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HYBRIDIZATION AND VARIATION OF PONDEROSA AND JEFFREY PINES ON MT. SAN ANTONIO, CALIFORNIA¹

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INTRODUCTION

The purpose of this study is to determine whether plants having the characteristics of *Pinus ponderosa* or *Pinus jeffreyi* occur in allopatric or sympatric patterns of ecological distribution. If ecological conditions do permit the two pines to exist in a sympatric situation, occurrences of hybridization would be significant.

Several authors have questioned the taxonomic and genetic interrelationships of the ponderosa (western yellow) pine, *Pinus ponderosa* Dougl. ex P. and C. Lawson, and the Jeffrey pine, *Pinus jeffreyi* Grev. and Balf. in A. Murr. Although two recognizable extremes do exist, the question of the degree of genetic continuity between the two pines is unsolved and at present controversial. In 1929, N. T. Mirov established numerous chemical differences between the resins of the ponderosa and Jeffrey pines. The resin of *P. jeffreyi* contains traces of straight-chain aldehydes not found in the terpene mixture unique to *P. ponderosa*. He found that these chemical differences rarely combine in supposed hybrid individuals.

In 1953, D. A. Johansen established morphological criteria for the specific validity of the Jeffrey pine. He summarized some 14 archegonial characteristics of the megagametophyte which differed markedly from those of the ponderosa pine. He also noted several pines in upper San Antonio Canyon (Mt. San Antonio, California) which had a combination of archegonial characteristics different from the ponderosa pine and unlike those of the Jeffrey pine. These trees were previously regarded as variations of *P. ponderosa*. However, Johansen's analysis of the archegonia showed the individuals to be either hybrids or a taxon constituting an unrecognized species.

L. D. Benson (1955) and a group of students made a survey of the ponderosa-Jeffrey pine complex on the southern and eastern slopes of Mt. Pinos (Santa Emigdio Range). At elevations approaching 7,750 ft., the combination of char-

¹Based on a thesis presented in partial fulfillment of the requirement for the degree of Master of Arts in the Claremont Graduate School. The work was done at the Rancho Santa Ana Botanic Garden under the supervision of Professors Lyman Benson, Sherwin Carlquist, and Robert Thorne.

acteristics followed a relatively pure *P. jeffreyi* segregation pattern. However, at the 6,300 ft. level, many individuals had characteristics of each species in nearly equal proportions. The data were derived through the quantification of five characteristics using a hybrid-index scale (Anderson, 1949).

An important later study by J. R. Haller (1962) also used Anderson's hybrid-index method. Fifteen characteristics were quantified and applied to an analysis of several ponderosa and Jeffrey pine populations throughout Californian montane regions. Haller found that the frequency of hybridization was very low in all areas. The marked diversity of characteristics within a given individual was attributed to the wide variability of the taxa. However, Haller's quantification of a given characteristic on only a three point scale (0=ponderosa-like, 1=intermediate, 2=Jeffrey-like) could obscure segregation of characteristics within a putative hybrid zone. A greater, yet reasonable numerical range for a given characteristic enables one to work with degrees of phenotypic differences. This type of analysis is more dimensional and should reveal the nature of hybridization in which multiple-factor segregation is occurring.

Various earlier studies and observations have suggested that hybridization between Jeffrey and ponderosa pine is actively occurring within a certain zone on Mt. San Antonio, California. Since past studies concerning the ponderosa-Jeffrey pine complexes have either been superficial or based upon too few criteria, I undertook an intensive study of the Mt. San Antonio area. Some four years of analysis and field work were undertaken to test the degree and nature of hybridization, to supply comparisons with "pure" populations, and to describe the ecological background of this hybridization. The "pure" or allopatric populations of both species were studied in isolated areas near Mt. San Antonio and elsewhere within the same mountain range (San Gabriel Range).

On completing this investigation, I co-operated with a colleague in making a comparative study of the bark chemistry of the ponderosa-Jeffrey pine complex on Mt. San Antonio. Chromatographic analysis of phenols and tannins revealed a distinct pattern difference between the two species.² Hybrid individuals detected by morphological methods in this paper were verified by plausible intermediate chromatogram patterns (unpublished data).

DISTRIBUTION AND ECOLOGY

In California, *Pinus ponderosa* is common in the montane forests from the Oregon border through the Cascades, the inner North Coast Ranges, and the western slopes of the Sierra Nevada. The species occurs sporadically through the South Coast Ranges, becoming more abundant in the higher mountains that comprise the Transverse and Peninsular ranges. The southern limit of the ponderosa pine in California is near Cuyamaca Reservoir in San Diego County.

