

# Natural Variation and Delineation of Clones of *Populus tremuloides* and *P. grandidentata* in Northern Lower Michigan

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The American aspens, unlike most tree species, are normally able to initiate multi-stemmed clones (BARNES 1966), the larger ones having an appearance of groves. Throughout the range of the aspens the clonal habit is typical, although in dense stands the clonal structure often becomes obscure. While the clonal habit of aspens is basic in identifying natural clones, it is the amount and nature of intra- and interclonal variation which provides the ultimate source of information needed to delineate them. Such information was used by ZAHNER and CRAWFORD (1965) and BERTENSHAW (1965) in investigating clonal structure related to site quality.

The purposes of this paper are to describe, illustrate, and quantify the natural variation of morphological and phenological characteristics in local populations of trembling aspen, *Populus tremuloides* MICHAUX and bigtooth aspen, *P. grandidentata* MICHAUX in northern Lower Michigan and to show how variation within and between clones may be used to separate members of naturally occurring clones.

Investigations of variation are valuable as a basis for silvicultural manipulation and genetic improvement of aspen stands. Furthermore, information on the nature and amount of diversity in local populations is basic for investigations of the genecology and the extent of natural hybridization of the species. For example, natural hybridization is relatively common in aspen populations in southeastern Michigan (BARNES 1961) and may have occurred in part of the range of the species in the Western United States (BARNES 1967). Information on the variation in populations in northern Lower Michigan where hybridization is rare is useful in assessing the rate and extent of hybridization in southern Lower Michigan and in other parts of the species' range.

## Research Sites and Methods

The establishment and development of aspen clones were studied intensively on forest land of the University of Michigan Biological Station. Two areas, termed the Pellston Plain and the Moraine research sites, were selected especially because of the ease of delineation of putative clones.

The Pellston Plain research site is part of a broad glacial outwash plain surrounding the village of Pellston, Michigan (Fig. 1). Cold air drains onto the Pellston Plain from surrounding moraines creating an unfavorable local climate for plant establishment and growth. A wide diurnal temperature range, as much as 65° F, characterizes the growing season. July was the only month free of freezing temperatures from 1942 to 1964 (U.S. Dept. Commerce 1942—1964). The soil is a ground-water podsol leached first by waters of glacial Lake Algonquin and subsequently by ground water. The silt and clay content of the A and B horizons averages about 8%.

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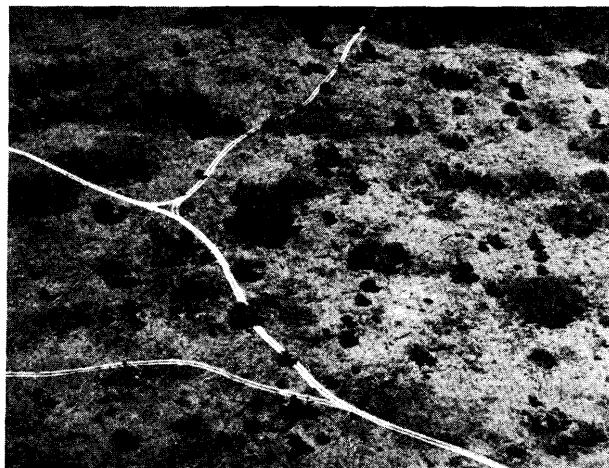


Fig. 1. — Aerial view of the flat, sandy outwash plain near Pellston, Michigan.

The substrate of the Moraine research site is composed of deposits of Valders till mantled by varying thicknesses of high-level outwash sands. The soil, classified by FOSTER et al. (1939) as Emmet Sandy Loam, has a silt and clay content of approximately 11% in the A and B horizons. The local climate is less severe than that of the Pellston Plain. Fires swept through both areas repeatedly until about 1935, when an effective fire protection and prevention system was developed. About 1850 both sites supported a forest of white pine, red pine, red and white oak, and probably other conifers and hardwoods (KILBURN 1957).

Thirty-one *Populus tremuloides* and 21 *P. grandidentata* clones were selected for detailed study on the basis of their separation, sharpness of boundaries, size, and vigor. The clone center was determined arbitrarily by driving the center stake near the largest tree or among a group of large trees in what presumably was the center of the clone. Each clone was mapped, average clone radius determined, and five sample trees selected. A clone was divided into five concentric zones from clone center to boundary. The cardinal direction line (N, E, S, or W) whose distance most closely approximated the average clone radius became the sample line, and the tree closest to this line in each of the five zones was chosen as a sample tree. All clones, except one, of *P. tremuloides* on the Pellston Plain site were sampled during July and August 1956. Five *P. tremuloides* and nine *P. grandidentata* clones on the Moraine site were sampled during the same period, and the remaining clones were sampled in summer 1958. Measurements of the diameter at breast height (DBH), stump diameter, total height, and crown class<sup>2)</sup> were taken while the trees were standing. Sample trees were felled and a section cut from the stump and at breast height. Age determinations were made either in the field or the laboratory. Bark color was determined with the help of the Villalobos color atlas (VILLALOBOS-

<sup>2)</sup> Crown classification: 1 — Dominant; 2 — Co-dominant; 3 — Intermediate; 4 — Intermediate to Suppressed; 5 — Suppressed (BARNES 1959).

DOMINGUEZ 1947). Stages of leaf-flushing (five were recognized) were observed on three different dates during the spring of 1958. Leaf coloration and leaf drop were observed in the fall of 1957 and 1958. Notes on the incidence of forking, frost cracks, poplar borer attack, sunscald, hypoxylon canker, and nectria canker, were taken.

Leaves of species of the genus *Populus* exhibit dimorphism (BURGER 1920; CRITCHFIELD 1960; HAMAYA and INOKUMA 1957). The two basic types of leaves may be termed "early" or "late" depending on the time of their initiation and differentiation (CRITCHFIELD 1960). Leaves which are formed in the bud the preceding year and develop in the early spring are termed early leaves. They lack marginal glands. Sometimes additional leaves are initiated during late spring and summer. These leaves are usually located at the tip of leader shoots in the upper crown and are termed late leaves. Late leaves are more variable in shape than early leaves and have gland-tipped teeth along their margin.

Leaf samples were collected in three different positions of each sample tree. Leaves were taken from terminal shoots, 5 to 18 in. long, in the top of sample-tree crowns. These long, heterophyllous shoots typically bore early leaves along the basal  $\frac{1}{4}$  to  $\frac{1}{2}$  of the shoot and late leaves on the remainder of it. Leaves of short, axillary shoots < 1 in. (0.3 to 0.9 in. long), situated just below the terminal shoot, were also collected. Finally, leaves were taken from terminal and lateral short shoots, 1 to 5 in. long, in the lower and inner portions of the crown. Only early leaves were borne on axillary and terminal short shoots. The leaves were pulled from the shoots, pressed, and dried.

The early and late leaves on long shoots were heavily damaged by leaf-chewing insects. Leader leaves of *P. grandidentata* were so mutilated that no samples were taken. In this study, almost all the leaves studied were early leaves.

Blade width, blade length, and petiole length of all leaves collected from short shoots 1–5 in. of the 52 clones were measured to the nearest cm. The mean value of each attribute for each sample tree in a clone was computed. The

five values (one for each sample tree) were then averaged and a clone mean derived for each attribute. To avoid bias in sampling underdeveloped or immature leaves, *P. tremuloides* leaves less than 2½ cm. in width and length, and *P. grandidentata* leaves less than 4 cm., were not used in computing the means. The ratio blade width/blade length (BW/BL) was computed for each sample tree in a clone and the clone ratio computed by averaging the ratios of the five sample trees. The standard deviations and coefficients of variation of blade width, blade length, and petiole length were computed for each sample tree and a clone mean determined (BARNES 1959). Leaves on short shoots < 1 in. of three *P. tremuloides* and two *grandidentata* clones were also measured.

