Invasion and Recovery of Vegetation after a Volcanic Eruption in Hawaii

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Summary

A major volcanic eruption on the island of Hawaii in December 1959 devastated an existing montane rain- and seasonal-forest covering an area of about 500 hectares (ha). The eruption resulted in a massive pahoehoe lava substrate on the crater floor of Kilauea Iki, in a new cinder cone, in an area covered with spatter and another with an extensive blanket of pumice varying along a fallout gradient from over 46 m to less than 2 cm deep. Six new habitats were recognized by kinds of substrate and remains of former vegetation. A study was made of plant invasion and recovery from the time of the disturbance till 9 years thereafter. Plant records consisted primarily of periodically listing species by cover-abundance in a large number of quadrats along a transect system that crossed the crater floor and extended about 3 km along the fallout gradient. The atmospheric environment was studied concurrently by records of rainfall, lateral rain- and steam-interception, and desiccating power. The substrates were examined for their soil moisture properties, temperatures, mineralogical properties, and available plant nutrients.

It was found that plants moved onto the crater floor within the first year. They progressed concentrically towards the crater center in correlation with a substrate-heat gradient that cooled progressively from the margin inward. Plant invasion on the cinder cone was delayed by 2-3 years, because of prolonged volcanic heating from below. A fast invasion took place on the spatter habitat where a surviving rain forest was nearby and where tree snags provided additional moisture locally at their base by intercepting wind-driven rains. Establishment at snag bases was also noted on the pumice, and, generally, plant invasion occurred by aggregation of plants in favorable microhabitats which included crevices and tree molds. On the pumice, invasion progressed at a relatively uniform rate in spite of differences in substrate depth and atmospheric environment. The increase in plant cover was much faster on the habitats with vegetation remains than on those without. On the latter, the plant cover was still insignificant in year 9 after the eruption, in spite of a near total spread of plants across these habitats.

The sequence of life form establishment on substrates without vegetation remnants was clearly algae first, then mosses and ferns, then lichens, then native woody seed plants, and finally exotic woody and herbaceous seed plants. On the substrates with former vegetation remains, exotic seed plants participated in the invasion process from the beginning. This was related to the availability of microhabitats with water relations favorable for plants with normal root systems and probably higher water requirements than the native sclerophyllous woody plants. A remarkable recovery occurred among *Metrosideros polymorpha* trees that were buried up to and over 2.5 m deep under pumice. Several native shrubs resprouted after their entire shoot system had been buried. The best herbaceous survivors were those with underground storage organs, which included both native and exotic species.

The invading exotics in no way interfered with the establishment of the native pioneer plants. Initial stages of succession were observed whereby native woody plants began to replace exotic woody plants. Among herbaceous plants, exotic species were far more numerous, because there are only very few native species in this group. A succession, in part caused by competitive replacement, was noted among the exotic herbaceous plants. Thus, there appears to be no threat of native plants to be replaced by exotics on these new volcanic substrates. The native forms are better adapted to these harsh environments. But exotic complementary life forms are expected to remain in association with the native vegetation because of a lack of life forms among the native species to fill the available niches.

1

Introduction

In December 1959 Kilauea Iki, a pit crater on the summit of Kilauea Volcano, erupted and deposited a blanket of ash over an area of 500 ha. The entire area was later named "Devastation Area" because of the widespread destruction of vegetation.

The devastated area provided an excellent opportunity to study the formation of new plant communities on a variety of new volcanic substrates. The question of how plant communities originate has been of great interest to ecologists for some time. A number of observations are recorded in the literature. Clements (1916, 1928) even developed his scheme of vegetation classification on general observations relating to the origin and succession of plant communities. Yet, many of his conclusions about vegetation origin and succession were based on side-by-side comparisons of different communities that are supposed to form a sequence in time, where in reality they form a sequence in space.

Observations of plant populations and vegetation changes on the same site over a period of time offers much more reliable information on community origin and succession than spatial comparisons. However, the opportunities for such studies are restricted to the occurrences of new substrates, and these are not often found in nature. Moreover, most observations on new volcanic substrates relate to rather general records of species occurrences (Uhe 1972). Rarely have studies been done that consist of annually repeated records in permanent quadrats.

When beginning this study, the following questions were asked:

1. In what sequence do plant life forms and species invade?
2. What is the rate of species increase on new volcanic substrates?
3. At what rate does plant life cover the barren surfaces?
4. How does volcanically damaged vegetation recover?
5. What are the environmental factors and factor intensities that limit plant invasion and recovery?

On the basis of information in the literature and preliminary observations, it was hypothesized that the invasion of plant life forms would follow the sequence of algae, lichens, mosses, ferns, and finally seed plants. It was also thought that succession would be more rapid on ash than lava rock and that invasion would be positively correlated with rainfall.

In terms of species invasion, there was a question as to whether endemic or exotic plant species would be more successful. The endemic flora in Hawaii originated from chance establishment of plants whose disseminules must have traveled great distances. In the development of this endemic flora into communities, one important evolutionary stress-factor was volcanism. Volcanism must have disturbed established plant communities from time to time in much the same way as it does today. Endemic plants may be said to be adapted by evolution to various forms of volcanic disturbances, while some exotic species are aggressive weed plants that may also be able to cope with drastic disturbances.

The question of exotic species invasion was of particular interest to the park resources managers, who are charged with the responsibility of keeping the national park in a pristine condition. Invasion of exotic species is looked upon as an unnatural phenomenon. Therefore, a study was necessary to find which group of species, exotic or endemic, would be more successful in forming the new communities.

2

Analysis of Previous Studies

Studies in Hawaii

A framework for ecological studies in the Hawaiian Islands has been given by several descriptions of vegetation zones (Hillebrand 1888; Rock 1913; Hosaka 1937; Egler 1939; Robyns and Lamb 1939; Hart and Neal 1940; Ripperton and Hosaka 1942; Krajina 1963; Knapp 1965). Three ecological studies were concerned with more local physiographic sections of Oahu (Hosaka 1937; Egler 1947; Hatheway 1952). Their emphasis was on the description of current plant communities. Fosberg (1961) provided a summary description of about 30 major ecosystems that are prevalent on nearly all the high islands.

Several ecological studies deal specifically with the island of Hawaii, which because of its recent volcanic surfaces, shows major unconformities in vegetation types to the other high islands. Doty and Mueller-Dombois (1966) reviewed all bioecological studies that had been done up to that time in Hawaii Volcanoes National Park. In addition, a detailed framework of ecosystem types was provided with this publication—an aerial photo vegetation map and five topographic vegetation profiles. These ecosystem types were further investigated for their phytosociological relationships (Newell 1968) and tree stand relative to soil characteristics (Rajput 1968). Mueller-Dombois (1967) analyzed in some detail the ecological relations in the alpine and subalpine vegetations on Mauna Loa volcano, and a comparison of east-flank vegetations on the still active Mauna Loa and the older, dormant Mauna Kea volcanoes was made (Mueller-Dombois and Krajina 1968). These studies provide the more specific ecological framework for studies dealing directly with succession on volcanic surfaces.

Studies directly concerned with aspects of vegetation dynamics on new volcanic material of Hawaii, the youngest island, were done by Forbes (1912), MacCaughey (1917), Robyns and Lamb (1939), Skottsberg (1941), Doty (1957, 1961, 1966, 1967a, 1967b), Miller (1960), Fosberg (1959), Mueller-Dombois (1967), Jackson (1969), Atkinson (1969, 1970), and Eggler (1971).

Forbes was the first to study plant succession on recent Hawaiian lava flows. His observations were confined to the summer-dry region on the lee side of Mauna Loa. Here he studied five lava flows with dates of 1859, 1884, 1887, 1907, and one of recent origin but not dated. His major conclusions with regard to plant invasion, succession, and climax on lava flows on the leeward side are summarized in the following points:

1. Appearance of lower cryptogams, eventually becoming conspicuous on the a'a.
2. Appearance of *Polypodium pellucidum* (folded form), *Sadleria cyatheoides,* and *Metrosideros polymorpha* (ohia), first on pahoehoe, and at a much later date on a'a.

3. Gradual development of the typical floral aspects of the immediate vicinity, if in the central region of an ohia forest.
4. Establishment of the final native vegetation, if in the central region of a koa forest.
5. A later stage may be the encroachment of the naturalized flora, due to a change of conditions brought about by human agency.

MacCaughey (1917) also confined his study to the xerophytic regions. He reported that the rate of invasion depended on rainfall and adjacent vegetation, and that his findings generally agreed with those of Forbes. In contrast he found that lichens occurred much sooner on a'a than on pahoehoe, while ferns and trees established earlier on the pahoehoe lava type.

Robyns and Lamb (1939) recognized and classified five major climax formations for Hawaii. In so doing they followed the monoclimax concept of Clements. They emphasized that climate controls the final form of vegetation, while the soil accounts only for developmental stages. They concluded that the rate of invasion and vegetation density increased with rainfall and that moisture is more important in plant establishment than age of the substrate. They reported the course of primary succession in the Kilauea region in three steps:

1. Invasion of cracks in the new flow by ferns and flowering plants that are common to the adjacent area, and supported by nonvascular cryptogams especially on the a'a lava.
2. Gradual building up of heavier plant covering, filling in between the cracks, producing a shrub stage in which *Dodonaea viscosa, Styphelia tameiameiae,* and *Metrosideros polymorpha* predominate.
3. Development of a plant community typical of the vegetation formation found in the surrounding area.

Skottsberg (1941) was the first investigator in Hawaii to make observations in the same locations after a lapse of time by using permanent quadrats to study plant succession. He established six 10 x 10-m quadrats in 1926. Four were laid out on the 1920 Kilauea flow in the Kau Desert in a summer-drought climate, the other two were established on the 1919 Mauna Loa flow in a rain-forest climate in southwest Hawaii. Within each of the flows, he compared a'a with pahoehoe sections. As expected, the plant invasion rate was very much faster on the 1919 flow (wet climate) than on the 1920 flow (dry climate), and the species diversity was greater in the moist climate. In general, he found invasion of vascular plants to be denser on pahoehoe, while cryptogams (mosses and lichens) were becoming widely established on the a'a lava. This supported the earlier observational studies. Skottsberg's work points out the need of distinguishing finer substrate differences in relating plant invasion to the type of volcanic surface material.

Doty (1957, 1961, 1967a, 1967b) made the most intensive study of plant succession on Hawaiian volcanic materials to date. His work was confined to the 1955 lava flow on the east flank of Kilauea Volcano, which is in a humid climate. He observed that blue-green algae were established 3 months after the flow had stopped. At 6 months the algae were followed by a large number of individuals of cryptogamic and vascular plants. These consisted of the following species: a fungus (not named); a tree, *Metrosideros polymorpha;* an herb, *Erechtites valerianaefolia;* an orchid, *Spathoglottis plicata;* a fern, *Nephrolepis exaltata;* and a moss, *Campylopus.* Doty reasoned that the vascular species were established because of abundant water from steam condensing (recylcing rainwater) on the flow surface. About 14 months after the eruption, large numbers of plants died. Doty assumed that a drought had developed on the flow. He believed this to be caused by a decline of vapor steaming. He attributed the reduction of steam condensation to the cooling of the flow-interior. During the drought, nonnative species disappeared completely and the number of native species was greatly reduced also. However, when rainy periods prevailed, native cryptogamic populations were found to form a succession. The blue-green alga *Scytonema* and then *Stigonema* were replaced by *Stereocaulon* lichens.

Fosberg (1959), after examining the alpine and subalpine zone of Mauna Loa, believed that the scattered, high altitude plants seem to have no ecological relation or dependence between them. He found that they occur in separate niches or isolated examples of the same niche. Contrary to Fosberg's findings, Mueller-Dombois (1967) found species successional relationships in the alpine scrub vegetation on Mauna Loa. He reports that where the shrubs *Vaccinium peleanum* and *Styphelia douglasii* grow together, the latter tends to replace the former.

Jackson (1969) studied the role of *Stereocaulon* lichen in rock weathering at low altitudes on eight dated Mauna Loa and two Kilauea flows that traverse different rainfall zones. He found that this lichen greatly accelerated the weathering of the basalt lava. A reddish-brown colloidal "gel" was isolated that consistently occurred in association with *Stereocaulon* on the lava flows in areas of higher rainfall. The gel was not found on rock surfaces not occupied by this lichen nor on those in dry climates, where *Stereocaulon* remained stunted or immature. The gel was identified as a polymorph of ferric (III) oxide containing minor amounts of aluminum and titanium oxides and traces of silicon. According to Jackson, this is the first record of this specific iron compound ever found in nature, and he tentatively gave it the name "lichenite."

Atkinson (1969, 1970) examined the successional trends in the humid and subhumid lowland to montane areas of Mauna Loa and Kilauea volcanoes from a side-by-side comparison of flows of different ages. He was trying to find a method to extend the dating of lava flows beyond the recorded dates, which go back about 200 years. By using the rate of calcium loss, pH change, and titanium gain, he believed that he had found a means of extending the lava flow dates in the humid and subhumid lowland to the montane ozone for another 200 years. On this basis, he described four chronosequences as being distinct, all beginning from volcanic rock. According to Atkinson, a coastal sequence terminates via a *Metrosideros* stage in a *Pandanus tectorius* forest; a humid upland sequence, in a *Metrosideros-Cibotium* forest; a humid lowland series, in a *Metrosideros* dominated forest with minor quantities of *Cibotium* tree ferns. A subhumid to summer-dry series is believed to terminate in a *Metrosideros-Diospyros ferrea* forest. Starting from barren lava, the development of these four different forest types is thought to take place in less than 400 years. No consistent differences in succession were observed in relation to a'a and pahoehoe lavas.

Eggler (1971) studied vegetation on 16 young lava flows on the island of Hawaii for approximately 3 years. These represented a'a and pahoehoe types found in both wet and dry climates. They ranged in age from prehistoric time (prior to 1778) to deposits made in 1965. Eggler said that he could find little evidence of a succession pattern among the vegetations on these flows. Further, he observed that the rate of establishment of plants on these flows may have differed greatly. After contending that there are no distinguishable patterns in succession and rate of establishment among Hawaiian laval vegetations, Eggler proposed a formula for predicting biomass accumulations on volcanic substrates. The factors in this formula were: age of lava flow x precipitation x lava type x soil factor = biomass/ha. It seems clear that Eggler's design of side-by-side comparisons of flow vegetations did not permit reliable conclusions on succession and rate of establishment. His biomass formula fails to reveal any phytosociological relationships. These would be important for an understanding of succession.

