

THE CLOSED-CONE PINES
OF THE NORTHERN CHANNEL ISLANDS¹

Y. B. Linhart, B. Burr, M. T. Conkle²

University of California, Berkeley
United States Forest Service, Berkeley

Our interest in the pines of the Northern Channel Islands developed in the course of our work with the California closed-cone pines. The focus of these investigations has been Monterey pine (*Pinus radiata* D. Don.), a species which is widely planted as a forest tree in New Zealand, Australia, Chile, South Africa, and Spain. Despite its wide use, *P. radiata* is not well known genetically and its performance in California, its native home, has not been fully assessed.

The first phase of the project on *Pinus radiata* entailed study and sampling of the three native stands on the mainland. Later, we sampled its southern variety (*P. radiata* var. *binata* Engelm.) on Guadalupe Island. This led to a consideration of the other insular populations of closed-cone pines and their relationship to mainland *P. radiata* and Bishop pine (*P. muricata* D. Don.). We thus became aware of the confusion and uncertainty relative to the taxonomic and biosystematic relationships within the *P. radiata-muricata* complex.

In the past, California has relied on virgin and second-growth forests as a source of timber. In the future, artificial regeneration will become of increasing importance, and hitherto unused species may gain status as prime wood and fiber producers. Most insular populations of closed-cone pines occur on sites marginal for good tree growth. If planted on better sites, they may prove to be economically valuable. Furthermore, it may be possible to

-
1. This work was supported in part by the National Science Foundation (NSF-GB-2550) and by the Wrasse Foundation.
 2. Respectively, Assistant Specialist, School of Forestry, University of California, Berkeley; Graduate Student, Department of Genetics, University of California, Berkeley; and Forest Geneticist, Pacific Southwest Forest and Range Experiment Station, United States Forest Service, Berkeley.

combine their ability to survive on poor sites with the fast-growth characteristics of other species or populations to produce strains suitable for wood production in less-than-optimal situations. The hybrid *Pinus attenuata* × *P. radiata* is a good example of the above possibility, combining the drought and cold resistance of knobcone pine (*P. attenuata* Lemmon) with the fast growth of *P. radiata*.

Such economic considerations, in addition to the biosystematic problems cited above, led us to study and sample the closed-cone pine populations on Guadalupe Island in February 1963, Cedros Island in April 1963, Santa Cruz Island in June 1964, and Santa Rosa Island in April 1965.

This paper contains descriptions of the populations of closed-cone pines on Santa Cruz and Santa Rosa islands, and analyses of data from specimens collected on these islands as well as related mainland populations of *Pinus muricata*. Our results and observations are then discussed in the light of present knowledge of the California closed-cone pines.

HISTORICAL REVIEW

The nomenclature of the closed-cone pines on Santa Cruz and Santa Rosa islands has been in doubt for as long as these pines have been known botanically. Howell (1941) mentioned that T. S. Brandegee and E. L. Greene, among the first botanists to visit the Northern Channel Islands, called the pines *Pinus insignis* var. *binata* Engelm. They have subsequently been called *P. radiata* or *P. radiata* var. *binata* (Howell, 1941). Mason visited Santa Cruz Island in September 1927, and found *P. muricata* resembling the mainland *P. muricata* growing on the island. In addition, he described a smooth-cone variant which he named *P. remorata* Mason (Mason, 1930). He separated *P. remorata* from *P. muricata* on the basis of three main differences: (1) its thicker needles, (2) its larger number of resin canals per needle - six to twelve for *P. remorata* and three to ten in southern populations of *P. muricata* (Duffield, 1951), and (3) its almost symmetrical cones with smooth, or slightly rounded scales bearing small prickles, as opposed to the heavily-armed asymmetric cones of *P. muricata*.

Pinus remorata was present on both Santa Cruz Island and the mainland during the Pleistocene, as evidenced by cones found on Santa Cruz Island (Chaney and Mason, 1930) and Carpinteria (Chaney and Mason, 1933). Mason (1949) reported that *P. remorata* is now restricted to Santa Cruz and Santa Rosa islands and speculated on its presence on Cedros and Guadalupe islands. Mason (1949) also noted that *P. remorata* and *P. muricata* on Santa Cruz Island were completely interfertile and hybridized freely, the pro-

jected result being a complete "genetic submergence" of *P. remorata*. At the same time, he stated that there was evidence for a gene flow from the islands to the mainland, which accounted for the presence of a hybrid swarm on La Purisima ridge and had contributed, over a long period of time, to the differentiation between the northern and southern populations of *P. muricata*.

Eastwood (1941) expressed doubt about the clear-cut distinctness between the cone variants, and Howell (1941) suggested that the variation found in the pines on Santa Cruz Island was parallel to the variability of *Pinus radiata* var. *binata* on Guadalupe Island. In his study of the natural variation in *P. muricata*, Duffield (1951) classified the closed-cone pines of the Northern Channel Islands as *P. muricata* var. *remorata* irrespective of cone type. On the basis of oleoresin analyses, Forde and Blight (1964) and Mirov et al. (1965) confirmed the distinctness of the Santa Cruz and Santa Rosa island pines from the San Luis Obispo, La Purisima, and San Vicente populations of *P. muricata*. This distinctness is of a quantitative nature rather than a specific discontinuity (table 1).

STAND DESCRIPTIONS

There are three main populations of closed-cone pines on Santa Cruz Island, and one on Santa Rosa Island (fig. 1). The nearest mainland populations of *Pinus muricata* are about 90 kilometers northwest from Santa Cruz Island and 80 kilometers north-northwest from Santa Rosa Island. About 20 kilometers separate the Santa Rosa Island pines from the nearest Santa Cruz Island pines.

Santa Cruz Island, eastern population

The easternmost of the Santa Cruz Island populations is scattered over the isthmus (see fig. 1). Trees in the northern portion of this population grow in relatively dense stands on four ridges above China Harbor. They occur at elevations of 150 to 400 meters, largely on north and northeast facing slopes, on sandy soils from a diatomaceous parent material. In many places, manzanita (*Arctostaphylos insularis* Greene) and occasionally scrub oak (*Quercus dumosa* Nutt.) and toyon (*Heteromeles arbutifolia* M. Roem.) grow in dense thickets among the pines. The majority of the pines have "remorata-type" or intermediate cones (fig. 2). *Remorata*-type cones are those corresponding to Mason's (1930) description as opposed to the typical cones of *Pinus muricata* which will be called "muricata-type". Most trees are 10-25 years of age, but occasional mature trees, snags, and fallen trunks are scattered throughout, providing evidence of older stands.