Pinus jeffreyi is restricted to southern Oregon, California, and northern Baja California and its distribution approximates the geographic range of the ponderosa pine. However, the Jeffrey pine is more abundant in the south and occurs in relatively large stands within the Sierra de San Pedro Mártir in Baja California.

²The concept of "species" in relation to *Pinus* will be discussed later.

Typically, *P. ponderosa* occupies lower, coastal-facing slopes of the major mountain axes, while *P. jeffreyi* is characteristic at higher elevations and on dry, desert-facing slopes.

Studies by other authors as well as my observations show that extremes of the ponderosa-Jeffrey pine complex are relatively homogenous. Within the mountain ranges of Southern California, *P. ponderosa* generally occurs between 5,000 and 7,000 ft., whereas *P. jeffreyi* characteristically occupies the 7,000–10,000 foot zones. On Mt. San Antonio, the stands between 5,600 and 6,600 ft. appear to be almost uniform *P. ponderosa*, whereas between 7,000 and 9,500 ft. most individuals are *P. jeffreyi*.

Apparently differential tolerances of the two species to various ecological factors partially dictate their elevational zonation. On the south-facing slope of Mt. San Antonio, the lower elevational limit of *P. ponderosa* is approximately 5,600 ft. Lack of adequate precipitation (under 25–28 inches annually) is often the limiting factor at this lower level. However, weather readings from the Camp Baldy Fire Station (1950–1963) indicate precipitation averaging some 31 inches per year at the 4,200 ft. level, a quantity in excess of the minimum water requirement for the ponderosa pine. Apparently other factors combine to limit *P. ponderosa* at the 5,600 ft. level. Occupation of this area by dense chaparral growth and other conifers may be a limiting factor. The ponderosa pine generally occurs in open montane forests where individual trees are well spaced from other vegetation. However, in this local situation, large numbers of *Pseudotsuga macrocarpa*, *Calocedrus decurrens*, *Pinus lambertiana*, *Quercus chrysolepis*, *Cercocarpus betuloides*, *Eriogonum fasciculatum*, and other species seem more successful than *Pinus ponderosa*.

High concentrations of soluble soil salts at this elevation may be correlated with the abundant chaparral vegetation. Using a salinity meter and soil cores, I measured the electrolytic conductivity of the soil. Negligible readings were found between 5,700 and 9,600 ft., while at 5,500 ft. the reading was 2.00 mm/per cm. Perhaps *P. ponderosa* cannot tolerate this saline condition, whereas the chaparral vegetation thrives in such a habitat.

The upper limits of *P. ponderosa* on this mountain (between 6,500 and 6,600 ft.) are probably controlled by low temperatures and lack of adequate precipitation. The cold, dry conditions of Mt. San Antonio's north face continue to some extent on the south-facing slopes. Apparently, environmental conditions enable only a narrow band of ponderosa pine to exist (a vertical 800–900 ft. zone), while the more drought-resistant and temperature-tolerant Jeffrey pine extends through a much wider elevational range (approximately 2,500 ft.). Wide temperature extremes in the Jeffrey pine belt are evidenced in statistics obtained from the Los Angeles County Flood Control District (1964). At 7,800 ft. (Mt. San Antonio Pass or "the Notch"), the average maximum temperature was 90°F and the average minimum was 4°F over the past six years. Such conditions appear magnified on the north-facing slopes where *P. jeffreyi* extends down to the 5,000 ft. level. Here the ponderosa pine is virtually absent.

The upper limits of *P. jeffreyi* on the south-facing slope of Mt. San Antonio are near the 9,500 ft. level. Here low temperatures, rapid fluctuations from day to night, and incessant drying winds permit development only of stunted specimens

of Jeffrey pine (Fig. 1). The climatic conditions here correspond closely with those encountered in a subalpine environment (Horton, 1960). Both species are restricted in their upper distributional limits by low temperature. However, as noted above, *P. jeffreyi* is tolerant of much lower temperatures than *P. ponderosa*.

Apparently, within a given range at either end of the elevational scale, stands of *Pinus ponderosa* (lower range) and *Pinus jeffreyi* (upper range) occur as distinct species. In summation, *P. jeffreyi* seems more tolerant of low temperatures and aridity than *P. ponderosa* and equally tolerant of high temperatures and high quantities of soil moisture (Haller, 1962).

