Successional Trends in the Coastal and Lowland Forest of Mauna Loa and Kilauea Volcanoes, Hawaii[1]

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ABSTRACT: Three trends in forest succession are described from the coastal and lowland lava flows (<1,000 feet) of Mauna Loa and Kilauea in Hawaii. All begin on bare rock in a region of high rainfall (75 to 150 inches). One trend is in coastal forest and involves the replacement of *Metrosideros polymorpha* vegetation by *Pandanus tectorius* forest. The other trends occur inland and give rise to *Metrosideros polymorpha* and *Metrosideros polymorpha/Diospyros ferrea* forests within 400 years. No consistent differences in successional trends were observed between pahoehoe and aa flows. Seasonal distribution of rainfall was considered to be important in differentiating the *Metrosideros/Diospyros* succession, while exposure to wind-carried salt may differentiate the *Pandanus* succession. There is need to protect representative areas of these forests for future study.

THIS PAPER gives information on some of the successions occurring during the first 400 years of forest development on aa and pahoehoe flows of Mauna Loa and Kilauea. The earliest stages in successions on Hawaiian lava flows have been reasonably well documented (Forbes, 1912; MacCaughey, 1917; Robyns and Lamb, 1939; Skottsberg, 1941; Doty and Mueller-Dombois, 1966; Smathers, 1966; Doty, 1967), but little has been written about later stages, particularly in regions of high rainfall. The observations recorded here are concerned with coastal and lowland flows less than 1,000 feet in altitude.

DESCRIPTION OF AREA STUDIED

Location

The area studied (Fig. 1) covers parts of the lower slopes (0–1,000 feet) of both Mauna Loa (13,677 feet) and Kilauea (4,090 feet). It includes: (1) the eastern slopes of Mauna Loa that lie south and southeast of Hilo, and (2) the northern and southeastern slopes of the Puna rift zone of Kilauea within 9 miles of Pahoa.

Climate

Climatic data for the area have been given by Blumenstock and Price (1967). Mean annual temperatures vary from 73.1° F near sea level (Hilo airport) to 69.9° F at 1,000 feet, based on a temperature lapse rate of 3.5° F per thousand feet (Mr. Saul Price, U. S. Weather Bureau, personal communication). Near sea level, mean summer and mean winter temperatures are 74.8° and 71.4° F, respectively. At 1,000 feet, approximate mean summer and winter temperatures are 71.3° and 67.9° F. The mean variation between warmest (August) and coldest (February) months is between 5° and 6° F and probably never exceeds 9° F. The area is frost free.

At sea level, mean annual rainfall increases northward from about 75 inches near Kaimu to 136 inches at Hilo airport. Inland at 1,000 feet altitude, annual rainfall is more than 140 inches in the Puna rift region and more than 150 inches on Mauna Loa. Rainfall is rather unevenly distributed, with the wettest month, December or March, often receiving more than twice the rainfall of the driest month, June. In areas where monthly averages are all above 10 inches, there may be occasional months with only 1 or 2 inches of rain. Rainfall intensities in excess of 9 inches in 24 hours occur once every 2 or 3 years at most localities. (Blumenstock and Price, 1967). Average relative humidities are between 70 and 80 percent.

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The eastern slopes of Mauna Loa are exposed to the northeasterly trade winds which blow more than 70 percent of the time. Storms are infrequent.

Geology

The surficial lava flows of the area are either late Pleistocene or Recent in age and include both pahoehoe and aa types of lava. Those