An open stand of more mature trees, with diameters of 40-60 centimeters and heights up to 14 meters, occurs along the main

Table 1
OLEORESIN COMPOSITION OF NORTHERN CHANNEL ISLAND PINES
AND RELATED MAINLAND *PINUS MURICATA*

Number of samples	α -PINENE		β -PINENE		SABINENE		TERPINO-LENE		OTHERS	
	m	r	m	r	m	r	m	r	m	r
SANTA CRUZ ISLAND										
Northern Population										
M	1	54.5	8.0	25.5	3.5	8.5				
M	1	40.5	13.5	25.5	10.5	10.0				
I	1	33.0	4.0	38.0	21.5	3.5				
I	1	35.5	4.5	34.0	20.5	5.5				
R	1	38.0	7.5	35.0	16.0	3.5				
Western Population										
I	1	34.5	5.0	40.5	17.0	3.0				
R	1	24.5	2.0	46.5	24.0	3.0				
R	1	14.0	4.0	55.5	23.5	3.0				
SANTA ROSA ISLAND										
	8	47.0 (20-59)	12.0 (2-20)	24.0 (8-46)	13.0 (8-24)	4.0				
LA PURISIMA										
	17	6.0 (4-12)	2.0 (1-4)	54.0 (44-73)	27.0 (8-32)	11.0				
SAN LUIS OBISPO										
	10	6.0 (4-9)	1.5 (1-5)	56.0 (53-62)	30.0 (25-35)	6.5				
SAN VICENTE										
	7	6.5 (5-8)	2.0 (1-2)	50.5 (41-62)	22.5 (3-30)	18.5				

Table 1. Oleoresin composition of Northern Channel Island pines and related mainland *Pinus muricata*. The numbers are percentages of total compositions. R, I, and M refer to *remorata*-, intermediate-, and *muricata*-type cones respectively.

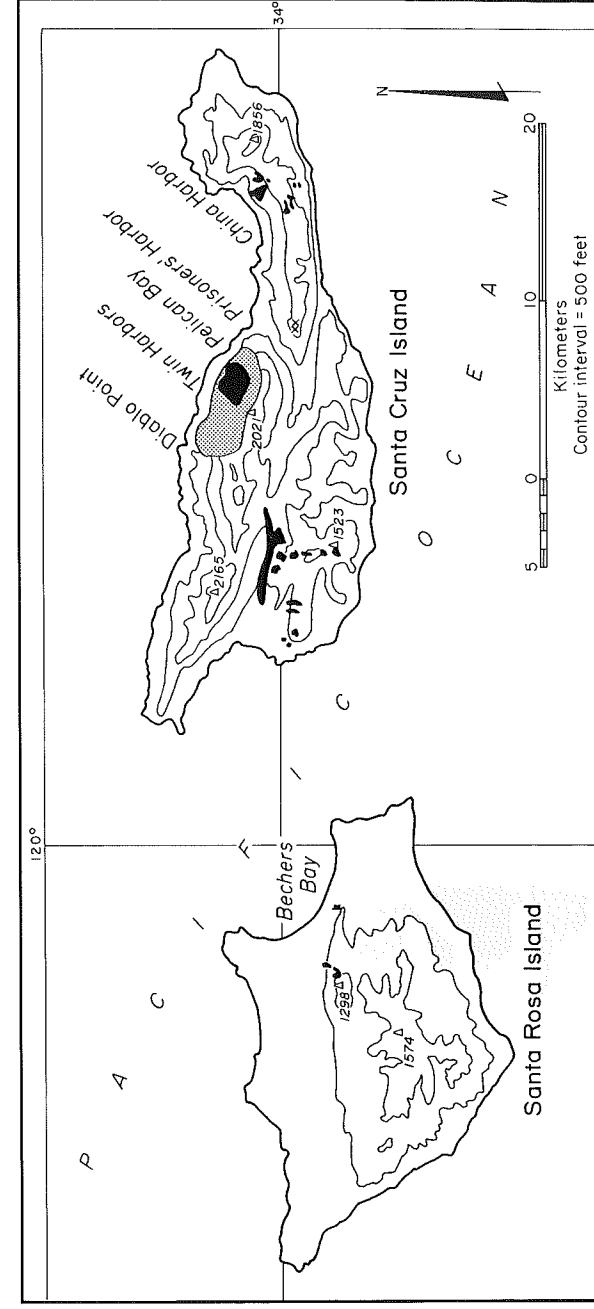


Fig. 1. Populations of closed-cone pines on the Northern Channel Islands. Elevations are in feet. The stippled area between Pelican Bay and Diablo Point indicates the distribution of individuals and small groups of pines scattered over that area, but not accurately mapped.

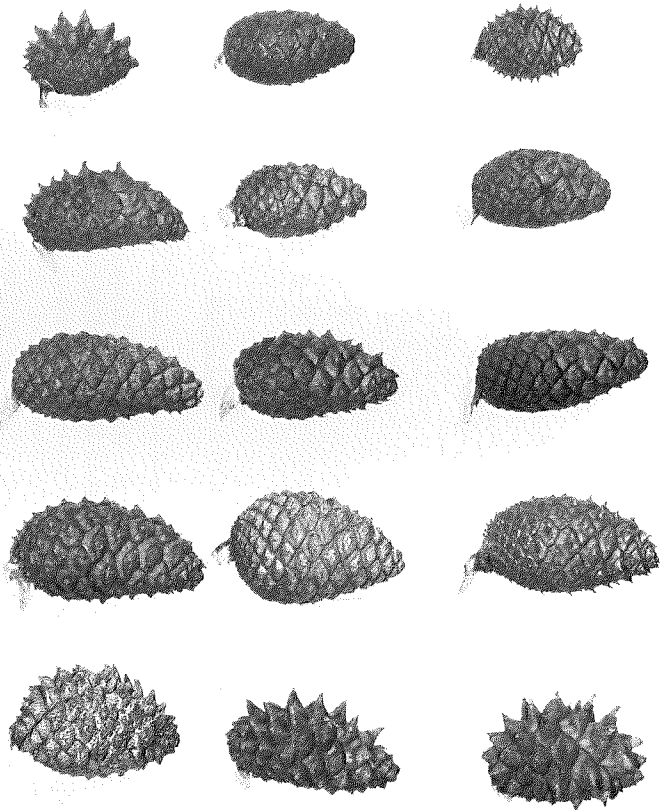


Fig. 2. Santa Cruz Island, eastern population. Variation in cone size and shape.

ridge of the isthmus at altitudes of 300 to 450 meters. Chamise (*Adenostoma fasciculatum* H. & A.) is a common associate in this area. Many of the trees have branches or tops broken by the wind and in general their cones are more intermediate or *muricata*-like. Two small clumps of similar character, with 25 to 35 trees each, are found south of the main ridge about 1 kilometer away.

Santa Cruz Island, northern population

The northern population is relatively extensive, the area of main concentration being within a mile of the coast and extending from Pelican Bay to a large canyon west of Twin Harbors. Occasional individuals and groups are scattered from Twin Harbors past Diablo Point. The soil in this section is derived from weathered basalt, but andesite outcrops are not uncommon on the ridges. The heaviest stands are on the north and northwest faces of ridges where ironwood (*Lyonothamnus floribundus* Gray) is a common associate. On the more exposed lower ridges, *Arctostaphylos insularis* forms thickets among the pines. The pines in this population are the most variable of the three groups on this island. The trees vary from windswept forms on the sea bluffs to straight-stemmed trees on the protected slopes. Many have long, horizontal branches. The cone type is also variable, and some unusual cones with markedly raised, pointed umbos were collected from this population (fig. 3). Crown gall (*Peridermium* sp.), was commonly found on trees in this area.

