A Study of the Ecology of Pioneer Lichens, Mosses, and Algae on Recent Hawaiian Lava Flows[1]

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ABSTRACT: The ecology of pioneer lichens, mosses, and blue-green algae on some recent Hawaiian lava flows was investigated quantitatively. Up to an elevation of at least 3,000 feet, the major variables of the physical environment are rainfall, rock texture, and sea breezes.

The lichen *Stereocaulon vulcani,* the most abundant and widespread pioneer organism, shows a marked preference for regions of higher rainfall, but all species of *Parmelia* and *Cladonia*, together with an unidentified crustose lichen, were found only in areas of lower rainfall. The mosses and blue-green algae prefer relatively humid regions, but *Campylopus densifolius* is able to grow in some areas that are too dry to permit growth of *Rhacomitrium lanuginosum.*

Rough aa lava provides a more favorable substrate for *Stereocaulon vulcani* than does the smoother pahoehoe, but this effect becomes less pronounced with increasing rainfall. Thus, aa creates a more moist environment than does pahoehoe, probably because its highly irregular, pitted surface is better able to trap and retain rainwater. A possible contributing factor is the greater susceptibility of aa to chemical weathering.

On some lavas, lichens and mosses preferentially colonize seaward-facing rock surfaces. This is ascribed to water vapor conveyed inland by sea breezes. Nutrients in wind-borne ocean salts may play a secondary role.

The net effect of rainfall, rock texture, and, in some cases, sea breezes determines the abundance and gross vegetative morphology of *Stereocaulon vulcani,* its ability to gain a foothold, and the level of maturity which it can attain. The successfulness of *S. vulcani* in colonizing lava can be ascribed to its ability to invade vesicles and narrow recesses in the rock, its ability (or that of its associated microflora, or both) to accelerate the chemical weathering of the rock, and its rapid rates of dispersal, establishment, and growth. Under optimal conditions, *S. vulcani* spreads rapidly over a fresh rock surface, and dominates the pioneer community, probably by preempting space which might otherwise be occupied by slower-growing species. In one particularly damp area, mosses and blue-green algae increase at the expense of *S. vulcani.* In one exceptionally dry area, *Stereocaulon* is initially the most abundant lichen on the aa flows, but it never attains maturity, and its numerical importance is gradually superseded by that of *Parmelia* and *Cladonia,* which are better adapted to dry conditions.

No evidence of "mat" formation was found. Vascular plants spring up in crevices, while lichens, mosses, and algae occupy the intervening rock surfaces.

THE ISLAND OF HAWAII has many historically recent lava flows colonized by pioneer lichens, mosses, algae, and vascular plants. Preliminary observations on the ecology of these plants were made by Forbes (1913) and Robyns and Lamb (1939), followed by the work of Skottsberg (1941), Miller (1960), Doty (1967), and Mueller-Dombois (1967). In the present study, the ecology of the pioneer lichens, mosses, and algae is investigated at a number of sampling stations representing lavas of different age and different surface properties situated in different

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climatic zones. The field work was performed during the summer of 1967.

FIELD AREA

Geology

The lava flows, which originated from eruptions by the volcanoes Mauna Loa and Kilauea, are composed of tholeiitic basalts of similar chemical composition and mineralogy (Macdonald and Katsura, 1962, 1964; Muir and Tilley, 1963; Powers, 1954, 1955; Nockolds and Allen, 1956; Macdonald, 1949). The lavas consist either of rough aa or relatively smooth pahoehoe, or both together (Macdonald, 1953). In contrast to aa, pahoehoe has a thin surface zone of glass.

The following lava flows, designated by year of eruption, were chosen for study: the Mauna Loa lavas of 1950 (east branch), 1926, 1919, 1907 (east branch and west branch), 1887, 1868, and 1859, and one prehistoric flow of unknown age, together with the Kilauea lava of 1955. The Mauna Loa lavas lie in the Kona district of western and southwestern Hawaii, and the Kilauea lava lies in the Puna district of eastern Hawaii (Fig. 1). The lavas of 1950, 1926, 1919, 1907 (both branches), 1887, and 1868, together with the prehistoric