A species is limited where the range of its tolerances is exceeded by the range of environmental factors. Since the ecological requirements of the two pines appear to overlap, some sympatry might be expected. In sympatric populations it is very possible that hybridization might occur if genetic barriers are not too strong. Within the 6,600–7,000 ft. elevational ranges on Mt. San Antonio, casual inspection reveals characteristics of both species in a seemingly random pattern. Protected cold pockets within this zone support some individuals of *P. jeffreyi* to about 6,700 ft., with some individuals having characteristics of Jeffrey pine scattered as low as 6,300 ft. Conversely, some individuals with character combinations approaching those of *P. ponderosa* appear to tolerate the low temperatures and may be found up to elevations of 7,500 ft. Above this level they are probably absent due to environmental extremes.

The net result of these overlapping ecological conditions in this narrow zone appears to be a situation wherein the individuals show character combinations from both taxa. In the center of this zone, about 6,750 ft., it appears that many individuals do not clearly conform to either species in question. Characteristics alien to *P. jeffreyi* decrease steadily above this zone, whereas individuals below this zone tend toward *P. ponderosa* with decrease in altitude.

MT. SAN ANTONIO TRANSECTS

GENERAL LOCATION AND TOPOGRAPHY

The major study area was on the south face of Mt. San Antonio (Mt. Baldy) and down the upper portion of San Antonio Canyon. Mt. San Antonio is in the San Gabriel Mountains, a large granitic mass of eroded and faulted ridges situated transversely (NE–SW) in relation to the Pacific Coast. The greater portion of this mountain lies in the Angeles National Forest, San Bernardino County. Mt. San Antonio is 13 air miles north of Upland and five air miles south of Wrightwood which borders the Mojave Desert. The Mt. San Antonio area is dissected into an intricate arrangement of deep, V-shaped canyons and sharp, narrow ridges which form a very rugged terrain (Fig. 2). The distance from the summit of Mt. San Antonio (10,064) to the Glacier Camp area (5,600) is only 2.5 air miles. This abrupt drop of some 4,400 ft. displays the entire ecological-distribu-

Fig. 1–2.—Fig. 1. A highly contorted and prostrate specimen of *Pinus jeffreyi* at the 9,500 ft. level.—Fig. 2. General topography of the Mt. San Antonio area. The open montane forest is a typical habitat of both *Pinus ponderosa* and *Pinus jeffreyi*.

tional range of the ponderosa-Jeffrey pine complex and is therefore an ideal location for a study of this nature.

LOCATION AND SIZE OF SAMPLE AREAS

A series of two closely parallel transects was run from the Mt. San Antonio Saddle (9,500 ft. level and the upper distributional limits of *P. jeffreyi*), along the Devil's Backbone to the Mt. Baldy Notch (Mt. San Antonio Pass, 7,800 ft.), down to the base of the first ski lift, and then along the valley floor of upper San Antonio Canyon to Glacier Camp (5,600 ft. and the lower distributional limits of *P. ponderosa*). The transect is shown in Fig. 3.

Analyses were made of the ponderosa-Jeffrey pine complex at approximately every 200 ft. rise along the transect line. The analyzed taxa were selected in a random manner within a close range of any given elevation. Attempts were made to select for study only trees on a south- or southeast-facing slope to minimize the effects of slight environmental changes.

SCORING TECHNIQUES

At approximately each of the 200 ft. elevational spans, 30 individuals were analyzed using the hybrid-index method (Anderson, 1949). During the study, two different transects were run in close proximity to one another. Thus, 15 individuals were studied at each designated elevation in each of the transects. Twelve morphological characteristics were quantified on a five point scale (0-4) giving a possible 0-48 point index range for each individual studied (Table 2). The average index score for the 15 individuals studied gives an index score for that particular elevation. A more accurate indication of the genetic situation for a given elevation is found by averaging the two sets of index scores. The index scores in Fig. 6 were determined by using this average. Although some of the characteristics in this analysis are more definitive than others, the use of 12 characteristics of equal index value minimizes the effect of a single feature and enables one to detect possible degrees of hybridization.

METHODS

Well spaced individuals were chosen for analysis at a given level to avoid effects of overcrowding which might detract from the true characteristics of the trees. Individuals in close proximity to one another were generally avoided to reduce the chances of sampling the progeny of one individual. Samples of foliage and ovulate cones were obtained by the use of pruning shears with a 25-ft. handle extension. Those samples used for quantitative analyses were selected to be as representative of the individual as possible. Contrary to views of some workers (Bradshaw, 1941), the two species are practically inseparable morphologically during juvenile stages. Thus, sampling included only mature individuals (150-350 years as determined by core samplings). Population samples of each individual studied were collected and catalogued as part of a verification record. Complete herbarium specimens of representative samples were collected for

Fig. 3. Map section showing transect route on Mt. San Antonio. Sections 4-6, 8-9, and 17 are within R. 7W, T. 2N. The broken line represents the transect routes, the two parallel lines the lower ski lift, and the thick, dark line the road running through San Antonio Canyon.

each elevation surveyed. These document the above evidence and form a foundation for the quantified hybrid-index. These samples are included on herbarium sheets (*Parratt* 459-473, POM). Complete herbarium specimens are recorded under the following numbers: Mt. San Antonio transect (*Parratt* 419-442, RSA); Charlton and Barley Flats (*Parratt* 620-623, RSA); Table Mountain (*Parratt* 601-608, RSA).

