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Arctostaphylos viscida Parry and A. canescens Eastw., two well-known and frequently encountered manzanitas in the Siskiyou Mountains in southwestern Oregon, are shown to hybridize and to produce an extensive series of morphological intermediates. The hybridization occurs wherever populations of these two species meet at contact zones of serpentine and non-serpentine soils. At these locations, A. viscida grows primarily on the serpentine, whereas A. canescens has never been observed on serpentine soils. Chromosome counts made of the two species show that they both have $n=13$, the haploid number in the genus.

Evidence regarding hybridization was obtained through morphological comparisons and the use of the hybrid index and pictorialized scatter diagram techniques. From their morphology, the hybrids are judged to include F_1 's, F_2 's and backcrossed individuals. Most of the identifiable hybrids

occur on soils of transitional and non-serpentine types whereas few occur on serpentine soil. This restriction in distribution is believed to be caused by more rigid edaphic selection on serpentine. The effect of differential selection on the survival of hybrid plants is to permit genes of A. viscida to infiltrate more easily the genotype of A. canescens than vice versa. Away from the areas of contact with serpentine soil separate populations of A. canescens are shown to be morphologically variable in the direction of A. viscida. The variability is inversely proportional to the geographical distance separating them from A. viscida populations.

The morphological intermediates between A. viscida and A. canescens are similar to six putative species of Arctostaphylos that were described by Thomas Howell in 1901 from specimens collected in this region of Oregon. These species--A. bracteata, A. strigosa, A. oblongifolia, A. parvifolia, A. cinerea and A. pulchella--have been maintained as valid species by several previous authors, even though they are known only from a few herbarium specimens and are extremely difficult to separate taxonomically either from each other or from A. viscida or A. canescens. Since these six putative species can be readily accounted for by hybridization, and since they do not exist as distinctive natural populations but only occur where populations of A. viscida and A. canescens come together, it is suggested that they no longer be given taxonomic recognition.

HYBRIDIZATION BETWEEN ARCTOSTAPHYLOS VISCIDA
AND A. CANESCENS IN OREGON

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LESLIE DAVID GOTTLIEB

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In Charge of Major

Redacted for Privacy

Head of Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

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HYBRIDIZATION BETWEEN ARCTOSTAPHYLOS VISCIDA
AND A. CANESCENS IN OREGON

INTRODUCTION

The species of manzanita, Arctostaphylos Adans., are some of the most frequently encountered shrubs in many parts of western Oregon and California. Unlike most other long-lived, woody groups of plants, these species are believed to be presently undergoing "rapid evolution" and to have added new species in geologically recent times (Stebbins, 1950, p. 551). Studies of speciation in woody genera are few, and the recent complex patterns of evolutionary development in the manzanitas make them a particularly rewarding subject for such studies. The Siskiyou Mountains in southwestern Oregon, with their unique and ancient diversity of habitats, are excellent study locations since several well-known manzanitas are widely distributed there. These are Arctostaphylos viscida Parry, A. canescens Eastw., A. nevadensis Gray, and A. patula Greene.

Despite the commonness of Arctostaphylos, its taxonomy is confusing and imperfect. For example, six additional species of Arctostaphylos have been described in the

Siskiyous that are extremely difficult to separate taxonomically either from viscida and canescens or from each other. They are A. bracteata, A. strigosa, A. oblongifolia, A. parvifolia, A. cinerea, and A. pulchella, all described by Thomas Howell in 1901 based on specimens collected in 1886. Although the identification and biology of Howell's species are obscure, since they are known only from a few herbarium specimens, several of them have been maintained as valid species in the standard taxonomic treatments that include the Siskiyous.

Many authors (Benson, 1930; Jepson, 1939; Adams, 1940) have commented on the difficulty of delimiting species of Arctostaphylos, especially on the basis of herbarium analyses of morphological features, because throughout the genus the flowers as well as the vegetative organs are very similar. Species have had to be separated primarily by characters of pubescence and geographical distribution. Additional criteria based on field studies have been sought to separate the species. For example, such characters as growth habit, manner of branching, and hue of foliage have been examined. Ecological data, particularly in regard to the reaction of the plants to fire, have been emphasized. However, the presence of overlapping characters has hindered efforts to obtain adequate species-delimiting criteria.

The present study was initiated to elucidate the biological relationships between viscida and canescens and the six species described by Howell, and thereby to clarify the perplexing taxonomic picture presented by this common shrubby genus in southwestern Oregon.

To understand Howell's six species of Arctostaphylos, preliminary information was obtained from intensive field studies. Arctostaphylos populations were located and identified in an area of several hundred square miles surrounding his original locations, Andersons and Waldo. These two 19th-century townsites are a few miles apart in southern Josephine County, just north of the Oregon-California state border. They are reached by U.S. Highway 199, the main highway between Grants Pass, Oregon, and Crescent City, California (figure 1).

Arctostaphylos viscida and A. canescens are widely distributed in this region, covering hillsides, roadcuts, and other fairly open areas, and are the two manzanitas most often encountered. Arctostaphylos patula and A. nevadensis are found primarily along the Onion Mountain Road northwest of Hayes Hill from U.S. Highway 199. A very few scattered plants of A. columbiana Piper and A. hispidula Howell also occur in this area.

The field sampling revealed an extensive series of morphological intermediates between viscida and canescens

which includes many plants that are similar to Howell's six species. In general, these intermediates occur where large populations of viscida and canescens come together. Morphological intermediates were not observed between either viscida or canescens and A. patula and A. nevadensis, the two other common species of Arctostaphylos present in the area.

Therefore, to develop evidence regarding Howell's species, studies were concentrated on viscida and canescens under the hypothesis that the morphological intermediates are the result of hybridization and that the putative species described by Howell are similar, if not identical, to these intermediates.

Although it is preferable to test such an hypothesis by artificial cross-fertilization and analyses of the artificial hybrids, such tests might require a minimum of three to five years before an F_1 generation would flower, much more time than was available. In addition, since little genetic work of this kind has been done within the genus, not much information is available regarding breeding systems, modes of inheritance and seed-germination requirements. Therefore detailed, quantitative morphological studies of the plants were made to accumulate relevant evidence. The data were then analyzed using the hybrid index and pictorialized

scatter diagram techniques developed by Edgar Anderson (1949). Also some chromosome counts and preliminary observations regarding breeding mechanisms were obtained.

LITERATURE SURVEY

The literature on experimental studies of hybridization is rich; however, only a small proportion of it deals with studies of slow-growing, long-lived perennial species. The long time period between generations in woody plants has caused researchers to shy away from them. When crossing experiments were made in woody genera such as Quercus, Ceanothus, Pinus, Platanus, Catalpa and other monophloid groups, it was found that species similar in external morphology generally form fertile hybrids (Stebbins, 1950).

Much of the discussion arising out of these studies involves the effects of hybridization on the production of species variability. One view, championed by Edgar Anderson (1948, 1949, 1951, 1953), is that hybridization results in increased variability in the participating species because of repeated backcrosses of the hybrids to one or both parents. Termed introgression, the process yields plants very much like the recurrent parent but with a few characteristics of the introgressing species. Another view discounts the effects of introgression by claiming that gene flow remains local and cannot be detected at a distance from the hybridizing taxa. Others consider that differential variability within species results from differential selection acting on flexible genetic systems, and not from

hybridization.

Examples of introgressive hybridization in woody genera may be found in studies of Quercus, Juniperus, Acer, Cowania and Purshia.

Quercus has been a favorite genus for such work.

Stebbins, Matzke, and Epling (1947) studied a hybridizing population of Q. marilandica and Q. ilicifolia in the Pine Barrens near Lakehurst, New Jersey. Using the hybrid-index technique, they found that Q. marilandica is introgressed by Q. ilicifolia in several characters. The variants form a continuous series from exact intermediates to typical Q. marilandica and, therefore, are thought to be backcrosses to Q. marilandica. The authors point out, however, that the genes of Q. ilicifolia have only a local effect on Q. marilandica and have not spread beyond the region of their mutual occurrence. The two species are kept distinct because they have a comparatively small number of generations per chronological time period. Since the Pleistocene ended 25,000 years ago and their present habitat was removed from the influence of glaciation, they are believed to have had only 250 generations and perhaps fewer than 100. Even a slight discrimination against the hybrid seedlings over such a small number of generations would be sufficient, the authors state, to keep the species distinct.

Tucker (1952) investigated intermediate populations between Q. douglasii and Q. turbinella and found that inheritance in oaks might be simple and governed by only a few gene differences. If this is so, then the number of generations required to wipe out interspecific differences in hybridizing species is considerably fewer than stated in the preceding example.

Other recent studies of hybridizing oaks include those of Cooperrider (1957), Silliman and Leisner (1958), and Forde and Paris (1962). The latter work is particularly relevant because it involves the serpentine endemic species, Q. durata. Hybrids between Q. durata and Q. dumosa, a non-serpentine species, are sometimes found in transitional soil zones. However, the authors discovered a large intermediate population on a non-serpentine ridgetop four miles distant from the nearest serpentine outcrop with Q. durata individuals. The ridgetop sampling reveals two kinds of variation among the oaks. One sample is a hybrid swarm whereas the other sample contains only a limited range of segregants with the Q. durata characters dominant, suggesting that it is Q. durata slightly introgressed by Q. dumosa. To explain the unexpected occurrence of Q. durata on non-serpentine soils, the authors tentatively concluded that the general inhospitality of the ridgetop, caused by its altitude and exposure as well as partial soil mineral deficiencies

(although not nearly as difficult a habitat as that typical of serpentine), favors Q. durata rather than Q. dumosa.

"Soils intermediate in properties better explain the occurrence of an introgressed population of Q. durata which can presumably compete better in such sites than pure stands of either parent" (Forde and Faris, p. 346). Unfortunately, the authors did not prove that the soils were indeed intermediate.

In a study of introgression in sugar maples in southern Quebec, Dansereau and Desmarais (1947) interpret the presence of slight leaf pubescence and a less-dissected leaf outline in certain populations of Acer saccharum as evidence of introgression from A. nigrum.

All populations of Purshia tridentata in Utah are believed to be introgressed by Cowania stansburyana (Stutz and Thomas, 1964). Purshia glandulosa is thought to be the stabilized product of this hybridization which occurs at the summits of north-south slopes where the two species meet, and in ravines where P. tridentata extends into territory occupied by C. stansburyana. Where only two contrasting slopes are present, only F_1 's and backcrosses were found at the summits; where the slopes are multidirectional, F_2 segregants were identified. The different populations of P. glandulosa appear to derive from separate hybridizations

since they are uniform for certain characters but not for others.

Hall (1952) has been able to trace the effects of introgressive hybridization in Juniperus virginiana and J. ashei for 1000 miles from Texas to Indiana. In a hybrid swarm examined near the Platt National Monument in Oklahoma, he found that the junipers respond very closely to environmental differences so that it is possible to describe the habitat by noting the pattern of variation of the junipers growing on it. The two junipers are very different morphologically, and Hall was able to demonstrate that in the hybrids the characters of each species tend to stay together rather than vary at random.

Research on hybridization in some other long-lived genera has failed to turn up evidence of introgression. The two sages, Salvia apiana and S. mellifera, are sympatric in southern California. Epling (1947b) observed that although they are isolated by ecological preferences, pollinator preferences, and differences in flowering times, occasional F_1 hybrids occur in disturbed habitats. The F_1 produces only two per cent viable seeds, but these are vigorous and the fertility increases in experimentally produced F_2 's. Populations of S. mellifera near S. apiana populations are not more variable than populations of S. mellifera outside the range of S. apiana; therefore, Epling

concluded that gene flow remains strictly localized without gene introgression.

Epling found a similar situation of hybridization without subsequent introgression in a study of Arctostaphylos mariposa Dudley and A. patula in Yosemite National Park in California (1947a). Specific differences in a representative leaf in slightly over 1000 individuals along a transect between the two species provide evidence that approximately five per cent are F_1 hybrids. The hybrids are vigorous and set fruit in the same proportion as the parents. The two species are kept distinct, he concluded, by the combined action of several mechanisms including limitations of pollen dispersal, seasonal flowering time differences, insect preferences, and limitations on seed dispersal in the hybrids. These environmental factors were considered just as effective in reducing gene flow as those genetic factors affecting the viability of hybrid zygotes in other species crosses.

In Ceanothus, section Cerastes, Nobs (1963) reported several different types of species distributions and stabilizations. Within the section, hybrids between the various taxa are as highly fertile as their parents and have regular meiosis, seed-set and pollen formation, and could be considered ecological races or ecotypes.

Where the habitat boundaries are sharp, as between the obligate serpentine endemic species, C. jepsonii, and the wide-ranging C. cuneatus, there is little natural hybrid survival except where the distinctness of the habitats has been sullied by man-caused or other disturbances. No evidence of introgression was found between C. jepsonii and C. cuneatus, or between C. jepsonii and C. ramulosus, another taxa with which it often occurs. Likewise, introgression does not occur between C. pumilus, another serpentine endemic, and C. cuneatus.

Where the habitat boundaries are not distinct and cover a broad zone of gradual change, hybrid derivatives are widespread. An example of this is found in the area between C. cuneatus which grows in the hot, dry inland foothills east of the North Coast Ranges in California and C. gloriosus which is restricted to the cool, moist coastal area north of San Francisco Bay. Between these distinct species, a series of intermediate populations occurs that exhibits a continuous series of intergrades. These intermediate populations include forms named C. ramulosus, C. sonomensis, and C. masonii.

A third type of differentiation in Ceanothus occurs within single species that occupy a range of different habitats. Three varieties are recognized within C. gloriosus: a prostrate form confined to the exposed ocean bluffs,

and erect or semi-erect forms inhabiting the chaparral farther inland. These differences in growth form are genetically stable and are maintained when the plants are brought into garden cultivation.

