

A COMPARISON OF THE MAINLAND
AND ISLAND POPULATIONS OF TORREY PINE

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Torrey pine (*Pinus torreyana* Parry ex Carr.) has one of the most limited ranges of any species in the genus, and occurs only in two highly restricted coastal localities about 175 miles apart: the mouth of Soledad Canyon, just south of Del Mar on the San Diego County mainland, and along the northeastern coast of Santa Rosa Island. Taxonomically, Torrey pine is placed with *P. coulteri* D. Don and *P. sabiniana* Dougl. in the group *Macrocarpae*, a group that is confined in its distribution to California and northern Baja California. All three of these species share such characters as very long, grayish needles; large, heavy cones with highly developed apophyses; and short, thickened seed wings. Torrey pine is apparently most closely related to *P. sabiniana*, both morphologically and genetically. Hybrids between these two species have recently been produced at the Institute of Forest Genetics at Placerville, but attempts to hybridize *P. coulteri* with *P. torreyana* have been unsuccessful (Critchfield, 1966).

The geographical isolation of the mainland and island populations of Torrey pine and the environmental differences between the two localities suggest that these two populations might show some degree of morphological differentiation. The purpose of the present study has, therefore, been to compare the mainland and island populations in a general way in order to gain an approximate idea of their morphological and evolutionary relationships. The results to this point must be considered highly tentative, owing to the small size of the samples, the small number of characters considered, and the difficulty of assessing the effects of the environment. Further investigations are being planned.

Three collections of about 10 trees each have been made from the two native populations: one collection from Santa Rosa Island and two from Torrey Pines State Reserve, on the mainland near Del Mar. The island grove runs for about a half-mile along the north slope of a ridge facing the Santa Barbara Channel. The lowest trees occur near the base of the slope at an elevation of

200 feet. The grove extends upward from these trees for about a quarter-mile, to an elevation of 500 feet, close to the top of the ridge. A series of small, north-south canyons dissects the entire area. The characteristic soil is a fine, sandy loam, but rock outcrops occur along the ridges. Shrubs such as *Adenostoma fasciculatum* and *Heteromeles arbutifolia* are scattered through the grove, but do not form the dense thickets characteristic of chaparral vegetation on the mainland. The openings between the trees are usually covered with grass.

All the trees on the exposed ridges in the island grove are severely wind-pruned, and even in the relatively sheltered sites none of the trees are more than about 35 feet tall. Nonetheless, most of the trees appear to be healthy, and young trees occur in the open places. In some parts of the area, mature trees with trunks two to three feet in diameter form a dense canopy. Cores of the trunks obtained with an increment borer by Ralph N. Philbrick and examined by Harold S. Gladwin show that in favorable sites the trees are sometimes able to grow continuously during the year. Most of the trees grow relatively slowly, however. One incomplete core from a slow-growing 30-foot tree in a relatively dry site showed more than 73 rings, thus making this tree about the same age as the well-known "Ward" Torrey pine, which was planted on the mainland at Carpinteria in 1890, and now reaches a height of more than 100 feet.

Although precipitation is relatively low at both localities where Torrey pine occurs naturally, the mainland locality at Del Mar is decidedly drier than Santa Rosa Island. The annual rainfall on the island is about 12 inches (Vail-Vickers Ranch weather records, 1941 to present); at Del Mar it is only 10 inches, and is much less reliable. The effects of the low rainfall at Del Mar are almost certainly compounded by the porous, sandy soil characteristic of that area but not of Santa Rosa Island. The aridity at Del Mar is reflected in the presence there of several species of cacti, and by the desert affinities of a number of other plants, such as *Yucca schidigera*.

The first of the two mainland sample areas is situated on the seaward-facing slope at Torrey Pines Reserve and is similar in elevation and exposure to the island grove, except for the slope direction which is primarily west rather than north. The ground is covered by a remarkably varied assemblage of plants, representing the coastal strand, coastal sage, chaparral, and desert communities. Most of these are relatively low-growing. The tallest of the pines are 35 feet high, as they are on the island, but they are usually much smaller at this locality. The trunk diameter is usually less than a foot, the crowns are generally far less dense than on the island, and the overall appearance of the trees is spindly and stunted. Most of the trees along the seaward edge

of the grove, as well as a considerable number farther back, have died within the last few years, apparently from a combination of drought and insect damage. Seedlings are uncommon within the sample area.

The second mainland sample was obtained approximately one-quarter mile inland from the first on a northeast-facing slope, sheltered from the prevailing westerly winds. The associated chaparral vegetation is taller, much denser, and less varied than on the seaward slopes. The pines are few in number and sparsely scattered through the chaparral. No young trees are evident. The existing trees were probably established when the chaparral was less dense, possibly following brush fires. All of the trees are well-formed and apparently healthy. There is little evidence of wind-pruning. Several trees have trunk diameters of three feet and reach 75 feet in height. Because the orientation of the slope provides protection from both the wind and the most direct rays of the sun, the habitat is more moist here than on the seaward slope and much more favorable for the growth of the pines, although not necessarily for their establishment.

