1975

Phenotypic variation of trembling aspen in western North America

B.V. Barnes

Phenotypic Variation of Trembling Aspen in Western North America

Dale

BURTON V. BARNES

Abstract. Phenotypic variation of leaf, bud, and twig characters was investigated in 1,257 trembling aspen clones at 206 locations in 7 states and 1 Canadian province. Early leaves from seasonally determinate shoots of the lower crown were sampled to minimize intraclonal variation. Univariate and multivariate analyses revealed a clinal south-north gradient in leaf shape, size, and tooth number from southern Utah to northern Montana and Idaho. Nearly all clones had pubescent buds and shoots; these characteristics were most pronounced in Vancouver Island populations. Leaves from the Colorado and Columbia Plateaus closely resembled leaves of fossil Pliocene and Miocene aspens. Clones from these mostly unglaciated areas are larger than those in the northern part of the study area. ***Forest Sci. 21:319–328.***

Additional key words. Multivariate analysis, paleobotany, morphology, *Populus tremuloides*, plant geography.

TREMBLING ASPEN, *Populus tremuloides* Michaux, is the most widely distributed native tree species in North America. Its geographic distribution in western North America in particular is enormous, spanning approximately 40 degrees of latitude from northern Mexico to northern Alaska. Diversity in the western populations has been documented by Pauley and others (1963) who found differential survival and growth among different sources.

Several taxa of western aspens have been described, the most important of which are *Populus aurea* Tidestrom and *P. vancouveriana* Trelease (Barnes 1967, 1969). The differences between them and typical *P. tremuloides* are minor and in this paper a broad concept of *P. tremuloides* adopted by most authors is used.

Barnes (1967) introduced evidence of morphological differences between *P. tremuloides* from Michigan and northern Idaho, western Montana, and Washington. The western clones consistently were more pubescent on the basal scales of terminal buds than eastern *P. tremuloides*. In addition, some of the western clones had markedly fewer serrations along the leaf blade than trembling aspen in Michigan. In pubescence and leaf serration these western clones resembled hybrids between *P. tremuloides* and *P. grandidentata* Michaux and certain Asian aspens. Therefore, a study of the leaf, bud, and shoot morphology of aspen clones in the West was undertaken to gain increased understanding of their phenotypic variation and to provide a basis for comparisons with eastern populations.

Methods and Study Area

Intact shoots bearing "early" leaves (preformed in the bud the previous season, Barnes 1969) were collected from 1,257 aspen clones at 206 locations in seven western states and British Columbia, Can-

The author is Professor of Forestry, School of Natural Resources, University of Michigan, Ann Arbor, Michigan. He thanks herbaria curators of the following institutions for lending specimens: University of California, Berkeley; Unisity of Colorado, Boulder; University of Montana, Missoula; Montana State University, Bozeman; University of New Mexico, Albuquerque; University of Wyoming, Laramie. He thanks Erich Steiner, University of Michigan Matthaei Botanical Gardens, for facilities and Gary E. Andrejak for assistance. Research supported by a grant from the Horace H. Rackham School of Graduate Studies, University of Michigan. Support by funds provided under the McIntyre-Stennis Law (P.L. 87-788) is acknowledged. Manuscript received July 18, 1974.