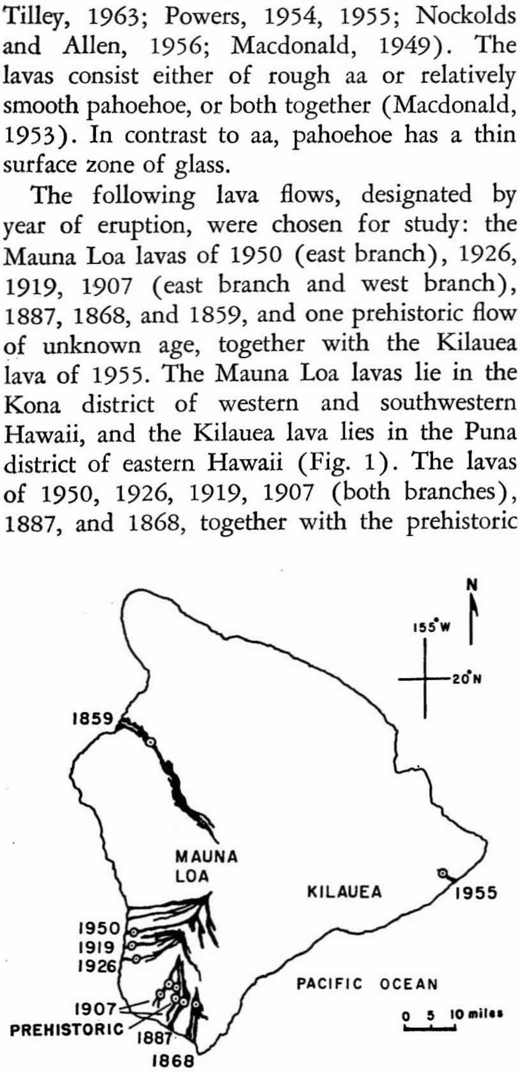

FIG. 1. Index map of the Island of Hawaii, showing the lava flows investigated and the sampling stations (encircled). The lower station on the east branch of the 1907 lava includes the prehistoric lava.

lava, which crops out through an opening in the east branch of the 1907 lava, were sampled near Route 11. The east and west branches of the 1907 lava were also sampled near the east end of Luau Drive and near the intersection of Tiki Lane and Hukilau Drive, respectively. The lava of 1859 was sampled near Route 19, and the lava of 1955 near Route 13. At the localities studied, the lavas of 1950, 1926, 1919, 1907, 1887, and the prehistoric lava consist exclusively of aa, whereas the lava of 1868 is entirely pahoehoe; the lavas of 1955 and 1859 are mixtures of aa and pahoehoe.

Climate

In the sampling area, the temperatures are equable, but rainfall varies considerably (Blumenstock, 1961; Stidd and Leopold, 1951). Even in regions of higher rainfall, the high rates of infiltration in the volcanic rocks make the environment of the rock surfaces relatively arid (Blumenstock, 1961).

The Puna district receives abundant rainfall from the trade winds and winter storms. However, the Kona district is dominated by a local monsoon consisting of a diurnal cycle: sea breezes in the daytime and land breezes at night, with frequent showers in the afternoon or evening (Leopold, 1949; Jones, 1939).

The annual rainfall at each sampling station was estimated from the maps of Blumenstock (1961) and Taliaferro (1959) (Table 1). The broad pattern of rainfall distribution shows that the sampling stations on the east branch of the 1907 lava, the prehistoric lava, and the lavas of 1887 and 1868, lie in a zone of relatively low rainfall which cuts across the southern end of the island, whereas the stations on the lavas of 1950, 1926, and 1919, and the west branch of the 1907 lava, lie in an adjacent zone of higher rainfall. On each branch of the 1907 lava, rainfall is more abundant at the higher-altitude than at the lower-altitude station. The 1955 lava lies in a wet region, and the 1859 lava in a dry one.

METHODS

Each sampling station was located more than 100 feet away from the road, and areas disturbed by human activity were avoided.

TABLE 1

ELEVATION AND APPROXIMATE ANNUAL RAINFALL AT THE SAMPLING STATIONS

LAVA FLOW	ELEVATION (feet)	ANNUAL RAINFALL (inches)	
		TALIAFERRO	BLUMENSTOCK
1955	840	105	103
1950	1,324	56.3	slightly less than 50
1926	1,720–1,760	64.7	slightly more than 50
1919	1,557	60.7	slightly less than 50
1907, west branch	3,000	75	>50, <75
1907, west branch	1,915	62.5	>50, <75
1907, east branch	3,030	66.7	slightly more than 50
1907, east branch	1,965	58.3	45
1887	1,933	53.8	42.2
1868	2,040–2,080	50	40
1859	2,160	22.5	26.7
prehistoric	1,945–1,950	58.3	45

NOTE: Rainfall data are median and mean values estimated from the maps of Taliaferro (1959) and Blumenstock (1961), respectively.