Both vegetative and cone characters were used to compare the trees from the three sample areas. Most of the former are apparently easily modified by the environment, while the latter are usually less subject to direct modification, as will be shown below. For the vegetative characters, two branches were selected from each tree: one from the windward side and one from the leeward side of the crown. The data from these two sets of branches were recorded separately.

Statistical significance of apparent differences between different localities or sets of branches was determined by use of the Mann-Whitney U Test (Siegel, 1956). All significant differences in the paragraphs below are at the 0.001 level unless noted otherwise.

The first character, the mean yearly length increment of the branches, is small on the seaward slope at Del Mar and large on the inland slope, reflecting the more favorable growing conditions at the latter site. The difference between these two immediately adjacent sites is statistically significant and is greater than the difference between either of these two and the mean of the island locality (table 1). The branches from the leeward side of the trees show no significant differences from those on the windward side at either mainland site, but on the island the difference between the windward and leeward branches is highly significant, and even larger than the difference between the means of the two mainland samples (table 1). This rapid growth of the leeward branches is an indication of the favorable growing conditions on the island when the effects of the wind are reduced.

Three-needle and four-needle fascicles, rather than the five-

TABLE 1. MORPHOLOGICAL RELATIONSHIPS OF THE MAINLAND AND ISLAND POPULATIONS OF TORREY PINE

	DEL MAR SEAWARD (Dry-windy)	DEL MAR INLAND (moist-non windy)	SANTA ROSA ISLAND (very moist-very windy)
Yearly Branch Growth (length)			
Windward Branches	5.56 cm	7.27 cm	4.57 cm
Leeward Branches	4.72	9.05	8.52
Average	5.14	8.16	6.74
Per Cent of 3 and 4-Needle Fascicles			
Windward Branches	10.7	1.2	4.0
Leeward Branches	8.2	6.1	4.0
Average	9.4	3.9	4.0
Needle Length			
Windward Branches	20.9 cm	24.1 cm	19.7 cm
Leeward Branches	21.8	24.1	22.0
Average	21.3	24.1	20.9
Needle Color			
Windward Branches	Yellow-Green	Yellow-Green	Blue-Green
Leeward Branches	Yellow-Green	Yellow-Green	Blue-Green
Cone Size (length + width)	21.0 cm	25.0 cm	27.5 cm
Cone Width/Length Ratio	0.98	1.03	1.19
Umbo Length/Scale Thickness Ratio	0.48	0.55	0.71

needle type characteristic of the species, are significantly more common (0.015 level) at the seaward Del Mar site than at the other two. In several other pine species, fascicles with less than the usual number of needles are characteristic of populations or individuals in particularly dry sites (Haller, 1965), and presumably the figures for the seaward Del Mar locality reflect the same phenomenon. This character shows no significant difference between windward and leeward branches at any site, including the windy island. Needle number, however, is probably determined in the summer, a relatively non-windy period, whereas growth of branches and needles occurs mostly during late winter and spring, the windiest time of the year.

Needle length is significantly greater at the inland Del Mar site than at the other two, again reflecting the favorable growing conditions there. The only significant difference between windward and leeward branches occurs on the island, where, not unexpectedly, the needles on the leeward branches are longer.

Each of the three characters considered above reflects a different aspect of the environment of the three sites, but certainly does not provide evidence of genetic difference between the mainland and island pine populations. The remaining characters, however, show a different pattern.

The needle color in both mainland sites, from leeward or windward branches, is a fairly consistent yellowish-green. On the other hand, all branches from the island trees bear needles of a distinctive bluish-green color. This difference would seem almost certainly to be genetically based, for two reasons: the uniformity of needle color in the two ecologically different but adjacent mainland sites, and the known general tendency of pine species or races to retain any differences in needle color when planted together at the same site (Weidman, 1939).

Cone size, since it depends directly on growth, is undoubtedly modified to some degree by the environment. Individual trees, for example, produce larger cones during favorable years than during unfavorable ones. This kind of environmental influence is probably indicated by the relatively large cones at the inland Del Mar locality as compared with those from the more severe seaward site. However, unlike the other size characters, cone size is significantly greater on the island than inland at Del Mar (fig. 1), thus suggesting that the difference in size between the mainland and island cones is based at least in part on a genetic difference. In other species of the genus *Pinus* the genetic basis of cone size has been clearly demonstrated. For example, the Rocky Mountain race of *P. ponderosa* produces relatively small cones both in its native habitat and when planted in the more moist, mild environment at the Institute of Forest Genetics in Placerville, California. The Californian race, however, produces rela-

