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## ARCTOSTAPHYLOS MYRTIFOLIA, ITS BIOLOGY AND RELATIONSHIP TO THE PROBLEM OF ENDEMISM

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*Abstract.* *Arctostaphylos myrtifolia* is a California endemic plant limited to only certain outcrops of an Eocene laterite in the Sierra Nevada foothills near Ione and to a kaolin-altered rhyolite and an acid sericitic schist eastward at higher altitudes of 500 m. Taxonomically the diploid species is isolated. Morphologically it resembles a low, sclerophyllous heath. The plants are killed by fire, but seedlings are favored by the ensuing bare areas. It flowers in late winter or very early spring. The climate where *A. myrtifolia* occurs is dry in summer, wet in winter. Frosts are infrequent and slight, but summer heat is severe. Only some 350 mm of actual evapotranspiration of water is calculated to take place in these environments, but leaching may amount to 200 mm at lower elevations and to 400 mm at higher. The stations for *A. myrtifolia* do not differ greatly in climate from surrounding areas where the plant does not occur, but they have a somewhat more maritime temperature regime. The soils at these stations are acid and presumably so low in nutrients as to exclude the normal, zonal, climax vegetation. The endemic plant thus is presumed to be a better competitor on the nonzonal sites of acid soil parent material.

Many cases of similarly disjunct plant distribution can be related to regionally peculiar soil parent materials whose evident effect is to exclude the regionally climax vegetation. With competition by zonal vegetation thus weakened, disjunct plants can and do occur. The vegetation associated with *A. myrtifolia* is poor, therophytic, and adapted to acid, seasonally wet sites. It shows similarities to the Cisto-Lavanduletea of the Mediterranean region. Historical factors of some kind, and not the contemporaneously acting ecological factors alone, are assumed to help account for the limited distribution of the species.

### INTRODUCTION

*Arctostaphylos myrtifolia* Parry is an endemic plant of the central Sierra Nevada foothills of California about 70 km (40 miles) southeast of Sacramento, almost limited in distribution to outcrops of the Eocene, lateritic Ione formation. Its known geographical distribution (Fig. 1) has been

discussed and extended from the originally described Ione area to include disjunct stations to the east near San Andreas (Gankin 1963). Explanation of the extreme localization of this plant was hypothesized to depend both on its environmental relationships in the Ione area, which is a local center of endemic and disjunct occurrences,

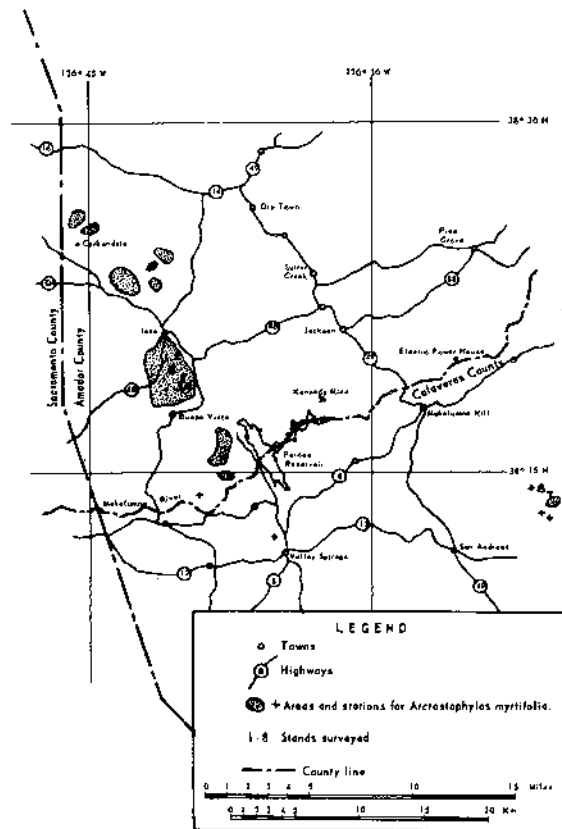


FIG. 1. Map of the distribution of *Arctostaphylos myrtifolia* in the Sierra Nevada foothills. Stations where stand surveys were made (Table IV) are numbered 1 to 8.

and also on its biosystematic relationships. This paper summarizes current information on the biology of this plant and also considers the general problem presented by the frequent occurrence of endemic and disjunct plants in many kinds of non-zonal ecosystems. The study was carried out intermittently from 1955 to the present.

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#### THE GENUS *Arctostaphylos*

The genus *Arctostaphylos* (excluding the circumpolar, deciduous *Arctous*) has a center of taxonomic diversity in California. The latest systematic treatment for California by Munz and Keck (1959) recognizes over 50 taxa. Eastwood earlier (1934b) listed well over 50 species, but many of her names have since been reduced to synonymy. Clearly the genus is a complicated one, and its taxonomy is still in a state of flux.

Of the species of *Arctostaphylos*, one is circumboreal (*A. uva-ursi* (L.) Spreng., cf. Major and

Bamberg 1963), and five more extend outside California to British Columbia, Texas, and Mexico as limits but mostly to Washington, Nevada, Utah, and Baja California. About four species are widespread within California, and all the rest are narrowly limited within the state, mostly in localized habitats near the Pacific Coast.

All the *Arctostaphylos* species of the United States occur also or mainly in California; however, *A. cratericola* Donn. Sm. is disjunct in the highlands of Guatemala. Mexican and Costa Rican taxa sometimes placed in *Arctostaphylos* can be considered species of *Comarostaphylis* or other, related genera.

The species of *Arctostaphylos* occupy a tremendous variety of habitats. Within California these include elevations from sea level to over 10,500 ft (3,200 m), the maritime northwestern coast on forest edges, windswept headlands, overdeveloped coastal podsollic soils, sandy areas, serpentine, sandstone, shale, granite, assorted extrusive rocks, dry chaparral-covered hillsides of many kinds, oak savannas, xeric pine forests, mountain coniferous forests, and others.

#### TAXONOMY OF *Arctostaphylos myrtifolia*

C. C. Parry (1887) published the original description of *Arctostaphylos myrtifolia*. He placed it in his section *Micrococcus* (Parry 1884: 36) and suggested possible affinities to *A. nummularia* Gray from near Ft. Bragg on the Pacific coast. His original description indicated only that it grew "on gravelly ridges east of Ione." Almost every subsequent description of the distribution of this species has given the same location.

Jepson (1922), following the proposed close relationship of *A. myrtifolia* to *A. nummularia* and *A. sensitiva* Jeps., reduced both *A. myrtifolia* and *A. sensitiva* to varietal status. All these taxa have small, similar-sized leaves, low or even semiprostrate habit, pubescent ovary, and similar fruit, but *A. myrtifolia* is 5-merous and *A. nummularia* and *A. sensitiva* are 4-merous. The former has stoma on both leaf surfaces, the latter two only below (Howell 1945).

Eastwood (1934a, 1937) segregated the genus *Schizococcus* from *Arctostaphylos* on the basis of readily splitting nutlets and thin pericarp. She included in this group *Arctostaphylos nummularia* (coastal Mendocino Co.), *A. sensitiva* Jepson (Mt. Tamalpais and the Santa Cruz Mts.), *A. nissenana* Merriam (a rare species near Placerville in El Dorado Co.), and *A. myrtifolia*. While these species do have the similarities named, weakness of *Schizococcus* as a genus is evident from Howell's (1955b) discussion of natural hybrids

of all of the species included by Eastwood in *Schizococcus* with other species of *Arctostaphylos* presumably not closely related to the *Schizococcus* group. If the genetic constitution of the species in the group is close enough to species outside the group to allow hybridization, there is little reason to maintain *Schizococcus* as a genus.

The latest monograph of *Arctostaphylos* (Adams 1940), as well as most recent floras, maintains *Arctostaphylos myrtifolia* as a species. Adams makes no sectional breakdown of the genus.

#### MORPHOLOGY

Plants of *Arctostaphylos myrtifolia* vary considerably in height, depending on age, site conditions, and genetic makeup. One plant 25 cm tall was approximately 8-10 years old while another 1.2 m tall was 30-40 years old. Generally, however, plants do not attain an age much older than 50 years and are not much taller than 1 m. Plants in the San Andreas region were found to be on the average much taller than those in the Ione region. An extraordinary plant was approximately 3 m tall. Soil fertility and moisture evidently affect the growth habit. The usual habit is low and semiprostrate with a tendency towards layering, so that the general aspect of an area where these plants predominate is one of low, sprawling, somewhat separated shrubs not much over 20-30 cm tall (Fig. 2). This aspect, along with a brownish color which contrasts with the greener surrounding vegetation, makes for easy recognition of a stand of *A. myrtifolia* (Fig. 3).