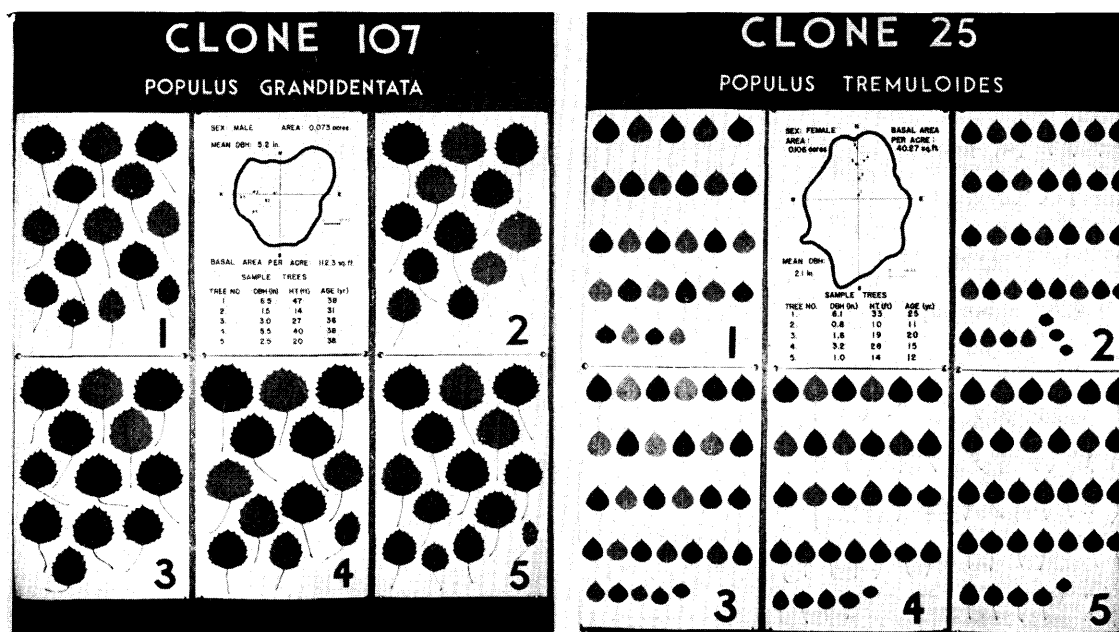
Intra- and interclonal variation were contrasted pictorially and analytically using leaves from medium-length shoots. Leaves of each ramet and the data summary for each clone were photographed (Fig. 2). Variance analyses were used to compute ratios of genetic variance to total variance ( $\frac{V_g}{V_g + V_e}$ ), i.e., heritability in the broad sense. Within-class and between-class correlations, and path coefficient analyses were used to study leaf variability in relation to shoot length and ramet height, diameter, and age.

DBH of all trees in one quadrant adjacent to the line of sampling was measured with calipers, and basal area was determined. In clones with less than 50 stems, the diameter of all trees was measured.

## Results and Discussion

The interaction of genotype and environment causes differences in phenotypic expression. Ordinarily it is impossible to distinguish the part of the variation due to the genetic constitution from that due to environmental factors. Thus, clonal tests and progeny tests have been employed to estimate the genetic and environmental components of variance. The multi-stemmed clone provides a natural clonal test, but it is not statistically valid because clones are not replicated. Despite this, the degree of genetic con-

Fig. 2. — Example of leaves and clone data prepared for all clones of both species. (Numerals on each sheet of leaves



indicate the sample tree whose relative position in the clone is shown on the clone map.)

trol of a given trait is more evident in a multi-stemmed clone than in species whose growth habit is non-clonal.

In the following sections, intraclonal variation of each character is reported followed by a description of interclonal variation. Due to space limitations only brief mention is made of the variation of many characters, and only variation in bark, foliage, and flower bracts is described in more detail.

#### Gross Appearance of the Clone, Growth Rate, and Suckering Ability

Intraclonal variation was observed in the size and density of ramets, growth rate, and suckering ability. Age, available growing space, and competition with adjacent ramets were the primary factors responsible for intraclonal differences.

Obvious interclonal differences appeared in the vertical profile and the density and homogeneity of ramets of both species. Clone size, total height, DBH, and basal area were used to determine clonal differences in growth rate and suckering ability (Table 1). On both sites only slight differences in *P. tremuloides* clone size, average diameter, mean annual height growth, and basal area per acre could

or crown class) for trembling aspen clones was about the same (.14) as that reported by VAN BUIJTENEN *et al.* (1959) for trembling aspen in natural stands, but the value they reported for total height (.52) was much higher.

Heritability estimates computed for ramets in naturally occurring clones might be lower or higher than those in a controlled clonal test of the same clones. In the former, age and growing space are not the same for all clones or all ramets within a given clone. To provide a more reliable estimate for naturally occurring clones an adjustment for non-genetic factors, age and crown class, was made using separate covariance analyses (Table 2). In every case the heritability value increased substantially due to a greater environmental difference between ramets within clones than that between clones.

The broad-sense heritability estimates are applicable only to the clones and sites studied. Because the clones are not replicated, the estimate of total genetic variance is probably biased upward. Despite this, the general level of genetic variance, particularly height growth of bigtooth aspen, is encouraging and may have economic significance. Since bigtooth clones can be propagated from root cuttings and phenotypic selection is facilitated by the clonal growth

Table 1. — Comparison of growth data for clones of *Populus tremuloides* and *P. grandidentata* on the research areas.

Species	Site	Sex	Number of clones	Average area	Mean BA <sup>1)</sup> per acre	Mean DBH <sup>2)</sup>	Mean annual DBH growth	Mean annual height growth	Average age sample trees
				(acres)	(sq. ft.)	(in.)	(in.)	(ft.)	(yr.)
<i>P. trem.</i>	P <sup>3)</sup>	F	10	0.075	27.1	1.7	0.12	1.00	16.9
<i>P. trem.</i>	P	M	10	0.076	23.4	1.5	0.13	1.10	15.9
<i>P. trem.</i>	P	M & F <sup>4)</sup>	20	0.075	25.2	1.6	0.12	1.05	16.4
<i>P. trem.</i>	M <sup>5)</sup>	F	6	0.048	86.0	3.4	0.10	0.78	35.0
<i>P. trem.</i>	M	M	4	0.050	52.9	3.4	0.11	0.82	35.7
<i>P. trem.</i>	M	M & F	10	0.049	69.5	3.4	0.11	0.80	35.3
<i>P. grand.</i>	P	M & F	3	0.080	51.5	3.7	0.20	1.32	23.0
<i>P. grand.</i>	M	F	9	0.079	138.4	5.3	0.17	1.27	36.4
<i>P. grand.</i>	M	M	8	0.060	123.5	5.0	0.15	1.16	35.3
<i>P. grand.</i>	M	M & F	17	0.070	131.0	5.2	0.16	1.22	26.0

<sup>1)</sup> BA = basal area

<sup>2)</sup> DBH = Diameter at breast height

<sup>3)</sup> P = Pellston Plain research site

<sup>4)</sup> M & F = male and female clones combined

<sup>5)</sup> M = Moraine research site

be attributed to sex. The average annual diameter and height growth for trembling aspen clones on the Moraine site were the same as or less than those of trembling aspen clones on the Pellston Plain site. However, the basal area of Moraine site clones was two to three times higher. This difference was largely due to a difference of approximately 17 years in the age of ramets on the respective sites.

No significant differences ( $P > 0.05$ ) were found between male and female clones of bigtooth aspen on the Moraine site in DBH, total height, and basal area per acre (Table 1), but several individual clones exhibited striking differences.

Suckering ability, as indicated by number of ramets per clone and clone size, was the most variable growth feature, particularly of bigtooth clones. This is not surprising since marked variation in suckering in *P. grandidentata* has been reported (FARMER<sup>5)</sup>, ALDEN<sup>6)</sup>, and GARRETT and ZAHNER 1964).

Between-clone differences of various growth attributes were tested statistically and heritabilities were determined (Table 2). The heritability of DBH (unadjusted for age

habit, the possibilities of clonal selection and testing (LIBBY 1964) should be explored.

#### Stem Form

A multitude of bole forms was observed, from extremely crooked to nearly straight. This attribute was particularly striking because of its great intraclonal uniformity. Clones exhibiting forking often differed markedly in forking habit. For example, almost every tree of bigtooth clone 116 was forked at about 20 to 30 feet above the ground. Ramets of clones 118 and 126, however, were consistently forked at ground level or slightly above the ground. Twenty-two of the 32 ramets in bigtooth clone 126 were forked at the base. Though environmental conditions were probably responsible for the marked differences in forking habit,

<sup>5)</sup> FARMER, ROBERT E., JR. 1961. Propagation of aspen using dormant and greenwood stem cuttings. Unpublished report, University of Michigan, July 1961, 37 p.

<sup>6)</sup> ALDEN, HOWARD. 1962. Aspen project progress report. Unpublished report, University of Michigan, 14. p.

Table 2. — Statistical significance and broad-sense heritability estimates for growth attributes of clones of *P. tremuloides* and *P. grandidentata*.<sup>1)</sup>

Species	Attribute	Significances <sup>2)</sup>			Heritability		
		Unadjusted	Adjusted <sup>3)</sup>		Un-adjusted	Adjusted	
			Age	Crown Class		Age	Crown Class
<i>P. tremuloides</i>	Total Height	P < .05	P < .01	P < .01	.13	.45	.43
<i>P. tremuloides</i>	DBH	P < .01	P < .01	P < .01	.13	.36	.28
<i>P. tremuloides</i>	Age	P > .05	—	—	—	—	—
<i>P. tremuloides</i>	Crown Class	P > .05	—	—	—	—	—
<i>P. grandidentata</i>	Total Height	P < .01	—	P < .01	.34	—	.58
<i>P. grandidentata</i>	Mean Annual Height Growth	P < .01	—	P < .01	.44	—	.61
<i>P. grandidentata</i>	DBH	P < .01	—	P < .01	.34	—	.43
<i>P. grandidentata</i>	Age	P > .05	—	—	—	—	—
<i>P. grandidentata</i>	Crown Class	P > .05	—	—	—	—	—

<sup>1)</sup> Basis: *P. tremuloides*, 20 clones on the Pellston Plain site.