Sheep are very common in the northern part of the island where they seem to be the major biotic factor. There is little regeneration of the trees or shrubs, and a browse line is noticeable on all pines. Most trees are 40 to 65 years old. Remains of much larger stands are scattered on the bare slopes; and it is not unusual to see mature pines standing completely alone, with no other associates (fig. 4a). In the canyon bottoms, however, the vegetation has fared better and younger trees are common. It is also evident that several stands have been destroyed by fire within the past 20 or 30 years.

Santa Cruz Island, western population

The western population is the most extensive of the three groups on Santa Cruz Island, and contains the majority of pines on the island (fig. 4b). The largest continuous stand stretches as a strip for about 5 kilometers along the upper end of the Cañada Cervada, and extends a short distance into the Central Valley. The width of the strip varies from 300 to 1,000 meters and the elevations vary from 100 to 300 meters. The soils are derived from granitic parent materials. The number of trees in this strip is on the order of 100,000. Trees dominate the upper slopes of

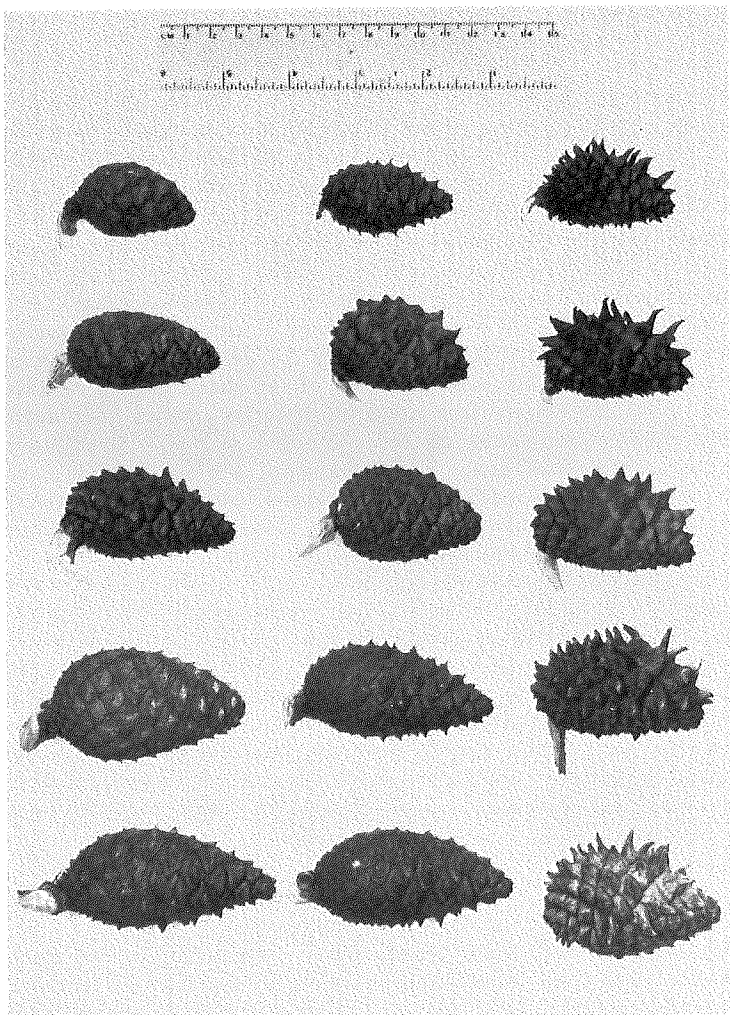


Fig. 3. Santa Cruz Island, northern population. Variation in cone size and shape. Note predominance of *muricata*-types and extremes in apophysis and umbo development.



Fig. 4a. Santa Cruz Island, northern population. Much of the ground cover is lacking in large portions of this population from which sheep have not been eliminated. It is probable that this area was more heavily forested in the past.



Fig. 4b. Santa Cruz Island, western population. This is a well forested slope with plentiful reproduction and many individuals of all age classes.

the ridge, where they apparently obtain moisture from fog drip, and become less abundant at lower elevations. The main associates are *Quercus dumosa* and *Arctostaphylos insularis*. The majority of the pines in this stand appear to be 15 to 25 years old. Seedlings and young trees two to ten years old are abundant and thriving, following exclusion of sheep by fencing. Cones are larger than in the other two populations and most of them are *remorata*-like (fig. 5). Cone production is precocious; seedlings two to three years old bear conelets and male strobili. *Peridermium* infections are most abundant along the ridge top.

A broad band composed of many small groups of pines extends south from the midsection of the main stand toward the Sierra Blanca. These groups grow predominantly on north-to-northwest-facing slopes at altitudes of 250 to 400 meters in groups of 10 to 50 mature trees. Where sheep are present, the stands have regressed to small patches of poorly-formed trees with no regeneration. In fenced areas, the mature trees are surrounded by abundant seedlings and young trees. A single tree in this area had abnormal clusters of conelets (fig. 6). The southernmost pines on the island occur on a single ridge leading up to Sierra Blanca Peak, a distance of 4 kilometers from the main population. The pines are in scattered groups on north-facing slopes along the flanks of the peak up to an altitude of 480 meters, within 15 meters of the summit.

In these scattered outliers, the great majority of the trees have *remorata*-type cones, with few intermediates or *muricata*-types. Occasional *Peridermium* infections were observed. Range grasses are associated with the pines in fenced areas, but wherever sheep are found the hillsides are essentially bare and heavily eroded.

On the hills overlooking the Christi Ranch, on the north face of the Cañada de los Sauces, are two clumps of 50-100 trees each, and a dozen individuals are scattered over the bluffs directly above Kinton Point. The latter are so twisted by the wind and misshapen that they no longer assume tree form, but rather are a mass of interlacing branches covered with cones. The two clumps are in protected draws. Most of these trees are 6 to 12 meters high, and are surrounded by numerous seedlings. All trees seem to have *remorata*-type cones. *Peridermium* was not seen.

Santa Rosa Island population

The closed-cone pines on Santa Rosa Island are almost all in one small area, 3.5 kilometers inland in a southwest direction from the Vail-Vickers Ranch headquarters on Bechers Bay (fig. 7). There is also one individual, reported by E. R. Blakley (personal communication) to be growing in the stand of Torrey pines about 4 kilometers southeast of the Ranch.

