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The Development Of Northern Red Oak In Mixed Stands In Central New England

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THE DEVELOPMENT OF NORTHERN RED OAK IN MIXED STANDS IN CENTRAL NEW ENGLAND

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ABSTRACT

Much of the upland forest of central New England consists of red oak (*Quercus rubra* 1.), red maple (*Acer rubrum* 1.), black birch (*Betula lenta* 1.), and other species. Such stands developed a definite vertical canopy stratification when started from clearcutting or similar disturbance. The few red oaks which ultimately occupied much of the upper continuous canopy were present since stand initiation but relatively inconspicuous at first. The more numerous maples, birches, and other species which dominated at first lapsed into the lower crown positions beneath the red oak after about the third decade.

The stands are commonly even-aged even though the broad range of diameters and crown classes developing after about 30 years gives an all-aged appearance.

For best diameter growth on individual red oak trees and optimum board-foot production per acre, it may be desirable to have only 45 well-placed red oak seedlings (or seedling sprouts) per acre in the reproduction, relying on the more numerous red maples, black birches, and other species to keep the red oaks pruned.

INTRODUCTION

Northern red oak is a characteristic dominant over much of the northern part of the eastern deciduous forest (Braun, 1950; Smith, 1962b). Nevertheless, when attempts are made to regenerate previously oak-dominated stands, the seedlings of this species seem peculiarly sparse and unresponsive to efforts to stimulate their growth. Most research has focused on stand developmenrs soon after cutting and the manipulation of old stands (White and Roach, 1971). This study links these two stages by tracing the development of old stands backward in time. It tests the hypothesis that full, dominant canopy cover of red oak results from emergence, at middle age, of small numbers of well-distributed saplings which burgeon while certain other species, initially dominanr, lapse into the lower canopy strata.

Silvicultural Problems with Red Oak Regeneration

When stands dominated by members of the red oak group are subjected to various methods of regeneration cutting, the seedlings of this group are almost invariably small in comparison to those of other species (Smith, 1970; Clark and Watt, 1971; Roach, 1971). Clark and Watt (1971) reviewed a number of preharvest thinning regimes designed to ensure adequate oak regeneration; Russell (1973) investigated a method of planting northern red oak at close spacing. Trimble 0972, 1973, 1974) examined red oak regeneration and early growth on various sites after the clearcutting of oak-dominated mixed stands in West Virginia. He found that other species were more numerous and generally taller than red oak on all sites five years after clearcurting and sometimes 12 years later. He also found that in these early stages red oak would not even show much growth acceleration after release in cleanings.

Species Stratification in Cenrral New England Deciduous Forests

Red oak often forms an essentially pure upper canopy stratum in older mixed stands on moist, well-drained sites in central New England (Goodlett and Zimmermann, 1973; Goodlett, 1974; and Harvard Forest Records, 1974). On upper slopes, red oak occupies the upper stratum in the moister drainages while black oak *(QuercuJ* *velutina* Lam.) and white oak (*Quercus alba* L.) predominate on the adjacent, drier ridges. White ash (*Fraxinus americana* L.) is found in the upper canopy position where microsites in the upland soils are too moist for red oak (Stout, 1952; Lyford, Goodlett, and Coates, 1963).

Red maple and black birch occupy the lower crown strata in virtually all middle-aged or old stands. Other species, such as the aspens (*Populus* species), the hickories (*Carya* species), black cherry (*Prunus serotina* Ehrh.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), and eastern while pine (*Pinus strobus* L.), were also observed in such stands. White birch (*Betula papyrifera* Marsh.) and gray birch (*Betula populifolia* Marsh.) are also present and so frequently hybridized (Remington, 1973, 1974) that they are referred to herein collectively as white-gray birch. Sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) become more abundant with increasing moisture.

Interpretations of the Size Distribution of Mixed Species Stands

The structure and development of mixed deciduous forests is complex and even bewildering. Many species and a broad range of individual tree heights and diameters can exist in small areas. Some observers regard this wide variation in diameter and height as indicating the all-aged condition or one which enables all-aged management. Others maintain that such aggregations are commonly even-aged.

Within a single stand, tree heights vary considerably, with smaller individuals existing beneath and between the crowns of the taller trees. Segregation by species often occurs, with some occupying the upper stratum and others, the lower strata. It was frequently assumed that the smaller trees were younger, were of shade tolerant species, and would eventually replace the taller ones in the upper canopy (Jones, 1945; Braun, 1950; Daubenmire, 1968). According to this explanation, a stratified stand of mixed species is constantly recruiting new trees, thus creating an all-aged condition.

Mixed stratified stands often have a broad range of diameters which, when arranged by diameter classes, may approach a reverse-J-shaped distribution, especially when the smaller diameter classes are not included in the sample. The explicit or implicit assumption that tree diameter indicates age can lead to the interpretation that such stands exhibit the all-aged or balanced uneven-aged condition, with geometrically decreasing numbers of stems in each successively older age class (Hough, 1932; Meyer and Stevenson, 1943; Worley and Meyer, 1951; Eyre and Zillgitt, 1953; Phillips, 1959; Piussi, 1966; Daubenmire, 1968; Minckler, 1974; and Mueller-Dombois and Ellenberg, 1974).

There is increasing evidence that a stratified canopy and/or a broad diameter distribution in a mixed deciduous stand do nOt necessarily indicate an all-aged condition, but may also exist in even-aged stands. In these cases the new stand may develop from advance growth, sprouts, new seedlings, or all in combination after removal of the previous stand (Raup, 1964; Smith, 1962a; Johnson, 1972; Drury and Nisbet, 1973). "The plants dominant in the later stages [of secondary succession} were present either from the beginning, or at least from a very early stage. Their inconspicuousness in the early stages appears to be a consequence of their slow growth and/or their suppression by other species (and to some extent, to the preoccupation of botanists with the dominant species)" (Drury and Nisbet, 1973). In such stands, the subordinate-layer species have smaller diameters but are of essentially the same age as their suppressors.

The effective stem age is dated from time of release of the suppressed seedlings living near the forest floor after overstory removal (Morris, 1948; Sprugel, 1974). By even-aged it is not meant that **all** trees start in precisely the same year, but that the range of ages is small compared to the life expectancy of the major components.

Wilson (1953) showed that an even-aged, second-growth, northern hardwood stand in New Hampshire had the reverse-J-shaped diameter distribution generally associated with all-aged stands. Putnam, Furnival, and McKnight (1960) presented data which, on analysis, show the J-shaped diameter distribution actually being better developed in even-aged than in uneven-aged southern bottomland hardwood stands. By following second-growth mixed hardwood stands in Connecticut for 30 years, Olson (965) found evidence suggesting that dominant trees were not necessarily older than their substratum associates. Gibbs (963) concluded that diameter was a poor indicator of tree age in mixed deciduous stands in West Virginia.

The interpretation of the reverse-J-shaped diameter distributions is crucial to the silvicultural manipulations of mixed hardwood stands. Minckler (1973; 1974) contended that this distribution is a sufficient precondition for uneven-aged selection management. Others (Marquis, 1973) stated that even-aged stands are difficult to convert to the uneven-aged condition even if the diameter distribution is of reverse-J-shape.

Previous Observations of Red Oak Growth

There has been evidence that red oaks maintain rapid diameter growth for more years than many associated species. This indirectly implies that eventual dominance in mixed stands does not necessarily depend on dominance in youth. In mixed hardwood stands in Connecticut Olson (1965) found that the proportion of basal area contributed by northern red oaks increased from age 40 to 70 even though the absolute number of them decreased. Karnig and Stout (1969) found that the diameter growth was much greater on red oak trees of larger diameter classes than smaller diameter classes in mixed forests of southern New York. Similar observations have been made of black oak in Missouri (Buchanan et aI., 1962).

Late acceleration in diameter growth of nonhern red oak has also been observed in Wisconsin (Scholz, 1948) and at the Harvard Forest (Yoder, 1941; Hoisington and Carr, 1949).

Northern red oak grows more slowly in height than its associated intolerant species during its first four or five years (Minuse, 1912; and Beck, 1970). Scholz (1952) attributed its presence only in even-aged patches in Minnesota to its lack of shade tolerance. Tryon and Carvell (1958) showed initial growth of oak regeneration beneath canopies to be closely correlated to the amount of sunlight incident on the forest floor. Seedlings of northern red oak grew taller and leafier with progressive increases of light from 8 to 100 percent of full sunlight (McGee, 1968).

There is evidence that the oaks which later dominate can first live as intermediates in the upper crown canopy. Scholz (1952) concluded that red oaks could develop into trees of sawtimber size under conditions of considerable crowding as long as they were not permanently overtopped. Ward (1964) also showed that they endured somewhat crowded conditions.

Later in stand development, when general height growth has slowed, Stephens and Waggoner (1970) found the crown canopy of mixed hardwood stands in Connecticut to become increasingly dominated by oaks. At this time northern red oak individuals seemed either to gain dominance in the stand or to die.

PROCEDURES

It was first necessary to test the view that a domination of middle-aged stands by red oak was a common and predictable event in stands arising after very heavy cuttings or severe blowdowns. This was done by analysis of a systematic sample of a typical central New England hardwood forest.

After red oak's dominance at middle age had been verified, the rest of this study involved reconstruction of the common species interactions which led to this condition. A series of middle-aged and old even-aged stands was examined; these were typical of the common condition, dominated by red oak, and had originated after heavy cutting or blowdown. The distributions of species by age and diameter were determined to verify that the stands were even-aged and to test the hypothesis that the red oaks usually became larger than common associates of equal age (especially red maple and black birch). Incidental to this was the observation that these mixed, even-aged stands could have tree diameter distributions approximating the reverse-J-shaped curve often interpreted as indicative of the uneven-aged condition.

Next, sample tree groups containing red oak dominants, red maples, black birches, and other species were dissected to reconstruct the growth patterns leading to red oak dominance. No dominant red oaks were found in this study which did not show a pattern of having emerged into such dominance at middle age.

Observations of very young stands by others in similar forests have suggested that red oak is not prominent in the early stages of stand development. Dead stems and stem remnants were systematically located and identified by species on several plots of varying ages in this study to verify this.

Finally, complete and detailed dissections were made of a red oak and all of its associates on a plot believed to be the most typical of those previously observed.

The study was undertaken on the Yale Forest in northeastern

Connecticut (Meyer and Plusnin, 1945) and the Harvard Forest in Petersham, (north-central) Massachusetts. These forests are representative of upland hardwood forests in central New England. Study areas were confined to upland sites on sandy, bouldery, strongly acid tills derived principally from granite and schist. Such soils are widespread in central New England and encompass the well-drained and moderately well-drained Gloucester, Brookfield, Paxron, Acton, and Woodbridge soils (Ilgen et al., 1966). Stands growing on these sites are described by Westveld (1956) as being in the Transition Hardwoods-White Pine-Hemlock Zone.

The study was further restricted to stands which arose from seeds and advance growth after very heavy cuttings such as the removal of old-field white pine. Such stands are now very common in central New England.

The study was completed over a two-year period beginning in the spring of 1972. For simplification all ages and diameters are referenced to December, 1971 unless otherwise stated. Diameter measutes inside bark were converted to diameter outside bark where necessary by regression equations developed for each species (see Appendix).

Reconstruction of Stand Histories

Much of the effort was concentrated on reconstructing in time a few representative stands by historical-development dissection of the present living and dead stems (Stephens, 1955; Henry and Swan, 1974; Oliver and Stephens, 1977). This method was used as an alternative to the more common practice of following the growth changes in initially young stands over a long time. The method involves stem analyses and detection of previous events such as cuttings and natural disturbances by living and nonliving evidence.

Clearcuttings of old-field white pines were detected in several ways. There were remnants of many closely spaced white pine stumps which had been cut near the ground in an area surrounded by a stone wall. Many suppressed seedlings living near the forest floor beneath the white pine were mowed, pushed over, or damaged at the root collar by the pine cutting (Parron, 1922; McKinnon et al., 1935). In this study, remnants of white pine logs in the forest floor lirrer were frequently found near points of early damage to presently living stems. The pine remnants indicated that these stems had been advanced regeneration, and that pine cutting was the cause of damage. Growth ring analyses indicated the time of the clearcutting.

Previous clearcutting of deciduous woodlots was deduced from high frequency of multiple-sprout (coppice) stems initiated at the same time (Frothingham, 1912), lack of a plow layer in the soil, and/or the mound-and-pit microrelief characteristic of unplowed soils in the area (Lutz, 1940; Stephens, 1956).

Blowdown by the 1938 hurricane was deduced from growth rings, windthrow mounds, or remains of trees blown over by southeast winds. Complete stand blowdown was obvious from the large number of windthrow mounds and parallel, blown-over stems (in the plots studied the downed trees had nOt been salvaged). Where only scattered trees were blown over, adjacent trees had expanded to close the canopy, leaving little evidence of the hurricane except windthrow mounds.

Patterns of Species Stratification

Thirty-five permanent point-sampling plots, located at random on a systematic grid (Zai, 1957) throughout the 7,800-acre (3,159 ha) Yale Forest, were reinspected to determine how commonly red oak gained ascendency in species stratification in the older upland hardwood stands. Plots or quadrants of plots were accepted if no cutting or silvicultural manipulation had occurred within the past 33 years and the previously stated criteria of till soil and stand origin from clearcutting or blowdown were met. Twenty-five of the 35 plots met these criteria.

Sample trees on each plot were those over one inch (2.5 cm) D.B.H. Each sample tree was described by species, D.B.H., and canopy stratum.

Four canopy strata were recognized, similar to those distinguished by Richards (1957): Emergent (A-stratum), *B*-, C-, and D-strata. A reproducible, objective method of distinction between crown strata was developed as described in detail in the Appendix. Essentially, the B-stratum formed a relatively smooth, continuous upper canopy surface with a few protruding "bumps" of taller, A-stratum trees. The C-stratum and even lower D-stratum tree crowns were either partially covered or completely overtopped, respectively, by taller trees. The C- and D-strata generally had less continuous upper surfaces than the B-stratum.

Special attention was given to the relative canopy positions of red oak and its common associates, red maple and black birch. The taller species was noted whenever a sample tree of one species overlapped at least one tree of the other species for more than one-half of any crown radius. This overlapping is defined herein as "interacting." Each interacting species would assume the higher position 50 percent of the time if there were only a perfectly random pattern in the interaction.

A large dominant, ring-porous tree (usually an oak) was aged at one foot (30.5 em) height with an increment borer in each sample plot to determine the range of ages of dominant trees in the entire 25-plot sample.

Intensive Study of Mixed Stands

Selection and Aging of Stands

The red oaks were quite consistently in the upper canopy in these stands. The next step was to reconstruct the patterns of stand development which led to the dominance by red oaks. The age distribution of the dominating oaks from several stands was first studied; then the relative ages and developmental history of the trees which had grown in their immediate vicinity were determined.

The six stands selected for this analysis were between 33 and 107 years old. The 107-year-old stand (Stand VII) was at the Harvard Forest and arose after a hardwood clearcutting. The other stands were at the Yale Forest. The 33-year-old stand (Stand VI) arose after 1938 hurricane blowdown; and all others began after white pine clearcuttings. Stand V was 45 years since clearcutting; stand IV was 74 years; and Stands I, II, and III were 60 years old. The 50-year heights of dominant red oaks (determined from stem analysis) in Stands I- IV ranged from 55 to 66 feet (17-20 m) and averaged 60 feet (18 m).

All seven stands were typical of the general stratification pattern found in such stands from the previous systematic sample, and met the stated criteria of soil and stand origin. Most intensive analyses were done in 60-year-old stands, since this age seemed within the rotation age of forest management, and since red oaks seemed to have reached the upper crown stratum by this age. Older and younger stands were examined less intensively to help clarify observations.

