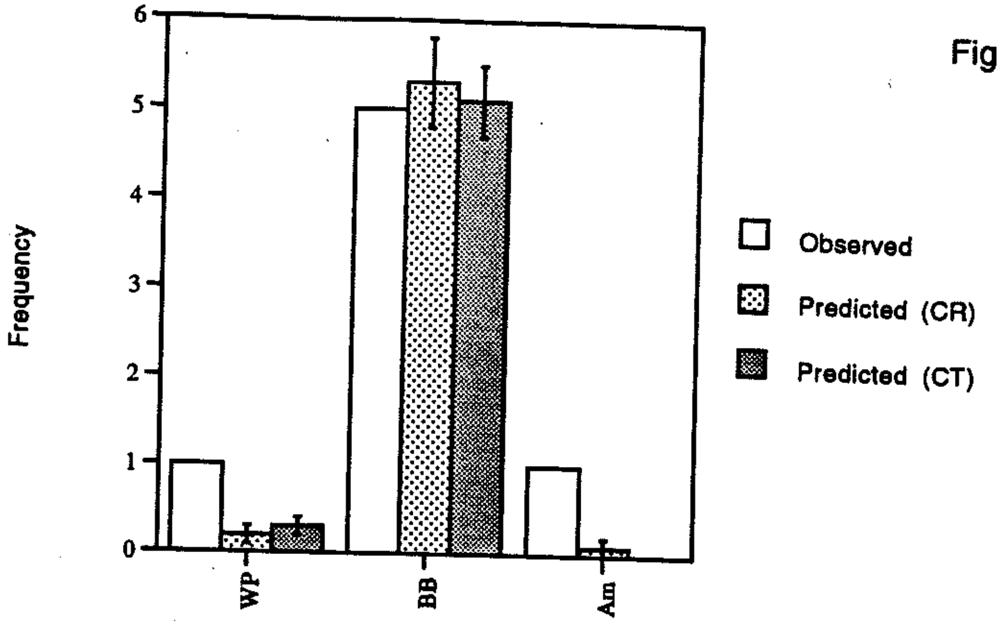


Fig. 33

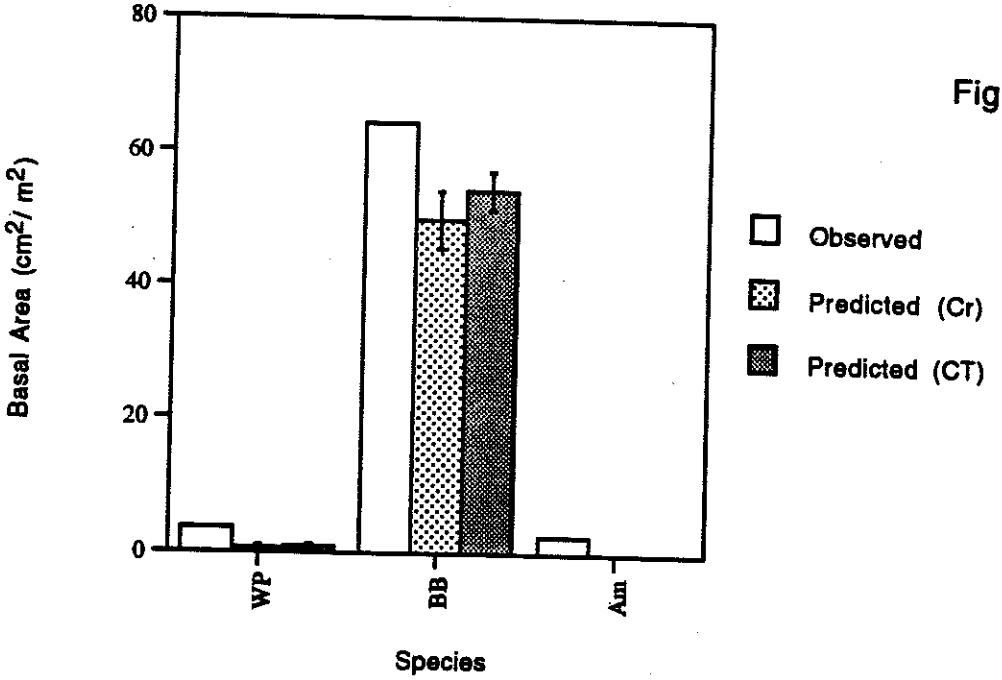


Fig. 32 and 33
JABOWA was run from 1936 to 1952 for plot 20 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (32) and basal area (33) of the species white pine (WP), black birch (BB), and amelanchier (Am) were compared with actual observations. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 22 - 1900 to 1952