All of these examples display the reaction of flexible genetic systems to the selective pressure of changing environments. A similar finding was reported in some Eucalyptus species in Tasmania by Barber and Jackson (1957). These workers demonstrated a strict clinal transition between leaf glaucousness and non-glaucousness across a rapidly changing altitude gradient. Although both types of seedlings are produced in both high and low elevation habitats, selection always eliminates glaucous seedlings at the bottom of the gradient and non-glaucous seedlings at the top of the gradient. Such strong selective pressure brings about genetic diversity without introgression in a complex pattern controlled by the environment.

FIELD STUDIES

Habitat

The Siskiyou Mountains straddle the Oregon-California border west of the Cascades. They have a rugged aspect and have been described as "a confusion of broken mountain ridges with steep and stony slopes and scanty soil" (Peck, 1961, p. 18). Exhibiting a complex history of uplift, subsidence and erosion, they have existed, at least as low mountains, since the close of the Cretaceous period (Whittaker, 1960). Complicated mosaics of different rock types with major peridotite and serpentine intrusions are conspicuous. Their heterogeneous topographies and soil types result in extremely varied habitats. Hot, dry summers and cool, wet winters characterize the region with the amount of precipitation generally decreasing from the coast inward.

The Siskiyou flora is especially rich in numbers of both species and endemics, a consequence of a long geological history undisturbed by glaciation, lava flows, or oceanic submergence. The location of the mountains as the meeting ground of Northwestern, Californian and arid Interior floras also contributes to the richness of the flora (Whittaker, 1960).

No topographical or altitudinal differences in habitat preferences were discerned between viscida and canescens. Either might be encountered in high or low elevations and on north- and south-facing slopes. Detling (1961, p. 349) noted, "In some places where it [viscida] would be expected, it is replaced by A. canescens."

However the two species do have distinct edaphic preferences. Canescens has never been observed on serpentine soils; viscida is found both on and off serpentine. South of Hayes Hill (figure 1), a divide between the Illinois River drainage to the south and the Applegate River drainage to the north, large populations of viscida are always found on serpentine; in this area off serpentine only scattered plants of viscida are found. To the north and east of Grants Pass, large populations of viscida have been located on non-serpentine soils.

A geological description and map that includes the study area between Hayes Hill and the Oregon-California border was prepared by Wells, Hotz, and Cater (1949). The following description of peridotite and serpentine soils accords with their designations.

Peridotites are medium-grained rocks, consisting of olivine with or without other mafic materials. Sometimes called ultramafic rocks, they have a high proportion of magnesium and iron. Serpentine is derived from peridotite

by hydrothermal alteration. Wells et al. use peridotite to designate all rocks of the group whose general physical appearance still resembles the original rocks. Freshly broken peridotite ranges from light yellow-green to green-black, depending on the degree of serpentization. The light-colored peridotite is little altered; the dark-colored, almost completely altered.

The rocks designated as serpentine are those peridotite masses or parts of peridotite masses that have been so completely altered to minerals of the serpentine group that the rocks are distinctive in outcrop. Such materials are found in major fault zones that cut across or follow the edges of the larger peridotite bodies. Outcrops of serpentine are generally green-gray, although they may range in color from honey to green to dark gray-green to even black. They are characterized by slick, curved, lustered surfaces. In the present study when the designation serpentine is used, it indicates that the area in question has been designated serpentine by Wells et al.; in other words, it has been more or less completely altered from peridotite to serpentine.

Serpentine soils are characterized by a shallow profile, gravelly texture, low clay content, extremely low calcium levels, heavy-metal toxicity, excessive magnesium which probably accentuates the low calcium levels, and low

available molybdenum. They are widely regarded as infertile, physiologically difficult soils for most plants (Walker, 1954).

Waldo Transect

Waldo, now deserted, but once a thriving mining town, is located about four miles north of the state border and three-and-one-half miles east of U.S. Highway 199 from O'Brien (figure 1). It is situated between the East and West Forks of the Illinois River. After gold was discovered in its vicinity in 1853, the area remained a center of gold, copper and platinum mining until well into the present century. The gold, primarily in the form of placers, was mined by directing jets of water at the stream beds to loosen gravel which was then worked through sluice boxes and undercurrents where the gold was collected. It is estimated that Waldo produced \$4,000,000 worth of gold as well as \$1,700,000 worth of copper (Shenon, 1933).

Such mining methods are particularly destructive of plant habitats. Not only is Waldo an extremely disturbed site, but the presence there of a great deal of serpentine also contributes to its inhospitality for many plant species. Figure 2 shows how the different soils are juxtaposed at Waldo.

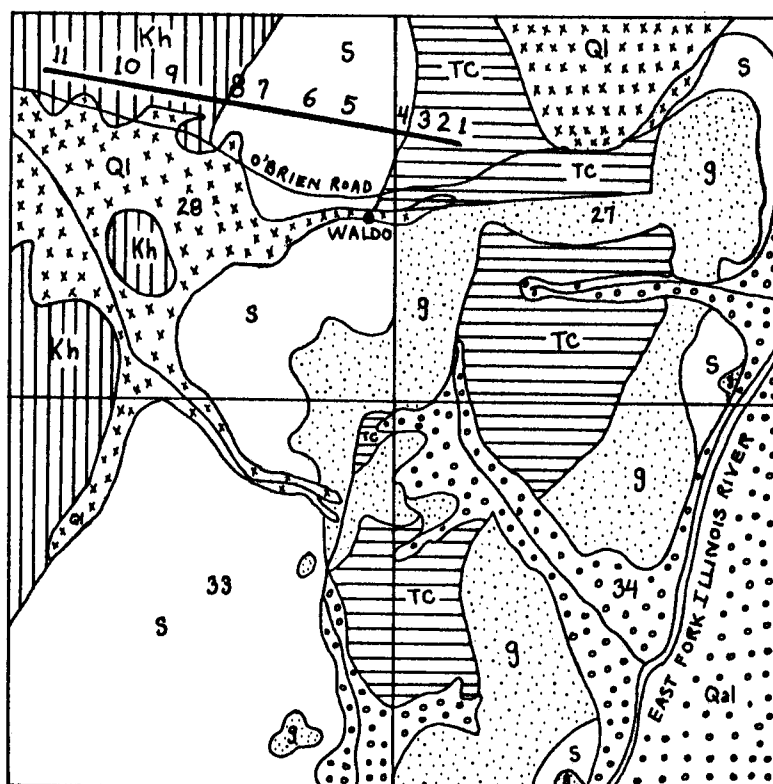
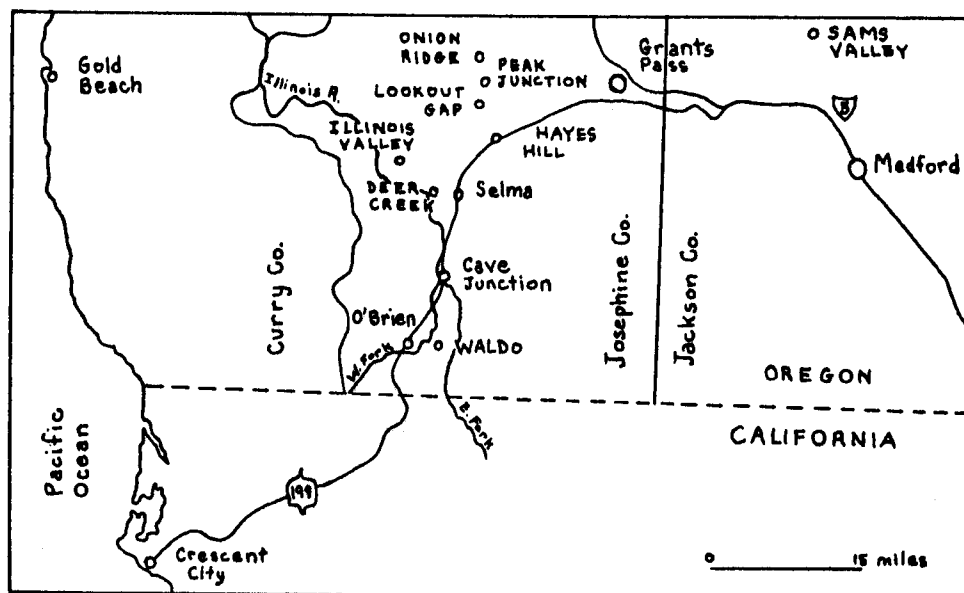


Figure 1. (Upper) MAP OF STUDY AREA.

Figure 2. (Lower) MAP OF WALDO SHOWING TRANSECT LOCATION AND SOIL TYPES. (Map and soil designations adapted from Shenon, 1933. S: serpentine; Tc: coarse conglomerate; Kh: indurated conglomerate; Ql: clay and sand; g: altered basalt and gabbros; Qal: alluviums.)

Normal erosion also mixes up the soils. The Waldo site is surrounded by hills composed of serpentine and non-serpentine rocks which wash down, intermix and overlap on the more level terrains.

The non-serpentine soils at Waldo consist primarily of coarse and indurated conglomerates, some clay, and altered basalt and gabbros. They support a medium-dense perennial vegetation of Pinus ponderosa, Arbutus menziesii, Pseudotsuga menziesii, Quercus kelloggii, Q. garryana, Rhus diversiloba, Rosa gymnocarpa and many annual species. The serpentine areas are open and gravelly textured and support a woody vegetation of only scattered Arctostaphylos shrubs, Ceanothus cuneatus, and Pinus jeffreyi. (Table I provides additional habitat data.)

A total of 110 Arctostaphylos plants were sampled at Waldo. The sampling procedure consisted of laying out a transect from canescens on non-serpentine soil to viscida on serpentine. The transect was located parallel to and on the north side of the O'Brien-Waldo road beginning at a point 1.1 miles west of the East Fork of the Illinois River and extending one mile to the west. The transect was divided into approximately 500-foot sampling intervals at each of which ten plants were selected for measurement. From east to west locations 1, 2 and 3 are off serpentine. Locations 4, 5, 6 and 7 are on serpentine. Location 8 is a zone of

Table I. HABITAT DATA FOR A. VISCIDA AND A. CANESCENS WHERE THEY MEET AT WALDO, OREGON. The sampling intervals are numbered from east to west and are approximately 500 feet apart. They are located on the north side of the O'Brien-Waldo road and extend from 1.1 to 2.2 miles west of the East Fork of the Illinois River. The transect is located in R. 8W., T.40S., Sections 27 and 28.

Sampling Interval	Soil Type*	Elevation (feet)	Associates
1.	Tc	1750	<u>Pinus ponderosa</u> , <u>Quercus kelloggii</u> , <u>Q. garryana</u> , <u>Arbutus menziesii</u> , <u>Rhus diversiloba</u>
2.	Tc	1725	<u>P. ponderosa</u> , <u>Q. kelloggii</u> , <u>Q. garryana</u> , <u>A. menziesii</u> , <u>R. diversiloba</u>
3.	Tc	1700	<u>P. ponderosa</u> , <u>Pseudotsuga menziesii</u> , <u>Q. kelloggii</u> , <u>Q. garryana</u> , <u>A. menziesii</u> , <u>R. diversiloba</u>
4.	S	1700	<u>Pinus jeffreyi</u>
5.	S	1625	<u>P. jeffreyi</u>
6.	S	1575	<u>P. jeffreyi</u> , <u>Ceanothus cuneatus</u>
7.	S	1550	<u>P. jeffreyi</u> , <u>C. cuneatus</u>
8.	S,Kh	1525	on S: <u>P. jeffreyi</u> , <u>C. cuneatus</u> on Kh: <u>Ps. menziesii</u> , <u>R. diversiloba</u> , <u>Fraxinus oreganus</u> , <u>Rosa gymnocarpa</u> , <u>Pyrus</u> sp., <u>Spirea douglasiana</u> , <u>Crataegus</u> sp., <u>Salix</u> sp.
9.	Kh	1525	<u>P. ponderosa</u> , <u>Q. kelloggii</u> , <u>Q. garryana</u> , <u>A. menziesii</u> , <u>R. diversiloba</u> , <u>C. cuneatus</u>
10.	Kh	1525	<u>P. ponderosa</u> , <u>R. gymnocarpa</u> , <u>Salix</u> sp.
11.	Kh	1500	<u>Ps. menziesii</u> , <u>R. diversiloba</u> , <u>A. menziesii</u> , <u>R. gymnocarpa</u>

*Tc = coarse conglomerate with sandstone beds near base

Kh = indurated conglomerate with sandstones

S = serpentine

obvious soil intermixing and overlap. Locations 9, 10 and 11 are off serpentine. All of these locations are on south or southwest slopes.

To eliminate personal bias, the first ten plants observed at each location that had set fruit were selected. The procedure was to clip and measure an upper branch on the south-facing portion of the shrub. Only a limited number of plants at each location had set fruit, probably because of insect predation. To obtain ten plants it was frequently necessary to cover an area with a radius of 75 to 100 feet from the approximate center of each location. If it was necessary to go as far as 100 feet, this distance was taken in a direction approximately 90 degrees to the axis of the transect in order to avoid merging the separate transect locations.

Other Study Areas

If edaphic factors are significant in permitting hybrid survival at Waldo, then hybrid survival should also occur elsewhere where the same edaphic factors are operating. To test this possibility, additional studies of viscida and canescens were made at other locations where the two species are growing adjacent to each other. Within the study region this only occurs at contacts of serpentine and non-serpentine soils. Two such areas were sampled: one at

Lookout Gap on the Onion Mountain Road, six-and-one-half miles west of U.S. Highway 199 from Hayes Hill; the other, approximately eight miles west of Selma in the Illinois Valley (figure 1). A third location about three miles east of Cave Junction on Route 46 was also surveyed, but the plants had not set fruit and it was not possible to make quantitative measurements. However many morphological intermediates were noted.