At each sampling station the species composition of the cryptogam community, and the cryptogamic plant cover, were estimated by taking randomly spaced point samples along line transects. The positions of the sample points were determined by means of a length of string on which points had been marked in ink; a table of random numbers was utilized to determine the distances between points. The length of a transect was about 80 feet, and the average number of sample points was 181 (with a range of 157–197), the distance between adjacent points ranging from 1 to 9 inches. From the raw data the following statistics were computed:

$$\text{Frequency} = \frac{\text{no. of points occupied by a species} \times 100}{\text{total points}}$$

$$\text{Plant cover} = \frac{\text{no. of points occupied by cryptogamic plants} \times 100}{\text{total points}}$$

Sampling by means of quadrats was impracticable, because most of the lichens consisted of myriads of small individuals generally clumped closely together.

RESULTS AND DISCUSSION

The quantitative data are recorded in Tables 2–4.

The fruticose lichen *Stereocaulon vulcani* is the most widespread and abundant pioneer cryptogam in the field area. The "juvenile" *Stereocaulon* species, whose immaturity prevents full identification, is probably *S. vulcani,* as no other species of *Stereocaulon* were found in the sampling area. These juvenile forms consist of tiny, rudimentary, crustose thalli. Magnusson and Zahlbruckner (1944) divided the Hawaiian *Stereocaulon* population into a number of species, whereas Hale (personal communication) recognized only one species, *S. vulcani,* among the mature thalli collected for the present study, despite variations in gross morphology. Similarly, Doty and Mueller-Dombois (1966) and Doty (1967) mention only the species *S. vulcani*. Probably this taxonomic confusion arises from the fact that the vegetative features of the genus are notoriously intergradational (Hale, 1961). In the present work, the writer will assume, tentatively, that there is only one species, *S. vulcani*, and that its vegetative morphology is modified by environment. On the basis of gross morphology, the "adult" *S. vulcani* thalli can be divided into two categories: (1) twiglike or tendrillike structures, arbitrarily termed "normal" and (2) thalli with a stunted, or scrubby,[3] appearance.

Other commonly encountered pioneer organisms include species of *Parmelia* and *Cladonia*, an unidentified crustose lichen, the mosses *Campylopus densifolius* and *Rhacomitrium lanuginosum*, and a species of blue-green alga (probably *Scytonema* sp.).

The Physical Ecology of the Pioneer Communities

Rainfall, rock texture, and sea breezes appear to be especially significant variables in the physical environment. Other factors, such as temperature and the chemical composition of the rock, do not vary greatly in the sampling area, and will not be discussed.

RAINFALL: The bifurcate lava of 1907 affords an opportunity to assess the ecological effects of rainfall, independent of such variables as the age and properties of the rock. The usefulness of this lava flow arises from the fact that the east branch of the lava lies in a relatively dry region, and the west branch in a wet region; moreover, the rainfall varies with altitude. The contrast between the floras on the east and west branches was noted by Skottsberg (1941).

The frequency of "adult" *Stereocaulon vulcani*, and the percentage of adult thalli in the *Stereocaulon* population, are highest on the west branch of the lava at 3,000 feet, where rainfall is highest. On the west branch at 1,915 feet, where rainfall is lower, the values for these parameters are much lower, and on the east branch at 3,030 feet they are lower still. On the east branch at 1,965 feet, where rainfall is lowest, no adult thalli were found, and the sparse, depauperate *Stereocaulon* population consists entirely of juvenile thalli. Nevertheless, *Stereocaulon* is by far the dominant pioneer organism at all four sampling stations. Rainfall influences not only the frequency of occurrence and rate of maturation of *S. vulcani*, but also the gross morphology of the adult thalli (Table 4). Thus, on the west branch of the 1907 lava at 3,000 feet all of the adult thalli have the normal morphology, whereas on the west branch at 1,915 feet about 42 percent of the adult thalli are scrubby; on the east branch at 3,030 feet all of the adult thalli are scrubby. In brief, *S. vulcani* has a strong preference for regions of higher rainfall, though it is able to subsist under a considerable range of rainfall regimes. We may also conclude that this lichen is the dominant pioneer cryptogam on aa lava in both wet and dry regions. *Rhacomitrium lanuginosum* and *Campylopus densifolius* also prefer regions of higher rainfall, as they were found only on the west branch of the lava, where they form minor components of the community.