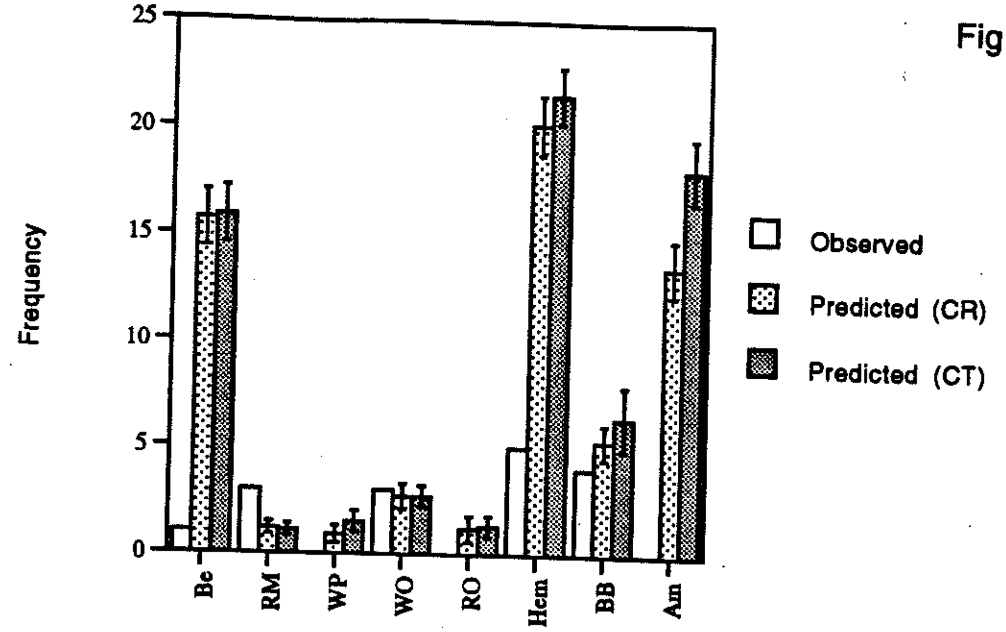


Fig. 34

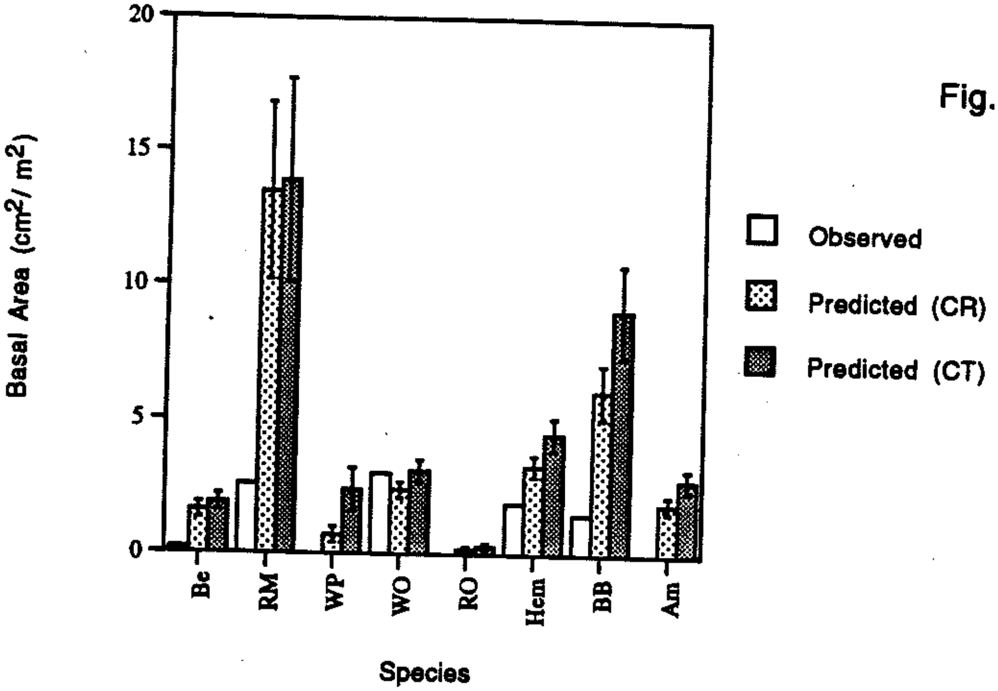


Fig. 35

Fig. 34 and 35

JABOWA was run from 1900 to 1952 for plot 22 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (34) and basal area (35) of the species beech (Be), red maple (RM), white pine (WP), white oak (WO), red oak (RO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observ. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

