

GENETICS AND VARIATION

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The broad genotypic variability in quaking aspen (*Populus tremuloides* Michx.), that results in equally broad phenotypic variability among clones is important to the ecology and management of this species. This chapter considers principles of aspen genetics and variation, variation in aspen over its range, and local variation among clones. For a more detailed review of the genetics of quaking aspen, especially with wider geographic application and with emphasis on tree breeding, see Einspahr and Winton (1976).

General Principles

Cytogenetics

Aspen is typically dioecious—forming either male or female flowers on a tree, but seldom both. The haploid number of chromosomes in the gametophytes formed in these flowers is 19. Through sexual union, the nucleus in the cells of the resulting sporophyte (tree seedling) has a diploid number of chromosomes—38 in aspen (Einspahr and Winton 1976).

Sometimes the normal process of chromosome splitting and recombining during cell division goes awry. This can result in triploid, or even tetraploid or monoploid sporophytes. Polyploidy occurs in aspen, and can be induced for breeding purposes (Einspahr and Winton 1976). Triploid trees (clones) at times occur in nature.

Hybridization

Quaking aspen crosses readily with other species of *Populus* within the section *Leuce*, producing hybrids. Where quaking aspen grows near bigtooth aspen (*Populus grandidentata* Michx.) (Barnes 1961) or near introduced species, hybrids sometimes occur (Einspahr and Winton 1976). Quaking aspen also has been hybridized with other species, particularly *P. tremula*, *P. alba*, and *P. canescens* in tree breeding programs (Einspahr and Winton 1976).

Population Genetics

A population persisting in an environment has become genetically adapted to survive there. A species growing in a wide variety of environments exhibits genetic variation associated with the pattern of environmental variation (Spurr and Barnes 1973). Typically, tree species have a clinal or continuous pattern of genetic variation.

The term “aspen ecotypes” often is used. Ecotype implies a degree of genetic discontinuity between one population and other populations of the species, as distinguished from the more continuous variability across a cline (Ford-Robertson 1971, Society of American Foresters 1958, Spurr and Barnes 1973). The pattern of genetic variation in aspen, however, appears to be clinal. Therefore, the term “ecotype,” although commonly used in reference to aspen, is not entirely correct.

Genetic differences among populations usually reflect existing environmental differences, especially day length and other similar environmental gradients across the cline. They also can reflect past differences, past or current introgression of genes from other species, and genetic changes that accompanied past or existing barriers to gene flow.

Some selection of genotypes can be expected by different environments within a region, and even within a localized area, such as different elevations. However, even where local environmental differences are large, populations usually do not differ as much as those on different parts of the continent because of past gene flow between local sites.

Aspen has certain peculiarities that may have affected its evolution and certainly affect its ecology and management. In the West, a whole aspen stand may be a single genetic entity—a clone (see the MORPHOLOGY chapter). If clones are large, some areas with considerable acreage of aspen, therefore, may have only a few individuals (clones) available for sexual reproduction (Strain 1964).

In much of the West, even where there are many genotypes, the rarity of successful sexual reproduction results in restricted gene recombination, and, therefore, very limited selection of new genotypes in current environments. Local populations of aspen genotypes are virtually fixed on most western aspen sites.

Given occasional fire or comparable disturbance, aspen clones (genotypes) perpetuate themselves readily and abundantly by root suckering (see the VEGETATIVE REGENERATION chapter). Cottam (1954) suggested that most current clones in the Great Basin are at least 8,000 years old. Barnes (1975) speculated that an occasional Utah and Colorado clone may have originated as a seedling during the Pliocene, surviving the intervening 1 million years or more by suckering. Suitable conditions for widespread aspen seedling establishment apparently can be thousands of years apart without serious genetic impoverishment.

Except during periods of widespread seedling establishment, there may be essentially no competition between aspen genotypes except along clonal boundaries. There is no genetic competition within a stand of pure

aspen consisting of a single clone. Such a clone may not be as well adapted to its site as are other clones in the vicinity. But it became established under a set of previous conditions; and, once established, it was well enough adapted to persist.

Geographic Variation

Pauley et al. (1963a, Pauley 1963) grew quaking aspen seedlings in Massachusetts from seed sources throughout most of its range. Seedlings of Lake States origin survived and grew as well as seedlings from local New England sources. But western seedlings from a large range of latitudes (Arizona to the Yukon Territory) were weak, and almost all died by age 12. Daylength at different latitudes is important, as shown by Vaartaja (1960), who compared seedlings from Wisconsin and northern Saskatchewan sources. He found very different growth responses to short-day conditions.