Initially only B-stratum red oak ages were determined in the stands. The three stands 60 years of age (Stands I, II, and III) contained B-strata composed largely of red oaks, with lower strata of red maples, black birches, and many of the other species found in the initial 25-plot inventory of upland stands. Sixty-three randomly selected B-stratum red oaks were cored at breast height in these three stands to determine diameter growth and age patterns. The piths were not reached in 28 of the trees after repeated corings because of the commonly eccentric growth pattern (Sorensen and Wilson, 1964). Consequently, 35 trees were used for age determinations and all 63 were used to document diameter growth patterns. Crown projection maps of a subsample of 25 red oaks of known age were made for later comparison with basal area growth.

Less intensive samples of the B-stratum red oaks were taken in the other four stands. Three red oaks were aged in the 74-year-old stand; seven oaks were aged in the 45-year-old stand; and five each in the 33- and 107-year-old stands.

Selection and Analyses of Plots

Fourteen plots were selected in the seven stands for more intensive studies of the pattern by which red oak attained ascendency over its associates. All of these plots had red maple and/or black birch beneath the red oak. The oaks in the plots chosen all had ages and diameters near the center of the range of values of the previously sampled B-stratum red oaks from the same stand. Plot areas differed because of variations of crown sizes and degrees of stratification at different stand ages.

Seven plots were established in the three 60-year-old stands (Plots 1-1, 1-2; II-I, 11-2; and III-I, 111-2, and 111-3); three plots were located in the 74-year-old stand (plots IV-1, IV-2, and IV-3). Each plot was the area vertically beneath the crown of a chosen B-stratum red oak. Plots of one-fiftieth acre (0.008 ha) were randomly located in younger stands; two in the 45-year-old (Stand V) and one in the 33-year-old Stand VI.

The plot in the 107-year-old stand at the Harvard Forest (Stand

VII) consisted of a B-straturn red oak overtopping a black birch and a sugar maple.

All stems within the 60-, 74-, and 107-year-old plots were mapped and sectioned at one foot (0.3 m) and breast height for later age and diameter growth analyses, except for the red oak in the 107-year-old plot, which was sampled by climbing the tree and coring it at four-foot intervals to 16 feet (4.9 m). The tallest red maple and black birch present, the upper canopy red oak, and other selected individuals were also analyzed for height growth by sectioning each tree every four feet (1.2 m) ro the tOP, beginning at eight feet (2.4 m). The sections were then aged and measured, as described in the Appendix. The positions of all forks, breaks, and major branches were recorded. By this method, height-age curves were constructed for the stems. Less detailed height-age curves were obtained for trees in the 45- and 33-year-old plots by aging each tree at one foot (0.3 m) and breast height and finding its total height.

Fifty-two trees were studied within the seven plots in the 60-year-old stands. Three trees were studied in the 107-year-old stand; 26 trees on three plots in the 74-year-old stand; 43 trees in twO plots in the 45-year-old stand; and 28 trees in a single plot in the 33-year-old stand.

To determine if trees beyond the oak crowns behaved differently, two plots in the 60-year-old stand were extended beyond the crown of the central B-stratum red oak to beneath the crowns of the surrounding B-stratum trees. Vertical crown projections were mapped of the surrounding B-stratum trees (all were red oaks) and the central B-stratum tree of each of the two plots. Root collar positions of all living trees were also mapped. Supplemental stem analyses were performed on all trees not previously analyzed.

Additional information on the relative height growth of competing red oaks, red maples, and black birches was obtained from unpublished data collected by E. P. Stephens (Stephens, 1955) at the Harvard Forest between 1951 and 1955. His study wason aO.89 acre (0.36 ha) plot in a stand with species and soils similar to the others of this study. All living trees on the plot had been mapped, sectioned, and aged at stump height, breast height, and every four feet (1.2 m) above that. The data were used from four red oaks growing in even-aged associations with red maples and five red oaks growing with black birches.

Development of an Individual Red Oak and Its Associates

More intensive study was undertaken on a typical individual red oak and its substratum associates in a 60-year-old plot. Plot 1-2 was used because it characterized developments observed on other plots. All living stems beneath and extending beyond the central oak crown periphery were mapped. Stems that died since the clearcutting of the old-field white pine (to be discussed in more detail later) and stumps of the cut pines were also mapped and identified. Living branches of the central red oak were mapped in three dimensional space by means of triangulation with surveyors' transits. This oak was then cut down and sections were taken every four feet (1.2 m) along its stem and major branches to determine the ages. All trees of other species within the plot were similarly analyzed.

Analysis of Initial Species Stocking

To determine the initial species composition of stands, estimates were made of the total number of stems of each species which had been present since stand initiation on five plots in three stands of 60, 45, and 33 years of age (Stands I, V, and VI).

Two of the 60-year-old plots (Plots 1-1 and 1-2) were enlarged to include the area within the vertical projection of the crown periphery of a B-stratum red oak and extending outward from this for one-half the distance to the vertical projections of the crown peripheries of the immediately surrounding B-stratum trees. In this way any parr of the stand area could conceivably be divided into a number of unequal sized plots.

The Land F soil horizons on twO 60-year-old plots, (plots 1-1 and 1-2) were carefully removed. Stumps, stump holes, dead stems, and other evidence of previous trees were mapped. The species were identified from wood or bark samples; the diameters and extent of decay of the stumps were noted. The harvest of the previous old-field stands of white pine had been very complete, as observed elsewhere by McKinnon et al. (1935). Except for the large rot-resistant stumps of the cut white pines, it is very probable that all stem remnants indicated trees which had been part of the present stand. All living stems in the 13 original plots, ranging from 33 to 107 years of age, were found to have starred either from released advance growth or seeds soon after stand-initiating disturbances and it is probable that the dead stems found in this study had simultaneous origin.

The remains of dead stems were in all stages of decay, of many species, and as small as 2.2 inches (5.6 em) in diameter at the root collar. It is probable that remnants of most stems larger than three inches (7.6 em) basal diameter at the time of death were found. This enabled an approximation of all trees that reached sapling size and a minimum estimate of the total number of trees per acre.

Three other plots were examined ro provide supplementary evidence of the total number of each species initiated per unit area. Circular one-fifth acre (0.08 ha) plots were established concentric to the two randomly placed one-fiftieth acre (0.008 ha) plots (Plots V-I and V-2) in the 45-year-old stand and one one-tenth acre (0.04 ha) plot was established in the 33-year-old stand concentric to Plot VI-I. All living and dead stems in these plots were identified by species.

RESULTS AND DISCUSSION

Pattern of Species Stratification

Examination of the broad sample of 25 permanent inventory plots at the Yale Forest verified that there was a definite pattern of stand development leading to dominance by red oak at middle age. The stand ages of this sample ranged from 33 to 100 years and red oak was a sample tree or interacted with a sample tree in 22 of the 25 plots.

The most common and important interaction involved the assertion of dominance of red oak over red maple and black birch. Red oak and red maple interacted on 16 plots with a total of 50 interactions. Red oak subordinated or overtopped the red maple in all 50 interactions. Red oak likewise dominated black birch in 30 of 31 interactions on 13 plots. The probability that the red oak might, as a matter of random chance, be above the red maple in all 50 instances or above the black birch in 30 instances out of 31 is infinitesimally small. Therefore, red oak can be expected to be in a canopy stratum equal to or higher than red maple or black birch where red oak between 33 and 100 years is found with either of these species in such upland stands.

Red oak occupied the B-stratum either as a single species, along with other oak species, or with maples, birches, and hemlocks where they were free of oak competition.

The diameter distribution of all trees in the 25-plot sample is shown in Figure 1. Figure 2 shows the diameter distribution by strata. Red oak was in the larger diameter classes, while red maple and black birch were found with increasing frequency at smaller diameters. Trees of larger diameters were found in the B-stratum, or upper continuous canopy, with the exception of hemlock. Progressively smaller trees were relegated to lower canopy strata. Red oak accounted for over 40 percent of the stems in the upper continuous canopy (B-stratum) although it comprised less than 8 percent of all stems. Red maple and black birch, on the other hand, were found primarily in the lower (C- and D-) strata. Seventy-five percent of the red oaks found in the lower two strata were subordinate to other red oak trees, and not to other species.

Age and Diameter Distributions in Stratified Stands

Age Distribution of B-stratum Red Oaks

The B-stratum red oaks in the stands studied were found to begin (probably from advanced regeneration) soon after the disturbance initiating each stand. Of the 35 red oaks aged at breast height in the three 60-year-old stands, all but 5 had reached breast height within 7 years of the disturbance. Four of these five had reached breast height within 10 years and the fifth was about 12 years younger (at breast height) than the disturbance.

The four additional stands represented a wide range of ages (33 to 107 years) and originated from three forms of disturbance (old field white pine clearcutting, hurricane blowdown, and deciduous forest clearcutting). Examination of the red oaks in these stands indicated that they had originated and developed in the same way as those of the 60-year-old stands.

The three 60-year-old stands (Stands I, II, and III) contained B-stratum red oaks which had diameters and ages whose means were not significantly different by analysis of variance (5 percent level).

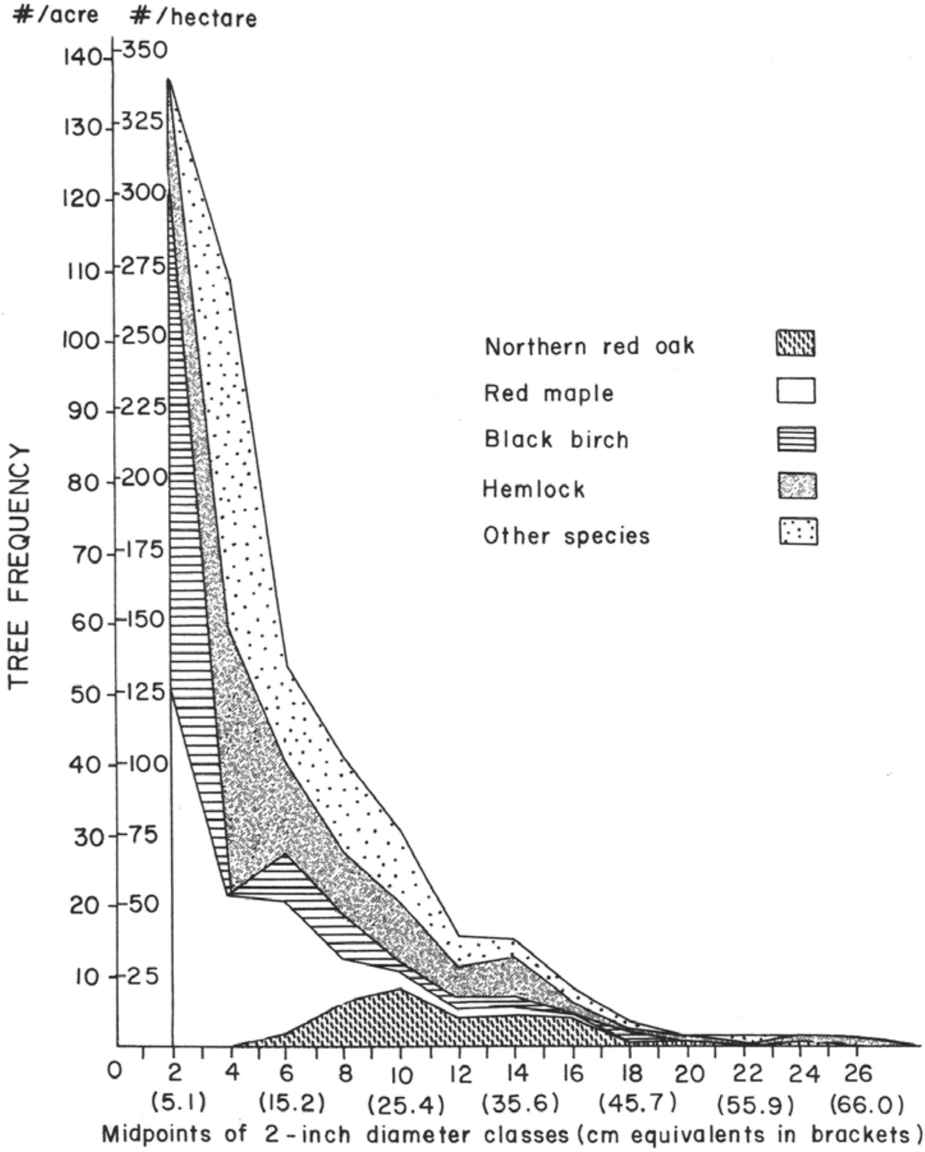


Figure 1. Distribution of all trees of upland forests in the Yale Forest in northern Connecticut based on point sampling of 25 plots.

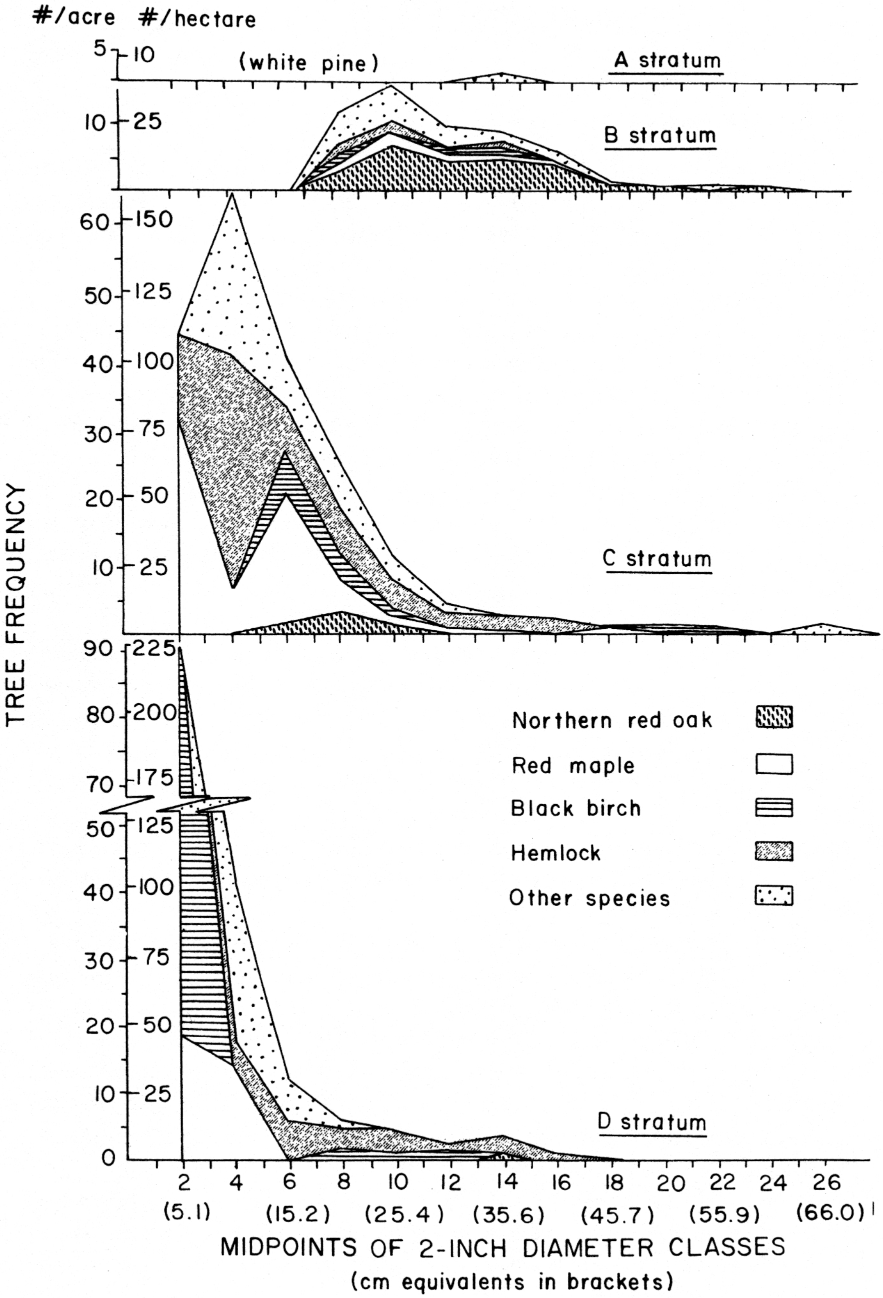


Figure 2. Vertical stratification of trees of Figure 1.