OTHER STUDY AREAS

In order to establish a comparative norm for using this hybrid-index scale, known allopatric populations of both taxa were analyzed in nearby locations on the same mountain range. An analysis of relatively homogenous populations of either species enables one to determine the ranges of morphological variation within a given population without the attendant effects of intergradation. After one establishes the range of phenotypic variation in a relatively stable and isolated population, results can be transposed to corresponding populations on Mt. San Antonio. This provides for a more meaningful interpretation of the putative hybrid zone.

Additional study areas were selected from isolated populations which included the full range of ecological conditions encountered on Mt. San Antonio for both species. Analysis of each study area included a local population sample of 25 individuals. Each individual was scored on the same hybrid-index scale used for the Mt. San Antonio transects.

The study areas for *Pinus ponderosa* included Barley and Charlton Flats, just off the Angeles Crest Highway (Los Angeles County; Angeles National Forest). The Barley Flats area of State Detention Camp No. 16 is located northwest of Redbox Ranger Station and 1.5 miles north of the Angeles Crest Highway. Twenty-five individuals were sampled on a dry, south-facing slope at the 5,500–5,600 ft. level. This area was near the lower elevational limits of *Pinus ponderosa* as indicated by the dominance of *Pinus coulteri*. The Charlton Flats Recreation Area is located nine miles northwest of Redbox Ranger Station and southwest of the Angeles Crest Highway. A sample from a local population of 25 individuals was collected on a gentle southern slope and another sample was taken from a north-facing slope. This area was selected because it included a number of large stands of *P. ponderosa* within the 5,300–5,400 ft. elevational range.

The sample of *Pinus jeffreyi* was located within the Table Mountain Recreation Area, approximately three miles north of Big Pines Ranger Station and seven miles northwest of Wrightwood (Los Angeles County; Angeles National Forest). At an elevation of 7,200 ft., local population samples were taken on both north- and south-facing slopes. Although varying north-facing slopes are found, the entire area is cold and dry much of the year and compares with ecological conditions on the north face of Mt. San Antonio. The individual trees were, for the most part, as large as any Jeffrey pine found in any other area.

MORPHOLOGY AND DEFINITIVE CHARACTERISTICS

Table 1 presents a comparative survey of the various characteristics which may be used to distinguish *Pinus ponderosa* from *Pinus jeffreyi*. This table is

⁵Refers to an expression of mass per unit volume of the cones. A description of this method is discussed by Haller (1962).

⁶Cone phyllotaxy refers to the spiral arrangement of the cone scales, usually arranged at right angles to one another. Cones of *P. ponderosa* generally have serial rows of five and eight, whereas *P. jeffreyi* cones have eight and thirteen rows.

⁷This comparison refers to the ratio of the wing length to the seed length. Impressions in the cone scales are very useful in obtaining this ratio if the actual winged seeds are missing.

⁸A new chromatography test developed by Parratt and Sherwin (unpublished).

TABLE 1. *Comparison of characteristics distinguishing allopatric populations of Pinus ponderosa and Pinus jeffreyi.*

BARK CHARACTERISTICS:

	<i>P. ponderosa</i>	<i>P. jeffreyi</i>
1. fissures: ³	widely spaced and shallow	narrowly spaced and deep
2. color of outer bark:	light yellow or yellow tan	red or reddish brown
3. scales—inner surface:	soft; bright yellow to sulfur color	hard and brittle; cream, pink, gray, or tan color
4. bark odor:	resinous	vanilla-like

BRANCH AND NEEDLE CHARACTERISTICS:

5. young branchlets:	non-pruinose; orange odor; yellow to green	pruinose; violet odor; purple
6. needle color:	deep yellow-green; surface smooth and glossy	deep gray-green; surface glaucous
7. needle width:	1.4–1.6 mm	1.7–2.2 mm
8. bud resin:	abundant	lacking
9. bud scales:	red to brown with dark hairs	light brown with longer white hairs

OVULATE CONES:

10. size-volume: ⁴	120–500 cc	600–2,000 cc
11. density: ⁵ (weight/volume)	light; 0.06–0.10	heavy; 0.12–0.18
12. cone length:	7–13 cm	15–25 cm
13. phyllotaxy: ⁶	5 and 8	8 and 13
14. prickly direction:	pointing outward; prickly on handling	pointing downward
15. scale color:	brown to black on dorsal surfaces and light brown on ventral surfaces	light buff or tan on both surfaces
16. wing length/ seed length: ⁷	4.5–2.9	2.4–1.5
17. cone separation:	basal scales often left on tree	complete separation of cone from tree

STAMINATE CONES:

18. elongation during growth:	early in growing season	later in season
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CHEMICAL:

19. aldehyde:	absent; no color change with Schiff's reagent	present; purple color with Schiff's reagent
20. bark chemistry: ⁸	differential chromatographic associations	pattern of phenol-tannin

GENERAL:

21. nature of tree crown:	less symmetrical; more rounded due to pendulous nature of branches	more symmetrical; long, narrow, and tapering
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³Figs. 4-5 show a comparison of the fissure differences between the two species.⁴The formula for this volume measurement was developed by Haller (1957) and is discussed adequately in that work.

compiled from the findings of Sudworth (1908), Jepson (1923), Bradshaw (1941), Munz (1959), Haller (1962), and my own studies. Of the characteristics listed, only 12 are quantified and used in this study (Table 2). It would be impractical in this work to use all available characteristics, many of which are only slightly definitive or are technically difficult to measure. One such characteristic is the chemical test for resin aldehydes found in the two pines. *Pinus jeffreyi* contains traces of straight chain aldehydes which are lacking in the resins of *P. ponderosa* (Mirov, 1929). In colorimetric tests using leuco-basic fuchsin (Schiff's reagent), resin samples of *P. jeffreyi* turn a deep purple, whereas the

Fig. 4-5. Bark fissure comparison on *Pinus jeffreyi* and *Pinus ponderosa*.—Fig. 4. Specimen of *Pinus jeffreyi*. Note the narrow plates and deep fissures.—Fig. 5. Basal portion of *Pinus ponderosa* showing wide, flat plates and the widely spaced, shallow fissures.

ponderosa resin remains a yellow or tan color. Intermediate colors are supposedly found in hybrid individuals (Haller, 1962). However, tests by Haller (1962) at the Institute of Forest Genetics, Placerville, California, showed a portion of the test to be invalid. All of the cultivated F_1 hybrids for which *P. jeffreyi* was the female parent displayed the Jeffrey-pine aldehyde reaction. The only individual for which *P. ponderosa* was the female parent displayed an intermediate reaction. Thus, a considerable amount of testing on known hybrid derivatives should be conducted, in my opinion, to determine the actual value of this test. If part of the known F_1 hybrids give inaccurate colorimetric readings, perhaps

the test should not be included in a detailed taxonomic survey of the two species.

RESULTS

The results of the quantification of characteristics for the Mt. San Antonio transects are given in Fig. 6 where each index score represents an average of the 30 individuals sampled for each given elevation within the two transects.

An insight into the possible variational ranges for both species was derived from analysis of the three allopatric populations in the vicinity of Mt. San Antonio. Although these populations are relatively homogenous and within a small elevational range, they are useful in establishing comparative norm for delimiting the species zones in the Mt. San Antonio transects. Investigation areas for *Pinus ponderosa* included Barley and Charlton Flats. The mean index scores for these areas were as follows: Barley Flats, 5.98; Charlton Flats, 7.11. The mean index score for the *Pinus jeffreyi* population on Table Mountain was 42.88. These results indicated more variability in allopatric populations of the two taxa than previously thought and proved the ponderosa pine slightly more variable in this particular comparison.

Thus, allowing an arbitrary ten-point range for the species variational range on either end of the Mt. San Antonio transect scale, *P. ponderosa* is included in the elevational range between 5,600 and 6,600 ft. *Pinus jeffreyi* includes a larger range at the top of the elevational scale from 7,000 to 9,500 ft. (Figure 6). The arbitrary ten-point range was taken from the highest index score for each species. This ten-point range was established to compensate for the possible human error factor and for the obvious polymorphism in populations of the two species. The average index grouping for the Jeffrey pine is therefore between 32.73 and 41.33. The average index grouping for the ponderosa pine is between 5.61 and 9.40 (Figure 6). These results indicate that *P. jeffreyi* is only slightly more variable than *P. ponderosa*.