*P. grandidentata*, 11 clones on the Moraine site.

<sup>2)</sup> Expressed to show whether the probability (P) of differences in a given attribute were significantly different at levels greater (>) or less (<) than 1 in 20 (.05) or 1 in 100 (.01).

<sup>3)</sup> Adjusted using covariance analysis.

some clones apparently were more highly predisposed to forking than others.

#### Leaf Flushing

Three types of intraclonal variation in leaf flushing were observed. First, smaller ramets lagged somewhat behind larger, more vigorous ramets in flushing stage. Second, flushing was usually more advanced in the upper crown than in the lower crown. Below a line about six feet above the ground flushing was substantially retarded. These types of variation probably were due to temperature inversions. Third, ramets growing in the southwest quadrant of a clone had a slightly more advanced flushing stage than ramets in the northeast quadrant.

#### Interclonal variation in *P. tremuloides*:

Marked differences in leaf flushing between clones in natural environments have been observed by BAKER (1921), COTTAM (1954), DANILOV (1954), EGEBERG (1963), and STRAIN (1966), and this study was no exception. Striking differences in flushing time were observed between sites. Clones on the Moraine site flushed at least an average of two weeks prior to that of clones on the Pellston Plain; the maximum difference was about six weeks. The cold air drainage onto the Pellston Plain was probably responsible for retarding flushing.

Within sites there was at least a three-week difference in flushing stage between earliest and latest clones. Two of the three clones growing on part of the Pellston Plain site having soils with a slightly higher silt-plus-clay content were among the early-flushing clones. However, the third clone was a late-flushing clone.

The early flushing of Moraine site clones was not necessarily an advantage since the leaves of several clones were damaged by frost. Marked differences in color of immature leaves on the Moraine site were observed. Several clones exhibited a reddish color while the more typical colors were yellow-green and pale green.

#### Interclonal variation in *P. grandidentata*:

The intraclonal uniformity and showy appearance of bigtooth aspen flushing emphasized interclonal differences in flushing time. The colors of immature bigtooth leaves of different clones were light green, yellow-green, reddish-green, or reddish brown. The initial color was a silver-

white due to dense pubescence on the undersurface. The typical lustrous green color gradually appeared as the leaves matured.

Bigtooth clones generally flushed two to four weeks later than trembling aspen clones. For bigtooth aspen the difference between sites, two to three weeks, was greater than within-site differences between clones (about two weeks). Late flushing might be a fitness advantage over trembling aspen. Bigtooth clones on both sites flushed late enough in the spring to escape damage by killing frosts.

#### Autumnal Leaf Color and Leaf Fall

A yellow coloration of aspen leaves in autumn has been reported by numerous authors (BRITTON and SHAFER 1908, COLLINGWOOD 1947, DAME and BROOKS 1904, HARLOW and HARRAR 1958, PEATTIE 1950, and many others). The occurrence of clones with red foliage is generally known to keen observers of western trembling aspen, but has only been reported by COTTAM (1966). The duration of the leaf-coloration period for trembling aspen in the Lake States is approximately one month (STROTHMANN and ZASADA 1957). Sometime during this period most aspen leaves do attain some shade of yellow. However, at the height of coloration the range of color of aspens on the research sites was unexpectedly broad — green, yellow, orange-red, violet-red, and dark brown.

Ramets at the edge of a clone exhibited somewhat more intense leaf coloration than the innermost stems. Greater exposure to direct radiation was probably the cause of the more intense foliage color of the ramets in the southwest quadrant compared to those in other quadrants. Stem size apparently played a companion role since the larger, centrally located ramets lagged somewhat behind the exterior ramets in color change and intensity. Leaf fall typically progressed from the lower to the upper part of the crown.

Although there was a striking range of variation in color among trembling aspen clones within sites, no consistent color difference between sites was observed. Interclonal differences in leaf fall were more conspicuous during the later part of the leaf-fall period. The three clones flushing earliest were the last to those their leaves.

Bigtooth aspens dropped their leaves earlier and exhibited a greater variety and range of colors, green, yellow,

red and brown, than trembling aspen. Differences in leaf fall were often more striking than differences in coloration. Occasionally, bigtooth clones devoid of foliage were observed growing alongside clones retaining all their leaves. For both species coloration and the sequence of leaf fall were similar in both years.

### Bark

The following observations were limited to the gross appearance of the surfaces of the boles. The typical aspen sapling develops a distinctive smooth, gray or tan surface more or less covered with a powdery excrescence. The smooth-barked condition may be retained for three or more decades, but it is usually replaced, at least at the base of the ramet or on one side, with rough bark, the surface shallowly or deeply grooved and dark gray or blackish in color.

#### Intraclonal variation in color and texture:

Intraclonal variation in color and texture among ramets of clones of both species was marked. Much of the subtle change in color on the bole surface was due to a powdery layer whose thickness and color were not uniform on a ramet.

The color difference between the north and south sides of most *P. grandidentata* clones was striking. South and west sides were typically bright and green-yellow or bronze in color whereas the north and east sides were usually dark, lusterless, and gray to greenish-black.

Bark texture varied from smooth to rough and plated.

Although most *P. grandidentata* and *P. tremuloides* ramets were smooth-barked, except for roughened areas near the base, ramets of one *P. grandidentata* and one *P. tremuloides* clone exhibited an unusually rough and plated bark. Ramets in the center of the bigtooth clone had rough bark on all sides of the lower portion of their boles (Fig. 3 a). At about 15 feet above the ground, however, the rough bark was gradually replaced by smooth bark. Ramets growing at the edge of the clone had rough bark on the portion of the bole facing the interior of the clone but smooth bark on the opposite side facing an opening around the clone (Fig. 3 b).

Bark texture on the south, north, and east sides of typical ramets of several bigtooth clones is illustrated in Fig. 4. The north and south sides of the corresponding sections are consistently different in color and texture. Prominent horizontal ridges were observed only on the east side of certain clones (106 A, 125, 126, and 133 in Fig. 4 c).

#### Interclonal variation in color:

BAKER (1921), COTTAM (1954, 1966), MARR (1947), OJAMAA (1961), and PEARSON and LAWRENCE (1958) reported differences in color of aspen bark. Interclonal differences in bark color on both sites in Michigan were very striking.

The bark colors of *P. tremuloides* clones on the Pellston Plain site were predominantly yellow and green-yellow. (For the color ratings of individual clones see BARNES 1959.) In contrast to the Pellston Plain clones, bark color of Mo-  
raine site clones was chiefly yellow and light orange-yel-



Fig. 3 a. — Rough-barked ramets in the interior of *P. grandidentata* clone 110 (above).

Fig. 3 b. — Smooth bark on the side of ramets facing the west edge of clone 110 (below).

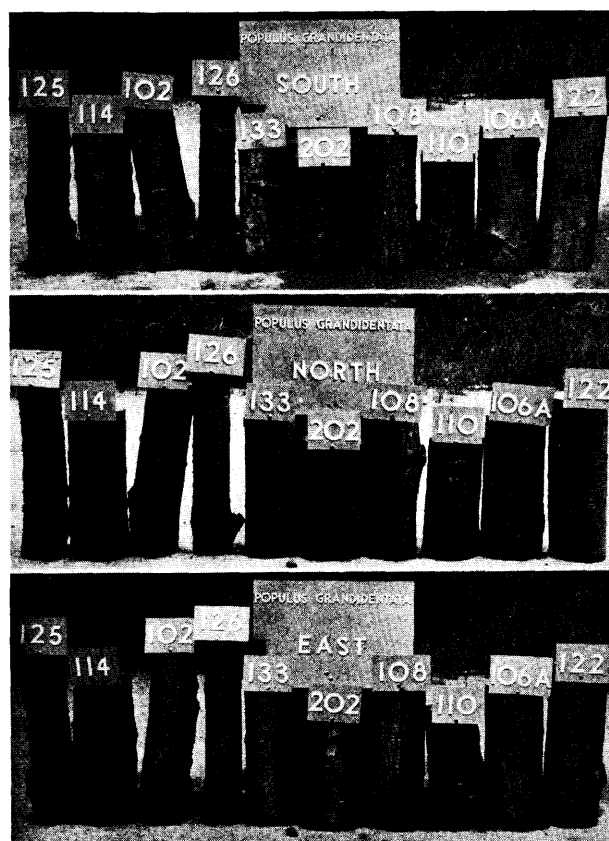


Fig. 4 a. — Bark typical of the south side of several *P. grandidentata* clones.