In general, the data for the other lava flows are consistent with the conclusions reached for the 1907 lava. The lavas of 1955, 1950, 1926, and 1919, which lie in regions of moderate to high rainfall, are largely carpeted with *Stereocaulon vulcani,* and all or most of the thalli are "normal" adults. In contrast, the adult *S. vulcani* thalli on the relatively dry lavas of 1859 and 1868 all have the scrubby habit, and on the lava of 1887 and the prehistoric lava *Stereocaulon* occurs exclusively in the juvenile phase. The fact that all of the *Stereocaulon* thalli on the prehistoric lava are juvenile, despite the relatively great age of the lava, strongly suggests that in a sufficiently dry area the lichen is never able to attain maturiy, even though its propagules may be able to gain a foothold.

In the areas studied, *Rhacomitrium lanuginosum* and the unknown species of blue-green alga are restricted to regions of higher rainfall, attaining their highest and second highest frequencies on the lavas of 1926 and 1919, respectively (in fact, the blue-green alga was found only on these two lavas). However, Mueller-Dombois (1967 and personal communication) observed that *R. lanuginosum* is able to grow in higher-altitude regions of low rainfall, owing to its ability to absorb water from clouds. *Campylopus densifolius* appears to be more tolerant of dry conditions, as it is able to grow on the lavas of 1859 and 1868. The data for *Rhacomitrium lanuginosum* and the blue-green alga suggest that the lavas of 1926 and 1919—especially the former—lie in a localized zone of

[3] As used in this report, the term "scrubby" means stunted, or shrubby, and refers to the life form of the thallus.

TABLE 2

FREQUENCY DATA FOR LICHEN, MOSS, AND BLUE-GREEN ALGAL SPECIES GROWING ON THE LAVA FLOWS*

NAME OF ORGANISM	LAVA FLOW 1955 (AA)	1955 (PAHOEHOE)	1950	1926	1919	1907 WEST BRANCH AT 3,000 FEET	1907 WEST BRANCH AT 1,915 FEET
Lichens							
Stereocaulon vulcani (Bory) Ach.	80	57.4	67	52.3	73.3	80.2	27.3
Stereocaulon sp. (juvenile phase)			9.95	8.89	4.92	10.9	43.2
Parmelia cetrata Ach.							
Parmelia subramigera Gyel.							
Parmelia sp.							
Cladonia skottsbergii Magn.							
Cladonia sp.							
unidentified pale green sp.				1.11			
unidentified crustose sp.							
Mosses							
Campylopus densifolius Angstr.				3.34	0.547		0.547
Rhacomitrium lanuginosum (Hedw.) Brid.			4.19	16.8	8.75	1.21	0.547
Algae							
blue-green sp. (probably *Scytonema* sp.)				7.78	2.19		
Other Plants Present	A few mosses, ferns, and small seed plants	Same as found on 1955 aa	A few ferns; no trees	Many vascular plants	A number of small trees and ferns	Scattered trees and ferns	Some ferns and higher plants

$$\text{* Frequency} = \frac{(\text{No. of points occupied by a given species}) \times 100}{\text{total points}}$$

anomalously high rainfall or high atmospheric humidity. This interpretation is supported by the noticeable dampness of the area (see Skottsberg, 1941) and by the fact that the *Stereocaulon vulcani* thalli on the 1926 lava are anomalously rich in silicon, aluminum, iron, and calcium (Jackson, 1968; Jackson and Keller, in press), suggesting high rates of chemical weathering and plant metabolism.

In contrast to the organisms discussed previously, the lichens of the genera *Parmelia* and *Cladonia*, together with the unidentified crustose lichen, are restricted to regions of relatively low rainfall. *Parmelia* and *Cladonia* were found only on the lavas of 1887, 1868, 1859, and the prehistoric lava; the crustose lichen was found only on the lavas of 1868 and 1859, and the prehistoric lava.