In an old stand of this species, very often the plants arise from a subsurface crown or stem, that is, there are several stems arising from below the surface of the soil. In such cases a branch may be connected to a plant several decimeters away and bear roots wherever it has come in contact

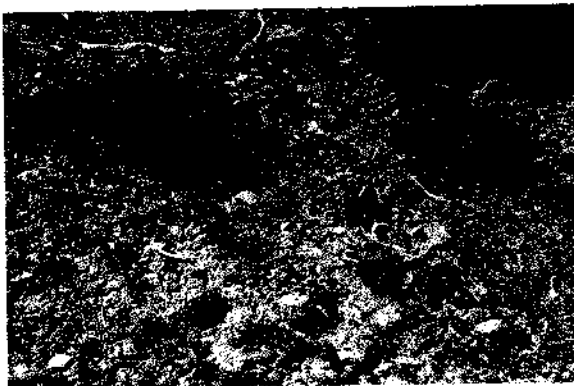


FIG. 2. Part of stand 4 of Table IV with shrubs of *Arctostaphylos myrtifolia* and in the foreground a tussock of *Juncus confusus* (right) and pedestaled *Eriogonum apricum* (left). The reddish soil is almost covered by a desert pavement of lateritic ironstone chunks.



FIG. 3. A dense stand of dark *Arctostaphylos myrtifolia* near Ione with light-colored *A. viscida* interspersed and as a band above. To the upper left is an open, ridgetop stand of *A. myrtifolia* with a gully eroding in white, kaolinitic clay.

with the soil. This capacity for vegetative reproduction makes it difficult to determine age of individual plants, let alone define an individual. Some plants that have layered are perhaps of considerable age.

Adams (1934) observed that older stems of *A. myrtifolia* had a very gnarled or flattened appearance, for cambial activity was restricted to only one edge of a branch, leading out to an apparently healthy set of branchlets, and the rest of the main branch was dead. The live portion of the stem usually occurred on the lower surface, but it might even spiral its way around the dead portion of the stem. This stem morphology is also known in *A. viscida* Parry. Adams thought the condition was caused by a parasitic fungus, but detailed observations on serial sections of the stems revealed none.

The wood of *A. myrtifolia* is semi-ring porous. Wood macerations show a preponderance of small vessel elements having simple perforation plates, which are approximately transverse. A second type of vessel element is much longer, with a simple but smaller perforation plate occurring at an angle of about 45°. Rarely there occurs a similar type of vessel element with several very thick bars forming a scalariform perforation plate.

Older portions of the bark of the stems and trunk produce a chaff, and the outer portion of the bark peels. These peelings along with leaves often form a considerable amount of the sparse duff cover at the base of the plant. This peeling of the bark should not be confused with the sloughing off of the dried epidermal layer on the branchlets. The epidermis of the branchlets is usually densely covered with both glandular and non-

glandular hairs. The rate at which the plant as a whole grows and the rate at which the epidermis is sloughed off, governing the amount of pubescence, may be varying genetic characters.

Several characters in *A. myrtifolia* are not constant and vary from individual to individual. Leaf shape and especially size vary considerably. Pubescence on the branchlets varies considerably in both length and density. Certain populations, however, are more constant than others. The phenotypic variation of many morphological characters is apparently due more to genetic differences than to responses of the individual to different environments. Considerable variability in a narrowly endemic taxon is an anomaly (Stebbins 1942).

Daubennire (1959:229) indicated that certain plants of sunny habitats orient their leaves vertically. This vertical orientation is common in *A. myrtifolia* on the vertical branchlets, while on the horizontal ones the leaves are more or less at right angles to the path of light. Morphological differences between the upper and lower surfaces of these sclerophyllous leaves are slight, although the leaves do become somewhat concave on the adaxial surface on drying.

The general structure of the flowers in all species of *Arctostaphylos* is notably alike, with greatest differences in ovary pubescence. Meiotic behavior is normal with 13 pairs of chromosomes (Fig. 4). This is the diploid number in the genus. Slides and voucher specimens are deposited in the Department of Botany, University of California, Davis.

The intine and exine are formed simultaneously



FIG. 4. Camera-lucida drawings of three meiotic sets of chromosomes of *Arctostaphylos myrtifolia*.

about the pollen mother cell resulting in four coalesced pollen grains. There are no distinctive markings on the pollen grains that would serve as a possible method of differentiating between *A. myrtifolia* and other species of *Arctostaphylos*. Pollen grains of *Arctostaphylos uva-ursi* (L.) Spreng., *Arctostaphylos tomentosa* (Pursh.) Lindl., and the closely allied *Xylococcus bicolor* Nutt. do not differ in sculpturing or coalescence. Erdtman (1952) stated that coalescence is frequent in the Ericaceae although he did not mention any members of the tribe *Arbuteae* to which *Arctostaphylos* belongs.

The pericarp of the berry is thin and papery, sometimes brownish or even whitish at maturity. The nutlets within are never coalesced but are free-splitting.

#### PHENOLOGY

First-year seedlings of *Arctostaphylos myrtifolia* were collected on a recently cleared road-bank. Each plant had 5 to 10 leaves, all of which were smaller than leaves of mature plants in that region. In several cases cotyledons were still attached to the seedlings. Seedlings have not been seen in an established colony of mature plants. They always occur on some sort of recently disturbed site such as clearings, road fills, road cuts, or burns. Seeds of *Arctostaphylos myrtifolia* are apparently widely spread in the local Ione area, but conditions favorable for germination and establishment of seedlings do not commonly occur. Instead, competition with old plants inhibits establishment of new individuals.

Since the species does not crown sprout, a severe fire will eliminate a population. In species of *Arctostaphylos* in California vegetative reproduction following fire occurs only by sprouting from an enlarged root crown. Root sprouts, such as occur in the chaparral species *Pickeringia montana* Nutt., are unknown in *Arctostaphylos*. Presence or absence of a root crown is an excellent species criterion according to Jepson (1939:29-32). Following fire-elimination of a stand of *Arctostaphylos myrtifolia*, seedlings become established from seeds newly distributed from adjacent, unburned populations and, possibly, from soil-stored seed. Thus the last fire in a particular area can be dated fairly accurately by checking ages of the oldest plants.

Flowering can occur in the very early ontogeny of the plant, probably after the second season's growth. Flowering plants may have but one or two branchlets and stand no higher than 8 or 10 cm. Inflorescences are formed in midsummer after vegetative growth has been completed, and they

remain nascent into the winter. Meiosis occurs just prior to flowering. Immediately the buds begin to swell. Flowering starts in mid-January and lasts into early March.

Apparently bees and bumblebees pollinate the flowers since they have been observed visiting them. These insects are too large actually to enter the small opening to the base of the corolla to obtain the nectar. The two recurved awns on the stamens may aid in pollination, acting as a tripping mechanism for shedding the pollen. The pollen would then be picked up by the retracting proboscis, thus facilitating cross pollination when the bee visits another plant. Cross pollination must take place because occasional hybrids occur, presumably between *A. myrtifolia* and *A. viscida*.

The fertilized flowers drop their corollas and stamens, and the calyx envelops the developing ovary. Nonfertilized flowers drop off. Eventually the calyx is shed from the developing ovary, and the berries, fully developed by late spring or early summer, are shed when dry. Means of dissemination are unknown, but dispersal to considerable distances (as to San Andreas from Ione) in the seats of berry-eating animals such as coyotes is improbable.

The rachis of the inflorescence is not necessarily shed after the berries are dropped and may persist on the plant at least one season. By the time the berries are well-formed new foliage begins to appear and eventually the nascent inflorescences are produced.

#### HABITAT

*Arctostaphylos myrtifolia* occupies a more or less continuous area on the flats and rolling hills near Ione at elevations of 300-450 ft (90-140 m) (Fig. 1). Stations and sometimes quite extensive stands scattered south of Buena Vista to the Mokelumne River are at slightly higher elevations. Stands extending northwest of Ione to Carbondale occur on the Ione type of terrain but at elevations as low as 200 ft (60 m). The Valley Springs Peak station is on the north side at an elevation of 900 ft (280 m). Along the Fillippini Ranch road north of San Andreas the plant occurs at elevations from 1,650 to 1,900 ft (500-580 m).