In addition to collections made at serpentine contact zones, the two species were sampled in more distant populations in order to obtain the range of variation in each species when it is growing separately from the other. Viscida was sampled on serpentine soil at Deer Creek, west of Selma, and also on a non-serpentine soil at Sams Valley, northeast of Grants Pass (figure 1). Canescens was sampled at Peak Junction, eight miles west of Hayes Hill on the Onion Mountain Road, and also at Onion Ridge 11 miles west of Hayes Hill on the same road (figure 1). These sites are all on south or southwest slopes. The canescens population growing along the roadcut at Hayes Hill was also sampled; however, it was found to be a slightly hybridized population and was not used in the determination of the range of variation in each species. (Table II provides habitat data on these locations.)

Table II. HABITAT DATA FOR ADDITIONAL POPULATIONS OF A. VISCIDA AND A. CANESCENS.

Population	Soil Type*	Elevation (feet)	Associates
LOOKOUT GAP 6 1/2 miles west of U.S. Highway 199; R.8W., T.37 S., on section line be- tween sections 15 and 16	S, Jgv	3575	on S: <u>Pinus jeffreyi</u> , <u>Libocedrus decurrens</u> , <u>Ceanothus cuneatus</u> , <u>Arctostaphylos patula</u> on Jgv: <u>Pseudotsuga menziesii</u> , <u>P. lambert-</u> <u>iana</u> , <u>Quercus vaccinifolia</u> , <u>Castanopsis</u> <u>chrysophylla</u> , <u>Lithocarpus densiflora</u> , <u>Arbu-</u> <u>tus menziesii</u> , <u>Prunus emarginata</u> , <u>Ceanothus</u> <u>velutinus</u> , <u>C. integerrimus</u> , <u>C. cordulatus</u> , <u>A. patula</u>
ILLINOIS VALLEY 7.8 miles west of Selma on Forest Service Road 3504; R.9W., T.38S., Sec. 2	S, Jgc, Qag	1750	on S: <u>P. jeffreyi</u> , <u>C. cuneatus</u> , <u>Eriodictyon</u> <u>californicum</u> on Jgc and Qag: <u>Ps. menziesii</u> , <u>L. densi-</u> <u>flora</u> , <u>Q. kelloggii</u> , <u>C. integerrimus</u> , <u>Rhus</u> <u>diversiloba</u>
DEER CREEK 2 1/2 miles west of Selma on Forest Service Road 3504; R.8W., T.38S., Sec.9	S	1550	<u>P. jeffreyi</u> , <u>L. densiflora</u> , <u>Q. breweri</u> , <u>Um-</u> <u>bellularia californica</u>
SAMS VALLEY 1/2 mile north of Sams Valley Road at Perry Road; R.2W., T.38S.	Teu	1500	<u>P. ponderosa</u> , <u>P. lambertiana</u> , <u>Q. kelloggii</u> , <u>Q. garryana</u> , <u>R. diversiloba</u> , <u>C. cuneatus</u>

Table II (Continued)

Population	Soil Type*	Elevation (feet)	Associates
PEAK JUNCTION 8 miles west of U.S. Highway 199 on Onion Mt. Road; R.8W., T. 37S., Sec. 9	Jgv	3900	<u>Ps. menziesii</u> , <u>P. lambertiana</u> , <u>P. attenuata</u> , <u>Q. vaccinifolia</u> , <u>L. densiflora</u> , <u>C. cordulatus</u> , <u>A. patula</u> , <u>A. nevadensis</u> , <u>C. chryso- phylla</u>
ONION RIDGE 11 miles west of U.S. Highway 199 on Onion Mt. Road; R.8W., T.36S., Sec.34	Jgv	3800	<u>Ps. menziesii</u> , <u>P. lambertiana</u> , <u>L. decurrens</u> , <u>Q. vaccinifolia</u> , <u>L. densiflora</u> , <u>C. chryso- phylla</u> , <u>A. patula</u>
HAYES HILL on U.S. Highway 199 just south of Hayes Hill summit; R.8W., T.37S., Sec. 24	Jgs	1600	<u>Ps. menziesii</u> , <u>P. ponderosa</u> , <u>P. lambertiana</u> , <u>L. decurrens</u> , <u>C. cuneatus</u> , <u>C. integerrimus</u> , <u>A. menziesii</u> , <u>Q. kelloggii</u> , <u>R. diversiloba</u> , <u>Rosa gymnocarpa</u>

* S = serpentine

Jgv = andesite flows, mainly polyphyritic with breccias and tuffs

Jgc = similar to Jgv, with slightly different composition

Jgs = similar to Jgv, with slightly different composition

Qag = gold-bearing stream gravels; a conglomerate of cobbles and boulders in matrix of sandy clay

Teu = buff sandstones, shale and conglomerates

Morphological Measurements

Epidermal Characters

Field analysis calls for a set of clear-cut, easily measured or easily recognized characters if species limits are to be understood and intermediates recognized. The traditional taxonomic descriptions of viscida and canescens are not helpful in this type of analysis because, reflecting the need to label specimens, these taxonomic descriptions are too broad and include a diversity of forms. Thus Adams, who monographed Arctostaphylos, describes viscida as having, "branchlets...typically glabrous and glaucous, or sometimes sparsely glandular-hairy or pubescent" (1940, p. 30). He describes canescens as having, "pedicels pubescent or occasionally somewhat glandular-pubescent" (1940, p. 34).

Such inclusive descriptions tend to obscure the limits of variation of morphological characters of the separate species. The writer believes that an accurate understanding of species differences in Arctostaphylos will be achieved only when morphological, ecological and other descriptions are precisely defined and rigidly applied. Since epidermal characteristics have always been the basis of several of the major distinctions in the descriptions of viscida and canescens, it was necessary for the purposes of the present

study to define operationally these features of the two species as follows:

Viscida is defined as having branchlets glabrous or rarely with very sparse, often deciduous minute stalked glands; leaves glabrous; fruit glabrous and viscid or sometimes with sparse and minute stalked glands; and pedicels with stalked glands.

Canescens is defined as having branchlets, leaves and pedicels densely covered with a short, white non-glandular pubescence; and fruit with a sparse, short, white non-glandular pubescence (the ovary has dense, white hairs some of which are lost when it enlarges into fruit).

Thus when viscida is not glabrous, it has only stalked glands. Canescens never has stalked glands (and is never glabrous).

The purpose of these definitions is to test the hypothesis that viscida and canescens hybridize and produce plants with morphological features intermediate to those of the parents. The definitions supply a set of operational limits such that after examination of each character in the field with an ordinary 10x hand-lens, it can be assigned as typical of one or the other parent or as having some degree of intermediacy. The recognition of intermediacy is the sine qua non for the determination of hybridization by this type of analysis.

The accuracy of observations of these epidermal features depends on the resolving power of the instrument of observation. With the hand-lens in the field, it is

relatively easy to observe the presence, absence or intermixture of hairs and stalked glands. However, in the laboratory with a 25x or 40x stereoscopic microscope an entirely new dimension of resolution is attained. When the observations made with the hand-lens were checked with the stereoscopic microscope, the categories of intermediacy were upheld, but the extreme conditions of pubescence, i.e., all hairs or all stalked glands, were not.

The problem is most evident on the observations of the pedicels where glands and hairs are sometimes found together. Thus when the hand-lens reported only hairs or only stalked glands present on a pedicel, examination under the 40x microscope often revealed perhaps five to ten stalked glands on a pedicel densely covered with hundreds of nonglandular hairs, or perhaps five to ten hairs on a pedicel covered with glands.

The degree of accuracy available with the hand-lens is sufficient to assess and assign a character to its proper category. Absolute statements regarding the extreme conditions of hairs without glands or glands without hairs are not necessary to assign characters. The presence of even a few glands on a hairy pedicel or a few hairs on a glandular pedicel is significant, and will be discussed later, but does not disrupt the present operational definitions of character differences.

Several categories of surfaces on the branchlets, fruit and pedicels were set up to reflect the presence of different epidermal features. (Several intermediate canescens plants growing at the Hayes Hill, Waldo and Illinois Valley locations have a small number of peculiar longer, branched hairs on the branchlets in addition to the usual short, white pubescence. The source of this unusual trichome is not known.) Leaf surface pubescence was not recorded as a separate trait because it tends to duplicate branchlet surface, and because pubescence may fall off the older leaves. The following categories were made:

Branchlet Surface

- Class A. Glabrous or with very sparse stalked glands.
- Class B. Sparse pubescence.
- Class C. Dense but minute pubescence or dense pubescence with some longer branched hairs.
- Class D. Dense pubescence.

Fruit Surface

- Class A. Glabrous and viscid or sometimes with a sparse covering of stalked glands.
- Class B. Some short white hairs and some stalked glands.
- Class C. Only short white hairs.

Pedicel Surface

- Class A. Only stalked glands.
- Class B. Mostly stalked glands and some short white hairs.
- Class C. Half stalked glands and half short white hairs.
- Class D. Some stalked glands and mostly short white hairs.
- Class E. Only short white hairs.

Other Characters

In addition to the epidermal characteristics, 11 different quantitative measurements were taken on each sampled plant. Seven of these involved various measurements on the inflorescence (figure 3). Many authors (Jepson, 1939; Adams, 1940; Abrams, 1951; Peck, 1961) have commented on the differences of the openness of the inflorescences of viscida and canescens, although generally they were not directly contrasting these two particular species. Viscida is said to have an open or loose panicle and canescens a short and dense panicle. The writer's own preliminary investigations tended to confirm this, and therefore measurements of the structures that cause the inflorescence to appear open or dense were taken. It was hoped that such measurements would prove valuable in differentiating the two species and might provide a subtle means of discerning hybrid plants.

The other four measurements were made on leaf shape. An earlier study of hybridization between A. patula and A. mariposa had also used leaf-shape differences (Epling, 1947a). All measurements were made on plants that were maturing fruits.

Inflorescence Measurements

1. Length of rachis from apex to highest rachilla.
2. Lengths of rachis between rachillae.
3. Lengths of rachillae.
4. Length of the longest pedicel between the apex and highest rachilla.
5. Width of same pedicel.

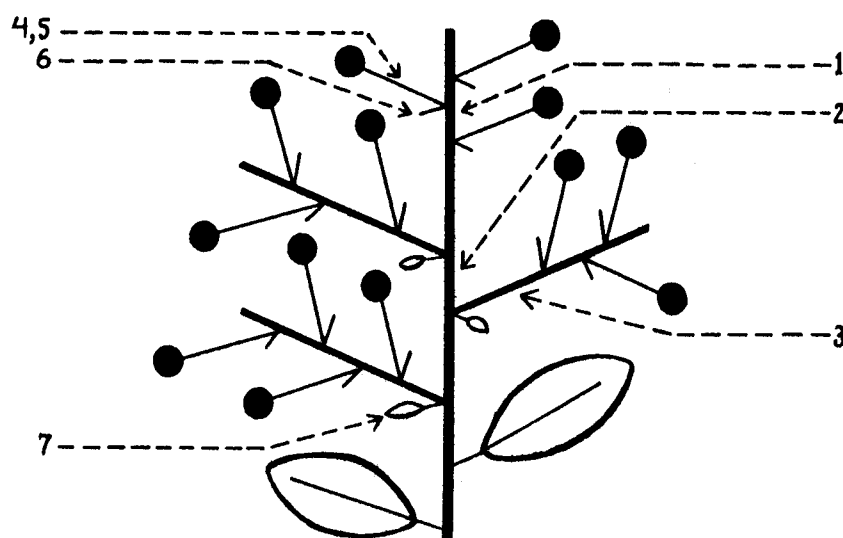


Figure 3. SCHEMATIC DIAGRAM OF ARCTOSTAPHYLOS INFLORESCENCE.
(See page 29 for identification of numbered structures.)

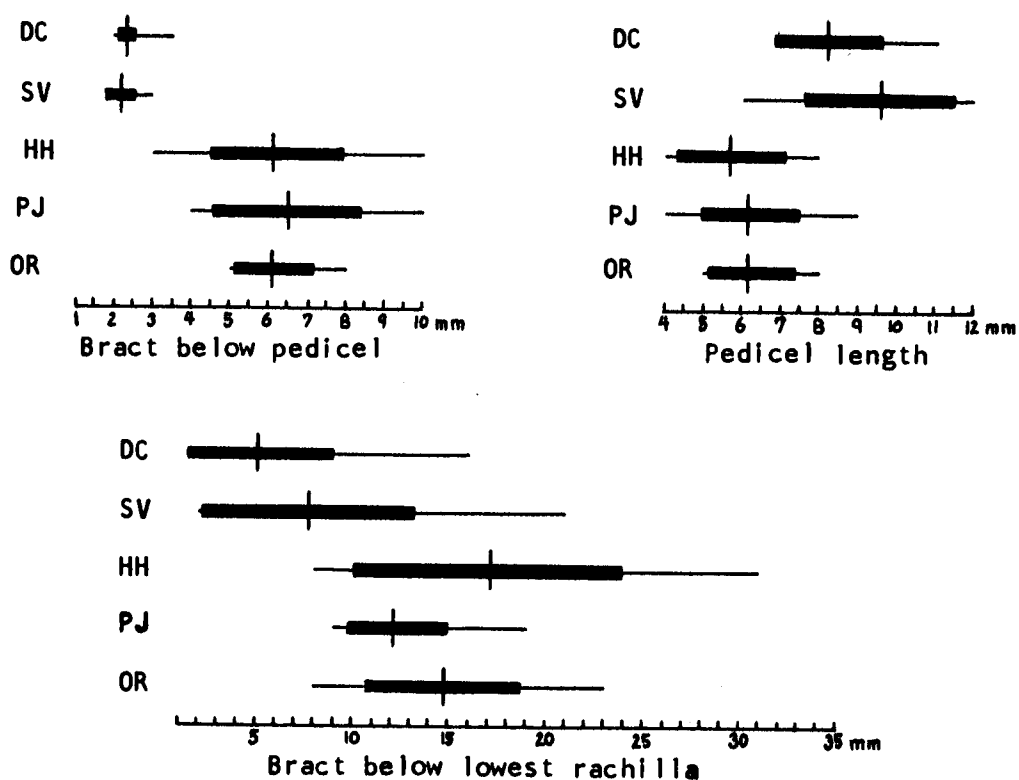


Figure 4. MEANS, STANDARD DEVIATIONS AND SAMPLE RANGES FOR THREE QUANTITATIVE CHARACTERS IN A. VISCIDA AT DEER CREEK (DC) AND SAMS VALLEY (SV), AND IN A. CANESCENS AT HAYES HILL (HH), PEAK JUNCTION (PJ) AND ONION RIDGE (OR).