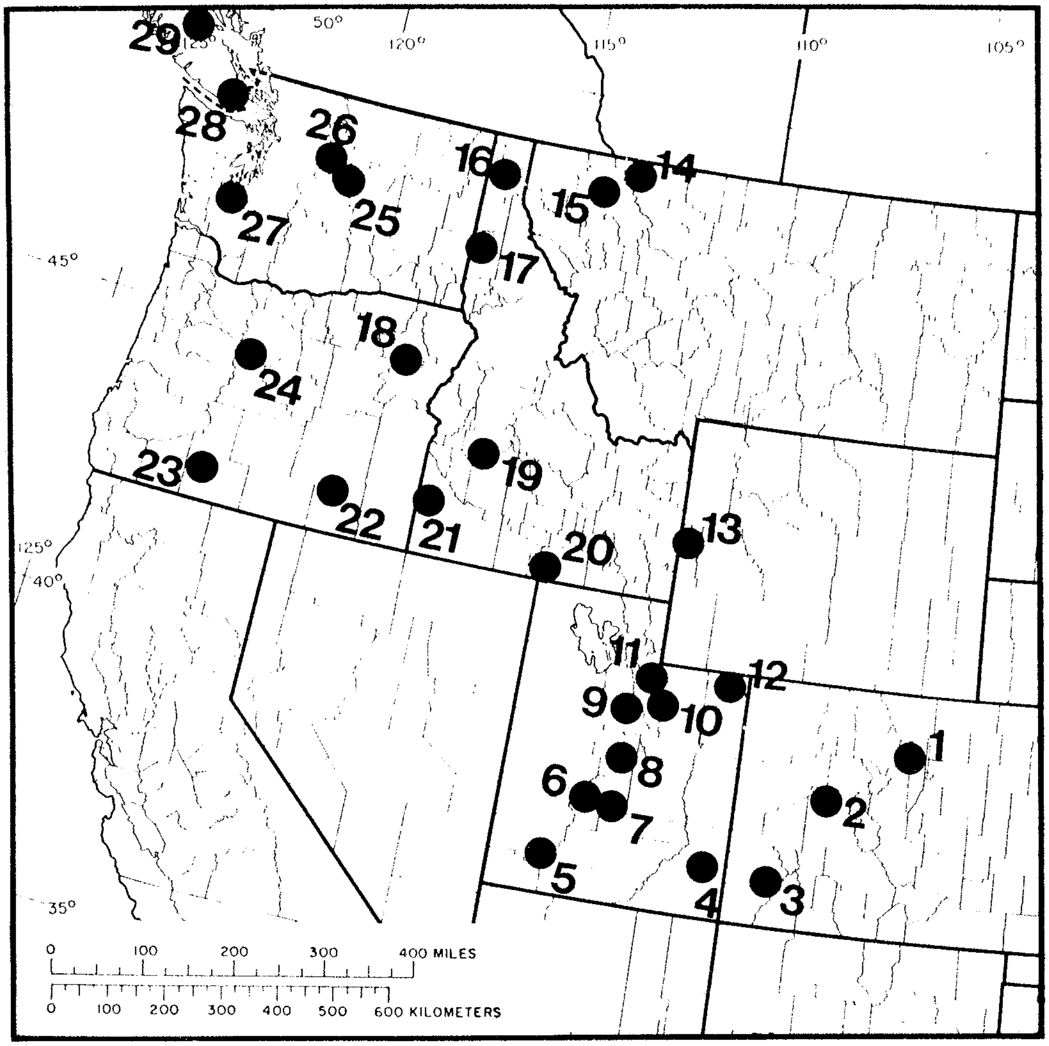


FIGURE 1. *Areas of collection for the 29 basic populations of trembling aspen.*

ada (Fig. 1). Five shoots, 2–8 cm long, were collected from the lower portion of the crown of one ramet in each clone. Clones were distinguished by leaf, bark, sex, and form characteristics (Barnes 1969). The local population was the first level of study and wherever possible six clones from each locality were sampled. The entire collection totalled 206 local-population samples.

Nine characters were measured or scored for each of five leaves per clone, each leaf usually from a different shoot. Only the middle leaf (or the one below it) of each shoot was measured. The characters were

blade width (mm)
blade length (mm)
point of maximum blade width (distance from base of blade along midrib to the point where the blade is widest) (mm)
petiole length (mm)
number of teeth along one side of the leaf blade
tooth size (scored 1–5)
bud pubescence (scored 0–6)
shoot pubescence (scored 0–6)
ratio of blade width/blade length

Within-clone variation in leaf and bud

TABLE 1. Location and means of leaf and bud characteristics for 29 basic trembling aspen populations in western North America.

