

GROWTH

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This chapter considers aspen growth as a process, and discusses some characteristics of the growth and development of trees and stands. For the most part, factors affecting growth are discussed elsewhere, particularly in the GENETICS AND VARIATION chapter and in chapters in PART II. ECOLOGY. Aspen growth as it relates to wood production is examined in the WOOD RESOURCE chapter.

LIFE-TIME PATTERNS

In the West, a stand of aspen may persist for more than 200 years. On a good site in southwestern Colorado, sample dominants in one stand averaged 215 years old and 107 feet (33 m) tall. The stand was still intact but had a very high decay frequency. That study (Jones 1966, 1967b) included 71 plots in mature and overmature aspen, mostly in Colorado but with a few plots in northern New Mexico and Arizona. The age-class distribution was as follows:

Age (years)	Number of plots
< 60	1
60-79	12
80-99	22
100-119	12
120-129	8
140-159	6
160-179	6
180-199	2
≥ 200	2

Although that was not a random sample, it gives some idea of the ages of mature and overmature stands encountered in Colorado, New Mexico, and Arizona.

In the Lake States, aspen lives notably longer on good sites than on poor sites (Zehngraff 1947, 1949; Graham et al. 1963; Fralish 1972). This also has been reported in the West (Baker 1925).¹ But on at least some poor western sites, aspen stands survive a long time. Of the 10 plots (Jones 1966, 1967b) in stands 160 years or older, 3 had site indexes that were rather poor by Colorado standards. Strain (1964) reported an uneven-aged stand in California's White Mountains with a sample tree 226 years old and only 39 feet (12 m) tall. That indicates a very poor site; however, it has what seems to be the oldest reported quaking aspen. Greene (1971) sampled clones in Colorado over a gradient from 5,500 to 11,250

¹USDA Forest Service. 1962. *Timber management guide for aspen*. 14 p. USDA Forest Service, Rocky Mountain Region, Denver, Colo.

feet (1,700 m to 3,400 m) elevation. Her data suggested that although aspen may live longer near timberline, growth was very slow there because of the short growing season.

Height Growth

The result of a lifetime of aspen growth can vary from a shrub in the Colorado krummholz to a tree in central Utah 120 feet (37 m) tall and 54 inches (137 cm) d.b.h. (Harlow and Harrar 1958). Beetle (1974) reported that in Jackson Hole, Wyo., aspen seldom grows taller than 60 to 70 feet (18 m to 21 m), or in marginal climates 20 to 40 feet (6 m to 12 m). Baker (1925) described a stand in central Utah as representative of better stands in the region. Its dominants averaged 64 feet (20 m) tall at age 80 and 75.5 feet (23 m) at 150. In a few southwestern areas, trees taller than 100 feet (30 m) are common, notably in the White Mountains of eastern Arizona and part of the San Juan Mountains near Pagosa Springs, Colo. Aspen taller than 90 feet (27 m) are frequent in various parts of the San Juans, in the Jemez Mountains of northern New Mexico, and on the San Francisco Peaks in northern Arizona. Aspen occasionally reaches these sizes elsewhere in the West (Hofer 1920).

Early Growth Rates

Stem analyses of mature and overmature dominants on Jones' (1967b) 71 plots show that most took 2 to 5 years to reach breast height (4.5 feet (1.5 m)); but some had taken only 1 year. A few had taken more than 5 years, perhaps because of dieback, browsing, or competition from shrubs, herbs, or residual overstory.

Dominant saplings on a 4-year-old Arizona clearcut averaged 10.5 feet (3 m) tall, and most were only three summers old (Jones 1975). The tallest, four summers old, was 17.4 feet (5 m). That was better than juvenile growth determined on other southwestern areas by stem analysis of mature dominants, and indicates the growth rate that can be attained under good circumstances (Jones 1975). Some of the dominants came up the same summer after the spring cut. Their first-year growth averaged somewhat less than that of dominants which came up the following year (fig. 1); but 3 years later, they still had a greater average height because of their earlier start. The greatest growth made by any sucker during its first summer was 4.9 feet (1.5 m).