## Plot 22 - 1936 to 1952

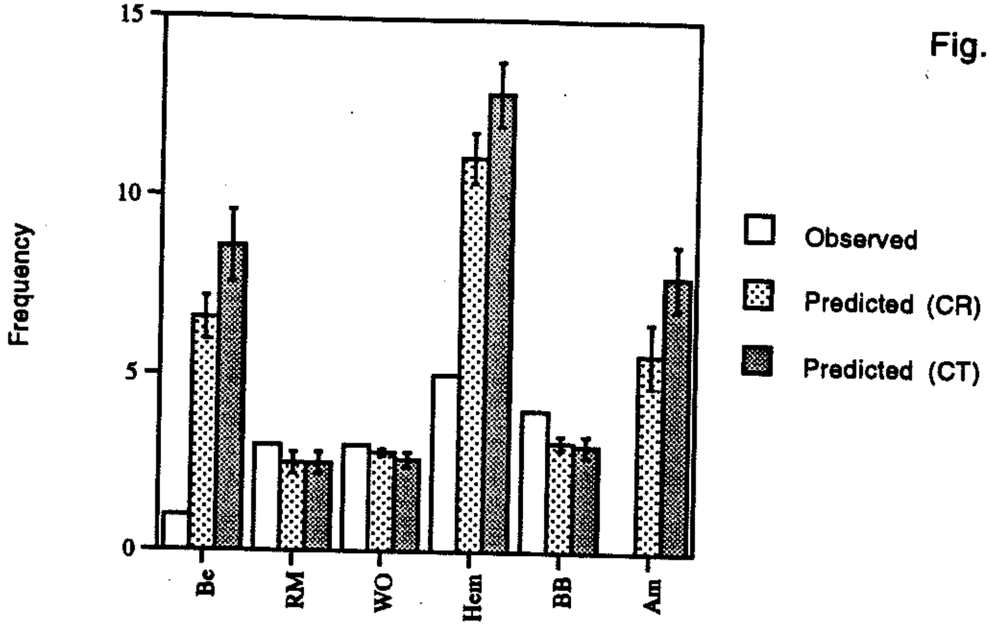


Fig. 36

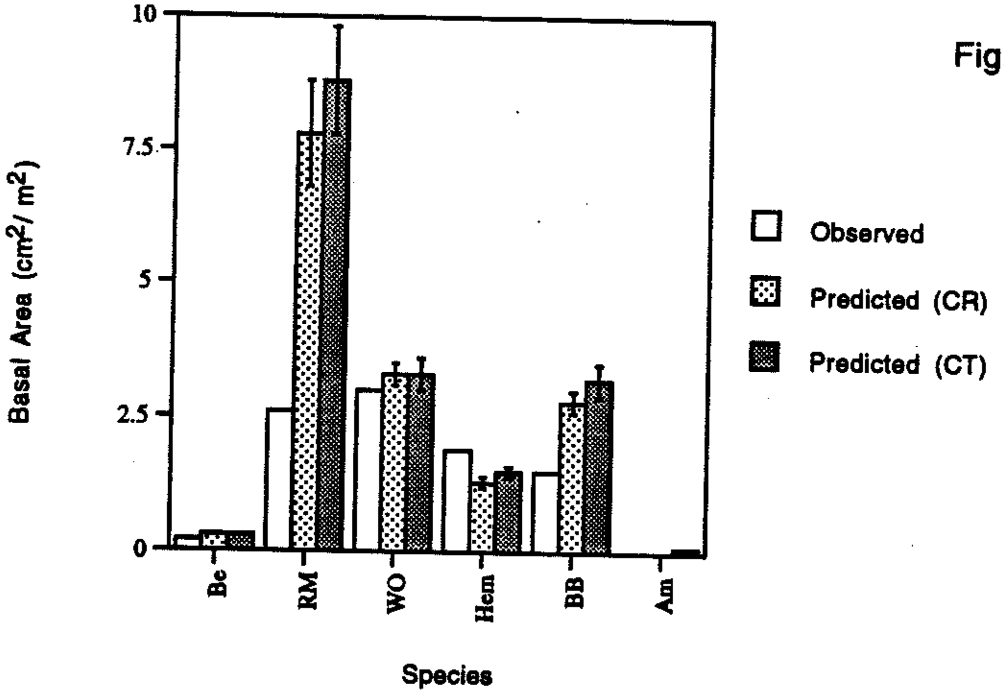


Fig. 37

Fig. 36 and 37

JABOWA was run from 1936 to 1952 for plot 22 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (36) and basal area (37) of the species beech (Be), red maple (RM), white oak (WO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Plot 27 - 1898 to 1952

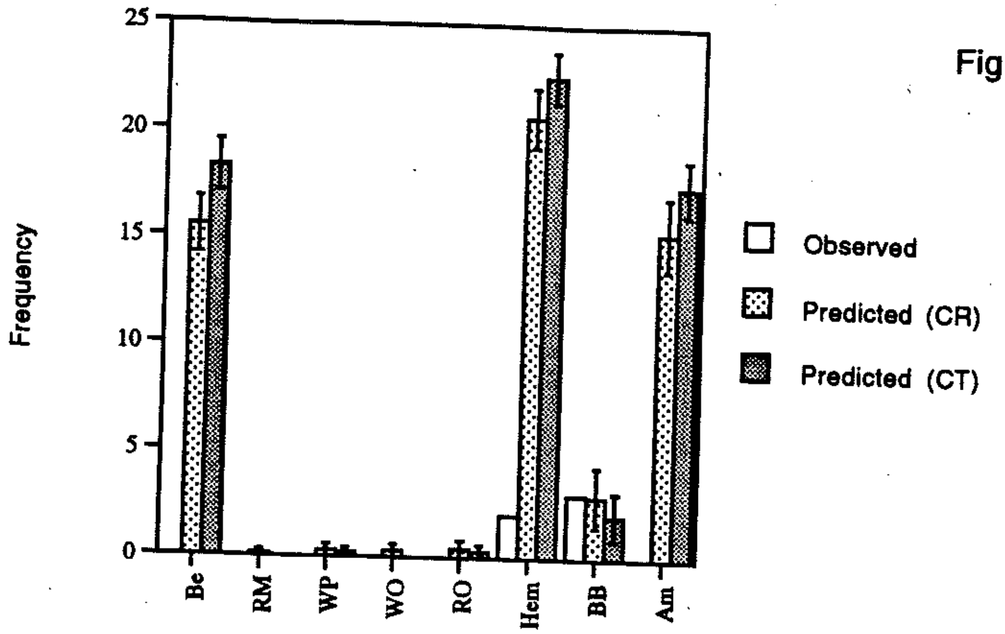


Fig. 38

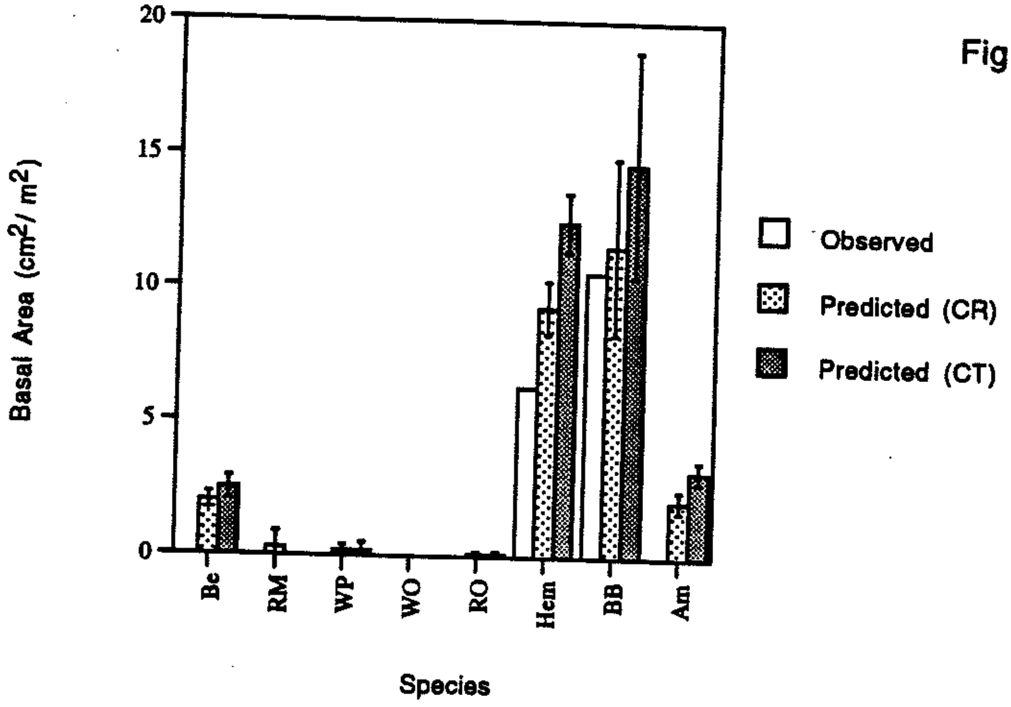


Fig. 39

**Fig. 38 and 39**
JABOWA was run from 1898 to 1952 for plot 27 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (38) and basal area (39) of the species beech (Be), red maple (RM), white pine (WP), white oak (WO), red oak (RO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observ. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