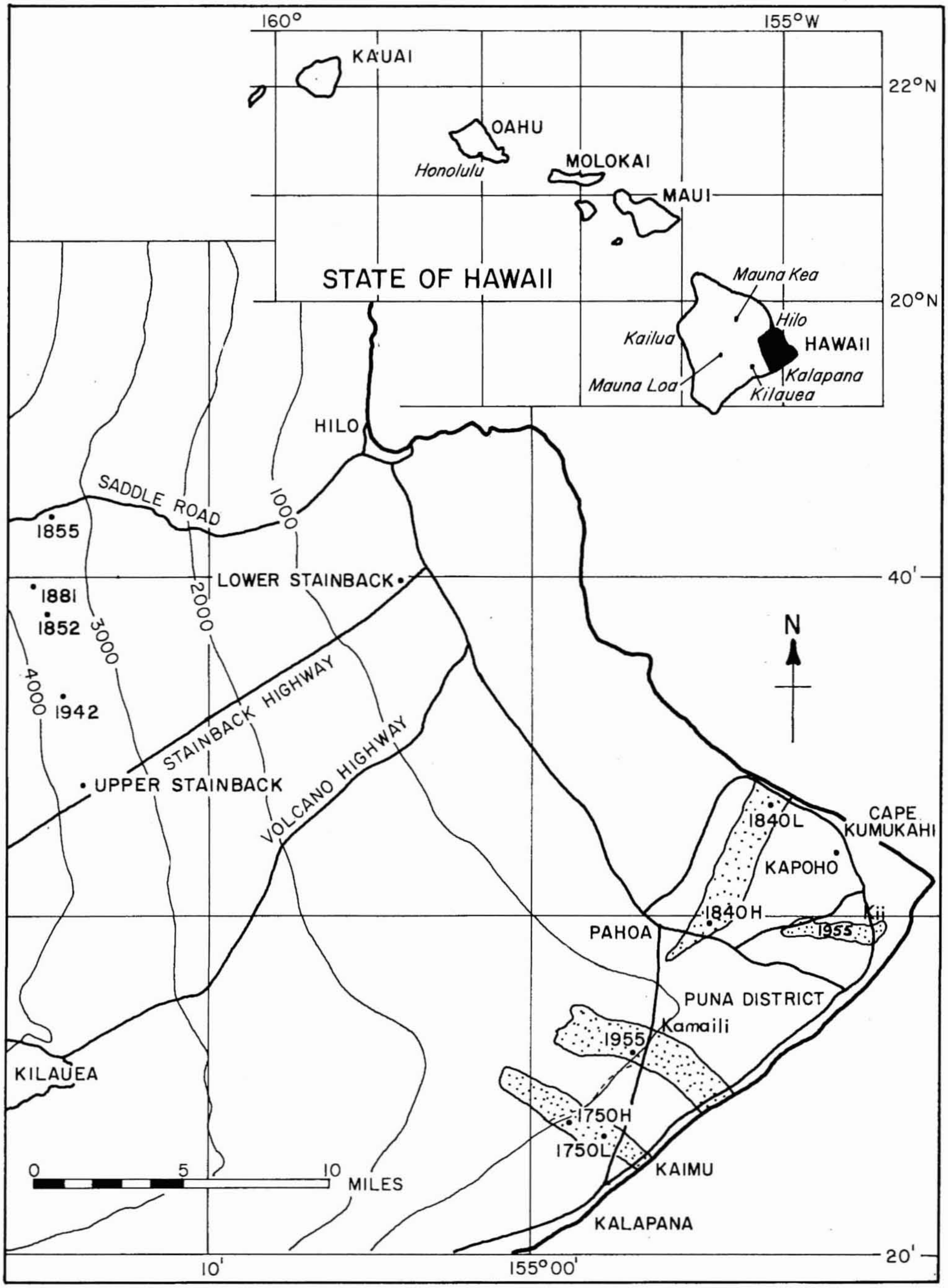

FIG. 1. Location of area studied and positions of sampling sites.

of Mauna Loa belong to the Kau Volcanic Series and those of Kilauea to the Puna Series (Stearns and Macdonald, 1946). The only dated flows in the study area are the 1750, 1840, and 1955 flows of Kilauea. All of these originated as flank eruptions from the Puna rift zone. The age of the flow tentatively dated as 1750 is uncertain, the only reference being that of Hitchcock (1911, p. 164) who gives the period 1730 to 1754 as the time of an eruption at Kaimu. The 1750 date used here, is that given on the geologic map of Hawaii (Stearns and Macdonald, 1946). All other flows in the region are prehistoric (i.e., earlier than 1750). Lavas of the area studied belong to the tholeiitic suite defined by Macdonald and Katsura (1962) and include olivine basalts, basalts, and oceanites (Macdonald and Katsura, 1964).

Patches of Pahala ash, dated from charcoal as last glacial (Rubin and Berthold, 1961), occur locally, but soils from this material are now largely under sugar cane. Pumice deposits, associated with cones and craters, cover small areas (Stearns and Macdonald, 1946), and historic eruptions of Mauna Loa and Kilauea have spread small amounts of ash and dust over wide areas of Hawaii Island (Wentworth, 1938). However, profile observations on the flows studied show that the contribution of ash to soil formation is small. Thus the successional trends described below are essentially those on ash-free lava.

Topography and Soils

Because of their youth, lava flows of the area are undissected and without permanent streams. Their highly permeable nature restricts surface water to small unfissured areas on a few pahoehoe flows. General slopes are long and gentle, averaging about 3° to 4° on Mauna Loa and 1° to 4° in the Puna rift region of Kilauea. The land surface is usually undulating except where broken by the more craggy surface of recent aa flows.

Soil development on the flows studied is restricted to a surficial layer of organic matter, 0 to 2 cm in depth, overlying weathering basalt. Depending on the age of the flow, some accumulation of organic matter and mineral particles has occurred in cracks between rocks. Cline (1955) mapped the soils of the later prehistoric and historic flows as lithosols. According to the U. S. Comprehensive Classification these soils are entisols and lithic folists in the order histosols (Soil Survey Staff, 1968).

Vegetation and Land Use

Forest dominated by *Metrosideros polymorpha* covered most of the study area in the past, but much of it has now been replaced by settlements and cultivated crops. A general description of the present vegetation of the area is given by Fosberg (1961). Doty and Mueller-Dombois (1966) described the *Metrosideros* forests on prehistoric flows adjacent to two flows of the 1955 Kilauea eruption: the Kii flow at 100 feet altitude and the Kamaili flow at 900 feet altitude (Fig. 1).

