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ALTITUDINAL ECOTYPES IN HAWAIIAN METROSIDEROS

Carolyn A. Corn and William M. Hiesey

Department of Botany
University of Hawaii
Honolulu, Hawaii

ISLAND ECOSYSTEMS IRP

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ABSTRACT

Hawaiian *Metrosideros* distribution extends from tropical to cool-temperature climates throughout the six major islands of the Hawaiian Island chain. It forms a highly polymorphic complex that occurs in a continuous distribution over areas with average annual rainfalls ranging from 30 to 450 inches and at elevations from sea-level to 8500 feet, and in diverse pedological and topographical habitats. All of these plants are probably derived from one or a very small number of ancestral introductions that arrived within the last 20 million years by long-distance dispersal.

Seeds collected from diverse altitudinal sites on the islands of Hawaii and Maui and grown under uniform greenhouse conditions show evidence of ecotypic differentiation along altitudinal gradients. The seedlings, although from islands separated by 50 miles of ocean, show a parallelism in their altitudinal intra-population variation that strongly overlaps from site to site.

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INTRODUCTION

In the Hawaiian Islands the most prevalent native tree is a polymorphic taxon with ill-defined taxonomic boundaries, referred to here as the *Metrosideros polymorpha* complex. From herbarium evidence at the Bishop Museum it appears that the taxon prior to this century occurred from sea-level on wetter slopes up to 8500 feet elevation in a broad continuous distribution over the six largest islands in areas with an annual average rainfall ranging from 30 to 450 inches. Although *Metrosideros* is successful in disturbed habitats such as recent lava flows and landslides, it rarely prospers in areas markedly disturbed by man. Within the last 200 years since Captain Cook's arrival the taxon's extensive range appears to be receding most rapidly where there has been extensive animal grazing and biotic competition from introduced plant species.

The *M. polymorpha* complex is variable in every discernable character. Where the group colonizes open lava flows, it occurs as a tree or shrub; in wet fern forests with deep ash soil, it is found as a tree 70 feet or more tall. On exposed ridges it becomes a small tree or shrub; and in bogs it occurs as a prostrate shrub flowering when less than 8 inches tall. It appears to be most variable at mid-elevations, 1000 to 4000 feet, on a weathered substrate.

The genus *Metrosideros* is also distributed on other oceanic high islands of the Pacific Ocean, including Samoa, Fiji, Tahiti, and the Marquesas, with the largest number of species located in New Zealand. Since species from other oceanic islands appear to be closely related to Hawaiian material and the Hawaiian Islands are volcanic and less than 20 million years of age (Stearns, 1967) with no apparent relic forms to be found, living or fossilized, members of the genus are assumed to have migrated to the island chain by long-distance dispersal. Fosberg (1948) calculated that the present total native angiosperm flora of Hawaii could have been derived from only 272 immigrants leaving many niches unfilled

(Carlquist, 1970).

Metrosideros seeds were probably carried to the islands by wind, although floatation by sea cannot be entirely discounted (Corn, 1972). How many times material has arrived and successfully established itself in the Hawaiian Islands is unknown, but the probability of many introductions is small. The single or few early ancestors upon establishment apparently radiated to new habitats among the numerous edaphic, climatic and topographic niches available in the islands. Isolation of local populations now exists in the form of (1) oceanic barriers between the islands; (2) topographic differences caused by erosion of the land on the older islands, in the form of dissected cliffs and valleys; and (3) kipukas (islands of vegetation surrounded by new lava flows) on the newer islands with active volcanism. The separation and subsequent rejoining of populations appear to be currently taking place, with apparent hybrids between such populations.

The extreme polymorphism of the Hawaiian _Metrosideros_ has long attracted the interest of biologists, and the classification of the many forms has been and still is in a state of confusion (Hillebrand, 1888; Rock, 1917; Skottsberg, 1944). It is evident that an experimental biosystematic approach is needed to clarify the relations between its diverse components. Since the Hawaiian _Metrosideros polymorpha_ complex is distributed over a wide altitudinal range, and in areas differing appreciably in rainfall and in soil substrate, a basic question that arises is: do genetically differentiated races or ecotypes occur in contrasting environments? If so, do populations on separate islands in similar habitats have similar ecotypes?

Several difficulties in establishing a clear answer to these basic questions arise. There is striking individual variability among members of any population growing together within a given area. A problem arises when one tries to distinguish how much of each variation is due to phenotypic modifications and how much is contributed by inherited, genotypic differences. The highly variable topographic and edaphic discontinuities within short distances so characteristic of Hawaii result in a multitude of micro-climatic niches over which the populations are distributed and further accentuate the problem of separating the environmental and genetic components of variation, thus tending to obscure the broader over-all trends of variation across major climatic gradients.

The present study is concerned primarily with the comparative growth responses and morphological characteristics of population samples of Metrosideros polymorpha across altitudinal transects on Mauna Loa, Hawaii, and on Maui, when grown in the same environment. Three major climatic gradients exist in Hawaii : one is with reference to altitude; another is with respect to precipitation patterns which in turn, are determined primarily by topographic features in relation to the trade winds; and finally, with respect to slope or wind exposure. The first two of the above climatic gradients relate especially to the sample populations used in this study area, with the third climatic variable, wind exposure, becoming prominent only at one site, on a dissected ridge in western Maui.