No.	Location and Population Name	LAT. (deg)	ELEV. (m)	CHARACTER: Blade Width (mm)	Blade Length (mm)	Max. Width (mm)	No. Teeth	Tooth Size (score)	Petiole Lgth. (mm)	Bud Pubescence (score)	Shoot Pubescence (score)	Ratio: BW/BL
1.	Nederland, Colo.	40.03	2926	48.9	45.3	17.6	21.0	2.5	30.0	2.9	2.5	1.08
2.	West-Central, Colo.	39.12	2499	52.4	50.6	19.2	20.3	2.6	36.3	2.9	2.7	1.04
3.	Dolores, Colo.	37.75	2377	46.2	44.6	16.7	20.5	1.9	32.7	3.2	2.4	1.04
4.	Blue Mts. Ut.	37.88	2743	55.5	52.8	20.2	19.8	2.8	39.8	2.7	2.3	1.05
5.	Cedar City, Ut.	37.60	2865	55.2	51.2	19.1	22.0	2.4	36.5	3.0	2.6	1.08
6.	Rockwood-Koosharem, Ut.	38.58	2591	58.9	53.7	23.3	20.9	2.5	40.4	2.9	2.6	1.10
7.	Fish Lake, Ut.	38.55	2743	53.6	49.0	19.8	19.4	2.5	35.3	2.6	2.3	1.10
8.	Ephraim. Ut.	39.33	2743	53.3	50.5	20.6	19.3	2.5	36.6	3.2	3.1	1.06
9.	Payson-Mt. Timp., Ut.	40.36	2134	52.5	53.3	21.0	22.0	2.7	38.9	3.2	2.9	0.99
10.	Elkhorn, Ut.	40.48	2499	51.8	48.7	20.0	20.7	2.5	36.2	2.7	2.0	1.10
11.	Kamas, Ut.	40.75	2438	53.8	53.9	20.3	20.1	2.9	36.1	3.0	2.6	1.00
12.	Flaming Gorge, Ut.	40.87	2621	49.3	47.6	19.6	20.2	2.5	33.4	2.8	2.2	1.04
13.	Logan-Yellowstone, Ut., Wyo., Mont.	43.49	1981	49.7	50.6	18.0	22.6	2.2	36.7	3.2	2.6	0.98
14.	Glacier-East, Mont.	48.80	1433	52.0	49.0	17.2	23.0	2.4	35.3	3.0	2.3	1.06
15.	Glacier-West, Mont.	48.63	914	44.3	48.4	17.2	25.5	2.0	36.2	2.5	1.7	0.92
16.	Priest River, Id.	48.27	762	51.3	56.2	19.2	28.0	2.1	38.1	3.0	2.6	0.91
17.	Moscow, Id.	47.00	823	51.4	54.9	19.3	24.7	1.8	42.0	2.9	2.5	0.94
18.	Blue Mts., Ore.	45.00	1402	51.0	53.4	19.4	23.2	1.9	35.9	3.0	2.4	0.96
19.	Idaho City, Id.	43.83	1341	50.7	52.6	19.5	23.7	2.0	37.5	3.2	2.3	0.96
20.	Oakley, Id.	42.22	1329	49.1	47.9	18.0	22.8	2.4	38.5	2.8	2.3	1.03
21.	Reynolds Cr., Id.	43.07	1829	54.2	53.2	19.7	25.8	2.5	39.6	3.0	2.5	1.02
22.	Frenchglen, Ore.	42.73	2195	49.4	49.0	18.2	21.3	2.6	35.9	3.3	2.8	1.01
23.	Chiloquin, Ore.	42.70	1280	48.6	48.2	17.8	21.4	2.0	40.0	3.1	1.9	1.01
24.	Sisters, Ore.	44.42	975	48.4	51.3	19.5	23.6	2.2	36.1	2.6	1.8	0.95
25.	Mission-Entiat, Wash.	47.70	732	56.1	56.0	20.3	26.0	1.9	37.4	3.2	2.9	1.00
26.	Lake Wenatchee, Wash.	47.82	671	60.1	64.4	22.8	25.5	2.0	38.9	3.1	2.7	0.94
27.	Puget Sound, Wash.	46.83	61	61.5	64.4	23.2	29.6	2.8	41.7	3.1	2.5	0.96
28.	Vancouver Is. (So.), B. C.	48.48	30	62.1	63.6	23.2	32.0	2.7	40.6	3.9	3.1	0.98
29.	Vancouver Is. (Cent.), B. C.	49.27	91	63.3	65.4	23.1	29.8	2.5	48.3	3.4	2.1	0.97

Tabulated values are based on 13 to 189 observations.

characters was minimized in four ways by controlling (1) crown position from which leaves were collected, (2) kind of leaves and shoot (early leaves on seasonally determinate shoots), (3) length of the shoot, and (4) position of leaf on the shoot. This sampling system together with use of characters performed the previous year increases the likelihood of uncovering genetic differences among populations.

To facilitate comparisons, populations were grouped at three levels. First, the 206 populations were grouped into 79 geographically related populations based on single and multivariate analyses. Second, the 79 populations were grouped into 29 basic populations (Fig. 1) based on single and multiple analysis of variance (MANOVA), Hotelling's T-square, and canonical variates analysis (Seal 1964). The 29 basic populations were generally composed of local populations whose characteristics were not significantly different ($P < .05$) within each basic population. The 29 basic populations were grouped into 9 physiographic regions, and canonical variates analysis used to examine differences among regional populations. The grouping represented progressive agglomeration into populations having less and less similar environments.

Area and number of ramets of each clone were also estimated, as well as stem form and bark color.