The literature survey of plant succession studies on Hawaii shows that the information is still only fragmentary. This is due in part to the great range of environmental conditions available and in part to the differential intensity of the studies. Three general questions have been partially answered for limited types of climates and substrates. These are:

1. What kinds of plants are the invaders on new lava materials and what are their followers?
2. Which type of lava is more rapidly invaded: the rough a'a or the smooth pahoehoe?
3. How long does it take for a forest to develop from the time of lava flow origin?

No attention has as yet been paid to succession on other types of volcanic substrates, for example, the various kinds of pyroclastics. Ash substrates are as prevalent as are lava rock substrates in Hawaii, but ash or pyroclastic substrates have received no attention in succession studies. From a fundamental viewpoint, plant invasion and succession on pyroclastic materials are equally significant. Also, little is known about the rate of species increase in the initial stages of succession. Only three studies were based on periodic observations of the same places. All others relate to conclusions drawn from adjacent observations that are presumed to form chronosequences, and these are still very general.

Studies in Other Volcanic Areas

A comprehensive review of work done in other volcanic areas of the world, including the Hawaiian Islands, was recently presented by Uhe (1972).

The more pertinent aspects relative to the present investigation may be summarized in three points: (1) Damage to existing vegetation and its recovery after volcanic activity; (2) New colonizers; (3) Invasion rates with respect to different materials.

1. Partial destruction of existing vegetation from deposits of the same volcanic material was found to have a selective effect on species composition and size within species. Eggler (1948, 1963) observed a better recovery of oaks than of other tree species and found that medium-sized pines were favored over small- and large-sized pines under deposits of ash on the slopes of El Parícutin, Mexico. Such effects may have contributed to differences in current species composition of vegetation islands on Mauna Loa. Eggler (1967) also found that the diameter of survival trees in the ash fallout area increased greatly. After examining the increased xylem tissue, he believed that in some cases the rapid increase in growth rate was caused by a decrease of competition. In another instance, he suggested that auxin increase, decrease, or destruction could have accounted for various rates of growth. A similar increase of the diameter of ash-buried survival trees was reported by Griggs (1922) from Mount Katmai.

Several investigators have reported that survival plants appeared to accelerate the rate of invasion of new colonizers and the revegetation process as a whole. Sands (1912) had observed great differences in the rate of vegetation reestablishment on St. Vincent Volcano (West Indies) as related to the depth of the ash blanket. Where the ash cover was shallow (implying a depth range of 30-150 cm), vegetation reestablished rather quickly. He attributed this to plant parts that survived under the ash and stated that much of the vegetation recovered from buried root systems and also from seeds. However, the latter explanation is rather questionable and would need reexamination. Gates (1914), studying the plant succession on Taal Volcano in the Philippines, also observed that where plants survived the eruption, either with their aerial parts or roots, the reestablishment of vegetation was faster. In habitats where there was no evidence of plant survival and where the volcanic substrate contained no residual organic material, the revegetation process was much slower. Aston (1916) also attributed the fast recovery of vegetation on the Tarawera Mountain eruption site (New Zealand) in part to hold-over plants. Griggs (1918, 1922) reported that at Mount Katmai, Alaska, the first plants to appear originated from buried root systems. Some of these, such as *Equisetum arvense,* were found to grow through 30-36 inches of ash. The hold-over plant recovery was so rapid in areas of ash fallout that he had to transfer his study to more deeply-buried sites. Griggs (1933), in particular, stressed the importance of distinguishing between hold-over plants and new colonizers.

2. Upon complete destruction of existing plant communities, seed sources for new colonization may become a limiting factor (Rigg 1914; Eggler 1963) and new substrates may lack organic nitrogen entirely (Griggs 1933; Tezuka 1961) or the level of organic nitrogen may be very low (Eggler 1963). From these studies it becomes apparent that the type of colonizers may be in part a function of the destruction effects.

Griggs (1933) found that the first colonizers on the deep ash deposits on Katmai were members of the *Jungermanniaceae* (liverworts), which apparently can grow on substrates almost devoid of organic nitrogen. Mosses and algae invaded only after nitrogen levels had increased. A local increase of nitrogen levels on new materials was observed beneath mosses (Eggler 1963; Tagawa 1964). In some tropical habitats the first colonizers have been algae (Treub 1888; Booth 1941; Doty 1961, 1967b). However, there are obviously great differences with regard to species, population density, and habitat. Some investigators thought that algae may supply nitrogen for higher plants. Treub observed thick carpets of blue-green algae on the new substrates of Krakatoa. He believed that these *Cyanophyceae* were the first plant colonizers forming the germination medium for the establishment of ferns. Booth (1941) reports that algae were among the first colonizers of eroded soils in the south-central United States. He found a complete covering of *Myxophyceae* that extended over hundreds of acres. When Brown et al. (1917) found no algae on the volcanic soils of Mt. Taal, they concluded that this condition explained the paucity of vascular species. In contrast, Doty (1967b) observed that the initial colonizing algae had little or no effect in aiding the establishment of higher plants.

Some investigators (e.g., Treub 1888) have contended that higher plants colonizing new volcanic substrates must get their nitrogen from sources other than nitrogen-fixing algae. Ernst (1908) and Campbell (1909), in continuing the Krakatoa study, found an aerobic nitrogen-fixing bacterium in the new soil. They also found abundant nitrogen-fixing bacteria in the root nodules of several leguminous plants on new volcanic substrates. Campbell assumed that bacteria were among the first pioneer colonizers, and that their presence helped to establish higher plants by providing organic nitrogen. Gates (1914) reported that a leguminous shrub, *Acacia farnesiana,* quickly became established on the new sterile soil of Taal Volcano, because the plant was associated with nitrogen-fixing bacteria.

Apparently, algae do not play such an important role in other tropical habitats. Hasselo and Swarbrick (1960), studying a section of the 1959 lava flow or Cameroons Mountain, found that creeping herbs that were rooted in undisturbed neighboring soil were the first colonizers. While they noted no definite algal stage, they found algae covered about 20% of the surface. They also drew attention to seasonal variations which were shown particularly by mosses and herbaceous plants. Tagawa (1964), working on Sakurajima, found early development characterized by bryophytes and lichens and he drew attention to the invasional differences between bryophytes, lichens, and higher plants; the cryptogams have more universal means of distribution and the higher plants are more directionally distributed from seed source centers. Tezuka (1961) found that mosses and lichens were not important on Oshima and that their role as pioneer invaders had been exaggerated by Clements. He also could not recognize the so-called ''herbage'' stage. However, a distinct herbaceous stage was recognized by Tagawa (1964) on Sakurajima. Also, Millener (1953) claimed that the classical sequence of algae-moss-fern-higher plant arrival was not applicable in many habitats on Rangitoto Volcano (New Zealand). Instead, he claimed that woody plants, *Metrosideros excelsa,* were pioneer colonizers. He explained the mode of pioneer colonization by woody plants as expansion of islands of forests that became established as circular colonizers in various places on an otherwise uniform lava surface. Millener (1965) also observed that of the 400 species of vascular plants found on the lava flows more than half were non-natives.

Similar to Forbes' (1912) and Skottsberg's (1941) findings on the island of Hawaii, a fern stage was recognized by Keay (1959) on Cameroons Mountain, which was well established 14 years after deposition of the 1922 lava flow in a very wet region. Shrubs were established 29 years after the eruption, while ferns persisted. Keay reported 12 species of *Ficus* as pioneer trees.

Tagawa (1966, 1968) also studied disseminule dispersal with cotton traps on Sakurajima. He found that several pioneer mosses were wind-dispersed by shoot fragments that would produce new plants. Spores were produced only during dry periods. The main reproductive mode appeared to be vegetative. He also noted that where topography influenced wind movement, this factor was important in disseminule dispersal, perhaps even more so than the direct distance to the seed source.

3. Different rates of invasion with regard to differences in substrates were observed by Eggler (1963) on El Parícutin. Plants were able to start on lava but not on unmodified ash. Mosses started in lava cracks where run-off water accumulated. Invasion rates were related to accumulation of wind-deposited ash that had sifted into cracks rather than to the differences of a'a and pahoehoe lava. This observation is similar to that of Skottsberg (1941) on Hawaii. Eggler also observed faster colonization of mosses where soil water was locally augmented by condensation near steam vents. Earlier, however, Eggler (1941) noted a slower vegetation succession on a'a lava in southern Idaho, as did Forbes (1912) on Hawaii. Tagawa (1964) also found more mosses and lichens on rough lava (a'a) than on smooth at Sakurajima. Taylor (1957) found ash-particle size to be one of the major factors causing differences in plant establishment on recent volcanic deposits in New Guinea (Mt. Lamington, Waiowa Volcano, Mt. Victory). Plants tended to get started earlier and increase more in cover on thin ash deposits than on deep ones. He attributed this to the finer material that was sorted out at the margin of the ash blanket. Here, the fine material was assumed to hold more water than the coarser ash in the deeper parts. Similarly, Treub (1888) described the deep Krakatoa pumice material as a very dry substrate. Dilmy (1965) observed that the hard-crusted soil on the 1963 Agung Volcano eruption site impeded new plant establishment. Survival plants were among the first to appear in the devastated area. However, both

these and pioneer plants could only become established along small rivers and on moist sites.

Schwabe (1969) and Behre and Schwabe (1969) reported briefly about the initial plant colonization of Surtsey, the volcanic island near Iceland that surfaced in 1963. Activity had ceased in 1967. Within one year after that, they noted a dense cryptogamic flora in and around fumarolic areas. They listed eight species of blue-green algae (one of them a nitrogen-fixer), three species of mosses, and a large number of diatoms. This initial colonization was associated particularly with small ash mounds near fumaroles. The vapor steam of the fumaroles had apparently caused the formation of these miniature dunes by binding fine, air-blown ash particles through moisture condensation. The authors refer to these locally favorable substrates as "oases" and say that they make up about 13% of the total new surface area. Occasional germinants of herbaceous seed plants were observed near the coastal points where seed was apparently inadvertently introduced with supplies. However, none of these higher plants have exhibited a community-type establishment.

The analysis of previous studies has shown that although some significant invasion patterns have been recognized, there are still gaps in the knowledge. For example, algae always seem to be among the first invaders, particularly where there are no surviving plants. But their significance in terms of abundance and interaction with other life forms has been evaluated very differently. In some studies algae are believed to provide the necessary organic nitrogen for higher plants or to form at least an important germination medium for these, while from other studies the role of algae seems completely independent and without relation to the other plant-life forms. Lichens and bryophytes appear to be significant only in certain climates. Ferns seem even further restricted because their presence is not often emphasized outside the tropics. Vascular plants can be among the first pioneers, but their appearance seems to be related to the degree of volcanic destruction, which makes their role as "true" pioneers somewhat questionable.

The review shows also that it seems difficult to define habitats before any definite community pattern is established. This is reflected in the rather general descriptions of volcanic environments.

Long-term observations of the same areas are fragmentary at best. This relates to the listing of species and life forms as well as the assessment of associated habitat factors. Very little emphasis has been placed on the relationship of life forms to one another and to the habitat complex. Changes in vegetation structure are only vaguely documented. Photographic records of the same volcanic habitats over a period of time are almost unavailable. There seems to be a near total lack of systematic and quantitative records. While species lists have been published for certain pioneer and later successional stages, there seem to be no continuous records of increase and fluctuation in species numbers in the same area through a sequence of years.

3

The Study Area

Geology

The pit crater Kilauea Iki and the area devastated in 1959 are adjacent to the northeastern rim of the Kilauea volcano caldera in Hawaii Volcanoes National Park on the island of Hawaii (Fig. 1). The whole area is nearly 1200 m in elevation.

Kilauea is a shield volcano that rises approximately 6100 m from the ocean floor and 1239 m above sea level. Its summit area consists of a caldera that is 4 km long and 3.2 km wide. This caldera formed by subsidence when magma was withdrawn from beneath the summit (Stone 1926). The main vent of Kilauea is a collapsed crater in the floor of the summit caldera, called Halemaumau.

Until the 1959 eruption, the volcano had erupted about once every 4 years. A chronology of the historic eruptions for Kilauea and Mauna Loa has been published by Macdonald and Hubbard (1966). Macdonald (1962) reports that two historic eruptions have occurred in or adjacent to Kilauea Iki prior to the 1959 eruption. In 1868 a fissure opened in the southwest wall and lava poured into the crater. In 1832 there was an eruption on Byron Ledge, a rim that separates Kilauea Iki from the main caldera. At that time, lava poured into both Kilauea caldera and Kilauea Iki.

The most common lava of the Hawaiian volcanoes is olivine basalt (Macdonald and Katsura 1961).

The December 1959 Eruption

Wentworth (1966) described the devastating character of the eruption. As lava poured into the crater from a rift in the crater wall, it consumed the ohia *(Metrosideros)* forest on the floor and all vegetation on the crater wall up to 115 m from the rim. Prior to the 1959 eruption, Kilauea Iki crater was approximately 250 m deep. After the eruption, the lava lake in the crater rose to a depth of 140 m. Heat from the rising lava lake soon superdried the remaining vegetation and numerous fires occurred which burned vegetation in strips on the upper sides of the crater wall.

The devastated vegetation took on a different character where the pyroclastic material fell. Wentworth observed that during the short violent phases of fountaining, cinders and cobble-sized chunks of lava accumulated at the southwestern side at the rate of several decimeters in depth per hour. These ejecta buried a considerable area of forest and stripped the trees in the leeward and surrounding area of their leaves, bark, and small branches.

Wentworth recognized four major belts of destruction as the pumice and spatter blanket developed. In the first belt, southeast of the vent, there were no remains of the former vegetation because it was covered with a deep mantle of pyroclastics. This is the area of the pumice cone and its surroundings.

Next to this was an area of tree molds, where many trees exploded from overheating and were then consumed by fire. The tree molds are trunk-sized imprints in the spatter blanket that were formed through sudden chilling of the glowing pyroclastic fallout, where it surrounded tree trunks in this zone.

This tree-snag zone was replaced at a further distance by another zone where the trees were severely excoriated from fallen pumice and clots of lava, but showed signs of recovery in a few weeks. Their trunks became heavily covered with a new growth of leaves. Within weeks after the eruption, these surviving *Metrosideros* trees showed abundant flowering.

Although Wentworth reported fume damage to some of the vegetation outside the devastated area, he considered the damage minor as compared to past eruptions. However, the fume was surprisingly acid at least locally. Murata (1966) found the steam condensate from the cinder cone during the eruption to have a 1.9 N HCl concentration.

Climate

The climate of the study area is tropical montane. This implies that the temperature is moderately cool throughout the year.

The mean monthly air temperature values remain below 20°C throughout the year, and may vary little, between about 14°C in the winter to about 17°C in the summer. The mean annual temperature at Hawaii Volcanoes National Park Headquarters (near 1200 m elevation) is 15.9°C (Doty and Mueller-Dombois 1966). The park headquarters station is about 2 km northeast of Kilauea Iki, at approximately the same elevation. Frost has never been recorded in the meteorological shelter, but minimum temperatures as low as 3-4°C are not uncommon in February. However, ground frost occurred in December 1969 in all lower lying areas at the Kilauea summit level.