METHODS

Seeds were harvested from mature trees (8 to 15 trees/locality) in natural habitats along two altitudinal transects; the first extended from 200 feet to 8300 feet elevation on the slopes of Mauna Loa, Hawaii, and the second, from 750 to 6600 feet on Maui. Seed samples from thirteen sites were sown in August 1970, and grown under uniform conditions in a greenhouse at the University of Hawaii at Honolulu at 200 feet elevation. Photographs and measurements of the seedlings were made in July 1972.

The seeds were germinated in 5-inch plastic pots on a mixture of equal parts of shredded tree fern, peat moss, and top soil, and were kept under 100 percent humidity at 28°C and 24 hour light at 200 foot-candles until the seedlings were one inch tall. They were then grown under mist and 30 percent shade cloth at temperatures ranging from 16°C to 35°C until they became root bound, approximately 10 months later. They were then repotted in larger pots and placed under natural day light on a greenhouse bench where temperatures ranged from 16°C to 40°C, with relative humidity averaging 60 percent. Day lengths varied from 10 hours 50 minutes to 13 hours 20 minutes. The plants were watered uniformly every two days.

MATERIALS

Figures 1 and 2 show the site localities and elevations from which the seeds were collected. Tables 1 and 2 list pertinent climatic, soil, and biotic data for each of the sites indicated in Figures 1 and 2. Most of the sites of the Mauna Loa, Hawaii, series are on recent lava flows, either pahoehoe or aa, with some flows occurring within the last 200 years. Many of these flows do not have any soil accumulation evident, since *Metrosideros* germinates and grows on the fresh lava. In contrast, the series of Maui sites are on older weathered lava soils. The sites M-1 and M-2 are on laterite soils with very little humus, while at the M-3 site the substrate is composed of a deep ash soil that is high in organic content.

Average annual rainfall on Mauna Loa, Hawaii, is highest at the middle elevations, 2500 to 4000 feet, with a decrease of rainfall above this altitude. On Maui, sites 1 and 2 recieve higher amounts of rainfall than site 3. Associated species found at each site reflect these climatic differences.

Annual average temperatures decrease with elevation, as shown in Tables 1 and 2. In sites where weather data are not available, temperature is computed from the lapse rate of -1.7°Centigrade per thousand feet elevation.