Results and Discussion

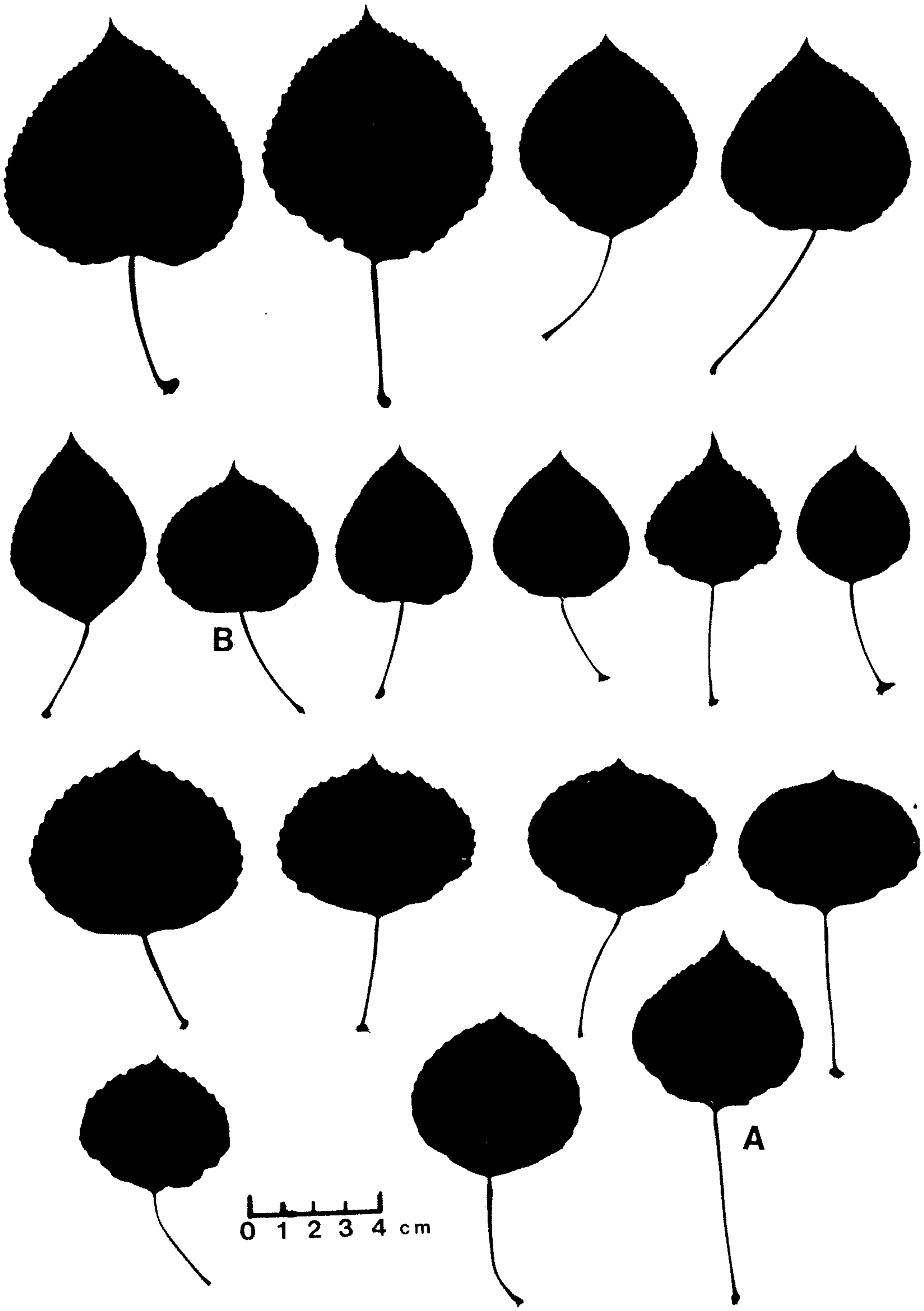
Univariate Comparisons. Considerable variation was found among the 29 populations in all traits. In leaves, size (blade width and length), shape (blade width/blade length), and number of teeth were the most important differences. Along a south-north gradient from southern Utah to northern Montana and Idaho, leaf size, primarily blade width, decreased markedly (Table 1). The trend for blade width was significantly correlated with increasing latitude ($r = -0.67$) and decreasing elevation ($r = 0.59$). The south-north trend was reversed farther to the west where small leaves were characteristic of central and southern Oregon populations 22 to 24 (Fig. 1) and large leaves typical of populations from western Washington and Vancouver Island (for blade width and latitude $r = 0.91$; for blade length and latitude $r = 0.92$).

Populations with the largest leaves (27–29, Table 1) were from western Washington and Vancouver Island, the highest latitudes and lowest elevations in the study. These areas are characterized by a mild, moist climate and a long growing season. Favorable growing conditions may explain the marked size difference between these populations and those in more arid climates west of the Cascade Mountains in Oregon (22–24) and in southern Idaho (19–21). Large leaves are also prominent in southern and central Utah (populations 4–9) and may be due in part to the high elevation with its increased rainfall and cooler climate. Nevertheless, leaves of these population were unusually large compared to other populations of high elevations in southern Idaho, northern Utah, and Colorado.