Fig. 4 b. — Bark typical of the north side of several *P. grandidentata* clones.

Fig. 4 c. — Bark typical of the east side of several *P. grandidentata* clones.

low. Wide interclonal differences were observed. In many instances adjacent clones could be distinguished readily by bark color alone.

The bark color of *P. grandidentata* clones on both research sites was predominantly yellow-orange and light orange-yellow. Clone 110 was undoubtedly the most striking clone; its black, slightly furrowed bark was unlike that of any other clone on either site (Fig. 3).

#### Interclonal variation in texture:

Besides the typical smooth bark of most ramets of both species, several types of rough bark were found (Fig. 5). First, a rough, fissured bark often replaced the superficial periderm at the base of the bole. KAUFERT (1937) attributed this to abrasion by grass and other vegetation. Second, aspen trees in very shaded locations typically had rough, plated bark extending 10 feet or more up the bole. As evidenced by differences in the texture of the north and south surfaces of aspen ramets, most aspen clones probably show a somewhat similar increase of rough bark to reduction in light intensity. Certain clones, however, whose genetic constitution apparently was more sensitive to reductions in light intensity, possessed a rough, fissured bark while adjacent clones typically had smooth-bark ramets (Fig. 5, clone 204).

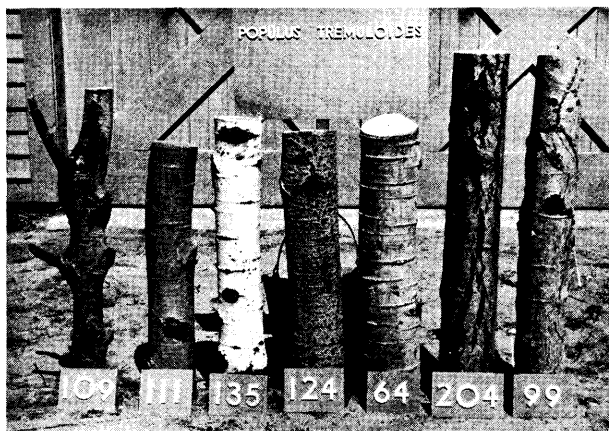


Fig. 5. — Stem sections of ramets in *P. tremuloides* clones illustrating the variety of bark texture and color.

Third, ramets of some bigtooth clones may have one or more bands of rough, plated bark from several inches to several feet in height (Fig. 4, clone 108). KAUFERT (1937) reported that this type of rough bark was caused by the fungus *Macrophoma tumafaciens*.

Damage by intense heat may also cause the formation of rough bark. On areas known to have had repeated fires, bark of bigtooth ramets was invariably rough, often to a height of 10 to 20 feet, where it was replaced by smooth bark. Since bark texture is known to have adaptive value in tree species and rough-bark clones may be resistant to insect attack, environmental and genetic factors affecting the induction of rough bark should receive attention.

#### Leaf Morphology

Polymorphism characterizes leaf variation in the aspens, birches (JENTYS-SZAFEROWA 1937, 1955), sweetgum (DUNCAN 1959) and many other species.

Several components of intraclonal leaf variation were recognized in both aspens. First, there were marked differences in leaf size and shape depending on the time of initiation and differentiation of the leaf, i. e., early and

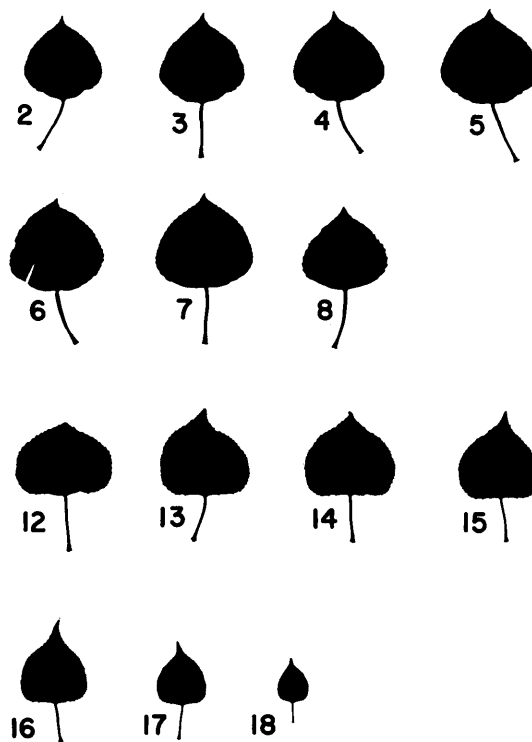


Fig. 6. — Leaf silhouettes of a long shoot of *P. tremuloides* ( $\times \frac{1}{3.6}$ ); leaves 2—7 are typical early leaves, 8 is a transition form to late leaves, and leaves 12—18 are typical late leaves.

late leaves. Second, diversity existed in leaf size and shape among the three shoot types: short shoots < 1 in., short shoots 1—5 in., and long shoots. Third, substantial variation existed within a given shoot type and crown position.

#### Early and late leaves contrasted:

Early leaves on short shoots < 1 in. of clones of both species were uniformly and significantly smaller and more elongate than early leaves from short shoots 1—5 in. and long shoots (Table 3). Early leaves borne on long shoots were approximately the same size as leaves of short shoots 1—5 in. Late leaves were highly variable; many were wider and shorter than leaves from short shoots 1—5 in. The petiole length of late leaves on long shoots was substantially shorter than that of early leaves of short shoots. However, insufficient material was available to provide detailed comparisons of early and late leaves. Furthermore, the size and shape of early and late leaves varied greatly by their location on the shoot and this would have to be carefully considered when comparing them (see below).

Early and late leaves on a single shoot 6.4 in. long are illustrated in Fig. 6. Initially the shoot grew 1.8 in. and early leaves 2—7 were located on this portion. The transition to late leaves is evident in leaf 8. Later the shoot grew 4.6 in. and late leaves 9—18 were located along this portion. Leaves 9, 10, and 11 were not found, presumably eaten by defoliating insects. Leaves in this transition stage are typically small, and often destroyed by insects.

KOZLOWSKI and CLAUSEN (1966) studied shoot-growth characteristics of both aspens and found all embryonic leaves to be of similar developmental stage, differing only gradually in length, i. e., all early leaves. Since heterophylly is common on terminal shoots of the upper crown of both species, failure to observe late leaves was apparently due to sampling terminal and lateral buds and shoots only in the lower crown.

Table 3. — A comparison of early and late leaves borne on short and long shoots of *P. tremuloides* and *P. grandidentata*<sup>1)</sup>

Type of Shoot and Foliage	<i>Populus tremuloides</i>			<i>Populus grandidentata</i>	
	Pellston Plain site			Moraine site	
	Clone Number			Clone Number	
	16	27	51	103	106
Mean Blade Width (cm)					
Short shoot < 1 in., early leaves	3.0	3.1	3.0	4.8	5.3
Short shoot 1—5 in., early leaves	3.6 <sup>2)</sup>	3.8	3.6	7.0	7.6
Long shoot					
Early leaves	3.8	3.7	3.5	—	—
Late leaves	4.2	4.5	—	—	—
Mean Blade Length (cm)					
Short shoot < 1 in., early leaves	3.7	4.1	3.4	6.3	5.8
Short shoot 1—5 in., early leaves	4.1	4.7	3.9	8.7	7.7
Long shoot					
Early leaves	4.1	4.6	3.7	—	—
Late leaves	4.1	4.2	—	—	—
Mean Petiole Length (cm)					
Short shoot < 1 in., early leaves	3.0	3.9	2.6	5.6	3.8
Short shoot 1—5 in., early leaves	3.0	3.8	2.8	7.0	4.6
Long shoot					
Early leaves	3.2	3.9	2.6	—	—
Late leaves	2.5	2.7	—	—	—
Mean of Ratio: Blade Width/Blade Length (BW/BL)					
Short shoot < 1 in., early leaves	0.81	0.74	0.89	0.75	0.90
Short shoot 1—5 in., early leaves	0.88	0.80	0.93	0.80	0.99
Long shoot					
Early leaves	0.93	0.80	0.94	—	—
Late leaves	1.02	1.08	—	—	—

<sup>1)</sup> Early leaf data are based on measurements from leaves on 5 ramets in each clone. (Clone 16 average of 44 leaves per ramet; clone 27, 37 leaves per ramet, clone 103, 38 leaves per ramet; clone 106, 28 leaves per ramet).