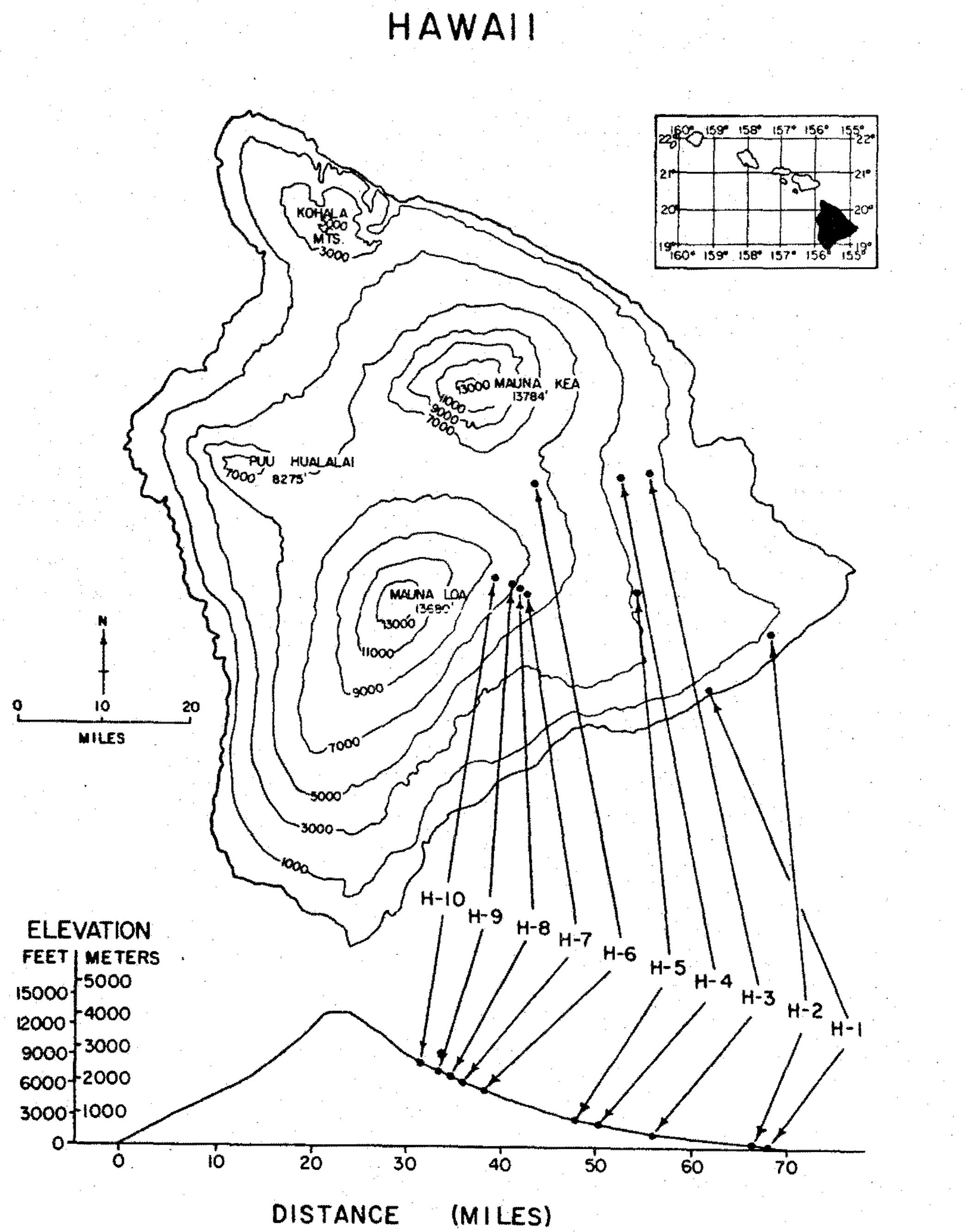


FIG. 1. Location and elevation of the Metrosideros seed sampling sites, H-1 to H-10, on the Island of Hawaii. See also TABLE 1.

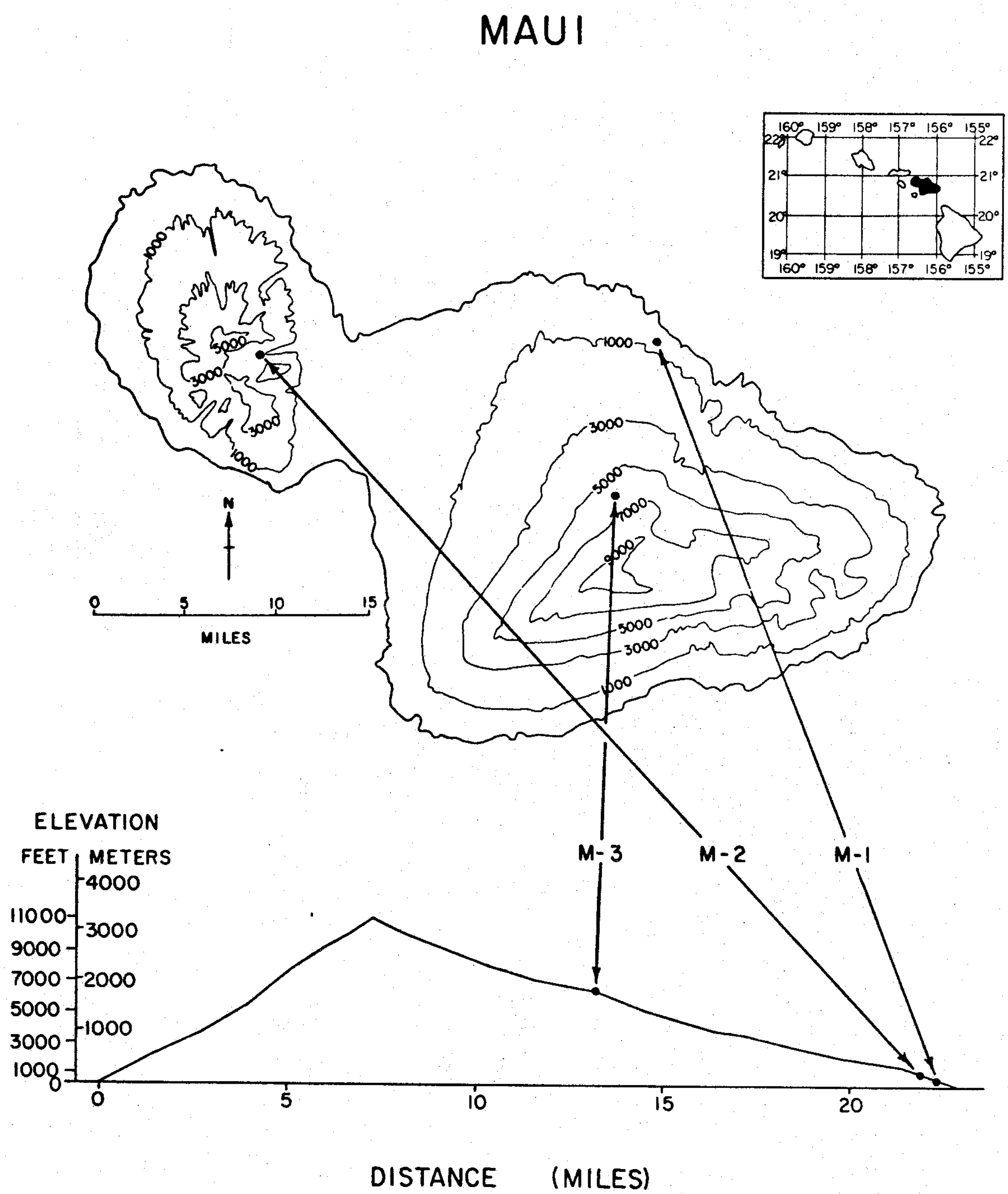


FIG. 2. Location and elevation of the Metrosideros seed sampling sites, M-1 to M-3, on the Island of Maui. See also TABLE 2.

TABLE 1. Description of sites of seed collections of *Metrosideros* at different elevations on the Island of Hawaii. See also Figure 1.