The mean annual rainfall at Kilauea Iki is at least as high as at the headquarter's station, for which long-term records are available. The 24-year mean annual rainfall at the headquarters is 2400 mm. For the years 1967 and 1968 the mean was 2873 mm, when the record for the same period in Kilauea Iki crater showed 3280 mm (Fig. 3). Annual rainfall at the headquarters has varied from as high as 4350 mm in 1918 to as low as 1210 mm in 1908. These are the greatest extremes recorded since 1899. Inspection of the annual records (Doty and Mueller-Dombois 1966) shows that during 67% of the years the values are between 2000 and 2500 mm. Similar annual rainfall variations can be expected at Kilauea Iki. Both areas are surrounded by *Metrosideros-Cibotium* rain forests.

The mean monthly rainfall at the headquarters station is in excess of 100 mm each month except June, when it may drop to 90 mm.

A gradient of about 1000 mm drop in annual rainfall was found to occur from Kilauea Iki to the south end of the study area in the upper Kau Desert. Here, in the upper Kau Desert, the 2-year mean for 1967-68 was 2203 mm as shown in Fig. 3. In accordance with the 2-year and long-term mean difference at headquarters, one may subtract about 500 mm to obtain a long-term mean rainfall of about 1700 mm in the upper Kau Desert at the end of transect AA' (Fig. 2). The long-term mean at Halemaumau crater was 1300 mm (Doty and

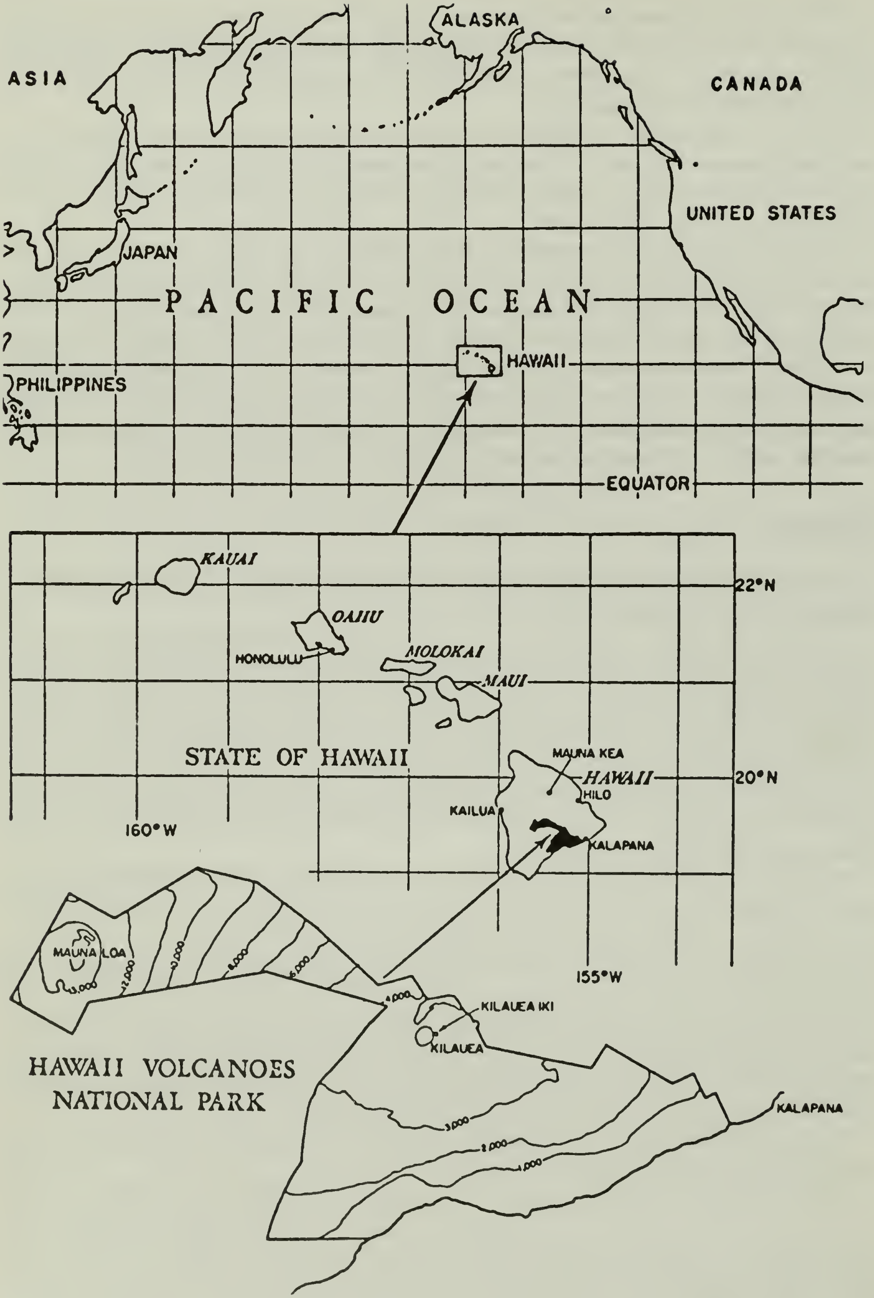

Fig. 1. Map showing location of Kilauea Iki crater in reference to Hawaii Volcanoes National Park and the Pacific Basin.

Mueller-Dombois 1966). Here a summer drought prevails from June through September, which appears to occur also in the southern study area, although of somewhat lessened intensity.

Thus, the study area extends from a montane tropical rain forest climate in the north (Kilauea Iki) to a montane tropical seasonal forest climate in the south (upper Kau Desert). This is indicated also by the original vegetation type boundary as shown in Fig. 2.

The Original Vegetation

The vegetation that was present before the 1959 eruption had never been sampled directly. However, a vegetation map at the scale of 1:12,000 was prepared for the whole park area (Doty and Mueller-Dombois 1966). This map was based on air photos taken in 1954. Three major vegetation types were recognized in the study area before the eruption. They form a sequence from north (Kilauea Iki crater) to south (Kau Desert) along the rainfall gradient previously discussed.

1. Closed *Metrosideros-Cibotium* forest [symbol cM(C) in Fig. 2]. This is the dominant rain-forest type in the park, which occurred formerly in the northern part of the devastated area. The forest is characterized by an upper, almost pure, layer of *Metrosideros polymorpha* trees and a shrub layer, dominated by *Cibotium glaucum* tree ferns. Another tall fern, *Sadleria cyatheoides,* is commonly associated with *Cibotium* in this area. Scattered small trees and tall shrubs include *Myrsine lessertiana, Ilex anomala, Gouldia terminalis, Vaccinium calycinum,* among others. The herbaceous undergrowth is usually thin and includes *Briza minor, Isachne distichophylla, Gahnia gahniaeformis, Hedyotis centranthoides,* and *Cibotium* seedlings. A more complete description is given by Mueller-Dombois (1966) and Newell (1968).
2. Closed *Metrosideros* with native shrubs [symbol cM(ns) in Fig. 2]. *Cibotium* is absent and the most common shrubs are *Styphelia tameiameiae, Vaccinium reticulatum, Dodonaea viscosa, Dubautia ciliolata, Wikstroemia sandwicensis,* and *Coprosma ernodeoides*. The tall fern, *Sadleria cyatheoides,* is often present also in this type, but the shrub composition is otherwise quite different from the first described rain-forest type. This forest joins the *Metrosideros-Cibotium* forest where rainfall becomes more seasonal. (The boundary is indicated in Fig. 2.)
3. Open *Metrosideros* forest with native shrubs and *Andropogon* grass species [symbol cM(ns-A)]. The two *Andropogon* species are the introduced *A. virginicus* and *A. glomeratus,* which occupy a dominant position in the herb layer. Otherwise, this vegetation type is floristically similar to the above. The *Andropogon* grass species were a minor part of the vegetation in 1954; however, when field checks of the 1954 aerial photos were made in 1966, these species formed a conspicuous component.

The New Volcanic Habitats

A survey of the devastated area after the eruption revealed several different habitats. It was reasoned that these could not be lumped together at the start, but would have to be studied individually to evaluate effectively the revegetation processes at Kilauea. There were areas where all the original vegetation was completely buried by new volcanic

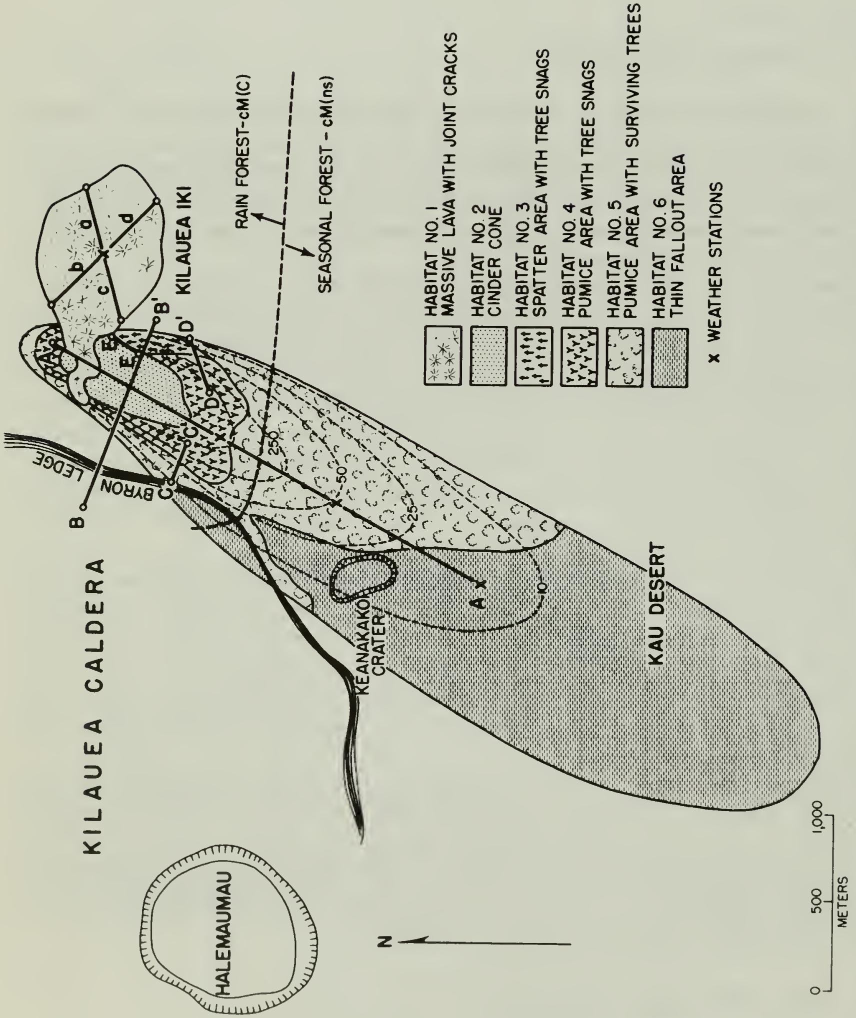

Fig. 2. Habitat types of the 1959 Kilauea Iki eruption site (crater floor and pyroclastic deposit).

materials, with no residues of organic matter left at the surface. Other areas showed dead standing and fallen trees. These were in part blanketed with different kinds of pyroclastics (spatter and pumice). Still other areas showed plants that survived the ash fallout.

Superimposed on these variations in volcanic destruction was the climatic gradient from humid to summer drought. In the latter climate, vegetative growth had always been sparse and of desert-like character. The area is known as the upper Kau Desert. Yet, the desert character of this area is not attributable to the summer-drought climate, but rather to certain peculiarities of the substrate, which will be discussed later. The habitats were classified according to the presence or absence of remnant vegetation and the associated volcanic substrate. It was assumed that differences in succession could be expected in habitats free of organic residues and in those where dead or living plant materials remained.

Following is a description of the six habitats recognized. Their geographic outlines are mapped in Fig. 2. The habitats are sketched in profile on the two diagrams (Figs. 3 and 4).

Habitat 1. Massive lava with joint cracks (56 ha)

This habitat includes the lava lake and high slump scarps on the Kilauea Iki crater floor (Fig. 3, segment 1). The lava lake consists of massive pahoehoe lava, with many joint cracks and crevices. After the eruption, this area was completely barren of life. Many crevices became fumaroles as rainwater permeated the lava lake's thin crust and came in contact with the hot interior.

The wall on the northeast side of the crater rises to 115 m. From this direction the prevailing trade wind carries some dust and organic materials (leaves, seeds, etc.) from the adjacent rain forest onto the crater floor. The major disseminule supply can be considered to come from the surrounding undevastated closed *Metrosideros-Cibotium* rain forest.

Habitat 2. Cinder cone (19 ha)

Included here are the summit and sides of the cinder cone Puu Puai which is 46 m high above the crater rim (Figs. 3 and 4, segment 2). The cone consists of pyroclastic materials that vary from light-weight, glassy, pumiceous particles to thick, heavy, welded masses of spatter. The hot interior has steamed continuously for several years, and at the summit area large amounts of secondary minerals have been deposited. The summit has numerous deep fissures, and on its northeast side, large slough-offs have occurred. Only the southwestern part of the summit and slopes exhibit stability. The climate here is similarly humid as in habitat 1. However, the trade winds blow strongly and continuously over the cone. During some periods, winds of 65-75 kph have been measured. Similar to habitat 1, the cone habitat consists entirely of barren volcanic materials. Its major disseminule source can also be considered to come from the northeast from the closed *Metrosideros-Cibotium* rain forest.