Age and Diameter Distributions of All Strata

Frequency distributions by diameter and age classes of all trees in the combined seven 60-year-old plots are shown in Figure 3 (A and B). The other trees, as well as the B-straturn oaks, essentially began soon after the disturbance. In the two plots extended to determine if trees beyond the oak crowns behaved differently, all studied trees were divided into two groups: those whose stems originated outside the projected crown of any B-stratum tree, and those trees within the projected crown area. Student's t-distribution analysis showed no significant difference (at the five percent level) between the ages of trees growing beneath and beyond B-stratum oak canopies.

Diameter and age distributions for the 74-, 45-, and 33-year-old stands are shown in Figures 4, 5, and 6. For the 107-year-old plot, all three trees were the same age (106 years at one foot) although the red oak was 19.2 inches D.B.H. (48.8 cm); the black birch, 7.9 inches (20.1 cm); and the sugar maple, 6.1 inches (15.5 cm).

All of the mixed species stands studied had a vertical stratification of crown canopies by species and all approached the reverse-J-shaped *diameter* distribution so often assumed to be indicative of the all-aged condition. However, the breast-high *ages* were narrowly distributed about a mean age slightly younger than that of the time of initial disturbance rather than being disturbed in the reverse-J-shaped manner. The total number of trees per unit area became fewer as the stands became older, but the essentially even-aged condition was maintained.

The largest of the few trees of each species which attained breast height much later grew less in diameter than could be explained solely on the basis of their younger age. The disadvantage of competing with earlier established vegetation for limited soil and light resources may explain this slow growth of slightly younger trees. Similarly, the competitive disadvantages of younger vegetation may explain why there was nOt a continuous recruitment of young trees, leading to the all-aged forest.

Small disturbances, primarily the 1938 hurricane, occurred in some of the plots. These did not create a new age class as a permanent component of the stands, but only increased the growth rate of the remaining older trees.

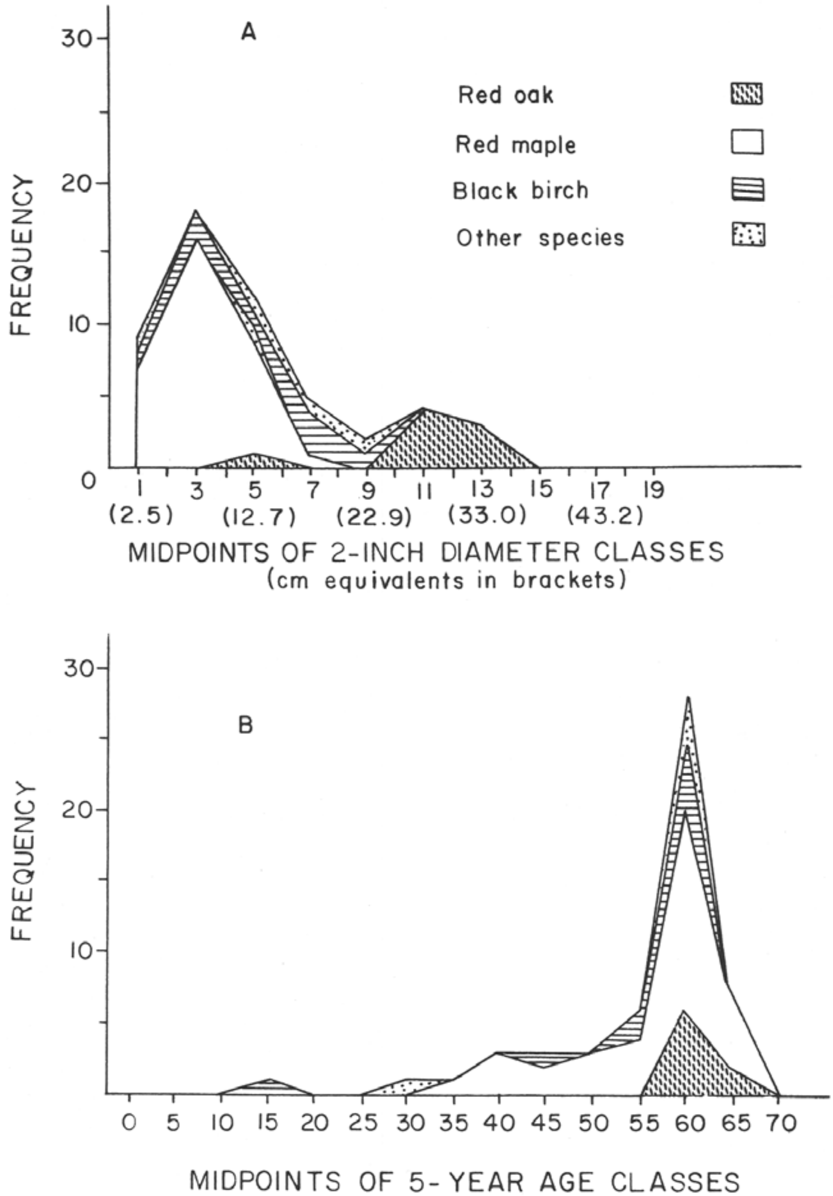


Figure 3. Distribution of diameters (Fig. A) and ages (Fig. B) of all trees in seven selected plots dominated by northern red oak in stands (Stands I, II, and III) beginning after clearcutting old field white pine approximately 60 years ago.

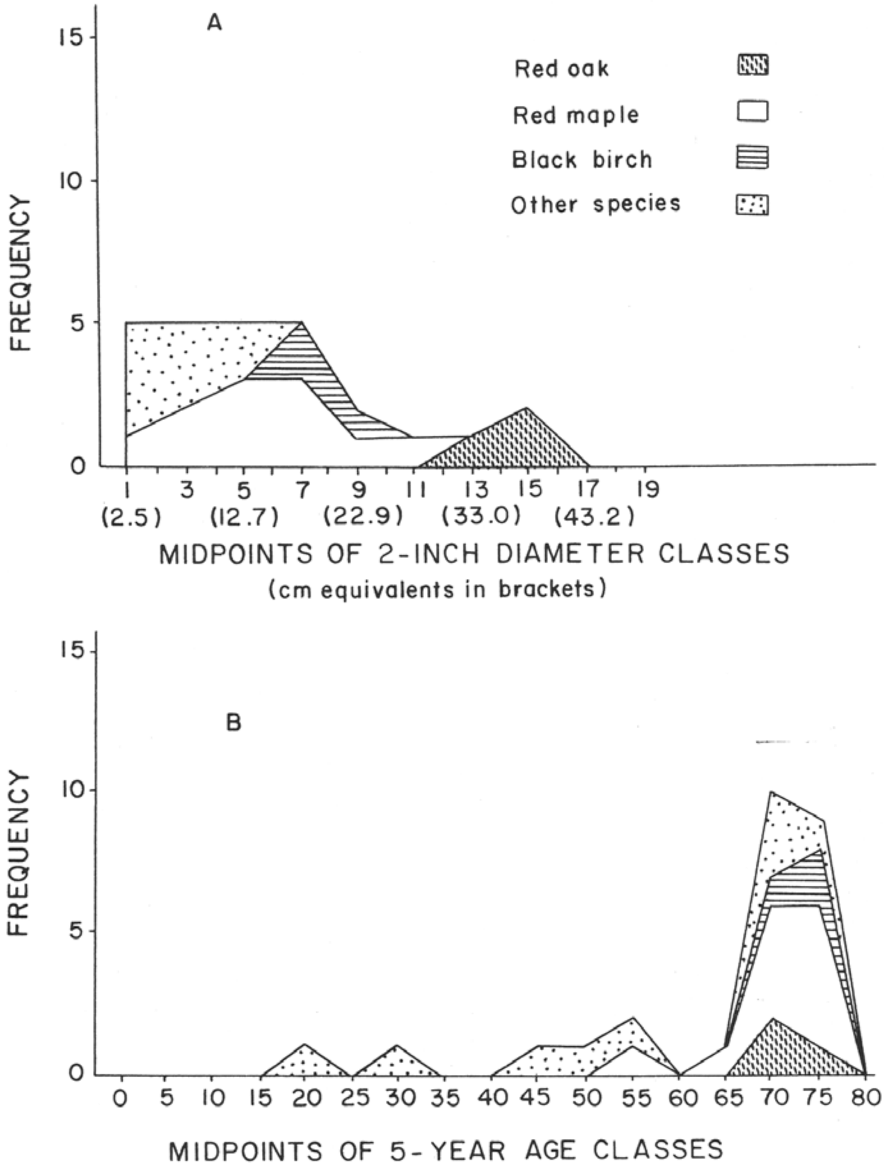


Figure 4. Distribution of diameters (Fig. A) and ages (Fig. B) of all trees in three selected plots with red oaks in the B-stratum in Stand IV. The stand resulted from clearcutting of an old-field-white pine stand approximately 74 years ago.

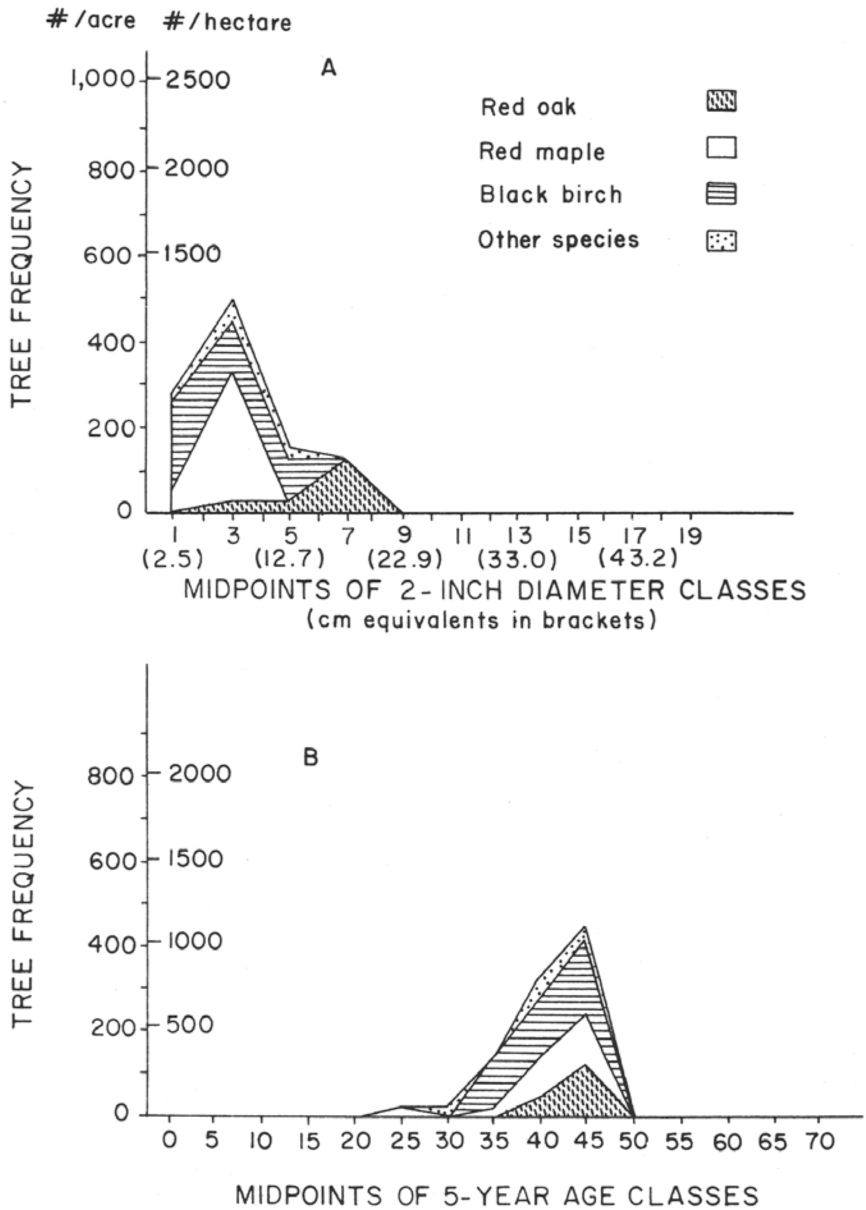


Figure 5. Distribution of diameters (Fig. A) and ages (Fig. B) of trees per acre resulting from clearcutting of white pine stand approximately 45 years earlier (Stand V).

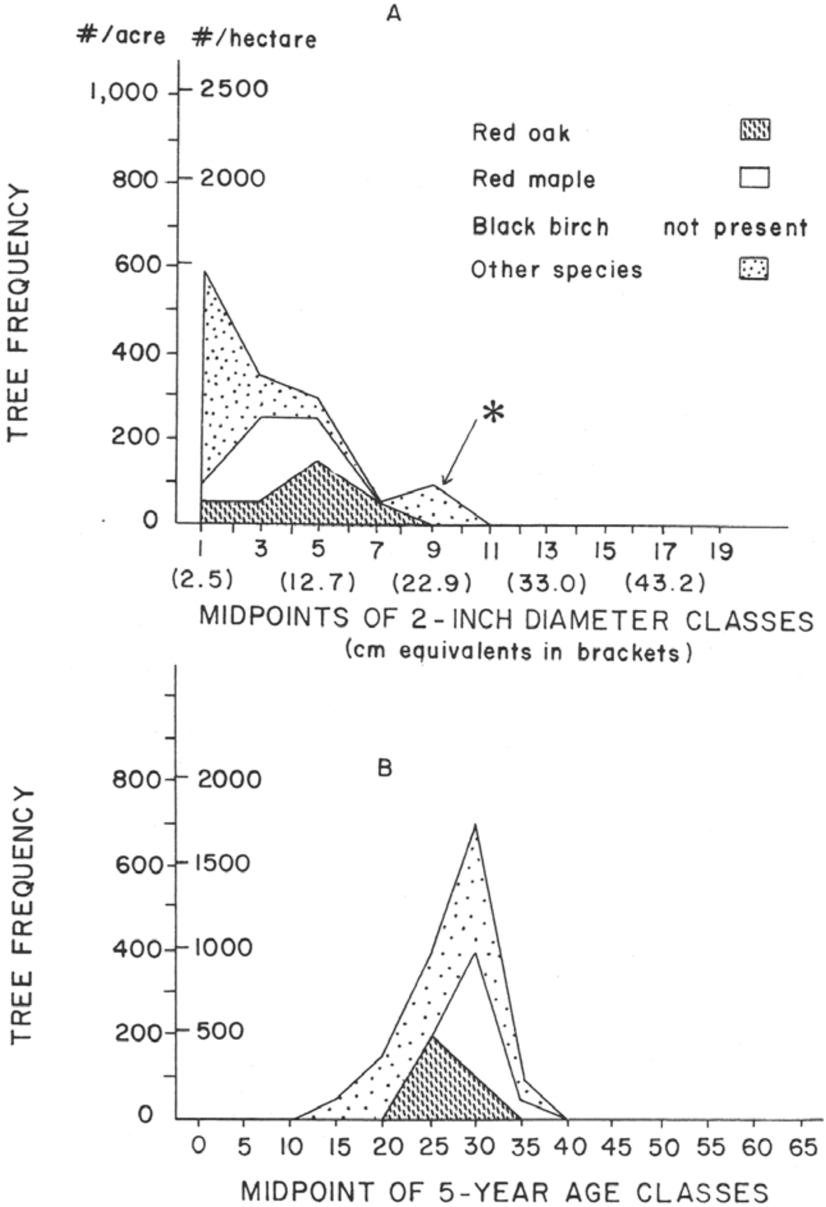


Figure 6. Distribution of diameters (Fig. A) and ages (Fig. B) of trees per acre resulting from hurricane blowdown of white pine stand 33 years previously (Stand VI). Asterisk denotes an aspen and one white pine lateral branch which grew vertically after windthrow.