# Plot 27 - 1936 to 1952

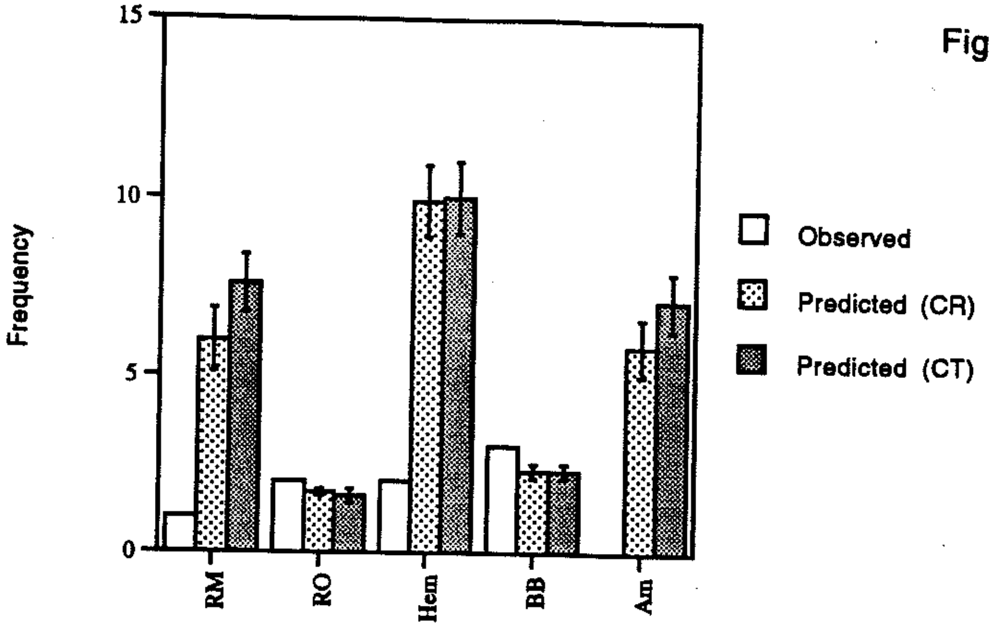


Fig. 40

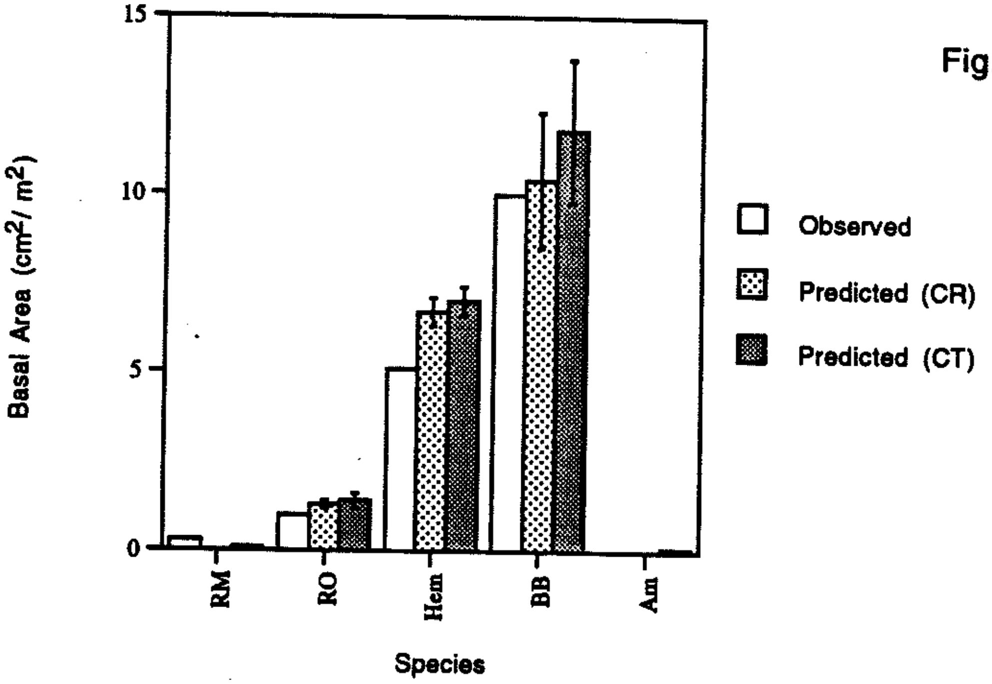


Fig. 41

**Fig. 40 and 41**

JABOWA was run from 1936 to 1952 for plot 27 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (40) and basal area (41) of the species red maple (RM), red oak (RO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