Habitat 3. Spatter area with tree snags (6 ha)

The surface substrate consists of thick welded spatter (a form of pyroclastic material with a density > 1) which piled up to a meter or more around the forest trees, killing most of them (Fig. 4, segment 3). Where the spatter was thin at the margin of this fallout, a few trees

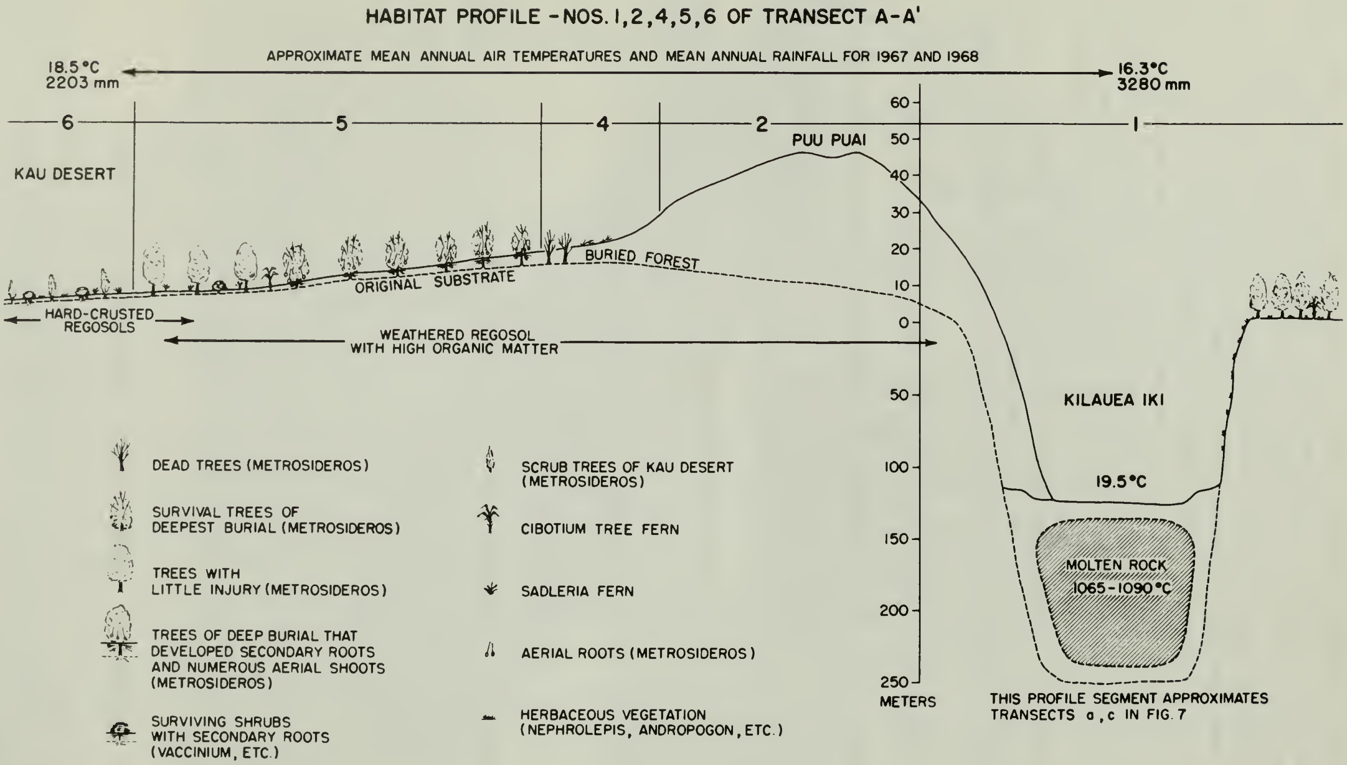

Fig. 3. Northeast-southwest profile of eruption site extending from Kilauea Iki crater to upper Kau Desert.

survived. They later resprouted from buried trunk bases or root systems. The rainfall on this habitat was about 3000 mm per year for the years 1967-68, similar to habitats 1 and 2 (see Figs. 3 and 4). The position of habitat 3, next to a relatively undisturbed, species-rich closed *Metrosideros-Cibotium* forest, provided for a more abundant supply of disseminules than those arriving in habitat 2. A board walk for park visitors was constructed through habitat 3. This also may have contributed to an occasional arrival of man-carried disseminules. Many of the dead trees in habitat 3 remained standing. They acted as local interceptors of wind-driven rain. In this manner, they provided favorable microhabitats for pioneer plants and animals.

Habitat 4. Pumice area with tree snags (31 ha)

The pumice depth varied from approximately 12 m to 30 cm in this habitat. Pumice is defined as pyroclastic material with a density < 1. Much of this area is on the leeward side of the cinder cone (Fig. 3, segment 4). This resulted in some protection from the prevailing winds. Rainfall is less over this habitat compared to the other three (see rainfall gradient indicated in Fig. 3). Here, the original forest was deeply buried, so that only dead trees remained with their top parts above the ash blanket. They seldom fell under the wind pressure except at the eastern and western edges of the habitat where the ash blanket was thin.

This habitat probably received a less abundant supply of disseminules than the other three habitats because of greater distance from the surrounding undestroyed vegetation.

In several places along the deepest part of the fallout (Fig. 3, transect AA′) in this habitat, and that of habitat 5, several small crater-like slumps occurred where ash filtered, after the blanket had formed, into earthquake cracks in the old substratum. These areas of subsidence vary from one to several meters in width or diameter and they can be up to 5 m deep.

Habitat 5. Pumice area with surviving trees (125 ha)

The pumice layer varies from approximately 3 m to 30 cm in depth along transect AA′ (Figs. 2 and 3). Here, nearly all *Metrosideros* trees survived. Because it is lee of the cone and slopes gently in a southwesterly direction, this habitat is somewhat protected from the prevailing wind. However, it receives greater insolation in the lower sectors because of decreased cloud cover. The joint boundary with habitat 4 across transect AA' coincides approximately with the mapped boundary between the original rain and seasonal forest (Fig. 2).

Habitat 6. Thin fallout area (263 ha)

Here, in the upper Kau Desert, the pumice begins with a depth of 30 cm and decreases at the south end of the fallout area to 2.5 cm or less (Fig. 3). Because of the thin cover of pumice with a density of < 1, the pumice particles may be moved about easily during heavy showers. This movement is further facilitated by a partially cemented ash-crust that formed

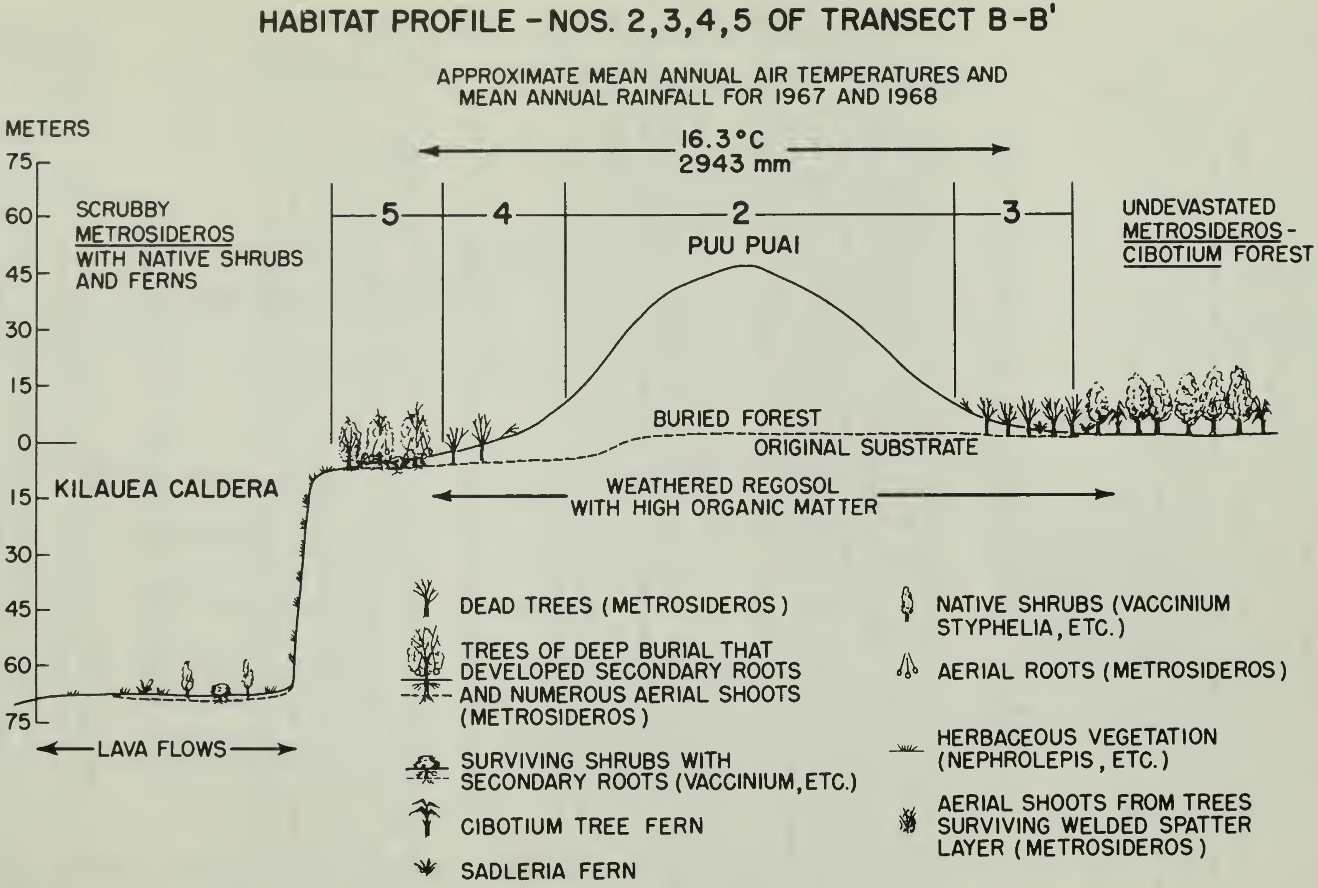

Fig. 4. Southeast-northwest profile of eruption site extending from the undevastated forest into Kilauea caldera.

the former habitat surface. The partial cementation of this former surface was the result of phreatic explosions at Halemaumau (Powers 1948). The substrate is thus very unstable. The pumice is of finer particle size than in other habitats and is made up largely of fine, black, glass-like fragments and some long, thin threads of glass, called Pele's hair. The vegetation is characterized by widely scattered, short *Metrosideros* trees and native shrubs. The woody plants grow in cracks and crevices and in deposits of the hard-crusted ash. A cloud cover seldom extends to this habitat, while cloud cover is a regular phenomenon over habitats 1 through 5. Therefore, habitat 6 receives a larger amount of sunshine than the others. Many deformed shrubby *Metrosideros* trees are bent toward the southwest away from the direction of the trade wind that blows from the summit area of Kilauea.

4

Methods

Vegetation Sampling

Plant species were listed periodically in permanent plots. These plots were arranged in a transect-system across the study area (Fig. 2).

On Kilauea Iki crater floor (habitat 1) four 1-m wide belt transects were laid out. Each of these begins at the crater floor margin; transect a at the NE side, b at the NW side, c at the SW side, and d at the SE side. The four transects join in the center of the crater floor in the form of a cross. Each 1-m wide belt transect was subdivided into 1-m segments, forming contiguous square meter plots. The number of square meter plots was determined by the transect length, transect a = 325 m, b = 385 m, c = 340 m, and d = 400 m.

The other five habitats were sampled with five transects. One transect, AA′, extends in a NE direction parallel to the prevailing trade winds; a second one, BB′, is at a right angle to the trade winds. This forms a cross with the first one (AA′) on the cinder cone (habitat 2). The remaining three transects CC′, DD′, were laid out in the habitats next to the cinder cone.

A number of 10 × 10-m plots were established along these five transects. These are distributed by habitats as shown in Table 1.

Plots are arranged contiguously along the transects except along the long transect, AA′. Here, the plots are distributed at intervals, but uniformly, through habitats 4, 5, and 6.

A species list was prepared for the entire "Devastation Area," which was updated at each resurvey. The species found in the plots were checked off by assigning a Braun-Blanquet symbol (1965). In addition to the presence-record, this method provided for an estimate of abundance and cover of each species. These records began in January 1960 right after the eruption had ceased and were repeated five times in 1961, 1962, 1963, 1966, and 1968. The final year was 9 years after the eruption. The species list record was restricted by necessity to macroscopic plants. Algae were thus recognized only if they formed visible colonies, which appeared usually as dark blotches on the volcanic surfaces. It is quite possible that small-sized colonies may have been overlooked occasionally in a few quadrats. But the repeated observation of a large number of quadrats makes the appearance-record of the macroscopic algae for each habitat quite certain.

In addition to these records, photographs were taken periodically at 13 permanently fixed photo stations along the transects. The photographs were to serve as a visual documentation of the vegetation recovery in different habitats. The photographs were taken of exactly the same landscape segments in four quadrants around the central point of each photo station.

Environmental Measurements

A few environmental measurements were made in an attempt to find at least a partial explanation for the plant invasion and recovery patterns that were expected to emerge.

Climate

A general analysis of local climate (Doty and Mueller-Dombois 1966) gave an indication of a sharp rainfall gradient along transect AA′, with a decrease from the Kilauea Iki area from about 2400 mm per year to about 1300 mm per year near the end of transect AA′ in the upper Kau Desert. It seemed appropriate to verify this trend and to establish the amounts of rainfall for the observational years. Therefore, rain gauges were established in habitats 1, 4, 5, and 6 in 1964. Records were taken weekly or bi-weekly through 1968. The rain gauge locations are shown by the crosses on Fig. 2.

On the crater floor of Kilauea Iki, steam came from the cracks in the pahoehoe lava almost continuously throughout the period of observation. It was thought that this moisture source may have had an influence on plant establishment on the crater floor. In order to assess the contributions of this moisture source to objects standing out from the crater floor, Grunow fog interceptors were installed on rain gauges. Four such gauges equipped with an interceptor each were set out near the beginning of each transect. A rain gauge without interceptor was put next to an interceptor-gauge for comparison. Recordings were made from January 1967 through December 1968. A paired set of gauges was also established at the end of transect AA′ in habitat 6.

Two hygrothermographs were installed in Stevenson screens (at 1.5 m heights), one on the floor of the crater in habitat 1, the other in habitat 6 at the end of transect AA′. In addition, the relative desiccation power of the environment was analyzed by Livingston white and black bulb atmometers mounted 30 cm above the ground near the rain gauges in habitats 1, 4, 5, and 6.

Substrate

Substrate sampling was done in various ways to obtain descriptive information on the edaphic properties of the new habitats and to verify hypotheses about the causes of certain observed plant invasion patterns.

Edaphic properties sampled in different locations were ash density, water-holding capacity and rate of water loss, available nutrients, pH, and degree of mineralization.

Ash density was used to separate the spatter area (habitat 3) from the pumice area (habitats 4, 5, and 6). The former showed densities greater than 1. Pumice was defined as ash with densities less than 1.

Water-holding capacity was tested on ash samples from habitats 2 through 6 by immersing pyroclastic fragments in water for 48 hours. After excess water had been allowed to drip off, the material was weighed for its holding capacity (here termed field capacity).

Thereafter, it was reweighed every 24 hours in a room with a mean air temperature of 21 °C and a mean relative humidity of 65% to determine the rate of water loss. Permanent wilting percentage was determined with a Richard's pressure plate at 15 atm.

Available nutrients tested were the cations (Ca, Mg, K, Na), nitrogen, and phosphorus. The method followed for cation extraction was the one described by Jackson (1958). Quantities were determined with a Perkin-Elmer spectrophotometer.