Physiognomic Development of Mixed Species Stands

As shown above, the mixed, even-aged stands that arose after clearcuttings or similar disturbances developed a vertical species stratification with red oaks in the upper stratum. Growth histories of several of the oak-dominated stands of the present study were reconstructed to determine their patterns of development and to shed some light on the oak regeneration problem.

Sequential Development of Typical Stand

Many of the data were consolidated into a composite diagram (Fig. 7) to show the development of a typical stand. The schematic was constructed from the height-age curves, plot maps, and data on stem branching and forks; this consisted of the B-stratum oaks of the seven 60-year-old plots (Plots 1-1,1-2, II-I, 11-2, III-I, 111-2, 111-3) and the tallest associated red maples and black birches as well as other red maples and black birches. The diagram shows development at 15-year intervals beginning in 1911. Height growth, relative spacing of trees within each plot, and positions of branches, forks, and irregularities in the trunks *are all to scale and based on direct measurements.* The plots were not all contiguous as implied in the figure. Only living stems along narrow transects within each plot are shown; other living red maples and black birches and other species were present. Many trees and species such as gray birches and aspens which died before the forest was 60 years old are not shown.

Development of an Individual Red Oak and Its Associates

Figures 8A-H show a reconstruction of the development of a typical red oak and its associates (Plot 1-2) as viewed from the south at 10 year intervals from 1901 to 1971. The stems shown in Figure 8H were living in 1971 and are depicted in their measured dimensions. The additional trees shown in Figures 8B-G represent the probable growth patterns of the stems for which only a root collar and possibly a fallen or standing dead stem were found. The size obtained by these stems and the time of their death is estimated from height-age curves of similar living trees analyzed throughout this study, as well as from the size and extent of decay of the dead stem remnants. Figure 8A,

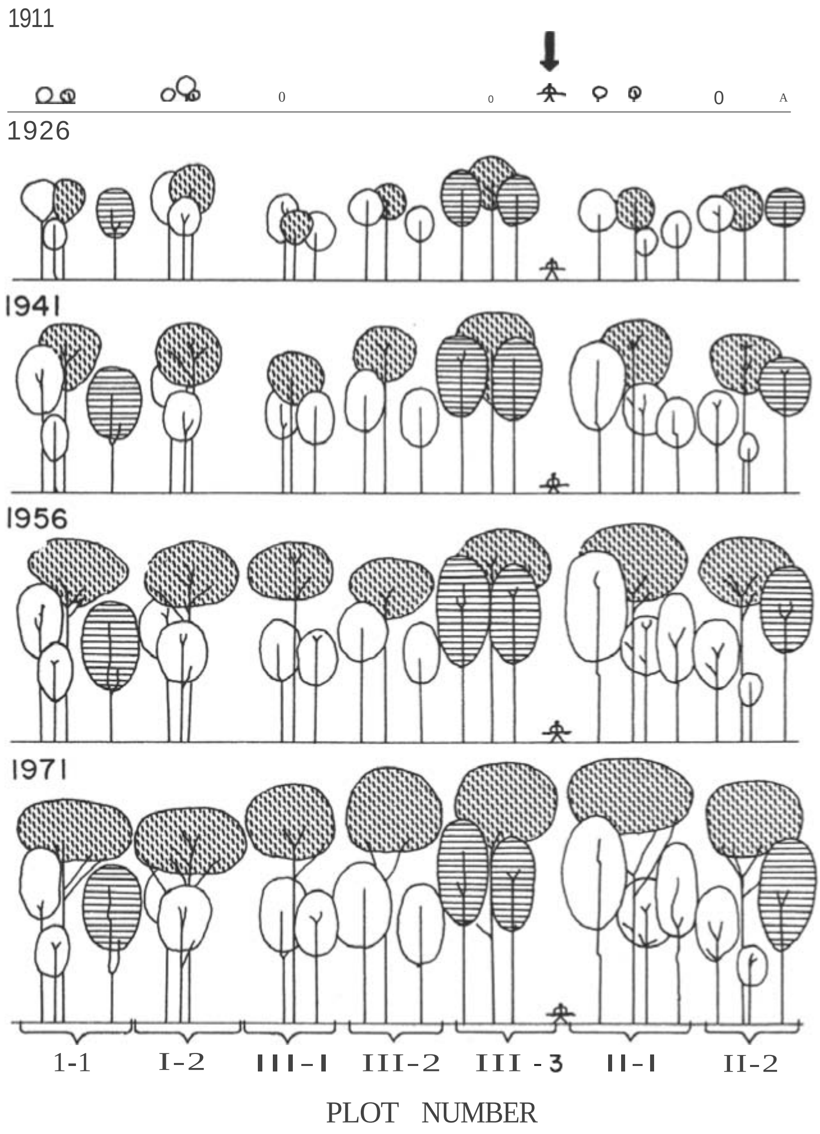


Figure 7. Growth of even-aged composite stand consisting of seven B-stratum red oaks (dotted crowns) and tallest red maple (plain crowns) and/or black birch (horizontally striped crowns) and other red maples and black birches with stems beneath vertical projection of crown of B-stratum red oak. Person (see arrow) is six feet (1.8 m) tall and holds a stick ten feet (3.1 m) long.

based on stump remnants, shows what the previous old field white pine stand probably looked like before clearcutting.

Red Oak Crown Development

Figure 9 shows the development, as seen from above, of the central red oak of Figure 8H, the red oaks which eventually became contiguous to it in the B-stratum, and the remnants of dead red oaks found within the area. The only branches analyzed were those living in 1971; branches dead before then may have made the crowns wider and deeper during the early years.

Discussion

The stands shown growing in Figures 7, 8, and 9 originated after old field white pine clearcutting of about 1910. Many of the trees initiating growth after the cutting arose from new seeds or from seedlings existing beneath the previous white pine stand. Not all trees started immediately after the clearcutting, but most did so within a short time.

What eventually became a stand with red oaks in the upper stratum and more numerous red maples and black birches in the lower strata began as an even-aged stand after a disturbance. The oaks ascended to dominant positions without any further disturbance by cutting, fire, or grazing. The red maples and black birches did not lose their position by dying; instead they simply lapsed into the lower strata. This result is not what would be anticipated from studies such as those of Clark and Watt (1971) and Roach (1971), of early developmental stages.

If the stands of this study had been examined during the first 25 years as they appeared in the stages shown in Figures 8B and 8e, it would have seemed very unlikely that the limited numbers of red oaks would ever dominate the main canopy as shown in Figure 8H. Not only were they vastly outnumbered by red maples, black birches, and other species, but their comparatively low stature would also lead one co infer that they were more likely to be suppressed than to ascend to dominance.

The lowest lateral branch still alive on the central red oak at 60 years (Fig. 8H) appeared co have started just as the tree began co emerge. The lowest living branches on seven 60-year-old B-stratum red oaks (in Plots 1-1, 1-2, 11-1,11-2, III-I, 111-2, and 111-3) in similar stands ranged from 30 to 41 feet (9.2 to 12.5 meters) above the ground and averaged 36 feet (11.0 meters). The long lateral (or "scaffolding") branches seen also in Figures 8 and 9 produced the broad, flat-topped, irregular shape of the typical red-oak crown. They may also have been instrumental in suppressing the lower trees by wind-whipping terminals of maples and birches protruding into these crowns.

The hurricane of September 21, 1938, blew down a hemlock and a red oak shown in Figure 8. These trees were adjacent to large rocks which did not permit adequate root anchorage on the windward sides.

When viewed from above (Fig. 9), the crowns of the widely spaced oaks are at first isolated among other species but eventually joined into a pure upper canopy stratum. Where red oaks grew close together, they segregated into the conventionally recognized dominant, codominant, and intermediate positions *within* the same canopy stratum. (Note the oaks in the southwest quadrant of Fig. 9.) This crown differentiation among closely spaced upper-stratum oaks is slow. Closely growing oaks each occupied a part of the canopy space with virtually no overlap of foliage between crowns. Where red oaks were more widely spaced, there was more room for the crowns of an individual tree to spread. Where oaks were in lower strata it was mainly because other oaks had excluded them from the B-stratum.

The suppression of oaks primarily by other oaks is supported by the observation made during the study of the permanent sample plots on the Yale Forest that 75 percent of the red oaks not found in the upper canopy were beneath the canopies of other red oaks. Few red oaks in the stands over 33 years old lived in the suppressed state. Only seven per acre (17/ha) were found alive below the upper continuous canopy stratum compared to an average of 23 per acre (57/ha) in the upper contInUOUS stratum.

Three oaks depicted in Figure 9 died before 1971. The 1938 hurricane blew over one (in Fig. 8); another (not in Fig. 8) was apparently suppressed by adjacent oaks to its southwest; there is no clear explanation for the death of the third (in Fig. 8).

FIGURE 8. (A - H) Reconstruction of development of a typical stand after clearcutting, about 1910, of old-field white pine. Diagrams show sequential stages in Plot I-2 viewed from south edge. Arrows point to trees still living in 1971. Tree "A" is red oak which ultimately predominated and is central tree of Plot 1-2.

Legend.