Late leaves were available only on one ramet of clone 16 (22 leaves) and an average of only 7 leaves per ramet of clone 27.

<sup>2)</sup> All early leaf data were subjected to statistical analysis. All early-leaf means not connected by the vertical line are significantly different ( $P < .025$ ).

For both species, the size and BW/BL of early leaves from short shoots < 1 in. differed significantly from those of short shoots 1—5 in. This difference is probably due more to differences in buds (axillary or terminal) and position in the tree (upper crown or lower inside crown) than shoot length per se. Nevertheless, early leaves, despite fluctuations of size and shape, showed little resemblance to late leaves of the same clone, regardless of where early leaves were sampled.

#### Intraclonal variation of leaves on short shoots 1—5 in.:

The size and shape of leaves on short shoots 1—5 in. were relatively consistent among ramets of a given clone (Fig. 2). Nevertheless, significant differences in leaf size and shape were found related to (1) ramet age, height, diameter, and crown class, and (2) position of leaf along the shoot.

The association of one leaf character, blade width, with ramet age, height, and diameter was investigated. Because between-clone variation is large and may mask consistent within-clone relationships, within-class correlations were employed. For 12 *P. grandidentata* clones sampled in 1958, DBH, total height, and age were not significantly associated with blade width ( $P > 0.10$ , Table 4). In contrast, within-class correlation coefficients of blade width and total height, DBH, crown class, and age for *P. tremuloides* clones on the Pellston Plain site were highly significant. Path coefficient analyses showed that total height, DBH, and age accounted for 47 percent of the variation in blade width.

Differences between the two species in respect to the relationship of blade width to age, height, and diameter of ramets (Table 4) are probably due to the development of the respective sets of clones. The diameter, height, and age of ramets of clones of *P. tremuloides* on the Pellston Plain decreased progressively from clone center to the boundary. However, ramets of *P. grandidentata* clones on the Moraine site apparently arose nearly simultaneously and exhibited very little variation in these traits from clone center to the boundary. *P. tremuloides* clones on the Moraine site had a somewhat similar growth habit to *P. tremuloides* clones on the Pellston Plain and also showed highly significant correlations of blade width with height and diameter. The ramets arose, however, at approximately the same

Table 4. — Within-class correlations of total height, diameter breast height, and age with blade width.

Variable	<i>P. grandidentata</i>	<i>P. tremuloides</i>	
	Moraine Site <sup>1)</sup>	Moraine Site <sup>2)</sup>	Pellston Plain Site <sup>3)</sup>
Total Height	0.006	0.515**	0.635**
Diameter			
Breast Height	—0.032	0.528**	0.492**
Age	—0.015	0.210	0.502

<sup>1)</sup> Basis: 12 clones

<sup>2)</sup> Basis: 7 clones

<sup>3)</sup> Basis: 19 clones

\*\* Significant at  $P < .01$



time so that age and blade width were not significantly correlated. For these clones only 29 percent of the variation in blade width was explained by variation in height, diameter, and age. These data suggest that age, height, and diameter were closely related to leaf size. Therefore, leaf size is not a reliable characteristic to use in clone identification when ramets differ markedly in these traits.

The relationship of crown class and leaf size was examined only for *P. tremuloides* clones on the Pellston Plain site. Total correlation coefficients for crown class vs. blade width ( $-0.54$ ) and blade length ( $-0.44$ ) were highly significant ( $P < .01$ ). Thus, as expected, as ramets receive less light and growing space, leaf size decreased.

Variation in leaf size due to fluctuations in shoot length was investigated by measuring the length of all short shoots 1–5 in. from which leaves were collected from 12 *P. grandidentata* clones on the Moraine site in 1958 and by computing the correlation with blade width. The within-class correlation of shoot length and blade width for these clones was not significant ( $r = 0.11$ ). No definite trend was found for all clones, but for certain individuals significant and contrasting coefficients were found, e. g., one clone exhibited a correlation of  $+0.68$  while that of another was  $-0.71$ .

The relative position of the leaf on a shoot was the greatest source of variation in leaf size and shape within a given crown position and short-shoot class. The lowermost and uppermost leaves on a shoot were often markedly different from leaves borne in the central portion (Fig. 8). Smaller leaves were characteristic at the uppermost and lowermost positions on short shoots 1–5 in. of *P. grandidentata* clones (Fig. 7). The shape of the lowermost leaf

was often somewhat more round or compressed, and the uppermost leaf was usually more elongate than leaves in the middle portion of the shoot. In *P. tremuloides* a similar pattern was found. The lowermost leaf was typically smaller and often more reniform, and the uppermost leaf was typically smaller and almost always more elongate (lower BW/BL ratio) than leaves borne in the central portion of the shoot. Although the above pattern seems to be standard in both species, clones differ and a rigid rule cannot be given.

Variation in morphological characteristics can be minimized by restricting the sampling to leaves near the center of the shoot. For example, the mean and standard deviation of blade width and blade length for all leaves on a short shoot 1–5 in. selected at random from *P. grandidentata* clone 118 were  $6.25 \pm 0.85$  cm. and  $6.20 \pm 0.69$  cm., respectively. When the uppermost and lowermost leaves were not included, the mean and standard deviation were  $6.68 \pm 0.23$  cm. and  $6.35 \pm 0.25$  cm., respectively. Two leaves per ramet taken from the central portion of short shoots 1–5 in. should be sufficient to characterize the leaf morphology of the clone for the purposes of rapid field delineation or for mass sampling of populations.

BROEKHUIZEN (1961) has reported a somewhat different but not unexpected situation for clones of black poplar hybrids (*P. × euramericana* [DODE] GUINIER). He found considerable fluctuation in leaf morphology in the first 15–17 leaves formed. Thereafter, leaves 17–30, leaf morphology was relatively constant. The relatively uniform leaves were formed after the beginning of July. Again, knowing the pattern of intraclonal variability, one can minimize this variation and make more effective comparisons between clones.

#### Interclonal variation of leaves on short shoots 1–5 in.: *P. tremuloides*. —

Although the general leaf form may be regarded as ovate, a great diversity in leaf size and shape was discovered (Fig. 8); circular, rhomboid, elliptical, and reniform shapes also may be considered typical. Highly significant differences ( $P < 0.01$ ) in blade width, blade length, petiole length, and BW/BL were found between clones on the Pellston Plain site. The heritability of these attributes before and after ( ) adjusting for crown class were .75(.80), .73(.81), .79(.82), and .80(.86), respectively. The variance ratios confirm observations of great uniformity within clones, and suggest that early-leaf characters are under much stronger genetic control than growth attributes. This is not surprising since early leaves are pre-formed in the bud. Such morphological characters, imprinted at an early stage of development, are less subject to external modification than attributes related to elongation and absolute size.

Great diversity was found in leaf size and shape (Fig. 8), and shape differences were contrasted using BW/BL ratios. Significant differences ( $P < .001$ ) were found between sites and between clones within each site. On the Pellston Plain site the average ratio for all clones was 0.91; the range was .80 to 1.05. Male clones had a significantly greater ratio than female clones ( $P < .025$ ). The average ratio on the Moraine site was 1.08; the range was .90 to 1.32.

Immature leaves were characterized by numerous silky hairs on the lower surface and margin. The mature leaves were glabrous on the upper and lower surfaces, but ciliate along the margin. The most variable character of the leaf margin was the degree of serration. Some clones had nearly

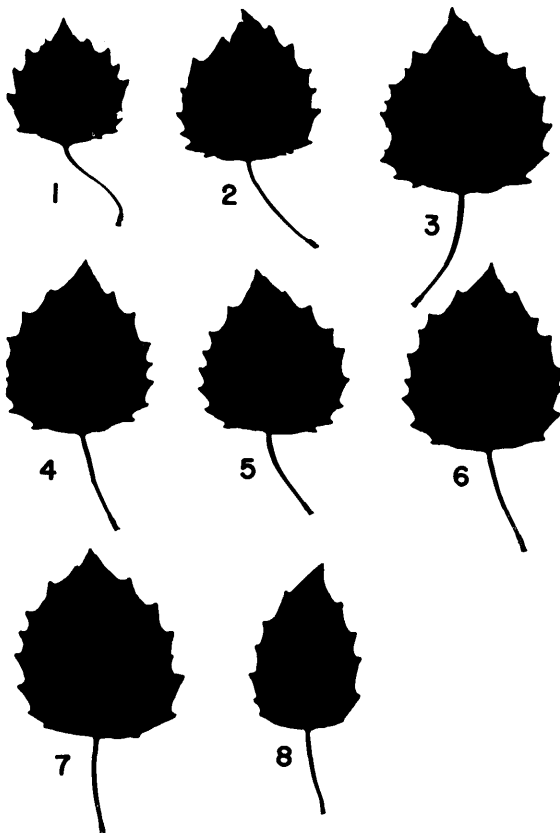


Fig. 7. — Silhouettes of early leaves from a short shoot 1–5 in. of *P. grandidentata* ( $\times \frac{1}{3.6}$ ). Leaf 1 was located at the base of the shoot, leaf 8 at the tip.