Site No.	Elevation Ft	Elevation M	Approximate Mean Annual Temperature °F	Approximate Mean Annual Temperature °C	Approximate Mean Annual Rainfall In	Approximate Mean Annual Rainfall Mm	Soil Type	Major Plant Associates*
H-1	200	61	74	23.3	40	1016	Pahoehoe lava, undated flow	Some *Sida fallax*
H-2	750	229	72	22.2	90	2286	Aa lava, 1955 flow	*Nephrolepis exaltata*, *Arundina bambusaefolia*, *Spathoglottis plicata*, *Stereocaulon vulcani*
H-3	1500	457	69	20.6	250	6350	Aa lava, 1880 flow	*Tibouchina urvilleana*, *Dicranopteris linearis*, *Machaerina angustifolia*, *Arundina bambusaefolia*
H-4	2500	762	65	18.3	250	6350	Aa lava, 1855 flow	*Dicranopteris linearis*, *Sadleria cyatheoides*, *Machaerina angustifolia*, *Polypodium pellucidum*
H-5	2900	884	64	17.8	130	3302	Aa lava, 1855 flow	*Dicranopteris linearis*, *Sadleria cyatheoides*, *Machaerina angustifolia*, *Lycopodium cernuum*
H-6	5500	1677	58	14.4	90	2286	Aa lava, 1855 flow	*Styphelia tameiameiae*, *Coprosma ernodeoides*, *Sadleria cyatheoides*, *Polypodium pellucidum*, *Stereocaulon vulcani*
H-7	6600	2012	55	12.8	40	1016	Weathered pahoehoe lava	*Acacia koa*, *Styphelia* sp., *Dodonaea viscosa*, *Pteridium aquilinum*, *Vaccinium reticulatum*, *Coprosma ernodeoides*, *C. montana*

TABLE 1 Concluded.

Site No.	Elevation Ft	Elevation M	Approximate Mean Annual Temperature °F	Approximate Mean Annual Temperature °C	Approximate Mean Annual Rainfall In	Approximate Mean Annual Rainfall Mm	Soil Type	Major Plant Associates*
H-8	6900	2104	54	12.2	40	1016	Aa lava, undated flow	*Sophora chrysophylla*, *Coprosma montana*, *Geranium cuneatum* var. *hypoleucum*, *Pteridium aquilinum*, *Dodonaea viscosa*, *Vaccinium pelearium*, *Styphelia douglasii*
H-9	7500	2287	52	11.1	40	1016	Aa lava, undated flow	*Sophora chrysophylla*, *Coprosma montana*, *Dubautia scabra*, *Pteridium aquilinum*, *Asplenium adiantum-nigrum*
H-10	8300	2530	50	10.0	35	889	Aa lava, undated flow	*Coprosma montana*, *Styphelia douglasii*, *Vaccinium reticulatum*, *Argyroxiphium sandwicense*, *Dodonaea viscosa*, *Agrostis sandwichensis*

* further descriptions of H-1, H-2, H-7, H-8, H-9, and H-10 sites are described by Doty and Mueller-Dombois (1966).

TABLE 2. Description of sites of seed collections of *Metrosideros* on the Island of Maui. See also Figure 2.

Site No.	Elevation Ft	Elevation M	Approximate Mean Annual Temperature °F	Approximate Mean Annual Temperature °C	Approximate Mean Annual Rainfall In	Approximate Mean Annual Rainfall Cm	Soil Type	Major Plant Associates
M-1	750	229	73	22.8	160	4064	red laterite	*Acacia koa*, *Psidium guajava*, *Cibotium* sp., *Polypodium pellucidum*, *Dicranopteris linearis*, *Pityrogramma calomelanos*, *Sphenomeris chusana*
M-2	1100	335	71	21.7	130	3302	red laterite	*Psidium guajava*, *Psilotum nudum*, *Styphelia tameiameiae*, *Sphenomeris chinensis*, *Setaria geniculata*, *Lantana camara*, *Cordyline* sp.
M-3	6600	2012	55	12.8	90	2286	dark brown ash soil with high organic content	*Sophora chrysophylla*, *Vaccinium reticulatum*, *Coprosma montana*, *Styphelia tameiameiae*, *Sadleria cyatheoides*, *Dicranopteris linearis*, *Agrostis* sp.

RESULTS

At the end of the 23-month growth period the seedlings displayed wide variation in their growth and physiological characteristics. Table 3 lists the variation in plant characteristics for 20 individual seedlings from four parent trees at the H-4 site. The population means and standard deviations of the sampled individuals are listed at the bottom of the table. These correspond to the mean value of the populations listed in Tables 4 and 5.

A linear regression analysis between the elevation of collection sites and the plant characters listed in Tables 4 and 5 result in significant correlation coefficients. Significant at the 1% level are plant height, plant width, mature leaf length and width. Internode length is significant at the 6% level. No significant correlation ($P = 0.05$) is obtained between elevation and leaf thickness, pubescence, or amount of anthocyanin present in the leaves and petioles.

Developmental changes occur as a seedling acquires its adult form, including changes in leaf size, internode length, leaf pubescence and thickness. Some seedlings begin to express these characteristics when only nine months old and 15 centimeters tall, while others at 23 months after germination are just developing some of these features. Possibly some plants may acquire added characteristics with a further increase of size and age. Adult plants from the same localities may therefore show correlations between characteristics with elevation that are not apparent in the seedlings.