The most striking difference among the 29 basic populations was the change in leaf shape, indicated by the blade width/blade length ratio (Fig. 2, Table 1). The ratio changed from an average 1.08 in southern Utah to 0.98 in the transition zone of northern Utah and southern Montana to 0.92 in northern Idaho and northwestern Montana. Moreover, the proportion of clones with a ratio greater than 1.00 decreased markedly from 83 percent in southern Utah to 44 percent in the transition zone to only 18 percent in the northern Idaho-Montana area. Other northern populations having a low ratio included those in the Blue Mountains of Oregon, the Wenatchee, Washington areas, western Washington, and Vancouver Island. Lower latitude populations in more arid climates (1–3, 19–24) had a high ratio, 1.02, and a preponderance of clones with a ratio greater than 1.00 (59 percent). Thus, leaf shape was strongly correlated with latitude

→

FIGURE 2. *Silhouettes of representative early leaves of trembling aspen from central Utah (populations 6 and 7, bottom two rows), northwestern Montana and northern Idaho (populations 15 and 16, third row from bottom), and Vancouver Island (population 28, top row). Each leaf represents a different clone. Leaves A and B illustrate rare leaf types not typical of the respective areas.*


B
A
0 1 2 3 4 cm

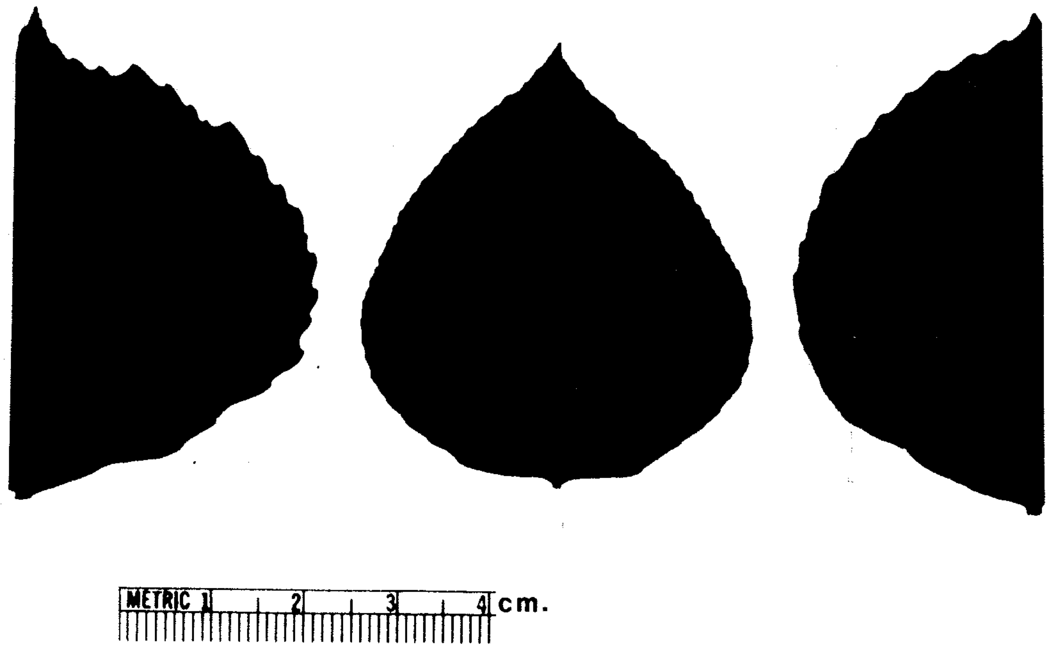


FIGURE 3. *Silhouettes of early leaves of trembling aspen from central Utah (population 7, left and right) and northwestern Montana (population 15, center) illustrating differences in serration.*

($r = -0.74$, $P < .01$) and elevation ($r = 0.78$, $P < .01$) for all 29 populations. Subsequent collections from two populations in Alberta and British Columbia, Canada (latitudes 52.03° and 50.18°) and two populations in New Mexico (latitudes 36.10° and 35.73°) confirmed the above findings. These Canadian populations had ratios of 0.90 and 0.91, those in New Mexico, 1.04 and 1.11. Herbarium material also confirmed this pattern from south to north.

A striking exception was the Glacier-East population (14, Fig. 1) which had a southern leaf shape and size (ratio—1.06; 68 percent of the clones had a ratio greater than 1.00). The Glacier-West population, just 50 air miles across the mountains, had a ratio of 0.92 and only 9 percent of its clones had a ratio greater than 1.00. The reason for the marked difference may lie in the dry, rainshadow conditions east of the Continental Divide as in more southern parts of the range. It is also possible that being separated by the northern Rocky Mountains, the two areas were repopulated in post-pleistocene times by different races.

Leaf shape differences among southern and northern populations were also demonstrated by variations in the point of maximum width. The widest portion of the leaf occurred proportionally higher in populations from southern and central Utah (at about 40 percent of the length) than in any other region. At the other extreme were clones from northern Idaho with a lower point of maximum width (34 percent; Fig. 2). For the 29 populations point of maximum width was significantly ($P < .01$) and strongly correlated with latitude ($r = -0.76$).

