Observations on Vegetation Patterns and Dynamics on Hawaiian and Galapageian Volcanoes

by F. R. FOSBERG

Smithsonian Institution, Washington, D. C.

The islands in the Pacific Basin east of the "Andesite Line" (which runs from east of Japan down along the Bonins, Marianas, through the western Carolines, turns east north of New Guinea and Melanesia to Fiji, and south along the Tonga, Kermadec, New Zealand alignment) are either coral islands or shield-type volcanoes of olivine basalt. The coral islands or atolls are in all likelihood ancient, now submerged volcanoes of this same type. In a few of the archipelagoes, such as Samoa, Hawaii, and the Galapagos, there are still active or dormant volcanoes that exhibit recently deposited substrata of fresh volcanic materials, and in some of them even the processes of destruction of vegetation by volcanic action and the reestablishment of pioneer species on new pyroclastic or flow materials may be observed. I have had the good fortune to watch these processes in Hawaii and, to a minor extent, in the Galapagos. The following observations are selected as of possible interest to participants in this symposium*, but some of them form part of a larger body of information to be included in a projected paper on the Hawaii National Park by Professor Mueller-Dombois and myself.

Oceanic shield-type volcanoes are broad, dome-shaped, laminated masses of basalt extruded from fissures or vents in the sea-bottom and, eventually, as successive flows are added, reaching the sea-surface and extending above it to almost 4600 meters (Mauna Kea, Hawaii). The above-water part is, while still new and not much eroded, a broad, gently sloping dome, with minor irregularities in form of cinder cones and spatter cones, as well as collapse craters, and with major summit depressions or calderas. The surface is mostly a mosaic of smooth or ropy *pahoehoe* lava, rough clinkery *aa* lava, and beds of pyroclastic material varying from fine ash to lapilli, pumice, and mixtures of these with volcanic bombs and ejected fragments of all sizes. Some of the pyroclastic deposits present a very similar appearance to sedimentary beds, even to becoming variously consolidated. This mosaic can be very intricate because of the braided and irregular nature of the flows, a fact of very great significance in determining the patterns of vegetation.

The Hawaiian Islands lie in the central North Pacific, in a single chain over 3000 kilometers long, extending from W.N.W. to E.S.E., with the two easternmost islands, Maui and Hawaii, the largest and youngest. These two are the ones of interest to us in this paper, as on Hawaii there is still frequent volcanic activity and on Maui the last such activity occurred only about 200 years ago. The Hawaiian Islands lie directly in the Northeast Trade Wind Belt and the

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climate, though somewhat seasonal, is not strongly so.

The Galapagos are apparently younger than the Hawaiian Islands, and lie in an irregular group directly on the Equator, 1000 kilometers west of the coast of South America. They are situated in a much drier and very strongly seasonal climate, with only a short rainy season in February to April. There is an alternation of northeast trades, doldrums, and southeast trades, rather than predominantly northeast trade winds, as in Hawaii.

The floras of both groups are relatively small, as tropical floras go, that of Hawaii being larger with a total of somewhat under 2000 indigenous species and varieties. Its affinities are predominantly with the Southwest Pacific and the Indo-Malaysian regions, while those of the Galapagos are almost entirely American. The floras of both groups show a high degree of endemism, that of Hawaii reaching about 95% of the indigenous flora. Among the endemics are many isolated relicts of ancient floras, as well as swarms of recently evolved varieties and species resulting from "adaptive radiation" in response to new and diverse environmental conditions and from "genetic drift," so likely in small insular populations.

The ecological behavior of these endemics, especially those resulting from recent local evolution, is reasonably easy to observe and understand when seen under undisturbed conditions, and when the situation is not complicated by the introduction of exotic plants. However, in Hawaii there are no areas still free from exotics, and in the Galapagos very few. However, I had the good fortune to see three localities in the Galapagos, one of them the site of very recent volcanism, where exotics had not yet become established. Another most unfortunate consequence of the presence of introduced plants in these open, pioneer situations is the crowding out and eventual complete elimination of many of the indigenous species, thus altering the vegetation pattern profoundly.

For convenience in discussion, the vegetation patterns on these islands may be divided into two categories: major patterns, corresponding to regional or local climatic patterns; and minor ones, related to differences in substratum and microclimate. This separation is not always very clear but will aid in understanding the bewildering array of variations in vegetation that are immediately apparent to the field observer.