Hemlock 

White Pine 

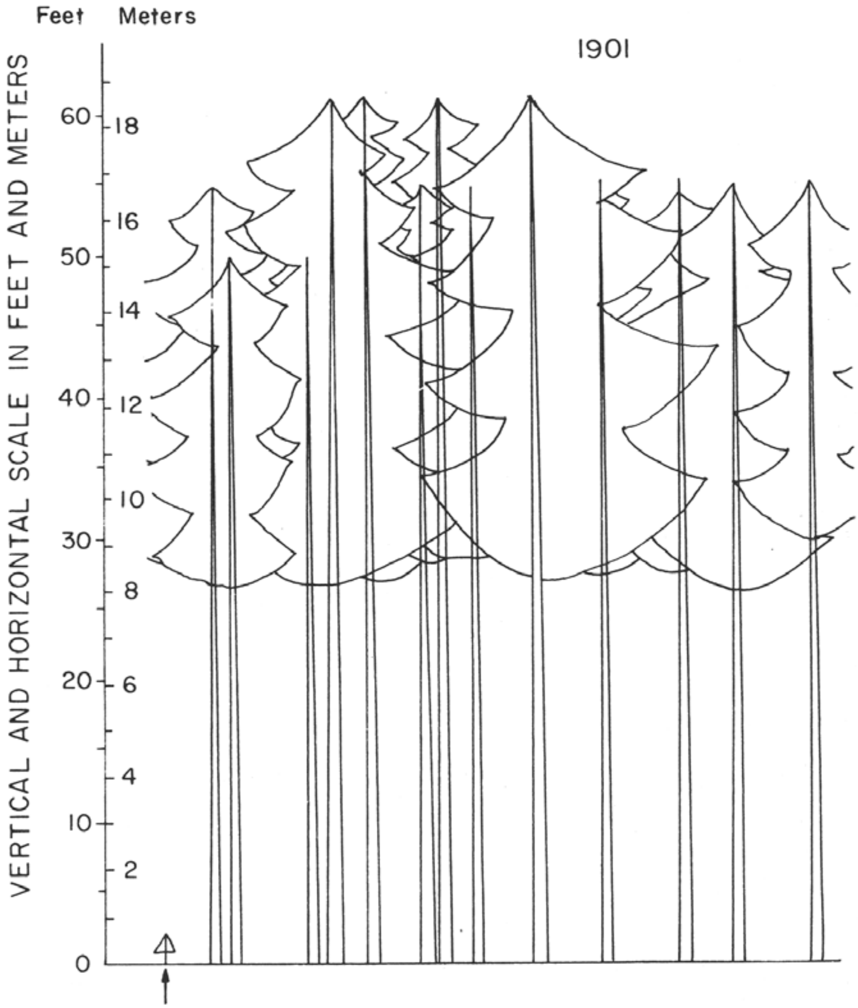
Birches 

Maples 

Oaks 

Not identifiable

A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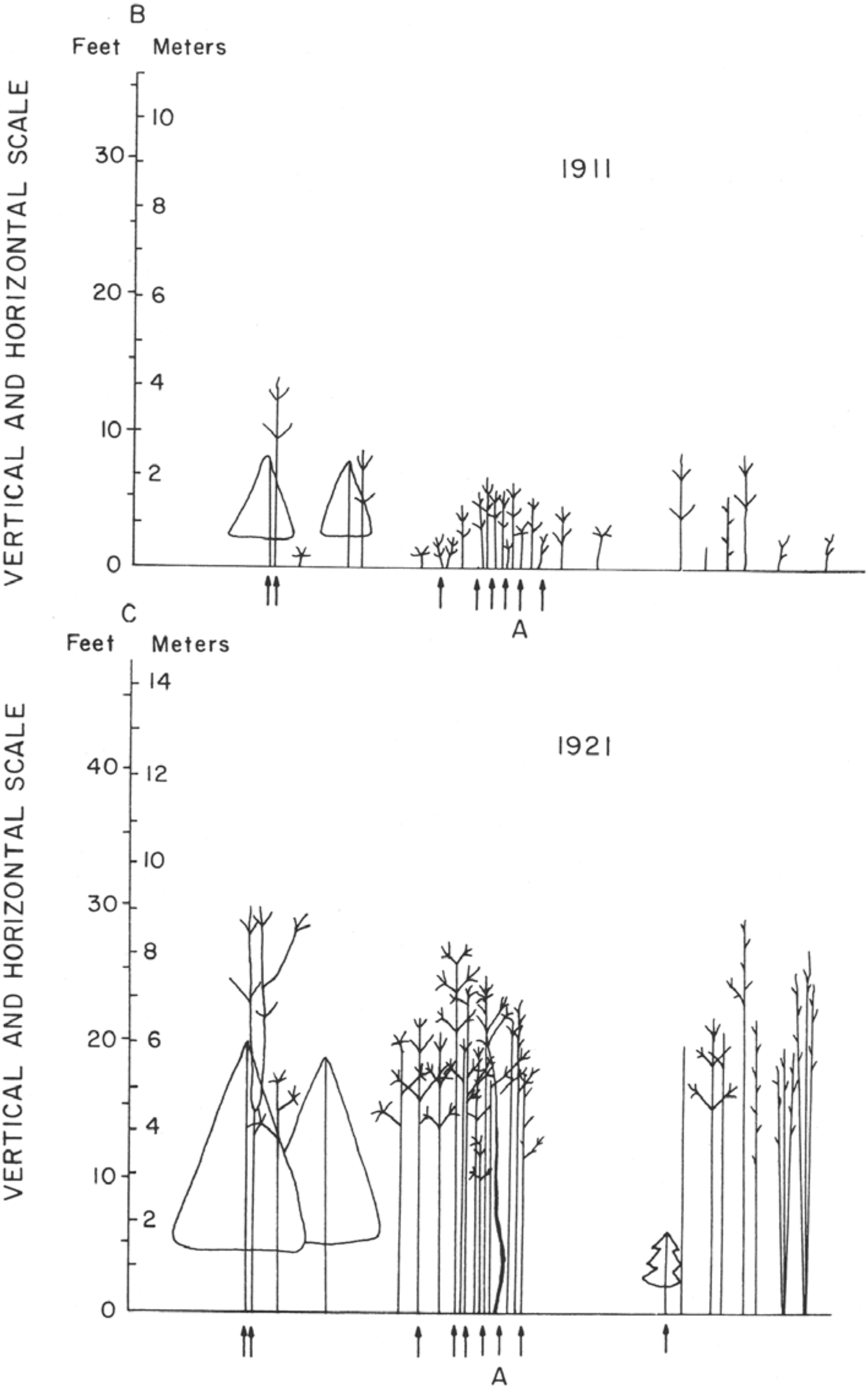
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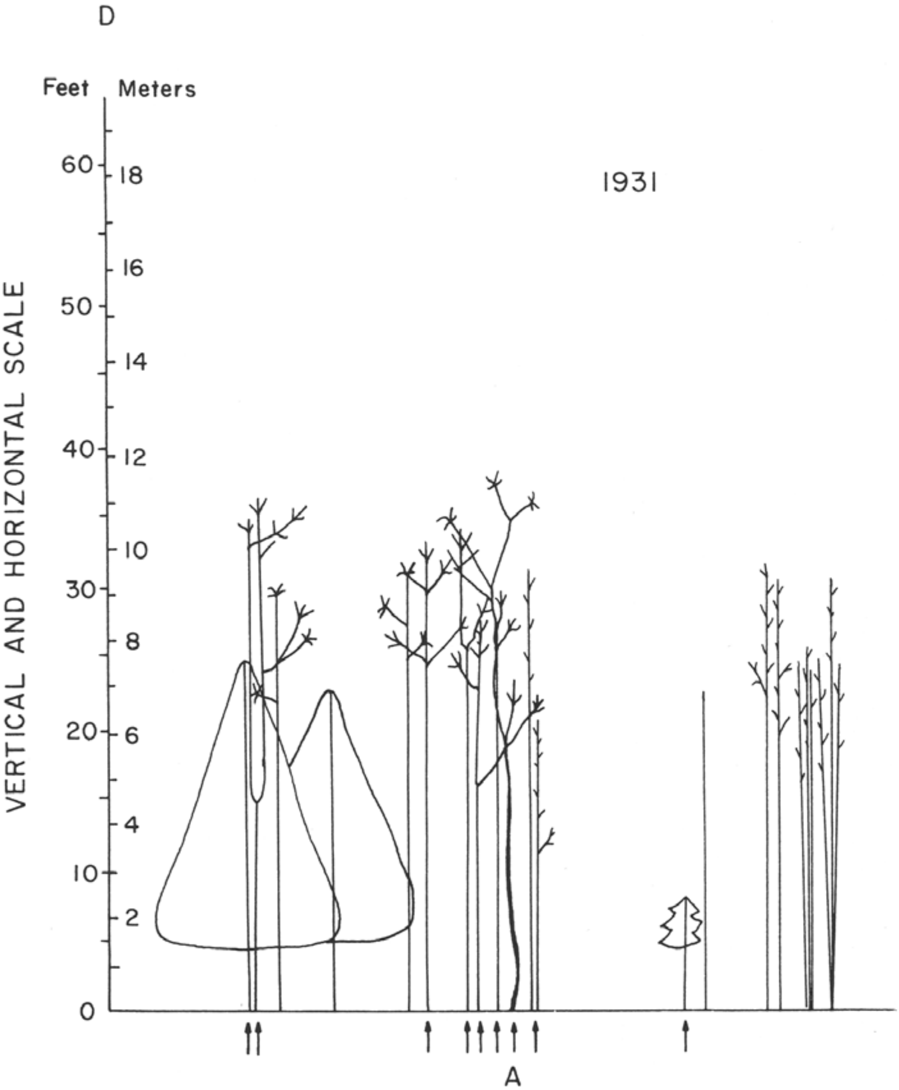
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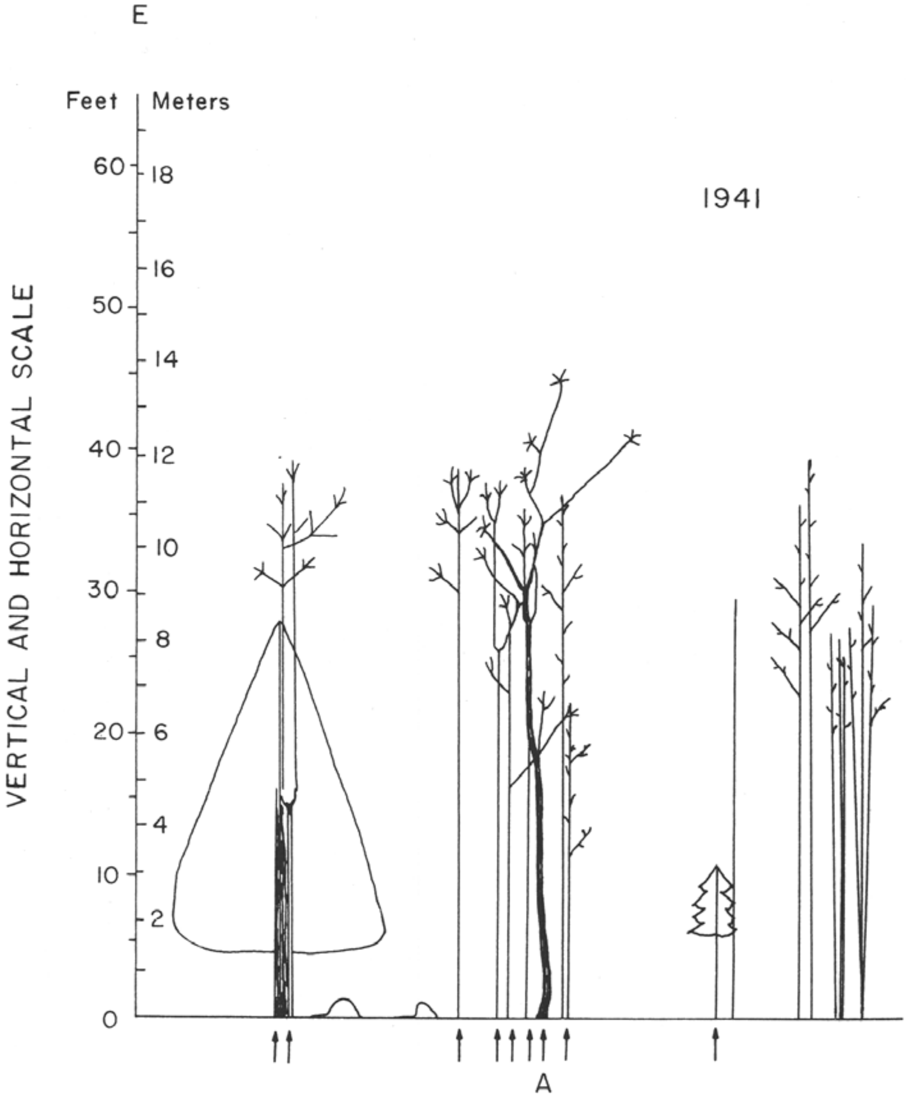
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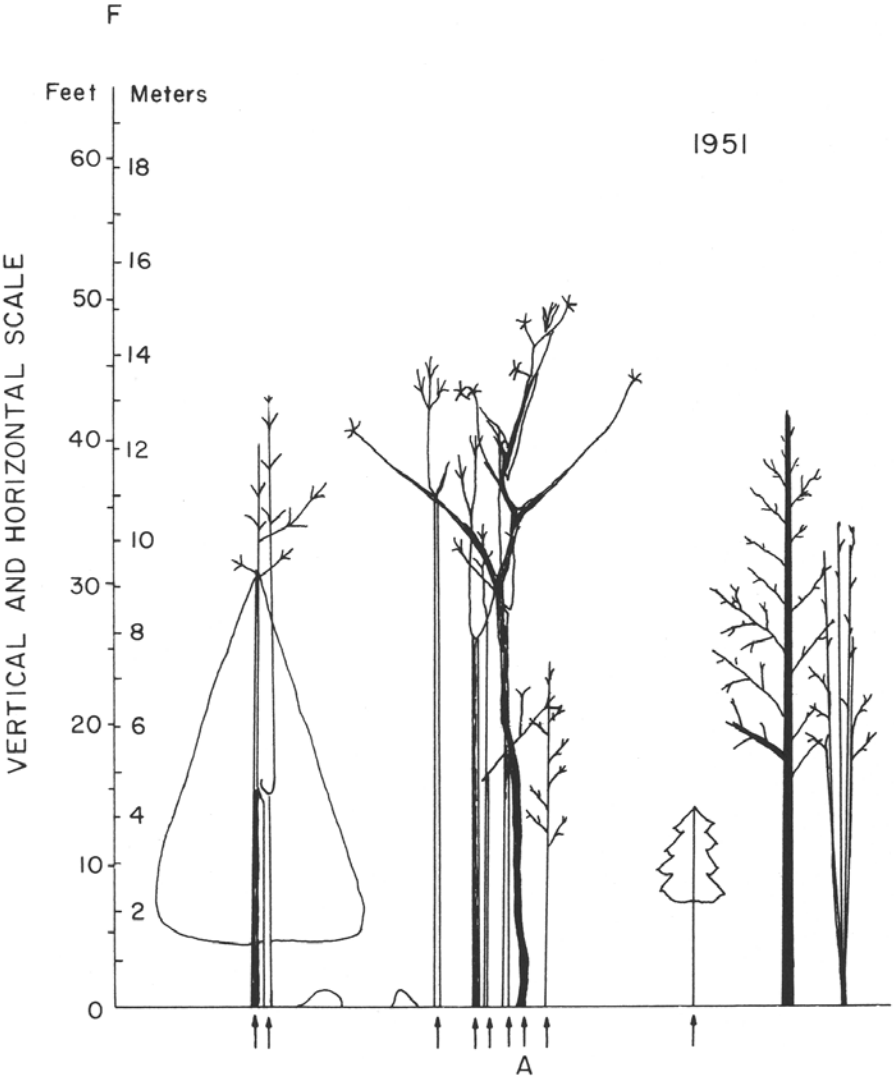
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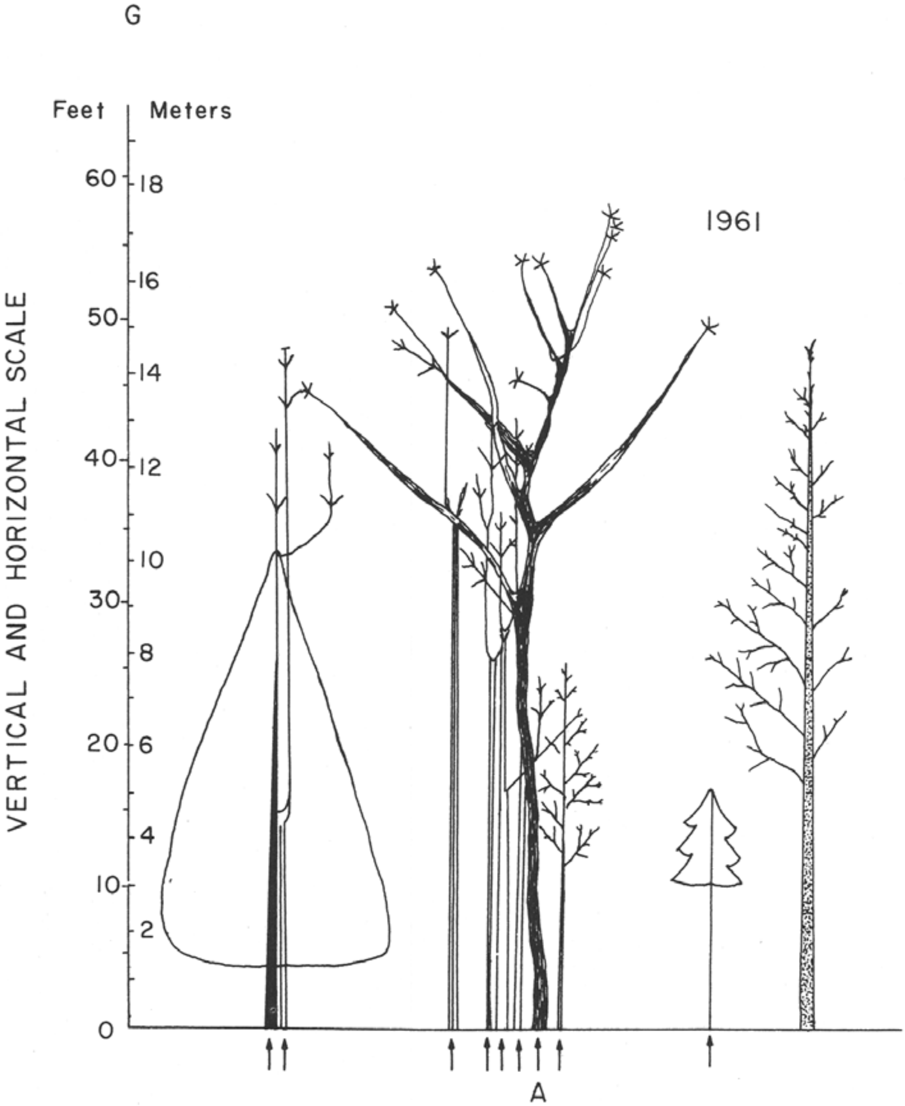
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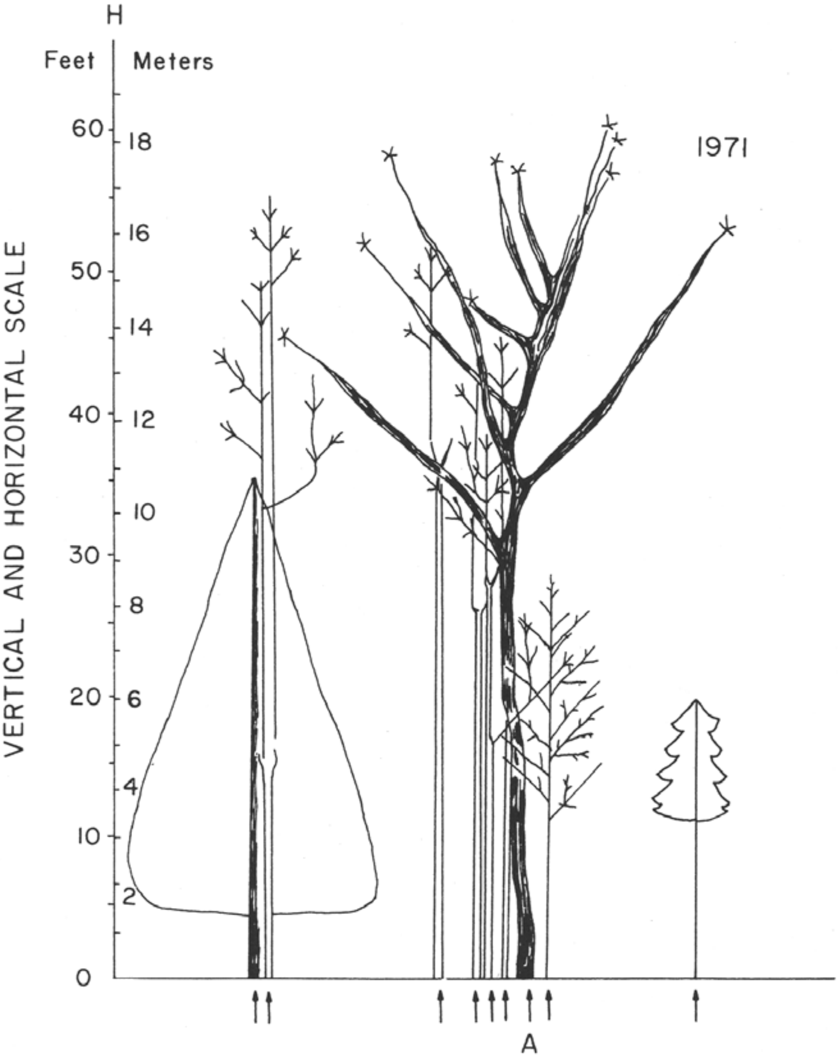
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It is probably easier silviculturally to grow northern red oaks, and perhaps other oaks, in mixture with other hardwood species than to attempt to create pure oak stands. Species such as maples, birches, and hemlocks may keep the oak stems well pruned. The emergence of the red oaks into the upper stratum and the submergence of the other species, coupled with the initial paucity ofoak regeneration, induces a natural thinning effect. If one could create a pure oak stand with hundreds ofoaks per acre, very intensive artificial thinnings would be required to produce a similar result.