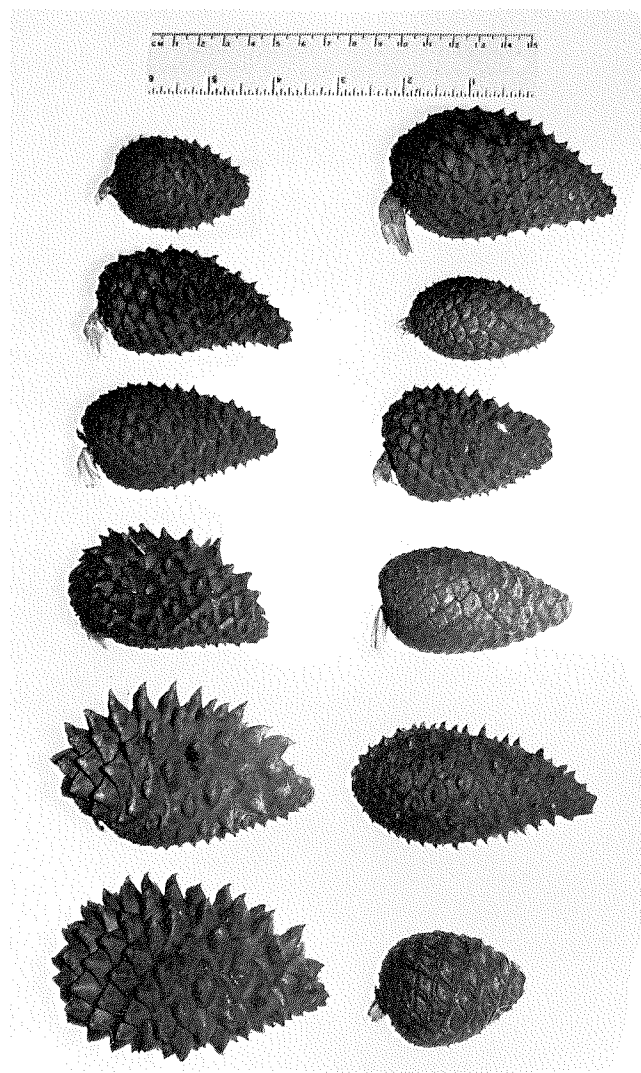


Fig. 5. Santa Cruz Island, western population. Variation in cone size and shape. Note large cones and predominance of *remorata*-types.



Fig. 6. Santa Cruz Island, western population. Abnormal clusters of conelets.



Fig. 7. Santa Rosa Island. This photo shows about half of the total Santa Rosa Island population. The remainder is within a few hundred meters of this area.

The pines on Santa Rosa Island seldom attain tree size except in sheltered situations. They are apparently subjected to some wind and animal damage. The majority of the trees have *remorata*-type cones and most others have intermediate-type cones (fig. 8). The only tree with *muricata*-type cones observed on Santa Rosa was one of five young trees growing as a group around a dead snag, which appears to have been their common parent. Other trees in this group have smooth cones. That single tree had retained most of its pollen at the time of observation (April 13), in contrast to its neighbors which had shed most of their pollen, as had all other pines of the island.

In general, the trees on Santa Rosa Island are found on north to west facing slopes at altitudes of 200 to 300 meters on siliceous soil from the Monterey formation. While *Quercus dumosa*, *Arctostaphylos subcordata* var. *confertiflora*, (Eastw.) Munz, and *Adenostoma fasciculatum* grow in the same locations as the pines, the association is not a close one. The pines tend to grow in scattered groups rather than stands and their total number is much smaller than on Santa Cruz Island: the total is on the order of 200-300 individuals. Seedling reproduction is rare. As on Santa Cruz Island, young trees produce cones at a very early age. *Peridermium* infections are frequent, usually on branches.

SAMPLING METHODS

The primary goal of our expedition was to obtain material that would include the range of genetic variability present in the island populations. In large stands we chose trees scattered over the whole area of the stand. Wherever small groups occurred, we attempted to sample at least one tree per group. We also collected from individuals isolated by at least several hundred meters from other trees, expecting to find a high frequency of selfed seed. We specifically included trees with *remorata*-type cones within groups of trees where the *muricata*-type predominated, and vice-versa. Similarly, we collected from *Peridermium*-free trees in infected areas and vice-versa. Levels of infection by *Peridermium* are of interest because it is a common and damaging pathogen on *Pinus radiata* and attacks *P. attenuata* and *P. muricata* as well, distorting trunks and branches of infected trees.

In addition to collecting cones, we collected needles, resin samples, and on a few occasions, wood samples. Twenty-one trees on Santa Rosa Island and 149 trees on Santa Cruz Island were sampled in this manner. Cones, needles, and resin were also collected from trees in the mainland populations at San Luis Obispo (San Luis Obispo County), La Purisima (Santa Barbara County), and San Vicente (Baja California). The data from mainland populations were used as a basis for comparison with Channel Island samples.

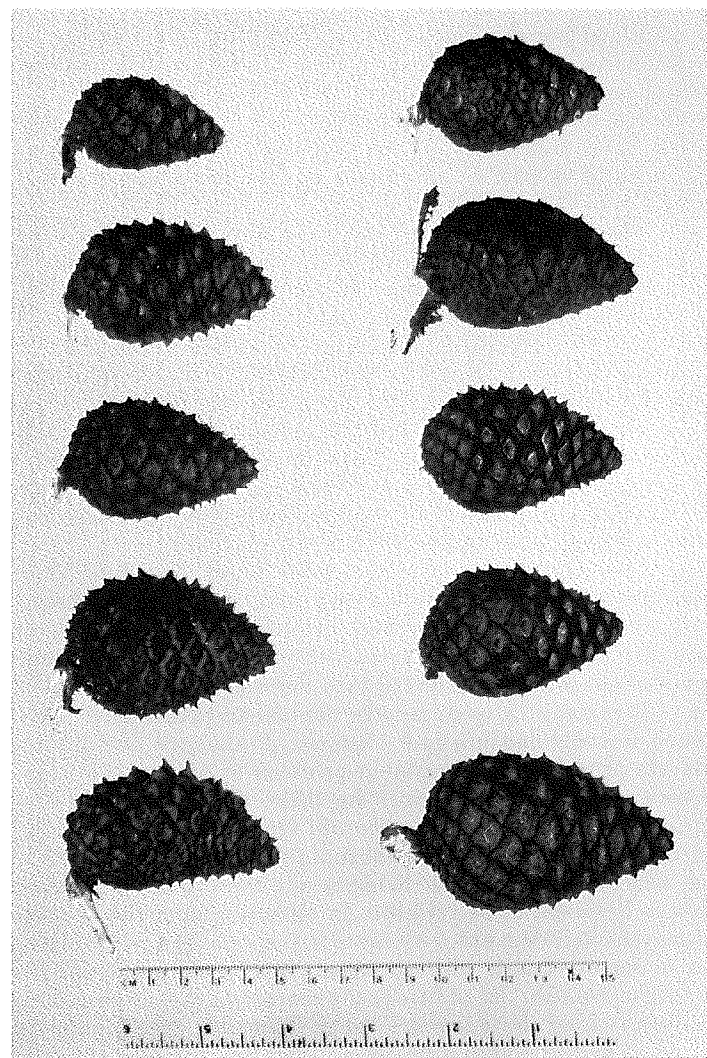


Fig. 8. Santa Rosa Island. Variation in cone size and shape. Note the predominance of *remorata*-types. Cone in upper left-hand corner was only *muricata*-type found on this island.

ANALYSIS OF DATA

The needle, cone, and resin samples were analysed to provide at least tentative answers to several questions. We wanted to know how much variation there is in the Northern Channel Island populations, how this variation compares with similar data from related mainland populations of *Pinus muricata*, and whether our sample supports published descriptions of differences between *P. muricata* and *P. remorata* (Mason, 1930, 1932, 1949).