## Plot 30 - 1925 to 1952

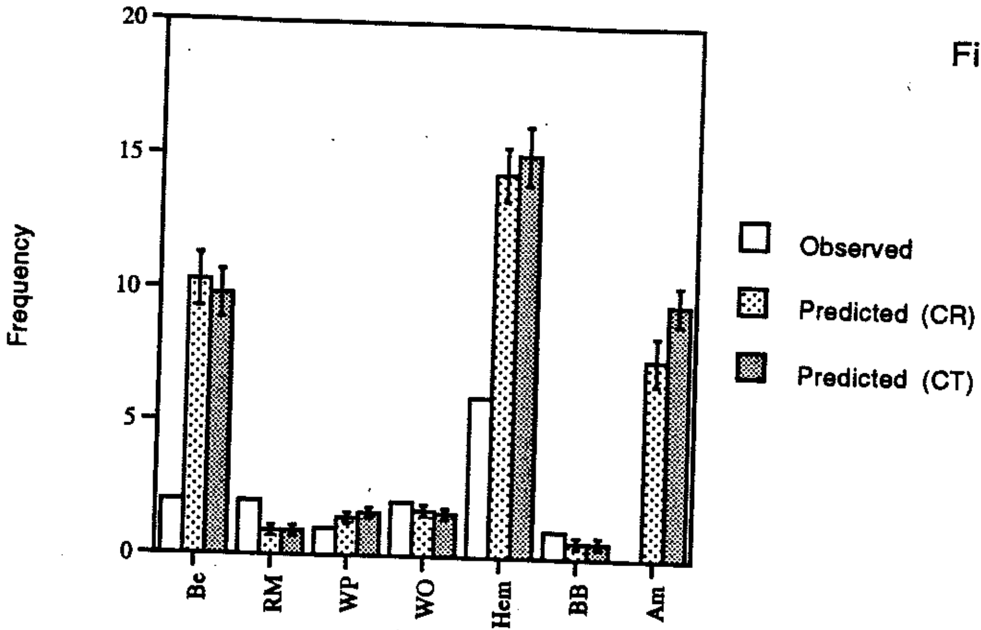


Fig. 42

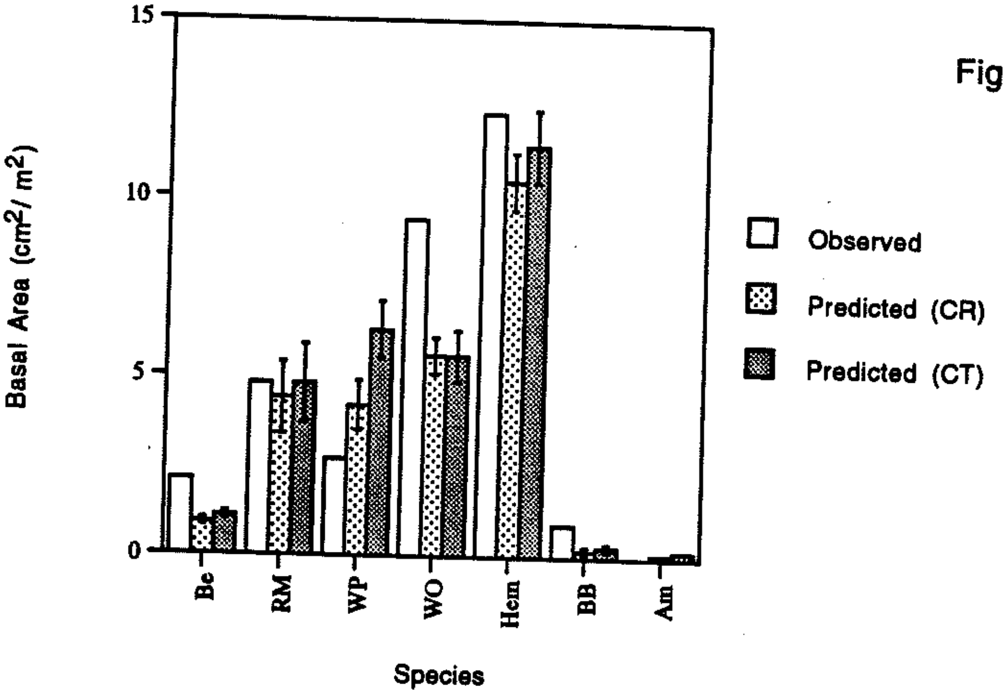


Fig. 43

Fig. 42 and 43
JABOWA was run from 1925 to 1952 for plot 30 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (42) and basal area (43) of the species beech (Be), red maple (RM), white pine (WP), white oak (WO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