The major vegetation patterns in both groups of islands seem to be controlled by elevation and the consequent climatic patterns. The most obvious effect of increased elevation on local climate is, of course, the steady decrease in temperature. Increased insolation is also usual except in cloudy areas, and winds are often much more severe, especially on crests and in passes and gaps. Much more striking, in its effect on vegetation, is the production of "orographic" rainfall, increased precipitation, resulting from cooling of the air as it rises to go over mountain ridges. One can stand on the crest of the Koolau Range, Oahu, Hawaiian Islands, and watch clouds form as the trade wind hits the cliffs below and rises, and feel and be wet by the orographic rainfall that occurs when these clouds reach a critical height and begin to lose their moisture. Even more conspicuous is the effect, in the Hawaiian Islands, of prevailing winds from one direction, in creating "rain shadows," dry areas on the leeward sides of the mountains, where the vegetation contrasts sharply with that on the wet windward sides, and where the altitudinal zones are deflected sharply upward on the leeward sides in relation to their elevations on the windward sides. Both Maui and Hawaii are high enough that they extend above the height to which the trade winds are lifted on encountering the mountains, so that above about 2500 meters, even on the windward sides the climate is rather dry. The island of Hawaii is large enough to produce still another peculiarity. On the leeward side (called the Kona Coast) there is a zone between sea-level and about 1500 or 2000 meters elevation, wet by convection showers that occur in the late afternoons. Locally topographic irregularities, especially resulting from faulting and from the clustering of several volcanic domes, cause complications in the simplified climatic picture drawn here.

In the Galapagos the lowlands, generally, are dry, though mostly rather well vegetated. Moisture gradually increases upward and at higher elevations, from about 200 meters upward, is a belt where a nocturnal stratus cloud layer intersects the mountain slopes, providing a very considerable moisture supply from condensation, even during the dry seasons. In these islands the dry season is very long, extending from May through January.

The major vegetation patterns generally correspond very well with these moisture patterns. On windward slopes in the Hawaiian Islands hygrophilous forests extend from sea-level to the elevations where orographic rainfall diminishes so that drought conditions are likely.

It is interesting that the two tree genera that, one or the other, are dominant in most of the Hawaiian hygrophilous forests, *Metrosideros* and *Acacia*, are both strongly xeromorphic in their morphology. The significance of this is not altogether clear, but several things may be said:

1. Neither of these genera is endemic in the Hawaiian Islands. They presumably colonized the islands in somewhat their present form. The *Acacia* belongs to the phyllodinous group, presumably evolved under arid conditions in Australia. *Metrosideros* principally inhabits volcanic islands, except for parts of New Zealand (much of which is volcanic) and New Caledonia, where its habitat is not too well known to me.

2. Out of many colonists of diverse habit, these two have been the most successful in occupying large areas of the Hawaiian Islands.

3. The new lava and ash substrata, which have apparently been prominent in the Hawaiian Islands from their beginnings, favor at least facultative xerophytes because of extreme drainage and high temperatures.

4. Present distribution of these trees, though prominently in mesophytic or hygrophilous forests, extends well into very dry regions, precisely on new lava substrata.

Hygrophilous vegetation also characterizes the convection belt on Hawaii, this forest being very tall and fine in the middle, moister elevations in this strip. There are also a number of other areas of hygrophilous forest on the leeward slopes of Hawaii, where, apparently, local topographic conditions result in rainfall either of orographic or convection origin. The environmental relations of these areas have not yet been adequately studied.

Transitions to xerophilous forest are usually rather rapid but the changes are continuous, rather than sharp. The dominance of the xeromorphic *Metrosideros* and *Acacia koa* makes these transitions seem much more gradual than they actually are. The more mesophytic character of the vegetation in old "kipukas" of deeply weathered soil in xerophytic regions suggests that the raw lava substratum accentuates the effects of dry weather, as might be expected from the lack of clay and other materials with enormous surface area and capillary effectiveness.

In lowland and middle elevation xerophytic areas, both open forest and scrub are prominent vegetation types. The shrubs and trees are strongly xeromorphic and their spacing tends to be open, and the rates of development of vegetation are exceedingly slow in comparison with those in mesophytic areas at the same elevations.

At middle to fairly high elevations native grassland with scattered trees and shrubs becomes an extensive type, alternating with almost bare younger lava flows.

At higher elevations the character of the substratum seems to exert a strong effect. Mauna Loa, almost entirely covered by recent lava, has little vegetation above 2600 meters. Mauna Kea and Haleakala, with more predominantly pyroclastic surfaces, have vegetation—mostly a rather "open to sparse" sclerophyll scrub—up much higher to the summit of Haleakala and to 3300 meters on Mauna Kea. Above that, there is very little vegetation of any sort.

In the Galapagos, except for new lava, the lowlands are covered by a highly xerophytic rather open forest, largely of *Bursera* or *Croton*, but with arborescent cacti and spiny leguminous trees. Upward this becomes more mesophytic and hygrophilous until, where the cloud belt is well developed, it is a broad-leafed forest, dominated by *Psidium* or *Scalesia*, and festooned with hepatics and other epiphytes. Ferns are abundant at these levels. Such vegetation is found in suitable places at least up to 1500 meters. However, extensive areas on the larger and higher islands are covered by such recent lava that closed vegetation has not had time to develop.

Minor vegetation patterns are superimposed on the broad patterns just described. They are controlled by a number of localized factors of which volcanism is the most conspicuous, and moisture availability is probably just as important. These are so intricately interrelated that clear correlations are not easily established. Succession, also, is of profound importance in determining vegetation patterns, as are the differing rates of succession on similar substrata under different climatic regimes.