Our choice of diagnostic characteristics was based on characteristics used previously in the investigations of *Pinus muricata* by Duffield (1951), *P. attenuata* by Newcomb (1962) and *P. radiata* by Forde (1964b, 1964c).

Needle shape and cone size data were analysed by the Dice-Leraas (1936) method which Duffield (1951) used in his study of *Pinus muricata*. Ranges, means, standard deviations, and confidence limits at the 5% level were obtained. In figs. 10 and 12, the horizontal line indicates the range of values for a specific characteristic within a group or population. The vertical line indicates the arithmetic mean; the open bar, the mean plus and minus one standard deviation; and the cross-hatching, the confidence limits at the 5% level. Data on resin canal frequency (fig. 9) are presented by bar graphs instead of the Dice-Leraas scheme since, as Forde (1964b) pointed out, the variation does not follow a normal distribution.

Cones were classified on a numerical index based on three characteristics: symmetry, apophysis shape, and umbo prominence. Cone symmetry was divided into three classes: (1) symmetrical; (2) slightly asymmetrical; (3) strongly asymmetrical. Apophysis shape was also divided into three classes: (1) flat-to-rounded; (2) raised; (3) prominently conical-to-pyramidal. Umbo prominence was divided into four classes: (1) absence of prickles; (2) moderate prickles; (3) prominent prickles or spines; (4) claw-shaped umbos. Total index values for these three characteristics ranging from 3 to 5 designated *remorata*-type cones, 6 to 8 intermediate-type cones, and 9 to 10 *muricata*-type cones. Because of the high degree of correlation between all three characteristics, the index is believed to be reliable. In other words, in the species studied, symmetric cones with swollen apophyses and strong prickles or smooth cones with strong asymmetry do not occur (for example figs. 2-3, 5). In addition, the cone length was measured with calipers along the geometric axis, from the cone tip to the farthest point on the dorsal side, away from the tip.

The needle characteristics studied were: number of resin canals per needle and relative needle stoutness expressed as a ratio of length over fascicle diameter. Four fascicles per tree were scored and the averages calculated. Other anatomical details such as number of vascular bundles per needle, number of

cell layers in the hypoderm, and the stomatal anatomy were also examined. All cross-sections were taken at one-third of the total needle length from the base.

Oleoresin analyses were performed by Dr. Eugene Zavarin of the Forest Products Laboratory, University of California, using vapor-phase chromatography methods (Mirov et al., 1966). Studies of oleoresin composition in pines have shown it to be a reliable characteristic for separating populations or species from one another. Forde (1964a) has demonstrated the high degree to which oleoresin composition is inherited. She found little variability within clones of an F_2 progeny of *Pinus attenuata* \times *P. radiata*, and also showed that this characteristic followed the expected pattern of intermediacy in F_1 and segregation in F_2 progeny of *P. radiata* and *P. attenuata*. Forde and Blight (1964) also supported Duffield's findings on the morphological variation between the groups within *P. muricata* on the basis of their oleoresin analyses. Other workers have found there is little variability in oleoresin composition due either to the different times of sampling or to the environment in which a species is planted (Mirov, 1961).

RESULTS

Needle Characteristics

Comparisons of resin canal numbers between populations are shown in Figure 9. In the Santa Cruz Island pines, the ranges of variation within populations are large: from 3 to 10 (mean 6.8), 2 to 11 (mean 7.1), and 2 to 9 (mean 6.4) in the eastern, northern and western populations, respectively. Within cone types, they are equally large: 2 to 10 (mean 6.1), 3 to 10 (mean 7.1), and 2 to 11 (mean 7.5) for *muricata*-, intermediate-, and *remorata*-types respectively. The western population has the smallest average and the northern population the highest average number of resin canals per needle. Santa Rosa Island trees exhibit less variation in resin canal number (3 to 6 per tree) and their mean, 4.4, is smaller than the Santa Cruz means. The San Luis Obispo and Purisima populations have means close to that of the Santa Rosa population. The San Vicente populations vary widely, ranging from a mean of 4 canals per needle in one distinct population to between 9 and 11 for four other populations, with an overall mean of 8.3.

Relative needle stoutness, used in the characterization of *Pinus remorata*, was calculated for all populations (fig. 10). In the Santa Cruz Island populations, variation within and between populations is not consistent for this characteristic. Averages by cone type and by populations give a better picture of the situation. Trees with *remorata*-type cones have, on the average,

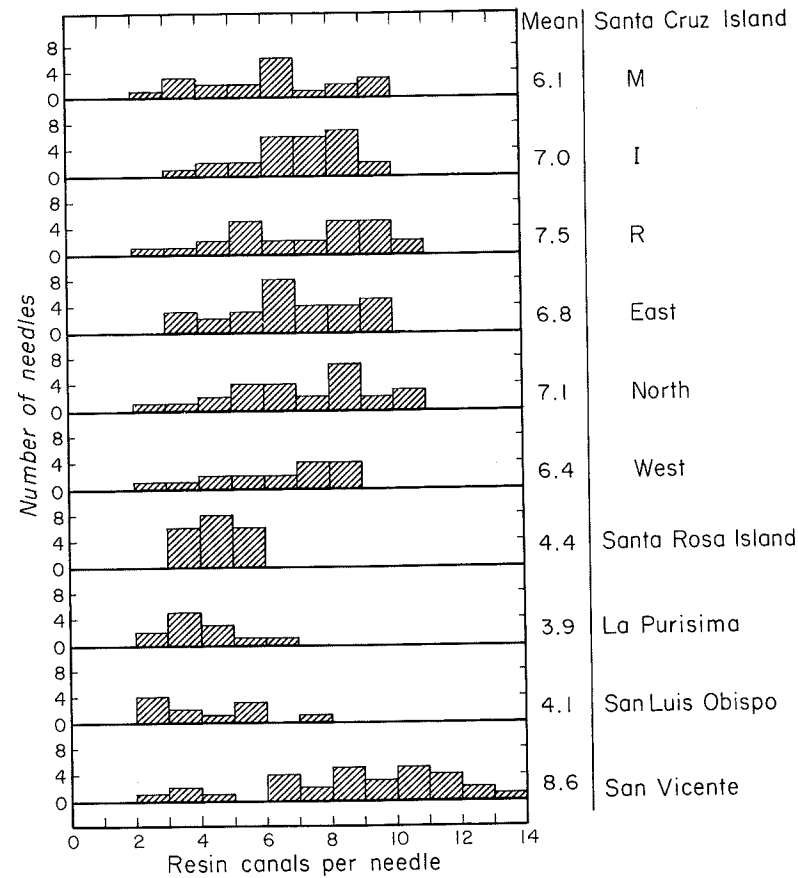


Fig. 9. Variation in resin-canal number in island and mainland populations of closed-cone pines. R, I, and M refers to *Pinus remorata*, intermediate, and *P. muricata* cone types.

slightly stouter needles; but standard deviations and confidence limits are so overlapping that there are no clear-cut differences. The western Santa Cruz population differs in having trees with markedly stouter needles than trees in other Santa Cruz populations. The needles of Santa Rosa trees are intermediate in stoutness between those of the western Santa Cruz trees and those of the eastern and northern Santa Cruz trees. Comparisons of island and mainland populations show that all three mainland populations studied have wide ranges of variation, with standard deviations and confidence intervals overlapping those of the island populations. Means of mainland populations show them to have needles intermediate in stoutness between Santa Rosa trees and trees of the eastern and northern Santa Cruz populations.