Available ammonia and nitrates were analyzed by Kjeldahl distillation (Harper 1924; Olsen 1929) and available phosphorus by a photometric method (Bray and Kurtz 1959). Substrate pH was determined for the upper 20 cm depths on a number of samples with a Beckman Expandomatic meter.

Degree of mineralization was analyzed with a Norelco X-ray diffractometer and thin sections of rocks were analyzed under the microscope for primary mineral occurrence and alterations.

Observed plant invasion patterns on the Kilauea Iki crater floor were believed to be related to substrate temperatures. Therefore, temperature measurements were made along the transects in numerous pahoehoe cracks with a Yellow Springs Telethermometer Model 43TC. These measurements were repeated several times during the warmest period of the day at intervals of 3, 30, 300, and 500 m from the crater floor edge to the center.

Another plant invasion pattern on the ash habitats showed a high correlation with the bases of tree snags. Soil moisture samples were taken at various points at the base of tree snags and away from them to verify the hypothesis that substrate moisture distribution was unequal over the ash surface and that the tree snags added to soil moisture by interception of rain water.

5

Plant Invasion Patterns

Kilauea Iki Lava Lake (Habitat 1)

Progress of invasion

A clearly directional progression of plant life was observed on the Kilauea Iki crater floor. Here plants invaded the new lava habitat from the margin toward the center in a pattern shown in Table 1A.

The species within each life form are listed in Appendix I. The term plant life form is used in a general sense in this book for designating such broad taxonomic groups as algae, mosses, lichens, ferns, and seed plants as shown in Table 1A. The term is also used for subdivisions of these groups, such as woody and herbaceous plants within seed plants. More detailed subdivisions of morphological forms as given by Raunkiaer (1918) or Ellenberg and Mueller-Dombois (1967) are likewise referred to as life forms.

In year 1, after the eruption, i.e., 6 months after formation of habitat 1, plant life was found only along transect a (NE side of crater floor, Fig. 2). A fern *(Nephrolepis exaltata)* and an alga *(Stigonema panniforme)* had progressed 11 m of the 325-m stretch toward the center. Two mosses *(Campylopus densifolius* and *C. exasperatus)* followed closely up to 5 m inward.

In year 2, no further progress beyond the 11-m point occurred along transect a, but plant life was found along the SE transect d to the 3-m point. The same species occurred there. In addition, one more alga was found, *Scytonema myochrous*. Also, a second fern species *(Sadleria cyatheoides)* occurred on transect a.

In year 3, invasion began along the two remaining transects (b and c) from the W side where the source of the lava outpour had occurred. Here, the same two algae *(Stigonema* and *Scytonema)* were found as the plants that had progressed farthest away from the edge, to 10 and 15 m, and two additional algae, *Anacystis montana* and *Hapalosiphon,* had joined the group. The same fern *(Nephrolepis exaltata)* and the same two *Campylopus* mosses appeared at the beginning of both transects. In addition, a third moss *(Rhacomitrium lanuginosum* var. *pruinosum)* appeared. A new cryptogamic life form occurred in the third year, the lichen *Stereocaulon volcani*. It appeared simultaneously on all transects, but advanced farther inward on the two southern transects (c and d). Here it occurred closest to the center together with the algae, the mosses, and the fern. On transect c (SW), *Stereocaulon* occurred even ahead of the other life forms, at 30 m toward the center by being present on every square meter. Thus, four pioneer algae were found in the third year, and these were generally closer to the center than the fern and moss species.

TABLE 1. Number of 10 × 10-m plots by habitats and transects as used for the plant records (transects and habitat outlines in Fig. 2).

Habitat	Transect	No. of plots	
2 Cinder cone	AA′	50	85
	BB′	35	
3 Spatter area with tree snags	BB′	6	21
	EE′	15	
4 Pumice area with tree snags	AA′	2	72
	BB′	12	
	CC′	32	
	DD′	26	
5 Pumice area with surviving trees	AA′	9	32
	BB′	6	
	CC′	14	
	DD′	3	
6 Thin fall-out area, upper Kau Desert	AA′		5
		Total	215

In year 4, the algae progressed to 22 m on transect a, while they advanced to 40 m, together with the *Stereocaulon* lichen, on transect c and to 30 m on transect b. A moss, *Campylopus densifolius,* progressed to 48 m on transect d. A second lichen, *Cladonia skottsbergii,* appeared along the first few meters on all four transects. Transect a did not continue to show the farthest center-ward progression as it did the first 2 years. The farthest center-ward progression (48 m) was found on transect d (SE). However, the two eastern transects (a and d) exhibited the first seed plants in the fourth year. There were four sclerophyllous (hard-leaved) woody plants *(Metrosideros polymorpha,* a potential tree, *Vaccinium reticulatum, Dubautia scabra,* both potential shrubs, and *Hedyotis centranthoides,* a semi-woody herb). These four are endemic species. A fifth seed plant species, *Lythrum maritimum* (a creeping herb and introduced species) made its appearance from the NW on transect b. After the fourth year, records were not taken until the seventh year (1966) following the eruption.

In year 7, plant life had progressed farthest on transect a to 150 m. This was almost half the distance to the center of the crater floor. The other transect on the east side, transect d, showed the second most forward advance (90 m inward), and the two west-side transects showed plant life to 80 m (on b) and 60 m (on c), respectively. The number of seed plant species had increased to eight, but *Lythrum maritimum* had disappeared. The other life forms showed increases of one species each, except the lichens.

TABLE 1A. Progression of plant life from crater floor edge towards center in habitat 1.

Direction on crater floor	Year after eruption	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968	Total distance to center
NE	Transect a	11 m	11 m	31 m	22 m	150 m	250 m	325 m
NW	b	—	—	10 m	30 m	80 m	120 m	385 m
SW	c	—	—	30 m	40 m	60 m	120 m	340 m
SE	d	—	3 m	40 m	48 m	90 m	120 m	400 m
	No. species	4	6	10	17	23	30	
	Life forms:							
	algae	1	2	4	4	5	5	
	mosses	2	2	3	3	4	5	
	ferns	1	2	2	3	4	5	
	lichens	—	—	1	2	2	2	
	seed plants	—	—	—	5	8	13	

Community formation

In year 9 (1968), two distribution groups among the seed plants became evident, one appearing all around the crater, and one entering from one side only.

Group 1 contained the four native species that were recorded already in the fourth year, *Metrosideros polymorpha, Vaccinium reticulatum, Dubautia scabra,* and *Hedyotis centranthoides.* Except for *Hedyotis,* they occurred around the crater on all four transects. These species had advanced most on the east side (transects a and d). On transect a they were found from 72 m *(Dubautia)* to 114 m *(Vaccinium)* inward; on transect d they were found between 34 m *(Dubautia)* and 51 m *(Vaccinium)* inward. *Metrosideros* on each of these transects occurred between these two species.

Group 2, which started to enter the crater floor on the east side along transect a, contained four species in 1966 (a potential tree *Buddleja asiatica,* a shrub *Cyrtandra* sp., a grass *Paspalum conjugatum,* and a forb *Anemone japonica).* In 1968 the group increased to nine species. Seven of these were exotics and two were natives. The two native species were the shrubs *Cyrtandra* sp. and *Coprosma ochracea.* The remaining five species were the weed-tree *Buddleja asiatica;* the forbs *Cuphea carthaginensis* (semi-woody), *Anemone japonica, Fragaria vesca* var. *alba;* and three grasses *Paspalum dilatatum, Andropogon virginicus,* and *Setaria geniculata. Paspalum conjugatum* had disappeared. The progress of these species was found within the first 7 m on transect a only, but a single *Andropogon* was at 110 m on transect b. Group 1 also persisted together with Group 2 as well as with the 15 species of cryptogams (algae, mosses, and ferns) that were found already in the third year on all four transects. This shows that a more complex community was now beginning to form at the east side of the crater floor.

Three communities had become evident:

1. A cryptogamic pioneer community consisting of algae, mosses, ferns, and lichens. This community occurred all around the crater and had advanced furthest toward the center.
2. A phanerogamic pioneer community consisting of the above life forms plus four native seed plants. This community also occurred all around the crater, but had not yet advanced as far to the center as the pure cryptogamic community.
3. A more complex phanerogamic pioneer community, which consisted of several exotic seed plants plus the above four native seed plants and the cryptogams. The additional plants were all daphnous (= soft-leaved) perennials including two native species in this group *(Cyrtandra* sp. and *Coprosma ochracea).* Their life forms are thus different from the sclerophyllous seed plants in the first phanerogamic community. This third community was more complex, because it now included a larger complement of life forms, potential shrubs, perennial herbs, and grasses. However, in the ninth year (1968), the final year of recording, this community had only entered the first few meters of one transect (a) on the east side of the crater floor.

In all, plant life had progressed to 250 m on transect a and to 120 m on the other three transects. In terms of overall distance to the center, this was approximately one-third.

Densification of colonization

In spite of the considerable progression of plant life toward the center of the crater floor, the vegetation cover was as yet so small in year 9 (1968) that, on superficial view, the surface looked practically barren.

Two parameters were recorded that convey the process of densification of plant life on the lava surface. One was frequency of the species in the square-meter quadrats along the four transects, the other was cover as estimated by the Braun-Blanquet scale in each contiguous square-meter plot. Density, in terms of number of individuals, was not recorded because of complications in recognizing individuals.

Frequency gives an idea of the uniformity of distribution along the transects. It is summarized for each of the five major life forms (algae, mosses, lichens, ferns, and seed plants) in Table 2. Here, their frequency is stated in relation to the cumulative transect area occupied by plant life per year of recording. The cumulative transect area was obtained from summing (Table 1A) the distances for each transect to which plant life had progressed from the crater-floor edge. The cumulative transect area shows the plant invasion zones as they enlarged during the six observational periods. The frequency values for each life form (Table 2) are derived from the maximum number of quadrats occupied by that life form at the time of observation. The number of quadrats occupied are expressed as percent of cumulative transect area occupied by all life forms. For example, in year 1, ferns occupied 3 quadrats out of 11 that were occupied by plant life (in this case algae). The fern frequency for 1960 thus was 27%.

Algae were uniformly distributed, showing from 87 to 100% frequency with any enlargement of the invasion zones, except in year 3. The reduction in algal presence in the third year (1962) is related to an exceptionally low rainfall. A rain gauge was not installed on the crater floor in 1962, but the record from the nearby park headquarters station showed a mean rainfall of only 1550 mm for that year, which was 1000 mm less than the amount recorded during the other years of observation. Because of abnormally low rainfall, vapor steaming from lava flow fissures must have been low also during 1962. This may explain the low frequency of algae in that year.

TABLE 2. Frequency (%) of plant life on crater floor area occupied.

Year after eruption	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968
Cumulative transect area occupied (meters)	11	14	111	140	380	610
Algae	100	93	43	87	97	97
Mosses	0.9	29	22	22	21	20
Lichens	—	—	26	51	92	77
Ferns	27	50	11	16	20	18
Seed plants	—	—	—	0.4	0.6	0.6

While the uniformity of algal distribution proved to be high throughout the study period (except for the drop in 1962), in terms of cover, the algae occupied very little surface. The Braun-Blanquet values for algae were never greater than +. This means that algae were present in the square-meter quadrats with insignificant cover, but usually with more than one colony of algal growth. Insignificant cover was arbitrarily defined as 0.1%, which implies a mean of 10 cm^2/m^2. This seemed to represent a realistic estimate.

The record of algae as presented in study does not include microscopic plant life. Algae were recorded only if they formed macroscopically visible patches or colonies. This may have introduced a source of error in the observations recorded.

The mosses filled the expanding plant invasion zone suddenly in year 2, reaching a maximum frequency of 29% (Table 2). From then on their frequency remained relatively stable, near 20%, within the rapidly expanding invasion zone.

As in the algae, the surface cover of the mosses was minimal, not exceeding 0.1% for any one species. When the + values (translated into 0.1% mean cover) are added for the individual species, their combined cover reaches only 0.2%, in spite of five moss species being present on the crater floor in the final year of observation.

The lichens made their appearance in the third year with 26% frequency, a value closely similar to that of the mosses. But from then on, their presence increased rapidly across the expanding invasion zone of the crater floor. In the seventh year their uniformity of distribution was almost complete, with 92% frequency which is comparable to that of the algae. A slight drop to 77% frequency occurred in the final year, when the plant-life zone transect area nearly doubled from 380 to 610 m^2. This slight drop may be explained by the presence of still unfavorable microhabitats for lichens in the algae-expanded invasion zone. In contrast to the algae and mosses, the lichens were never found near steaming lava cracks.

In terms of surface cover, the lichens occupied an insignificant part of the lava surface until the final year of observation, when their mean cover rose to an estimated 2.5% *(Stereocaulon volcani)*.

The ferns showed a relatively high frequency of 50% in the second year (Table 2). Thereafter, their frequency dropped sharply to 11% in the third year. This correlates with the reduction of algal frequency and was probably also caused by the exceptionally low rainfall in 1962. In the fourth, seventh, and ninth year, fern frequency appeared to stabilize between 15-20%.

In contrast to the algae, mosses, and lichens, the ferns grew only in lava cracks (Fig. 5). Their frequency, therefore, is a function of the lava crack frequency per sampling quadrat. On the average, cracks or crevices ran through every fourth or fifth quadrat. On this basis, ferns occurred with a high frequency (from 60 to 100%) in these microhabitats, although their frequency, in terms of the whole lava flow surface in the invasion zones, was only between 11 to 20% as shown in Table 2. The initial high frequency of 27 and 50% was related to the greater abundance of cracks near the crater floor edge when the invasion zone had not yet extended much toward the center.

In terms of surface cover, the ferns were as insignificant as the algae and mosses throughout the 9-year observation period.

The seed plants, which appeared only in year 4 (1963), exhibited a very low frequency value of 0.4%, which increased to only 0.6% at the last two observations (1966, 1968). This reveals that they were either widely scattered and sparse or locally clumped. The sclerophyllous native seed plants *(Metrosideros, Vaccinium, Dubautia,* and *Hedyotis)*

Fig. 5. Floor of Kilauea Iki, habitat 1, 1967. Ferns (*Nephrolepis exaltata*) established in joint cracks and crevices.

recognized by their progression onto the crater floor as group 1, fit more or less the first distributional pattern. The soft-leaved, more complex life form group (trees, shrubs, herbs, and grasses) described before as group 2, fits more or less the second distributional pattern. The latter became established only at the beginning of transect a, where they were locally clumped. In terms of cover, the seed plants were still as insignificant as the other life forms in the final year of observation.