The vegetation of the Ione region can be characterized as chaparral (Fig. 3). As with most sites which support chaparral vegetation, seasonal aridity and infertility of the soil are characteristic. Fire is an important factor in most chaparral regions and is of extreme importance in the Ione region. Fire kills *A. myrtifolia* outright with no crown-sprouting since the species has no root crown. It makes possible the establishment of

young plants. It may leave an area so bare of vegetation as to promote soil erosion. As with most non-crown-sprouting species of *Arctostaphylos* which form persisting plant communities, mortality is usually due to fire. Depending upon the intensity of the fire, the vegetation may be killed completely, only damaged, or both the vegetation and the soil litter may be destroyed.

#### Climate

Long periods of warm and rainless weather predominate in the Ione region, but there is just sufficient precipitation during the winter months to prevent the area from being a desert.

Climatic data for the Ione area indicate that the need for water and supply from precipitation are exactly out of phase (Fig. 5, Table I). A calculated yearly potential evapotranspiration (Thornthwaite 1948) of 830 mm of water is only very partially supplied by the annual average pre-

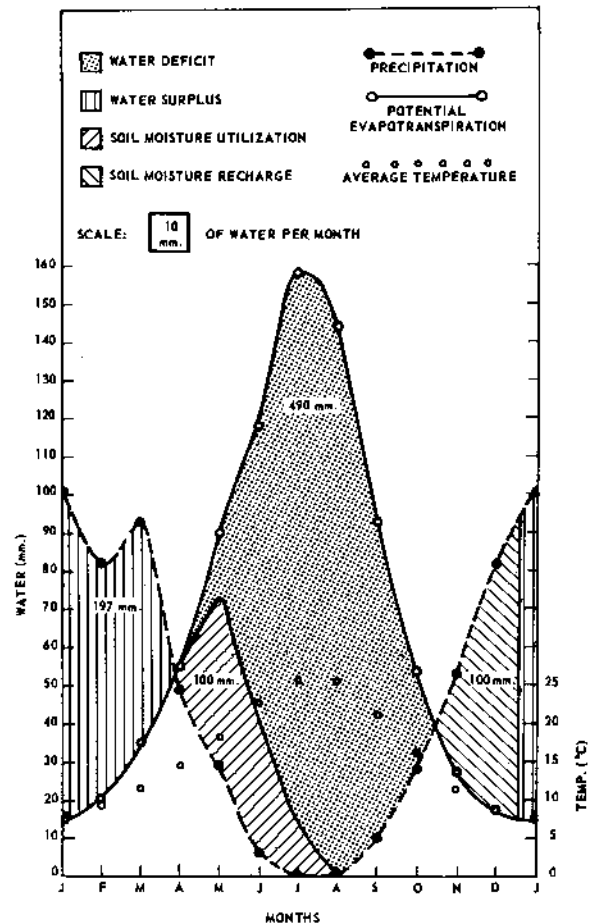


FIG. 5. Monthly balance between potential evapotranspiration (Thornthwaite 1948) and precipitation for Ione. Other data in Table I. 100 mm of available water stored in the soil, of decreasing availability as used, has been assumed.

TABLE I. Climatic data for the Ione area (U.S. Weather Bureau 1930, 1958)

Item	Station			
	Ione	Electra Powerhouse	San Andreas	Kennedy Mine
Latitude (°N)	38°23'	38°20'	38°09'	38°21'
Longitude (°W)	120°57'	120°40'	120°41'	120°35'
Elevation (m)	88	218	336	467
Average temperature (°C)	16.1	16.2	—	—
Precipitation (mm)	533	776	719	790
PE (mm) <sup>1</sup>	826	840	—	—
AE (mm) <sup>2</sup>	336	358	—	—
Water surplus (mm) <sup>3</sup>	197	411	—	—
Water deficit (mm)	490	486	—	—

<sup>1</sup>Calculated potential evapotranspiration (Thorntwaite 1948).

<sup>2</sup>Calculated actual evapotranspiration.

<sup>3</sup>100 mm of available water stored in the soil, of decreasing availability as used, has been assumed.

precipitation of 533 mm at Ione and about 800 mm for the higher altitude *Arctostaphylos myrtifolia* areas to the east. Calculated actual evapotranspiration is only 336 mm at Ione and only 22 mm more with an additional 243 mm of precipitation at the higher altitudes. The additional precipitation at higher altitudes to the east mainly serves to increase the water surplus, which appears as winter runoff. Potential losses of water by evapotranspiration in the winter are less than 20 mm a month.

At the higher stations the monthly rainfall is remarkably similar to that at Ione itself. The late spring to early fall months of May-September have the same (low) precipitation; the winter months may have up to 150 mm per month.

Prolonged periods of intense summer heat are common throughout the central part of the low Sierra Nevada foothills with an absolute maximum temperature of 46.6°C recorded at Ione for the 1878-1915 period. Highest temperatures have exceeded 23.9°C in every month. Freezing temperatures are infrequent, but winter temperatures are low enough so plant growth is nil. The absolute minimum was -10.0°C. The three summer months have had absolute minima above +10.0°C. With increasing elevation, temperatures show no decisive drop over the slight range of altitudes for which we have data. The Electra Powerhouse has slightly higher fall temperatures.

The Ione area is directly opposite the Golden Gate and San Francisco Bay through which maritime air pours into the Central Valley. The range of mean monthly temperatures in the Ione area is less extreme than at the same foothill elevations both to north and south (Table II). The valley and its eastern edge show a smaller range of mean monthly temperatures than does the foothill belt immediately above (transect A versus transect B of Table II). The variation

in latitude within these transects should alone cause some variation in mean monthly temperatures since the sun stands lower at the solstices with increasing latitude, or seasonal contrasts in the sun's radiation are greater. Over the extreme range of latitudes listed, however, this variation in monthly mean temperatures should be only 0.4°C (0.7°F) (Khromov 1957), and within the latitudinal range where the Ione geological formation outcrops from Oroville to Friant near Madera it should be only about 0.2°C (0.3°F). The north-south temperature differences outside the range of *Arctostaphylos myrtifolia* can be almost matched within the present range of the plant by east-west differences (transect C). Higher altitudes have less maritime climates in this region. Whether the occurrence of *A. myrtifolia* is related to the slightly more maritime climate in which it is now found will only be determined by comparative studies of heat tolerances and requirements of the species and the taxa associated with it. The data of Table II may have some bearing on the history of *Arctostaphylos myrtifolia* in glacial times when these temperature belts would have shifted geographically (see below). At the present time there appear to be no very outstanding climatic differences between the areas where *A. myrtifolia* now occurs and the nearby, surrounding regions where it is absent.

### Soils

*Arctostaphylos myrtifolia* is strikingly limited in the Ione region to outcrops of the Ione formation or to sediments derived from its outcrops. The Ione formation is composed of kaolinitic clay minerals, quartz sand, and ironstone. It is an Eocene, subaerial, and deltaic deposit derived from adjacent laterites formed in a tropical climate (Allen 1929, Pask and Turner 1952). It outcrops along the Sierra Nevada foothills from Table Mountain near Oroville at the north southward to Friant, a distance of 210 miles (340 km). As a lateritic deposit, the Ione formation is highly variable. Pure kaolinitic clay and pure quartz sand alternate with indurated ironstone. Local sedimentary deposits from the poorly vegetated formation are common. *A. myrtifolia* occupies those habitats which are low in fertility.