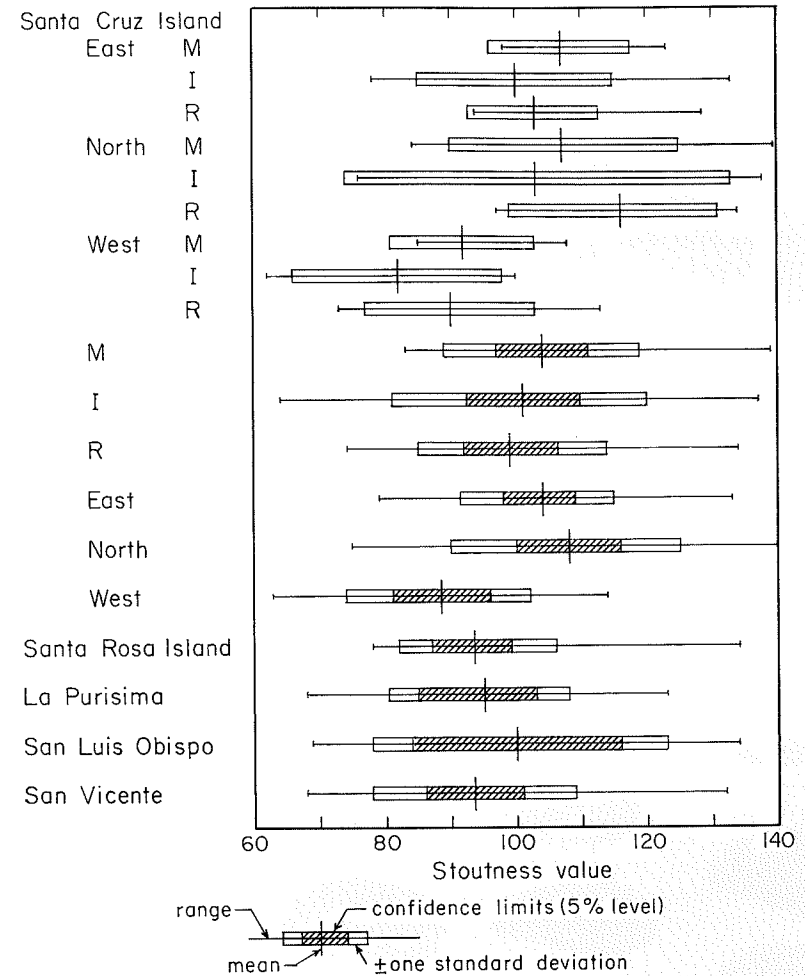


Fig. 10. Variation in needle stoutness in island and mainland populations of closed-cone pines. Low values indicate stout needles, high values, slender needles. R, I, and M refer to *Pinus remorata*, intermediate and *P. muricata* cone types.

Both island and mainland pines have, in general, two vascular bundles per needle and two layers of cells in the hypoderm. The frequency of deviations from these numbers was on the order of one to two per cent and appeared to occur randomly in all populations and cone types. In stomatal anatomy, the island pines, irrespective of cone type, resemble *Pinus muricata* from the southern mainland populations as described by Duffield (1951). Their

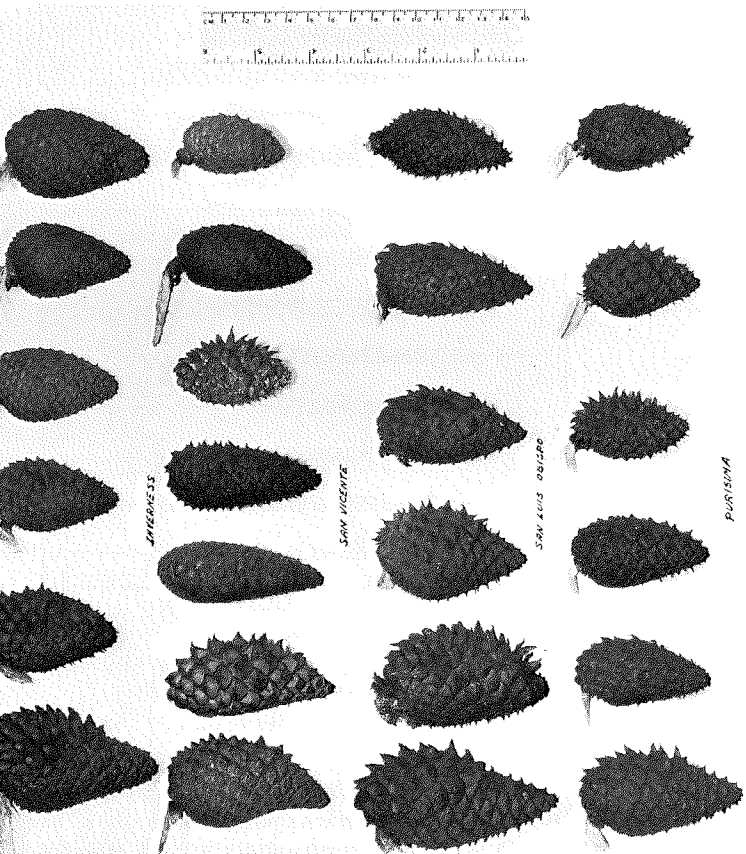


Fig. 11. Variation in cone size and shape in mainland populations of *Pinus muricata*.

stomata, when seen in cross-section, have a vestibule partly closed by the strongly over-arching lips of the accessory cells. In contrast, *P. muricata* from the northern mainland populations has a wide open wax-filled stomatal vestibule, with the lips of the accessory cells inconspicuous.

Cone Characteristics

Exact frequencies of cone types in island and mainland populations cannot be ascertained from our data, since our sampling methods were not designed to do this. We observed on Santa Cruz Island that trees with *muricata*- and intermediate-type cones are most abundant in the northern populations and least abundant in the western populations. On Santa Rosa, only 1 *muricata*-type was found and 5 intermediates collected. On the mainland, we collected intermediates at La Purisima and less frequently at San Luis Obispo. We also found intermediates and *remorata*-types at Pine Ridge, near La Purisima. At San Vicente, *remorata*-, *muricata*-, and intermediate-types are present in varying frequencies, depending on the population. Some populations have exclusively *muricata*-types, others have all three kinds, and one has predominantly *remorata*-types. We also collected *remorata*-types on Inverness ridge in Marin County (fig. 11).

Cone length is variable in all populations on Santa Cruz Island and in all cone types (fig. 12). Average cone length is essentially equal for the three cone types (about 62 mm). The standard deviations are similar and the ranges comparable. Cone lengths are similar in the eastern and northern populations (means, 56 and 58 mm), but the western population has much larger cones (mean 71 mm). Sizes of Santa Rosa Island, Purisima, and San Vicente cones are comparable to the eastern and northern Santa Cruz populations, while the San Luis Obispo populations resemble the western Santa Cruz Island group.