Height Growth and Species Stratification

Early height growth of red oak is governed by the size (and hence physiological condition) of the root system from which it developed (Sander, 1971). Similarly, early height growth of red maple (and probably other species) varies with such factors as size of root system and time of release (Wilson, 1968).

For each of the nine plots in 60- and 74-year-old stands and nine plots from Stephens' study (described in the Procedures), height of the red oaks at each five-year interval following stand initiation was compared with the simultaneous height of the tallest surviving red maple and/or black birch. There were 12 comparisons between red oak and red maple, and 10 between red oak and black birch. A paired variates test (Student's t-distribution) was used to compare height at each five-year interval between red oak and red maple or black birch within the same plot.

Mean height growth patterns of 18 red oaks, 12 red maples, and 10 black birches representing the tallest tree of each species found<>n each plot are shown in Figure IDA. The t-statistic of differences between paired variates (red oak-red maple and red oak-black birch) are shown in Figure IOB. For the red oak-red maples comparison, $t_{.95} = 2.201$ (df = 11); for the red oak-red maples comparison, $t_{.95} = 2.262$ (df = 9).

The red maple stems may actually have been taller than the red oaks for the first ten years ofgrowth. (Note that the t-statistics ofFig. IOB for red oak-red maple comparisons are negative until the tenth year.) The same relationship was observed for other red maples of the present study as well. Arend and Scholz (1969) also found red oak

FIGURE 9. Reconstruction of growth between 1931 and 1971 of crown of central northern red oak in Plot I-2 and crown growth of surrounding northern red oaks as viewed from the top. These oaks are widely spaced with red maple, black birch, and other species (not shown) in between. Note competition within B-stratum for closely spaced oaks in southwest quadrant.

Legend.

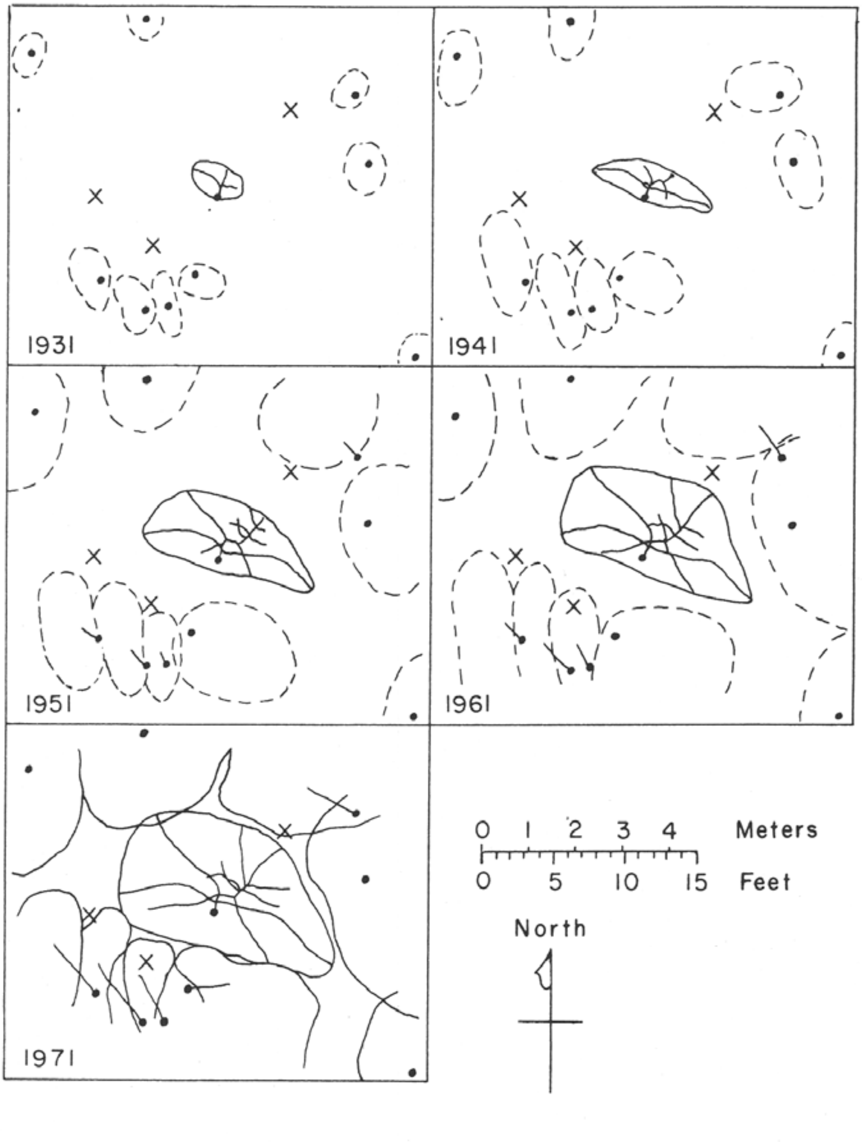
Root collars of northern red oaks living in 1971 •

Dead northern red oak stump positions. ×

Estimates of crown projections of B-stratum red oaks:

Crown size and branch positions of B-stratum red oak of Plot I-2 based on stem analysis:

Known crown projections of B-stratum red oaks: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regeneration to be shorter than associated species immediately following cutting in southern Wisconsin. These early years before crown stratification have been referred to by Gingrich (1971) as the "brushy" stage. The slow early height growth of oaks during this stage has sometimes led silviculturists examining only young stands to infer that the oaks would not survive. Between the ages of 20 and 25, the tallest red maples decelerated in growth, becoming very significantly (one percent level) shorter than the associated red oaks by 25 years. After this they tended to grow relatively little in height, becoming relegated to the lower canopy strata.

Black birches did not exhibit the rapid early height growth of the red maples but maintained a steady rate for a longer period (Figs. 10A and 10B). The tallest black birches eventually reached a height plateau slightly above the red maples.

Similar patterns of relative height-growth were found for these three species in the younger and older plots, where it was not unusual to find that either red maples or black birches had been taller than red oaks during the first 25 years. As observed earlier, the growth of red oaks over red maples and black birches seems to be consistent on the broad range of till sites in central New England.

Diameter Growth

A study of the breast height diameter growth rates of the 63 upper canopy red oaks from three 60-year-old stands (Stands I, II, and III) revealed two growth patterns: (1) an essentially linear diameter growth with slight acceleration or, more often, slight deceleration with increasing age; and (2) an abrupt increase in growth during or shortly after 1939. The remains of trees blown down by the 1938 hurricane were found beside all but one of the 15 oaks that showed the abrupt diameter increase after 1938. Upper-canopy oaks of the 45-, 74-, and 107-year-old stands also exhibited similarly the two diameter-growth patterns.

Emphasis in this study was placed on those trees which did not show growth acceleration after release by the 1938 hurricane. The sustained rapid and uniform diameter growth of unreleased oaks in these mixed stands probably resulted from the emergence of oaks from surrounding competition. Early in their lives the oaks were

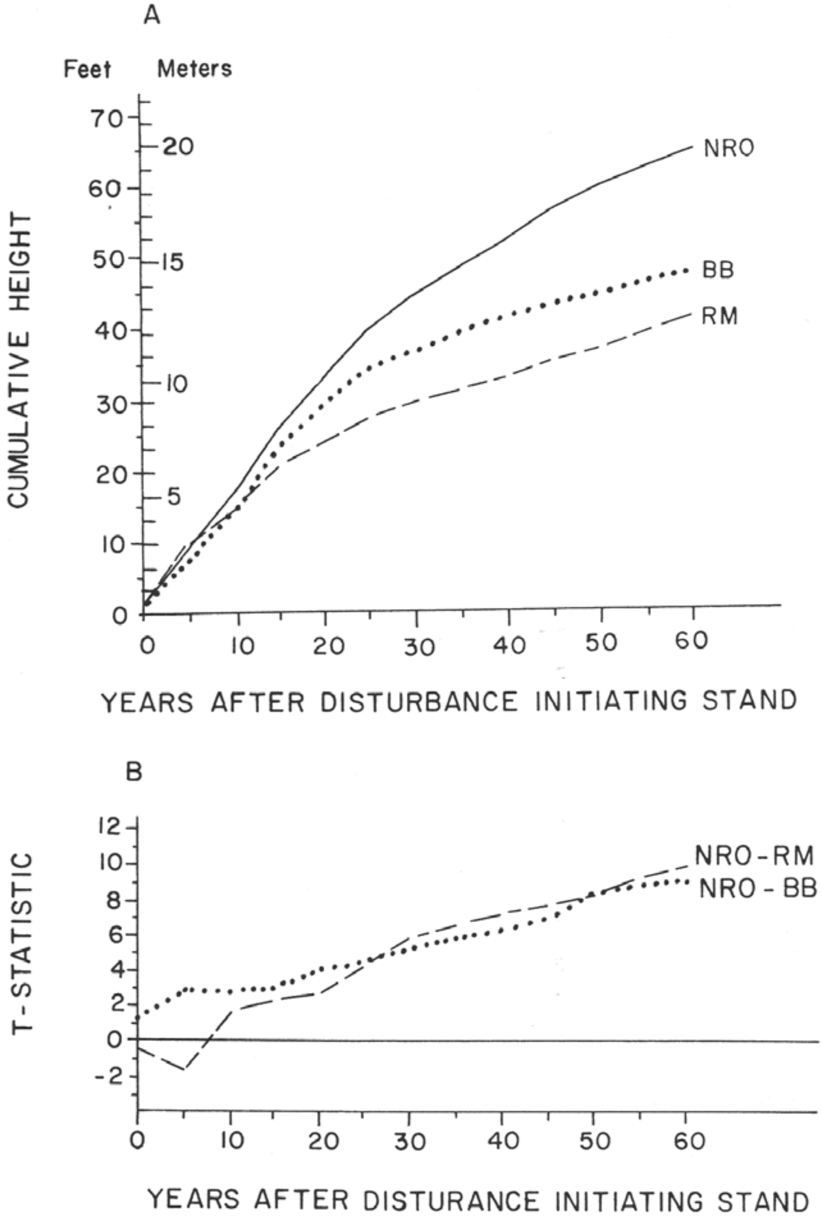

Figure 10. *A*. Cumulative height growth patterns of northern red oak, red maple, and black birch. *B*. T-statistic of paired variants for mean height of red oak and red maple (dotted line) and red oak and black birch (dashed line) for each five-year interval. T-statistic is positive when red oak is taller.

subjected to intense crown competition. The oak crowns expanded as they emerged above other species, enabling a rapid late growth rate (Holsoe, 1948) which, when put on over larger surface areas in the outer rings, caused the annual rings to be of approximately equal radial thickness.

Breast-height diameters at 5-year intervals for 10 red oaks, 8 red maples, and 6 black birches - all representing the largest of each species on 10 plots in the 60-, 74-, and 107-year-old stands-are shown as means in Figure 11A. None of the red oaks were ones that showed abrupt release after 1938 or at any other time. As with the comparison of height, the paired variates test was applied to differences in diameter between red oak and the other species. Best estimates of the standard deviations of the populations of differences between paired variates are shown in Figure 11B. For the red oak-red maple comparison, $t_{.95}$ = 2.365 (df = 7); for red oak-black birch comparison, $t_{.95}$ = 2.571 (df = 5).

Red maples generally remained smaller in diameter than their oak competitors (Figs. 11A and 11B), although the maples may have been taller (Fig. 10A) for the first few years. Red oaks were highly significantly (one percent level) larger in diameter than the red maples by the time the stands were approximately 15 years old. Black birches were at first smaller in diameter than both the red maples and red oaks. They soon grew larger than the red maples and maintained a high diameter growth rate for about 45 years. Similar diameter growth patterns were found in both the older and the younger stands studied. As with early height growth, it was not unusual for either red maples or black birches to be larger in diameter than the red oaks during the first 25 years.

Red oaks did not attain a dominant position in the stands until approximately 25 years after stand initiation. At that time red oaks were 30 to 45 feet (9 to 14 m) tall and four to six inches (10 to 15 cm) in diameter. Before 25 years, it would have been easy, without knowledge of subsequent events, to conclude that the young (0- to 25-year-old) stands would not develop a red oak B-stratum.

Initial Species Stocking and Changes with Time

The observed numbers of living stems by species in each intensively reconstructed stand and the detectable numbers of dead stems

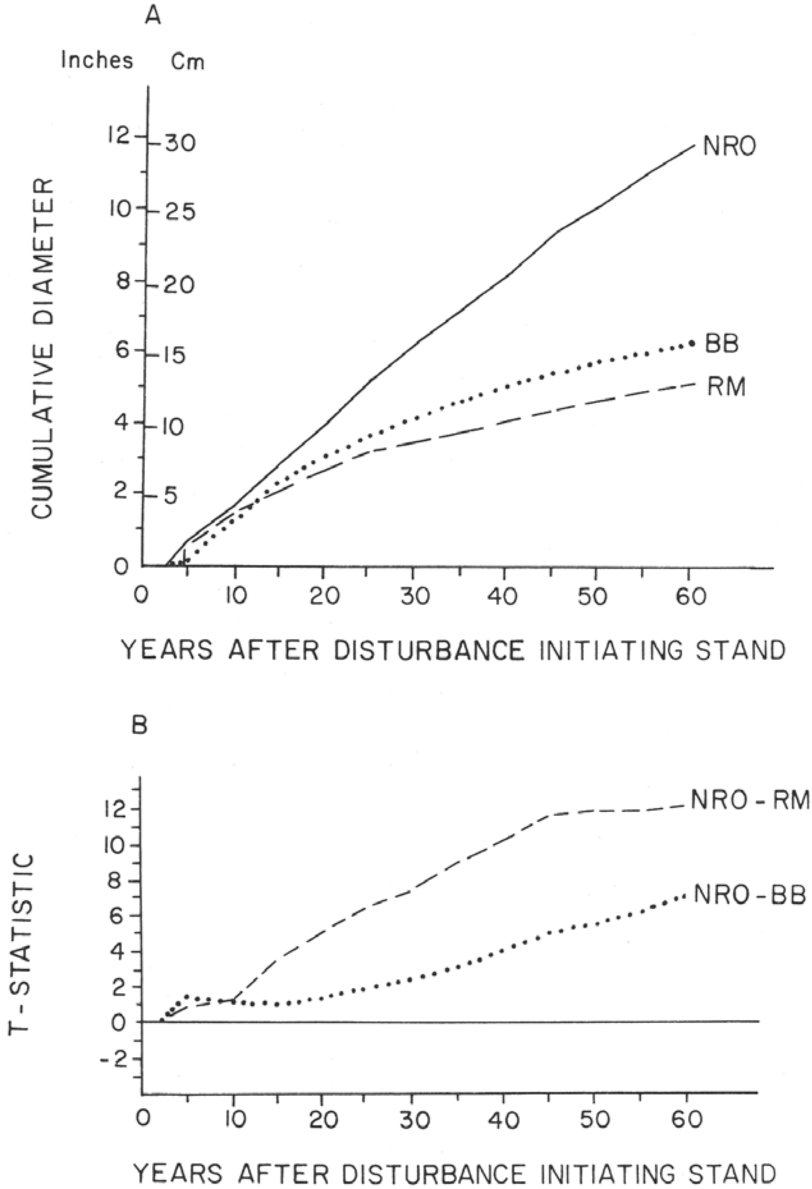

Figure 11. *A*. Cumulative diameter-growth patterns (based on 5-year increments) of northern red oak, red maple, and black birch. *B*. T-statistic of paired variates for mean diameter growth of red oak and black birch (dotted line) and red oak for red maples (dashed line) for each five-year interval. T-statistic is positive when red oak is larger.

are shown in Table 1. The sum of these values is the minimum number of trees present in each stand initially, exclusive of those dead ones for which no remnants remained. The greatest number of red oaks detected in any stand for any past time was 152 per acre (375/ha), or about 10 percent of a total stand comprising 1,631 saplings of all species per acre (4,029/ha). Red maples comprised 21 to 49 percent of the total saplings and black birches had varied from 8 to 35 percent of the total. At age 60, red oaks forming a pure B-stratum averaged only 97 stems per acre (242/ha), or 17 percent of the currently living stems.