Tooth number was strongly related to pattern of leaf shape variation. Utah populations, especially those in southern Utah, had significantly ($P < .01$) fewer teeth than those in the northern Idaho-northwestern Montana area (Figs. 1 and 3); the former populations had 20 teeth, the latter 27. Clones of central and western Washington and Vancouver Island in particular had many teeth. This is probably related to their large leaves developed under favorable growing conditions. In contrast, leaves of dry, eastern Oregon and southern Idaho were small and had few teeth (Table 1). Tooth number was moderately correlated with leaf size in the clones of Vancouver Island, western Washington, eastern Oregon, and southern Idaho (r, blade width = 0.55, $P < .01$; r, blade length = 0.57, $P < .01$). The Utah clones, however, differed markedly; they had large leaves and few teeth (Fig. 3). They probably reduced the overall correlation of leaf size and tooth number in all clones of the 29 populations. The correlation was nevertheless significant (r, blade width = 0.25, $P < .01$; r, blade length = 0.44, $P < .01$).

Bud and shoot pubescence characterized virtually all western clones during the growing season. All but one of the 1,257 clones examined had pubescent basal scales of terminal buds and only 16 clones (one percent) lacked it on the current shoot. To determine how deciduous this pubescence was, certain clones were examined in early July, late August, and in mid-April of the following year, just before bud break. Pubescence decreased slightly from early July to late August and then to about half in winter. Thus, pubescence is partly deciduous, but is readily found on buds in winter. In striking contrast, buds of eastern American aspens are sparsely pubescent, and their shoots are typically glabrous. Hybrids between *P. grandidentata* and *P. tremuloides* are moderately pubescent on upper as well as lower bud scales. Such pubescence was not observed on buds of typical western aspens. No clinal trends in degree of pubescence were found among the western clones. Clones from Vancouver Island, however, were much more pubescent than clones in other parts of the collection area.

No major differences were found in amount of within-population variation for the nine characters among the 29 populations. At two sites, one in northern Idaho and another in central Utah, 82 and 62 clones, respectively, were collected for studying within-site variation. The coefficient of variation for the nine characters showed clones from these sites were neither more nor less variable than those elsewhere in the study area.

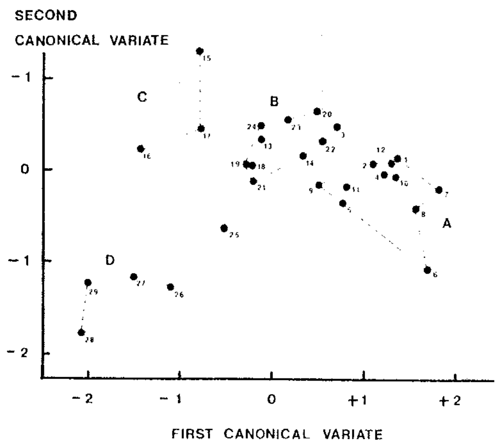


FIGURE 4. *Plot of first (horizontal axis) and second (vertical axis) canonical variates of nine morphological characteristics of 29 populations of trembling aspen in western North America.*

Multivariate Comparisons. Multicharacter analysis using MANOVA in pairwise comparisons showed populations were so different, even those closest geographically and ecologically, that only 17 of the 406 possible comparisons were not significantly different ($P > 0.05$). A more effective method of understanding population relationships using all characters simultaneously was plotting the first and second canonical variates (Fig. 4). The important characters separating populations along the horizontal axis were ratio, bud pubescence, and shoot pubescence; along the vertical axis, ratio, bud pubescence, and tooth size. The most distinctive differences were among central Utah populations (Fig. 1, A, 6–8), northern Idaho and northwestern Montana populations (C, 15–17), and the Pacific coast populations (D, 27–29). The Utah populations were distinguished from the two other groups primarily along the horizontal axis by leaf shape (ratio). The latter two groups were more northern and differentiated chiefly along the vertical axis on the basis of leaf shape, bud pubes-

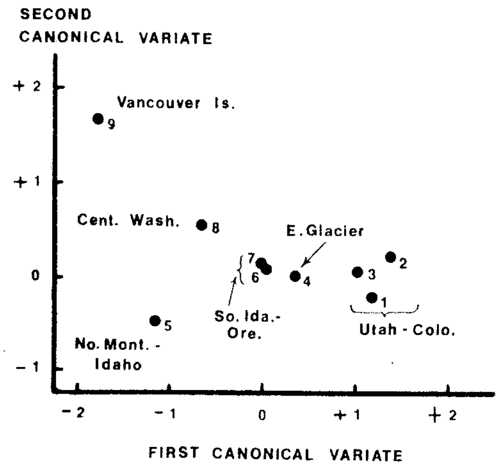


FIGURE 5. *Plot of first (horizontal axis) and second (vertical axis) canonical variates of nine regional populations of trembling aspen of western North America. The number, region, and basic populations (Fig. 1) included are as follows: 1 = central Colorado (1–2), 2 = southern Utah (3–7), 3 = central Utah (8–12), 4 = East Glacier (14), 5 = northern Montana and Idaho (15–17), 6 = southern Idaho and eastern Oregon (18–22), 7 = central Oregon (23–24), 8 = central Washington (25–26), 9 = Vancouver Island (27–29).*

cence, and tooth size. Pacific Coast populations had greater pubescence and larger teeth.