Cinder Cone (Habitat 2)

Here, and in the other four habitats on pyroclastic materials, the quadrat size was 10 × 10 m, because of the expected wide scatter of plant arrival. The frequency records on the pyroclastic habitats (2 through 6) are thus comparable among each other, but not with the frequency record on the Kilauea crater floor (habitat 1), which was taken in square-meter quadrats. However, the qualitative records, such as species arrival, number, and diversity, are comparable.

Appendix II shows the sequence of life form and species arrival patterns as well as the quantitative spread or distribution of species over the 9-year observation period.

Arrival pattern in comparison to habitat 1

In contrast to the lava lake (habitat 1) on which four species of cryptogams became established in year 1, plant life on the cinder cone became established only in year 3 (1962). Appendix II shows that the life form arrival sequence on the cinder cone was:

year 3 algae (one species, *Scytonema myochrous)*
year 4 algae plus mosses, lichens, and ferns
year 7 the same plus woody seed plants
year 9 additional arrival of a herbaceous seed plant, a grass *(Agrostis avenacea)*

Apart from the 3-year delay period, the life-form arrival sequence was very similar on habitats 1 and 2. The simultaneous arrival on the lava lake of algae, mosses, and ferns in year 1, as shown in Appendix I, is somewhat generalized. The more detailed analysis of progression of plant life toward the center of the lava lake (as discussed under progress of invasion, habitat 1) revealed the algae to be in most cases somewhat ahead of the ferns and mosses. This coincides with the pioneer sequence on habitat 2. Also, on both habitats lichens appeared after the algae. In habitat 1, they arrived after the mosses and ferns had become established; in habitat 2, lichens appeared together with the mosses and ferns. Woody seed plants arrived as the fifth major life-form group, distinctly after the cryptogams on both habitats. On the Kilauea Iki lava floor, they arrived in year 4; on the cinder cone, they arrived in year 7. Thus, the delay period of 3 years on the cinder cone was similar to that of the cryptogam arrival. Grasses became established in year 7 on the lava floor and in year 9 on the cinder cone.

Therefore, on the two habitats (1 and 2) that had no organic residues, the similarity in life-form arrival sequence can be summarized. Algae were the first, these were followed by ferns and mosses that arrived simultaneously, lichens arrived as the third group. These were followed by woody seed plants and these, in turn, by herbaceous seed plants.

The difference in arrival pattern was primarily the delay on the cinder cone and the lower number of species. The probable reasons for the arrival delay will be discussed later.

Number and kind of species in comparison to habitat 1

Comparison of Appendices I and II shows that the number of species was greater on the Kilauea Iki lava floor (habitat 1 = 32) than on the cinder cone (habitat 2 = 18) in year 9. This is not surprising if one considers that the colonization started later on the cinder cone. The number of species in year 4 on the crater floor = 17 compares closely to that in year 9 on the cinder cone. It is interesting that these are also almost the same kinds of species.

Using the Sφrenson (1948) index of similarity for the crater floor and cinder cone flora for these comparable years of pioneer plant invasion shows the following similarity percent.

$$IS = \frac{2c}{A + B} \times 100(\%) = \frac{28}{17 + 18} \times 100 = 80\%$$

where IS = index of similarity

c = number of common species = (3 algae+ 3 mosses+ 2 lichens+3 ferns+ 3 woody seed plants) = 14
A = total number of species on site A, here crater floor = 17
B = total number of species on site B, here cinder cone = 18

The floristic similarity between the two habitats decreased in year 9 to 67%. The greater difference is caused primarily by the exotic grasses and forbs that entered the crater floor habitat in 1968. These species had not yet arrived on the cinder cone. Since the exotic grasses and forbs fill a niche that is not occupied by native pioneer plants, it is likely that the same trend of exotic invasion of herbaceous plants will also occur on the cinder cone at some future date.

Quantitative spread of species

A comparison of the two transects on the cinder cone revealed no difference in the direction of spread with respect to the prevailing winds. Therefore, the transect quadrats could be treated as one group of 85 as in Appendix II.

The rate of spread across the cinder cone habitat is shown for selected species in each life-form group on Fig. 6. The rate of spread refers to the occurrence of individual plants or colonies in the 10 x 10-m quadrats along the transects going through habitat 2.

Figure 6 shows that the lichen *Stereocaulon volcani*, though being a slower starter than the alga *Scytonema myochrous*, was the fastest invader in terms of quantitative occupation of the habitat. In year 9 the lichen occupied over 80% of the habitat surface. The next most rapid invader in terms of habitat occupation was the alga *Scytonema myochrous*. The other two algae *(Stigonema panniforme* and *Anacystis montana)* invaded with an equally fast rate (Appendix II), so that the algae occupied about 60% of the habitat terrain in year 9. The third fastest spreader was the fern *Nephrolepis exaltata*, which occupied 40% of the habitat surface in year 9. This was followed by the moss *Rhacomitrium lanuginosum* var. *pruinosum*, which had invaded about 20% of the surface area. The rate of spread was the same for the moss *Campylopus exasperatus* (Appendix II). The woody seed plants were the slowest invaders because they entered the habitat as the last of the five life-form groups. Therefore, in year 9 they had not yet occupied 20% of the surface. Their rate of spread, however, compares closely to that of the mosses. None of the species, shown as representatives of the five life-form groups in Fig. 6, indicated any slowdown in rate of spread in year 9. Therefore, the curves may be extrapolated to 100% frequency, and the time of total occupation on the cinder cone can be estimated for the lichen to occur at approximately year

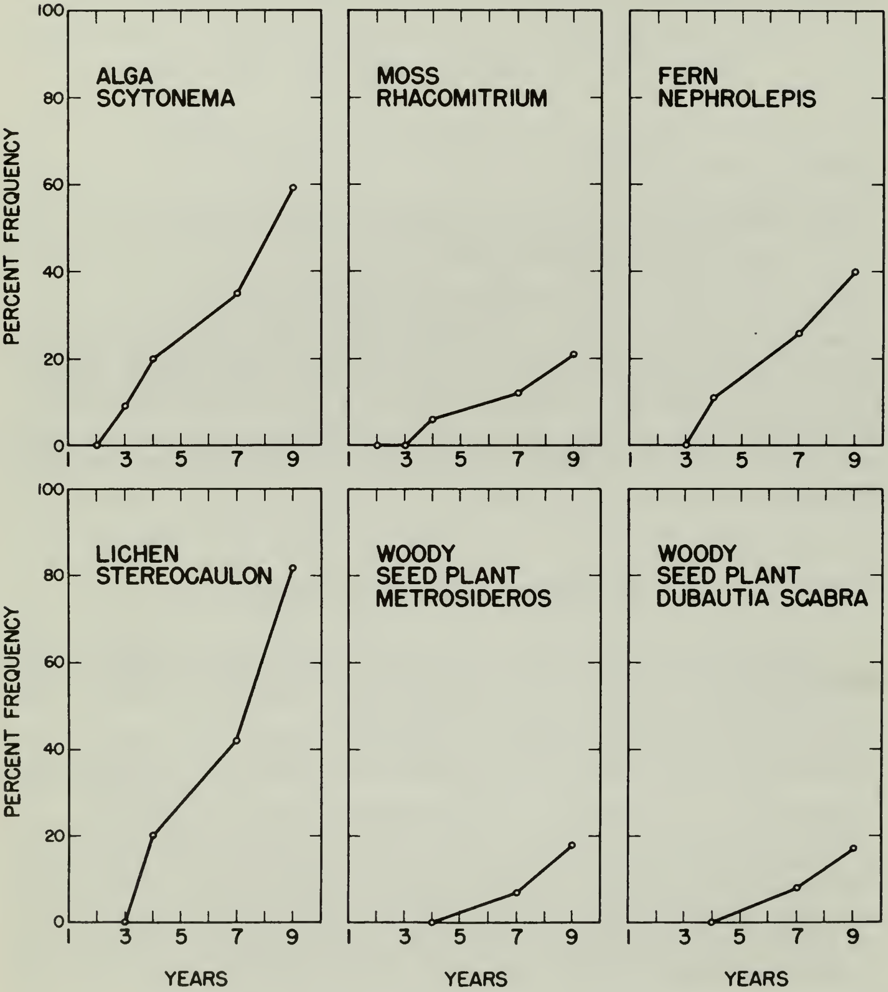

Fig. 6. Rate of spread across the cinder-cone habitat (2) for selected species in five life-form groups.

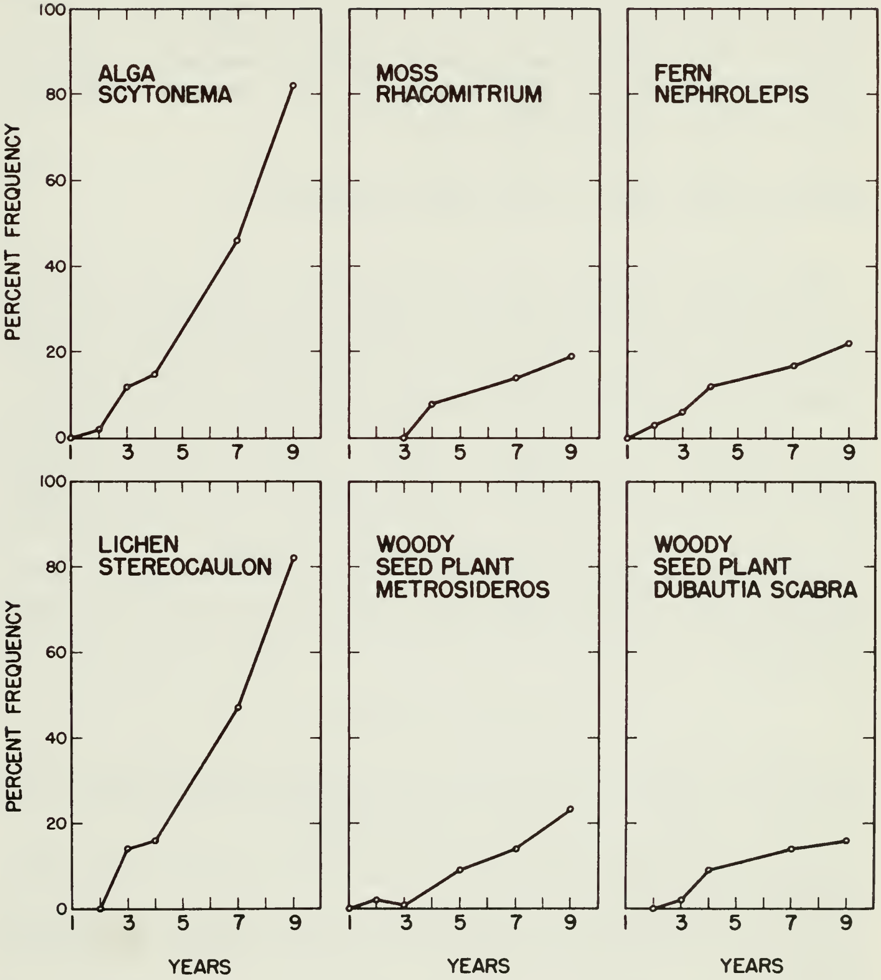

Fig. 7. Rate of spread across pumice-with-snags habitat (4) for selected species in five life-form groups.

10; for the algae, near year 12; for the fern *Nephrolepis,* near year 18; for the mosses and woody seed plants, near year 24. This trend can be predicted, provided that the rainfall pattern remains relatively the same as during the year of observation. However, it must be understood that the spread of plant life across the habitat has little to do with cover of the species. Cover, defined as the vertical projection of shoot mass per species or colony size, was still quite insignificant for all invading species in year 9. As on the crater floor, the cinder cone surface looked practically barren in 1968.

Spatter Area with Tree Snags (Habitat 3)

This is the relatively small, narrow, and elongated habitat adjacent east of the cinder cone (habitat 2) and adjacent south of Kilauea Iki (Fig. 2). It was defined in outline by the presence of *Metrosideros* tree snags that remained standing or fell down after the flowing-hot pyroclastic fallout was deposited. The new surface consisted of ''welded spatter,'' i.e., relatively large chunks of cinder-like particles that were still soft from heat and became welded upon deposition. The presence of completely defoliated trees (=snags) provided a convenient, mapable outline of habitat 3, which was bordered on the east side by the surviving, still well-foliated *Metrosideros* stand. On the north side it was bordered by the lower slope of the cinder cone habitat. In the first year after the eruption, the National Park Service built a board walk through habitat 3 for the use of visitors.

Vegetation was sampled by two transects: BB′, 60 m long, with six contiguous 10 x 10-m plots running east-west from the intact forest to the cinder cone slope, and EE′, with 15 contiguous 10 x 10-m plots running north-south on the cinder cone side, 5-10 m parallel to the board walk.

Progress of invasion

A directional advance of invasion of new species across habitat 3 was recorded by species presence in the six 10 x 10-m-contiguous quadrats running from the undisturbed forest edge to the cinder cone slope, over a distance of 60 m (Table 3).

It can be seen that algae were present over the 60-m belt-transect in all six quadrats beginning with the first year after the eruption.

Mosses arrived in the second year within the first 20 m off the forest edge and then spread across habitat 3 by advancing less than 10 m per year. In year 7, mosses were found in all six quadrats.

The lichen *Stereocaulon volcani* arrived together with the mosses in the second year and spread faster than 10 m per year across habitat 3.

The fern *Nephrolepis exaltata* arrived in the first year and then spread with a rate similar to *Stereocaulon* across the habitat.

Because of the high number of seed plant species that arrived early in the habitat, this group has been further separated into grasses, sedges, forbs, shrubs, and tree seedlings in Table 3.

Grasses arrived in the first year and spread with much the same speed (i.e., 10 m/year) across habitat 3. The first grasses were three exotic perennials: *Setaria geniculata, Paspalum dilatatum,* and *Sporobolus africanus.*

TABLE 3. Progression of invaders from undisturbed forest edge across habitat 3 towards cinder cone along the 60-m belt-transect BB′ (Fig. 2).

Life forms	Year after eruption	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968
Algae		60 m	60 m	60 m	60 m	60 m	60 m
Mosses		—	20 m	20 m	30 m	60 m	60 m
Lichens		—	30 m	30 m	50 m	60 m	60 m
Ferns		20 m	20 m	20 m	50 m	60 m	60 m
Grasses		10 m	20 m	30 m	40 m	50 m	60 m
Sedges							
native		—	—	—	—	—	50 m
exotic		—	—	20 m	20 m	50 m	50 m
Forbs							
native		10 m	10 m	20 m	20 m	20 m	50 m
exotic		10 m	20 m	30 m	60 m	60 m	60 m
Shrubs							
native		—	20 m	30 m	50 m	60 m	60 m
exotic		10 m	20 m	30 m	40 m	30 m	40 m
Tree seedlings							
native		—	—	20 m	30 m	60 m	60 m
exotic		—	—	20 m	40 m	60 m	60 m

A separation into native and exotic species aids in the interpretation of the result of the following seed plant groups:

Exotic sedges arrived after the second year and penetrated 50 m into habitat 3 in the seventh year, where they remained through the ninth year. At that time, a native sedge, *Carex wahuensis,* made its entrance at the 50-m part of the transect, but this species occurred only in one of the five quadrats.