However, early (1-5 years) height growth of aspen is not necessarily an indication of later growth potential of a stand. Jones and Trujillo (1975a), examining dissected

stems of trees from a well-stocked 22-year-old Arizona stand, found that trees on poorer sites reached 10 feet (3 m) tall almost as soon as those on good sites. On several sites in Colorado and the Southwest, Jones (1967b) found only a weak correlation ($R = 0.41$) between the height of dominant aspen at age 80 (site index) and the number of years it had taken them to reach breast height.

Site Index as a Measurement of Growth

For stands beyond the small sapling stage, site index is commonly used to represent the course of height growth for the dominant aspen trees in the stands of a given region. Site index curves are generalized regional representations and are unlikely to portray the growth curves of a specific site or stand very closely (Spurr 1952, 1956).

Baker (1925) presented a table of height-age coordinates for four aspen site classes in the Interior West. They were developed about 1912, mostly from measurements made on a single watershed. The methods widely used in later years to develop site index curves had not yet been described. Baker's height-age coordinates did not, nor were they intended to, represent the curves of height growth for any actual or hypothetical stand.

Jones (1967b) dissected many dominant aspens in the southern Rocky Mountains and reconstructed the course of their height growth. Each of his site index curves (fig. 2) is based on height-age data from plots whose dominant heights at age 80 were near the age-80 height for that site class. Curves were smoothed with the help of data from adjacent classes. Age was defined as the number of rings at breast height. This avoided the poor relationship of initial growth to apparent site quality, as well as the problems of counting rings at the base of trees with butt rot. The curves are available as an equation for computer application (Brickell 1970) and as a table for easy field and office use (Jones 1966).

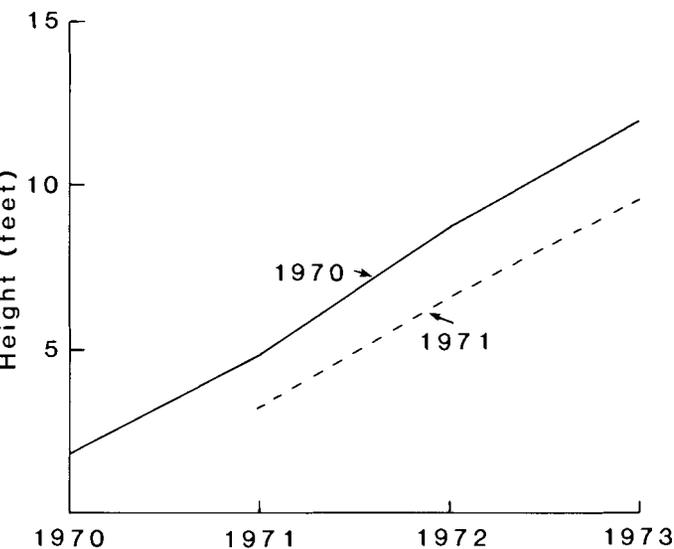


Figure 1.—Height growth of dominant 1970- and 1971-origin suckers on an Arizona clearcut (Jones 1975), Apache National Forest.

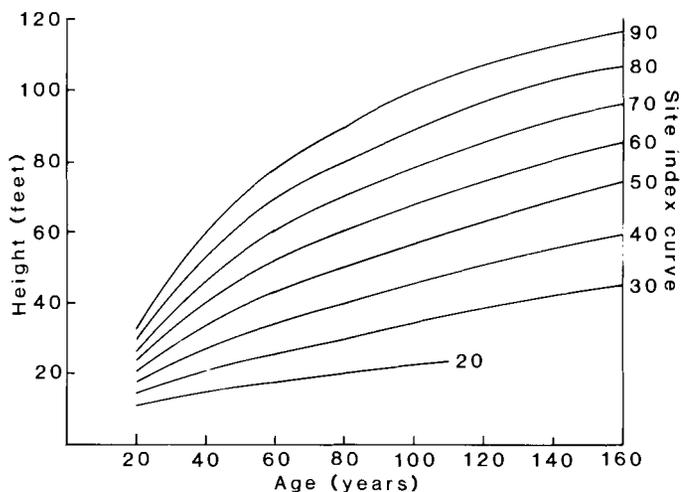


Figure 2.—Aspen site index curves for Colorado and New Mexico, using breast height age (Jones 1967b). The index age is 80 years.