Four relatively distinct groups resulted (dashed lines in Fig. 4). Three were separated along the horizontal axis from lower right to upper left by decreasing leaf ratio, and bud and shoot pubescence. They differed markedly from the Pacific Coast sources (D) along the vertical axis due to a further decrease in this group of leaf ratio, larger teeth, and more bud pubescence. The "A" populations are from southern and central Utah and Colorado. The "B" populations are primarily those from the dry portions of Oregon east of the Cascades, southern Idaho, the transition area (13) between Utah and northern Idaho and Montana, and the Glacier-East area (14). As indicated above, many characters of the exceptional northern population 14 were much more similar to those in Utah than to clones in northwestern Montana west of the crest of the Rocky Mountains. There was a significant clinal progression in morphology from south to north—from the Colorado Plateau Province (Fenneman 1931) of Utah and Colorado (A) through the Central Rocky Mountains to the Northern Rocky Mountains (C). Clones in parts of the Columbia Plateau (B) were intermediate between those of the extreme types of the southern Colorado Plateau and the Pacific Coast (D). This picture conformed well with subjective impressions throughout the study in field observations, in measuring the leaves, and in studying univariate character means and variation.

To examine regional relationships further, the 29 populations were combined into a set of nine populations representing the major physiographic regions sampled. A canonical analysis employing nine characters was performed on this group (Fig. 5). The results demonstrated the similarity of the central Colorado and Utah populations (1, 2, and 3) and also those of eastern Oregon and southern Idaho (6 and 7). They also showed the clinal progression of populations from the Colorado Plateaus to northern Idaho and Montana. Populations from northern Idaho and northwestern Montana, central Washington, and the Pacific Coast were sharply separated on leaf ratio and bud and shoot pubescence.

Genetic Basis of Phenotypic Differences. Woody species of the North Temperate Zone are known to exhibit genetic differences in growth, phenology, and morphology along south-north gradients related to the photoperiodic regime at each point on the gradient. The major morphological differences demonstrated above, especially those between physiographic regions, probably indicate genetic differences among the populations. Using only those characters with strongest genetic control (ratio, shoot and bud pubescence, tooth number, and maximum width) canonical variates analyses were performed again on the 29 basic populations and the 9 regional populations. The same major differences were found as in the nine-character analyses (Figs. 4 and 5) suggesting a genetic basis for the major phenotypic difference.

Clone Size and Occurrence. Aspens of the Utah and Colorado collection areas (populations 1–12) differ not only in morphology from northern areas (populations 15, 16, 28, 29) but also exhibit larger clone sizes and occur in greater abundance. In the former area aspen is typically a dominant forest type at middle elevations often in pure stands. In Utah aspen dominates more mountainous terrain at altitudes between 7,000 and 10,000 feet than any other forest species (Cottam 1954). Aspen stands comprise multistemmed clones with striking differences in stem form, branching, bark color, and leaf-flushing time (Cottam 1954). Some clones are unusually large, such that Baker (1921) presumed two clones to be different races. Kemperman[1] studied 36 clones of the Fish Lake population and although most clones were less than one acre (0.4 ha) two clones were found to occupy 25 and 107 acres (11 and 43 ha). They contained about 15,000 and 47,000 ramets respectively. In contrast, clones of the northern areas were much smaller, relegated to recently cut or burned sites, and relatively infrequent in the conifer-dominated forest. Seedlings are much more common in the northern range and often appear in fresh clear cuts and burned-over sites (Barnes 1966). In one area south of Priest River, Idaho, 82 clones were sampled (mostly one-tree clones) in a pasture that could easily have supported one of the large clones of central Utah or western Colorado. Nevertheless, seedling aspens, although rare, have been reported in Utah by Ellison (1943), Larson (1944), and Every and Wiens (1971).