Varying tendencies of instability of features within established ponderosa and Jeffrey pine populations are probably the result of a complex of interacting factors. One micro-ecological situation at a given elevation might favor selection of a certain genetic combination not favored in the next elevational zone. Within the established zone for *P. ponderosa*, the constancy of characteristics vary at different elevations. A similar trend is prevalent for the segregation of characteristics in the zone of *P. jeffreyi*. Even a stable genotype might have a number of possible phenotypic expressions which could be found throughout the population. If the genetic factors of the two species are expressed through multifactoral inheritance, almost unlimited combinations of characteristics are possible.

Additionally, the level of genetic variability throughout the population would be raised by the occasional formation of interspecific hybrids (Grant, 1963). As first suggested by casual observation and later indicated by the hybrid-index scale, there exists a small hybrid zone between the elevations of 6,600 and 7,000 ft. The hybrid zone shows a gradation of characteristics quite different from other areas in this transect. Individual index scores from the hybrid zone indicate a few individuals like F₁ hybrids, a larger number of samples with varying

TABLE 2. Quantification of characteristics used in the study for the purpose of forming a hybrid-index scale.⁹

BARK CHARACTERS:

1. *Fissures*

- 0= widely spaced and shallow; forming plates
- 1= not as widely spaced; plates more numerous
- 2= intermediate fissures; both wide and deep or narrow and deep
- 3= tending to narrow spacing and ridge-effect of plating
- 4= narrowly spaced and deep; forming ridges rather than plates

2. *Color*

- 0= light and dark yellow to tan
- 1= tending to more red or brown in yellow pigmentations
- 2= intermediate color tracings from both extremes
- 3= reddish brown to lighter brown
- 4= darker red to red-brown

3. *Scales: inner surface*

- 0= soft texture; bright yellow to yellow-tan
- 1= brown pigmentation in yellow or tan base colors
- 2= mixed brown to yellow with corresponding textures
- 3= yellow-brown to brown-tan in predominately Jeffrey-like scales
- 4= hard texture; light cream, pinkish, or chocolate red-brown

4. *Odor*

- 0= resinous odor from bark; if so, dark resin pits under scales
- 2= neither odor discernable
- 4= obvious vanilla-like odor on peeling scales; no resin pits

BRANCH AND NEEDLE COLORS:

5. *Needle color*

- 0= deep yellow green; surfaces smooth and shiny
- 2= dark yellow to gray green; surfaces non-glaucous
- 4= deep dull gray-green; surfaces glaucous

6. *Needle width*¹⁰

- 0= 1.4-1.6 mm
- 2= 1.6-1.7 mm
- 4= 1.7-2.2 mm

7. *Bud resin*

- 0= abundant to merely present
- 4= lacking

8. *Bud scales*

- 0= reddish-brown with dark terminal hairs
- 2= intermediate or graded colorations
- 4= light brown with longer white hairs

OVULATE CONES:¹¹9. *Phyllotaxy*

- 0= 5 and 8
- 2= variable, mixed or intermediate
- 4= 13 and 8

⁹On this scale, 0= *P. ponderosa*, 1-3= intermediate phases, and 4= *P. jeffreyi*. Therefore, any number between 1 and 3 would indicate phases of characteristics approaching one species or the other. Quantification of 12 such characteristics on a hybrid-index scale would give: 0= "good" ponderosa, 24= intermediate hybrid, and 48= "good" Jeffrey pine.

¹⁰Needle width measurements were taken by micrometer calipers.

¹¹Cones were generally the last crop and were cut or picked with a representative selection from each tree surveyed.

TABLE 2. Quantification of characteristics used in the study for the purpose of forming a hybrid-index scale (continued).

OVULATE CONES:

10. Scale color

- 0= dark black-brown on dorsal side
- 1= lighter black-brown dorsal coloration
- 2= intermediate; dorsal coloration of light brown to buff
- 3= darker buff on both scale sides
- 4= coloration similar on both sides; usually buff to tan

11. Prickle direction

- 0= pointing outward; prickly on handling
- 1= inclined more inward than in 0
- 2= vertical (relative) or of mixed angles; not in set pattern
- 3= outward inclination from 4
- 4= tucked under scale or strongly tending inward; not prickly

12. Cone length

- 0= 7-13 cm
- 2= 13-15 cm
- 4= 15-25 cm

combinations of characteristics from both species, and some individuals assignable to one species or the other. Introgressive hybridization probably explains a number of hybrid individuals with diverse and varying combinations of characteristics. These individuals are unlike the variants found within either species zone. The overlapping ecological requirements of the two pines makes possible the selection of characteristics from both species in all possible combinations.

Some taxonomists believe that the morphological characteristics differentiating these species are controlled by the environment. The expression of quantitative characteristics is affected to a slight degree by the environment. However, the major controlling factors must be considered genetic, because extremes of bark color, fissures, and other segregating characteristics are found in individuals growing side by side in a given area.