The vegetation pattern of the early 19th century can be inferred from surviving stands. A dense scrub of *Scaevola taccada* and *Hibiscus tiliaceus* grew along the shoreline. Behind this, *Pandanus tectorius* forest, up to 10 meters high, dominated the coastal fringe, and this changed with increasing distance from the coast to a *Pandanus-Metrosideros* forest that extended half a mile or more inland. Further from the sea, *Metrosideros* forest, up to 30 meters high, formed the main plant cover, its height and understorey composition varying with age. This general pattern would have been broken in places by clearings of the early Hawaiians, where a number of introduced plants such as coconut would have grown.

In the present vegetation of some prehistoric flows, the *Metrosideros* trees are smaller and more widely spaced on pahoehoe flows than they are on aa flows of similar age. Between the trees, and sometimes growing over them, are dense thickets of the fern *Dicranopteris linearis*. On very recent flows the whitish-colored lichen *Stereocaulon vulcani* is sometimes abundant and the only common tree seedling is *Metrosideros*. Introduced species are uncommon on such flows.

Land clearing, fires, and introduced animals, particularly pigs and cattle, have modified or destroyed the original vegetation in many places, allowing several introduced plants to become widespread. The most abundant are *Psidium guajava, Pluchea odorata,* and *Melastoma malabathricum.* In the Puna district, large areas of *Metrosideros/Dicranopteris* fernland have been burned, and the regrowth is dominated by grasses, particularly the introduced *Andropogon virginicus*. Also, plantations of coconut, papaya, banana, and coffee are growing here on recent lava flows. On late prehistoric flows of Mauna Loa, north of Olaa, additions of volcanic ash and fertilizers have made possible the establishment of a large macadamia nut farm.

METHODS

The flows sampled in this study were chosen during the course of an investigation into methods of aging lava-flow ecosystems (Atkinson, 1969). Sampling of the vegetation considered in this paper was restricted to seven sites on five flows of either late prehistoric or known age, and located at altitudes useful for the problem of determining ages. These sites are considered to be representative of the flows sampled. However, the trends discussed in this paper are based on observations made on many flows in addition to those sampled.

The exact position of each sampling site was determined by sighting across the general slope of the particular flow chosen to a distant object. Following this line, 50 paces were stepped off from the edge of the flow to clear the sample from conditions peculiar to the flow edge. The site was then checked to see if (1) its general slope was less than 10 percent (so that slope would be relatively constant throughout sampling), and (2) its surface and vegetation were representative of the flow in that area. If these conditions were not met, another 50 paces were traversed, and this procedure repeated if necessary until a suitable site was reached. In practice, no pacing repetitions were needed. At the point where pacing ended, a 100-meter line transect was oriented in the same direction, that is, across the general slope of the flow.

At each site, 10 or more trees within 2 meters of the line transect were measured for height (using abney level and eye estimates) and diameter at breast height (d.b.h.), that is, 1.4 meters above the ground. The stem diameter of trees less than 1.5 meters high was measured halfway up the stem. A tree volume index was obtained from the relationship: tree volume index = height × basal area where basal area $= \pi r^2$ and r = d.b.h./2.

The term *canopy* was used to denote the plant crowns that form the skyward surface of the vegetation and it was applied to all types of vegetation, for example, lichenfield, fernland, or forest. The percentage of ground area covered by the canopy (canopy cover) and the percentage covered by each species in the canopy were measured by recording the plants appearing vertically above 50 points spaced 2 meters apart along the 100-meter transect. For shorter vegetation, such as lichenfields, the 50 points were spaced at 60-cm intervals along a 30-meter transect.

The pteridophyte and spermatophyte species represented by three or more plants were listed for each site in an area of about 50 × 50 meters oriented parallel to the line transect (see Appendix).

Because of the variety of vegetation structure encountered on Hawaiian lava flows a convenient naming system is desirable. Terms such as forest, lichenfield, and rockland are used here according to whichever type of growth-form or ground material constituted the uppermost surface. The term *treeland,* rather than *forest,* is used for a tree-dominated vegetation if the canopy cover of trees was less than 80 percent. The type of forest or fernland is designated from the generic names of the major canopy species, that is, those with canopy cover equal to or greater than 20 percent. A slant line (/) between generic names indicates that the first species (e.g., *Metrosideros*) forms a separate stratum *above* the second species (e.g., *Dicranopteris*). When necessary, a hyphen is used to separate species in the same stratum. This naming system enables one to convey information on both composition and structure of the vegetation.

SUCCESSIONAL TRENDS

Three main trends in forest succession were recognized, all beginning on bare lava.