The shape of actual plot curves varied from these. In figure 3, comparison of Plots 14 and 71, and of Plots 12 and 69, show how different heights at maturity may be on plots where heights had been similar at age 30 or 40. Each plot probably was within a single clone.

Even stands that grow rapidly in height the first few decades often grow somewhat more slowly in height at maturity. The factors which cause height growth to slow as stands get older may be related more to the size than the age of trees.

The difference in mature height between some tall stands and some that are much shorter sometimes results entirely from large differences in immature height growth. Later growth rates may be quite similar. This is reflected in Jones' (1967b) site index curves (fig. 2), which are roughly parallel beyond the index age (80 years).

Diameter Growth

There is little information on patterns of diameter growth in aspen. Presumably, progressive crown or root deterioration results in markedly reduced diameter growth near the end of a tree's life. But there is no strong evidence that diameter growth of healthy, dominant aspen declines substantially with age.

At least during the first few decades, changes in the diameter growth of dominant trees seem to be short-term responses to external factors instead of forming a strong, age-conditioned pattern. Various workers, for example Churchill et al. (1964), have documented the severe diameter growth reduction in aspen caused by outbreaks of defoliating insects. Such reductions typically are followed by complete recovery. In Michigan, Graham et al. (1963) described periods of intensifying competition between immature canopy trees. These periods, ending with marked mortality, cause short-term diameter growth fluctuations which tend to obscure any possible long-term patterns.

In subordinate crown classes, however, diameter growth rates decline over time. This reflects not age, but decreasing availability of growth requisites as competitive position deteriorates. In an Arizona study (Jones and Trujillo 1975a), 22-year-old intermediates had been codominants earlier, and some were dominants before that. With each reduction in competitive position, their supply of sunlight and perhaps also of water and nutrients became less, and relative ring widths decreased. Trees that became overtopped formed still narrower rings; and, during their final years, these light-deprived trees formed rings that were barely visible under a microscope.

In a particular year, weather may cause exceptionally good or poor diameter growth. In widespread samples from throughout the southern Rocky Mountains, Jones (1967b) found that on a given plot, the rings for certain years were notably wider or narrower than the several rings on both sides. Often there were several such distinctive rings common to every sample dominant on a plot.

Aspen diameter growth is not related to site the same way that height growth is. A stand may have much larger diameters, yet, may be considerably shorter than another of similar age (fig. 4). The site characteristics that limited heights on Plot 15, in comparison to heights on Plot 14, did not limit relative diameter growth. Stand density has only a modest effect on the final diameters of dominants (see the INTERMEDIATE TREATMENTS chapter).

SEASONAL PATTERNS

Shoot Growth

Aspen buds begin to swell during the first warm period in spring, when minimum temperatures are still below freezing (Ahlgren 1957). Photoperiod is not a critical factor in determining the timing of bud opening. The beginning of bud activity may vary several weeks

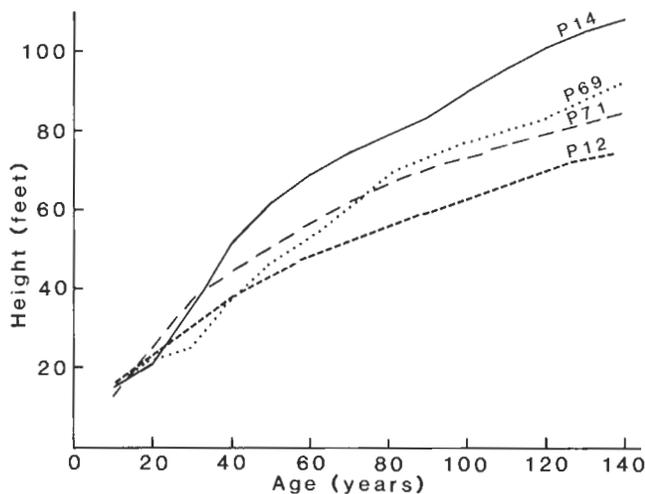


Figure 3.—Later height divergence on plots with similar heights at age 30 (Plots 14 and 71) and age 40 (Plots 69 and 12).