TABLE 2 (*continued*)

LAVA FLOW							
1907 EAST BRANCH AT 3,030 FEET	1907 EAST BRANCH AT 1,965 FEET	1887	1868 AT LEVEL OF ROAD	1868 ATOP CLIFF 17 FEET HIGH	1859 (AA)	1859 (PAHOEHOE)	PRE-HISTORIC
0.701			4.47	32.5	39.6		
66.3	8.56	32.4	49.2	19.9	6.78		9.32
		0.56	0.558			4.89	9.93
		0.56		0.524	0.521	4.89	
							0.621
			1.12	1.05			
			1.12		0.521		0.621
				0.524		0.544	0.621
			1.68	3.66	2.60		
A few vascular plants	A few foliose lichens	*Cladonia skottsbergii* (rare occurrences)	*Usnea* sp.; *Parmelia reticulata;* some ferns and higher plants		Much tall grass	*Ramalina* sp.; much tall grass	Some grass and trees

ROCK TEXTURE: Aa and pahoehoe differ in their suitability as substrates for pioneer plants (Forbes, 1913; Robyns and Lamb, 1939; Skottsberg, 1941; Magnusson and Zahlbruckner, 1944). The lavas of 1859 and 1955 are ideally suited for a comparative study of the ecological effects of aa and pahoehoe, because (1) each flow has coexisting aa and pahoehoe; and (2) the 1859 flow lies in a dry region, whereas the 1955 flow lies in a wet region.

The dominant species on the aa phase of the 1859 lava is *Stereocaulon vulcani* (mostly scrubby adults with a few juveniles), accompanied by minor occurrences of *Campylopus densifolius, Parmelia subramigera,* and *Cladonia* sp., the total plant cover being about 50 percent. On the pahoehoe phase, however, the most abundant species are *Parmelia subramigera* and *P. cetrata,* the unidentified crustose lichen occurs as a minor component of the community, and

TABLE 3

PLANT COVER AND TOTAL NUMBER OF SAMPLE POINTS

LAVA FLOW	PLANT COVER	TOTAL SAMPLE POINTS
1955 (aa)	80	184
1955 (pahoehoe)	57.4	197
1950	81.2	191
1926	90	180
1919	89.7	183
1907, west branch at 3,000 feet	92.2	166
1907, west branch at 1,915 feet	71.6	183
1907, east branch at 3,030 feet	66.9	157
1907, east branch at 1,965 feet	8.56	187
1887	50.4	185
1868, at level of road	58.2	179
1868, atop cliff 17 feet high	58.2	191
1859 (aa)	50.0	192
1859 (pahoehoe)	1.03	184
Prehistoric	21.1	161

TABLE 4

THE PHYSIOGNOMY OF THE *Stereocaulon* POPULATIONS

LAVA	PERCENTAGE OF "ADULT" *S. vulcani* IN TOTAL *Stereocaulon* POPULATION	MORPHOLOGY OF *Stereocaulon*
1955 (aa)	100	normal
1955 (pahoehoe)	100	normal
1950	87.2	normal + juvenile
1926	85.4	normal + juvenile
1919	93.7	normal + juvenile
1907, west branch at 3,000 ft	88.1	normal + juvenile
1907, west branch at 1,915 ft	38.7	normal + scrubby + juvenile (42% of the adult forms are scrubby)
1907, east branch at 3,030 ft	0.953	scrubby + juvenile
1907, east branch at 1,965 ft	0	juvenile
1887	0	juvenile
1868, at level of road	8.33	scrubby + juvenile
1868, atop cliff 17 ft high	62	scrubby + juvenile
1859 (aa)	85.3	scrubby + juvenile
1859 (pahoehoe)	—	—
prehistoric	0	juvenile

the plant cover is only about 1 percent; no *Stereocaulon* thalli whatsoever—not even juvenile ones—were found on the pahoehoe. These findings appear to indicate that the pahoehoe provides a drier environment than does the aa. Evidently the pahoehoe texture aggravates the drought due to low rainfall; the combination of low rainfall and unfavorable substrate is sufficient to prevent *Stereocaulon* from gaining a foothold. However, in the case of the 1955 lava *Stereocaulon vulcani* was found to be the dominant species on both the aa and the pahoehoe, though the organism occurs with considerably greater frequency on the aa. Probably the steady abundance of rainfall largely compensates for the "dryness" of the pahoehoe, thus permitting *S. vulcani* to grow there. Hence, the contrast between the aa and pahoehoe communities is much less extreme on the 1955 than on the 1859 lava.