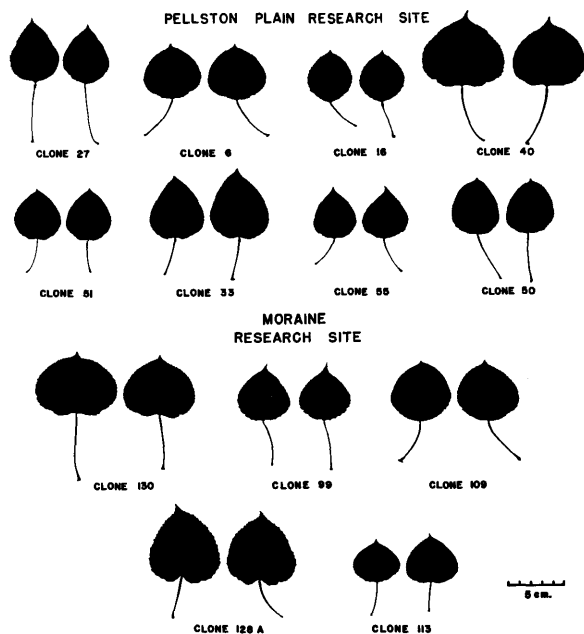


Fig. 8. — Leaf silhouettes of selected clones of *P. tremuloides* ( $\times \frac{1}{7.0}$ ). Early leaves from central portion of short shoots 1–5 in.

entire leaf margins while those of other clones were distinctly serrate. The average number of teeth per leaf side on the Pellston Plain was 29.4, range 22–39. On the Moraine site clones had 32.7 teeth per leaf side; the range was 28–36.

Blade tips were characterized using RICKETT'S (1956) classification. Cuspidate tips predominated on both sites, but acute, acuminate, and mucronate tips were also recognized.

Six blade base shapes were recognized: cuneate, rounded, truncate, concave, subcordate, and cordate. Blade bases in several clones were decurrent. On the Pellston Plain site this feature was associated with clones having cuneate and concave bases. Rounded and concave base shapes were most common on the Pellston Plain site while subcordate and concave bases predominated on the Moraine site.

Highly significant differences ( $P < 0.01$ ) in the petiole length were found among clones on the Pellston Plain site. The mean petiole length for these clones was 3.3 cm.; the range was 2.6 to 4.5 cm. In general, the clones with larger leaves had longer petioles. Clones on the Moraine site had longer petioles (mean = 2.9 cm.) and a greater range (2.4 to 4.7 cm.) than those of clones on the Pellston Plain site.

#### Interclonal variation of leaves of short shoots 1–5 in.: *P. grandidentata*. —

Significant differences in blade width, blade length, and petiole length were found between clones on the Moraine site ( $P < .001$ ). Two extreme leaf shapes termed "circular" and "elongate", and a complete range of intermediates were found; examples of each are illustrated in Fig. 9. A nearly continuous series of BW/BL ratios was found for the 18 clones on the Moraine site (range .75 to 1.02; mean .88). Highly significant differences in BW/BL ( $P < .001$ ) were found between these clones, and leaves of male clones had a significantly greater BW/BL ratio than leaves of female clones ( $P < .05$ ).

Blade tip variation was not pronounced; tips were acute or acuminate. Eight clones on the Moraine site had leaves

with cuneate bases (clones 107, 126, and 104 in Fig. 9). The number of clones characterized by rounded, truncate, and concave bases was five, two, and three respectively.

The leaf margin of all clones was distinctly toothed. The average number of teeth per leaf side for Moraine site clones ranged from 6.6 to 12.3; the mean of all clones was 9.8. The range for individual leaves was 5 to 15. There was no substantial difference between male and female clones nor between circular and elongate forms. A nonsignificant correlation was found between the number of teeth and blade width and blade length. Although the dentation of leaves of many clones was regular, irregular dentation (characterized by distance between teeth, size of teeth, and angle of teeth with the midrib) was found in seven of the eighteen clones. Clonal differences also existed in the shape of the individual teeth; blunt, sharp pointed, and recurved types were found.

#### Morphology of Flower Bracts

The bracts of the aspen catkin subtend the pedicellate flowers. The pedicels at the base of the catkin were short, but became longer toward the tip. The bracts were attached to the pedicel of the flower and were shaped somewhat like a hand. Along the margin of the bract of both species arose several to many stiff, silky hairs.

A gradual diminution in size of bracts was found from the base to the tip of the catkin in both species (Fig. 10). The large and irregular bracts at the base of male and female catkins was typical.

The lowermost flower was usually subtended by a long, scale-like bract (A in Fig. 10). Occasionally located near the base of the catkin were double-lobed bracts (B in Fig. 10). Between the two long lobes of this bract was a small papilla, covered with stiff, silky hairs. This appendage is probably an aborted central bract lobe. Often just above or near this type of bract were found one or more triple-lobed bracts (C in Fig. 10). The two side lobes were reduced somewhat in size and the margin of the two lobes was often dissected into two or more digits. The side lobes and center lobes seemed to fuse together to form the typical one-lobed

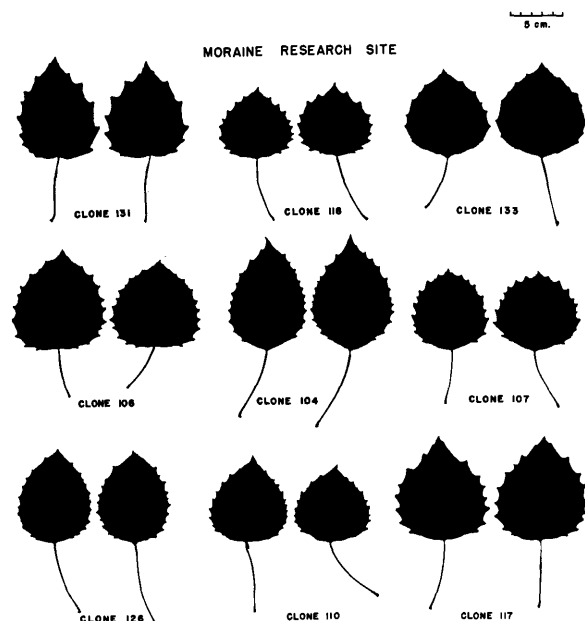


Fig. 9. — Leaf silhouettes of selected clones of *P. grandidentata* ( $\times \frac{1}{7.0}$ ). Early leaves from central portion of short shoots 1–5 in.

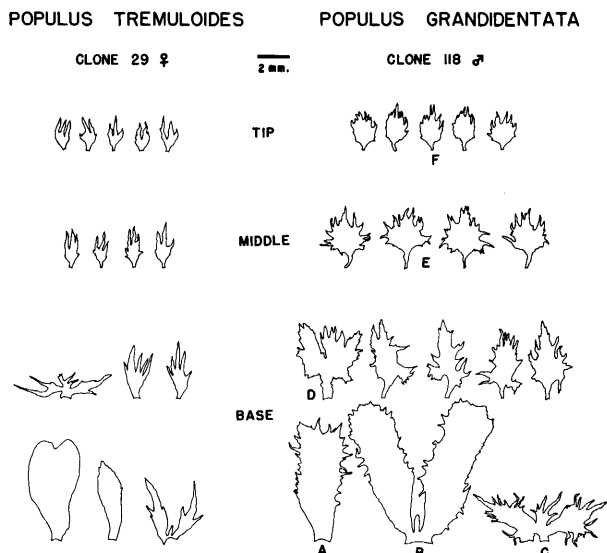


Fig. 10. — Tracing of flower bracts of *P. tremuloides* and *P. grandidentata* illustrating intraclonal differences in size and shape.

multi-appendaged bract. An intermediate stage between the three-lobed and single-lobed form was occasionally found (D in Fig. 10).

The basal forms of the bract were located on approximately the basal  $\frac{1}{10}$  of the catkin. Throughout the central portion of the catkin, there was only a slight decrease in bract size (E in Fig. 10). Bracts became markedly smaller in the upper  $\frac{1}{3}$  of the catkin (F in Fig. 10).

Bracts dissected from the central third of one catkin from one ramet in each of four male and four female clones of trembling aspen and bigtooth aspen are shown in Fig. 11. Differences existed in the size and shape of the bract and the number and length of the digits. Bracts of trembling aspen had from three to eight long and narrow digits; bracts of bigtooth aspen had from five to twelve digits and were not as deeply cleft. The uniformity of bract characters within a clone suggests that, like some leaf attributes, their genetic control is very strong. Interclonal differences in bract size, bract color, and number and length of digits were also found among six clones of trembling aspen on the Moraine site.