The clay substratum has long been recognized for its ceramic properties, and for years clay mines have operated in the Ione region. More recently the sand fraction has been recognized to be of excellent quality for use in glassmaking because it is relatively free of iron. The upper surface, or lentil, of the area has been termed Cheney Hill clay containing white Ione sand. The soils of

TABLE II. Maximum, minimum, and range of mean monthly temperatures of some climatic stations near Ione

Station	Latitude (°N)	Longitude (°W)	Elevation (m)	Temperature (°F)		
				Maximum (July)	Minimum (January)	Range
<b>A. North-South transect along the east side of the Central Valley</b>						
Chico	39°42'	121°47'	58	78.6	44.4	34.2
Marysville	39°09'	121°35'	19	79.1	45.8	33.3
Sacramento City	38°35'	121°29'	7	75.3	45.2	30.1
Lodi, Ione	38°07'	121°17'	12	62.3	44.4	27.9
Stockton	37°58'	121°18'	3	74.4	44.5	29.9
Modesto	37°39'	121°00'	28	76.0	44.6	31.4
Turlock	37°32'	120°51'	32	76.0	42.3	33.7
Merced	37°18'	120°29'	52	78.6	44.5	34.1
Hanford	36°20'	119°40'	74	80.5	44.9	35.6
<b>B. North-South transect along the Sierra Nevada foothills</b>						
Red Bluff	40°09'	122°15'	104	83.2	45.1	38.1
Oroville	39°30'	121°35'	76	79.4	43.3	36.1
Rocklin	38°48'	121°14'	73	77.9	44.2	33.7
Folsom	38°42'	121°10'	77	79.4	46.4	33.0
Ione	38°23'	120°57'	88	78.1	46.1	32.0
Oakdale	37°52'	120°52'	66	77.6	44.5	33.1
Madera	36°58'	120°04'	82	79.8	45.2	34.6
Fresno	36°46'	119°42'	101	82.1	44.7	37.4
Bakersfield	35°25'	119°03'	149	84.2	46.9	37.3
<b>C. East-West transect through the Ione area</b>						
San Francisco	37°47'	122°25'	16	61.6	50.1	11.5
Berkeley	37°52'	122°15'	76	63.2	49.2	14.0
Antioch	38°01'	121°46'	9	76.0	46.7	29.3
Lodi, Ione	38°07'	121°17'	12	72.3	44.4	27.9
Electra Powerhouse	38°20'	120°40'	218	77.7	45.7	32.0
Placerville	38°44'	120°48'	576	73.5	40.2	33.3
Colfax	39°06'	120°58'	736	77.0	43.5	33.5
Gold Run	39°12'	120°52'	987	75.2	40.4	34.8

the region, which have been classified into the Hornitos series, are mostly residual, extremely shallow, and in at least their second cycle of weathering. They are easily eroded away during heavy rains where protective plant cover is lacking. Often puddled clay occurs at the lower ends of blocked gullies. As a result the vegetation may often become established directly on the exposed, residual parent material.

Soil profiles are only 25-35 cm deep to the C horizon. A friable A horizon somewhat stained with brown organic matter may extend to 5-15 cm depth or may be missing entirely. The clay fraction in most cases increases with profile depth, and the sand fraction decreases. The silt fraction remains fairly constant throughout. B horizons may be quite red and clayey; C horizons are hard and yellowish in color. During soil genesis, therefore, the clay moves downward in the profile, or the clay fraction may be washed away to form sedimentary deposits in low-lying areas. The surface of the Ione soils is strewn with sandstone rocks and lateritic ironstone chunks, as well as andesites and greenstones of pre- and post-Ione formations. A "desert pavement" frequently forms (Fig. 2).

The soils of the San Andreas region are derived from a Jurassic, micaceous schist. The sand percentage can vary widely, clay percentage varies inversely with the amount of sand, and silt is quite constant. Due to the different parent materials in the Ione and San Andreas regions, it is difficult to compare the soils in the two areas. At neither the Ione nor San Andreas sites have zonal soils formed.

The striking fact about the soils in both regions, and one that could have an important bearing on the occurrence of *A. myrtifolia*, is strong acidity. In all cases measured, the soils have a phenomenally low pH. A low of 2.9 and a high of 3.95 were recorded for the Ione region. Whereas most agricultural soils range from slightly acid to neutral, the hydrogen-ion concentrations of the soils of the Ione region are from 1,000 to 10,000 times higher. High acidity is expected in the lateritic residues of the Ione formation, but it is quite unexpected in the apparently quite undeveloped soils near San Andreas where *Arctostaphylos myrtifolia* occurs. The sericitic schist is evidently naturally low in bases, with pH values of 4.6 in the subsoil.

The Valley Springs Peak disjunct station of *Arctostaphylos myrtifolia* is on a third type of soil parent material, namely a kaolinitic-altered rhyolite. This highly weathered and leached deposit has in common with the lateritic formation of the Ione region and the sericitic schist of the San Andreas region a naturally low base content, i.e., low natural soil fertility.

The high acidity under *Arctostaphylos myrtifolia* is not a result of great organic matter additions to the ecosystem. Organic matter production is very low in this kind of vegetation for soil fertility is very low and the climate is most unfavorable for plant growth. Nor is the high acidity a result of present processes of soil formation. Adjacent Californian chaparral soils are acid, but their acidity is much less (2 + pH units) than that of the soils in areas of *Arctostaphylos myrtifolia*. The high acidity found in soils under this plant is an inheritance from the soil parent material. It is an independent factor of the ecosystem (Major 1951), and on it the localized occurrence of *Arctostaphylos myrtifolia* probably depends.

Crocker (1956) described another case of low soil pH inherited from an acid parent material found on mesas near San Diego, California. The low pH is quite discordant with the present climatic processes of soil formation. In fact, parent material of these San Diego soils is more acid than the present surface soils themselves (pH 3-6 versus 5-7). Current soil formation has concentrated calcium in the surface horizons and on calcareous parent materials has produced pedocals of neutral to alkaline reaction. The climate of the area is mediterranean, warm (15.9°C average temperature even in this maritime climate with amplitude of monthly means only 5.0°C), and arid. Precipitation is 20 mm a month or less during 8 months. Total precipitation is 262 mm; potential evapotranspiration (Thornthwaite 1948) is 785 mm; summer water deficit is 523 mm; and there is no winter water surplus. With a soil storage capacity of only 50 mm of available water no leaching could occur. This area of acid, non-zonal soils has a very notable group of endemic or disjunct plants (Gander 1938, Purer 1939).

Low pH is correlated with a high exchangeable aluminum content in soils (Russell 1950:94, Jenny 1961). Thus, *Arctostaphylos myrtifolia* must not only be tolerant of high soil acidity but also of high content of soluble aluminum. These two inseparable factors evidently provide the unique and disjunct environments in which this endemic plant occurs because it can out-compete a great

variety of other, zonal plants under such conditions.

Surface soils at Ione are uniformly less acid (by 0.5 pH unit) than lower horizons. Evidently bases brought to the surface by the vegetation slightly increase soil fertility. There is no evidence, however, that over most of its area *Arctostaphylos myrtifolia* would be replaced in time by other vegetation, the regional climax for example. *Arctostaphylos myrtifolia* characterizes a persisting plant community.

The sericitic schist found near San Andreas is marked in its scattered outcrops along the lower elevations of the Sierra Nevada by peculiar and persisting plant communities. The station for the rare *Arctostaphylos nissenana* Merriam described by Howell (1936) as "on sterile schistose rock" is this substratum. In other places *Pinus attenuata* Lemmon, with such associates as *Arctostaphylos viscida* Parry, *Boschniaka strobilacea* Gray, *Ceanothus tomentosus* Parry (Table III), *Chamaebatia foliolosa* Benth., *Quercus chrysolepis* Liebm., and *Festuca megalura* Nutt. in openings, occurs on this distinctive soil parent material. *Adenostema fasciculatum* H. & A. also occurs where the rock outcrops at lower elevations. All of these specialized communities occur in a regional climax or zonal vegetation characterized by *Pinus ponderosa* Dougl.; apparently the unique communities are better competitors of the infertile soils derived from the peculiar schist than are the zonal plants.

#### ENDEMIC AND DISJUNCT PLANTS AS SPECIALISTS IN NON-ZONAL SITES

Other floristic and ecological situations are known where a site which is non-zonal for some reason, such as a peculiar soil parent material, is occupied by a peculiar flora of disjunct or endemic species. We believe these situations arise where zonal vegetation is weakened in its competitive ability by a singular environment, and therefore exceptional plants can survive there. Since the phenomenon is a general one, the solution to it should also be general. No solution based on a specific physiological mechanism seems adequate to explain the great variety of cases.

For example, the New Jersey pine barrens have a distinctive flora and a consequently distinctive vegetation (Harshberger 1916, Seifriz 1953). Tedrow (1952) points out that the podsol soils developed on sandy parent materials are "geographically out of place." We suggest that lack of competition by the regional, zonal vegetation adapted to the zonal gray-brown podsol soils allows establishment of the distinctive flora.