1. ROCKLAND → *Metrosideros* TREELAND → *Pandanus* FOREST

This succession occurs in a quarter-mile-wide coastal zone on pahoehoe and aa flows having more than 70 inches of annual rainfall. Ferns (*Nephrolepis* sp.) establish in cracks, and the

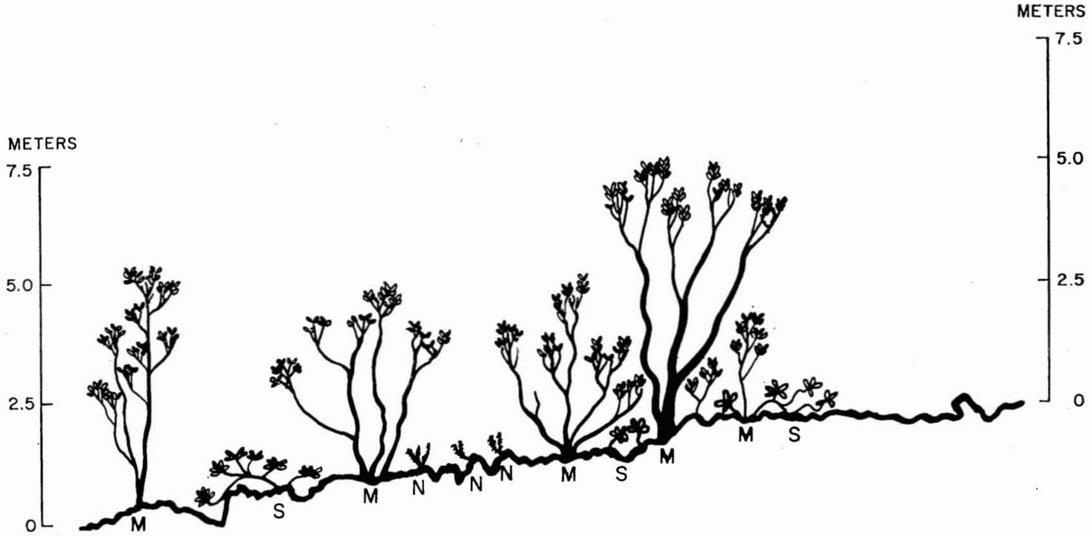

FIG. 2. Profile diagram of *Metrosideros* rockland on the 1840 aa flow of Kilauea (1840 L sampling site, 40 feet altitude). *M* = *Metrosideros polymorpha, N* = *Nephrolepis hirsutula, S* = *Scaevola taccada.*

lichen *Stereocaulon vulcani* enters on boulders within 5 years of flow formation. *Metrosideros polymorpha* is the pioneer tree species, appearing within 10 years, and a rockland with scattered trees develops as on the 1840 flow (Fig. 2). The height-class distribution of *Metrosideros* from this same site (Table 1) shows that young plants are still entering the community even after 120 years. *Pandanus tectorius* is absent from the 1840 and 1750 flows. Thus it must sometimes be more than 200 years before this species appears in the succession. However, on late prehistoric flows located between the 1750 flow and the 1960 Kapoho flow, juvenile *Pandanus* can be seen among the *Metrosideros* on sites which are apparently no different from the 1840 and 1750 flows, apart from their greater age (Fig. 3). On older prehistoric flows, both between and south of these flows, *Pandanus-Metrosideros* forest occurs. In advanced stages of the succession, *Metrosideros* apparently decreases and may disappear altogether, as for example on a prehistoric flow north of Kapoho (Fig. 4).

TABLE 1

HEIGHT-CLASS DISTRIBUTION OF *Metrosideros polymorpha* ON THE 1840 KILAUEA LAVA-FLOW AT 40 FEET ALTITUDE

HEIGHT CLASS (meters)	PERCENTAGE OF TOTAL*
0–1	13
1–2	16
2–3	13
3–4	20
4–5	16
>5	22

* Number of plants sampled = 45.

2. ROCKLAND → *Dicranopteris* FERNLAND → *Metrosideros/Dicranopteris* TREELAND→ *Metrosideros* FOREST

This is the most widespread trend of succession on aa and pahoehoe flows below 1,000 feet altitude. The earliest stages have been detailed by Doty and Mueller-Dombois (1966) and Doty (1967). Mats of *Stereocaulon* are sometimes prominent on young flows, particularly where the porosity of individual rocks is high. During intermediate stages of the succession, there is wide variation in the proportions of *Dicranopteris linearis* and *Metrosideros* forming the canopy, and all gradations from fernland to treeland can sometimes be found on the same flow.

Metrosideros seedlings are absent in the treeland, possibly because of the dense fern cover. Increase in *Metrosideros* cover appears to be taking place by lateral spread of crowns and resprouting from prostrate branches. Judged by

FIG. 3. Juvenile *Pandanus tectorius* growing in *Metrosideros* treeland on a late prehistoric aa lava flow south of Kapoho (50 feet altitude).