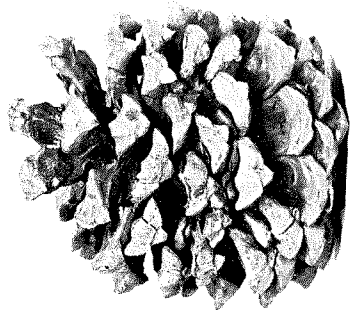
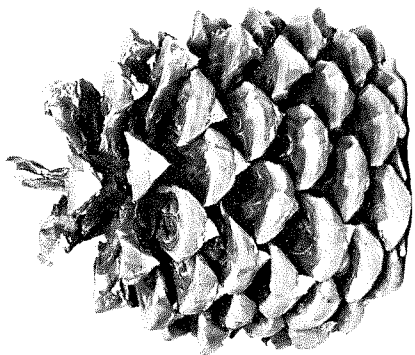
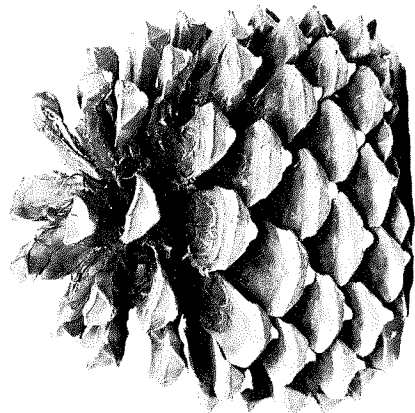


Fig. 1. Typical female cones from three samples of Torrey pine, $\times 2/5$. Left, Del Mar, seaward slope; center, Del Mar, inland slope; right, Santa Rosa Island. Note large diameter of island cone relative to its height.

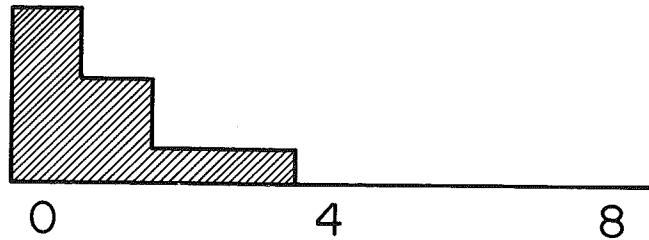
tively large cones at the Institute of Forest Genetics as well as in most other parts of the state (Haller, 1962, unpublished).

The final two characters considered are ratios involving several features of the cone that are independent of size and are no doubt largely genetically determined. Both show the island population to be significantly distinct from the two mainland samples, which resemble each other closely. The cones on the island are broader in relation to their length and have more pronounced projections on the ends of their scales than those from the mainland population (fig. 1).

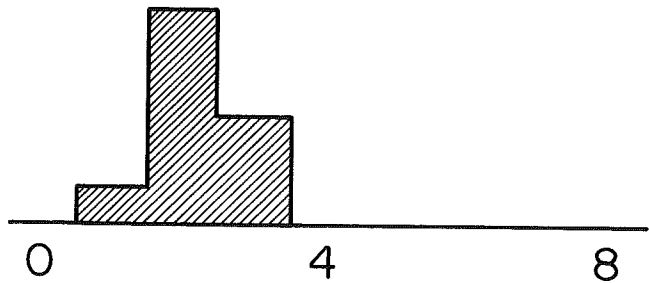
Summarizing the morphological comparisons, at least four characters, presumably genetically determined, show significant statistical differences between the island and mainland populations. However, all of these characters except needle color show considerable overlap between the two localities, and the impression received from any single character is that the two populations are not very distinct. But a different picture emerges if the last four characters in fig. 1 are combined into a simple hybrid index, and the total index score of every individual is plotted into a histogram (fig. 2). The two mainland samples overlap almost completely, and differ by little more than one point in average index score. The island sample, on the other hand, is completely distinct from both mainland samples, and differs by an average of five points from the inland Del Mar sample and by six points from the seaward sample.

After the survey of the two native stands was completed, it was called to my attention by Professor Carl Hubbs that an experimental planting of mainland and island Torrey pines had been made some years ago at the U.S. Department of Agriculture station near La Jolla, just two miles from the native Del Mar stand. When this site was visited, about 20 trees from each of the two native stands were found growing in contiguous plots. The tallest trees were about 50 feet high, and most of them had been producing cones for a number of years. Ten trees were sampled from each of the two groups. The data from these samples tend to confirm the overall impression obtained from the natural stands, although most of the individual characters behave somewhat differently than their counterparts in the wild. For example, the proportion of three and four needle fascicles was lower, and the needles were significantly shorter, in the planted trees from Santa Rosa Island than in the adjacent planting of mainland trees. This agrees with the data from the natural populations but also suggests a genetic difference that could not have been assumed from the original data. Another apparent genetic difference between the two planted stands that could not have been predicted was that the mainland trees tended to grow taller and showed a more definite single trunk than the bushier, more freely branched island