Disjuncts and endemics of the Appalachian



TABLE III. Plants of restricted or disjunct distribution occurring in the Ione area of Amador County, California, in addition to *Arctostaphylos myrsinifolia*<sup>1</sup>

Species	Distribution	References
<b>RESTRICTED</b>		
<i>Ceanothus tomentosus</i> Parry	Placer to Mariposa Counties	Munz and Keck 1959: 979
<i>Erigonum apricum</i> Howell	On otherwise almost bare slopes near Ione	Howell 1955a
<i>Helianthemum suffrutescens</i> Schreib.	Amador County only	Munz and Keck 1959: 174
<i>Horkelia parryi</i> Greene	Placerville in El Dorado County, Ione- Buena Vista area in Amador County, and at El Dorado Reservoir near San Andreas in Calaveras County	Keck 1938: 89
<i>Mimulus viscidus</i> Congd.	Amador plus Calaveras to Tulare Counties	Munz and Keck 1959: 619, modified
<i>Plagiobothrys scriptus</i> (Greene) Jtn.	Ione and La Grange in Stanislaus County	Munz and Keck 1959: 582
<b>DISJUNCT</b>		
<i>Agrostis exigua</i> Thurb.	Napa and Sonoma Counties, Central Valley from Shasta and Butte to Stanislaus County, foothills of Sierra Nevada in Amador County	Crampton 1961: 155
<i>Aira elegans</i> Willd.	Introduced from the Mediterranean, N. Africa, and the Balkans to adjacent Asia into Amador, Marin, Sonoma, and Humboldt Counties in California and Oregon west of the Cascades plus the U.S. southern coastal plain from New Jersey and Maryland to Florida, Tennessee, Arkansas, and Texas	Hermann 1956: 122, Munz and Keck 1959: 1514, Hitchcock and Chase 1950: 299
<i>Eleocharis pachycarpa</i> Desv.	Introduced from Chile and Argentina to Humboldt, El Dorado, and Amador Counties in California and east side of Lake Tahoe in Nevada, plus Sydney, Australia	Mason 1957: 287 Svenson 1957: 540
<i>Juncus confusus</i> Cov.	Amador County foothills at Ione plus montane Trinity and Tuolumne Counties and northward to British Columbia, southern Alberta, and southwestern Saskatchewan and Rockies from northern New Mexico and Arizona north of the Grand Canyon northward	Munz and Keck 1959: 1406, plus local floras
<i>Lotus balsamiferus</i> (Kell.) Greene	Siskiyou to Lake and Mariposa Counties	Abrams 1944: 541
<i>Ophioglossum californicum</i> Prantl.	Formerly Ione, at Monterey, San Diego to Baja California and Mexico	Munz and Keck 1959: 29
<i>Polygonum maritimum</i> Willd.	Introduced from southern Europe, North Africa to the Near East and Turkestan into Shasta County, the Sierra foothills in Tuolumne, Stanislaus, and Amador Counties, in the Sacramento Valley into Butte and Colusa Counties, Coast Ranges from Humboldt, Lake, Napa, Sonoma, Marin, Alameda, and San Luis Obispo Counties	Rubtsoff 1961: 169
<i>Scribneria bolanderi</i> (Thurb.) Hack.	Scattered in sterile places from Washington south through California to Tulare County in the Sierra Nevada, to Fresno County, in the Central Valley, and to Santa Barbara County in the Coast Ranges	Crampton 1955, Raven 1960
<i>Tillaea muscosa</i> L.	Introduced (?) at Ione and San Andreas from Mediterranean and Atlantic Europe	Munz and Keck 1959: 719, Gankin 1962

<sup>1</sup>Contributory data from John Thomas Howell.

shale barrens (Platt 1951) occur on the open sites which the zonal vegetation cannot fully occupy. The granitic flat-rocks of the southeastern United States (McVaugh 1943, Keever, Oosting, and Anderson 1951) have disjuncts whose presence similarly seems to be related to competition. This hypothesis was demonstrated to be correct for *Diamorpha cymosa* (Nutt.) Britt., a crassulaceous endemic of such sites, by Wiggs and Platt (1962). Although this plant's physiology would allow it to grow outside the shallow depressions weathered in the granitic outcrops, competition with plants normally found in the zonal vegetation off the

flat-rocks limits its occurrence to the extreme environments in which it is found and in which the zonal plants cannot grow. The species' ecological tolerance is narrowed drastically from its physiological tolerance (Ellenberg 1953, Walter 1960: 15). The glades of Missouri to Tennessee similarly have non-climax vegetation and a distinctive flora on a peculiar soil parent material which produces drouthy and shallow soils (Quarterman 1950a and b, Braun 1950: 131, Kucera and Martin 1957).

Similarly, the flora and vegetation of the Gaspé Peninsula (Scoggan 1950, Rune 1953, 1954) are

distinctive. The remarkable disjuncts occur on the regionally distinctively different ferromagnesian or calcareous rocks or in such persisting communities as form on river shingle or calcareous rock. Zonal vegetation occupies none of these substrates.

The inability of known plant physiological data alone to explain the geographical occurrence of plants is particularly well shown by the Gaspé Peninsula disjuncts (Mason and Stout 1954, Wells 1959, Major 1961). Here rare and disjunct plants occur either on serpentine or limestone, some on both. The immature soils formed from the first soil parent material are extraordinarily low in percentage saturation of the soil cation exchange complex with calcium; those from the second are obviously high. The paradox of the same plant species being unique to both such soils, has no physiological explanation at present. The zonal vegetation of this maritime, humid climate with some 300-500 mm of surplus water available for leaching through the soil each year (climatic data from Scoggan 1950: 15; climatic calculations according to Thornthwaite 1948) is adapted to leached and acid soils formed from granite and other acid rocks. Serpentine with its low percentage exchangeable calcium on the soil cation exchange complex behaves toward plants in many ways as an acid soil. Percentage calcium saturation is low when magnesium is high (Vlamin 1949). Examples of plant responses are mentioned below. We conclude *both* the calcium-poor serpentine and the calcium-rich limestone habitats of the Gaspé are open sites since the zonal vegetation cannot grow there. The famous disjuncts can. Why they can is unknown, and we recommend the problem to plant physiologists.

In Albania, again, the same endemics occur on both serpentine and hard limestone (Markgraf 1932: 101, 118 according to Krause 1958: 795).

Similar situations with distinctive floras containing many, at least locally, specialist species and producing non-zonal vegetation have been described by Rune (1953) from northern Scandinavia on serpentine, by Coombe and Frost (1956) from the Cornish serpentines, by Louseley (1950) and Pigott (1956) from limestone areas in England, and by Lüdi (1952), Louseley (1950), and others for Irish limestones. In many of these cases arctic-alpine plants occur at very low elevations where the zonal vegetation adapted to acid (leached) soils is interrupted by calcareous soil parent materials. The extraordinary flora of Öland and Gotland are well known, and their open, steppe-like alvar vegetation is related to the distinctive occurrence of limestone on the

islands (Sjörs 1956: 130). Romell (1957) has described open sites in Sweden where rare plants have persisted due to man's maintenance of non-zonal vegetation. Braun-Blanquet (1951) and Krause (1958) discuss the peculiar vegetation (and flora) on areas marked by such extremely varied, non-zonal kinds of soil parent materials as those high in gypsum, serpentine, zinc and lead, copper, selenium, and sodium chloride and sulfate.

McMillan (1956) has described the edaphic restrictions of many species in California to non-zonal soils formed from serpentine or acid parent materials whose common feature may be low calcium saturation of the base exchange complex. Disjunct and endemic plants on the acid and clearly non-zonal soils of the San Diego mesa were referred to above.

Recently Howell and Twisselmann (1963) described the new species *Eriogonum temblorense* from the arid southern San Joaquin Valley of California. It is confined to outcrops of a white shale which is generally devoid of plants. Where it occurs in areas with a better plant cover of the widespread annuals it grows only on shale outcrops or similar spots not occupied by the annuals.

This suggests that there may be two principal factors that determine the Temblor buckwheat's limited and local distribution. First, it has a tolerance for extreme aridity and for the edaphic peculiarities of white and brown shale, particularly the Miocene white shales along the west side of the upper San Joaquin Valley. Secondly, in common with many plants of localized distribution in the region that tolerate unusual edaphic situations, it is unable to compete with the aggressive annuals in places with good soil. . . . its restriction is probably more the result of its inability to compete successfully under normal soil and moisture conditions than the obligate need for any specialized qualities of the white and brown shales (Howell and Twisselmann 1963: 44).

Griffin (1963) has mentioned two disjunct foothill woodland communities in California. One is isolated in a Great Basin pine forest-juniper woodland area and the other in a Klamath Mountains mixed coniferous forest area. Each is on a "locally unique deposit," i.e., on a unique soil parent material. The first is on unique Pliocene sediments in a region of recent volcanics, and the second is on unique Cretaceous sediments in the midst of a pre-Silurian metamorphic region. The contrast in properties between the unique soil parent material and surrounding rocks seems to be of decisive importance for the plants concerned—not the specific properties of the unique sediments.