Resin analyses

The first thing that became evident during our field collections was the paucity of resin production in the island pines of all types: only 8 of 100 trees sampled on Santa Cruz and 3 of 35 trees sampled on Santa Rosa yielded analysable amounts (2 to 3 drops) of resin over a 24-hour period. In contrast, *Pinus muricata* sampled on the mainland at San Luis Obispo and Purisima yielded analysable amounts in 10 of 20 and 5 of 12 attempts, respectively. The poor resin flow in these trees observed during our sampling and in previous attempts at Placerville, on trees of Northern Channel Island origin, may have an anatomical basis such as plugging or small number of wood resin canals.

Analyses of our samples and of previous samples reported by Mirov et al. (1966) are presented in Table 1. The island popula-

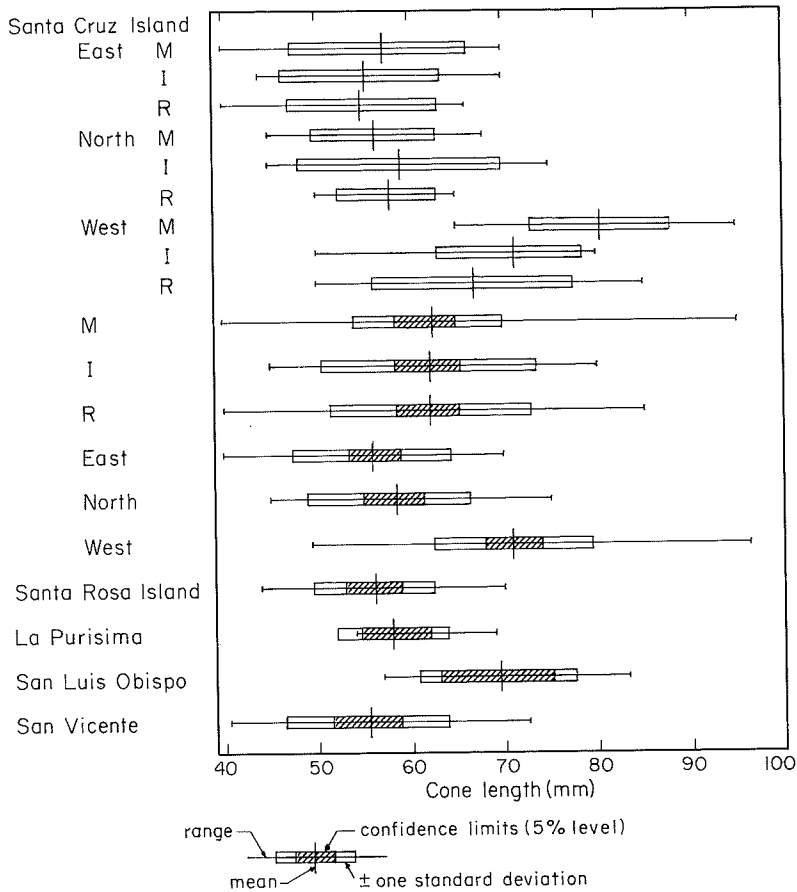


Fig. 12. Variation in cone length in island and mainland populations of closed-cone pines. Lengths are in millimeters. R, I, and M refer to *Pinus remorata*, intermediate, and *P. muricata* cone types.

tions differ from the mainland populations of *Pinus muricata* in a higher relative content of α -pinene and correspondingly lower relative contents of sabinene and terpinolene. Within the island populations there are marked differences between northern and western populations on Santa Cruz Island. Comparisons between oleoresin compositions of trees with different cone types from Santa Cruz Island give interesting results. The number of samples is very small, involving two, three, and three samples in the *muricata*-, intermediate-, and *remorata*-types, respectively. Differences between cone types are noticeable but in general, oleoresin composition seems to be related to the population from

which the tree originates more than to its cone type. Note the similarity between the Santa Cruz northern population where *muricata* and intermediates predominate and the Santa Rosa population which has almost exclusively *remorata*-types.

DISCUSSION

Mason (1930) distinguished *Pinus remorata* from *P. muricata* on the basis of stout rather than slender needles with 6 to 12 rather than 3 to 10 resin canals, and symmetrical cones with smooth scales rather than asymmetrical cones with raised umbos. On the basis of these characteristics, *P. remorata* apparently does not exist as a distinct species on Santa Cruz or Santa Rosa islands, nor in any of the mainland populations. Trees with *remorata*-type cones do not possess a unique or constant set of characteristics. Figs. 9, 10, and 12 show that the number of resin canals, needle stoutness, and cone size are not associated with cone type; i.e., specific values for these three characters, when grouped by the cone type with which they occur, form random arrays rather than discrete sets. In our samples, some trees with *remorata*-type cones had slender needles with resin canal numbers in the range described for *P. muricata*. Conversely, some trees with *muricata*-type cones had stout needles with high numbers of resin canals. Even when trends in associations between needle and cone characteristics are sought, these trends fail to be consistent from population to population (see figs. 9-10 and 12). Larger differences in these characteristics are found between populations than between the *remorata*-type and *muricata*-type trees within populations.

Unfortunately, we had only a small number of resin samples for comparison: five from the northern and three from the western Santa Cruz Island populations, and eight from Santa Rosa Island. Perhaps the lack of correlation with cone type that we observed occurred only by chance. Our data, however, indicate a moderate difference between populations on Santa Cruz Island and between the two islands. (The northern Santa Cruz Island population and the Santa Rosa Island population have higher α -pinene compositions than does the western Santa Cruz Island population.) The Northern Channel Island populations appear to have higher amounts of α -pinene and proportionately less sabinene and terpinolene than do any of the mainland populations of *Pinus muricata* (see table 1).

Overall, our data indicate that *Pinus remorata* is primarily a name given to a particular cone type in a variable species. We agree with Duffield's conclusion about the island pines: they do not deserve status as a species, for that would indicate a level of distinctness similar to *P. attenuata*, *P. muricata*, and *P. radiata*. Mason's (1949) suggestion that pines with the *muricata*-type cones

had migrated to Santa Cruz Island and were swamping the *remorata*-type cone characteristic on that island provides a reasonable explanation for the variability of cone type found currently on Santa Cruz Island. However, this hypothesis does not explain similar patterns of variation in cone shape found in southern mainland populations of *P. muricata*, *P. attenuata*, and *P. radiata*.

Trees with *remorata*-type cones are found today in *Pinus muricata* populations at San Vicente (Baja California), La Purisima Ridge (Santa Barbara County), and as far north as Inverness Ridge (Marin County), over 500 kilometers from Santa Rosa Island (fig. 11). It seems probable that the two cone variants have been together for a long time over a wide range, and that Santa Cruz Island is but one of the places where both occur. Similarly, individual trees with smooth cones and relatively thin scales are found in the Ensenada (Baja California) population of *P. attenuata* (Newcomb, 1962). In *P. radiata* var. *binata* on Guadalupe Island, Howell (1941) noted a high degree of cone variability, ranging from smooth, symmetrical cones to typical *radiata*-type cones, with many intermediates. We found this to be true in our visit, and verified Howell's observations of complete intergradation of cone types. On Cedros Island, the situation is similar to that on Guadalupe Island.