Barnes (1975) studied phenotypic variation of leaves of western aspen from southern Utah and Colorado northward to the Canadian border. While there was a great deal of variation within areas, the differences between areas were even more striking. Proceeding northward, he found that leaves tended to be smaller, and narrower, with one exception—aspens leaves were largest on Vancouver Island and the coast of Washington. Leaves in northern Idaho and northern Montana resembled those of central Canada and the Great Lakes region. Leaves from the Columbia and Colorado Plateaus, however, closely resembled those of preglacial aspens. He suggested that this resemblance to Tertiary aspens reflects the relatively small number of sexual generations over the hundreds of thousands of intervening years. In contrast, in northern Idaho and northern Montana, aspen regeneration from seed is comparatively common, as it is in central Canada and in the glaciated East. Presumably, many more sexual generations in these areas have been exposed to the evolutionary pressures of environmental stresses and competition than those in the Columbia and Colorado Plateaus.

Airborne aspen pollen has been found 200 miles (320 km) from its nearest possible source (Bassett and Crompton 1969). Most female trees, however, probably are pollinated by nearby male trees. Gene flow between widely separated populations of aspen must be slow and uncertain, even under the most favorable conditions.

Local Variation Among Clones

Patterns

Almost every conceivable combination of morphological and phenological characteristics has been reported¹ in aspen clones (Cottam 1954, Egeberg 1963, Morgan 1969, Strain 1961).

¹Montgomery, D. H. 1957. *A phenological study of aspen in the Medicine Bow Mountains*. 25 p. Unpublished paper at the University of Wyoming, cited by Strain (1961, 1964).

There is strong evidence of selection of genotypes by extreme sites. Aspen is morphologically, and presumably genetically, most uniform at its lowest and highest elevations, where environmental stresses are most severe. The greatest variation in form occurs at intermediate elevations (Greene 1971), suggesting a broader spectrum of genotypes there. However, the occurrence of large differences in ecologically adaptive characters between neighboring clones on the same site indicates that selection through much of the aspen elevational zone has not been rigorous.

Phenology

Adjacent clones of the same sex show considerable interclonal variation in bursting of floral buds (Greene 1971). Generally, clones that break dormancy relatively early in one year do the same in other years.

Marked differences in timing of leaf flushing between clones have been observed (Baker 1921, Barnes 1969, Cottam 1954, Egeberg 1963, Strain 1966). The clonal variation does not result entirely from genetic differences between clones; site has a considerable effect on leaf flushing, also.

Egeberg (1963) sampled 60 clones on one Colorado hillside, all at similar elevations and facing the same direction. They leafed out over a 3-week period. Morgan (1969) reported clones that leafed out 2 weeks earlier than neighboring clones, but also turned yellow 2 weeks earlier. Greene (1971), however, found that clones which flushed earliest were not necessarily the first to change color in autumn. Cottam (1954) found that saplings transplanted to the University of Utah campus retained their leafing differences.

A tendency to later leafing and earlier yellowing could be expected at higher elevations. Near Santa Fe, N. Mex., Covington (1975) found that clones at the lowest elevations (8,000 feet (2,450 m)) leafed out as much as 5 weeks earlier than those at the highest (10,700 feet (3,250 m)), and turned yellow 3 to 5 weeks later. He attributed this largely to climatic difference across the 2,700 feet (800 m) of elevation.

Growth Rates

Growth rates are of major interest to foresters. (See the GROWTH chapter for a discussion of the specific characteristics of the growth and development of aspen trees and stands.) Zahner and Crawford (1965) documented large differences in growth rates of adjacent bigtooth aspen clones on the same site. Barnes (1969) found that growth rates varied among different quaking aspen clones on the same sites in Michigan. When differences were adjusted for crown class, he found heritabilities of 0.58 and 0.43 for total height and diameter at breast height, respectively.

In Utah, Warner and Harper (1972) commonly observed large height differences between contiguous clones on apparently uniform sites. Clonal differences in

diameter growth also have been found. In many clones in the Colorado Front Range, Mitton and Grant (1980) found a significant positive relationship between clone heterozygosity and mean annual diameter growth.

Jones and Trujillo (1975a, 1975b) dissected dominant aspen along the common boundaries of paired clones in Arizona. Their data suggested that, while substantial differences are often seen, most clones which share a site do not differ much in height. Where there are height differences between clones on a shared site, they often develop during the early to mid-sapling stage. Subsequent height growth in both clones may be similar, and the height difference may remain about the same for many years (fig. 1). Height contrasts often are most conspicuous, therefore, when the stand is young (Jones and Trujillo 1975a, 1975b).

Zahner and Crawford (1965) pointed out that clonal height variation can introduce a major error when site index is used to characterize the production potential of a site. That is a problem primarily where the site is occupied by several to many clones, and site index is unwittingly based on only one or two.