# Plot 30 - 1936 to 1952

**Fig. 44**

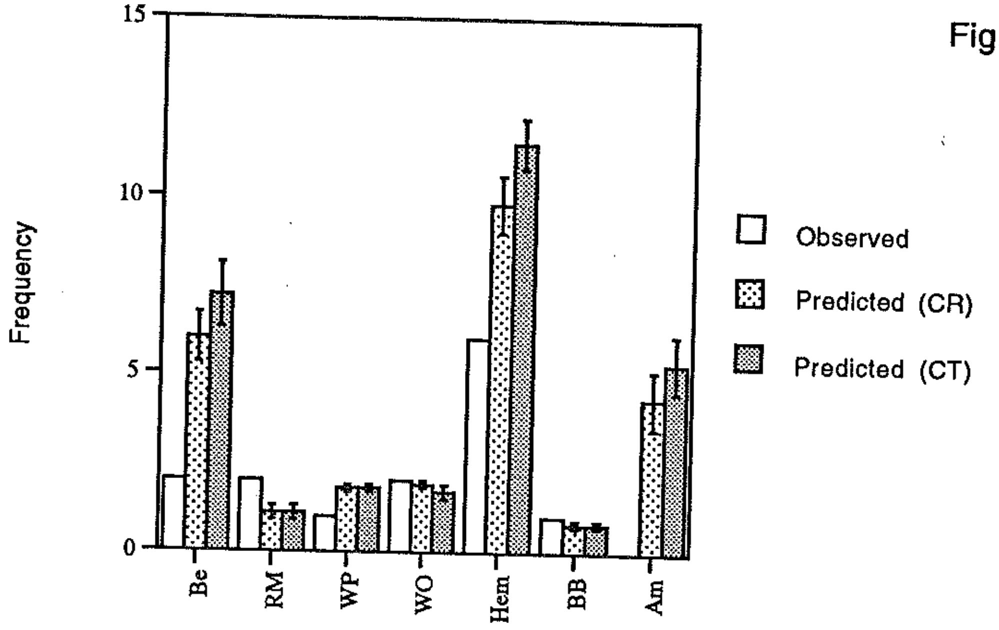


**Fig. 45**

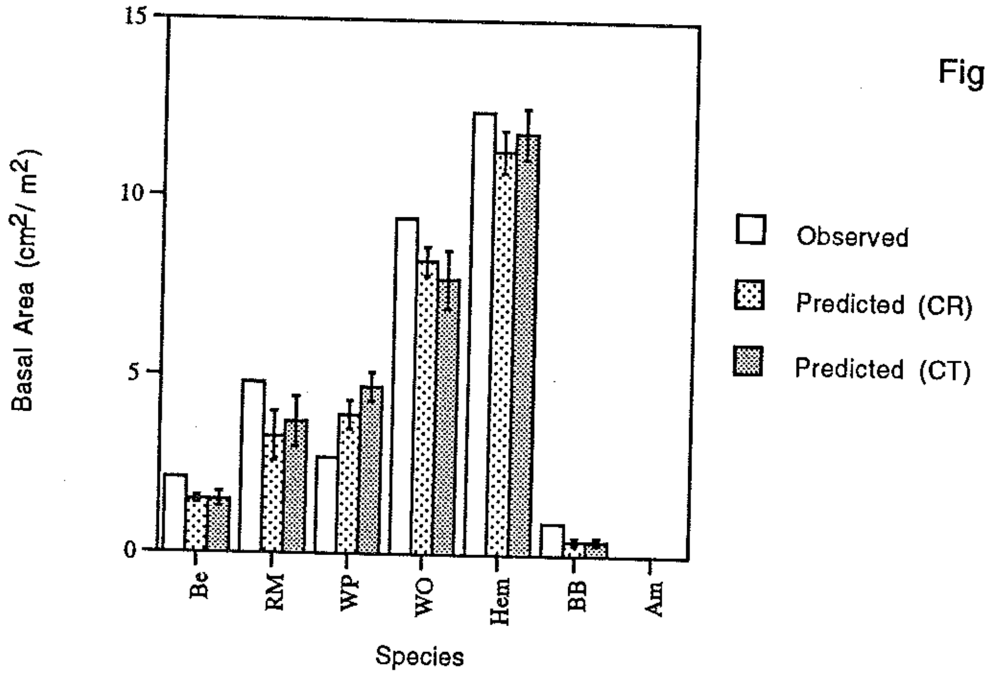


Fig. 44 and 45

JABOWA was run from 1936 to 1952 for plot 30 using the Charlton (CR) and Chatfield (CT) soil series for site calibration. Predicted frequency (44) and basal area (45) of the species beech (Be), red maple (RM), white pine (WP), white oak (WO), hemlock (Hem), black birch (BB), and amelanchier (Am) were compared with actual observations. Confidence intervals for the predicted values were obtained from 40 iterations of the run.

Table 1
Three soil series (Charlton, Chatfield, and Hollis) were used to characterize the Harvard Forest plot. JABOWA requires calibration for a site by the characteristics listed below.

| Soil series | Soil depth (m) | Water table depth (m) | Soil texture (mmH2O/m depth) | % rock |
|---|---|---|---|---|
| Charlton | 1.7 | 1.7 | 138.6 | 0.05 |
| Chatfield | 0.7 | 1.7 | 109.2 | 0.05 |
| Hollis | 0.4 | 1.7 | 147.1 | 0.08 |

## Plot 12

### 1886-1952

Table 2

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Red Maple | -25.0 | -45.0 | 81.3 | 4.7 |
| White Pine | 0.0 | 0.0 | 0.0 | 0.0 |
| White Oak | -20.0 | -5.0 | -95.2 | -95.2 |
| Red Oak | 160.0 | 280.0 | -72.5 | -42.5 |
| Hemlock | 318.0 | 338.0 | -64.7 | -60.1 |
| Black Birch | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Amelanchier | 0.0 + | 0.0 + | 0.0 + | 0.0 + |

### 1936-1952

Table 3

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 - | 0.0 + | 0.0 - | 0.0 - |
| Red Maple | -30.0 | -45.0 | 3.1 | -26.6 |
| White Oak | -5.0 | -10.0 | -19.0 | -14.3 |
| Red Oak | -15.0 | -10.0 | 12.5 | 225.0 |
| Hemlock | 72.0 | 108.0 | -25.2 | 19.3 |
| Amelanchier | 0.0 - | 0.0 + | 0.0 - | 0.0 - |

Table 2 - 16
Percent difference between predicted and observed values [(P - Obs)/Obs * 100] of species density and species basal area for the Charlton and Chatfield soil series. Entries marked 0.0+ represent model predictions in the absence of actual trees. Entries marked 0.0- represent the lack of model predictions where species occurred. Zero values without a (+) or (-) signify a completely accurate prediction.

# Plot 13

## 1915-1952

Table 4

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Red Maple | -60.0 | -66.7 | 94.7 | 76.3 |
| White Oak | -23.3 | -16.7 | -30.8 | 0.0 |
| Hemlock | 138.9 | 161.1 | -14.4 | -0.7 |
| Black Birch | -45.0 | -40.0 | -15.6 | 8.9 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 + | 0.0 + |

## 1936-1952

Table 5

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 + | 0.0 + | 0.0 - | 0.0 - |
| Red Maple | -3.3 | -20.0 | 60.5 | 50.0 |
| White Oak | -6.7 | -6.7 | 7.7 | 23.1 |
| Hemlock | 58.9 | 74.4 | -17.1 | -12.5 |
| Black Birch | -20.0 | -20.0 | 4.4 | 11.1 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 - | 0.0 - |

# Plot 14

## 1890-1952

Table 6

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Paper Birch | -100.0 | -100.0 | -100.0 | -106.0 |
| Red Maple | 30.0 | 40.0 | 449.2 | 481.9 |
| White Pine | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| White Oak | -23.3 | -43.3 | -94.4 | -94.4 |
| Red Oak | 460.0 | 640.0 | -57.9 | -10.5 |
| Hemlock | 129.0 | 135.0 | 48.2 | 73.5 |
| Black Birch | 715.0 | 725.0 | 155.6 | 190.7 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 + | 0.0 + |

## 1936-1952

Table 7

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 + | 0.0 + | 0.0 - | 0.0 - |
| Paper Birch | -100.0 | -100.0 | -100.0 | -100.0 |
| Red Maple | -30.0 | -30.0 | 230.0 | 39.3 |
| White Oak | -133.0 | -10.0 | -22.2 | -11.1 |
| Red Oak | -20.0 | -10.0 | -31.6 | -53.0 |
| Hemlock | 54.0 | 59.0 | 2.4 | 12.0 |
| Black Birch | -20.0 | -30.0 | 16.7 | 14.8 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 - | 0.0 - |

# Plot 20

## 1855-1952

Table 9

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Red Maple | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| White Pine | 380.0 | 460.0 | 2528.0 | 619.4 |
| White Oak | 0.0 + | 0.0 - | 0.0 - | 0.0 - |
| Red Oak | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Hemlock | 304.0 | 230.0 | -78.8 | -78.4 |
| Black Birch | 830.0 | 370.0 | 336.0 | 204.0 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 + | 0.0 + |

## 1879-1952

Table 10

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| White Pine | 10.0 | 0.0 | 13.3 | 33.3 |
| Hemlock | 106.7 | 130.0 | -4.6 | -1.8 |
| Black Birch | 0.0 + | 0.0 + | 0.0 - | 0.0 - |
| Amelanchier | 0.0 - | 0.0 + | 0.0 - | 0.0 - |

## 1936-1952

Table 11

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| White Pine | -80.0 | -70.0 | -83.3 | -75.0 |
| Hemlock | 6.0 | 2.0 | -22.6 | -15.7 |
| Black Birch | -90.0 | -100.0 | -100.0 | -100.0 |

# Plot 22

## 1900-1952

Table 12

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 1470.0 | 1490.0 | 700.0 | 850.0 |
| Red Maple | -60.0 | -63.3 | 419.2 | 434.6 |
| White Pine | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| White Oak | -10.0 | -10.0 | -20.0 | 3.3 |
| Red Oak | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Hemlock | 304.0 | 332.0 | 73.7 | 136.8 |
| Black Birch | 325.0 | 60.0 | 306.7 | 506.7 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 + | 0.0 + |