Marked differences in the size of bracts subtending male and female flowers of bigtooth aspen were found (Fig. 11).

Bracts of seven female clones were significantly smaller than those of seven male clones ( $P < 0.001$ ). Bracts of trembling aspen were longer than bracts of male bigtooth and wider and larger than the bracts of female bigtooth clones.

#### Other Characteristics

Clonal differences were found in a number of additional characteristics which are often very useful in delineating ramets of adjacent clones: summer leaf color, terminal bud shape, leaf thickness, size of stomata, presence of aphid galls, and susceptibility to insect attack (*Saperda calcarata*, *Dicerca* spp., *Agromyza* sp.) sunscald, frost cracking, and *Melampsora* sp.

#### Naming of Varieties and Forms of Aspens

A number of infraspecific scientific names have been created for aspen variants involving leaf shape or gross appearance (Table 5). On the basis of the evidence presented earlier, I do not feel that such taxonomic names for alleged "varieties" or "forms" should be applied to individual clones or extreme variants.

Table 5. — Species, varieties and forms of trembling and bigtooth aspen based on leaf morphology and gross appearance.<sup>1)</sup>

Infraspecific Name, Rank, and Author	Reference
<i>P. aurea</i> TIDESTROM	TIDESTROM (1911)
<i>P. tremuloides</i> var. <i>aurea</i> (TIDESTROM) DANIELS	DANIELS (1911)
<i>P. vancouveriana</i> TRELEASE ex TIDESTROM	PIPER and BEATTIE (1915)
<i>P. tremuloides</i> var. <i>vancouveriana</i> (TRELEASE) SARGENT	SARGENT (1919)
<i>P. cercidiphylla</i> BRITTON	BRITTON & SHAFER (1908)
<i>P. tremuloides cercidiphylla</i> (BRITTON) SUDWORTH	SUDWORTH (1927)
<i>P. tremuloides</i> var. <i>intermedia</i> VICTORIN	VICTORIN (1930)
<i>P. tremuloides</i> var. <i>rhomboidea</i> VICTORIN	VICTORIN (1930)
<i>P. tremuloides</i> var. <i>magnifica</i> VICTORIN	VICTORIN (1930)
<i>P. tremuloides</i> f. <i>Davisiana</i> TIDESTROM	TIDESTROM (1911, 1914)
<i>P. tremuloides</i> f. <i>reniformis</i> TIDESTROM	TIDESTROM (1914)
<i>P. tremuloides</i> f. <i>pendula</i> JAEGER and BEISM.	VICTORIN (1930)
<i>P. tremuloides</i> f. <i>minor</i> COCKERELL and <i>P. tremuloides</i> f. <i>nana</i> COCKERELL	COCKERELL (1891a, 1891b)
<i>P. pseudograndidentata</i> DODE	DODE (1905)
<i>P. grandidentata</i> f. <i>septentrionalis</i> TIDESTROM	TIDESTROM (1914)
<i>P. grandidentata</i> f. <i>meridionalis</i> TIDESTROM	TIDESTROM (1914)
<i>P. grandidentata</i> f. <i>coelestina</i> TIDESTROM	TIDESTROM (1914)
<i>P. grandidentata</i> var. <i>angustata</i> VICTORIN	VICTORIN (1930)
<i>P. grandidentata</i> var. <i>subcordata</i> VICTORIN	VICTORIN (1930)

<sup>1)</sup> Based on a list by LITTLE (1953) and the other sources cited.

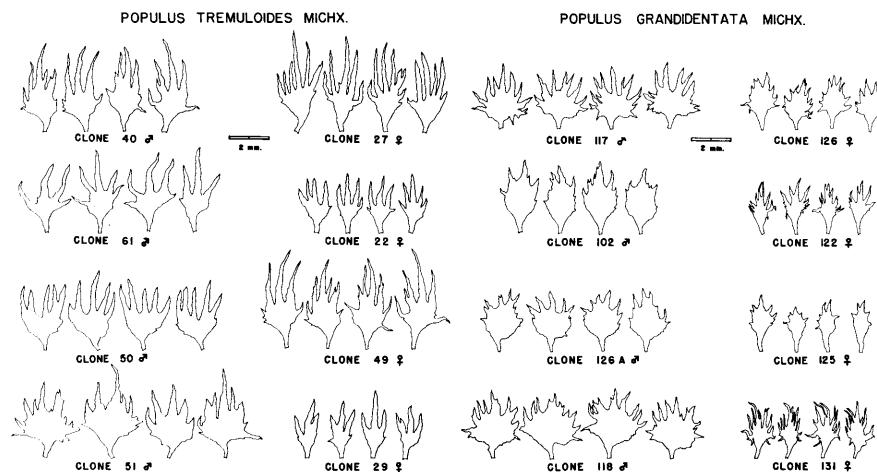


Fig. 11. — Tracings of flower bracts of *P. tremuloides* and *P. grandidentata* illustrating interclonal differences in size and shape.

After studying the descriptions, illustrations, and in many cases, authentic specimens of these taxa, I agree with LITTLE (1953) who recognized only two species, *P. tremuloides* and *P. grandidentata*, and synonymized the so-called "varieties" and "forms" as not worthy of recognition. Many of the varieties and forms were apparently based upon but a single clone, and the range of variation of leaf shape and other characters for the species as a whole was not realized. I observed or collected leaves from aspens on the two research sites which conformed to practically all of the described varieties and forms. For the present, therefore, I do not believe it wise to subdivide aspens into infraspecific taxa unless there is compelling evidence. Indeed, I suspect the number of such names could be multiplied almost indefinitely, judging from the populations I studied, which are probably representative of what may be expected throughout the ranges. There is some evidence that certain populations of western trembling aspen may be different (BARNES 1967), but this has not yet been conclusively shown.

Taxonomically it is more accurate to establish a broad concept of the two aspen species which recognizes the great extent of variation and differentiation between clones.

### Clone Identification

Identification of clones of many species is becoming increasingly important in forest genetics and ecological studies. Of the many variable traits described above only one or a few may be sufficient to distinguish clones. In other instances many traits may be necessary and multivariate analyses may be required. For many years European workers have investigated the problem of identifying clonally propagated poplars and aspens and use many of the traits described above (BROEKHUIZEN 1961, 1964; FRÖHLICH and BAUMEISTER 1963; HATTEMER 1966; MARCET 1956, 1961; MELCHIOR and HATTEMER 1966; MÜLLER 1957; MÜLLER and SAUER 1958; SAUER 1958).

In Table 6 characteristics of aspens are ranked by season in decreasing order of their usefulness and precision in delineating adjacent natural clones. Spring is probably the best season to distinguish adjacent clones through the marked differences in flushing and flowering. BLAKE (1963) reported a rapid method of delineating clones in spring using colored aerial photographs. Four flowering conditions, male, female, bisexual, and no flowering, are very useful in clone identification. Many authors have reported the bisexual condition in Section *Leuce* (BARNES 1959, LESTER 1963) and the aspens are regarded as subdioecious species, i. e., some bisexual plants occur regularly in nature in addition to completely male and female plants (WESTERGAARD 1958). In some years ramets of certain clones bear no flowers, and female clones seem to be much less regular in flowering than male clones (LANGHAMMER 1963). However, when a good flowering year occurs, LANGHAMMER reported that the male-female ratio was approximately 50—50.

Leaves are extremely useful in clone identification and two leaves on the central portion of a short shoot 1—5 in. long from the lower crown should suffice for comparisons. Finally, because of the amount of intraclonal diversity in most characters, the intraclonal variation pattern for each should be well understood before making comparisons among clones.

### Summary and Conclusions

This paper reports an investigation of the natural variation of morphological and phenological characteristics of

Table 6. — Characteristics for field identification of aspen clones ranked by season in decreasing order of usefulness.

A. Spring
1. Sex
2. Time of flowering and floral characteristics
3. Time, color, and progression of leaf flushing
B. Autumn
4. Leaf coloration
5. Time and progression of leaf fall
C. Summer
Leaf Characteristics
6. Leaf shape (BW/BL ratio) color, and size
7. Configuration of blade base
8. Leaf margin: tooth number, size, and shape
9. Configuration of blade tip
D. All seasons
Bark Characteristics
10. Bark texture
11. Bark color
Stem Characteristics
12. Stem form.
13. Branching habit (branch angle, branch length, internode length)
14. Susceptibility to injury
a. Sun-scald
b. Frost crack
c. Insect and disease injury
15. Miscellaneous characteristics
a. Pruning ability
b. Leaf rust
c. Aphid galls
16. Vertical profile

the aspens, *Populus tremuloides* MICHX. and *P. grandidentata* MICHX. in two localities in northern Lower Michigan. Clones were selected for study on two relatively uniform sites, and five trees were systematically sampled in each of 31 *P. tremuloides* and of 21 *P. grandidentata* clones of both sexes. In addition to phenological data for each clone, leaves from shoots of three different lengths, and data on total height, age, crown class, and diameter at breast height (DBH) were obtained from each sample tree.