In the West, however, a site will often be occupied entirely by one clone. The site index of that clone is normally the only relevant one, unless the area is to be regenerated by planting. Perhaps the best aspen site indexes in the West are the result of superior genotypes growing on good to excellent sites. Conversely, the poorest result from inferior genotypes growing on poor sites. (See the section on site index in the GROWTH chapter.)

Regeneration

In Arizona and Utah, regeneration and subsequent stocking sometimes differ among clones (Jones and Trujillo 1975a, Schier 1975a, Schier and Campbell 1980). In Arizona, at age 22, some clones with more

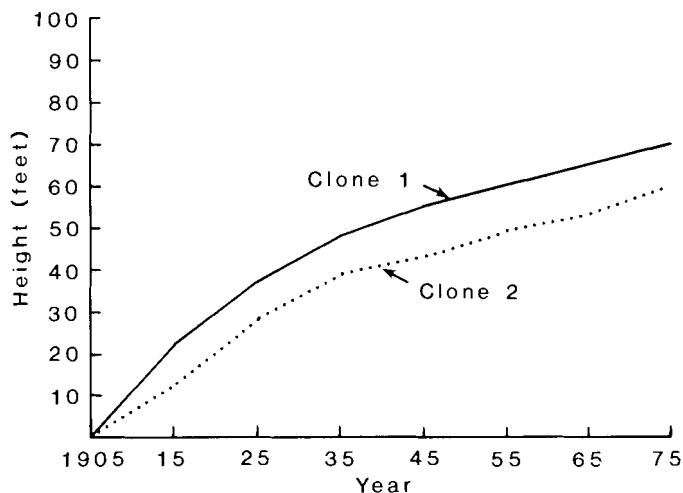


Figure 1.—Height growth curves of two clones on the same plot and site (Jones and Trujillo 1975b). Apache National Forest, Arizona.

trees per acre also had larger trees, in both height and diameter, than neighboring clones on the same site, despite considerably greater crowding (Jones and Trujillo 1975a).

There are numerous reports of clonal differences in the suckering capacity of excised roots (Farmer 1962a, Maini 1967, Schier 1974, Schier and Campbell 1980, Tew 1970a, Zufa 1971). Sucker cuttings also show clonal differences in rooting ability (Schier 1974, Schier and Campbell 1980). (See the VEGETATIVE REGENERATION chapter for a fuller discussion of variation in suckering potential within and among clones.)

Susceptibility to Diseases and Insects

In Manitoba, Wall (1971) found that the incidence of decay, percent of volume decayed, position of rot columns in the trunks, and shape of rot columns, differed among clones. Where clonal boundaries crossed the boundaries of different sites, clonal responses to site change were not always the same. Decay might increase in some clones but decrease in others. In Michigan, susceptibility to Hypoxylon canker varied markedly among clones on four different sites (Copoly and Barnes 1974).

A late-flushing clone in Alberta was damaged by leaf beetles year after year. The older and less succulent leaves of nearby clones were less attractive to the beetles and were not damaged.² In contrast, populations of tortricid caterpillars infested primarily the leaves of early-flushing clones (Witter and Waisanen 1978).

Ploidy

Differences in growth rates and wood characteristics have been demonstrated between naturally occurring triploid clones and associated diploid clones (Einspahr et al. 1967; Van Buijtenen et al. 1958a, 1958b). But it was not established that the differences were greater than those between some diploid clones. Van Buijtenen et al. (1958b) reported that clues for recognizing triploids were their larger trees and larger leaves. But the triploids they described presumably were found and recognized because they looked different. There may have been other triploid clones in the vicinity that were not recognized, whose trees and leaves were not larger than many of the nearby diploid clones. This is suggested by Every and Wiens (1971). In studying 18 Utah clones, they found that three were triploids and one was a tetraploid. Yet, there were no morphological differences that distinguished them from the associated highly varied diploid clones. This suggests that polyploids may be more common and some of them less conspicuous than generally realized.

²Personal communication from A. K. Hellum, University of Alberta.

Other Characteristics

In Manitoba, Wall et al. (1971) noted that some clones became chlorotic on nutrient-deficient sites where others did not. Research with cottonwood clones (Curlin 1967) suggests that differences among aspen clones in response to soil fertilization might be expected.

Carbohydrate reserves in roots vary from clone to clone (Schier and Johnston 1971, Tew 1970a) (see the VEGETATIVE REGENERATION chapter). Tew (1970b) found differences between clones in chemical composition of leaves that would influence their browse quality for animals.

Some clones have very slender twigs, while the twigs are relatively stout on others. On some they are quite crooked; on others they are comparatively straight. Barnes (1969) and Strain (1964) mentioned clonal differences in branching habit. Barnes (1969) also noted variation in time of flowering.