The observed numbers are consistent with those reported by others. McKinnon et al. (1935) studied hardwood reproduction following old field white pine clearcuttings in central New England. Excluding red maples and aspens, they found an average of 689 "crop trees" per acre (1,702/ha) on the better till soils five years after the clearcut (slightly fewer on the poorer soils). Red oaks averaged 241 trees per acre (595/ha) on better soils and 139 per acre (343/ha) on poorer soils immediately after clearcutting. Here, too, they observed oaks dominating as the stands became older. In the same circumstances, Patton (1922) observed 3,800 hardwood stems per acre (9,386/ha) at age 13; only eight percent of these were red oaks. Trimble and Hart (1961) observed several thousand stems per acre arising after clearcutting northern Appalachian hardwood stands and only a small fraction were northern red oaks. Similar conditions in young stands have led observers such as Clark and Watt (1971) and Roach (1971) to doubt whether red oaks would ever become prominent. It seems clear from the present study that northern red oaks do have the capacity to assume ultimate dominance over many other species after "clearcutting" or similar disturbances *provided they are initially present as advance growth.* This will occur even though the red oaks remain in a subordinate position for two decades or more.

Red oak saplings have a low mortality rate compared with many other species. For example, in Stand I, 75 percent of all red oak initially present were alive after 60 years, compared with 55 percent for red maples; 20 percent for black birches, and 44 percent for all species combined.

Table 1. Minimum estimates of living (1971) and dead trees per acre present since stand initiation in three stands of different ages. Numbers per hectare are in parentheses.

Stand age	60 years	45 years	33 years
Species	*#/acre (ha)*	*#/acre (ha)*	*#/acre(ha}*
Northern red oak			
-total	129 (319/ha)	152 (375)	150 (370
-living	97 (240)	134 (331)	130 (321)
Red maple			
-total	645 (1593)	565(396)	390 (963)
-living	355 (877)	377 (931)	360 (889)
Black birch			
-total	323 (798)	578(1428)	150 (370)
-living	65 (161)	270 (667)	40 (99)
Other			
-total	226 (558)	336 (830)	1170(2890)
-living	64 (158)	258 (637)	790(1951)
All species			
-total	1323 (3268)	1631(4029)	1860(4594)
-living	581 (1435)	1039(2566)	1320(3260)
No. of plots	2	2	1
Plot area			
acres	0.031	0.40	0.10
hectares	0.012	0.162	0.04

Silvicultural Considerations of Stocking and Volume Growth

Emergent red oaks have relatively broad, flat-topped crowns with a thin layer of foliage along their upper surfaces and essentially no lower layers of foliage. Therefore, the surface area of a vertical projection of a crown periphery on a horizontal plane—an approximate index of a red oak's photosynthetic surface area—would be expected to be closely related to the accumulated basal area of the tree stem where there had been relatively little disturbance. A close relation has been found between basal-area growth and crown projection area by Holsoe (1948) in red oaks and white ashes, by Berlyn (1962) in eastern cottonwoods (*Populus deltoides* Bartr.), and by Stout (1962) in a larger number of deciduous and coniferous species.

Basal areas and areas of crown projections of 25 trees in the three stands (Stands I, II, and III) of approximately 60 years age were measured. There was no evidence of stand disturbance except for the 1938 hurricane, which had caused acceleration in diameter growth of some trees. There was a close correlation ($r^2 = 0.83$) between basal area and crown projection area for these trees as shown in Figure 12 and expressed by the equation:

$$BA = (0.0013 \times SA) + 0.0718$$

where BA = basal area per red oak in the upper canopy stratum at 60 years age; and SA = surface area of a vertical projection of the red oak crown on a horizontal plane. A very similar relation was found by Patton (1922) and Stout (1962).

On a crown map of a stand with a B-stratum of red oaks, the intercanopy area was divided equally among adjacent B-stratum crowns. A low correlation ($r^2 = 0.335$) was found between crown size and amount of ascribed intercanopy area; this area averaged 60.2 square feet (5.6 centares) per tree and varied little with crown size.

By adding this 60.2 square feet (5.6 centares) of intercanopy area to the horizontally projected surface area of each upper canopy tree, the number of trees of any given average diameter which can be grown on an acre can be approximated. Figure 13 shows graphically the estimated change in basal area (BA) per tree and DBH of each B-stratum red oak with the change in number of individuals in a uniform, square spacing.

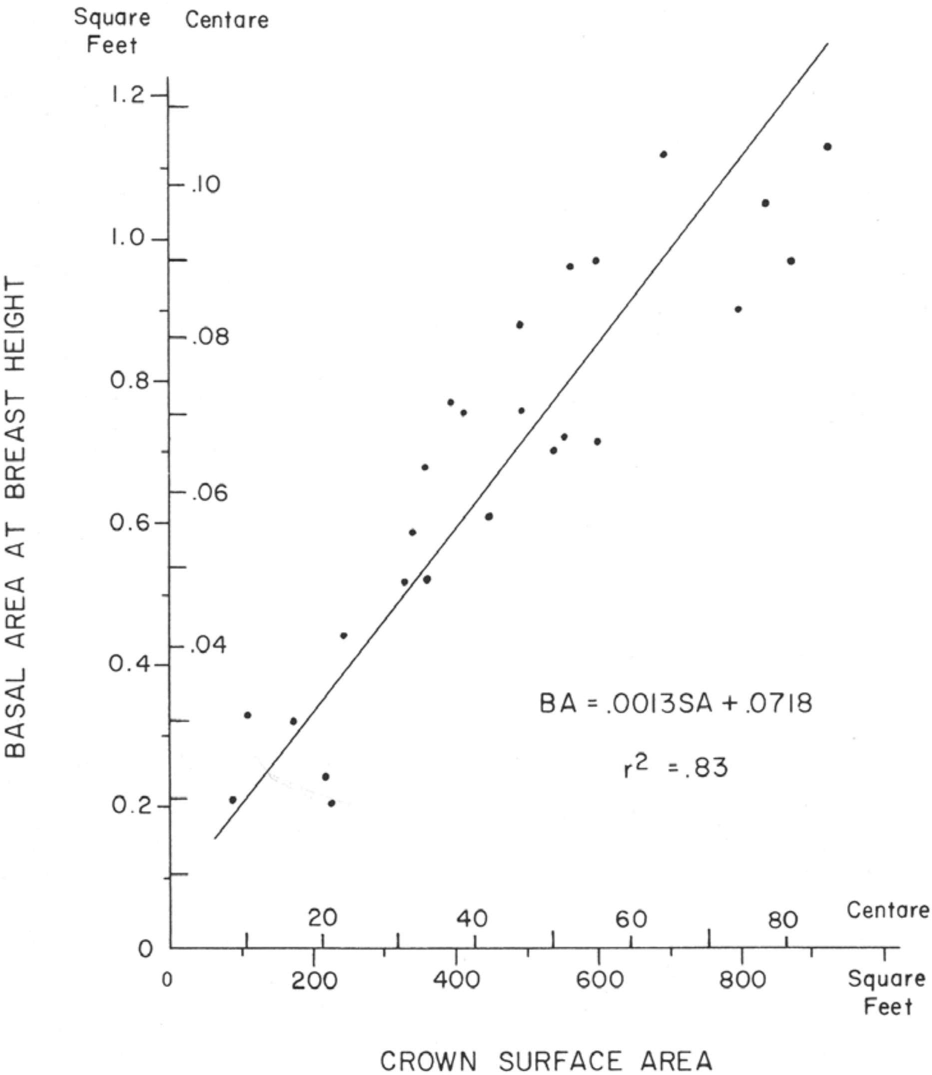

Figure 12. Relationship of basal area to the area of crown surface, projected to a horizontal plane, in red oak trees.

Figure 14 shows the board foot volume per red oak for all red oaks per acre forming a pure B-stratum. These values are based on Figures 13 and 12 and the International ¼ - inch scale (Form Class 78; Forbes, 1955). It also assumes two logs (32 feet; 9.8 m) of merchantable timber per tree-an assumption derived from the earlier observation that the height of the lowest living branch of seven sampled 60-year-old red oaks averaged 36 feet (11 m).

Given these simple assumptions, the beSt board foot volume obtainable at 60 years is with not more than 45 upper canopy red oak stems per acre (111/ha). This also assumes that the oak component had been at this density since age 30. The other portion of the stand, perhaps amounting to 1500 stems per acre (3,672/ha), would be of other species and subordinate to the oaks. Somewhat higher oak stocking may, however, result in greater board foot volumes and better quality material than might be inferred from Figure 14 because competition between the oaks would cause higher pruning and hence longer merchantable boles (Patton, 1922; Gevorkiantz and Hosley, 1929).

This study shows that it is not only unnecessary but undesirable to have large numbers of red oaks in mixed stands. The capacity of the red oaks to emerge after two decades above most associated species results in the same effect as thinning, provided that the red oaks in the mixed stands are not so close together that they compete with each other. The optimum number of red oaks is indeed so small that they are not readily obvious to casual observation among the more numerous associated species during the early stages of stand development.

GENERAL DISCUSSION AND CONCLUSIONS

Possible Causes of Delayed Oak Dominance

Root Systems 0/Associated Species

The average depth of woody lateral roots growing in a deciduous forest follows a pattern of stratification by species, with oaks in the deepest strata (Stout, 1956; Lyford, 1974). The generally deep root

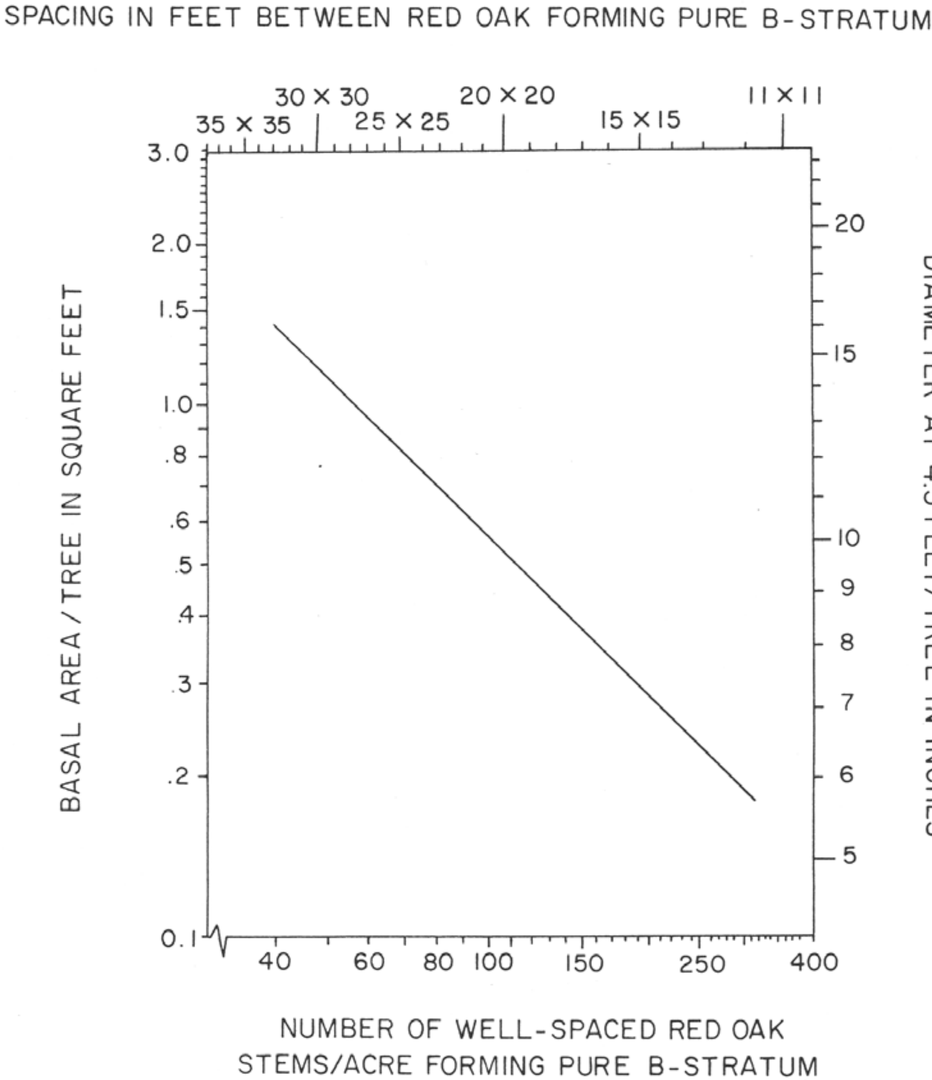

Figure 13. Diameter and basal area expected from northern red oak at 60 years when forming a pure B-stratum if thinned to given spacing (or number per acre) at no later than 25 years.

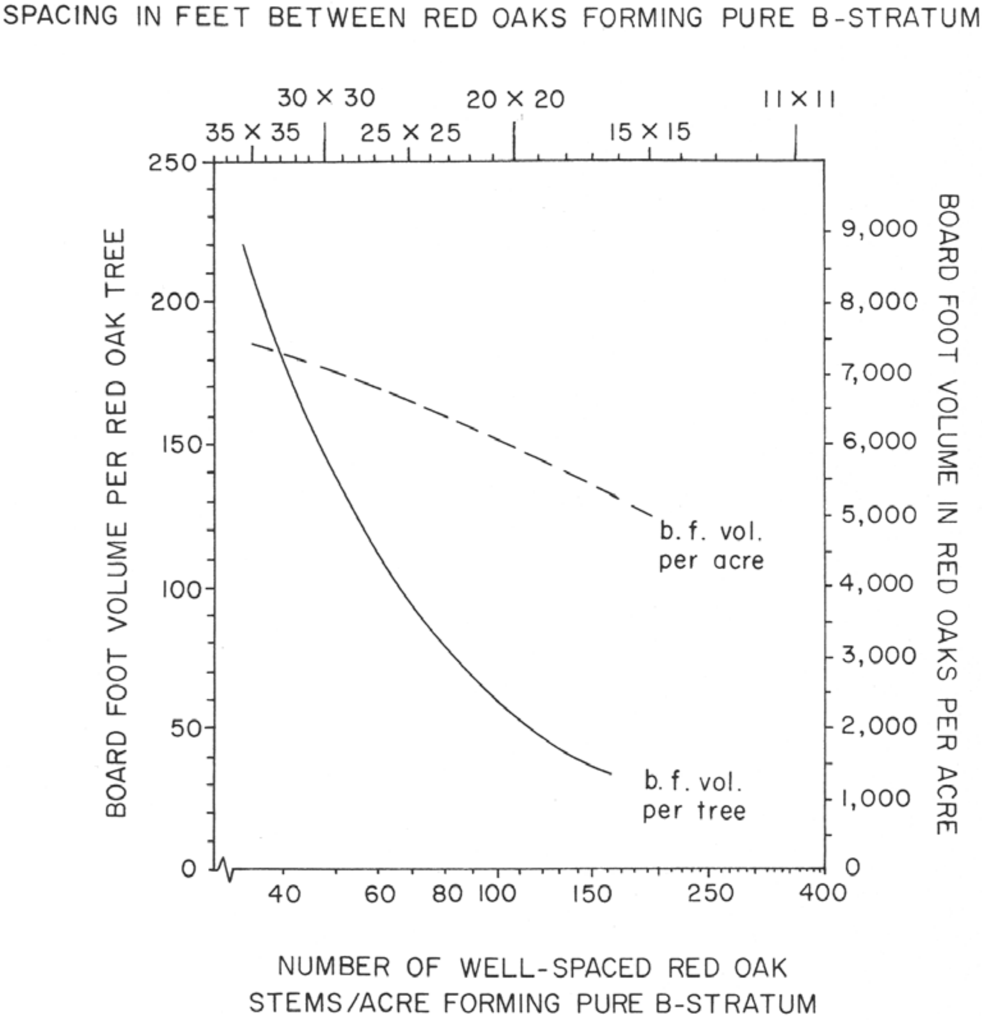

Figure 14. Board foot volume (International 1/4 inch rule, Form Class 78) per tree (solid line and scale on left) and per acre (dashed line and scale on right) of varying numbers of well-spaced red oaks in pure B-stratum when not thinned since 25 years. Based on Figures 12 and 13.

systems of red oak seedlings compared to red maples and black birches may account for their slow initial growth and sustained later growth. Red oak growth may be directed at the development of a deep root system during its early stages rather than at fast shoot growth. Later, the well-developed root system may allow oak to maintain steady height growth longer than its more superficially rooted competitors.