On the lava of 1887, the east branch of the lava of 1907 at 1,965 feet, and the prehistoric lava, all of which consist of aa, the rainfall is suboptimal, but the substrate is favorable; the result is that *Stereocaulon* has gained a foothold but is unable to attain maturity. The lava of 1868, which consists of pahoehoe and receives more rainfall than the lava of 1859 but less than the lava of 1955, is able to support a sizable, though stunted, *Stereocaulon* population. On the 1868 lava, a sloping surface was found which was largely devoid of mature *S. vulcani,* although it was sparsely inhabited by *Cladonia* (?) sp. In places where the surface rock had sloughed off, exposing the rougher, vesicular rock underneath, *S. vulcani* was quite abundant.

Why should aa provide a more moist environment than pahoehoe? As suggested by Skottsberg (1941), the most plausible explanation seems to be that the rough, pitted aa surface is better able to trap and retain rainwater than is the relatively smooth, impervious pahoehoe surface. Factors other than availability of water should also be considered. The glassy surface of pahoehoe is more resistant to chemical weathering than the crystalline surface of aa (Forbes, 1913; Macdonald, 1953), and this may aggravate the harshness of the environment by increasing the difficulty with which the lichens extract nutrients from the substrate. Further, aa is probably more effective in trapping dust and windborne propagules (Skottsberg, 1941), though the cracks and folds of pahoehoe also trap these particles (Forbes, 1913). Another possible contributing factor is that aa and pahoehoe may differ in abrasion pH, but this hypothesis was ruled out by the discovery that the abrasion pH of both the aa and the pahoehoe of the lavas of 1859 and 1955 is approximately 9.

SEA BREEZES: On the lavas of 1950 and 1859 (both aa and pahoehoe), the seaward-facing rock surfaces are populated by pioneer organisms, whereas the landward-facing surfaces are practically bare. This strongly suggests that sea breezes perform an essential ecological function for the pioneer cryptogams on these two lavas. The daily occurrence of sea breezes in the Kona district tends to support this interpretation. The sampling sites on the lavas of 1950 and 1859 are approximately 1.5 and 7.5 miles, respectively, from the shoreline, and, judging from the data of Eriksson (1957) and Junge (1957), they are close enough to the ocean to be influenced by it. A possible alternative explanation is that the distribution of organisms is determined by degree of exposure to solar radiation, but this is unlikely for the following reasons: (1) on the 1950 lava the rock surfaces in question face almost due east and west, whereas effects due to the angle of the sun should appear only on north- and south-facing slopes; (2) the lava surfaces are very irregular, and the slope angles of the lichen-covered and lichen-free surfaces do not seem to differ systematically; and (3) the effect was not seen on other lavas lying farther south and east.

A likely explanation for the phenomenon is that water vapor conveyed inland by the sea breezes condenses preferentially on seaward-facing surfaces. This would account for the seemingly paradoxical fact that the aa lava of 1859 supports "adult" *Stereocaulon vulcani* and *Campylopus densifolius*, whereas the lava of 1887, the east branch of the 1907 lava at 1,965 feet, and the prehistoric lava do not support adult populations, even though they receive more rainfall per year than does the 1859 lava. Furthermore, the distribution of lichens on the lavas of 1887, 1907, and the prehistoric lava does not seem to be influenced by sea breezes. Thus, it would seem that sea breezes, by furnishing a steady supply of supplementary water, permit the growth of moisture-loving organisms on the 1859 aa (and on the 1950 lava, whose yearly supply of rainwater is only moderate), and that a lack of sea breezes at the southern end of the island makes the lava flows in that region effectively drier than the 1859 aa, even though they receive more rain. The tentatively assumed absence or feebleness of diurnal sea breezes at the southern end of the island can be explained by orographic influences. This region lies in the rain shadow of Mauna Loa and, therefore, receives a reduced rainfall; but the southern spur of the mountain is apparently not high enough to prevent the water-depleted air from sweeping across the region at ground level, thereby suppressing the Kona monsoon (see climate diagrams in Doty and Mueller-Dombois, 1966, p. 87). Farther north, of course, the mountains are so high that the Kona Coast is shielded from the trade winds, and the monsoon is well developed.

In addition to water vapor, sea breezes carry fine particles of ocean salt, which would tend to be deposited on ocean-facing surfaces (Oosting, 1956). Possibly this contributes to the favorable influence of the sea breezes by providing nutrients.