FIG. 4. Profile diagram of *Pandanus* forest on a prehistoric aa flow north of Kapoho (90 feet altitude). *A = Aleurites moluccana, An = Asplenium nidus, Mc = Morinda citrifolia, P = Pandanus tectorius, Pg = Psidium guajava.*

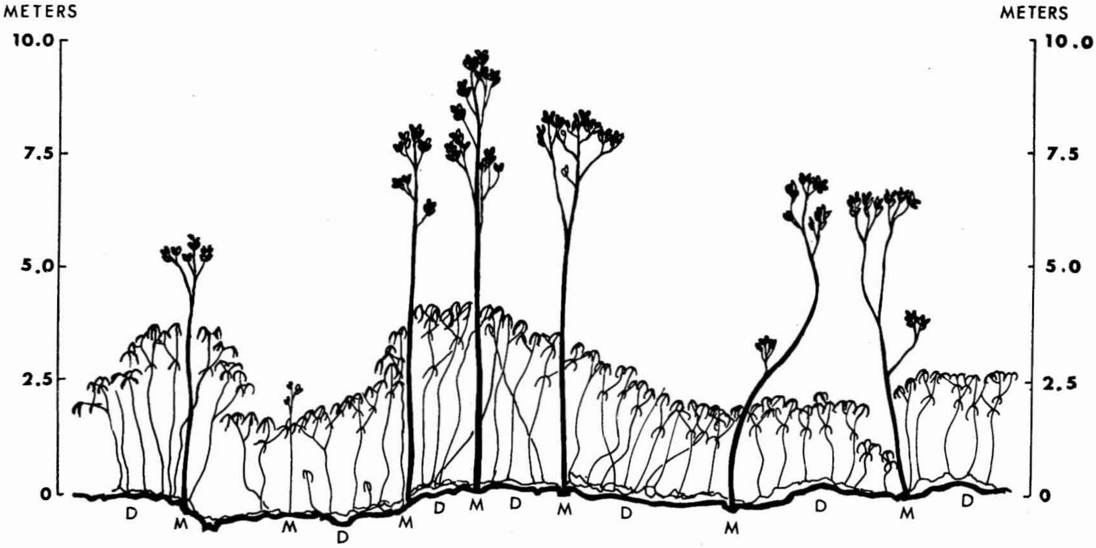

FIG. 5. Profile diagram of *Metrosideros/Dicranopteris* treeland on the 1840 aa flow of Kilauea (1840 H sampling site, 650 feet altitude. *D* = *Dicranopteris linearis, M* = *Metrosideros polymorpha.*

the vegetation of the upper half of the 1840 flow, the treeland stage of this succession can be reached within 120 years (Table 2 and Fig. 5). Replacement of the treeland by *Metrosideros* forest is inferred from the presence of *Metrosideros* stands on older aa flows nearby. However, there are extensive prehistoric pahoehoe flows in the Pahoa district which are still in the *Metrosideros/Dicranopteris* treeland stage. Even allowing for past fires, it appears that the rate of succession on pahoehoe is extremely slow.

Stages in this succession can be found where the rainfall is 80 to 140 inches per annum, but with higher rainfall, tree ferns (*Cibotium* spp.) form an increasing proportion of the canopy and the succession moves toward *Metrosideros/ Cibotium* forest. Some *Cibotium* is present on a prehistoric site sampled at 300 feet altitude near the Stainback Highway south of Hilo, the "Lower Stainback" site (Fig. 1 and Table 2). The rainfall here is approximately 140 inches, and the *Metrosideros* stand sampled has an understorey of *Cibotium* tree ferns, *Psidium guajava,* and *Coffea* sp. The mean tree volume for this sample is smaller than that from some historic flows (Table 2), and this, together with the rather close spacing of the *Metrosideros* trees, suggests that the Lower Stainback forest may be secondary in origin.

In the very high rainfall zone above 1,000 feet altitude (>150 inches per annum) on the northeastern slopes of Mauna Loa, the successional trends are more complex, with many species entering the canopy besides *Cibotium* tree ferns.

3. ROCKLAND → *Metrosideros* FOREST → *Metrosideros/Diospyros* FOREST

Stages in this succession were found only on aa flows below 1,000 feet in the western Puna rift district where mean annual rainfall is 110 inches or less. As with the other trends described, *Metrosideros polymorpha* is the pioneer tree species, but in this succession the fern *Dicranopteris* appears to be unimportant. A site sampled on the 1750 flow (Fig. 6) illustrates an intermediate stage where *Diospyros ferrea* is still only an upper understorey species. That it will ultimately form part of the canopy can be inferred from the absence of both *Metrosideros* juveniles (i.e., seedlings and saplings) and resprouts, and the presence of juvenile *Diospyros* of various heights. This particular site was at an altitude of 990 feet. At 300 feet altitude on the same flow, where a closed forest canopy has not yet developed, *Diospyros* was absent.