Forbs occurred together with the algae, ferns, and grasses in the first year after the eruption. One of these was a native species, *Astelia menziesiana;* another, an exotic, *Eupatorium riparium.* Exotic herbs penetrated rapidly across the transect, reaching the 60-m part in the fourth year after the eruption. *Astelia* advanced another 10 m into habitat 3 in the third year. It remained in the first two quadrats throughout the 9-year observational period. But a second native herb, *Hedyotis centranthoides,* was recorded in two quadrats in the ninth year. One of these was the fifth quadrat.

An exotic shrub, *Rubus rosaefolius,* appeared in the first year after the eruption in the first quadrat. Thereafter, it was joined by several other species, for example, *Rubus penetrans,* in the second year. However, this group did not advance beyond the 40-m section of the transect.

In contrast, a native shrub, *Dubautia scabra,* did not appear until the second year. It was then joined by other native shrubs in the fourth year, notably *Vaccinium reticulatum* and *V. calycinum.* Both *Dubautia* and *V. reticulatum* spread rapidly to the sixth plot, where they were recorded in the seventh year.

Tree seedlings did not arrive until the third year. These included only two species, the native *Metrosideros polymorpha* and the introduced weed-tree *Buddleja asiatica.* Both trees spread with the same rate across the 60-m transect and were found in the sixth plot in the seventh year (1966).

Although directional progress was not measured along transect EE′ (Fig. 2), plants were observed to arrive slowly in the northeast sector and to progress toward the southwest.

Floristic pattern in comparison to habitats 1 and 2

As pointed out previously, the arrival sequence of life forms and species differed from those in habitats 1 and 2. Appendix III shows that seed plants were among the first invaders, together with the alga *Stigonema panniforme* and the fern *Nephrolepis exaltata.* Mosses and lichens arrived in the second year. Thus, within the group of cryptogams, the sequence of arrival remained similar to that on the two previously discussed habitats, but the arrival of seed plants together with the cryptogams is a significant departure for habitat 3. It is also of interest that these first seed plant pioneers were all exotics except one, the forb *Astelia menziesiana.* This species grows normally as an epiphyte on very old *Metrosideros* trees in the montane rain forest. In habitat 3, *Astelia* grew directly on the ash. The exotics that appeared as first arrivals in year 1 were a shrub *(Rubus rosaefolius),* three grasses *(Paspalum dilatatum, Setaria geniculata,* and *Sporobolus africanus),* and one forb *(Eupatorium riparium).* Except for the shrub life form, there are very few native species among the grasses and forbs in this climatic zone (Doty and Mueller-Dombois 1966) that could be expected as early invaders.

A second, remarkable departure from the species invasion pattern of habitats 1 and 2 is the very rapid increase in the number of species in habitat 3. They increased from 8 in year 1 to 64 in year 9. This increase in species is particularly noteworthy in the group of mosses, grasses, sedges, and forbs.

The first three moss species in Appendix III are the common pioneer mosses found also in habitats 1 and 2; the other 12 mosses are unique to this habitat. The increase in number of moss species was explosive in year 7. This correlates with a rather sudden recovery of the woody plants that began to provide shade over much of the spatter surface on habitat 3. This woody-plant recovery is documented by the photographic record (Fig. 9). Except for *Ceratodon purpureus,* the mosses that invaded habitat 3 in year 7 and 9 are species of the rain forest. Thus, the sudden increase in moss species indicates a significant change in microclimate near the ground in habitat 3. The change to a continually more moist microclimate near the ground began in year 4 with the arrival of *Bryum crassicostatum* and *Macromitrium owaihense.*

The second major floristic difference from the first two habitats is in the early establishment of a species-rich herbaceous component in habitat 3. This also indicates much more mesic conditions. Only two species in the herbaceous component are endemic, the sedge *Carex wahuensis* and the forb *Astelia menziesiana.* All 9 grasses, 3 sedges, and 20 forb species are exotics. It seems apparent that these exotic herbs fill an almost empty niche in the invasion process on new volcanic materials. Some of these had already made their entrance on the crater floor (habitat 1), and it is to be expected that many, if not all, of the exotic herbs listed in Appendix III will also become established in the other new habitats in the rain-forest climate.

Succession

The species frequency data in Appendix III shows a rapid rate of spread over habitat 3 for a number of species. For example, the algae were found in all 21 quadrats in year 4; the moss *Campylopus exasperatus* and the lichen *Cladonia skottsbergii,* in year 7; and the pioneer fern *Nephrolepis exaltata* had spread across nearly the entire habitat in year 9. This indicates a much faster rate of occupation than was shown for the cinder cone (habitat 2).

A few species showed a decline in territorial gains over the 9-year period in habitat 3. This is significant because the decline may indicate the beginnings of a succession.

A definite territorial reduction was shown by the moss *Campylopus densifolius,* which showed its peak spread with 95% frequency in year 7 and thereafter was found only in 10% of the plots. Here, a successional replacement with one or several of the rain-forest mosses is indicated in the ground layer.

Among the shrubs, a definite territorial decline was shown in the two *Rubus* species *(R. rosaefolius* and *R. penetrans)* from their peak distribution in year 4. It was observed that spaces occupied by certain individuals of these exotic species were later invaded by individuals of the native shrubs *Dubautia scabra* and *Vaccinium reticulatum.* Thus, in these cases, a successional replacement of exotic by native shrubs was indicated. The same phenomenon was observed with the exotic weed-tree *Buddleja asiatica,* which showed significant territorial reduction in year 9. A large number of mature individuals of *Buddleja* were dying off rather suddenly. The *Buddleja*-dying took place particularly among those individuals that grew at the bases of *Metrosideros* snags that had resprouted from the base. The possibility of competitive replacement of *Buddleja* trees by *Metrosideros* trees was indicated.

Among the grasses, definite territorial reductions occurred in *Paspalum dilatatum* and *Setaria geniculata. Sporobolus africanus* disappeared completely from the plots in year 7. These three grass species were those that occurred in year 1. Their peak distribution was in year 4. Their decline coincides with the appearance of the mosses, which indicated a change in microclimate near the ground caused by increased shading of the woody plants. However, the decline of the grasses was noted also in unshaded places. Here the grasses *Holcus lanatus* and *Pennisetum clandestinum* and the sedge *Cyperus polystachyos* took over some of the space of the above declining species, indicating competitive replacement.

Similar replacement relations were observed among the forbs. After year 4, the first invader *Eupatorium riparium* lost much of its territory by die-back. Significant decreases occurred also in *Geranium carolinianum, Sonchus oleraceus,* and *Erechtites valerianaefolia.* Later invaders and definite increasers were *Commelina diffusa, Hypochoeris radicata,* and *Epilobium cinereum.*

Therefore, succession through competition was definitely indicated in habitat 3. While among the woody plants there was a trend toward greater habitat occupation by native plants at the expense of exotic shrubs, the competition in the herbaceous group was strictly among exotics.

Pumice Area with Tree Snags (Habitat 4)

This habitat consists of the area where the first snag tops of buried trees began to appear above the pumice blanket. The boundary extends to the survival tree line of habitat 5, where the maximum pumice depth was about 3 m (Figs. 2 and 3). A single tree fern *(Cibotium glaucum)* was the only plant that was observed to survive the deep burial and pumice blast. In the ninth year this plant still displayed good vigor, but no additional specimens had appeared. Since most of this habitat area already lies in the area of the former seasonal forest (Fig. 2), no additional tree fern specimens were expected. The tree fern *C. glaucum* is a characteristic plant of the rain forest.

Arrival pattern in comparison to habitats 1, 2, and 3

The general direction of invasion was from both the eastern and western boundaries of the habitat toward the center, but the new plants became established in a widely scattered formation.

Appendix IV shows the invading species for the 72 quadrats. No new plant was recorded in year 1. In year 2, seed plants became established together with the first cryptogams. Simultaneous arrival of seed plants and cryptogams was also noted in habitat 3. Both these habitats (3 and 4) were characterized by the standing tree snags. Therefore, there is a correlation of immediate seed plant establishment and presence of significant organic residues of a former vegetation (here, the tree snags) on new volcanic surfaces. The pioneer seed plants arriving in year 2 in habitat 4 were the exotic shrub *Rubus rosaefolius*, the native tree *Metrosideros polymorpha* (as seedling), and the composite weed *Erechtites valerianaefolia*.

The cryptogam-arrival sequence was similar to that on the previously discussed habitats, except that the potential semi-tree fern *Sadleria cyatheoides* appeared together with *Nephrolepis exaltata* in year 2. In habitats 1 and 2, *Sadleria* appeared a year after *Nephrolepis*. Again, the lichen *Stereocaulon volcani* arrived a year after the other cryptogams (algae, mosses, and ferns).

Among the seed plants, several more woody species became established in year 3 (two exotics *Rubus penetrans* and *Buddleja asiatica* and one native *Dubautia scabra*), while only two additional forbs appeared. These were also weedy composites *(Sonchus oleraceus* and *Hypochoeris radicata*). In contrast to habitat 3, grasses arrived very late, only in year 7 *(Andropogon virginicus)*. Only one more grass species *(Holcus lanatus)* became associated in year 9. Also, the rain-forest mosses found in habitat 3 never arrived in habitat 4.

The comparison with habitat 3 is of interest because both habitats had the tree snags in common. Table 4 shows the number of seed plant species found in the two habitats.

Habitat 3 received more rainfall than habitat 4 (see rainfall gradient, Fig. 3). Habitat 3 was in the rain-forest terrain and habitat 4 in what was formerly mapped as seasonal forest (see boundary in Fig. 2). This difference in moisture may in part explain the different pattern in seed plant establishment on the two habitats. Another difference is in the greater water-holding capacity of the spatter in habitat 3 as compared to that of the pumice in habitat 4.

This will be discussed later. The greater distance away from an intact, surviving stand, of course, also was important. The disseminules reaching habitat 4 had to be carried over a greater distance. This may have eliminated the establishment of a number of grass species in habitat 4 that were present in habitat 3. However, the disseminule dispersal limitation was probably a lesser factor among the moss species. The absence of rain-forest mosses in habitat 4 points to water rather than to dispersal as the more important limiting factor in early species diversity.

TABLE 4. Number of seed plant species in the two pyroclastic habitats with tree snags (habitats 3 and 4).

Life form and habitat	Year	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968
Woody plants							
habitat 3		1	3	6	9	9	11
habitat 4		—	2	5	5	5	7
Grasses							
habitat 3		3	3	5	8	6	7
habitat 4		—	—	—	—	1	2
Sedges							
habitat 3		—	—	2	3	3	4
habitat 4		—	—	—	—	—	—
Forbs							
habitat 3		2	4	4	14	18	21
habitat 4		—	1	3	5	9	12

Quantitative spread of species in comparison to habitat 2

Figure 7 shows the rates of spread in 10 x 10 m squares of six selected species over the surface area of habitat 4. The six species were the most widely distributed in habitat 4. A comparison of Fig. 7 with Fig. 6 shows that the rates of spread were quite similar on both the cinder cone and pumice-with-tree-snags habitat. The pioneer algae and lichens on both habitats showed the fastest rate of spread. The pioneer moss *Rhacomitrium* and the woody plant seedlings also displayed similar, but much slower, rates than the algae and lichens. The fern *Nephrolepis exaltata* progressed only half as rapidly in habitat 4 (Fig. 7) as on the cinder cone (Fig. 6). This is undoubtedly related to the number of fissures in the substrate surface. There were many more cracks and crevasses on the cinder cone surface than on the pumice-with-snags habitat. While *Nephrolepis* became established also on the level pumice surface, it takes a foothold much more readily in cracks, as noted particularly for habitat 1 (Fig. 5).

Pumice Area with Surviving Trees (Habitat 5)

This habitat was covered with a blanket of pumice varying from 3 m depth at its boundary with habitat 4 to about 25 cm depth at its boundary with habitat 6 (Figs. 2 and 3).

Under this ash deposit, most *Metrosideros* trees plus 22 other species survived. Their recovery will be discussed later.

A separate record was kept of new invaders and survival plants. The list of new invaders is shown in Appendix V.

Similarly, as in habitat 4, no new invader was noted in year 1. In year 2, the typical pioneer cryptogams arrived (an alga, *Stigonema;* a moss, *Campylopus densifolius;* and the fern, *Nephrolepis exaltata).* Again, the first lichen *(Stereocaulon volcani)* was the last of the cryptogamic life forms, arriving in year 3, but it was noted all over the habitat. Of significance also is the arrival of seed plants together with the pioneer cryptogams in the first arrival year. Thus, the same life-form arrival sequence was recorded as in the habitats with snags (3 and 4). The first seed plants were an exotic sedge *(Cyperus brevifolius)* and an exotic forb *(Eupatorium riparium). Eupatorium riparium* was also the first forb to vigorously invade habitat 3, and *C. brevifolius* also was the first sedge together with *C. rotundus* to invade habitat 3 in year 3.

There are other floristic similarities between habitats 3 and 5 in spite of the fact that habitat 4 separates the two (Fig. 2). This closer floristic similarity of habitat 5 with 3 is shown, for example, in the mosses, among which, in addition to the usual pioneers, three shade-mosses became established *(Bryum argentum* var. *lanatum, Dicranum speirophyllum,* and *Thuidium plicatum).* These arrived in year 9, indicating a change in microclimate near the ground at that time. This change was caused by the expanding crown-cover of the surviving *Metrosideros* trees. Other plants indicating similarities in microenvironment with habitat 3 were the grass *Paspalum dilatatum,* the sedges *Cyperus polystachyos* and *Gahnia gahniaeformis,* and the forbs *Fragaria vesca* var. *alba, Cirsium vulgare, Anemone japonica,* and *Eupatorium riparium,* which were common to only these two habitats (3 and 5).

It is interesting that no native woody plant invaded habitat 5. The only woody invaders were the exotic shrubs *Rubus rosaefolius* and *R. penetrans.*

Thin Fallout Area, Upper Kau Desert (Habitat 6)

This habitat had the least volcanic disturbance among the six. The pumice blanket varied from less than 25 cm to about 2 cm depth (Fig. 2). The habitat had been sparingly stocked with low-growing woody plants before the eruption. The scattered *Metrosideros* trees were scarcely more than 2-3 m tall. Recovery of surviving plants was of importance here, but a number of new invaders were recorded also.