Thomas (1961: 23) mentions the disjunct *Pinus ponderosa* Dougl. stands on the peculiar, deep sands in Santa Cruz County, California, with their

peculiar flora and vegetation. Billings (1950) has discussed the disjunct *Pinus ponderosa* on acidified rhyolite near Carson City, Nevada, located in a sea of sagebrush (*Artemisia tridentata* Nutt.) on zonal, arid brown to sierozem soils (cf. Oosting 1956: 198, 351). Salisbury (1954, 1964) has discussed a similar situation at the Big Rock Candy Mountain in central Utah. In the California case the pine is a xeric disjunct; in the two Great Basin cases the pine is a mesic disjunct. Neither is a pre- or post-climax phenomenon in any real plant successional sense, but again, they are parts of persisting plant communities related to peculiar soil parent materials. In all three cases the pine is on "poorer" soils from a nutritional standpoint and is behaving as a soil specialist and not as a climax or zonal plant.

It is not inferred in the above case that the pine is physiologically homogeneous. Squillace and Silen (1962) have reviewed long-term provenance trials of this species and have demonstrated that geographically different seed sources are different climatic races so far as growth is concerned. "Attempts to relate growth with soil characteristics. . . could not be made because reliable indices of these factors could not be found" (p. 13). Although *Pinus ponderosa* consists of many ecotypes, all of them are more similar to one another than any is to the plants with which the species is in contact, such as the extreme examples *Atriplex confertifolia* (Torr. & Frem.) S. Wats. and *Sequoia sempervirens* (Lamb.) Endl.

The classic study by Baker and Korstian (1931) of the gap in the Great Basin between the Pacific and Rocky Mountain areas of *Pinus ponderosa* discusses the disjunct individuals found in the Wasatch Mountains. These plants are on coarse talus. Zonal, finer textured soils support *Quercus gambelii* Nutt. and other shrubs. Again, disjunct stations of the pine are found along the east edge of the Wasatch Plateau only on sandstone outcrops. In these areas of Utah *Pinus ponderosa* is rare and disjunct. It is not a zonal or climax species and is found only on sites where zonal vegetation competes poorly.

Commonly in California serpentine outcrops harbor plants out of their normal range of distribution as well as endemics limited to such non-zonal sites. The xeric *Pinus sabiniana* Dougl. occurs at higher elevations in the Sierra Nevada and in more moist climates of the northern Coast Ranges than normal on serpentine. On the other hand the mesic, mountain, and northern coastal azalea *Rhododendron occidentale* (T. & G.) Gray, which ordinarily occurs on acid soils, in the arid central Coast Ranges is in drier than usual regional

climates on serpentine (Major 1958) along with *Pseudotsuga menziesii* (Mirb.) Franco. Or the mountain trees *Calocedrus decurrens* (Torr.) Florin and *Pinus jeffreyi* Grev & Balf. occur in the northern Coast Ranges to extraordinarily low altitudes of a few hundred feet on serpentine. They are accompanied by a profusion of such uncommon plants (for the area in question) as *Calypso bulbosa* (L.) Oakes and *Goodyera oblongifolia* Raf. or *Crocidium multicaule* Hook. and *Onychium densum* Brack. (= *Cheilanthes siliquosa* Maxon) in forest stands and on rocky sites respectively. Hardham (1962) has described the *Cupressus sargentii* Jeps. groves in the South Coast Ranges of San Luis Obispo County in California. The groves are on serpentine, therefore do not support zonal vegetation, and harbor a number of local endemics plus northern species here near or at the southern limit of their distributions and at low altitudes. Examples are *Parnassia palustris* L. var. *californica* Gray, *Habenaria dilatata* (Pursh) Hook. var. *leucostachys* (Lindl.) Ames, *Carex luzulina* Olney, and *C. mendocinensis* Olney.

At Ione, on an extraordinarily leached and acid soil parent material, the Rocky Mountain meadow species *Juncus confusus* Cov. occurs more than 1,000 m and one or two life zones below its normal habitat.

*Eleocharis pachycarpa* Desv. occurs near Buena Vista (Fig. 1) on presumably acid soils, in moist soil near salt marshes in Humboldt County, in serpentine barrens in the foothills of El Dorado County, and on the east side of Lake Tahoe (Mason 1957: 287). While the disrupted but widespread range of this plant introduced from Chile must be due to spread by sheep (also to Sydney, Australia, about 1845 according to Svenson in correspondence) (Svenson 1957), its ecological distribution is physiologically explicable only on the basis of lack of competition at the sites where it occurs.

Also in California an assemblage of widely disjunct, Cordilleran boreal plants has been found in the single, large area of calcareous rock known in the predominantly granitic Sierra Nevada at the head of Convict Creek (Major and Bamberg 1963). In the same area lowland xerophytes such as *Stipa comata* Trin. & Rupr., *Koeleria cristata* (L.) Pers., *Oryzopsis hymenoides* (R. & S.) Rick., and *Artemisia tridentata* Nutt. extend to timberline. A reasonable hypothesis is that on the marble and its detritus zonal alpine and sub-alpine vegetation cannot exist, so the disjuncts do. Both groups of species, which are so ecologically unlike, illustrate the principle that pe-

ripheral, disjunct populations of plant species occur on regionally or zonally unique substrates.

Even such a pronounced acidophile as *Picea mariana* (Mill.) BSP occurs on calcareous alluvium—a non-zonal site—near its southern limit in the Athabasca River valley of Jasper National Park in Alberta, Canada (Porsild 1959). Here it occurs with obligate calcicoles and not with members of the zonal vegetation.

The above examples could be expanded, evidently indefinitely (Krause 1958). Once this principle of disjunct and endemic plant occurrence on non-zonal sites is accepted, examples become almost too numerous. In all these cases explanations of why the rare plants occur where they do in terms of plant physiological reactions are completely lacking. Judging from the cases cited, they would have to be conflicting. The only explanation which fits the diversity of facts—that is, plants occurring at higher or lower altitudes than normal, in wetter habitats or drier, with less calcium or more—is in terms of plant competition. All the cases fit the conclusion that rare or disjunct (non-zonal) plants can occur in a given area where competition is decreased by some kind of extraordinary soil parent material or other continuously effective disturbance of climax vegetation development (Pigott and Walters 1954).

#### VEGETATION ASSOCIATIONS

The species associated with *Arctostaphylos myrtifolia* provide the most ready interpretation of the ecology of this plant. These associations can be characterized structurally. Some physical and chemical factors of the environment which condition the vegetation have been described above. A consideration of floristic relationships offers a means of comparing ecological relationships between kinds of vegetation widely separated in space and in which measurements of habitats may not be made by comparable means. While the habitat measurements are not a subject of universal agreement among botanists, the names of associated species are.

The Ione area with its peculiar edaphic conditions contains other plants of restricted distribution besides *Arctostaphylos myrtifolia* (Table III). All these species are specialists found in open, non-zonal habitats. None are members of zonal, climax vegetation. The more widely distributed California plants typical of chaparral and foothill woodland which are also in the Ione area include *Adenostema fasciculatum* H. & A., *Arctostaphylos viscida* Parry, *Arctostaphylos manzanita* Parry, *Quercus wislizenii* A. DC and var. *frutescens* Engelm., *Rhamnus californica* Esch. ssp.

*tomentella* (Benth.) C. B. Wolf, *Heteromeles arbutifolia* (Ait.) Roem., *Pinus sabiniana* Dougl., *Eriodictyon californicum* (H. & A.) Torr., *Lotus scoparius* (Nutt. in T. & G.) Ottley, and others.

At the higher elevation San Andreas sites (Fig. 6) north slopes are occupied by such plants of the



FIG. 6. A ridgetop stand of *Arctostaphylos myrtifolia* above San Andreas. The zonal vegetation in the canyon below includes *Pinus lambertiana* and *P. ponderosa*.

mid-altitude, mixed, Sierran coniferous forests as *Pinus lambertiana* Dougl., *Chamaebatia foliosa* Benth., and *Meconella californica* Torr. On the south and west-facing slopes where *Arctostaphylos myrtifolia* occurs are such woody plants as *Pinus ponderosa*, *Pinus sabiniana*, *Arctostaphylos viscida*, *Heteromeles arbutifolia*, *Eriodictyon californicum* (indicating a recent fire), *Adenostema fasciculatum*, and *Castilleja foliolosa* H. & A.