Polymorphism of reproductive organs is unusual within species, and the genus *Pinus* is no exception. Why this polymorphism should exist in the southern populations of the closed-cone pines, and why there should be such a high incidence of *remorata*-types on Santa Cruz and Santa Rosa islands are important questions suggested by recent studies of these pines. One possible explanation is that *remorata*-type cones are present in larger or smaller proportions in different populations because of the "founder phenomenon" (Mayr, 1942). By chance, trees with *remorata*-type cones could have been the only ones left after a fire, and thus would have been the ones to reseed that particular area. Such fires have occurred on Santa Cruz Island in the past (Williams, 1954). Again, by chance, seeds from trees with *remorata*-type cones may have been the ones to migrate to a new area and establish a new population. It is possible that the occurrence of nearly-uniform *remorata*-types and the small amount of variability in the Santa Rosa Island population may be due to colonizing in this way by one or a few individuals.

Another possibility is that one or the other cone type is present to a greater or lesser degree in the natural populations because these cone characteristics have a differing selective advantage under the different environments, both past and present, of these populations. Shaw (1914) and others have suggested that strong deflection towards the branch coupled with thick scales and prominent apophyses of the closed-cone pines are of value in hot, arid climates with a high incidence of fire. Vegeta-

tion growing on the islands may have been subjected to fewer fires than that on the mainland. Thus, trees with smooth, thin-scaled cones would not be at a disadvantage on such islands. The predominance of such trees on all four islands visited is strongly suggestive. The postulated increase in *muricata*-types on Santa Cruz may be a result of repeated fires over centuries of Indian occupation. Such fires still occur as noted above. Williams (1954) refers to fires which destroyed large stands on the slopes near Pelican Bay about 30 years ago. These fires may account, at least in part, for the predominance of *muricata*-types in the northern population.

It is likely that both the founder's effect and differing selective advantages have been responsible for the variability within and between populations that are found in the present insular populations.

In conclusion, we have found:

1. *Pinus remorata*, as described (Mason, 1930, 1932), does not currently exist as a separate species on the Northern Channel Islands.
2. The variability in cone shape found in the Santa Cruz Island populations parallels that in other southern populations of the California closed-cone pines.
3. The closed-cone pines of the Northern Channel Islands are similar to the *Pinus muricata* populations of San Luis Obispo, La Purisima, and San Vicente. The island pines differ quantitatively in several morphological and chemical characters; they do not, however, deserve specific rank, and even the varietal rank proposed by Duffield (1951) may be premature.

As Mason (1949) pointed out, it is too early to make definitive statements regarding the nature and relationship of the populations within this complex. We must still examine the inheritance of cone type, and attempt to assess its possible selective advantage. Relationships which we missed in the natural populations may be discovered when progenies from all these populations are established in replicated common gardens. In such a situation, characteristics can be measured in a series of relatively uniform environments, and material for a complete series of cross-pollinations will be available. The information gained from such studies will be valuable in elucidating the relationship of the island pines to the other populations of closed-cone pines.

ACKNOWLEDGEMENTS

We are very grateful to Mrs. Edwin L. Stanton and Dr. Carey Q. Stanton and to Messrs. A. L. and N. R. Vail for allowing us to visit Santa Cruz and Santa Rosa and extending to us their hospitality. Mr. and Mrs. John Tappeiner were very kind and helpful

in allowing us to use their home as a base of operations and furnishing us with transportation to Santa Rosa Island. Dr. Donald Weaver was of great help in matters of general information and advice and offered us the hospitality of the University of California, Santa Barbara Geology Summer Camp. From the inception of this study to its completion, Dr. William J. Libby has supported, advised, helped us in our work, and reviewed the manuscript, as did Dr. W. B. Critchfield. Miss A. Laton and Mr. S. De Keijzer helped in data compilations and drawing of figures.

LITERATURE CITED

- Chaney, R. W., and H. L. Mason. 1930. A Pleistocene flora from Santa Cruz Island, California. *Carnegie Inst. Wash. Pub.*, 415: 1-24.
- Chaney, R. W., and H. L. Mason. 1933. A Pleistocene flora from the asphalt deposits at Carpinteria, California. *Carnegie Inst. Wash. Pub.*, 415: 45-79.
- Dice, L. R., and H. J. Leraas. 1936. A graphic method for comparing several sets of measurements. *Contrib. Lab. Vertebrate Genet., Univ. Michigan*, 3:1-3.
- Duffield, J. W. 1951. Interrelationships of the California closed-cone pines with special reference to *Pinus muricata* D. Don. Ph.D. thesis. Univ. Calif., Berkeley. 114 pp.
- Eastwood, A. 1941. The islands of southern California and a list of the recorded plants. I. *Leafl. West. Bot.*, 3(2):27-36.
- Forde, M. 1964a. Inheritance of turpentine composition in *Pinus attenuata* X *radiata* hybrids. *New Zealand J. Bot.*, 2(1):53-59.
- Forde, M. 1964b. Variation in natural populations of *Pinus radiata* in California. I. Sampling methods and branch characters. II. Needle characters. *New Zealand J. Bot.*, 2(3):213-257.
- Forde, M. 1964c. Variation in natural populations of *Pinus radiata* in California. III. Cone characters. IV. Discussion. *New Zealand J. Bot.*, 2(4):459-485.
- Forde, M., and M. M. Blight. 1964. Geographical variation in the turpentine of Bishop pine. *New Zealand J. Bot.*, 2(1):44-52.
- Howell, J. T. 1941. The closed-cone pines of insular California. *Leafl. West. Bot.*, 3(1):1-8.
- Mason, H. L. 1930. The Santa Cruz Island pine. *Madroño*, 2(1): 8-10.
- Mason, H. L. 1932. A phylogenetic series of the California closed-cone pines suggested by the fossil record. *Madroño*, 2(3):49-55.
- Mason, H. L. 1949. Evidence for the genetic submergence of *Pinus remorata*. In *Genetics, paleontology and evolution*, pp. 356-362.
- Mayr, E. 1942. *Systematics and the origin of species*. New York. 334 pp.

- Mirov, N. T. 1961. Composition of gum turpentines of pines. U.S. Dept. Agric., Forest Service Tech. Bull., 1239:1-158.
- Mirov, N. T., E. Zavarin, K. Snajberg, and K. Costello. 1966. Further studies of turpentine composition of *Pinus muricata* in relation to its taxonomy. *Phytochemistry*, 5:343-355.
- Newcomb, G. B. 1962. Geographic variation in *Pinus attenuata* Lem. Ph.D. thesis. Univ. Calif., Berkeley. 191 pp.
- Shaw, G. R. 1914. The genus *Pinus*. Cambridge. 96 pp.
- Williams, M. W. 1954. California's offshore islands. *Pacific Discovery*, 7(1):16-17.