The most obvious vegetation feature controlled by volcanism is the "kipuka" phenomenon. A kipuka is an "island" of vegetation surrounded and isolated by lava flows which have covered and destroyed all except the kipuka of the preexisting vegetation in the vicinity. Kipukas occur in all or most areas of lava flows and are of all sizes and ages. One of the best known examples is the Kipuka Puaulu or Bird Park, at Kilauea, Hawaii. Here is an area of an ancient surface of deeply weathered volcanic soil with forest that is completely different from anything in the vicinity and containing a number of tree species found nowhere else in the world.

The pattern of early pioneer vegetation on *pahoehoe* (smooth) lava and that on *aa* (rough) lava show strong contrasts. On *pahoehoe*, plants gain a foothold principally in the numerous cracks that form in the surface, and in accumulations of ash in folds and depressions. These are mostly herbaceous flowering plants, ferns and shrubs. The gray moss *Rhacomitrium*, may be abundant. On *aa*, fern sporelings appear in sheltered spots. Lichens, especially *Stereocaulon*, appear abundantly on all surfaces except in the very driest areas. *Metrosideros* seedlings, which in other areas frequently start as epiphytes, become established and send their roots down through the glassy sponge-like surface to tap water that accumulates on top of the dense inner part of the flow.

Lines of vegetation following the direction of a flow may mark collapsed lava tubes or low cliffs left by the subsidence of the central part of the flow as fluid lava is drained from beneath the surface. The vegetation seems to be encouraged by the shade given by the clifflet during a part of the day. In the collapsed lava tubes there are probably both shading and perhaps intermittent running water.

Clumps of vegetation mark subsidence craters and broken lava bubbles.

Fumarole areas and hot spots, even in forested areas, have sparse, dwarfed vegetation, of very different composition from that of surrounding areas.

Drifting sulphur-dioxide fumes from eruptions have a strong effect on vegetation, killing many species and defoliating or killing back the tips of others.

The general appearance from the air of the vegetation on lava flow slopes on the wet or moist sides of the mountain is that of an intricate mosaic of patches of green of different shades and textures, corresponding to vegetation on flow surfaces of many different ages, left by braided flow patterns superimposed upon each other. In other words, this is a vast aggregation of kipukas.

On the dry sides of the mountains there is likewise such a mosaic, but the scrub vegetation here is sparse enough so that the browns and blacks of the lava showing through dominate the color in most places. Areas of green represent very old kipukas on which forest has had time to develop.

Ash beds are commonly more extensive and have more uniform vegetation. An interesting example of this is a tall scrub of *Chenopodium oahuense* on deep ash in the Humuula Saddle between Mauna Kea and Mauna Loa. Ash beds on very dry areas at low elevations on the leeward side of Hawaii are covered by sparse grasses and sedges, but in places form dunes with little vegetation.

The southeast coast of Hawaii is mostly lined by low wave-cut cliffs, cut in relatively recent lava flows. The vegetation changes along the coast, back from the cliffs, going southwestward, from sclerophyll forest to scrub, and to almost no vegetation at all. At the top of this cliff is a completely bare strip, splashed by salt spray. A few clumps of *Fimbristylis cymosa* are found within 10 or 15 meters of the edge. From here back *Sesuvium portulacastrum*, *Scaevola taccada*, and several other strand species become rapidly more abundant, until there is a closed scrub which gradually fades into the sclerophyll forest. Where the general vegetation becomes sparse, so does the strand belt described above gradually disappear.

The above observations are on Hawaiian vegetation patterns. In the Galapagos I am only able to describe one local situation that is correlated with volcanic features. Narborough Island is for the most part covered by great sheet-flows of rather new lava. Here and there are kipukas, but they are much less frequent than those on Hawaii. On the new lava, in some areas, are scattered cacti—mostly two species of *Cereus*—and in some areas, scattered trees, probably *Bursera* (seen only from the air). On the southwest slope of the island is a continuous strip of green vegetation running from the sea to the summit, at about 1500 meters. This, as would be expected, changes gradually upward from xerophytic to mesophytic vegetation. About one third of the way up is a conspicuous area of grass, surrounded by scrub and sparse forest. The forest is mostly *Zanthoxylum fagara*. In the grass are scattered a number of species of shrubs of diverse affinities, several of them with a remarkable unbranched or virgate habit. Several arborescent *Opuntia* plants are to be seen. With the grass are quite a number of species of broad-leafed herbs. Land iguana burrows are very common. The substratum in the grassland is a finely broken pumice. The surrounding rough lava, in the immediate vicinity of the pumice area, is covered by rather thick scrub, with some trees and patches of low forest. The scrub extends up two small cinder cones but disappears when newer lava is reached on either side of the strip. This area has the distinction of being one of the few areas of relatively open vegetation that I have seen which almost completely lacks exotic species. One individual of *Sonchus oleraceus*, a wind-dispersed species, was seen.