In the Ione region *A. myrtifolia* occurs in almost pure, heath-like stands. Characteristically it occupies the tops of knolls, ridges, or other interfluvial areas. It may form over 50% cover, but the soil surface between is almost bare. A few annuals, lichens, and mosses occur under the shrubs. Shrub cover increases with age of the colony.

Colonies may be considered local populations since they are often separated from each other by intervening hedges of such other, taller plants as *Arctostaphylos viscida* (Fig. 3) and *A. manzanita* found only rarely within the colonies of *A. myrtifolia* itself. The colonies thus form a mosaic. There probably is gene flow from one local population to another, but it is clear that gene interchange between populations is less than that within them.

The vegetation at Ione is arranged in a zonation pattern. In the ideal case the local population of *A. myrtifolia* forms the center of a series of concentric rings. The first ring outward from *A. myrtifolia* is made up mostly of gray *A. viscida* which grades off into the tall *A. manzanita*. The next zone is heterogeneous in composition with the two

TABLE IV. Location, descriptive data, and species abundance<sup>1</sup> in selected *Arctostaphylos myrtifolia* stands

Stand description and species	Life form <sup>2</sup>	Stand								Origin of species
		1	2	3	4	5	6	7	8	
Location		Ione	Ione	Ione	Ione	Ione	Ione	San Andres	San Andreas	
Elevation (m)		120	155	150	145	145	110	580	500	
Cover (%)		35	60	55	30	35	25	45	40	
Slope		Flat	Flat	5°NE	10°SE	Flat	Flat	10-15°S	15°W	
Area (m <sup>2</sup> )		50	25	50	50	100	25	25	50	
Species										
<i>Arctostaphylos myrtifolia</i> Parry	NPH	3	4	4	2	3	2	3	3	Native
<i>A. viscida</i> Parry	NPH	.	(+)	+	+	+	.	+	.	Native
<i>Quercus wislizenii</i> A. DC var <i>frutescens</i> Engelm.	NPh	r	.	(+)	(+)	+	.	.	.	Native
<i>Helianthemum suffrutescens</i> Schreih.	NPh	.	.	.	.	(+)	+	1	.	Native
<i>Festuca megalura</i> Nutt.	Th	r	1	+	.	+	1	.	.	Native
<i>Lotus micranthus</i> Benth.	Th	.	.	.	.	.	+	+	.	Native
<i>Agrostis diegoensis</i> Vasey	H	.	.	.	.	.	1	1	.	Native
<i>Psilocarphus tenellus</i> Nutt.	Th	.	+	.	.	.	.	+	.	Native
<i>Tillaea erecta</i> H. & A.	Th	.	.	.	.	.	.	r	+	Native
<i>Aira caryophylla</i> L.	Th	+	.	.	.	r	+	r	+	Introduced
<i>Hypochoeris glabra</i> L.	Th	.	+	r	.	r	.	.	.	Introduced
<i>Filago gallica</i> L.	Th	.	.	.	.	+	.	.	+	Introduced
<i>Polytrichum juniperinum</i> Willd.	Soil	.	+	+	+	.	?	?	?	Native
<i>Polytrichum</i>										
(?) <i>piliferum</i> Schreb.	Soil	+	.	.	.	.	?	+	?	Native
<i>Cladonia verticillata</i> (Hoffm.) Schaer.	Soil	1	1	+	.	+	?	?	?	Native
<i>Parmelia conspersa</i> (Ehrt.) Ach.	Rock	+	+	.	.	r	?	?	?	Native
Total number of species in stand		10	8	7	6	10	6	13	4	

<sup>1</sup> Abundance is given according to Braun-Blanquet's scale (1951).

<sup>2</sup> Life forms according to Raunkiaer (Braun-Blanquet 1951) NPh=nanophanerophyte with perennating buds less than 2/m and more than 25 cm above the ground surface; H=hemicryptophyte with perennating buds at the ground surface; Th=therophyte with seeds as the perennating organs. The substratum is indicated for cryptogams.

large *Arctostaphylos* species plus scrub *Quercus wislizenii*, *Heteromeles arbutifolia*, and an occasional *Ceanothus tomentosus* or *Rhamnus californica* ssp. *tomentella*. This zone often passes into a dense stand of *Adenostema fasciculatum*. Woodland follows concentrically with arboreal *Quercus wislizenii*, *Pinus sabiniana*, and an occasional, very slow-growing *Pinus ponderosa* even at this low elevation, larger shrubs of *Heteromeles arbutifolia*, and some annual grasses. Outside this region is the common oak-grassland of the Sierra Nevada foothills.

Topography modifies the vegetation. On exposed slopes and on the tops of ridges *A. myrtifolia* forms almost pure stands. In gullies and washes other plants such as *Arctostaphylos viscida*, *Adenostema fasciculatum*, and scrub *Quercus wislizenii* are associated with it.

The populations in the San Andreas region occur as islands. They are abruptly bordered by zonal vegetation with abundant *Adenostema fasciculatum*.

The vegetation of eight stands of *Arctostaphylos myrtifolia* (Fig. 1) has been surveyed and described (Table IV). Few stand surveys have been published for California vegetation. Methods of vegetation description follow Braun-Blanquet

(1951). Minimal areas in this vegetation are less than about 10 m<sup>2</sup>. Data for cryptogams are only sketchy, and Table IV gives an incomplete picture of the vegetation characterized by *Arctostaphylos myrtifolia*. Abundance is given according to Braun-Blanquet's scale with cover decreasing logarithmically from 5 to +, r indicating rare occurrence, and life forms are according to Raunkiaer's system (Braun-Blanquet 1951).

Stand 1 was recorded May 4, 1962, in the NW1/4S31, T6N, R10E. Besides the species listed in Table IV, the following occurred: scattered *Parmelia caperata* (L.) Ach. which with *P. conspersa* was on lateritic ironstone rocks, *Letharia californica* (Lev.) Hue, and *Festuca microstachys* Nutt. (Th). The last name according to Niehaus (1961) includes the eight arid-site *Vulpia*'s with spreading spikelets, usually listed for California. In addition members of the genera *Dermatocarpon*, *Lecidia*, *Cladonia*, *Cetraria*, *Ramalina*, *Acarospora*, *Umbilicaria*, and *Lecanora* also occurred in the stand. Dr. Eilif Dahl very kindly made the tentative field identifications of the lichens; any errors are ours. Some annuals may have dried up and disappeared from this stand.

Stands 2 through 5 were recorded April 21,

1963, during an extremely wet and late spring. Stand 2 was on a ridge top in the SW1/4S30, T6N, R10E. Stand 3 was in the SW1/4S5, T5N, R10E. Stand 4 (Fig. 2) was nearby at the foot of a slope where *Eriogonum apricum* Howell grows in pure stand above and *Juncus confusus* Cov. in pure stand in a temporary seep below (Howell 1955a). The stand actually occupied a small ridge crest, however. It contained besides the plants listed in Table IV *Eriogonum apricum* (H) and *Juncus confusus* (H). No therophytes could be found in it. Stand 5 was just north of 3 and 4 on the top of a hillock. The soil surface was mostly covered with ironstone fragments, and, as in most *Arctostaphylos myrtifolia* vegetation, therophytes occurred mostly under the shrubs.

*Juncus confusus* is a strange associate in this lowland plant community. It is described by Munz and Keck (1959:1406) as an occasional mountain plant of the Sierra Nevada in California at altitudes of 4,000-6,000 ft (1,200-1,800 m). Its distribution extends north to British Columbia, southern Alberta, and southeastern Saskatchewan and southward in the Rockies to Nebraska, northern New Mexico, and to the Grand Canyon in Arizona. In Colorado Harrington (1954:149) says it may occur up to 11,000 ft (3,350 m).

Stand 6 was recorded April 15, 1956. Stand 7 was recorded March 8, 1956, on the eastern edge of the SE1/4S4, T4N, R12E. The stand was bordered diffusely by woody plants such as *Pinus sabiniana* (Ph), *P. ponderosa* (Ph), *Eriodictyon californicum* (NPh), *Adenostema fasciculatum* (NPh), and *Heteromeles arbutifolia* (NPh). It contained besides the plants listed in Table IV the scattered therophytes *Lotus strigosus* Nutt., *Agrostis* (?) *microphylla* Steud., *Micropus californicus* F. & M., and a depauperate *Trifolium* sp. Stand 8 was recorded April 12, 1961, in the NW1/4S4, T4N, R12E and contained besides the plants tabulated *Tillaea muscosa* L. (Gankin 1962) and *Riccia* sp. A complete list was probably not obtained. In February 1964 *Tillaea* was abundant in *Arctostaphylos myrtifolia* sites at Lone as well.