Three general conclusions were reached: the aspens exhibit an enormous amount of interclonal variation even in local populations in a fragmentary part of their range. Thus a broad concept of these species which recognizes the great diversity existing in local populations should be adopted. Second, ramets of one clone usually can be distinguished from those of a neighboring clone by one or more morphological and phenological traits. Phenological characteristics are extremely useful to distinguish clones in the spring and fall while, during the summer, leaf morphology is especially helpful in delineating them. Intraclonal variation, particularly the differences in early and late leaves, shoot length, and position of leaves on the shoot, should be thoroughly understood before extensive interclonal comparisons are initiated. Third, the methods and data contained herein may be used as an aid in circumscribing the variation of the two basic aspen species, and have already been shown (BARNES 1961, 1967) to be of value in estimating the role of hybridization between them.

#### Specific conclusions:

1. In gross appearance ramets of a clone were typically uniform in stem form, leaf flushing, autumnal leaf coloration, and leaf fall. Minor fluctuations in flushing and fall coloration were observed from the center of the clone to its boundary, in the upper and lower parts of the crown of individual ramets, and in different quadrants of the clone. These variations were attributed primarily to differences in sunlight, temperature, and stem size.
2. Noticeable differences between clones occurred in clone

profile, density of ramets, suckering ability, and growth rate. A significant difference was found between *P. tremuloides* clones on the Pellston Plain site in total height ( $P < .05$ ) and in DBH ( $P < .01$ ). Broad-sense heritability for total height and DBH, adjusting for age by covariance analyses, were .45 and .36 respectively. Statistically significant differences ( $P < .01$ ) in total height, DBH, and mean annual height growth were found for *P. grandidentata* clones on the Moraine site. Heritabilities for total height and DBH, adjusted for crown class, were .58 and .43. No differences in growth capacity were found attributable to sex.

3. There was marked phenological diversity between sites and between clones on a given site. Trembling aspen clones flushed earlier, and retained their leaves longer in the autumn, than bigtooth clones. On a given site trembling aspen clones varied two to three weeks in reaching a given flushing stage, bigtooth aspen by one to two weeks.

4. Aspen clones displayed a wide range of foliage colors, yellow to violet-red, at a given time in the autumn. Bigtooth aspen exhibited a more intense and wider array of colors than trembling aspen.

5. Within clones only minor variations were observed in bark color and texture as long as stems were viewed from the same direction. Large fluctuations in color and texture, however, were observed between the north and south sides of the bole. The south side of *P. grandidentata* stems was typically smooth and green-yellow in color. The north side of the same ramets was often corky in texture and usually dark gray or gray-green.

6. Conspicuous interclonal differences in both species were found in bark color and texture. Smooth bark was typical of pole-sized stems but several clones had unusually rough, plated bark.

7. Intraclonal leaf variation was striking and greater than interclonal variation in some instances. Intraclonal differences were attributed to time of initiation of leaves (early vs. late leaves), age, size, and crown class of the ramet, position of leaves in the tree crown, type of bud (axillary or terminal), length of the leaf-bearing short shoot, and position of leaves along the shoot. Of these sources of variation, time of initiation of leaves, type of bud and short-shoot length, and position of the leaf on the shoot were the most important.

8. Extensive interclonal variation in leaf morphology, size, shape, number of teeth, configuration of the blade tip and base, was found. In trembling aspen ovate, circular, elliptical, rhomboid, and reniform shapes were observed. In bigtooth aspen two extreme shapes, circular and elongate, and a complete range of intermediates were found.

Statistically significant differences ( $P < .001$ ) in the blade width, blade length, petiole length, and the ratio of blade width to blade length (BW/BL) were found between *P. tremuloides* clones. Broad-sense heritabilities for these attributes, adjusted for crown class, were .80, .81, .82, and .86, respectively. The BW/BL ratio was used to contrast leaf shapes of all clones; significant differences ( $P < .001$ ) were found between clones of each species. For both species leaves of male clones had a significantly greater ( $P < .05$ ) BW/BL ratio than leaves of female clones.

The average number of teeth per leaf side for *P. tremuloides* clones was approximately 30; the average for *P. grandidentata* was approximately 10.

9. Bracts subtending male and female flowers of both species exhibited several different forms at the base of the catkin. Along the remainder of the catkin, the bracts were relatively uniform in shape, but decreased in size toward the tip. Striking interclonal differences were observed in the shape of bracts. Bracts subtending female *P. grandidentata* flowers were significantly smaller ( $P < .05$ ) than bracts subtending male flowers.

10. Delineation of ramets of naturally occurring clones is

possible through use of one or many characters (Table 5). It is accomplished most readily in the spring using flower, flushing, bark, and bole traits. In the summer two leaves per ramet selected from the central portion of short shoots 1–3 in. from the lower portion of the crown should be sufficient for comparisons. Since leaf size is significantly related to ramet age, height, diameter, and crown class, it may not be a reliable character when ramets differ markedly in those traits. Leaf shape, leaf base configuration and number of teeth are the best leaf characteristics to use.

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## Chimären mit di-, tri- und tetraploiden Chromosomenzahlen in einer Nachkommenschaft von *Chamaecyparis pisifera plumosa aurea*

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Die starke Variabilität morphologischer und physiologischer Merkmale in der Nachkommenschaft einer isoliert stehenden frei abgeblühten *Chamaecyparis pisifera plumosa aurea* (4), (5) legte eine cytologische Untersuchung nahe. Diese wurde am Mutterbaum selbst durchgeführt, der sich als diploid erwies. Weiterhin wurden zunächst an 20 im Gewächshaus eingetopften Stecklingsklonen der 4 in der Nachkommenschaft ausgeschiedenen Benadelungstypen (*sr* = *squarrosa*, *sp* = *squarrosa-plumosa*, *p* = *plumosa*, *sm* = *squamosa*) Chromosomenzählungen vorgenommen. Diese ergaben in 5 bis 6 Wurzelspitzen je Klon bei Auszählungen von je 15 bis 20 Metaphasen für 13 Klone reine Diploidie ( $2n = 22$ ). Unabhängig von der Benadelungsart wurden im Gewebe von 6 Klonen diploide und triploide Zellen (22, 33)

und in einem Klon noch zusätzlich tetraploide Chromosomenzahlen (22, 33, 44) nebeneinander gefunden (Abb. 1). Dieses Ergebnis unterscheidet sich insoweit von einem bei *Picea abies* gefundenen, als dort bei ähnlichen Untersuchungen neben normalen diploiden auch Pflanzen gefunden wurden, deren Gewebe aus Zellen mit eu- und aneuploiden Chromosomenzahlen (24–70 Chromosomen) zusammengesetzt waren. Auch rein triploide und haploide Individuen traten bei *Picea abies* auf (1), (2), (3). Eine Parallele zu dem Auftreten reiner Haplonten bei *Picea abies* fand inzwischen POHLHEIM (6) auch bei den *Cupressaceen*. Die Mutante *Thuja gigantea gracilis* erwies sich als haploid.

Weitere Aufschlüsse zu den hier vorgelegten cytologischen Befunden werden von der Untersuchung eines vom normalen abweichenden Blühverlaufs dieser *Ch. pisifera plumosa aurea* erwartet. Vom Februar bis zum Abschluß dieser Mitteilungen Anfang August (1968) wurden immer neue Entwicklungsstadien weiblicher Blüten festgestellt, die sich zu Zapfen weiter entwickelten. Diese Art der Blütenentwicklung scheint auch in ähnlicher Weise an je einem Baum von *Chamaecyparis nootkatensis* und *Ch. lawsoniana* sowie bei einem Klon von *Ch. lawsoniana* Triomf van Boskoop aufzutreten.

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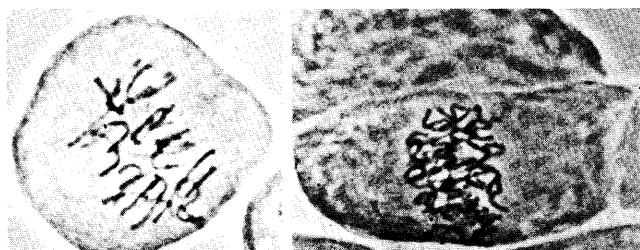


Abb. 1. — Diploide (links) und triploide (rechts) Zelle aus dem Gewebe einer Wurzelspitze. (phot. VILLWOCK)

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