Figure 4.—Diameter comparison of two stands. The scale board above the plot numbers is 2 feet (61 cm) long. Each sample dominant on Plot 15 (bottom) exceeded 24 inches (61 cm) d.b.h. at 137 years, with an average height of 84 feet (26 m). No tree on Plot 14 (top) was larger than 20 inches (51 cm) d.b.h. at 148 years, although the sample dominants averaged 110 feet (34 m) tall. Apache National Forest, Arizona.

from one year to the next, depending on the weather. Warm weather early in the spring will advance the time of flushing; cold weather will retard it. Adjacent clones may show marked differences in timing and progression of leaf flushing (Barnes 1969).

Observation suggests that at typical aspen elevations in Colorado and the Southwest, aspen commonly leaf out in late May or early June, depending on locale and clone. In a southern Wyoming study at 8,700 feet (2,650 m), aspen leaves were unrolled but not fully expanded on June 1 (Strain 1961, Strain and Johnson 1963). In south-central Utah, Dixon (1935) reported that the highest elevation aspen observed, a dwarfed gnarled stand at 10,000 feet (3,050 m), was just leafing out on June 21. In northwestern Wyoming, Beetle (1974) noted that new terminal growth in aspen began in early to late June, depending on year and site. On the east slope of the Front Range in Colorado, Greene (1971) found that low-altitude (below 7,000 feet (2,150 m)) clones generally leaf out in early May, middle-altitude (8,000 to 10,000 feet (2,450 m to 3,050 m)) clones in late May or early June, and high altitude (above 10,500 feet (3,200 m)) clones at the end of June.

Observing shoot development of 60 aspen clones from 9,800 to 10,200 feet (3,000 m to 3,100 m) in elevation, on a southeast facing slope in northern Colorado, Egeberg (1963) found that more than 3½ weeks elapsed between the times the first and last clones flushed out. This wide clonal variation in timing of bud break resulted in clonal differences in susceptibility to frost damage.

Genetics strongly influence duration of shoot growth in aspen, which generally correlates with the frost-free season prevailing in the native habitat of each clone. Day length appears to determine duration of height growth. Clones from high latitudes or high elevations are among the first to cease growing and form terminal buds. Maini (1968) reported that basal branches ceased growth first; some 3 to 4 weeks later the branches in mid-crown stopped growing; and finally, some 3 or 4 weeks still later, the terminal stopped growing.

There is limited information on when shoot extension in western aspen ceases. Observation of trees in yards in Logan, Utah, indicates that bud set occurs in late July or early August. Strain (1961) found that aspen on a poor site in southern Wyoming ceased growing in height by June 26. In the Upper Peninsula of Michigan, the average period of height growth was about 80 days (Strothman and Zasada 1957). In Utah, Schier (1978c) found that 2-year-old aspen ramets were fully dormant by late August, as indicated by the failure of axillary buds to break following defoliation. (The shoots of dormant aspen require a cold period before they resume growth.)

Cambial Growth

Five to eight layers of undifferentiated cells overwinter in the cambial zone of aspen (Davis and Evert 1968). In the Lake States, cells on the phloem side of the cambial zone begin to divide in late March or early

April. Early cell division proceeds relatively slowly and primarily produces phloem. When xylem begins forming in mid-May, cambial activity increases and reaches a maximum in late May and June. Cambial activity drops sharply in early July; and by the end of July or early August dividing cells can no longer be found.

Cambial activity in bigtooth aspen (*Populus grandidentata* Michx.) begins about 3 weeks before the buds leaf out (Wilcox 1962). Brown (1935) reported that cambial activity in quaking aspen (*Populus tremuloides* Michx.) begins immediately below the leaf buds as they begin to swell, then progresses gradually down the stem and outward toward the root tips. It reaches the base of the trunk about the time the leaves emerge (Ahlgren 1957, Brown 1935), varying with the distance from the leafy crown to the tree base (Brown 1935). Cell division in the cambium probably is triggered by auxins from the elongation of new shoots (Wilcox 1962), which begins after the small early leaves have expanded (Strain 1961).

Cambial activity in aspen ends in different parts of the tree in the same order that it starts, stopping first in the twigs and persisting longest in the roots (Brown 1935). In general, the fastest growing trees have the longest growing season (Kozlowski and Winget 1962b).