This community shows the highest rate of growth among the historic stands sampled (Ta-

TABLE 2

MEAN TRUNK DIAMETERS, TREE VOLUMES, AND CANOPY COVER OF VEGETATION SAMPLED ON HAWAIIAN LAVA FLOWS

LAVA FLOW		ALTITUDE (feet)	MEAN ANNUAL RAINFALL (inches)	TYPE OF VEGETATION	NO. OF TREES SAMPLED	MEAN D.B.H. (cm)	MEAN TREE VOL. INDEX (cu dm)	CANOPY COVER %			
								TOTAL	*Metrosideros*	*Dicranopteris*	*Cibotium*
Kilauea	1955	930	100	*Stereocaulon* lichenfield	10	0.5	0.05	80	<1	0	<1
Kilauea	1840 H	650	130	*Metrosideros/Dicranopteris* treeland	10	5.7	21.5	100	52	48	0
Kilauea	1840 L	40	115	*Metrosideros* rockland	20	5.0	19.5	72	24	0	<1
Kilauea	1750 H	990	110	*Metrosideros* forest	10	63.0	7,545	100	76	0	12
Kilauea	1750 L	300	90	*Metrosideros* treeland	10	26.0	1,149	70	10	0	<1
Mauna Loa	Prehistoric Lower Stainback	300	140	*Metrosideros* forest	10	27.0	901	100	72	0	16
Kilauea	Prehistoric flow north of Kapoho	90	100	*Pandanus* forest	10	15.0	195	100	0	0	0

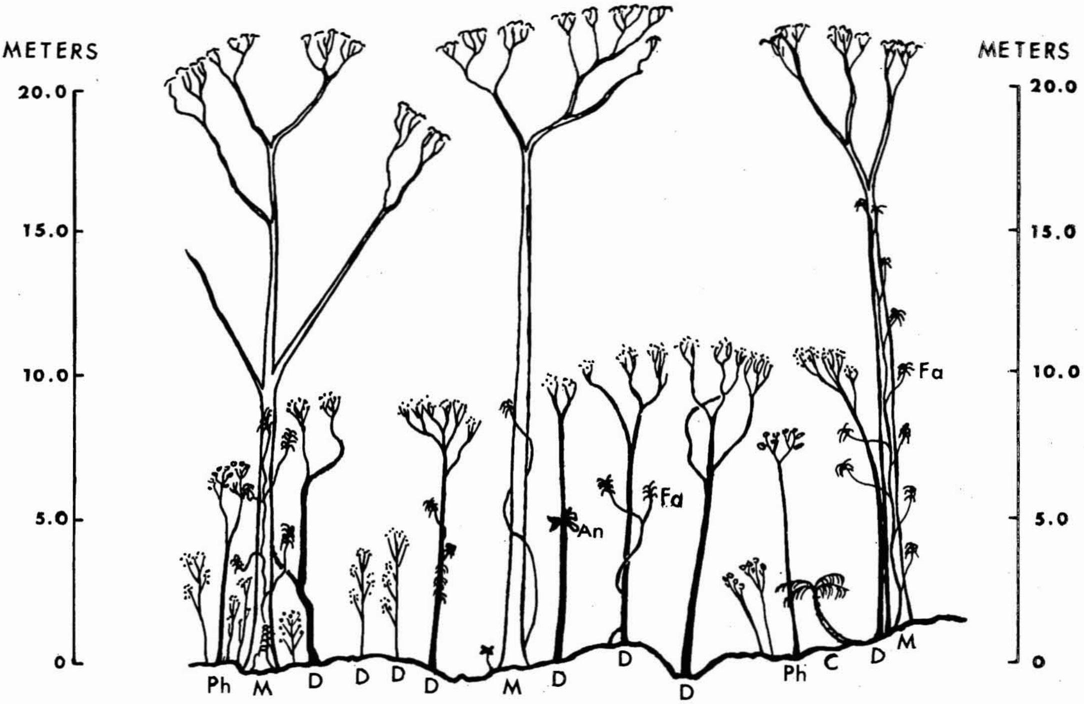

FIG. 6. Profile diagram of *Metrosideros* forest on the upper 1750 aa flow of Kilauea (1750 H sampling site, 990 feet altitude). *An = Asplenium nidus, D = Diospyros ferrea, Fa = Freycinetia arborea, M = Metrosideros polymorpha, Ph = Psychotria hawaiiensis.*

ble 2). At the time of sampling, logging of such stands was taking place in adjacent areas.

DISCUSSION

Trends of Succession

An important question is how the three trends described become differentiated from each other. Within the rainfall range studied, 75 to 150 inches per annum, succession to *Metrosideros* forest is the most general trend. The coastal trend towards *Pandanus* forest may possibly be related to the tolerance of *Pandanus tectorius* to wind-carried salt. The species was found up to 1.6 miles inland from the coast (north of Kaimu). Why *Pandanus* is generally restricted to a much narrower coastal belt is not known. It is surprising that *Pandanus* does not enter the succession earlier than it does, since there are often bare areas among *Metrosideros* trees that appear suitable for *Pandanus* establishment. Possibly the relatively heavy seed limits its dispersal. How much time is necessary before *Pandanus* replaces the *Metrosideros* completely is also unknown.