GENETIC BARRIERS AND EXPERIMENTAL HYBRIDIZATION

Artificial hybrids can be obtained between the two species (Richter and Duffield, 1951). The Institute of Forest Genetics at Placerville, California, planted 15 F_1 hybrids between *Pinus ponderosa* and *Pinus jeffreyi* in 1933. A limited number of ovulate cones from these individuals indicates that fertility is extremely variable. However, preliminary results from the experimental station indicate that seed set from the hybrid individuals is considerably lower than in crosses within either species.

The relatively few hybrids found in this study would perhaps indicate the existence of relatively strong isolating barriers or mechanisms. Several such barriers have been discussed in the literature and applied specifically to the ponderosa-Jeffrey hybrid situation. Haller (1962) suggests that the pines may be somewhat isolated reproductively due to differences in the time at which pollen is shed. Extensive hybridization would be limited by the fact that pine

pollen is usually short lived (Forest Service, 1948). In addition, McWilliam (1959) has found the receptive period of the ovulate cones to be rather brief. It is known that the cones of *P. ponderosa* mature somewhat earlier than those of *P. jeffreyi*. Probably the timing of events and conditions would have to coincide for successful natural crosses between the two species. This study would indicate that conditions do exist, in fact, which permit the two pines to interbreed in limited numbers. Johansen (personal communication) feels that the exact conditions which permit the formation of the *ponderosa* × *Jeffrey* pine-hybrids do not recur every year. He believes also that these conditions are more cyclic than annual, and that a cycle reaches its peak during the years of above-normal rainfall and drops considerably during the dry years.

Even if these hybrids are produced in quantity, the apparently limited area within the hybrid zone could support only a few trees. I feel that the main limitation to hybridization here is environmental rather than genetic. Thus, the pollen may be carried by the winds from one species level to the other with the resultant seedlings having very little chance for survival in the well-established colony of the female parent. In this situation, the F_1 hybrids between the two species would survive only in medial sections of the hybrid zone. As noted earlier, the greater possible adaptive nature of individuals repeating various degrees of backcrossing would constitute the bulk of the hybrid zone.

DISCUSSION AND CONCLUSIONS

EVOLUTIONARY HISTORY

Although fossil three-needle pines occur as far back in geological history as the Jurassic period, none may be assigned to the species in question (Mirov, 1938). Axelrod and Ting (1960, 1961) cite several findings of fossil pollen grains from the late Pliocene and early Pleistocene periods which are clearly *ponderosa*- and *Jeffrey*-like. However, these findings indicate only the presence of the two species and provide little evidence as to their probable evolutionary history.

McNair (1937) found that the average iodine count increases in value with the advance in evolutionary position of the two pines. On this basis, he hypoth-

Fig. 6. Hybrid-index analysis of the *ponderosa*-*Jeffrey* pine complex on the south-facing slope of Mt. San Antonio. The elevations surveyed in the study are listed on the left-hand edge of the graph. The mean index scores on the right-hand edge and correspond with each given elevation. The center portion listed as "index scores" graphically presents the hybrid-index range. Each mean index score represents an average of 30 individuals for each elevational level (15 individuals for each of the two transects). From 5,600–6,600 ft. are found individuals of *Pinus ponderosa*. At the opposite end of the transects, 7,000–9,500 ft., are found dense populations of *Pinus jeffreyi*. The diagonal lines in the 6,750–7,000 ft. zones represent the hybrid population between the two pines. (Note that throughout the paper, the hybrid zone was listed as including the 6,600–7,000 ft. elevations. This was done to accommodate the gradual termination of the hybrid zone into one or the other pine populations. Thus, the actual hybrid zone is slightly larger than shown on this graph.) With a 0–4 point range for each characteristic analyzed (a total of 12 characteristics), 0 would be a "good" score for *P. ponderosa*, 24 and intermediate hybrid, and 48 a "good" specimen of *P. jeffreyi*. It is difficult to find a group of individuals which would fit exactly into these three categories. Thus, the noted wide variational range is allotted each species.

esized that *P. jeffreyi* is considerably older than *P. ponderosa*. Johansen (1953) ranks the Jeffrey pine as clearly the archaic species. In recent studies, Johansen (1964) has found the following primitive features in the Jeffrey pine archegonium: binucleate archegonium, occurrence of double fertilization (dubiously primitive), and the formation of Araucarian-like proembryos.

With this meager phylogenetic evidence, it is difficult to develop an accurate evolutionary history of the two taxa. Perhaps the two species diverged from a common ancestor and have evolved through geologic time at different rates. This being the case, the Jeffrey pine archegonium designated primitive by Johansen might well be a retention of primitive characteristics, while that of *ponderosa* has become simplified.