SHOOT TYPES

Aspen trees have two types of shoots: short shoots and long shoots (Critchfield 1960, Kozlowski and Clausen 1966, Pollard 1970b). Short shoots are preformed or predetermined in the winter bud. Their growth is fixed, because it is completed when the preformed stem units have elongated. Growth of long shoots involves the elongation of preformed stem units, followed by a period of free growth during which new stem units begin and elongate simultaneously. Short shoots complete their growth during a brief period in the spring, whereas long shoots may continue elongating until late summer. Lateral long shoots vary from those growing slightly longer than short shoots to those growing as much as the terminal shoot.

The occurrence of both fixed and free growth in aspen results in leaf dimorphism (Critchfield 1960). The two basic types of leaves are called "early" or "late" depending on their time of initiation and differentiation. Both leaf types grow on long shoots (for this reason they are called heterophyllous shoots), whereas short shoots have only early leaves. Early leaves are embryonic leaves in the winter bud, and are the first set of leaves that appear in the spring (Critchfield 1960). The first late leaves are also present in the winter bud, but are arrested primordia. Succeeding late leaves begin and develop during free growth. Late leaves vary in shape more than early leaves and have gland-tipped teeth along their margins, which are lacking in early leaves (Barnes 1969).

The tendency for free growth and production of heterophyllous long shoots diminishes as the tree ages. The terminal and main lateral shoots of young aspen are comprised almost entirely of long shoots. As the crowns

increase in size, short shoots soon outnumber long shoots, and most of the foliage consists of early leaves. Pollard (1970b) found that long shoots made up 13% of the canopy in a 6-year-old stand, whereas they made up only 6% of the canopy in a 15-year-old stand. There were no long shoots at all in a 52-year-old stand. Kozłowski and Clausen (1966) also found that all shoots of adult aspen were preformed, and, therefore, all leaves were of the early type.

Aspen shoots normally do not begin branching until the second year. Elongation of lateral buds on the current year's growth is inhibited. Strain (1964), however, reported that suckers from an exceptionally shrubby clone branched during their first summer.

Free growth of leaders and many lateral shoots enables young aspen to grow rapidly and develop a canopy in a few years. Continuing height growth and branch extension far into the summer on good sites is not shared by any of the associated conifers, making aspen's rapid juvenile growth and stand development unique among the upland forest species in the Interior West.

PHOTOSYNTHESIS AND GROWTH

Aspen is classified as very shade intolerant when compared to other North American tree species (Baker 1949). Aspen's inability to survive under shade results from a low ratio of photosynthesis to respiration under low light intensity (Bazzaz 1979). Tolerant species have a more favorable carbon balance under low light than aspen, because they have higher photosynthetic rates and/or lower respiration rates.

Loach (1967) found that hardwood species ranging from very tolerant (beech) to very intolerant (aspen) all had lower photosynthetic rates in the shade. Respiratory adaptations to shade, however, were not similar. Leaves of tolerant species showed reduced respiration rates in the shade, but those of aspen did not.

Farmer (1963a) found that temperature regime has an important effect on response of aspen to low light intensity. Reduction of light intensity from 1,700 to 500 foot-candles reduced both height growth and dry weight increment at a 76°F (24°C) day/71°F (22°C) night regime. At a cooler regime (70°/66°F) (21°/19°C), however, dry weight increment was reduced, but height growth was not.

Attached aspen leaves attain their light saturation point at about 3,000 to 3,500 foot-candles (Loach 1967, Okafo and Hanover 1978). At this light intensity Okafo and Hanover (1978) found that the average net photosynthesis rate of Michigan aspen was 33.9 mg CO₂ dm⁻² hr⁻¹. There was considerable variation between genotypes. It ranged from 10.4 to 50.4 mg CO₂ dm⁻² hr⁻¹. Net photosynthesis rates for individual leaves exceeded the rates observed for the whole seedling by about four times. This was a result of mutual leaf shading and the occurrence on whole seedlings of young and old leaves, both of which have lower rates of photosynthesis.