Rainfall differences may explain the divergence of the *Metrosideros* and *Metrosideros/Diospyros* successions. Mueller-Dombois (1966) describes open *Metrosideros/Diospyros* forest on slopes within Hawaii Volcanoes National Park, and associates it with a summer-dry climate. Summer-dry conditions may occur to some extent in the Kilauea 1750 H site (*Metrosideros* forest with *Diospyros* understorey) where the rainfall is 110 inches, but they are unlikely in the *Metrosideros* forests of the Stainback area, Mauna Loa, with its 140 inches or more of rain per annum and frequent cloud cover. *Diospyros ferrea* occurs in the Stainback area but there is no indication that it will ever be an important species there. Thus it can be inferred that decrease in rainfall from 140 to 110 inches, or possibly the reduced cloud cover associated with this rainfall difference, has altered the trend of succession from *Metrosideros* to *Metrosideros/Diospyros* forest.

Comparison of the 1750 H site (990 feet) with the 1750 L site (300 feet altitude and 90-inch annual rainfall, Table 2) shows a reduced growth rate of *Metrosideros* on the latter site. The forest on the 1750 flow at the lower altitude is still quite open with many areas of bare lava. *Diospyros* was not present on the 1750 L site although open *Metrosideros/Diospyros* forest does occur in still lower rainfall areas within the National Park. Thus, although the rate of succession has been reduced in the area of lower rainfall, there is no reason to suppose that the trend of succession has been altered.

A second important question concerns the future composition of the forests described. In the absence of disturbance by man or introduced mammals, the *Pandanus* forest appears to be self maintaining. In both *Pandanus* and *Metrosideros* forests, wherever the canopy has been opened by cutting, fires, or animals, there has been extensive invasion of introduced plants, particularly *Psidium* species. Juvenile and mature trees of *Aleurites moluccana* present among the *Psidium* stands suggest that, in some places at least, *Aleurites* will dominate these disturbed forests in the future.

In undisturbed *Metrosideros* forests older than 100 years, the absence of *Metrosideros* seedlings from shaded ground indicates a decrease in *Metrosideros* cover in the future. It is not unlikely, however, that after several centuries replacement of *Metrosideros* could balance mortality. Such replacement can be effected through resprouts from old trees and by the occasional establishment of seedlings on tree fern trunks.

Factors Affecting the Rate of Succession

General observations on the island of Hawaii indicate that the most important factor influencing the rate of succession on lava is available moisture. This is governed by rainfall and edaphic factors, particularly the size distribution of boulders and stones, and the porosity of individual rocks. These edaphic factors are of greatest importance during early stages. Thus a flow composed mainly of large boulders tends to have a lower cover of *Metrosideros* trees than a flow containing a high proportion of stones and fine material. Presumably, moisture stress on flows of coarse material is too great to allow the *Metrosideros* trees to establish.

Rock porosity influences particularly the establishment of lichens. The 1955 Kamaili flow from Kilauea, for example, is particularly scoriaceous and porous, and here *Stereocaulon vulcani* is extremely abundant. Scoriaceous lava, with its numerous pores, can probably catch and hold lichen propagules more easily than can less porous rock.

On pahoehoe flows, the establishment of *Metrosideros* appears to be at least partly controlled by fissures and cracks, a point noted by Skottsberg (1941). A flow with few fissures tends to have a lower density of *Metrosideros* than a strongly fissured flow. The fissures act as traps for wind-blown dust and mineral nutrients released by the weathering of the pahoehoe crust. Accumulation of this fine material would increase moisture storage. Forbes (1912) remarked on the fertile soil that develops in pahoehoe cracks. In addition to these factors of nutrient and moisture supply, a fissure provides space for the development of roots. Thus, even though the density of *Metrosideros* trees is usually lower on pahoehoe than on aa flows, a highly fissured pahoehoe flow can support a *Metrosideros* stand of similar density to an adjacent aa flow of the same age.

Another effect of available moisture on the trend of succession concerns the fern *Dicranopteris linearis*. On both pahoehoe and aa flows, *Metrosideros* regeneration practically ceases as this fern spreads and forms dense tangled thickets. Establishment and growth of *Dicranopteris* appears to be very dependent on available moisture: on drier sites such as the lower part of the 1750 flow, this fern is infrequent or absent.

Representative Areas for Future Study

There is need to protect representative areas of the communities described for future study. Although a wide range of vegetation is protected in Hawaii Volcanoes National Park, there appears to be no reserve of the coastal *Pandanus* forest or the *Metrosideros/Diospyros* forest with a continuous canopy. The *Pandanus* forest southeast of Hilo is the lowermost forest in a sequence of vegetation that, though damaged or destroyed in places, extends with few breaks from sea level to the summit of Mauna Loa at 13,000 feet. There can be few places in the Pacific region where such a complete sequence of vegetation and soils can still be studied.

Comparison with New Zealand

It may be remarked in conclusion that in New Zealand four species of *Metrosideros* are early entrants of successions on rocky surfaces. *M. excelsa* and *M. excelsa* x *M. robusta* hybrids have established on the late prehistoric basalt flows of Rangitoto Island, near Auckland. *M. excelsa* dominates young forests on late prehistoric rhyolite flows of Mayor Island in the Bay of Plenty. *M. robusta,* widespread in the North Island of New Zealand, usually establishes epiphytically on other trees. This species and *M. umbellata,* widespread in the South Island, can colonize rocky surfaces such as fans of coarse debris or rock faces left by landslips. Finally, *M. kermadecensis* colonizes recent volcanic surfaces in the Kermadec Islands.