Figure 3 (bottom graphs) indicate the seedling plant heights and leaf sizes as they vary with elevation. Variation within the populations overlaps with neighboring populations, but the populations from extreme elevations, such as H-2 and H-10, have no overlap in their characteristics. Figure 4 (bottom row) illustrates seedlings from 5 of the 10 different elevations sampled along the

TABLE 3. Individual variation among seedlings from site H-4 on the Mauna Loa Transect grown under uniform greenhouse conditions at Honolulu.

Seedling No.	Plant: Height (cm)	Plant: Width (cm)	Plant: Growth Habit	Mature Leaf: Length (mm)[1]	Mature Leaf: Width (mm)[1]	Mature Leaf: Thickness (mm)[1]	Mature Leaf: Pubescence[3]	Mature Leaf: Color	Anthocyanin[4]	Length of Internodes (mm)[1]
1	30	18	erect	43	30	0.20	0	med.	1	21
2	30	23	semi-erect	47	29	0.20	++	med.	1	14
3	47	13	erect	52	30	0.20	+	med.	2	22
4	35	23	semi-erect	36	24	0.17	+	med.	1	21
5	30	13	erect	47	26	0.23	+	med.	2	17
6	31	22	semi-erect	47	29	0.20	0	med.	2	13
7	39	15	semi-erect	36	22	0.23	+	med.	2	14
8	39	5	erect	55	39	0.37	0	med.	1	21
9	34	9	erect	38	26	0.23	0	med.	1	13
10	25	16	erect	43	24	0.23	0	med.	2	13
11	30	18	semi-erect	43	27	0.27	0	med.	1	18
12	30	19	semi-erect	41	24	0.17	0	med.	1	17
13	55	35	semi-erect	53	35	0.23	0	med.	2	24
14	30	10	erect	36	25	0.20	0	med.	2	24
15	29	13	erect	35	20	0.20	0	med.	1	17
16	35	14	erect	50	33	0.27	0	med.	1	23
17	45	28	erect	49	31	0.23	0	med.	1	24
18	44	18	erect	46	32	0.27	0	med.	2	26
19	26	5	erect	48	29	0.23	0	med.	1	20
20	34	5	erect	52	33	0.20	+	med.	1	19
Average	34.9 ± 7.8	16.1 ± 7.7	erect	44.8 ± 6.3	28.4 ± 4.7	0.23 ± 0.04	0(70)[2]	med.	1(60)[2]	19.0 ± 4.2

[1] each value a mean measurement of 3 mature leaves or internodes
[2] number in parenthesis is the percent of seedlings having that characteristic
[3] 0 = no pubescence; + = some pubescence; ++ = very pubescent
[4] 1 = little or none; 2 = some; 3 = abundant

TABLE 4. Growth responses and description of *Metrosideros* seedlings originating from different altitudes on the Island of Hawaii after 23 month's growth under uniform greenhouse conditions at Honolulu. See also Figures 4 and 5.

			Plant			Mature Leaf						Mean length of Internode (mm)
Site No.	No. of Plants	Elevation (ft)	Mean Height (cm)	Mean Width (cm)	Growth Habit	Mean Length (mm)	Mean Width (mm)	Mean Thickness (mm)	Pubescence[1]	Color[2]	Anthrocyanin[3]	
H-1	2	200	48	36	semi-erect	40	28	0.26	+(100)[4]	+(100)[4]	1(100)[4]	18.8
H-2	27	750	41.7±7.8	19.6±7.1	erect	41.8±5.1	23.0±3.5	0.19±0.05	+(89)	+(96)	2(59)	18.7±5.5
H-3	12	1500	28.3±7.0	13.9±7.7	erect	42.1±5.0	22.8±3.2	0.22±0.03	+(50)	+(100)	1(58)	17.0±1.9
H-4	20	2500	34.9±7.8	16.1±7.7	erect	44.8±6.3	28.4±4.7	0.23±0.04	o(70)	+(100)	1(60)	19.0±4.2
H-5	12	2900	30.5±5.4	13.7±6.3	erect	33.1±12.1	21.6±4.9	0.24±0.04	+(83)	+(100)	1(50)	18.8±5.4
H-6	20	5500	23.0±6.1	7.4±4.2	erect	21.8±3.9	16.0±4.2	0.23±0.04	+(80)	+/++ (55/45)	1(75)	14.1±3.8
H-7	20	6600	29.6±6.4	11.6±10.3	erect	23.7±3.9	18.0±3.0	0.27±0.05	+(45) (30/70)	+/++ (30/70)	2(50)	18.6±4.1
H-8	20	6900	20.6±4.0	6.1±2.3	erect	19.2±3.2	12.8±2.5	0.28±0.07	+(85)	++(100)	2(50)	17.2±3.6
H-9	12	7500	19.4±3.6	5.6±2.2	erect	16.2±2.4	10.8±1.8	0.23±0.06	+(83)	++(100)	1(58)	15.1±2.4
H-10	8	8300	14.4±6.7	4.6±2.2	erect	15.1±1.6	9.8±1.7	0.18±0.03	+(62)	++(100)	1(88)	12.8±2.6

[1] Dominant character/population. Range: o = no pubescence; + = some pubescence; ++ = very pubescent.
[2] Dominant character/population. Range: o = light green; + = medium green; ++ = dark green.
[3] Dominant character/population. Range: 1 = little or none; 2 = some; 3 = abundant.
[4] Percent of plants with characteristic

TABLE 5. Growth responses and description of Metrosideros seedlings originating at different altitudes on the Island of Maui after 23 month's growth under uniform greenhouse conditions at Honolulu. See also Figures 4 and 5.