Because aspen produces new leaves over the entire growing season, the tree uses both reserves and cur-

rently synthesized carbohydrates for apical growth. The amount of current photosynthate utilized in shoot expansion depends upon the relative timing of leaf development and internode elongation. For about 2 weeks after spring bud break, elongating shoots largely depend upon reserve carbohydrates that move upward from storage tissue in stem and branches (Donnelly 1974). First-developing leaves begin to photosynthesize soon after bud break; but they assimilate and respire more metabolites than they produce. They begin to export substantial amounts of photosynthate when they are about 50% of their full size. More than half of the photosynthate is at first transported to the developing shoot, where it is utilized in internode elongation and in the expansion of terminal leaves. Then, as other leaves closer to the stem tip begin exporting photosynthate, meristems below the developing shoot become the major sinks for carbohydrates from the first formed or basal leaves.

There is a seasonal change in the relative proportion of photosynthate transported from the leaves to the stem tip and to the lower stem and roots (Donnelly 1974). Early in the growing season, most of the photosynthate is transported to vigorous sinks in developing shoots and leaves. As the season progresses, the downward translocation of photosynthate increases because of the increase in number of leaves exporting photosynthate and the decline in rate of shoot elongation. Channeling of photosynthate to the roots during the second half of the growing season is indicated by the buildup of carbohydrate concentrations in the roots (Schier and Zasada 1973).

The occurrence of chloroplasts in phelloderm and cortical parenchyma cells of the bark enable aspen stems and branches to carry on photosynthesis (Barr and Potter 1974). Foote and Schaedle (1976) reported that in 5- to 7-year-old aspen stems gross photosynthesis ranged from 0.0 mg CO₂ dm⁻² hr⁻¹ on winter days when the temperature was below 27°F (-3°C) to 5.5 mg CO₂ dm⁻² hr⁻¹ in July. The stem was not capable of net photosynthesis; but the respiratory loss of CO₂ from the stem was reduced all the way to zero, depending on the time of year and the level of illumination. Photosynthate produced in the bark is transported laterally in rays to xylem, phloem, and cambium (Shepard 1975).

The annual contribution of bark photosynthesis to the carbohydrate supply of a tree has been estimated to be only 1-2% (Foote and Schaedle 1978). This small contribution, however, may not reflect the actual importance of bark photosynthesis in satisfying the respiratory needs of the stem for maintenance and biosynthesis. During periods of high insolation, bark photosynthesis nearly equals stem respiration and could increase the chances of recovery of stressed trees after insect defoliation or after a severe late spring freeze.

DISTRIBUTION OF GROWTH WITHIN THE TREE

Diameter growth of woody stems typically is greatest near the source of photosynthates. In forest trees this is within or at the base of the live crown. Aspen is no ex-

ception. The annual diameter growth of the bole of mature Wisconsin aspen was considerably greater at 19 feet (6 m) than at 4.5 feet (1.5 m), with most of the difference developed late in the growing season (Kozlowski and Winget 1962b). In New Brunswick, "relatively young" aspen growing in the open had maximum ring widths for the year within the first five internodes from the apex (McDougall 1963). Jones and Trujillo (1975a) found that, in 22-year-old Arizona aspen, maximum diameter growth occurred in the upper bole within the crown.

Most of the aboveground biomass of mature aspen trees is made up of woody bole, bark, and branches. A sampling of trees in northern Utah and western Wyoming (Johnston and Bartos 1977) showed that the woody bole made up 50% or more of the aboveground biomass, the bark from 20% to 25%, and live branches from 10% to 17% of the biomass. The dry weight ratio of branches to bole decreases modestly with age (Schlaegel 1975a, Zavitkovsky 1971). The branch-to-bole ratio is greatest in dominants.

Much less is known about root growth than about top growth. Almost 20% of the total biomass of 40-year-old aspen consisted of roots greater than 0.2 inch (5 mm) diameter (Alban et al. 1978). Apparently the proportion of the tree that is below ground declines with age (Young and Carpenter 1967). Young trees 10 feet (3 m) tall had a ratio of 0.46, those 20 feet (6 m) tall 0.31, and older trees 35 feet (11 m) tall only 0.25. From an exploratory study in a small aspen population, Young et al. (1964) found that, for a given diameter, the taller trees have the greater root-to-top ratios; and, for a given height, trees with larger diameters have smaller ratios.

