Genetic Uifferences in Stem Form of Ponderosa Pine Grown in Michigan

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A major objective in most forest tree improvement programs is to select and breed geographic races and individual trees for superior growth. Many investigators have studied genetic variation in total height and diameter. However, only a few have studied the inheritance of stem form (Callaham and Liddicoet, 1961; Johnsson, 1960; Nilsson, 1968; Pederick, 1970; Squillace and Silen, 1962). Whether the objective is to produce timber or pulpwood, it is generally considered desirable to grow trees that have little taper (Johnsson, 1960; Larson, 1963). Trees with little taper have a more cylindrical stem and, hence, more wood volume than trees with much taper.

In uninodal species, stem form may be studied by measuring two or more diameters at the midpoints of different internodes. Hence, taper equals the diameter/diameter ratio — the method used here for studying variations in stem form.

The primary objective of this study was to determine if there are significant differences in taper for different geographic sources of ponderosa pine (Pinus ponderosa Laws.).

Materials and Methods

The observations for this study were made in a range-wide provenance test of ponderosa pine at the W. K. Kellogg Forest in southwestern Michigan. In this plantation, 55 seed collections were arranged in a randomized complete-block design with 7 replicates and 6-tree row plots. The sources represented a large portion of the species range in the western United States. The 2-0 seedlings were planted on a sandy loam soil at 8- by 8-foot spacing in 1962. Weed control was practiced for 3 years after planting. Wells (1964a, 1964b) reported on this material while it was in the nursery, and Wright et al. (1969) reported on the subsequent outplanting.

Three traits were measured at age 10 from seed: (1) total height; (2) basal diameter at 6 inches above ground; and (3) "mid-diameter", which was defined as the midpoint of the fourth internode from the top. Taper was then determined as the ratio of mid-diameter to basal diameter.

A disadvantage of this method of measuring taper is that the length of stem between diameters is an unknown variable. However, a compensating advantage is that the measurement of diameter at the midpoint of the same internode in all trees insures that physiological age is held constant, because that diameter represents a constant number of growth rings from the pith. Hence, internodal diameters and their ratios should not be confounded by year-to-year variations in radial growth resulting from fluctuations in annual rainfall. This method, based as it is on a constant age difference rather than on a constant stem length, means that taper as defined in this study is not comparable in a strict sense to taper as it is usually measured.

A two-level nested analysis of variance with unequal subclass numbers was used to detect the amount of variation between varieties and among ecotypes within varieties. Origin means were used as subsamples within ecotypes. For the analysis, two varieties of ponderosa pine, Pacific Coast variety ponderosa and Interior variety scopulorum, were compared (Figure 1). All trees west of the dashed line extending from western Montana to southern California are considered to be of the former, while those to the east of it are considered to be of the latter. A third variety, *Arizonica* (Engelm.) Shaw, was not considered. Although differences among ecotypes within varieties were found for certain traits of growth rate and stem form, they will not be discussed because this paper is concerned with varietal differences.

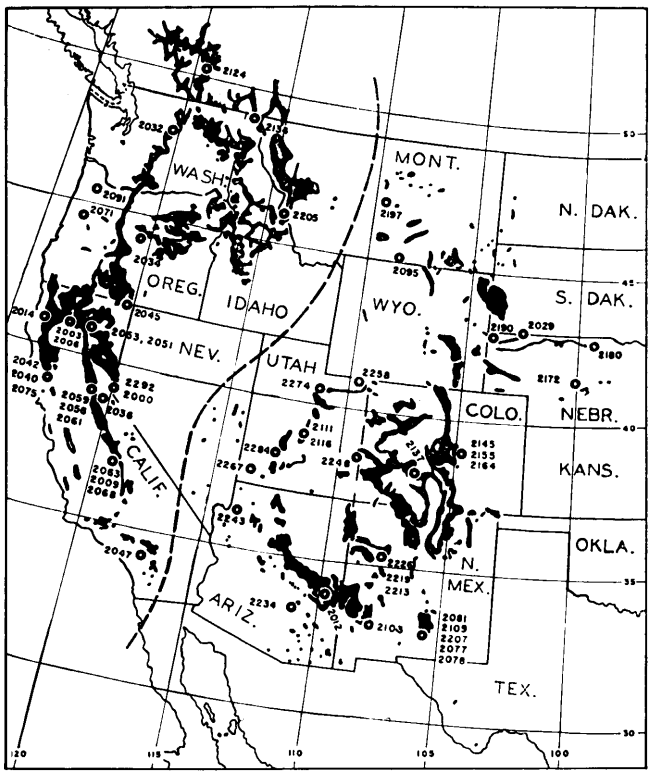

Figure 1. — Natural distribution of ponderosa pine, including thc origins of 55 seedlots comprising the provenance test at the W. K. Kellogg Forest (Wells, 1964 a).

The separations used in this paper are those originally proposed by Wells (1964 a, 1964 b). Although these separations may not be perfect natural entities, they seem to describe adequately the variation patterns considered.