## 1936-1952

Table 13

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 560.0 | 760.0 | 50.0 | 50.0 |
| Red Maple | -16.7 | -16.7 | 200.0 | 238.5 |
| White Oak | -6.7 | -13.3 | 10.0 | 10.0 |
| Hemlock | 122.0 | 158.0 | -31.6 | -21.1 |
| Black Birch | -22.5 | -25.0 | 86.7 | 113.3 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 - | 0.0 + |

## Plot 27

### 1898-1952

Table 14

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Red Maple | 0.0 + | 0.0 - | 0.0 + | 0.0 - |
| White Pine | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| White Oak | 0.0 + | 0.0 - | 0.0 - | 0.0 - |
| Red Oak | 0.0 + | 0.0 + | 0.0 + | 0.0 + |
| Hemlock | 935.0 | 1030.0 | 476.0 | 98.4 |
| Black Birch | -3.3 | -33.3 | 9.4 | 38.7 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 + | 0.0 + |

### 1936-1952

Table 15

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Red Maple | 500.0 | 660.0 | -100.0 | -66.7 |
| Red Oak | -15.0 | -20.0 | 30.0 | 40.0 |
| Hemlock | 395.0 | 400.0 | 31.4 | 37.3 |
| Black Birch | -23.3 | -23.3 | 4.0 | 18.0 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 - | 0.0 + |

## Plot 30

### 1925-1952

Table 16

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 415.0 | 390.0 | -57.1 | -47.6 |
| Red Maple | -55.0 | -55.0 | -8.3 | 0.0 |
| White Pine | 40.0 | 60.0 | 55.6 | 133.3 |
| White Oak | -15.0 | -20.0 | -40.4 | -40.4 |
| Hemlock | 140.0 | 151.7 | -15.3 | -7.3 |
| Black Birch | -40.0 | -40.0 | -77.8 | -66.7 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 + | 0.0 + |

### 1936-1952

Table 17

| Species | % Difference in Density (/100m2) | | % Difference in Basal Area (cm2/m2) | |
|---|---|---|---|---|
| | Charlton | Chatfield | Charlton | Chatfield |
| Beech | 200.0 | 260.0 | -28.6 | -28.6 |
| Red Maple | -45.0 | -45.0 | -313.0 | -22.9 |
| White Pine | 80.0 | 80.0 | 44.4 | 74.1 |
| White Oak | -5.0 | -15.0 | 12.8 | -18.1 |
| Hemlock | 63.3 | 91.7 | -8.9 | -4.8 |
| Black Birch | -20.0 | -20.0 | -55.6 | -55.6 |
| Amelanchier | 0.0 + | 0.0 + | 0.0 - | 0.0 + |

**Table 18**

Comparison of actual heights obtained in 1952 for different species with heights calculated from the JABOWA height equation. The dependent value for determining height in the model equation is diameter at breast height.

| Species | Sample Size | Mean of Actual | Std. Dev. of Actual | Mean of Predicted | Std. Dev. of Predicted |
|---|---|---|---|---|---|
| Chestnut | 16 | 15.57 | 4.30 | 9.81 | 3.98 |
| Hemlock | 221 | 8.97 | 4.47 | 6.57 | 3.76 |
| Red Maple | 86 | 3.60 | 1.83 | 6.27 | 3.19 |
| Red Oak | 29 | 14.39 | 5.98 | 4.94 | 2.20 |
| White Oak | 43 | 12.30 | 5.52 | 7.19 | 3.93 |
| White Pine | 13 | 11.89 | 4.16 | 12.48 | 4.05 |

# Appendix A

## I) Suggestions for addition to Stephens' long-term data

Further collection of data from Stephens' plot could lengthen the time interval of succession history. The newly collected data would most likely be more reliable than Stephens' data, because it would not be encumbered by the difficulties of reconstructing forest dynamics from dead tree fragments. The greatest challenge would be to relocate the exact boundary of the plot. To do this, one would need to consult the mound and pit map combined with the topographical map constructed by Stephens in his PhD thesis. Once key features were identified at the site, the distance to the plot's boundary could be measured and scaled from the maps. It would be useful to measure forest composition in $100m^2$ plots. In addition to species' density, DBH, height, and spatial arrangement, the soil characteristics necessary for calibration of JABOWA could be measured according to the protocol in Botkin (1993). Of special interest would be collection of available nitrogen values for as many plots as feasible.

Collection of the same data for the adjacent hemlock-dominated plot would allow for interesting experiments concerning the effects of clearcutting on species' regeneration. Comparison of available nitrogen values, organic matter and pH between the stand cut in 1952 and the adjacent plot could provide insights into the effects of clearcutting on those site parameters.

## II) Further exploration and use of Stephens' data

1) Comparison of the adjacent hemlock stand with the stand cut in 1952 to determine the effects of clearcutting
2) Testing the spatial competitive interactions between species by using analyses such as nearest-neighbor distance correllations
3) Determining the competitive advantage by species (when appropriate) of sprouting vs. sexually reproduced saplings
4) Analyzing the effect of the chestnut blight on chestnut compared to other species
5) Analyzing any difference between species for the effects of the gypsy moth infestation

# Appendix B

## I) Experimentation, verification and validation of JABOWA

1) Create growth curves for each species to be compared with present growth curves.
2) Determine species-specific growth parameter values according to Botkin's methodology mentioned in the discussion of the present paper and in Botkin (1993).
3) Create new height equations based on determination of new coefficient values from regression of Stephens' height data.
4) Obtain species-specific parameter values from field measurements and compare with Botkin's values.
5) Run the model for the initial plots listed in the files over a range of nitrogen values to test the sensitivity of the model to variation in the level of nitrogen.
6) Apply sensitivity analysis to a few model components.
7) Project the composition of Stephens' plot and determine whether or not it ever converges to the composition of the adjacent plot that was not clearcut in 1952. Project both sets of plots and determine whether or not either of the plots converge to a stable equilibrium with and without disturbance.

## II) Running JABOWA with ease

1) The manual is incomplete but is a good place to start understanding how to run JABOWA.