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APPENDIX

LIST OF VASCULAR PLANTS FOUND ON SAMPLING SITES
(* indicates introduced species)

	SAMPLING SITES WITH ALTITUDES						
SPECIES	1955 (930 ft)	1840 L (40 ft)	1840 H (650 ft)	1750 L (300 ft)	1750 H (990 ft)	Pre-historic Kapoho (90 ft)	Pre-historic Stainback (300 ft)
PTERIDOPHYTA							
ASPIDIACEAE							
Cyclosorus parasiticus (L.) Farwell					+		
C. truncatus (Poir.) Farwell						+	
ASPLENIACEAE							
Asplenium nidus L.					+	+	
Asplenium sp.			+			+	
BLECHNACEAE							
Sadleria cyatheoides Kaulf.		+	+	+			
DAVALLIACEAE							
**Nephrolepis hirsutula* (Forst. f.) Presl	+	+	+	+	+	+	+
GLEICHENIACEAE							
Dicranopteris linearis (Burm.) Underwood			+	+			
HYMENOPHYLLACEAE							
Vandenboschia cyrtotheca (Hilleb.) Copel.					+		+
LYCOPODIACEAE							
Lycopodium cernuum L.			+				
OPHIOGLOSSACEAE							
Ophioglossum pendulum (Presl) Clausen					+		+
POLYPODIACEAE							
Pleopeltis thunbergiana Kaulf.	+						

APPENDIX (*continued*)

	SAMPLING SITES WITH ALTITUDES						
SPECIES	1955 (930 ft)	1840 L (40 ft)	1840 H (650 ft)	1750 L (300 ft)	1750 H (990 ft)	Pre-historic Kapoho (90 ft)	Pre-historic Stainback (300 ft)
PSILOTACEAE							
Psilotum nudum (L.) Beauv.		+		+			
PTERIDACEAE							
Cibotium glaucum (Smith) Hook. et Arn.					+		+
MONOCOTYLEDONAE							
CYPERACEAE							
Fimbristylis cymosa R. Br.		+					
Machaerina angustifolia (Gaud.) Koyama			+				
GRAMINAE							
**Andropogon ? glomeratus* (Walt.) BSP.				+			
Oplismenus hirtellus (L.) Beauv.					+	+	
LILIACEAE							
Cordyline fruticosa (L.) Goepp.		+				+	
Smilax sandwicensis Kunth					+		
ORCHIDACEAE							
**Arundina bambusaefolia* Lindl.	+	+	+	+			
**Spathoglottis plicata* Bl.	+	+			+		+
PALMAE							
Cocos nucifera L.		+					
PANDANACEAE							
Freycinetia arborea Gaud.					+		+
Pandanus tectorius Park.						+	
DICOTYLEDONAE							
ANACARDIACEAE							
**Schinus terebinthifolius* Raddi				+			
APOCYNACEAE							
Alyxia olivaeformis Gaud.					+		
CASUARINACEAE							
**Casuarina equisetifolia* L.		+					
COMPOSITAE							
**Pluchea odorata* (L.) Cass.		+					
**Vernonia cinerea* (L.) Less		+					
EBENACEAE							
Diospyros ferrea var. *pubescens* Fosb.					+		+

APPENDIX (*continued*)

	SAMPLING SITES WITH ALTITUDES						
SPECIES	1955 (930 ft)	1840 L (40 ft)	1840 H (650 ft)	1750 L (300 ft)	1750 H (990 ft)	Pre-historic Kapoho (90 ft)	Pre-historic Stainback (300 ft)
EPACRIDACEAE							
Styphelia tameiameiae (Cham. et Schlecht.) F. Muell.		+	+	+			
ERICACEAE							
Vaccinium reticulatum Smith		+	+				
EUPHORBIACEAE							
Aleurites moluccana (L.) Willd.						+	
Antidesma ? platyphyllum Mann					+		
GOODENIACEAE							
Scaevola taccada (Gaertn.) Roxb.		+					
MORACEAE							
**Cecropia peltata* L.							+
MYRSINACEAE							
Ardisia elliptica Thunb.					+		
MYRTACEAE							
Metrosideros polymorpha Gaud.	+	+	+	+	+		+
**Psidium cattleianum* Sabine			+	+	+		
**P. guajava* L.			+			+	+
PIPERACEAE							
Peperomia sp.				+	+		
ROSACEAE							
Osteomeles anthyllidifolia (Sm.) Lindl.				+			
**Rubus rosaefolius* Sm.					+		
RUBIACEAE							
**Coffea* sp.							+
Morinda citrifolia L.						+	
Psychotria hawaiiensis Gray					+		+
URTICACEAE							
Pipturus sp.					+	+	