The *A. myrtifolia* community has a three-layered, discontinuous structure of low shrubs, scattered herbs, and mosses and lichens. The herbaceous layer is very poorly developed. Often only the shrub and epiphytic or soil- and rock-lichens are evident in a stand. Besides the plants listed for the eight stands, however, these annual plants also occurred in *Arctostaphylos myrtifolia* stands: *Evax acaulis* (Kell.) Greene, *Juncus bufonius* L., *Alchemilla occidentalis* Nutt., and *Pla-*

*giobothrys* (?) *tenellus* (Nutt.) Gray. *Salvia sonomensis* Greene is a chamaephyte and *Chlorogalum pomeridianum* (DC.) Kunth is a geophyte which are both found occasionally with *Arctostaphylos myrtifolia*. All of these plants are of wide distribution within California.

Judging from the stands recorded in Table IV, the *Arctostaphylos myrtifolia* vegetation of California is related through its exotic plants to the Mediterranean class Cisto-Lavanduletea (Braun-Blanquet, Roussine, and Negre 1952). It shares with this calcifuge, heath-like (*Cistus* spp.) and therophytic, anthropic vegetation the class characteristic species *Aira caryophylla*, *Cladonia verticillata*, *Polytrichum piliferum*, and *P. juniperinum*. Another class characteristic species, *Cynosurus echinatus* L., is now a California plant but occurs in shaded parts of oak savannas which are more fertile than those associated with *Arctostaphylos myrtifolia* vegetation. The California vegetation is related to the therophytic order and alliance named for *Helianthemum guttatum* (L.) Miller. *Filago gallica* L. and *Hypochoeris glabra* L. are characteristic species shared with the order. It would not be surprising if *Silene gallica* L., characteristic of the order, were to show up in the openings in *Arctostaphylos myrtifolia* vegetation in California since this exotic annual occurs in adjacent and somewhat similar but more fertile sites. Of the species characteristic of the alliance only *Tillaea muscosa* has been recorded in our stands; great efforts have been made in California to establish *Trifolium subterraneum* L.; *Vulpia dertonensis* (All.) Volkart (= *V. bromoides* (L.) S. F. Gray) is in similar but more fertile sites; and *Alchemilla microcarpa* Boiss. & Reut. may yet be found in California. Of the species characteristic of the association Helianthemum guttati, *Galium divaricatum* Link. and *Scleranthus annuus* L. are now naturalized California plants characteristic of poor, siliceous, open vegetation. *Juncus bufonius* L., which is sometimes found with *Arctostaphylos myrtifolia*, is a differential species for the Mediterranean subassociation characterized by *Tillaea muscosa*, *Sagina apetala* Ard. and *Juncus capitatus* Weig. are two other differential species for this subassociation which are naturalized in California but have not been recorded for *Arctostaphylos myrtifolia* vegetation.

Companions of high presence in the Mediterranean association which occur in California but not in the stands of Table IV include *Poa bulbosa* L., *Hypericum perforatum* L., *Cerastium holosteoides* Fr., *Erophila verna* (L.) Chevall., *Polygonum tetraphyllum* L., and *Trifolium arvense* L. The Tillaeetum muscosae of the alliance Helian-

themion guttati has in common with our community *Tillaea muscosa*, *Filago gallica*, and *Parmelia conspersa*. It adds the naturalized Californian plants *Herniaria cinerea* DC. as characteristic species and as companions *Lobularia* (= *Alyssum*) *maritima* (L.) Desv., *Erodium cicutarium* l'Her., *Galium murale* L., *Arenaria serpyllifolia* L., and *Sheardia arvensis* L. The Mediterranean class Isoeto-Nanojuncetea has some relationship to the California community since both are characterized in winter by standing rainwater and in summer by dried soil. The Isoetetum duriaei has *Aira caryophyllea*, *A. elegans*, *Juncus bufonius*, and *Tillaea muscosa* in common with the *Arctostaphylos myrtifolia* vegetation.

All the associates of *Arctostaphylos myrtifolia* indicate soils of very low fertility, acid, seasonally wet but summer dry, rocky to puddled clay, and open or at most shrub-covered. Most plants are dwarfed in this association, but seed production seems not to be seriously impaired. The two annuals *Lotus micranthus* and *L. strigosus* are examples, being only a few centimeters tall at maturity but producing numerous seedlings in spring, of which very few mature.

#### HISTORY

Without a fossil record statements on origin, evolution, and migration of *A. myrtifolia* must be speculative. The species is intimately related to a peculiar habitat in the Ione regions, namely to the Eocene Ione formation of kaolinitic clay minerals, quartz sand, and ironstone derived from adjacent laterites. From Eocene time to the present the Sierra Nevada has been rising. However, there is little chance that some such infertile habitats as those now occupied by *A. myrtifolia* near Ione could have been exposed continuously since Eocene time, for extensive deposits of early Miocene rhyolite and Miocene-Pliocene andesitic mud flows are known from adjacent areas. Also, *A. myrtifolia* is hardly a plant of lateritic environments, nor is it likely that its immediate precursors were either. The present widely scattered exposures of the Ione formation probably were uncovered by recent erosion. However, only at Ione does *A. myrtifolia* occur on the Ione formation.

The Valley Springs Peak disjunct station is not on the Ione formation but on a kaolinitic-altered rhyolite of the Valley Springs formation. The station near San Andreas is on a sericitic schist of originally Jurassic age. Both are infertile sites offering opportunities for establishment of non-zonal taxa.

If these last stations indicate a presently expand-

ing distribution, it is very difficult to account for the absence of the plant on other outcrops of the Ione formation than the ones at and near Ione. On the other hand, this spread to a variety of soil types, even if they all have infertility in common, hardly suggests a contracting distribution. Probably the plant has more or less reached its edaphic limits within the considerable climatic variation related to differences in altitude in the limited Ione to San Andreas area, but it has by no means reached its edaphic limits in the wider, but climatically more uniform region, of present Ione formation outcrops. Historical factors of some kind are helping to determine the plant's present distribution.

A hypothesis fitting many facts is that the present area of *A. myrtifolia* is a relic of a formerly more widespread area, possibly encompassing most of the present outcrops of the Ione geological formation from Oroville on the north to Friant on the south. The Pleistocene glacial (here pluvial) periods could have changed the climate to north and south of the present area of *A. myrtifolia* to be more similar to that of the present area. As shown in Table II the Ione area now has smaller monthly temperature ranges than occur to north and south, and this range is still less at lower altitudes. Thus, if the glacials had a more maritime climate, as seems likely, temperature extremes to north and south of Ione-San Andreas would have been more similar to present temperature ranges within that area. *A. myrtifolia* may be persisting in only that part of a former area least changed from glacial times. Unfortunately, reconstruction of glacial climates and vegetation in California has only begun.

The habitually similar and putatively closest relatives of *A. myrtifolia* occur isolated, all in mesic climates, on the podsollic soils near Ft. Bragg (*A. nummularia* Gray) (Gardner and Bradshaw 1954); as isolated colonies in sparse chaparral with *Pinus attenuata* Lemmon on poor soils in a forest climate from Mt. Tamalpais and Bolinas Ridge in Marin County through the Santa Cruz Mountains (*A. sensitiva* Jeps.) (Thomas 1961: 267); and scattered in forested, foothill elevations on infertile soils near Placerville in El Dorado County (*A. nissenana* Merriam). The last species is quite dissimilar. This distribution may be a fragmented relic of an originally more coherent one. All four species are edaphically limited in distribution, but many sites are known which to all appearances could support one of these species but in fact do not. Climatic or plant successional and soil formation vicissitudes perhaps related to postglacial events could at one time have

eliminated the plants from such sites, and re-immigration has not been possible. If the area of these four species was once coherent, it was broken up long enough ago for considerable separate evolution to have taken place.

The hypothesis that *A. myrtifolia* is a newly formed species which just fits its specialized habitat is not supported by its diploid chromosome number in a genus where polyploidy is common, by its lack of any immediate relatives in its vicinity, by the geological history of its site which involves no evident catastrophes (Lewis 1962) for this plant, or by its considerable variability which is incompatible with origin from a single individual (Mayr's "founder" principles (1952: 237)).

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