A statement as to the present evolutionary activity of the two pines is also difficult. I believe the two species are presently in a stage of divergent evolution which probably began in pre-Pliocene times. A long history of divergent evolution would have allowed adequate time for appreciable segregation between the two species. This would best explain the variable bimodal pattern by which the morphological characteristics of the two species are segregated. With this wide variational gamut, the two pines are considered species in a broad sense. Variational ranges noted in these pine species are not unlike those found in some species of other woody genera (*Ceanothus*, *Arctostaphylos*, and *Quercus*).

Variable phenotypic expressions of particular characteristics within each species were accounted for by means of allowances in the hybrid-index scale. This variability has often been mistaken and interpreted by taxonomists as varying degrees of hybridization. I believe that extensive study based upon a well-established character index is the only manner in which one may become familiar enough with this complex to distinguish hybridization from "normal" variation of a single species, thereby delimiting the two species.

FREQUENCY AND SIGNIFICANCE OF HYBRIDIZATION AND VARIATION

Haller (1962) found a low, yet constant rate of hybridization in all of his study areas. The average number of hybrids found in any proposed hybrid zone was slightly more than one out of every 25 individuals. I found that hybrids constitute 4.8% of the individuals sampled on Mt. San Antonio. This figure is only slightly higher than those found in Haller's studies.

Although the rate of hybridization may be low, the process may have very important implications. Some of the polymorphism expressed throughout the *ponderosa*-Jeffrey pine populations may be attributed to hybridization. A very low rate of hybridization over a number of years could greatly increase the amount of variability found in both species (Grant, 1963). Haller (1962) believes that hybridization between the two pines may have been more frequent in the past than at present. He feels that the disturbed conditions of the Pleistocene may have greatly shifted distribution patterns for the occurrence of hybridization. Additionally, I believe that the close genetic relationship between the two pines in an early stage of divergent evolution may have greatly increased the potential for hybridization.

Genetic variability, regardless of its source, is an important mechanism in providing and maintaining the adaptability of the two species in an unstable environment. The instability of the environment and of the species themselves, results in active evolution. The more important factors stimulating this evolution may be: (1) instability and diversification of the two species in a present phase of divergent evolution; (2) adaptation toward a more xerophytic habitat as directed by an increasingly dry climate in southern California (Los Angeles County Flood Control District, 1964); (3) the varying tolerances of both species to various conditions of slope direction, temperature, moisture, and edaphic factors. These factors are at least partially responsible for the distribution of the two species in an ecological pattern. Overlapping ecological conditions provide an opportunity for a limited amount of hybridization in sympatric associations of the two species.

SUMMARY

Various earlier studies and observations have suggested that hybridization between *Pinus ponderosa* P. & C. Lawson and *Pinus jeffreyi* Murr. is actively occurring within a certain zone on Mt. San Antonio, California. This study was undertaken to test the degree and nature of hybridization and variation present, to supply comparisons with "pure" populations, and to describe the ecological background of the entire complex.

Geographical ranges of the two species overlap to a great extent in southern California montane regions. Preliminary studies revealed that the effect of elevation and slope direction upon temperature, salinity, and moisture are partially responsible for the distribution of the two pines into species zones which merge at elevations between 6,600 and 7,000 ft. on Mt. San Antonio.

To aid in determining the relationships between *P. ponderosa* and *P. jeffreyi*, 12 distinguishing characteristics were quantified on a hybrid-index scale (Anderson, 1949). The index was used on two transects on Mt. San Antonio (south-facing slope) between the elevations of 5,600 and 9,500 ft., the complete ecological range of the two species. By this means, the traits of the two pines were summarized and scored on a comparative basis. Index scores from allopatric populations near Mt. San Antonio revealed a relatively wide, yet bimodal pattern of variation within the two species. Application of these results to the Mt. San Antonio transects aided in delimiting the species and in detecting possible hybridization. Index results verified observational findings of a small hybrid zone between the elevations of 6,600 and 7,000 ft. In this sympatric association of the two species, it appears that varying and overlapping ecological conditions create situations in which selection favors characteristics from both species in varying quantities and in many genetic combinations.

The total number of hybrid individuals in the population constituted 4.8% of the total transect analyses. The two pines are considered "species" in the broadest sense. A wide range of polymorphism is found within the two species, a feature not uncommon in many groups of woody plants. Hybridization may be important in maintaining the genetic variability and adaptability of the two species. Finally, the possible significance of evolutionary divergence on variation and hybridization is discussed in relation to the two species.

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