Relative Size of Xylem Vessels

The observation that species such as red maple are tolerant of shade and red oak is intolerant may lie in the relative sizes of the xylem vessels. Ring-potouS red oaks have much larger xylem vessels than do the diffuse-porous red maples and, because of embolization, must add new vessels each year to maintain evapotranspiration flow to the leaves (Zimmerman and Brown, 1971). Diffuse-porous maples can utilize older vessels for more years. Therefore, for red oaks to live they must produce enough net photosynthate each year to add an entire new complement of xylem vessels. Since these vessels are larger than the diffuse-porous maple and birch vessels, the net photosynthate needed to maintain an oak is greater. This larger requirement of dry matter for annual xylem formation may exclude the red oaks from living in the lower strata even though red oaks leaves may be no less efficient than red maples in net photosynthesis at low light intensities. Red maples were observed in this study living in the understory with annual radial xylem increments ofIess than 0.0016 inches (0.04 mm). Even in a dying red oak the smallest such increment was 0.0083 inches (0.21 mm).

The ascendance of the oak may also be triggered by the attainment of a certain diameter since the volume of oak xylem transport, being restricted primarily to the outer ring, would probably be closely influenced by the tree's diameter.

Also, the oak vessels may be instrumental in their more efficient height growth. The larger red oak vessels allow transport in the xylem to occur at a more efficient rate than the small-vesselled maples and birches (Zimmerman and Brown, 1971).

Terminal Growth Patterns

Many red maples and black birches had bayonet-like crooks in their stems where the terminal had died and a lateral branch assumed apical control. Height-age curves indicated a decline or temporary hiatus of height growth at about the time of the terminal death. From studies of the extent of xylem rot at the point of the crook, the terminal death occurred when the red maple and black birch twigs were generally less than 1.5 inches (3.75 cm) in diameter. These deaths were extremely common; bur it was not clear whether they were the result of sporadic episodes of acute damage (such as severe wind or glaze storms or insect ourbreaks) or if they were a quite regular, chronic phenomenon.

Times of breakage could be dated from height-age curves to within approximately three years. The approximate date of each injury to each red maple and black birch sectioned for height in the 60- and 74-year-old stands are shown in Figure 15. The frequency of injuries by years showed the injuries to have occurred on a quite regular basis. Even years of severe windstorms-1938, 1950, and 1954-showed no apparent rise in number of breakages.

Incidence of breakage was chronic rather than limited to a few specific years, but was greatest in the early life of the stands. Part of the chronic breakages may be caused by a combination of wind action and the frequent, minor glaze storms of the region. Red oaks, even with their stronger limbs, may suffer from this injury; however, another bud would more readily assume the terminal growth position than in the cases of maples and birches because the oak terminals assert less apical control than do the others (see Kozlowski, 1971; Zimmerman and Brown, 1971).

The relatively thin branches of birches and maples were observed to batter against the Stour lateral branches of oaks when blown about during windstorms and during ordinary glaze storms accompanied by winds. Such batterings probably contribute to theinjuries to the stems observed in this study. The relatively weak apical control of red oaks allows them to develop large, strong lateral branches which might act to inhibit the height growth of competing vegetation while protecting the terminal buds of the oaks from similar such injury.

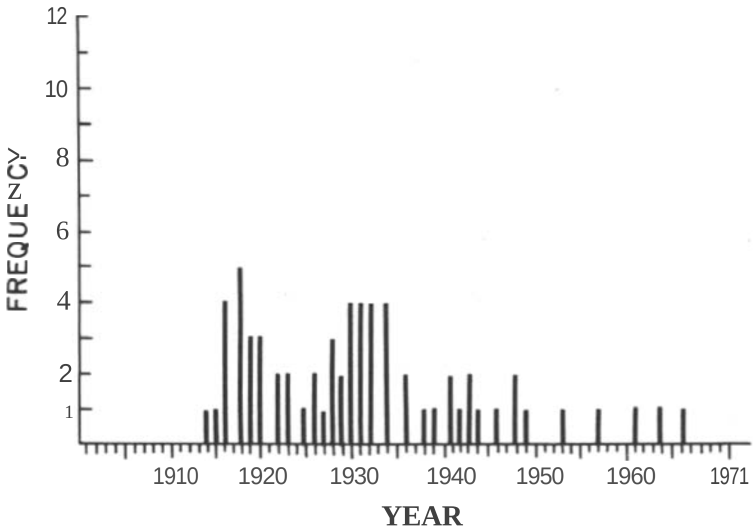

Figure 15. Frequency of black birch and red maple stem injuries for each year in trees sectioned in 60-year-old stands.

Another factor possibly contributing to the terminal breakages in maples and birches is the occasional seed setting and concurrent die-back or growth decline which has been observed in these species (Mello, 1974).

Stratification of Other Species

There also seemed to be a distinct pattern in the temporal and spatial stratification of other species within the stands studied. Height-age curves were developed only for red maples and black birches in their relation to red oaks; however, observations of other species suggest certain patterns.

Aspens seem to make rapid early height and diameter growth but do not live long.

One form of the white-gray birch complex maintains height and diameter growth characteristics similar to red oak for a longer period than do red maple and black birch, as was also observed by McKinnon et al. (935). Another form seemed to behave like an early pioneer and die in the first 20-30 years.

Hickories were not very prominent in these forests but seemed to be emerging into the B-stratum and competing with the red oaks in the 107-year-old stand.

Hemlock, generally relegated to the lower strata, responded to disturbances in the overstory by temporarily increasing its diameter growth rate, as was also found by Marshall (1927) and Lutz (1928).

Sugar maple behaved very similarly to red maple, often accompanying it or even replacing it on the better sites. More than any other species, sugar maple seemed able to germinate and survive at much later times during the life of the stand than other species. These younger saplings grew extremely slowly if not released.

Conclusions

In the even-aged stands of this study, oaks predominated ftom age 30 to age 100 in the larger sizes and superior canopy positions. Although continuously present and relatively few in number, oaks grew to the dominating position sometime after the second or third decade. Before this their small stature and infrequency relative to red maples and black birches easily leads to the assumption that red oak regeneration has been unsuccessful. In a mixed stand oaks did not have as high rate of mortality as the associated species studied.

If the management objective is to produce 60-year-old or older red oaks, they can be grown in even-aged stands. These oaks do not need to be grown in pure stands. In faer, it will simplify intermediate silvicultural operations such as thinnings and ptunings if one simply has a density and spacing of oaks approximating the desired rotation density and spacing (plus an insurance faeror of perhaps 33 percent).

The combination of a few large red oaks and the larger numbers of smaller subordinate trees of other species in the even-age stands studied exhibited a reverse-] -shaped curve of diameter distribution similar to that often ascribed only to all-aged stands.

APPENDIX

Species Stratification in Extensive Areas of Mixed Forests

Four crown strata were recognized, similar to those recognized by Richards (1957):

A stratum (Emergent crown class): those trees with one half of their live crown length above the height of the upper continuous crown canopy (B stratum). They do nOt form a continuous crown canopy and they are not close enough to have contact between lateral branches of other "outstanding" trees.

B stratum: those trees which are neither overtopped by nor subordinated by any tree except emergents. (Definitions of "overtopped" and "subordinated" are listed below.)

C *stratum:* those trees which are subordinated by at least one other tree, but are not overtopped by any.

D *stratum* (OveKopped crown class): those trees which are overtopped by at least one other tree.

A tree was defined as interacting with sample trees chosen by the point-sampling (prism) inventory method if the sample *subordinated* it, *overtopped* it, was *subordinated by* it, or was *overtopped by* it. *Overtopping* was defined as the situation in which the horizontal crown projection of one tree completely covered the crown of another. *Subordination* referred to situations in which trees of lower status were not overtopped but more than half of the horizontal distance from the center to the edge of the crown, along any radius, was covered by the horizontal projection of the upper crown.

Determination of Tree Ages

Age was determined, with adjustments as described below, by counting the nwnber of annual rings in each disk under a dissecting microscope. For ring-porous hardwoods, except for occasional razor cuttings, it was not necesary to smooth surfaces cut with a chain saw. Conifer and diffuse-porous hardwood sections were prepared by sanding with progressively finer sandpaper and sometimes steel wool. Where necessary, petroleum jelly was used to make the rings more visible. The width of each annual ring was then recorded by measuring each ring along an average radius using an Addo-X tree ring counter.

Rings or parts of rings may disappear near the basipetal portion of the trunk of suppressed trees (Larson, 1956; and Bormann, 1965). To determine more accurately the age near the base of the suppressed trees which were sectioned every four feet for their entire height, the following method was developed:

1. For each section measured, the radial width of each annual ring was plotted on the vertical axis; and the number of rings (roughly the age) away from the present cambium was plotted on the horizontal axis (Fig. 16).
2. Graphs of consecutive sections were placed above the next lower ones on parallel horizontal axes, and with the zeroes (cambial ring) of the horizontal axes in a vertical line, as can be seen in Figure 16.
3. Beginning with the uppermost section, patterns of large and small annual radial growths were observed. These patterns were traced to the next lower section, where the outer portions were less distinct. Patterns from inside rings not even present in the higher sections were found and traced to the lower sections where the outer patterns had become obscure. The number of years lost in counting because of small or disappeared rings could be traced from the top (where the outer rings were present) through progressively inward patterns. An example of four sections from a tree thus traced is shows in Figure 16.

For those stems sectioned only at one foot and 4.5 feet, the ring patterns were compared between the two sections.

Relation of Diameter Inside Bark to Diameter Outside Bark for Each Species Studied

For each species, trees were sectioned and measured inside and outside of the bark. Regression analyses of the natural log of the outside bark diameter (y) versus the natural log of the inside bark diameter (x) were performed to generate equations to be calculated in millimeter units.

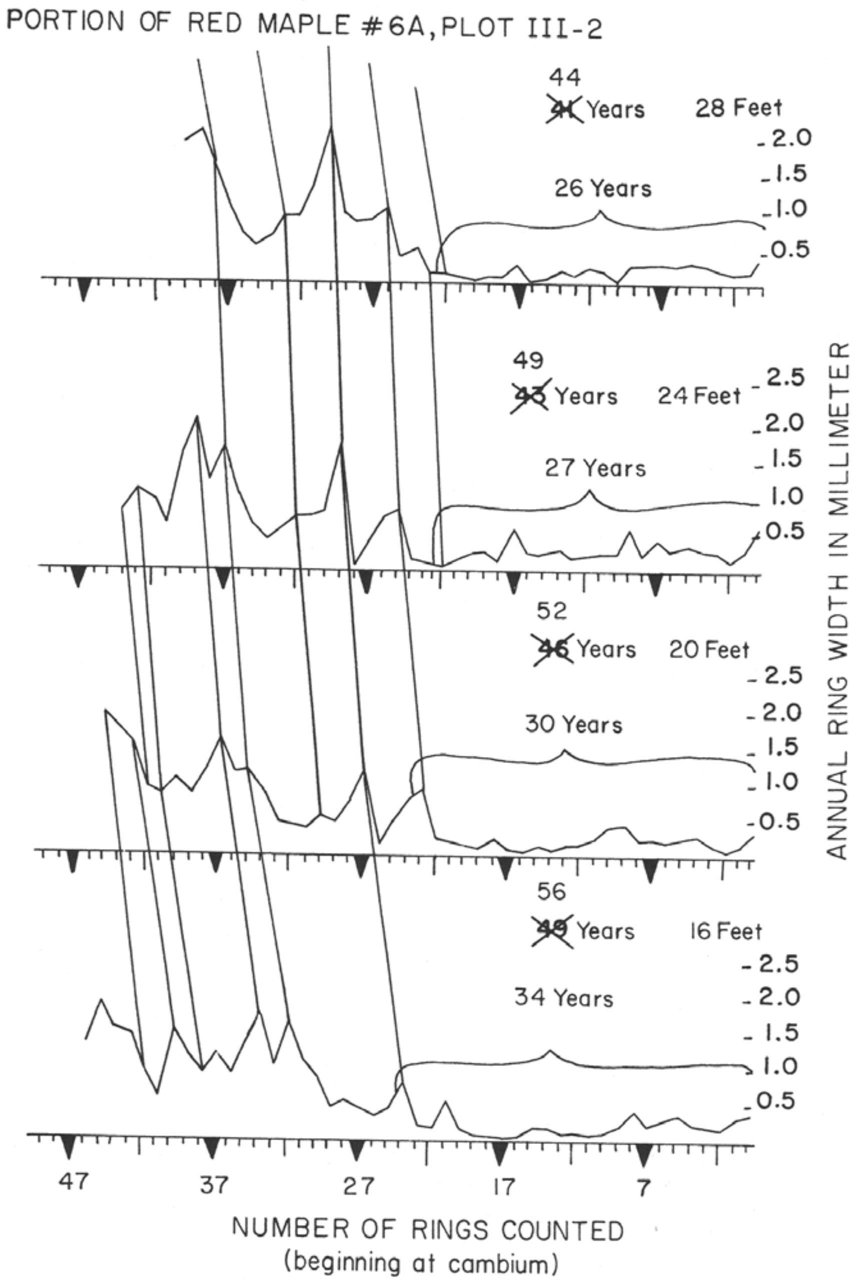

Figure 16. Example of method of determining age from sequential sections of a tree stem where lower outer rings may have disappeared or been miscounted because of their small size.

The equations followed the form:

$$y = Ax^E,$$

where A and E are as shown in the following table for each species studied. The lowest value of r^2 for any of the species was 0.988 and the standard errors of the residuals, expressed as percentage of the means, ranged from 0.4 to 1.3%.

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APPENDIX

Species	A	E	Nwnber in Sample	Range of DIB (mm)
Ash, white (*Fraxinus americana* 1.)	1.2049	0.9846	138	6.4-94.0
Aspen, Big tOoth (*Populus grandidentata Michx.)*	1.6119	0.9203	52	10.7-230.1
Birch, black (*Betula lenta* 1.)	1.2050	0.9781	159	14.2-254.1
Birch, grey and paper (*Betula populi/olia* Marsh. and *Betula papyri/era* Marsh.)	1.2381	0.9689	99	4.3-164.5
Birch, yellow (*Betula alleghaniensis* Britton)	1.2762	0.9601	99	7.3-164.0
Cherry, black (*Prunus serotina* Ehrh.)	1.1822	0.9803	116	6.8-113.8
Hemlock, eastern (*Tsuga canadensis* (1.) Carr.)	1.2594	0.9692	69	8.1-347.2
Hickory (*Carya* spp.)	1.2167	0.9833	148	17.9-80.2
Maple, red (*Acer rubrum* 1.)	1.1896	0.9748	354	5.6-286.0
Maple, sugar (*Acer sacchamm* Marsh.)	1. 1418	0.9887	112	8.0-277.5
Oak, black (*Quercus velutina* Lam.)	1.3609	0.9596	91	7.8-340.0
Oak, northern red (*Quercus rubra* 1.)	1.2821	0.9676	263	7.5-463.8
Oak, white (*Quercus alba* 1.)	1.5348	0.9279	65	28.6-218.0
Pine, eastern white (*Pinus strobus* 1.)	1.404	0.9458	86	7.1-154.7

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