STAND DEVELOPMENT

Uneven-aged aspen stands are common in many western areas, but their growth has not been studied (see the MORPHOLOGY chapter).

The development of even-aged stands has not received much attention aside from the yield studies that are reviewed in the WOOD RESOURCE chapter. The following generalized characteristics of even-aged stand growth are based on findings from the Great Lakes region (Graham et al. 1963, Pollard 1971), and a few western case histories (Jones 1975, Jones and Trujillo 1975a):

1. Rapid sucker growth. Early sucker growth ranges from less than 1 foot (30 cm) to more than 3 feet (1 m) per year for shoots having good competitive position. Rapid extension of lateral shoots on suckers more than 1 year old accompanies leader growth and results in early crown closure.
2. Quick definition of crown classes. After the canopy closes, trees stratify into crown classes quickly, despite genetic uniformity within clones (fig. 5). There is a fairly continual adjustment of trees to growing space, and a loss in competitive position of many trees making up the codominant, intermediate, and overtopped classes.

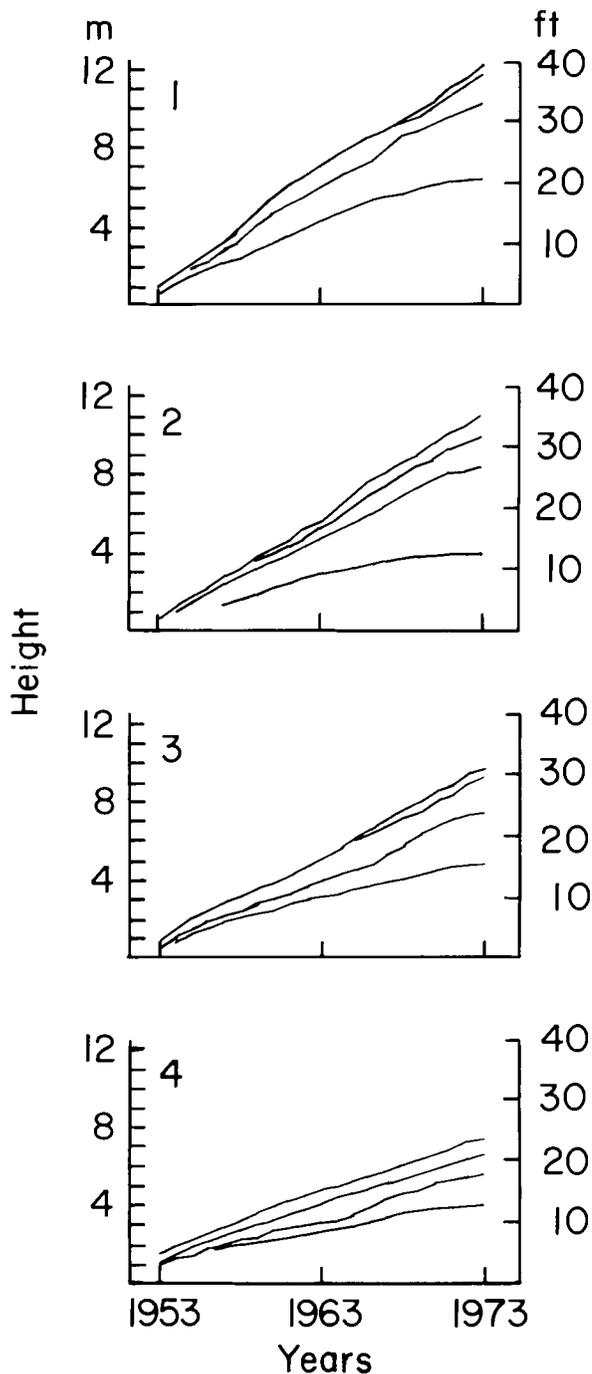


Figure 5.—Height growth curves for each live crown class on four Arizona plots (Jones and Trujillo 1975a).

3. Rapid natural thinning. When competition becomes intense enough to appreciably affect the diameter growth of dominants, mortality quickly reduces the number of trees in the lower crown classes. There are periodic surges in mortality, with a disproportionate number of trees, mostly those overtopped, dying within a short time. The adjustment in stocking may be severe enough to reduce dry weight increment for a time. Diameter growth, however, shows strong recovery with reduced competition.