As discussed in the MORPHOLOGY and GROWTH chapters, young aspen stands generally thin themselves effectively. Occasionally, however, a mature clone may be found which has not thinned itself (fig. 2). At age 70, the clone in figure 2 still had about 8,000 live but stunted stems per acre (19,800 per ha), despite several years of western tent caterpillar attacks. Nearby clones on the same ridge had typical stocking and much larger trees.

Sex-Related Differences

Reviewing genetics research on the genus *Populus*, Pauley (1949) felt there was considerable evidence that male *Populus* clones tend to grow faster and have better form and disease resistance than female clones. Rohmeder and Schonbach (1959) reported a tendency in male clones of European *P. tremula* to have better vigor and form than female clones. In a Saskatchewan study, female trees flowered and leafed out 4 to 5 days earlier than males, and the leaves also yellowed earlier (Maini 1968). Morgan (1969) reported that the female trees he saw flowering in an apparently small sample of Colorado clones all leafed out early, while no early-leafing



Figure 2.—An unusual, 70-year-old clone that had not become self-thinned. About 8,000 live stems per acre (19,800 per ha). Carson National Forest, New Mexico.

male trees were seen. In the Snowy Range, in Wyoming, Montgomery found that the time of flowering did not differ with sex.¹

Einspahr (1962) compared 49 male and 42 female clones in Upper Michigan and northern Wisconsin. He found no statistically significant difference between the sexes in any of the characteristics compared—age, height, diameter at breast height, volumes, form class, branch angle, branch weight, natural pruning, or crown volume. Barnes (1969) found sex and growth unrelated in Lower Michigan. In Colorado, however, Grant and Mitton (1979) found that at all elevations, female clones showed a consistently higher radial growth increment than male clones.

Whether clonal differences in form, growth, etc. tend to be sex-related seems generally unimportant from a management viewpoint. Clones usually are selected for the desired characteristics—form, vigor, phenology, etc. The sex of the clone usually is not a consideration except for seed collection or production.

Distinguishing Clones

The great genotypic variation in aspen is reflected in an equally great phenotypic variation among clones. Yet, the genotype uniformity within clones is equally striking—all the trees within a clone appear almost alike. This, plus the large size of most western clones, produces a mosaic on the western landscape (fig. 3). These clones can be distinguished by many characteristics, some very noticeable, and some quite subtle.

Forest managers seldom may be interested in the less noticeable clonal differences, such as leaf morphology. If a clone is markedly superior or inferior in terms of growth rate, stocking, stem form, pruning, beauty, or disease incidence, it usually will be easily recognized. Researchers, however, may want to distinguish clones that are not conspicuously different.

In Minnesota, Blake (1964) outlined what appeared to be different clones on low level color aerial photographs taken in spring. Ground checking confirmed the identification.

Barnes (1969) presented a summary of identifying characteristics for clones in northern Lower Michigan. They are equally applicable in the West. Modified slightly, they are presented in table 1, listed in order of decreasing usefulness within each season. Some characteristics, such as bark color, are useful only when viewing both clones from the same direction. The same tree often looks markedly different on opposite sides.

Leaves differ greatly within a clone, depending on the size, age, and crown class of the tree. They also differ on determinate and indeterminate shoots, on shoots of different lengths, and at different positions on the shoot. But within those subdivisions, they are relatively uniform within a clone. For example, a tree may be assigned to a clone on the basis of two leaves from the lower crown, taken from the central portion of a determinate shoot 1 to 5 inches (3 cm to 13 cm) long.



Figure 3.—A mosaic of aspen clones on Utah's northern mountains.

Greene (1971) listed six prominent features useful in differentiating clones in Colorado: (1) sex, (2) time of leafing and of leaf fall, (3) spring and autumn leaf color, (4) shape and size of leaves, (5) leaf serration, and (6) pubescence of dormant buds.

When possible, the ideal times to identify clones are the period of leafing out in late spring and the period of color change and leaf-fall in early autumn. Many clones that look much alike in midsummer contrast sharply at those times.

Table 1.—Criteria for distinguishing clones, by season and in order of usefulness. Adapted from Barnes (1969).

----- All Seasons -----	
Bark	
1.	Texture
2.	Color
Stem Characteristics	
3.	Form
4.	Branching habit (angle, length, and internode length)
Susceptibility to injury	
5.	Sunscald
6.	Frost crack
7.	Insect and disease injury
Miscellaneous	
8.	Self-pruning
9.	Galls
----- Spring -----	
1.	Sex
2.	Time of flowering, and flower characteristics
3.	Time, color, and rate of leaf flushing
----- Summer -----	
1.	Leaf shape (width/length ratio), color, and size
2.	Shape of leaf blade base
3.	Leaf margin; number, size, and shape of teeth
4.	Shape of leaf tip
5.	Leaf rust infection
----- Autumn -----	
1.	Leaf color
2.	Time and rate of leaf fall