6. Length of bract below a pedicel midway between the apex and highest rachilla.
7. Length of bract below the lowest rachilla.

Leaf Measurements

8. Length of the largest normal leaf blade produced in the prior two years.
9. Width of same leaf.
10. Length of petiole on same leaf.
11. Length from apex to the widest point of the blade on same leaf.

The Hybrid Index

The hybrid index is a method of comparing populations by scoring individual members of each population on a number of specific morphological differences (Anderson, 1949). Differences in the characters are scored as essentially like one species, essentially like the other, or as intermediate. One species is arbitrarily selected for the low end of the scale, the other for the high end. Thus, in a hybridizing population, plants exactly like the former species in all characters measured would score zero in each character and would have a total index value of zero. Plants exactly like the latter species would score, let us say, two in every character, and if six characters were being measured, such plants would score a total of 12. Plants intermediate in all characters would score a total of six. The frequency distribution of a sufficient sample of plants of a given population scored by this method indicates whether the population is essentially like one or the other of the

hybridizing entities or is intermediate to them. The value of the hybrid index is that it analyzes a hybrid population on the basis of a number of different characters any one of which may be insufficient by itself to indicate the hybrid nature of the population or of a particular plant.

Before the results of a hybrid index can be considered significant, the sensitivity of the index characters as measures of species differences must be determined. Characters that are considered more sensitive than others may be weighted to reflect their greater sensitivity.

The sensitivity of each character was determined by comparing the ranges of variation for the character in samples of 20 from two separate populations each of viscida and canescens. Each of the three qualitative characters of the pubescence proved diagnostic (figure 5). However, of the 11 quantitative measurements, only three were judged sufficiently satisfactory in terms of constancy and distinctiveness to permit them to be used as species-separating characters. These three are pedicel length, length of the bract below a pedicel, and length of the bract below the lowest rachilla (figure 4).

The impression of openness of the viscida panicle in contrast to the denseness of the canescens panicle was found to be a function of their different pedicel and bract lengths. In addition, the state of development of the

panicle, i.e., how many rachillae are present, how fully developed they are, how many fruits are present and the manner of their distribution, was found to be an important factor enhancing this impression.

The failure of eight different characters to separate the two species indicates the extent of their morphological similarity as well as the difficulty of designating intermediate plants in the field. In addition, it points up the historic problems associated with delimiting species in Arctostaphylos, since many of these characters have been used heretofore either directly or indirectly in the taxonomic descriptions of the species.

The six good characters were weighted according to their sensitivity in reflecting species differences. The weighting of the three quantitative characters was determined by the degree of separation of their means from each other (figure 4). The bracts below pedicels, which in the two species are abruptly different in length, were assigned a value of four points. Pedicel length, which was not as clearly defined, was valued two points. The length of the bract below the lowest rachilla is fairly sensitive; however, occasionally it is abnormally long in plants of viscida, perhaps because this structure is morphogenetically intermediate between a bract and a leaf. It is not a true part of the inflorescence, but instead marks the point of

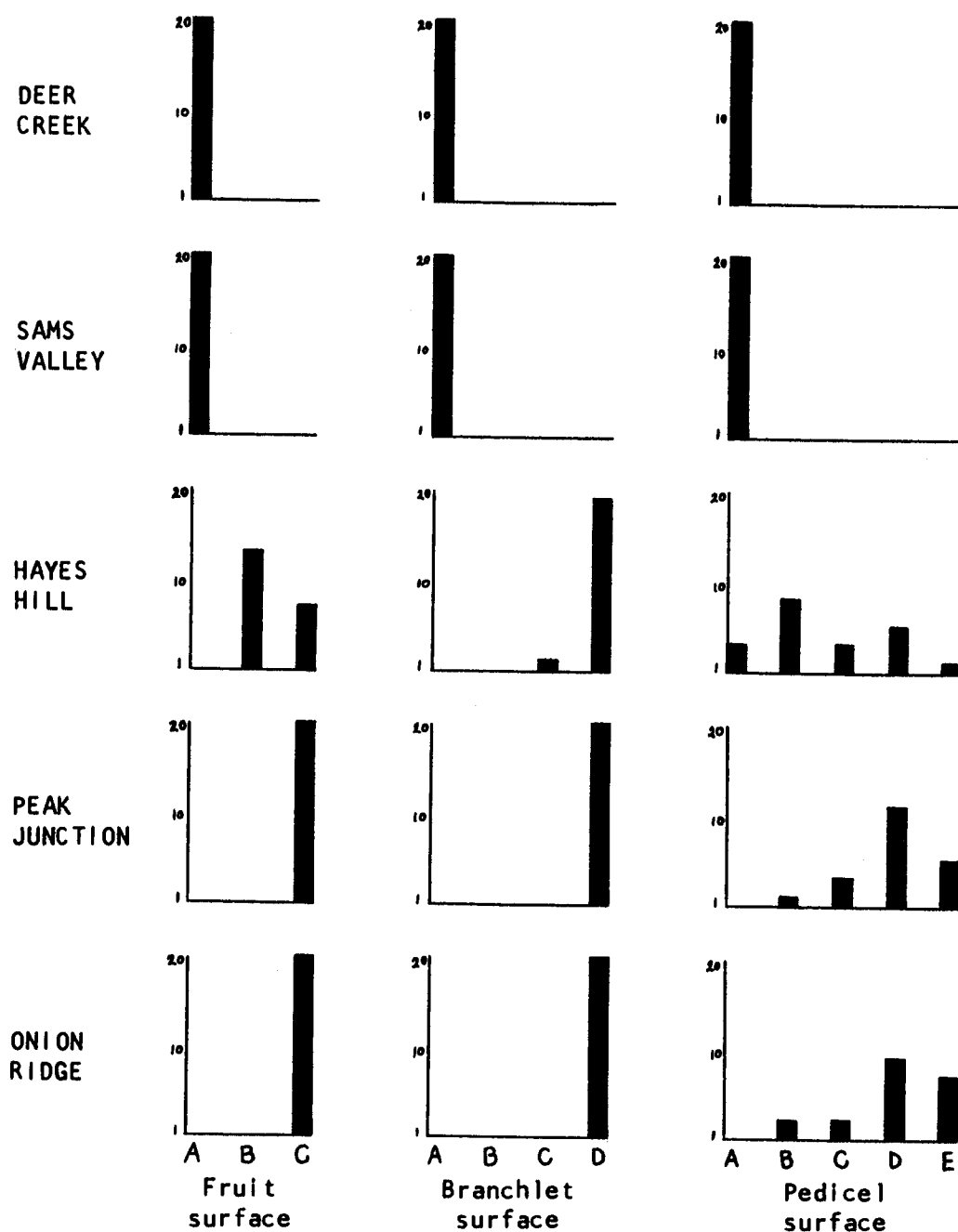


Figure 5. FREQUENCY DISTRIBUTIONS FOR THREE PUBESCENCE CHARACTERS IN *A. VISCIDA* AT DEER CREEK AND SAMS VALLEY, AND IN *A. CANESCENS* AT HAYES HILL, PEAK JUNCTION AND ONION RIDGE. (See page 28 for identification of letters.)

changeover from vegetative to reproductive organs. Thus, in certain plants otherwise indistinguishable from viscida, this bract may be leaf-like and similar in length to the corresponding structure on canescens. The feature was given three points in the hybrid index.

The three characters of surface pubescence were assigned a total of ten points. Branchlet surface was given four points because the addition of even the slightest amount of pubescence to the glabrous surface of viscida is easily noticed and reflects an obvious hybrid condition. Pedicel surface, which is an extremely sensitive character, was assigned five categories and also valued at four points. Fruit surface was valued at two points because it may be partially affected by the same genes affecting pubescence in the branchlets and pedicels.

The effect of this weighting procedure is to value approximately equally the quantitative and the qualitative characters. A "good" canescens plant is assigned the maximum amount of points for each of the six characters and therefore earns a total of 19 points. A "good" viscida plant scores the minimum for each character and earns a total of zero points. Plants that score intermediate totals are assumed to be hybrids.

The Pictorialized Scatter Diagrams

Another method of analyzing hybridization under natural conditions is by pictorialized scatter diagrams (Anderson, 1949). Such diagrams are particularly useful to demonstrate the presence or absence of genetic linkage between different polygenically determined morphological characters. The procedure is to score a number of individual plants simultaneously for two independent measurable characters and plot the results as a two-dimensional scatter diagram. Additional characters are represented by coloring or decorating the circles representing each individual plant.

In the present study, branchlet surface was plotted against the length of the bract below the pedicel (figures 8, 9, 10, 11 and 12). These two characters were selected to form the coordinates of the diagram because they have no apparent developmental relationship to each other, they can be measured accurately, and they can be graded in a series of categories. Three other characters--pedicel surface, pedicel length, and the length of the bract below the lowest rachilla--are represented on each circle and scored as either like viscida, like canescens or intermediate.

CYTOLOGY AND BREEDING SYSTEM

Flower buds of canescens from Hayes Hill and of viscida from Sams Valley were collected February 27, 1965, and fixed in a solution of four parts chloroform, three parts ethanol, and one part glacial acetic acid. In both species the bud scales and the tightly closed corollas prevent the stain from penetrating into the anthers. Piercing the buds with a needle before staining solved this problem. The buds were stained with acetocarmine and left in the stain for 72 hours at 55° C. to assure complete staining. The pollen mother cells were mounted and squashed in a freshly prepared mixture of Hoyer's medium and 45 per cent acetic acid (Beeks, 1955).

A number of satisfactory slides of meiosis in pollen mother cells were obtained. Both species show $n=13$. Meiosis was normal in all cells observed. Previous counts in the genus also reported this same haploid chromosome number (Gankin and Major, 1964).

Limited observations regarding the possibility of self-fertilization in canescens suggest that the species is self-incompatible. Fifteen inflorescences on canescens plants in three separate locations were bagged with glassine envelopes to prevent cross-pollination. None of the bagged inflorescences developed fruits although each of the bagged plants

set abundant fruits on its other unprotected inflorescences. The species is most likely pollinated by bees; at least three different species have been observed visiting the flowers.

RESULTS OF ANALYSES OF NATURAL POPULATIONS

The hybrid-index analyses of the populations of viscida at Sams Valley and Deer Creek and of canescens at Peak Junction and Onion Ridge show that the two species are clearly separated by the combination of six morphological characters (figure 6). The same analyses applied to the two species when they are growing adjacent to one another at Waldo, Lookout Gap, and Illinois Valley (figure 7) show the presence of numerous morphologically intermediate plants, believed to be hybrids.

The common factor in the three locations where intermediates are found is the presence of a contact zone of serpentine and non-serpentine soils. At each location viscida grows primarily on serpentine, although occasional individual viscida plants are found on nearby non-serpentine soils. The presence of viscida among canescens plants on non-serpentine further increases the possibilities of cross-fertilization and hybridization. Canescens has never been observed growing on serpentine.

The degree of soil mixing along the contact zones is greatest at Waldo, a consequence of both natural erosion and mining activities. At both the Illinois Valley and Lookout Gap locations, man's influence has been substantially less, primarily the construction of unpaved roadways. Also, at

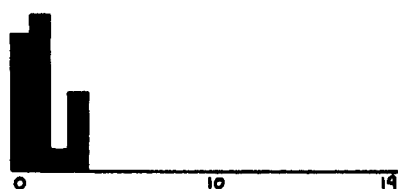
these locations the different soil types are situated side by side down the slopes of steep hillsides, so that erosion does not work one type of soil over the other in any substantial manner.

By far the greater number of hybrids and the greater proportion of hybrids to parents are also at Waldo (figures 7, 9, 10 and 11). The close connection between the extent of soil transition zones and the presence of hybrids is well known in groups of plants other than Arctostaphylos. The most relevant examples to the present study are in Nobs' (1963) study of Ceanothus, a shrubby genus quite similar to Arctostaphylos in distribution and ecological preferences and often found associated with it. Ceanothus pumilus is a serpentine endemic sometimes found growing with C. cuneatus, a wide-ranging species inhabiting hot, dry inland hills in the North Coast Ranges of California and southwestern Oregon. Under normal conditions no intermediates are found between these two species; however, under disturbed conditions hybrids are frequent. In the flood plain of the Illinois River, three miles north of Waldo, Nobs reported a population that contained 22 per cent intermediate plants out of a total of 50 surveyed. A similar series of hybrids was found in a serpentine contact zone two miles east of O'Brien (Nobs, 1963). Both of these locations are within a few miles of the Arctostaphylos hybrids found at Waldo.