DEL MAR (SEAWARD) $\bar{X}=0.8$



DEL MAR (INLAND) $\bar{X}=2.2$



SANTA ROSA ISLAND $\bar{X}=7.0$

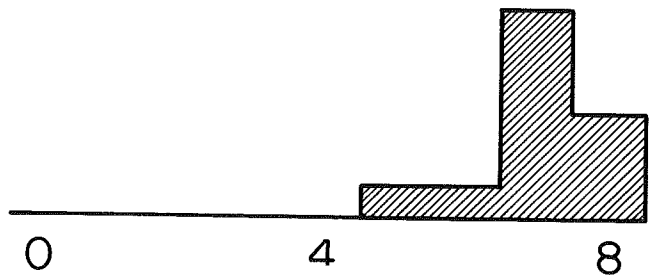


Fig. 2. Three samples of Torrey pine, scored with a hybrid index. Individuals with yellow-green needles, small, relatively elongated cones, and non-projecting apophyses are shown toward the left. Individuals with bluish-green needles, large, relatively broad cones, and projecting apophyses are shown toward the right.

trees. On the other hand, needle color and cone size failed to show as much difference between the two planted stands as between the natural populations. Cone length/width ratio was equally distinctive in both planted and natural stands. The lack of clear-cut differences between the planted mainland and island trees in respect to a few characters that were distinctive in the wild does not eliminate the possibility that these differences have a genetic basis. The highly unnatural situation of the experimental planting and the relative immaturity of the planted trees could easily cause the masking of subtly expressed genetic differences. It should also be noted that a few of the trees in the plantation could not be positively identified as to whether they originated from the mainland or island population, thus all of the summarized data from the experimental planting may be slightly erroneous.

The genetic distinctness of the mainland and island populations is hardly surprising in view of their geographic isolation and differing ecological conditions. Moreover, it is unnecessary to ascribe any special significance to the fact that one of the populations is on an island. Populations can be equally isolated and distinct from one another on the mainland. For example, the Monterey Peninsula and Cambria populations of *Pinus radiata* are about 80 miles apart, and show cone differences comparable with those in the two populations of *P. torreyana* (Forde, 1964). Even essentially continuous populations of plants or animals may show significant differences from one region to another, so that isolation in the sense of discrete populations may not be necessary to account for the differences between the two stands of Torrey pine.

It seems likely that the island population may represent the older of the two forms of Torrey pine, which has persisted through time with fewer changes than the mainland population, because of the greater similarity of the moist island climate to the still more mesic climate of California's past. There is no indication of this from the fossil record since there are no known fossils of Torrey pine, unlike the ecologically related "closed-cone pines". Whether it is more "primitive" or not, the island population, if left undisturbed, may outlast the one on the mainland, which is currently suffering from the combined intrusions of drought, insects, chaparral and *Homo sapiens*.

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DISCUSSION OF RELICTUAL AND DIVERGENT EVOLUTION

Dr. F. Harlan Lewis: As a basis for discussion, I would like to pose a question which is of particular interest to some of us. What changes have occurred in the island flora since it has been separated from the mainland — other than the fact that the goats have eaten a good deal of it? Dr. Haller has suggested, for example, that some of the characters that differentiate island and mainland populations of Torrey pine represent divergence on the island. This is what we have come to expect; when a population is separated on an island it ought to change. But I question this generalization.

Consider the differences between northern and southern populations of *Pinus muricata* on the mainland. If these populations can differ without one of them being on an island, I see no reason to assume that divergence on an island is the explanation for differences such as those between the Torrey pine populations. The island distribution may be irrelevant to the fact that they are different; perhaps the difference is older than the island. Do we have evidence that there has been divergence of the plants on the islands since they became separated from the mainland?

Dr. J. R. Haller: Divergence had to occur sometime.

Dr. Lewis: Of course, but if the divergence is not associated with the island, there is unlimited time for the occurrence of this divergence. It could be associated with any difference in environment during the Tertiary; and if you need to, you can go back even further. One of the reasons for studying islands, presumably, is to determine what happens to populations on an island that would not happen otherwise. Divergence apparently is not necessarily an island phenomenon.

Dr. Robert F. Thorne: Dr. Carlquist has recently written a book, *Island Life*, which we will all know about shortly, and also has two papers, I believe, in press now. One is on loss of dispersibility among island plants and animals and the other on loss of in-breeding (i.e., obligate cross-pollination from an increase in dioecism). I think he has some very pertinent things to say about divergence of island populations from their mainland relatives.

Dr. Lewis: I was not thinking of the floras of oceanic islands that have considerable age. I have no doubt that divergence has occurred in the Hawaiian Islands.