Biotic Factors: Adaptation and Competition

The successfulness of *Stereocaulon vulcani* in colonizing lava, even under suboptimal conditions, can be attributed largely to its ability to invade vesicles and narrow recesses, where water and dust may be trapped. Probably the lichen's wind-disseminated propagules initially become established in these protected pockets, having lodged there by chance. This concept is supported by polished sections showing thalli of *S. vulcani* occupying vesicles just beneath the rock surface (Jackson, 1968).

In addition, *S. vulcani,* or its associated microflora, or both together, has the advantage of being able to accelerate the chemical weathering of the rock on which it grows (Jackson and Keller, in press). This effects rapid release of nutrients, such as calcium, from the rock, and probably enhances the water-holding and ion-exchange capacity of the substrate.

Finally, it would seem that *S. vulcani* is characterized by rapid rates of dispersal and colonization, and, where water supply is adequate, by rapid rates of growth. The well-watered aa lava of 1955, which was only 12 years old when studied, was found to be about 80 percent covered with mature *S. vulcani,* and, because the lichen did not start growing there until 2 years after eruption of the volcano (Doty, 1967), this "population explosion" must have occurred within no more than 10 years. The west branch of the 1907 lava at 3,000 feet, where the annual rainfall is only second to that in the vicinity of the 1955 lava, was also found to be about 80 percent covered with adult *S. vulcani* thalli, and 11 percent covered with juvenile thalli. This indicates that, in a wet region, colonization of virgin rock by *S. vulcani* proceeds very rapidly once it has started, and then levels off at a high population density after just 10 years or less. On this hypothesis, *S. vulcani* dominates the cryptogam community by preempting space which might otherwise be occupied by slower-growing species.

Preemption of space by *S. vulcani* could explain in part why *Parmelia, Cladonia,* and the crustose lichen are restricted to dry regions, where growth of *S. vulcani* is more or less impeded. Nevertheless, *Parmelia, Cladonia,* and the crustose lichen also seem to be specifically adapted to dry conditions. The data from the east branch of the 1907 lava at 1,965 feet, the 1887 lava, and the prehistoric lava show that *Stereocaulon* initially invades the aa surfaces much more rapidly than any of the other lichens, even under dry conditions; but *Parmelia, Cladonia,* and the crustose lichen gradually proliferate and mature, while *Stereocaulon* remains indefinitely in an arrested stage of development.

It should be mentioned, too, that in dry regions inorganic weathering processes seem to be more important than the weathering action of lichens. Thus, on the prehistoric lava, which has a weathering crust a few millimeters thick, and raw soil lodged between the clinkers, the areas of bare rock appeared to be just as severely weathered as the areas covered by lichens. Comparison with the lavas of 1887 and 1907 (east branch at 1,965 feet) suggests that on the prehistoric lava the cumulative effects of chemical weathering acting slowly over a long stretch of time, together with accumulation of raw soil, have gradually made the substrate habitable by an ever increasing number of individual plants and plant species.

Though *S. vulcani* attains optimal growth in wet regions, the data from the lavas of 1926 and 1919 suggest that, when conditions become too damp, mosses and blue-green algae are able to encroach somewhat on the lichen's domain. Thus, the frequency of *S. vulcani* on the 1926 lava is lower than might be expected.

The subject of plant succession on the lavas has been treated by Doty (1967), Miller (1960), Skottsberg (1941), Robyns and Lamb (1939), and Forbes (1913). As emphasized by Miller (1960), the classical concept of the xerarch succession (Oosting, 1956) does not seem to apply here (see Cooper, 1928; Cooper and Rudolph, 1953). No evidence was found to indicate that the lichens or mosses create mats in which vascular plants become established. Instead, the vascular plants evidently spring up in crevices, while lichens and mosses occupy the intervening rock surfaces.

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LITERATURE CITED

BLUMENSTOCK, D. I. 1961. Climates of the states: Hawaii. Climatography of the United States, no. 60-51. Washington, D. C., U. S. Dept. of Commerce, Weather Bureau. 20 pp.

COOPER, R., and E. D. RUDOLPH. 1953. The role of lichens in soil formation and plant succession: Ecology, vol. 34, pp. 805–807.

COOPER, W. S. 1928. Seventeen years of successional change upon Isle Royale, Lake Superior. Ecology, vol. 9, pp. 1–5.

DOTY, M. S. 1967. Contrast between the pioneer populating process on land and shore. Bulletin of the Southern California Academy of Science, vol. 66, pp. 175–194.