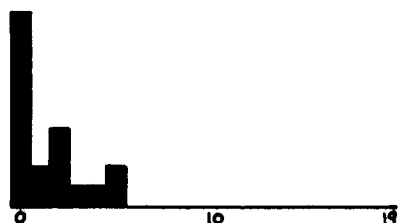
HYBRID INDEX KEY

CHARACTER	<u>A. VISCIDA</u>	INTER-MEDIATES	<u>A. CANESCENS</u>
Pedice! length	≥ 9 mm 0	8, 7mm 1	≤ 6 mm 2
Bract below pedice!	≤ 3 mm 0	4 mm 2	≥ 5 mm 4
Bract below lowest rachilla	≤ 5 mm 0	6-8, 9-11 1 2	≥ 12 mm 3
Pedice! surface*	A 0	B C D 1 2 3	E 4
Branchlet surface*	A 0	B C 2 3	D 4
Fruit surface*	A 0	B 1	C 2
TOTAL	0		19
* See page 28 for identification of letters.			

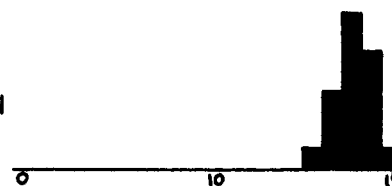
DEER
CREEK
n=20



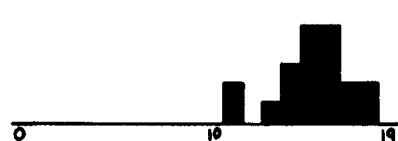
SAMS
VALLEY
n=20



PEAK
JUNCTION
n=20



HAYES
HILL
n=20



ONION
RIDGE
n=20

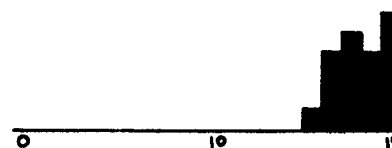


Figure 6. HYBRID INDICES FOR A. VISCIDA AT DEER CREEK AND SAMS VALLEY, AND FOR A. CANESCENS AT HAYES HILL, PEAK JUNCTION AND ONION RIDGE.

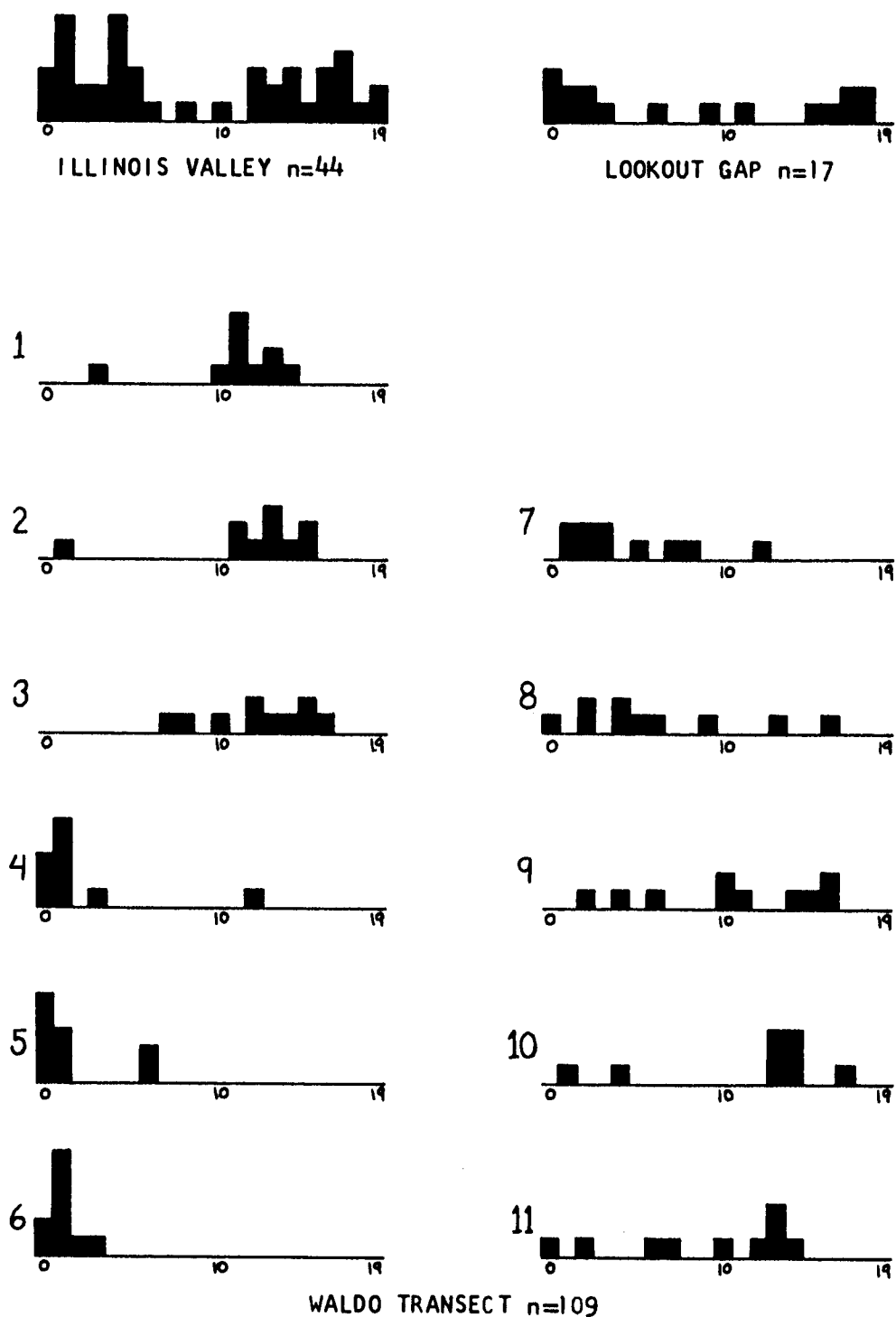


Figure 7. HYBRID INDICES FOR A. VISCIDA AND A. CANESCENS WHERE THEY MEET AT ILLINOIS VALLEY, LOOKOUT GAP AND WALDO (TRANSECT INTERVALS 1-11).

Nobs (1963) also reported the discovery of several intermediates between C. jepsonii var. albiflorus, another serpentine endemic, and C. prostratus var. occidentalis on a contact zone between serpentine and volcanically-derived soils.

Most of the hybrids between Arctostaphylos viscida and A. canescens survive on transitional or non-serpentine soils. These plants include F_1 intermediates, F_2 segregants as well as backcrosses to canescens indicated by a series of plants intergrading from the intermediate condition to those mostly like canescens.

Some hybrid plants also survive on serpentine and can be detected, for example, by the presence of sparse pubescence on their branchlets. Two plants on serpentine and four plants not on serpentine show this intermediate condition (figures 10, 11 and 12). The two serpentine plants are particularly interesting because in all their other morphological characters (except fruit surface, also intermediate and perhaps also affected by the same genes controlling branchlet pubescence), they closely resemble "good" viscida. Only five other plants out of the total of 52 sampled on serpentine show some other features suggestive of canescens, such as long bracts below pedicels or a high percentage of hairs on the pedicels.

CHARACTER	<u>A. VISCIDA</u>	INTER-MEDIATE	<u>A. CANESCENS</u>
Bract below lowest rachilla	≤ 5 mm ○	6-11 mm ○	≥ 12 mm ⊙
Pedicel length	≥ 9 mm ○	8, 7 mm ○	≤ 6 mm ○
Pedicel surface	glandular ○	both ○	all hairs ●

KEY

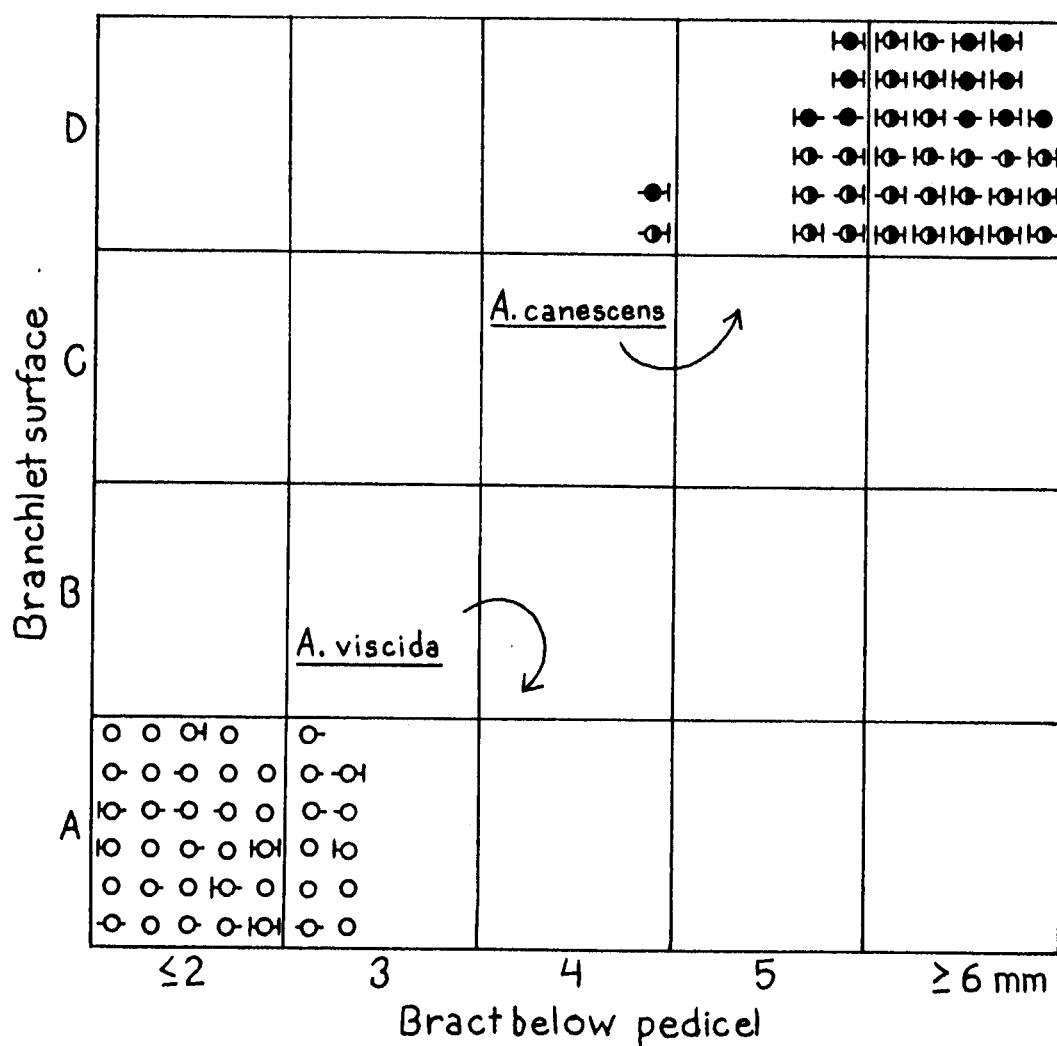


Figure 8. PICTORIALIZED SCATTER DIAGRAM FOR A. VISCIDA AT DEER CREEK AND SAMS VALLEY, AND FOR A. CANESCENS AT PEAK JUNCTION AND ONION RIDGE.

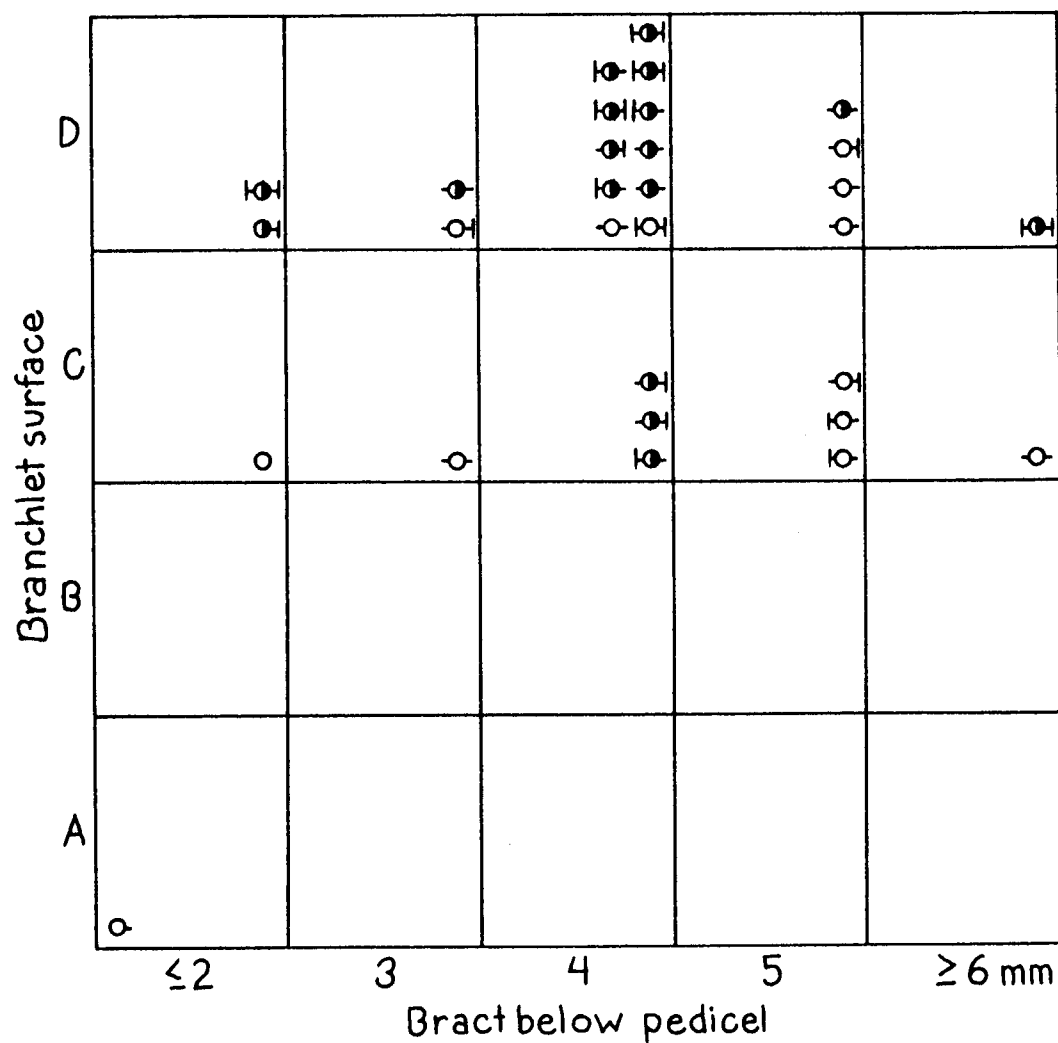


Figure 9. PICTORIALIZED SCATTER DIAGRAM FOR A. VISCIDA AND A. CANESCENS WHERE THEY MEET AT WALDO (TRANSECT INTERVALS 1, 2 AND 3).