2) Create initial plots by copying a previous plot._ file as a different name and editing with new values. Unless noted otherwise, save files as text by using Ctrl-F5 in WP.

3) Create species file by adding species to a copied species file. Be sure not to make a file with more than 40 species.

4) Create a climate file following the procedure in the manual.

5) Edit the existing Initvals. file and save as the same name. This will overwrite any previous values. When editing the initvals. file, make sure that the results interval divides the number of years in no more than 40 sections. The number of iterations should be set at least 40. List the species parameter file, the plot file and the climate file you created above. Check that the community number is set on 1 for Northeastern_Deciduous_Forest. Change the initvals. file any time you run the model with different data or values.

6) Exit WordPerfect

7) Type j to run JABOWA and -return-

8) Select menu 2 and choice 3 -return- -return-

9) Type stats

10) Type q for quattro. Under the menu bar select Tools-import-ASCII text file. Type newstat.out. For parsed data that can be edited select Comma and "" Delimited files and type newstat.out. One or both of these files should be saved before the next run.

# Appendix C

## List of files

All files are on the network's G:\ drive under the subdirectory \Mills\.

1) CUT1952 = All trees present on Stephens' plot in 1952 and the associated data from his thesis.

2) AV****.WQ1 = Initial plots created for JABOWA (100m2) from the mean of species frequency immediatedly before and after disturbance dates (listed in Stephens 1955)

3) Fin(plot number).WQ1 = Actual and predicted frequency and basal area for each of the 7 plots, soil series, and dates tested

4) HEIGHT.WQ1 = DBH, Ht and Ht predicted from JABOWA's height equation

5) INIT(plot number).WQ1 = The initial plots used to run JABOWA for my tests and the frequency and basal area in 1952

6) P(plot number)_(tree number).WQ1 = Ages at incremental heights for all trees on the 7 plots tested for which such data were available

7) TREE**.WQ1 = The same information as above but for some trees that were not in the plots used during the simulation

8) TABLE9(to 21).WQ1 = The sum of trees per species according to DBH size class before and after disturbance dates

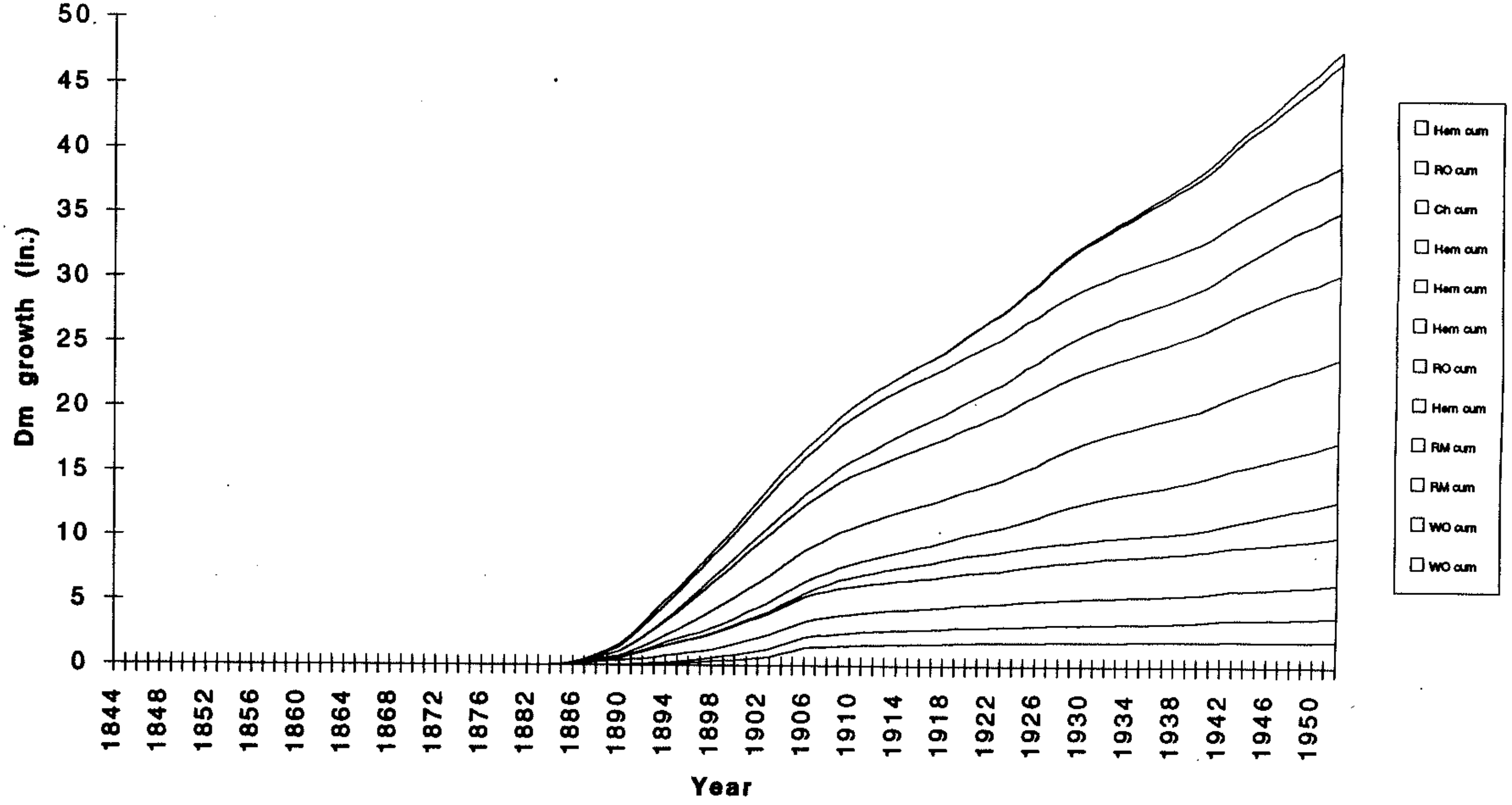
9) HARVFOR.NOR = Harvard Forest climate data file used for JABOWA

10) SPECIESH.SPP = Harvard Forest species file

# Appendix D

Cumulative individual growth graphs were created for plots 12 and 14. Dominance by species is observable from these graphs and is informative when compared with the diameter increment graphs of figs. (9-15).

# Cumulative Individual Tree Growth - Plot 12



## Cumulative Individual Tree Growth - Plot 14