DOTY, M. S., and D. MUELLER-DOMBOIS, 1966. Atlas for bioecology studies in Hawaii Volcanoes National Park. University of Hawaii, Hawaii Botanical Science Paper, no. 2.

ERIKSSON, E. 1957. The chemical composition of Hawaiian rainfall. Tellus, vol. 9, pp. 509–520.

FORBES, C. N. 1913. Preliminary observations concerning the plant invasion on some of the lava flows of Mauna Loa, Hawaii. Honolulu, Occasional Papers of the Bernice P. Bishop Museum of Polynesian Ethnology and Natural History, vol. 5, pp. 15–23.

HALE, M. E., JR. 1961. Lichen handbook. Washington, D. C., Smithsonian Institution. 178 pp.

JACKSON, T. A. 1968. The role of pioneer lichens in the chemical weathering of recent volcanic rocks on the Island of Hawaii. Ph.D. dissertation, University of Missouri (Columbia).

JACKSON, T. A., and W. D. KELLER. A comparative study of the role of lichens and "inorganic" processes in the chemical weathering of recent Hawaiian lava flows. American Journal of Science (in press).

JONES, S. B. 1939. The weather element in the Hawaiian climate. Annals of the Association of American Geographers, vol. 29, pp. 29–57.

JUNGE, C. E. 1957. Chemical analysis of aerosol particles and of gas traces on the Island of Hawaii. Tellus, vol. 9, pp. 528–537.

LEOPOLD, L. B. 1949. The interaction of trade wind and sea breeze, Hawaii. Journal of Meteorology, vol. 6, pp. 312–320.

MACDONALD, G. A. 1949. Petrography of the island of Hawaii. U. S. Geological Survey Professional Paper 214-D, pp. 51–96.

——— 1953. Pahoehoe, aa, and block lava. American Journal of Science, vol. 251, pp. 169–191.

MACDONALD, G. A., and T. KATSURA. 1962. Relationship of petrographic suites in Hawaii. In: The crust of the Pacific Basin. American Geophysical Union Geophysical Monograph 6 (National Academy of Science, National Research Council Publication 1035), pp. 187–195.

——— 1964. Chemical composition of Hawaiian lavas. Journal of Petrology, vol. 5, pp. 82–133.

MAGNUSSON, A. H., and A. ZAHLBRUCKNER. 1944. Hawaiian lichens. II. The families Lecideaceae to Parmeliaceae. Arkiv för Botanik, vol. 31-A, pp. 1–109.

MILLER, H. A. 1960. Remarks on the succession of bryophytes on Hawaiian lava flows. Pacific Science, vol. 14, pp. 246–247.

MUELLER-DOMBOIS, D. 1967. Ecological relations in the alpine and subalpine vegetation on Mauna Loa, Hawaii. Journal of the Indian Botanical Society, vol. 46, pp. 403–411.

MUIR, I. D., and C. E. TILLEY. 1963. Contributions to the petrology of Hawaiian basalts. II. The tholeiitic basalts of Mauna Loa and Kilauea. American Journal of Science, vol. 261, pp. 111–128.

NOCKOLDS, S. R., and R. ALLEN. 1956. The geochemistry of some igneous rock series, pt. 3. Geochimica et Cosmochimica Acta, vol. 9, pp. 34–77.

OOSTING, H. J. 1956. The study of plant communities. San Francisco, W. H. Freeman and Co. 440 pp.

POWERS, H. A. 1954. Basaltic magma at Hawaii is saturated in silica. Science, vol. 119, pp. 388–389.

——— 1955. Composition and origin of basaltic magma of the Hawaiian Islands. Geochimica et Cosmochimica Acta, vol. 7, pp. 77–107.

ROBYNS, W., and S. H. LAMB. 1939. Preliminary ecological survey of the Island of Hawaii. Bulletin du Jardin Botanique de Bruxelles, vol. 15, pp. 241–293.

SKOTTSBERG, C. 1941. Plant succession on recent lava flows in the Island of Hawaii: Göteborgs Kungl. Vetensk.-o. Vitterhets. Handl., följden 6, series B, band 1, no. 8, 32 pp.

STIDD, C. K., and L. B. LEOPOLD. 1951. The geographic distribution of average monthly rainfall, Hawaii. Meteorological Monographs, vol. 1, pp. 24–33.

TALIAFERRO, W. J. 1959. Rainfall of the Hawaiian Islands. Honolulu, Hawaii Water Authority. 394 pp.