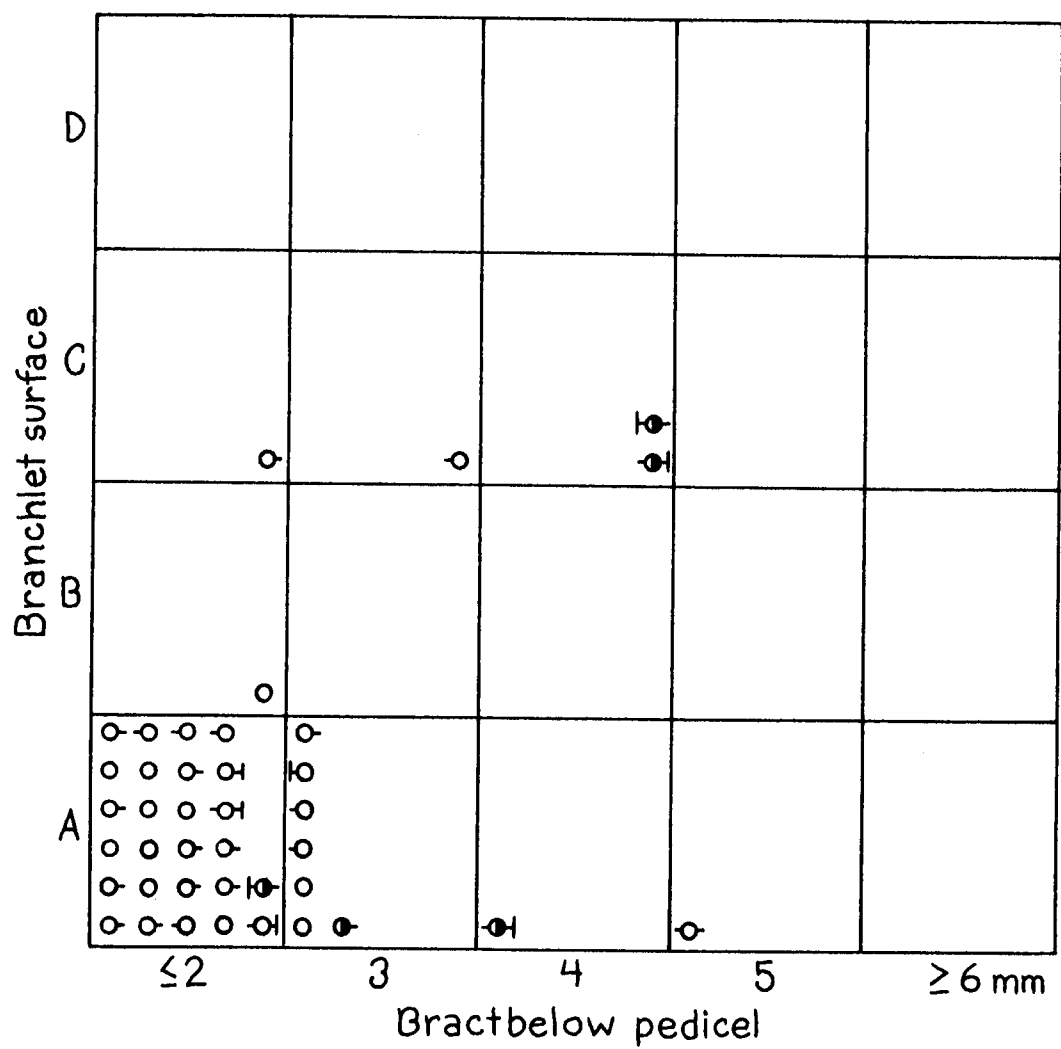


Figure 10. PICTORIALIZED SCATTER DIAGRAM FOR *A. VISCIDA* AND *A. CANESCENS* WHERE THEY MEET AT WALDO (TRANSECT INTERVALS 4, 5, 6 AND 7).

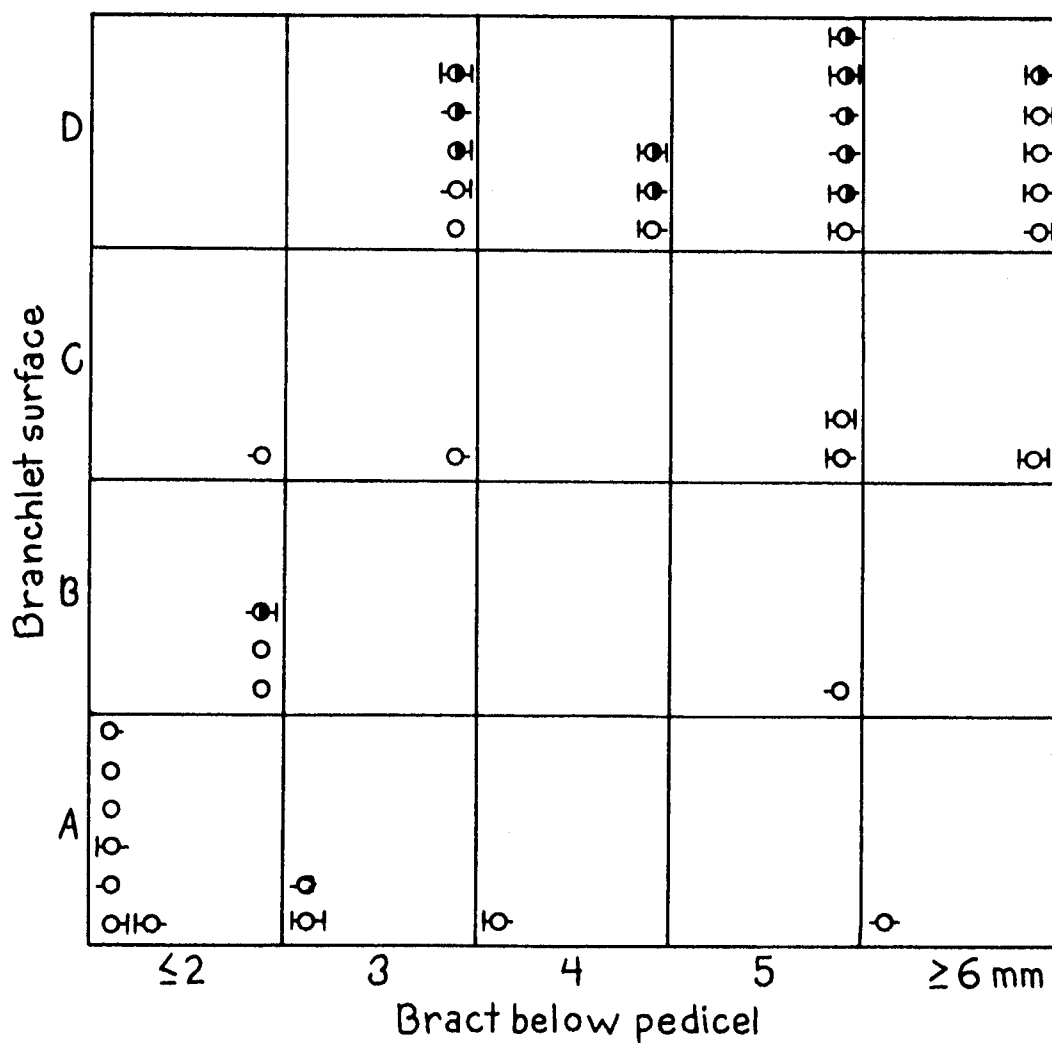


Figure 11. PICTORIALIZED SCATTER DIAGRAM FOR A. VISCIDA AND A. CANESCENS WHERE THEY MEET AT WALDO (TRANSECT INTERVALS 8, 9, 10 AND 11).

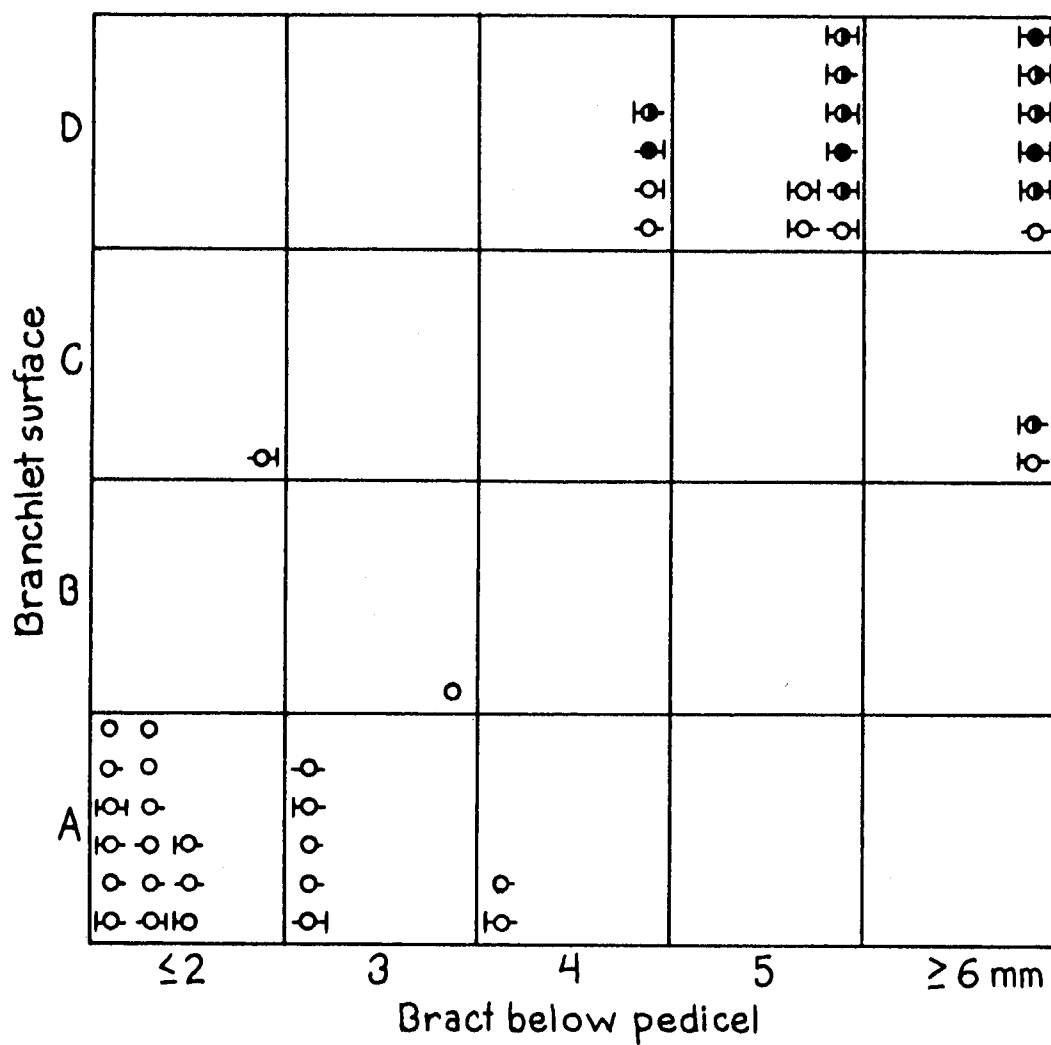


Figure 12. PICTORIALIZED SCATTER DIAGRAM FOR A. VISCIDA AND A. CANESCENS WHERE THEY MEET AT ILLINOIS VALLEY.

The question arises why so few of the plants on serpentine show canescens-like characteristics. The most likely answer is that strong edaphic selection is operating against those hybrid seedlings which do not have the minimum number of viscida genes necessary for serpentine tolerance. The ability to survive on serpentine is probably conditioned by a number of genes, for it involves a plant's reaction to several limiting factors including differential mineral availability and low soil moisture caused by low-clay, gravelly, shallow soils. If this is the case, then the hybrid plants which survive on serpentine must be at least second or third generation backcrosses to viscida, because the F_1 itself would only have half its genotype derived from viscida. The backcrossed plants will also look very much like viscida because of the effects of linkages between genes controlling physiology and morphology. The presence, for example, of sparse pubescence on the branchlets of the hybrid--a condition not found on either viscida or canescens (figure 5)--is a morphological expression of canescens genes after backcrossing.

Throughout the study region between Hayes Hill and the Oregon-California border, hybridization occurs wherever adjacent populations of viscida and canescens occur. It is believed, however, that genes of viscida can be recognized in canescens plants many miles distant from any contact

zone. Such influence is particularly evident in the finding of stalked glands intermixed with the short hairs on the pedicels of otherwise indistinguishably canescens-like individuals.