			Plant			Mature Leaf						
Site No.	No. of Plants	Elevation (ft)	Mean Height (cm)	Mean Width (cm)	Growth Habit	Mean Length (mm)	Mean Width (mm)	Mean Thickness (mm)	Pubescence[1]	Color[2]	Anthrocyanin[3]	Mean length of Internode (mm)
M-1	20	750	18.8±10.2	26.0±13.0	erect	58.6±7.6	31.4±5.4	0.17±0.04	+(60)[4]	o/+[4] (50/50)	1(60)[4]	26.8±3.2
M-2	20	1100	35.1±9.6	23.0±13.8	semi-erect	36.4±4.5	21.1±2.8	0.12±0.04	o(75)	+(95)	1(55)	17.4±4.8
M-3	10	6600	17.2±3.2	7.9±4.5	erect	19.0±3.2	13.2±2.0	0.22±0.03	+(80)	++(100)	1/2 (40/40)	12.9±3.3

1 Dominant character/population. Range: o = no pubescence; + = some pubescence; ++ = very pubescent.
2 Dominant character/population. Range: o = light green; + = medium green; ++ = dark green.
3 Dominant character/population. Range: 1 = little or none; 2 = some; 3 = abundant.
4 Percent of plants with characteristic.

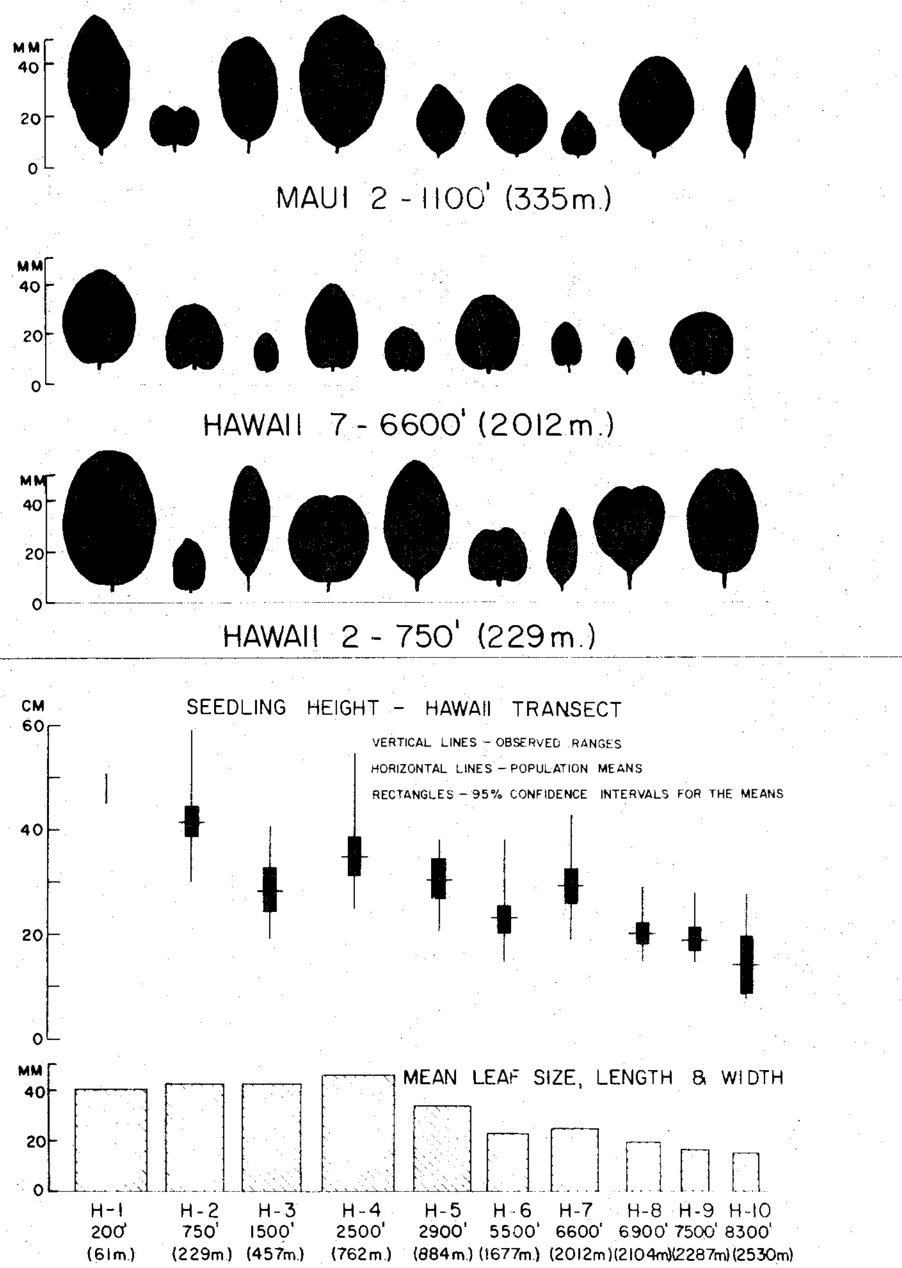


FIG. 3. Above: Outlines of leaves showing typical variation in size and shape among seedlings originating at three different sites, H-2, H-7, and M-2.
Below: Graphs showing mean dimensions of leaves and plant heights of 23 month-old seedlings of Metrosideros originating from different conditions at Honolulu. See also TABLE 4.