Results and Discussion

The Pacific Coast variety ponderosa had higher taper values (less taper) and thus was more cylindrical than the Interior variety scopulorum (Table 1). This strong difference was evident despite considerable variation in height and diameter growth within each variety (Table 2).

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Possible Adaptive Response to Regional Climatic Differences

Ponderosa pine occurs mostly within the arid transition zones of the West, where many climatic types occur.

Response to seasonal rainfall distribution. — The most striking difference between the regions occupied by the two varieties is in the ratio of July-August to annual precipitation. The Pacific Coast variety *ponderosa* occupies a summer-dry region in which only 1% to 8% (0.40 to 1.44 inches) of the total annual precipitation occurs during July and August. The Interior variety *scopulorum* occupies a summer-moist region in which 14% to 34% (3.22 to 7.82 inches) of the total annual precipitation occurs during the two summer months (U. S. Department of Agriculture, 1941).

The ratio of July-August to annual precipitation is the only observed factor which varies strongly between the two regions in a manner that parallels the difference in taper between the two varieties *(Tables 1 and 2).* There is no obvious selective advantage to cylindrical stems in a summer-dry environment. However, in such an environment, trees in which little or no photosynthate is translocated to the lower bole in the summer months may have a selective advantage over those which produce equal increments of summerwood over the total length of the stem. Although the radial growth responses of different genotypes to seasonal differences in water stress were not studied, it is reasonable to assume that, if taper responds in some way to water stress, water deficits occurring during July and August would exert the greatest selection pressure. Stem taper is a function of radial growth, and radial growth occurs later in the growing season than does height growth, most of which occurs in the spring (Larson, 1963). It follows that variations in stem form are most likely to be controlled by differences in summer rainfall, which affects the controls of radial growth.

Response to mean annual precipitation. — Total annual precipitation is generally greater in the region occupied by the Pacific Coast variety *ponderosa* than in that inhabited by the Interior variety *scopulorum.* However, because of considerable variation in total annual rainfall within each region (18—46 inches and 19—31 inches, respectively), the difference in total rainfall between regions is not as large as is the difference in the seasonal distribution of precipitation. Further, the relationship of annual precipitation to taper is not apparent.

Table 1. — Means for total height, basal diameter, mid-diameter, and taper according to variety and ecotype in ponderosa pine.[1])

Variety and ecotype	Total height	Diameter		Taper (= ratio of mid- to basal diameter)
		Basal	Mid	
	feet	*inches*	*inches*	*inches/inches*
ponderosa				
North. Plateau	9.2a	3.8a	2.4a	0.619a
Coastal Oregon	7.6b	3.4ab	2.1b	0.638a
Nevada	6.5b	3.2b	2.0b	0.638a
North. Calif.	6.7b	3.0b	2.0b	0.653a
South. Calif.	5.9c	2.8c	1.8b	0.646a
Average	7.0	3.2	2.0	0.636
scopulorum				
North. Interior	8.6a	3.5ab	1.9ab	0.536b
Colorado	6.8b	3.0b	1.7b	0.588a
Utah	6.4c	3.0b	1.7b	0.578ab
Utah — north. New Mexico	7.8ab	3.7a	2.1a	0.553ab
Ariz. — south New Mexico	7.6ab	3.6a	2.0ab	0.559ab
Average	7.6	3.4	1.9	0.560

[1]) Within each column for a variety, means not followed by the same letter are significantly different at the 5% level according to the Student-Newman-Keuls test.

Table 2. — Percentages of total variance in height, diameter, and taper accounted for by differences among varieties, ecotypes, and seedlots of ponderosa pine.

Source of variation	Percentages of total variance			
	Total height	Diameter		Taper (= ratio of mid- to basal diameter)
		Basal	Mid	
Variety	0	0	0	77***
Ecotype within variety	68***	56***	51***	4
Seedlot within ecotype	32	44	49	19
Total	100	100	100	100

***Significant at the 0.1% probability level on the basis of an analysis of variance with 1, 8, and 45 degrees of freedom for variety, ecotype, and seedlot, respectively.

Response to wetness of snow. — One environmental factor which is a function of both moisture and temperature is wetness of snow. Because the Pacific Coast region is warmer and more moist in winter than is the Interior, wet snow occurs there with greater frequency.

Selection for resistance to breakage of stems and branches by wet snow could affect stem form. A more cylindrical stem would seem to be structurally more resistant to breakage in its upper portion than would a conical stem. In areas of heavy snow, slender crowns permit maximum crown vigor while providing smaller branches which retain less snow than the long branches on wide crowns. Several investigators have observed more cylindrical stem form with increasing latitude and elevation in Scotch pine and have attributed this trend to resistance to snow breakage (Larson, 1963).

Response to wind velocity. — Another possible explanation of varietal differences is that conical stem taper bestows a selective advantage for resistance to wind. Larson (1963) reviewed literature relating stem form to wind resistance. Generally, tree boles in windy areas are more conical than those in areas with less wind.