Viscida is the only reasonable source in this region of genes determining the presence of stalked glands. The other Arctostaphylos species in southwestern Oregon either do not have this character or, for other reasons, cannot be considered the source of the glands. Arctostaphylos patula has glabrous pedicels; A. nevadensis is described as having either glabrous or moderately white-hairy pedicels. Only A. columbiana is described as having glands on the pedicels. However, this species also has distinct setose hairs on its branchlets, petioles and rachises and, since canescens has never been observed with setose hairs, it is difficult to believe that canescens received genes for pedicel glandularity from A. columbiana and yet never exhibits any indications of the setose hairs. In southwestern Oregon this leaves only viscida which could have supplied the genes for pedicel glandularity to canescens.

The farther apart large populations of the two species occur, the less the genetic influence of one on the other can be demonstrated (figure 6). The Onion Ridge canescens population is three miles farther from viscida at Lookout Gap than is the Peak Junction canescens population. Onion

Ridge has six individuals scoring a total of 19 points in the hybrid index, compared to only one such individual at Peak Junction. The Onion Ridge sample also has seven plants without glands on the pedicel, compared to five in the Peak Junction sample. The Hayes Hill canescens population, located on U.S. Highway 199 within a few miles of extensive populations of viscida at Deer Creek, has no individuals with a score of 19 and only two with 18. This sample of canescens has only a single individual without glands on the pedicel. At Waldo where the two species are adjacent, there are no individuals with a score of 18 or 19, and only one with 17 (figure 7). None of them has glandless pedicels.

Thus the hybrid indices which analyze the degree of morphological intermediacy in the populations also indicate the degree of geographical separation of the hybridizing species. The canescens populations at Onion Ridge and Peak Junction may not be "pure" canescens, but they are the best available canescens populations known to the writer in the region.

The viscida populations at Sams Valley and Deer Creek are substantially more uniform morphologically than the canescens populations. In terms of epidermal features and the length of bracts below pedicels, the viscida populations are remarkably constant (figures 4, 5). Nearly half (17 out of 40) of the viscida plants scored zero on the hybrid

index; ten scored only one (figure 6).

The higher scores of several of the viscida plants are the result of the two characters of pedicel length and length of the bract below the lowest rachilla. Both of these characters, particularly the latter, are probably influenced by environmental conditions. In combination, they may give an individual plant a maximum of five points on the hybrid index. The three plants at Sams Valley (figure 6) with scores of four or five are not considered by the writer to be any less "good" viscida than those plants scoring zero or one.

On the canescens side of the index scale, however, there are two reasons why scores equally close to the extreme, i.e., 14 and 15, are likely to represent hybrid individuals (figure 6). The intermixture of glands and hairs on the pedicels lowers the total score in many instances. Second, the effect of environmental influence is less relevant in the scoring because a given plant is scored as typically canescens if on either bract it measures at least a minimum length. Unusually excessive lengths have no effect on the scoring of these two characters as they do in viscida.

The viscida populations at Deer Creek and Sams Valley were compared to determine if there are any morphological differences in the species when it is growing on and off

serpentine. No significant differences are noted in the characters used in the hybrid index, although there are some slight differences in the mean of pedicel length and length of the bract below the lowest rachilla (figure 4). The differences in growth form, however, might simply reflect environmental influence. The plants at Sams Valley are almost arborescent (12 to 16 feet high) and are growing close to one another. At Deer Creek, the plants are shorter (from 3 to 9 feet high), spaced farther apart and, with the additional sunlight that this provides, are more rounded in outline. The leaves on the serpentine plants have a yellow-green hue while those off serpentine tend to be more gray-green.

On serpentine soils in the Illinois Valley and at Waldo, viscida plants frequently exhibit stem-layering. In certain locations this seems to be the chief method of reproduction, for no seedlings are observed. On non-serpentine soils at Waldo, viscida is taller and has larger leaves than the serpentine viscida at Waldo. Stem-layering is also observed in canescens at Peak Junction, Onion Ridge and elsewhere.

In places where either viscida or canescens occurs with other species and no indications of hybridization are present, differences in flowering time may be a significant isolating barrier. For example, at the Peak Junction

location where canescens is growing interspersed with A. patula, a distinct difference of perhaps several weeks is evident in the time of flowering of the two species. When the writer first visited this locality in early April, 1965, the A. patula plants were just finishing anthesis whereas the great majority of the canescens plants had not yet expanded their flower buds.

The pictorialized scatter diagrams are also effective methods of representing hybridization between viscida and canescens. The two species growing separately from each other occupy opposite corners of the diagram and have different decorations (figure 8). Where the two species are growing adjacent to each other in the contact zones at Waldo and the Illinois Valley, the diagrams (figures 9, 10, 11 and 12) show the effects of differential hybrid survival caused by the presence of serpentine soils. It has already been noted that most of the identifiable hybrids occur on transitional soils. Based on morphology, much of the variation in these hybrids is from an intermediate condition to the canescens-like extreme, and presumably they are backcrosses to canescens (figure 7). The effect of hybridization on viscida is much less because of the more rigid natural selection at locations on serpentine (figure 10).

The diagrams show that in geographically isolated viscida populations, glabrous or sparsely glandular

branchlets are always associated with totally glandular pedicels (figure 8). In isolated canescens populations, pubescent branchlets may be associated with several categories of pedicel surface features (figure 8). This finding supports the previous observation from the hybrid indices that viscida is more uniform than canescens.

In summary, the data provide evidence of hybridization and backcrossing at contact zones. The data also suggest that there may be a long-range flow of genes from viscida to canescens. Three observations support this latter possibility. First, in the contact zones, the effect of stricter differential edaphic selection of the hybrid seedlings on serpentine results in viscida more easily infiltrating canescens than vice versa. There is some backcrossing to viscida (as already pointed out), but this is apparently a localized phenomenon and cannot be detected in more distant viscida populations. Second, the lack of morphological uniformity in geographically separate canescens populations contrasts with the marked uniformity in separate viscida populations. Third, away from contact zones canescens populations contain individuals with various amounts of stalked glands mixed with hairs on their pedicels. The variability is inversely proportional to the geographical distance separating them from viscida populations.

The finding of hybridization at contact zones seems clear-cut. However, the suggestion of long-range gene flow from viscida to canescens remains speculative. One alternative explanation of the observations is that canescens is an inherently variable taxon, irrespective of its genetic contacts with viscida. It is not possible in the present study to rule out this alternative; canescens is primarily Californian in distribution and, unfortunately, field studies could not be conducted in the main part of its range. In a genus as complex and slightly differentiated morphologically as Arctostaphylos, only intensive field studies can reveal the actual pattern of variation in the different taxa. Examination of California herbarium material, without a knowledge of the ecological nature of the habitat from which the material came, would not be definitive and might be misleading.

TAXONOMIC HISTORY AND CONCLUSIONS

Arctostaphylos viscida was first described from Ione, Amador County, California, by C. C. Parry (1887) who was struck by the plant's conspicuous glandular-viscid pedicels. The species is found in the Sierra Nevada foothills from Calaveras to Shasta Counties and in the northern Coast Ranges from Napa to Del Norte and Siskiyou Counties in California, and into Josephine and Jackson Counties in Oregon.

Adams (1940, p. 30), who monographed the genus, gives the following description of A. viscida:

Erect shrub 1 to 4.5 m. high with several crooked stems from the base, with deep red, smooth bark; branchlets and peduncles slender and typically glabrous and glaucous, or sometimes sparsely glandular-hairy or pubescent; leaves pallid-glaucous, glabrous, orbicular, ovate, or elliptic, abruptly acute or obtuse and short-mucronate at apex, rounded or somewhat truncate at base, 2-4 cm. long; petioles slender, 5-8 mm. long; rachises typically glandular, or sometimes glabrous and glaucous; bracts inconspicuous, rarely more than 2 mm. long, ovate-acuminate, reddish, glandular-puberulent; pedicels slender, reddish, glandular-hairy, 6-10 mm. long; sepals ovate, acute, ciliate, pinkish, reflexed in fruit; corolla pink or almost white, 6 mm. long; ovary glabrous, or commonly glandular; fruit small, 6-8 mm. broad, flattened, deep red, glabrous or commonly very glandular; nutlets separable. No enlarged root-crown is produced; the shrubs kill under fire.

Arctostaphylos canescens was named by Alice Eastwood (1897) on the basis of a plant growing on Mt. Tamalpais, Marin County, California. The range of the species is the

North Coast Ranges from Marin to Del Norte Counties, California, and into southwestern Oregon in slightly modified form. Adams' (1940, p. 34-35) description of A. canescens follows:

Erect, straight-stemmed shrub 1 to 2 m. high, or in some situations a low (3 to 6 dm.) dense and knotty shrub; old stems with deep red smooth bark; branchlets densely white-tomentose or downy; young leaves very downy, pale, older ones less so, ovate, oblong-obovate to rotundish, spreading, mostly 2-4 cm. long, 1-2.5 cm. wide, on downy petioles 5-8 mm. long; peduncles and rachises white-tomentose or downy; panicle short, dense; bracts large, foliaceous, usually longer than the pedicels; pedicels pubescent or occasionally somewhat glandular-pubescent, 5-6 mm. long in flower, or up to 10 mm. in fruit; corolla pink, 8-9 mm. long; ovary densely white-hairy, non-glandular; fruit flattened-globose, usually pubescent or sometimes slightly glandular or glabrate and with a bloom; nutlets separable. No enlarged root crown is produced.

Thomas Howell named six species of Arctostaphylos from Waldo and Andersons in Josephine County, Oregon, in his Flora of Northwest America published in Portland, Oregon, in 1901. All of his species descriptions were based on specimens collected in April, 1886. Several of these taxa have been accepted and elaborated by later taxonomists. Other taxa have been merged in other species or given varietal status. Following is a taxon-by-taxon description of each of Howell's species and a survey of the relevant subsequent taxonomic opinion.

Howell (1901, p. 416) describes A. cinerea from near Waldo, Oregon:

Erect, 3-6 feet high, densely branched from the base, with rather light-colored bark and cinereous branchlets: leaves oblong or obovate, obtuse or acutish to acute, cuspidate, whitish-green, tapering below to a stout flat cinereous petiole, smooth: bracts not foliaceous, acuminate-lanceolate with a broad base, minutely cinereous; pedicels longer than the bracts, minutely tomentose: corolla dark rose-color to nearly white: filaments densely hairy: ovary hairy at the top: fruit globose, flattened at each end: some of the nutlets coalescent. Rocky hillsides along the eastern base of the Coast Mountains near Waldo, Oregon.

Adams (1940, p. 42-43) accepts the species and considers it "one of the more clearly marked of Howell's species." He goes on to say the species "produces an enlarged root crown from which sprouts arise after fire." He notes the lower bracts are "somewhat foliaceous." Benson (1930, p. 139) also accepts A. cinerea, but says it "is distinctly of the A. nevadensis type [note: a prostrate mountain species] and is probably only a pubescent form of it." He continues, "As is true of all the species proposed from this region, much more ample material and careful study is necessary before the true specific value of the various forms recognized can be determined. Aside from the type, the specimen cited is all that we have seen of this species." The species has also been accepted by Abrams (1951), McMinn (1939), Munz and Keck (1959), Eastwood (1934), and Peck (1961).

Howell (1901, p. 416) describes A. oblongifolia also from near Waldo, Oregon:

Densely branching from the base, with reddish-brown bark and cinereous branchlets, 4-6 feet high: leaves oblong or the lowest obovate, obtuse, cuspidate, usually abruptly contracted below to a rather long round petiole, whitish-green, smooth: bracts somewhat foliaceous, acuminate-lanceolate with a broad base, minutely pubescent: pedicels longer than the bracts, minutely pubescent and sparingly glandular: corolla white tinged with red: filaments very sparingly if at all hairy: ovary pubescent at the top. Rocky hillsides, eastern base of the Coast Mountains near Waldo, Oregon.

Examination of the holotype reveals that the two specimens on the specimen sheet are different in several significant characters. The righthand specimen has pedicels mostly with stalked glands and a few hairs, and ovary glabrous. The lefthand specimen has pedicels with a mixture of half-and-half stalked glands and hairs, and ovary densely white-hairy.

Adams (1940, p. 52) says the species has a root crown and, while noting that it needs further field study, says "it appears to be part of the non-glandular, pale-leaved northern phase of A. glandulosa Eastw." Benson (1930, p. 141) accepts A. oblongifolia and believes "the main relationships of this little-known species are with A. pulchella from which only the more or less pubescent ovary distinguishes it." Abrams (1951) merges it with A. intricata Howell, another dubious glandular-hispid species described by Howell from Gasquet, Del Norte County, California. Munz and Keck (1959) following this lead, place it

as a variety of A. intricata on the basis of branchlets and inflorescence being cinereous-pubescent. Eastwood (1934) accepts A. oblongifolia but relates it to A. viscida; McMin (1939) assigns it varietal status under A. viscida because of its pubescence.

Another Waldo species is A. bracteata (Howell, 1901, p. 417):

Strictly branched from the base, 4-6 feet high, with tomentose branchlets: leaves oblong, obtuse, obscurely cuspidate, minutely tomentose, contracted below to a flattish petiole: bracts foliaceous, lanceolate: pedicels pubescent, shorter than the bracts: filaments and ovary densely hairy. Near Waldo, Josephine Co., Oregon.

Adams (1940, p. 35) merges A. bracteata in A. canescens and considers it the "taller, large-leaved form" typical of northern California and southwestern Oregon. Abrams (1951) and B. O. Schreiber (1940) also merge A. bracteata in A. canescens Eastw. McMin (1939) calls it A. canescens var. sonomensis (Eastw.) Adams. Eastwood (1934) recognizes its species status based on its greener, less pubescent, large, broad leaves. Benson (1930, p. 143) considers that A. bracteata "has the floral characters of A. columbiana Piper but very distinct foliage, which is pale and glaucescent like that of A. pulchella Howell." He also points out its similarity to A. strigosa from which he says it "differs mainly...in having the leaf-blades long oval and similar at both ends except for an occasional small point at the apex.