FIG. 4. Seedling plants of *Metrosideros* originating from sites at different altitudes on the Islands of Hawaii (Below) and Maui (Above). All plants are 23 months old and were grown under uniform greenhouse conditions in Honolulu. Photographs are reproduced at the same scale; elevations of origin are indicated in feet.


5 CM M-1 750
5 CM M-2 1100
5 CM M-3 6600


5 CM H-2 750
5 CM H-4 2500
5 CM H-6 5500
5 CM H-8 6900
5 CM H-10 8300

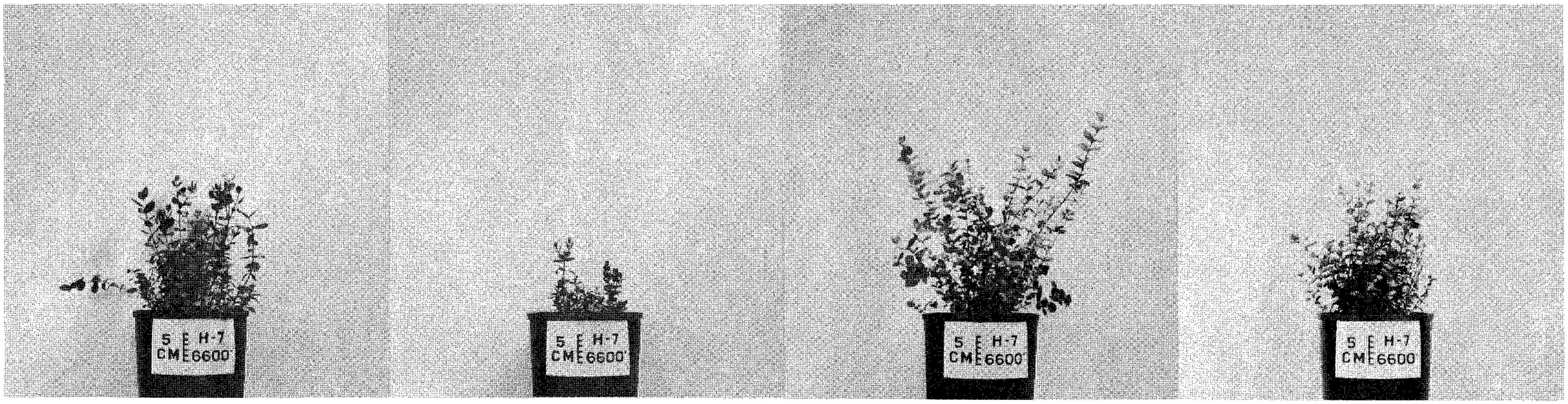
Mauna Loa transect. Differences are apparent in plant and leaf size. The plants along the Maui transect, shown in the top row of the same figure, show parallel differences in plant and leaf size. The leaves of plants along both transects become darker green with increased elevation (Tables 4 and 5).

A high degree of variation among individual seedlings at any one collection site is evident. Figure 5 illustrates the variation within a series of sample plants from two contrasting altitudinal sites on Hawaii that exemplifies the kind of intra-population variation generally found in Metrosideros. Figure 3 (center) illustrates the variation that can be found in leaves of the same two populations shown in Figure 5 along the Mauna Loa Transect, and also of another population(top row) from the M-2 Maui site. These outlines show typical differences in leaf size, petiole length, and leaf shape that are found among seedlings from any one locality.

Plants from the extreme low and high elevations are sufficiently distinct from each other in leaf color, leaf length, leaf width, and plant height so that there is little to no overlap in these characters. Seedlings from adjacent or intermediate altitudinal sites, however, do show a marked overlap.

The growth habit in mature Metrosideros may vary from prostrate to erect. Tables 4 and 5 indicate the average growth habit found among seedlings from each site. In two sites a high percentage of the progeny are semi-erect. The first is from a small sample of two plants within one-half mile of the ocean outside the salt spray zone (H-1). At the second site, on an exposed ridge in Maui (M-2), 70% of the seedlings are semi-erect. This site is the only one sampled that is located in an area of highly dissected topography exposed to strong winds, and its seedlings show the greatest diversity in form. This variability is reflected to some extent by the differences in leaves, shown in the upper part of Figure 3. The parent plants were low and shrubby, and it may be significant that a large percentage of their progeny tend to reflect this habit when grown in a greenhouse without exposure to winds. These observations suggest that growth habit may be determined largely by the genotype.