The conical boles of the Interior variety *scopulorum* are better adapted to wind stress than are the cylindrical boles of the Pacific Coast variety *ponderosa.* However, for this factor to be important, the trees of the Interior variety must be frequently exposed to more severe winds than are the trees of the Pacific Coast variety. Data obtained from the U. S. Department of Commerce (1969) revealed only slight differences in average and maximum wind speeds between the Pacifc Coast and Interior regions. Average wind velocity at 11 stations in the Pacific Coast region was 8.2 m.p.h., and maximum velocity was 65.0 m.p.h. The corresponding figures at 16 stations from the Interior region were 9.9 m.p.h. and 68.3 m.p.h.. The differences between regions were not significant.

In Australia, Jacobs (1954) showed that the diameter growth of pine trees prevented from swaying by guy wires was so reduced that they were no longer able to support themselves when the wires were removed. This reduction in growth suggests that the stems of pine trees have a considerable plasticity of responses to changes in wind

stress. Such plasticity would seem to preclude differences in average wind velocity of 1.7 m.p.h. or in maximum velocity of 3.3 m.p.h. as being large enough to cause this varietal difference.

Response to different habitats. — The habitats associated with each variety may affect stem form. Habitat is affected by each of the climatic factors discussed above. Exposure to wind varies with stand density, which differs between the two varieties. The higher annual precipitation of the Pacific Coast region favors relatively dense stands. Ponderosa pine typically grows in open, parklike stands in the Interior. Trees growing in dense stands are less exposed to wind stress than are trees growing in open stands. Hence, the trees of the Interior variety *scopulorum* might have developed a conical stem form as an adaptation to growth in open stands.

Adaptation Versus Genetic Drift

Finally, the possibility remains that taper evolved as a nonadaptive trait. It can be argued that isolation and restricted population sizes during glacial advances could have resulted in random genetic drift. However, the geological events of the last three epochs would seem to favor adaptation as the best explanation of the observed differences in stem form.

The Great Basin, in which ponderosa pine originally occurred, was formed by crustal uplift in the early and middle Miocene (Dunbar, 1960). However, the species was probably not divided into two populations until late Pliocene or middle Pleistocene times. According to Dunbar (1960), the greatest crustal upheaval in California occurred in the middle Pleistocene. Once crustal uplift had changed the terrain and climate of the Great Basin, the environment of this region could no longer support ponderosa pine. The species was forced to migrate to slightly moister sites at higher elevations both east and west of the Great Basin. Hence, two populations were created.

The Pleistocene is distinguished from the Pliocene by the occurrence of four major glaciations. The Great Basin was a nonglaciated region (Flint, 1957). However, Flint and Gale (1958) reported evidence of pluvial periods corresponding to the two most recent glaciations. Stratigraphic columns and radiocarbon dates from Lake Searles, California, indicate that the earliest pluvial period began about 46,000 years ago. Further, Roosma (1958) found juniper pollen in the mud portions of such columns and sagebrush pollen in the saline section. Pine pollen was not found.

Woodbury (1947) reported that a juniper-pinyon community in northern Arizona and Utah lies mainly within the 10- to 15-inch belt of annual precipitation. In contrast, the lower limit for ponderosa pine is about 15 inches. From this evidence, it appears that the climate within the Great Basin did not become sufficiently moist during pluvial periods for ponderosa pine to reoccupy the region. Hence, the two varieties were possibly separated as early as the Miocene and no later than the middle Pleistocene.

In the context of this geologic sequence, it seems most likely that differentiation between the two varieties is the result of adaptation to climatic and ecological changes that have been developing since the middle or early Pleistocene.

Varietal Differences in Other Traits

In this provenance test, strong differences between varieties have also been observed for other traits. Wright *et al.* (1969) showed that the Pacific Coast variety *ponderosa* has redder bud color, more appressed bud scales, and significantly greater amounts of N, P, K, B, and Ca than the Interior variety *scopulorum*. Also, in a Nebraska plantation containing the same ecotypes as the present study, Read (1971) observed that the Pacific Coast variety was more heavily browsed by jackrabbits.

The differences in these traits could have arisen independently, or selection could have caused the difference in one trait and differentiation in the other traits could have followed because of some genetic or physiological association. For example, foliar mineral content could affect metabolic activity in the crown in such a way as to affect auxin transport and, hence, wood formation in the stem.

Summary

In a rangewide provenance test of ponderosa pine grown in Michigan, taper differed strongly between varieties at age 10 from seed. (Taper was defined as the ratio of the diameter at the midpoint of the fourth internode from the top to basal diameter 6 inches from the ground.) The Pacific Coast variety *ponderosa* was the most cylindrical, whereas the Interior variety *scopulorum* was the most conical.

This strong difference is discussed in terms of possbile adaptive responses to regional differences in climate. The most striking is the ratio of July-August to annual precipitation, but the selective advantage to cylindrical stems in the summer-dry environment of the Pacific Coast is not clear. The other regional differences discussed are mean annual precipitation, wetness of snow, wind velocity, and habitat. The possibility of genetic drift following crustal upheaval in the Pleistocene and the resulting separation of the two populations is also considered.

Key words: Pinus ponderosa, taper, internode, variety, ecotype, provenance, pluvial, stratigraphic.

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