The leaves are also much smaller."

The fourth species is A. strigosa. Although Howell's published description of 1901 does not indicate the particular type locality, his hand-written label on the type specimen sheet records that the type locality is Waldo, Oregon.

Howell's description (1901, p. 417) of A. strigosa follows:

Erect and loosely branching, 8-10 feet high, with densely white-tomentose branchlets: leaves oblong or ovate, obscurely cuspidate, usually rounded at the apex, minutely white-tomentose, light green, abruptly contracted below to a round petiole: bracts foliaceous, lanceolate, strigose pubescent: pedicels shorter than the bracts, pubescent: filaments sparingly hairy: ovary densely pubescent. In the mountains of Josephine Co., Oregon.

Adams (1940), considering it very close to A. bracteata, also merges A. strigosa in A. canescens as the taller, large-leaved northern California form. Abrams (1951) and Schreiber (1940) agree with Adams. Shreiber also notes the occurrence of frequent intermediates between A. strigosa and A. bracteata and comments that there is no sharp distinction between the two. McMinn (1939) places A. strigosa in A. canescens var. sonomensis. Eastwood (1934) retains it as a species and says that its chief difference from A. bracteata is leaf color. Benson (1930) also hesitatingly accepts it.

Howell (1901, p. 416) describes A. parvifolia from near Andersons, Oregon:

Stems branching from the base, with light reddish bark and minutely white-tomentose branchlets: leaves small, oblong or cuneate-oblong, obtuse or

acutish, minutely cuspidate, whitish-green, on flattish petioles: bracts triangular, short-acuminate, minutely pubescent: pedicels not longer than the lower bracts, minutely pubescent: filaments sparingly hairy: ovary glabrous. On the high hills near Andersons, Josephine Co., Oregon.

Adams accepts A. parvifolia without comment. However, his description of the species differs both from Howell's original description and from the holotype. Adams (1940, p. 43) says the species has "ovary sparsely short white-hairy or occasionally densely so." The original description says the ovary is glabrous. Examination of the holotype clearly indicates Howell's description is accurate. Munz and Keck (1959) as well as Peck (1961) also accept the species. Abrams (1951) merges A. parvifolia into A. cinerea. Benson (1930, p. 139) says it "resembles both A. nevadensis Gray and A. cinerea and yet has very short pedicels. It has the foliage and glabrous ovary of the former and erect habit and pubescent pedicels of the latter." He does not give it species status. McMinna (1939) comments that A. parvifolia has been described as a hybrid between A. nevadensis and A. patula, an erect species common in the Cascades and Sierras and east to Colorado. Hitchcock (1959), without explanation, makes it a synonym of A. nevadensis.

Howell's published description of A. pulchella, like that of A. strigosa, does not indicate a particular type locality. However, his hand-written label on the type

specimen sheet records its locality as "west of Andersons."

His description (1901, p. 416) of A. pulchella follows:

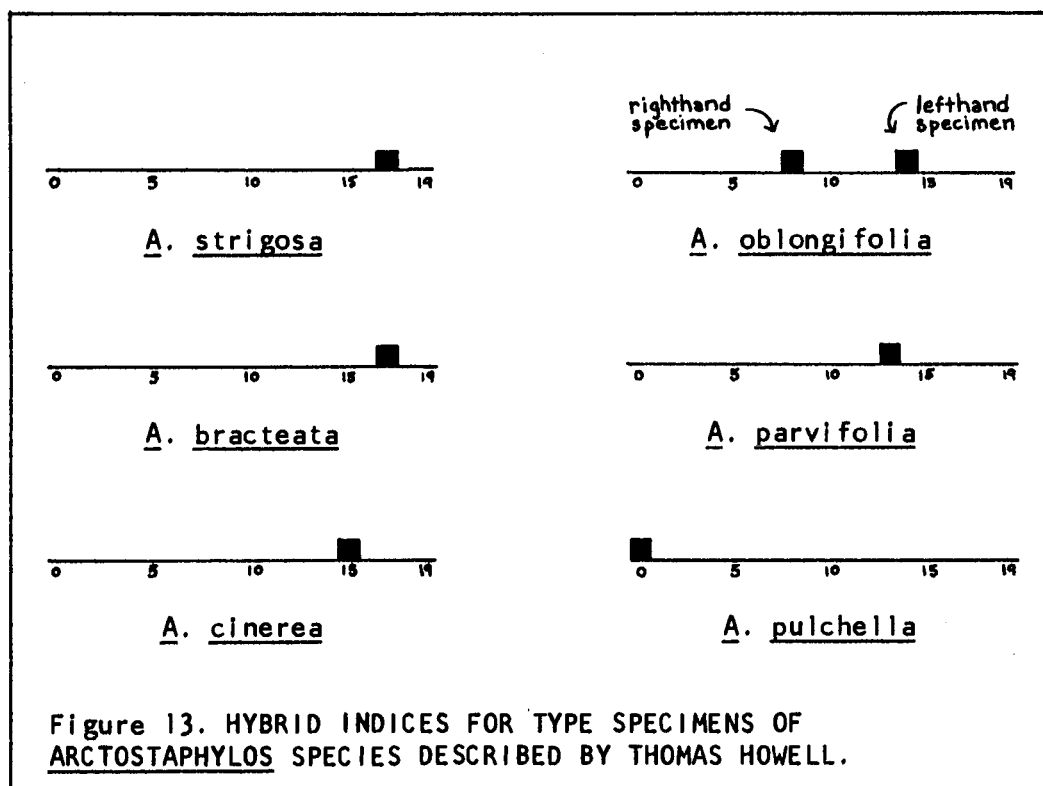
Arborescent, 6-12 feet high, branching from the base, with dark-colored bark and minutely pubescent branchlets: leaves obovate to oblong, obtuse, obscurely mucronate, smooth, cinereous-green: bracts acuminate-ovate with a very broad base, minutely pubescent: pedicels much longer than the bracts, sparingly glandular: filaments slightly hairy: ovary glabrous. On the mountains of Josephine Co., Oregon.

The type specimen has branchlets with sparse stalked glands.

Adams (1940, p. 31) considers A. pulchella "indistinguishable" from A. viscida except that its branchlets are "minutely pubescent" and therefore he merges it in the latter species. Abrams (1951) agrees. Benson (1930, p.141) accepts A. pulchella, but notes with apparent exasperation, "It is as well defined as a species as any of the lesser ones [note: of Howell's] that have been proposed."

Examination of the six holotypes reveals that none of them has any morphological features, singly or in combination, that are distinct from morphological features found either in A. viscida, A. canescens or their hybrids. The specimens were clipped in a middle stage of flowering, and do not show any signs of fruit development. Thus, technically, measurements of their inflorescences in the manner described for the hybrid index are not strictly comparable to measurements of fresh specimens in the field. However,

the differences are considered slight and do not affect the determination of epidermal characteristics. The hybrid index (figure 13) scores all of them as intermediates or mostly like A. canescens except A. pulchella, which scores zero and appears indistinguishable from A. viscida.



None of Howell's "species" exists as a natural population, unlike the intermediate populations between Ceanothus cuneatus and C. gloriosus cited earlier (Nobs, 1963). Many of his descriptive characters, such as leaf shape, bark color, branching pattern, filament pubescence, and flower color, are neither constant nor definitive features in these taxa.

Flower color, i.e., the quantity of redness on the corolla, varies on the same plant and may simply reflect the amount of sunlight that fell on the corolla. Leaf shape and size are also quite variable on the same plant. Branching patterns most likely reflect environmental influences. In short, many of Howell's descriptions either use characters of insufficient taxonomic value or in such an imprecise manner that, on the basis of his descriptions and type specimens, the writer believes it is impossible to make sense of his "species" or to identify them in the field.

Much of the diversity of taxonomic opinion on the manzanitas of southwestern Oregon results from Howell's imprecision as well as inadequate field analysis. Adams' statement that A. cinerea and A. oblongifolia have root crowns, a character Jepson (1916) first pointed out as having possible taxonomic significance, can only be considered his own opinion rather than an unquestioned morphological character of these "species," because Howell made no mention of such features and the type specimens do not show them.

The writer can find no evidence supporting McMinn's statement that A. parvifolia is a hybrid between A. nevadensis and A. patula. If these two latter species hybridize elsewhere, they do not seem to do so in the Illinois River drainage of the Siskiyou. Hitchcock's unexplained merging

of A. parvifolia in A. nevadensis is a mystery to the writer because Howell described it in his key as an erect shrub or low tree.

The taxonomy of Arctostaphylos in southwestern Oregon is most easily clarified if the intermediates between A. viscida and A. canescens are recognized as hybrids and not given taxonomic recognition as species. Since Howell described his specimens from an area where A. viscida and A. canescens are hybridizing fairly freely, and since his specimens are readily accounted for by such hybridization, it seems unwise to continue the use of his species names either in southwestern Oregon or elsewhere to identify putative hybrid individuals or stabilized hybrid populations, regardless of the degree of fit of his description to the plants being considered.

BIBLIOGRAPHY

- Abrams, Leroy. 1951. Illustrated flora of the Pacific states. Vol. 3. Stanford, California, Stanford University Press. 866 p.
- Adams, J. E. 1940. A systematic study of the genus Arctostaphylos Adans. Journal of the Elisha Mitchell Society 56:1-62.
- Anderson, Edgar. 1948. Hybridization of the habitat. Evolution 2:1-9.
- _____. 1949. Introgressive hybridization. New York, Wiley. 109 p.
- _____. 1951. Concordant versus discordant variation in relation to introgression. Evolution 5:133-141.
- _____. 1953. Introgressive hybridization. Biological Reviews 28:280-307.
- Barber, H. N. and W. D. Jackson. 1957. Natural selection in action in Eucalyptus. Nature 179:1267-1269.
- Beeks, R. M. 1955. Improvements in the squash technique for plant chromosomes. El Aliso 3:131-133.
- Benson, Gilbert Thereon. 1930. Trees and shrubs of western Oregon. Stanford, California, Stanford University Press. 170 p.
- Cooperrider, Miwako. 1957. Introgressive hybridization between Quercus marilandica and Q. velutina in Iowa. American Journal of Botany 44:804-810.
- Dansereau, Pierre and Yves Desmaris. 1947. Introgression in sugar maples. American Midland Naturalist 37:146-161.
- Detling, Leroy E. 1961. Chaparral formation of southwestern Oregon. Ecology 42:348-357.
- Eastwood, Alice. 1897. The manzanitas of Mt. Tamalpais. Proceedings of the California Academy of Sciences, ser. 3, 1:81-85.

_____. 1934. A revision of Arctostaphylos with key and descriptions. Leaflets of Western Botany 1:105-127.

Epling, Carl. 1947a. The genetic aspects of natural populations. American Naturalist 81:104-113.

_____. 1947b. Natural hybridization of Salvia apiana and S. mellifera. Evolution 1:69-78.

Forde, M. B. and D. G. Paris. 1962. Effect of introgression on the serpentine endemism of Quercus durata. Evolution 16:338-347.

Gankin, Roman and Jack Major. 1964. Arctostaphylos myrtifolia, its biology and relationship to the problem of endemism. Ecology 45:792-808.

Hall, Marion T. 1952. A hybrid swarm in Juniperus. Evolution 6:347-366.

Hitchcock, C. Leo et al. 1959. Vascular plants of the Pacific Northwest. Part 4. Seattle, Washington, University of Washington Press. 510 p.

Howell, Thomas. 1901. A flora of northwest America. Portland, Oregon. 792 p.

Jepson, W. L. 1939. A flora of California. Vol. 3. Part I. Berkeley, California, University of California Press. 128 p.

McMinn, Howard E. 1939. An illustrated manual of California shrubs. San Francisco, Stacey. 689 p.

Munz, Philip A. and David D. Keck. 1959. A California flora. Berkeley, California, University of California Press. 1681 p.

Nobs, Malcolm A. 1963. Experimental studies on species relationships in Ceanothus. Washington, D. C. 94 p. (Carnegie Institution of Washington Publication no. 623)

Parry, C. C. 1887. Californian manzanitas. Bulletin of the California Academy of Sciences 2:483-496.

Peck, Morton E. 1961. A manual of the higher plants of Oregon. 2d ed. Portland, Oregon, Binfords and Mort. 936 p.

Schreiber, Beryl O. 1940. The Arctostaphylos canescens complex. *American Midland Naturalist* 23:617-632.

Shenon, Philip J. 1933. Geology and ore deposits of the Takilma-Waldo district, including the Blue Creek district. Washington, D. C. p. 141-194. (U.S. Geological Survey Bulletin 846B)

Silliman, Francis E. and Robert S. Leisner. 1958. An analysis of a colony of hybrid oaks. *American Journal of Botany* 45:730-736.

Stebbins, G. Ledyard, Jr. 1950. Variation and evolution in plants. New York, Columbia University Press. 643 p.

Stebbins, G. L., Jr., E. B. Matzke and C. Epling. 1947. Hybridization in a population of Quercus marilandica and Quercus illicifolia. *Evolution* 1:79-88.

Stutz, Howard C. and L. Kay Thomas. 1964. Hybridization and introgression in Cowania and Purshia. *Evolution* 18: 183-195.

Tucker, John M. 1952. Evolution of the California oak, Quercus alvordiana. *Evolution* 6:162-180.

Walker, Richard B. 1954. The ecology of serpentine soils: factors affecting plant growth on serpentine soils. *Ecology* 35:259-266.

Wells, Francis G., Preston E. Hotz and Fred W. Cater, Jr. 1949. Preliminary description of the geology of the Kerby quadrangle, Oregon. Portland. 23 p. (State of Oregon. Department of Geology and Mineral Industries. Bulletin no. 40)

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.