FIG. 5. Seedling plants of _Metrosideros_ showing intra-population variability at two sites on the Island of Hawaii : _below_, H-2, from 750 feet (227 meters) elevation; _above_, H-7, from 6600 feet (2000 meters). All plants grown under uniform greenhouse conditions. Photographs all reproduced at the same scale.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CM 6600'
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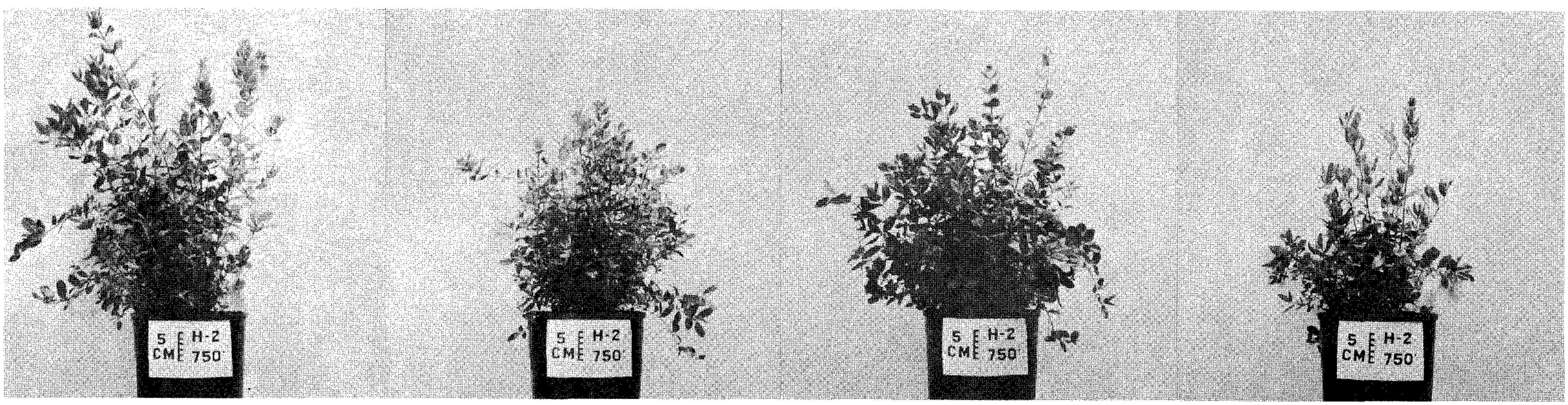
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5 H-2
CM 750'

DISCUSSION

The above data furnish evidence of the existence of genetically differentiated climatic races, or ecotypes, in a woody species on an oceanic island chain. The island of Hawaii is separated from Maui by 50 miles of ocean, and yet shows parallel changes in the composition of the native _Metrosideros_ populations with changes in altitude. Other environmental gradients such as precipitation and wind exposure probably also contribute to race formation through natural selection. For example, internode length, leaf pubescence and leaf size might possibly be correlated with rainfall patterns and the resultant effects on light intensities. Edaphic conditions most probably also exert an effect superimposed on the influence of altitude, resulting in the genetically heterogenous populations.

The altitudinal races, or ecotypes, in Hawaiian _Metrosideros_ appear to be essentially of the same nature as the ecotypes described by Turesson (1922). One major difference is in the highly overlapping individual variation found in _Metrosideros_ populations as contrasted with the relatively disjunct differentiation in the species described by Turesson. Natural selection in Hawaii may act quite differently from comparable continental areas for two reasons. First, the flora of a continental area is harmonic with many tree species competing for open habitats. In the disharmonic flora of Hawaii, _Metrosideros_ is a major tree without competition from any other, or very few, other tree species. Also no grazing animals are native to the environment that would have caused biotic competition and selection. Natural selection in Hawaii therefore may be governed primarily by physical factors, such as temperature, precipitation, wind, and soil, rather than by biotic selection. Second, in a maritime climate along the margin of a continental area, major climatic differences would normally require several degrees of latitude or hundreds of miles for large changes in rainfall and temperature to occur. In Hawaii these distances are telescoped into 25 to 50 miles from sea-level to 13,600 feet elevation. The average annual temperature varies 20° Centigrade between the base of Mauna Loa, Hawaii, and its summit 40 miles away. The rainfall varies from 20 inches at sea-level to more than 250 inches within 40 miles. Probably few other areas on earth combine such changes within such short distances, (cf. Britten, 1962). These strong selection pressures within small distances can be expected to exert important influences on natural selection of the vegetation present. The ubiquitous distribution of Metrosideros in large numbers with its high degree of genetic heterogeneity over the islands makes it an ideal object for studying the effects of natural selection pressures. The variation within populations of Metrosideros is probably considerably greater than that found in populations of Achillea by Clausen, Keck, and Hiesey (1948).

Variation in Metrosideros at each site overlaps with populations from sites at either higher or lower elevations, resulting in a cline across the altitudinal transects. Undoubtedly there is extensive outcrossing in this group, since the flowers are protandrous with sticky pollen that is transmitted by birds visiting the flowers for nectar.

A comparison of physiological characteristics of plants from contrasting altitudes is much needed and has been examined in an exploratory way. Seeds germinated from several altitudinal sites show differences in their abilities to survive freezing. Further studies under controlled conditions are contemplated.

ACKNOWLEDGEMENTS

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