Comparison With Fossil Aspens. The morphological differences among regional populations (Fig. 5) probably indicate genetically different races derived through adaptation to markedly different environments. The major differences between northern and southern populations may reflect evolutionary differences dating back at least to Pliocene or Miocene times. The fossil aspen record reveals that trembling aspen (*Populus pliotremuloides* Axelrod) was widespread in Pliocene times, perhaps even more so than today (Axelrod 1941). A somewhat larger-leaved type, principally *Populus voyana* Chaney and Axelrod, was present in Miocene times. Axelrod (1941) stated that leaves of *P. pliotremuloides* were indistinguishable from living aspens in the drier portions of their range in the western United States. Chaney (1938) and Wolfe (1964) also reported that fossil aspens closely resemble extant trembling aspen. Many fossil aspen leaves do closely resemble modern-day clones in the central and southern portions of this study. Almost all of the fossil early leaves are wider than long. For example, Chaney reported that *P. pliotremuloides* leaves of the Lower to Middle Pliocene Deschutes flora of eastern Oregon averaged 3.4 × 3 cm (ratio = 1.13). The leaf margins of the fossil leaves resemble those of the central and southern collection areas rather than those of the northern populations west of the Continental Divide. Existing clones of central and southern areas (populations 1–12, 19–24) seem to be much as they were in Pliocene or Miocene times. The areas occupied by these populations were mostly unglaciated. Compared to those in the northern areas, these clones may be far fewer sexual generations removed from their Pliocene ancestors. Perhaps a few are the very clones that were established in that early time and propagated vegetatively to the present. The enormous size of many of the clones in Utah and Colorado, compared to those in glaciated areas of both western and eastern North America, also suggests a much greater age.

Clone size, however, is also related to climatic and disturbance factors which affect the number of seedlings established, competition among clones, and competition between clones and tolerant invading species. Nevertheless, the severe effects of Pleistocene glaciation and the strong competition from more tolerant conifers has probably acted to reduce clone age in the north compared with clones of the mostly

[1] Kemperman, Jerry A. 1970. Study of a population of trembling aspen clones in south-central Utah. Master's thesis, University of Michigan, Ann Arbor. 42 p.

unglaciated southern areas. Large clone size in these areas may indicate that few seedlings were originally established.

Some clones of Utah populations resemble Asian aspens (*P. rotundifolia* and *P. bonati*) more closely than clones of the northern United States and adjacent Canada in the West or those typical of eastern North America. The possibility of close relationship of southern Rocky Mountain aspen populations to those in Asia is suggested by Weber's (1965) statement that:

> The Southern Rockies constitute one terminus of a track that once led from the mountains of Central Asia to the Mexican Plateau. On the American continent the area holds the greatest concentration of circumpolar species at their southern limits.

In contrast to aspens of the Southern Rocky Mountains, northern populations generally resemble eastern *P. tremuloides*, which is also found almost exclusively on glaciated terrain. Northern clones, like those in the East, are probably relatively young as indicated by their small size and their almost exclusive occurrence on recently disturbed sites.

Literature Cited

AXELROD, DANIEL I. 1941. The concept of ecospecies in Tertiary paleobotany. Proc Natl Acad Sci 27:545–551.

BAKER, F. S. 1921. Two races of aspen. J For 19:412–413.

BARNES, BURTON V. 1966. The clonal growth habit of American aspens. Ecology 47:439–447.

———. 1967. Indications of possible mid-Cenozoic hybridization in aspens of the Columbia Plateau. Rhodora 69:70–81.

———. 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. grandidentata* in northern Lower Michigan. Silvae Genetica 18:130–142.

CHANEY, RALPH W. 1938. The Deschutes flora of eastern Oregon. Carnegie Inst Wash Publ 476:185–216.

COTTAM, WALTER P. 1954. Prevernal leafing of aspen in Utah mountains. J Arnold Arbor 35:239–250.

ELLISON, LINCOLN. 1943. A natural seedling of western aspen. J For 41:767–768.

EVERY, A. DAVID, and DELBERT WIENS. 1971. Triploidy in Utah aspen. Madroño 21:138–147.

FENNEMAN, NEVIN M. 1931. Physiography of western United States. McGraw-Hill Book Co., New York. 534 p.

LARSON, GEORGE C. 1944. More on seedlings of western aspen. J For 42:452.

PAULEY, S., A. G. JOHNSON, and F. S. SANTAMOUR, JR. 1963. Results of aspen screening tests: I. Seed sources of quaking aspen (*P. tremuloides* Michaux). Minn For Notes 136, 2 p.

SEAL, HILARY L. 1964. Multivariate statistical analysis for biologists. Methuen & Co., Ltd., London. 209 p.

WEBER, W. A. 1965. Plant geography in the Southern Rocky Mountains. p. 453–468, *in* H. E. Wright, Jr., and David G. Frey (eds.), The Quaternary of the United States. Princeton Univ. Press, Princeton, N. J. 922 p.

WOLFE, J. A. 1964. Miocene floras from Fingerrock Wash., southwestern Nevada. US Geol Surv Prof Pap 454-N, 36 p.