Appendix VI shows the list of new invaders recorded in habitat 6. Algae arrived in year 2 and mosses, ferns, lichens, and seed plants (a small annual sedge, *Bulbostylis capillaris*) were added in year 3. Thus, seed plants arrived together with most other cryptogamic life forms in this habitat as in the others with snags or surviving plants. The early arrival of algae follows the general pattern observed in all other habitats. Thus, there is no significant departure in arrival sequence of life forms from the previous habitats, except two important pioneers were lacking. The moss *Rhacomitrium lanuginosum* var. *pruinosum* and the fern *Nephrolepis exaltata* did not appear among the pioneers. This is probably related to the lower rainfall. Another floristic difference is the appearance, among the pioneers, of the annual sedge *B. capillaris,* which is a characteristic plant on ash in the seasonal climate, but not found in the rain-forest climate (Doty and Mueller-Dombois 1966). The grass *Rhynchelytrum repens* also indicates the change to a drier climate in this habitat. The *Rubus* species did not invade; instead only two exotic woody plants *(Psidium cattleianum* and *Buddleja asiatica)* made their entrance in years 7 and 9 after the disturbance. As in habitat 5, *Metrosideros* tree seedlings did not appear in the 9-year observation period.

6

Recovery of Vegetation

Surviving Species

Table 5 shows a list of the species that survived the eruption in the "Devastation Area." No plant survived on the Kilauea crater floor (habitat 1) or the cinder cone (habitat 2).

In the spatter-with-tree-snags habitat (3), four species survived. Several of the *Metrosideros* tree snags, initially believed to be dead, resprouted from the base. These were trees near the eastern border of habitat 3, which adjoined the relatively undamaged rain forest (Fig. 2). The spatter was less than 30 cm deep where resprouting from the base occurred. The resprouting trees were larger than 20 cm diameter at the base. The flushing from the base of completely defoliated trees began at the border, where the spatter was shallowest. It progressed toward about 30 m from the border, where the spatter was about 50 cm deep. The territorial spread was reflected in increasing frequency values from 14% in year 1 to 38% in year 9. In contrast, survival of the two tree-fern species *(Cibotium glaucum* and *Sadleria cyatheoides)* was fairly constant throughout the observational period. After the ash fallout, all fronds were slashed off. New fronds began to resprout after 6 months (year 1). Tree ferns survived only where the apex of the stem was not buried. In contrast, in year 3 the exotic orchid *Spathoglottis plicata* appeared from bulbs that were buried under 10 cm of spatter near the rain-forest border.

In the pumice-with-tree-snags area (habitat 4), only one individual of *Cibotium glaucum* survived on transect DD′ (Fig. 2). The trunk of this individual was buried under about 1.5 m of ash and the top 50 cm remained above the surface. The tree fern regained full vigor soon after year 1 and maintained this vigor throughout the period of observation.

The largest number of species (23) survived in habitat 5. Compared to habitat 4, the ash blanket was shallower; it varied along transect AA′ from 300 cm at the border of habitat 4 to 25 cm at the border of habitat 6 (Fig. 2). The physical damage from the fallout itself was also much reduced in comparison to habitat 4. For example, most of the *Metrosideros* trees retained their bark on the leeward side near the border of habitat 4, but they retained bark all around the stem and even on smaller branches and on the few foliage remnants near the border of habitat 6. Recovery was almost immediate within a few months after the fallout.

In this habitat also, a large number of shrub species survived, namely, nine native and three exotic species (Table 5). Also, the two tree ferns plus two herbaceous ferns *(Nephrolepis hirsutula* and *Pteridium decompositum)* were among the survivors. The other surviving herbaceous plants were either rather tall (at least 30 cm), caespitose hemicryptophytes (the two sedges, the grass), or geophytes resprouting from bulbs or fleshy rhizomes *(Astelia, Tritonia, Hedychium,* and *Spathoglottis).* (In the older rain forests, *Astelia* grows

TABLE 5. Surviving species in 1968 by habitats. Values are in percent frequency.

Species	Habitat 3	4	5	6
TREES				
Metrosideros polymorpha	38	—	100	100
Persea americana	—	—	3	—
SHRUBS				
Vaccinium reticulatum	—	—	44	100
Dubautia scabra	—	—	34	—
Dubautia ciliolata	—	—	16	100
Styphelia tameiameiae	—	—	44	60
Dodonaea viscosa	—	—	13	100
Vaccinium calycinum	—	—	19	—
Wikstroemia sandwicensis	—	—	34	—
Coprosma ernodeoides	—	—	31	—
Osteomeles anthyllidifolia	—	—	3	—
Fuchsia magellanica var. *discolor*[1]	—	—	3	—
Psidium guajava[1]	—	—	3	—
Rosa sp.[1]	—	—	3	—
Rumex giganteus	—	—	—	60
FERNS				
Cibotium glaucum	10	1	3	—
Sadleria cyatheoides	14	—	31	100
Nephrolepis hirsutula	—	—	69	80
Pteridium decompositum	—	—	6	—
Pteris cretica	—	—	—	40
Polypodium pellucidum	—	—	—	60
Pityrogramma calomelanus[1]	—	—	—	60
SEDGES				
Machaerina angustifolia	—	—	9	40
Gahnia gahniaeformis	—	—	—	80
GRASS				
Deschampsia australis	—	—	28	—
FORBS (Geophytes)				
Dianella sandwicensis	—	—	—	60
Astelia menziesiana	—	—	13	—
Tritonia crocosiflora[1]	—	—	3	—
Hedychium coronarium[1]	—	—	3	—
Spathoglottis plicata[1]	10	—	—	—
Total species	4	1	23	14

[1] Exotic species.

normally as an epiphyte.) The herbaceous survivors occurred only in areas with less than 30 cm pumice deposit. The shrubs survived where the ash was less than 60 cm deep.

Among the shrubs, 7 of the 11 species were completely buried in year 1. The buried shrub species were five natives *(Vaccinium reticulatum, Dubautia scabra, Styphelia tameiameiae, Coprosma ernodeoides,* and *Osteomeles anthyllidifolia)* and two exotics *(Fuchsia magellanica* var. *discolor* and *Rosa* sp.). The two exotic shrubs occurred only where the ash blanket was less than 40 cm deep. Among the other native shrubs *(Dubautia ciliolata, Vaccinium calycinum, Wikstroemia sandwicensis,* and *Dodonaea viscosa)* were completely buried individuals that resprouted after the first examination in year 1. Thus, in contrast to the trees, all shrub species of habitat 5 were capable of resprouting after their shoot systems had been buried to the top or were broken off and buried by ash. This was not observed in the tree fern *Cibotium,* but instead it was observed in a few individuals of *Sadleria.* The reason why vegetative resprouting was not observed from fully buried trunks of *Cibotium* was probably because of rarity in the study area rather than its lack of capability. Among the herbaceous survivors, nearly all shoots of the geophyte species had disappeared under the ash. Their new shoots surfaced in year 2. Several individuals of buried caespitose hemicryptophytes *(Deschampsia australis, Machaerina angustifolia)* also resprouted after year 1.

In the thin fallout area (habitat 6), 14 species were found to survive under the 10-25-cm-deep pumice blanket. This smaller number of survivors in comparison to the 23 surviving species in habitat 5 is not related to the disturbance factor, but to the original edaphic and climatic difference. Here in habitat 6, the number of species was smaller to begin with. The original substrate under the new pumice blanket was a hard-crusted ash layer that had been deposited in association with moisture during an earlier explosion. The former surface resembled a pavement with fissures. The taller perennial plants were more or less restricted to growing in these fissures, while small annuals, such as the sedge *Bulbostylis capillaris*, and lichens grew on small, shallow, loose aeolian ash pockets on the pavement surfaces. These lichens and annuals had disappeared under the new thin fallout surface, but probably all perennial species survived. These included the tree *Metrosideros polymorpha*, five native shrubs (including a new species not originally found in any of the other habitats, *Rumex giganteus*), five fern species, two sedges, and one forb (see Table 5). In addition to the original edaphic peculiarity, the floristic difference of habitat 6 in comparison to habitat 5 was related to the lower annual rainfall, longer dry season, decreased cloud cover, and increased frequency of drying winds characteristic of the upper Kau Desert (habitat 6).

The surviving species were remarkable for their capacity to reproduce vegetatively. However, several of the surviving woody species also showed increased sexual reproduction. The success of their increased flowering, fruiting, and spore formation activity is reflected in the seedling frequency recorded in Table 6. These woody plant seedlings became established in most cases near surviving individuals so that a contagious pattern developed. *Vaccinium reticulatum* and *Styphelia tameiameiae* survivors produced abundant berries only in habitat 6. This is reflected in the seedling presence in this habitat. Abundant flowering occurred on nearly all recovered *Metrosideros* individuals in habitats 5 and 6 in year 1. The outcome was the successful establishment of *Metrosideros* seedlings in both habitats 2-4 years after the eruption (Table 6).

TABLE 6. Seedlings of surviving woody species in habitats 5 and 6 (% frequency).

	Year after	1	2	3	4	7	9
Species	eruption	1960	1961	1962	1963	1966	1968
HABITAT 5 (32 plots)							
Metrosideros polymorpha		—	—	—	38	69	90
Dubautia ciliolata		—	—	—	—	9	13
Dodonaea viscosa		—	—	—	—	9	6
Sadleria cyatheoides		—	3	3	3	19	31
Wikstroemia sandwicensis		—	—	—	9	13	6
HABITAT 6 (5 plots)							
Metrosideros polymorpha		—	20	40	40	40	60
Dubautia ciliolata		—	100	100	40	40	100
Dodonaea viscosa		—	—	—	—	100	100
Sadleria cyatheoides		—	—	40	40	20	40
Styphelia tameiameiae		—	—	40	20	40	60
Vaccinium reticulatum		—	60	20	40	60	100
Rumex giganteus		—	—	—	40	20	60

Plant Cover Development

The cover of the newly invaded plant species in habitats 1 and 2 was still under 1% in year 9 following the eruption. In contrast, the plant cover of some new invaders and of the surviving species became significant in habitats 3, 4, 5, and 6 during the period of observation. The development of the new plant cover in these habitats is shown by life-form spectra chronologies and photographs.

Life-form spectra are lists or diagrams that show the life-form composition of an area (Ellenberg 1956). In this case, the diagrams show the life-form composition of each habitat along the abscissa, while the height of each bar shows the percent cover for each life form from year 1 to 9 (Fig. 8). The percent cover was obtained from the Braun-Blanquet cover-abundance estimates given for each species in each plot. The mean cover value was first calculated for each species. Thereafter, these values were added for the species belonging to each life-form group.

Classification of each species into more detailed life-form groups appeared useful for several reasons. It was a means of identifying the developing synusiae, which are defined as groups of species of similar life form growing together in the same habitat (Ellenberg 1956). These species, because of similar morphological characteristics, are also probably the closest competitors for the same general niche (Mueller-Dombois and Sims 1966). Moreover, a detailed life-form classification focuses attention on the adaptive mechanisms of plants that are prevalent on different, new volcanic habitats. The life-form classification used for this purpose is based on the well-known life-form classification of Raunkiaer (1918).

Each diagram (Figs. 8, 10, 11, and 16) shows on the abscissa the five basic Raunkiaer life forms for vascular plants (phanerophytes, chamaephytes, hemicryptophytes, geophytes, and therophytes) plus two life-form groups for thallophytes. The latter include algae, mosses, and lichens. Subdivisions of each of these seven major life forms are based on the more detailed plant life-form key of Ellenberg and Mueller-Dombois (1967).

Macrophanerophytes (symbol PM) were here defined as trees over 2 m tall; Nanophanerophytes (symbol PN), as woody plants from 25 to 200 cm tall. Chamaephytes (symbol Ch) were defined as low shrubs or woody plant seedlings that were up to 25 cm tall at the time of observation. Chamae-hemicryptophytes [symbol Ch (H)] were defined as herbaceous perennials whose shoot system remained alive above the surface also when part of it died or dried up. Geophytes (symbol G) were defined as herbaceous perennials that could reproduce vegetatively from bulbs or rhizomes after shoot die-back. Therophytes (symbol T) were defined as herbaceous plants without the capacity of vegetative shoot reproduction. Thallo-chamaephytes included the cushion-forming bryophytes (symbol BrCh) and fruticose lichens (symbol LCh). The term "thallo-hemicryptophytes" was applied to flat-appressed mosses (symbol BrH) and the macroscopic algae (symbol Phyc H).

The subdivisions within these seven major life-form groups refer to more detailed morphological characteristics of the plants that suggest their structural adaptation to cope with the new volcanic environments. These symbols are defined in Appendix VII.

Habitat 3

Figure 8 shows that phanerophytes covered a considerable part of the surface area. These were primarily the invading daphnous, i.e., soft-leaved, evergreen small trees or shrubs (dPN) of *Buddleja asiatica, Rubus rosaefolius, Rubus penetrans,* and *Pluchea odorata.* All four species are exotics as indicated by cross-hatching in Fig. 8. The small cover of a native shrub in the dPN group which appeared in year 4 is from *Pipturus albidus.* Figure 8 also shows that the exotic shrubs covered more than 80% in the 25-200 cm height stratum in year 7, but their combined cover declined to about 60% in year 9, while the native shrub (*Pipturus*) maintained its position. Another well-represented life-form group in habitat 3 was the caespitose herbaceous chamae-hemicryptophytes [Ch(H) caesp]. These are primarily the exotic bunch grasses and sedges (Appendix III). It can be seen that their combined cover increased suddenly in year 3 to slightly over 30%. Their cover remained near 30% with some oscillation over the 9-year period. Among the geophytes, the native fern *Nephrolepis exaltata* (classifed as rhizomatous geophyte = G rhiz) attained a cover of from 5 to 10% in this habitat. Another important group in year 4 were the therophytes, represented by the composite weeds *Erechtites valerianaefolia* and *Sonchus oleraceus* (T scap). The caespitose forbs, *Physalis peruviana* and *Geranium carolinianum* (T caesp), became more important in year 9.

The general development of the new woody plant cover in habitat 3 is documented in the four photographs (Figs. 9.1, 9.2, 9.3, and 9.4). The photographs represent the change on the same habitat segment at the board walk, looking west toward the undisturbed rain forest (in the background). Figure 9.1 shows the disturbed forest in year 1 (1960), with only *Metrosideros* tree snags standing and few tree ferns (mostly *Sadleria cyatheoides*) at the outer limits of the spatter layer. The shrub *Rubus rosaefolius* is beginning to invade from the less disturbed forest edge. Figure 9.2 shows the same place in year 3 (1962). *Rubus rosaefolius* and *R. penetrans* cover almost half of the area. Grasses (*Paspalum dilatatum, Setaria geniculata*) fill much of the matrix between the shrubs and are hidden from the view.

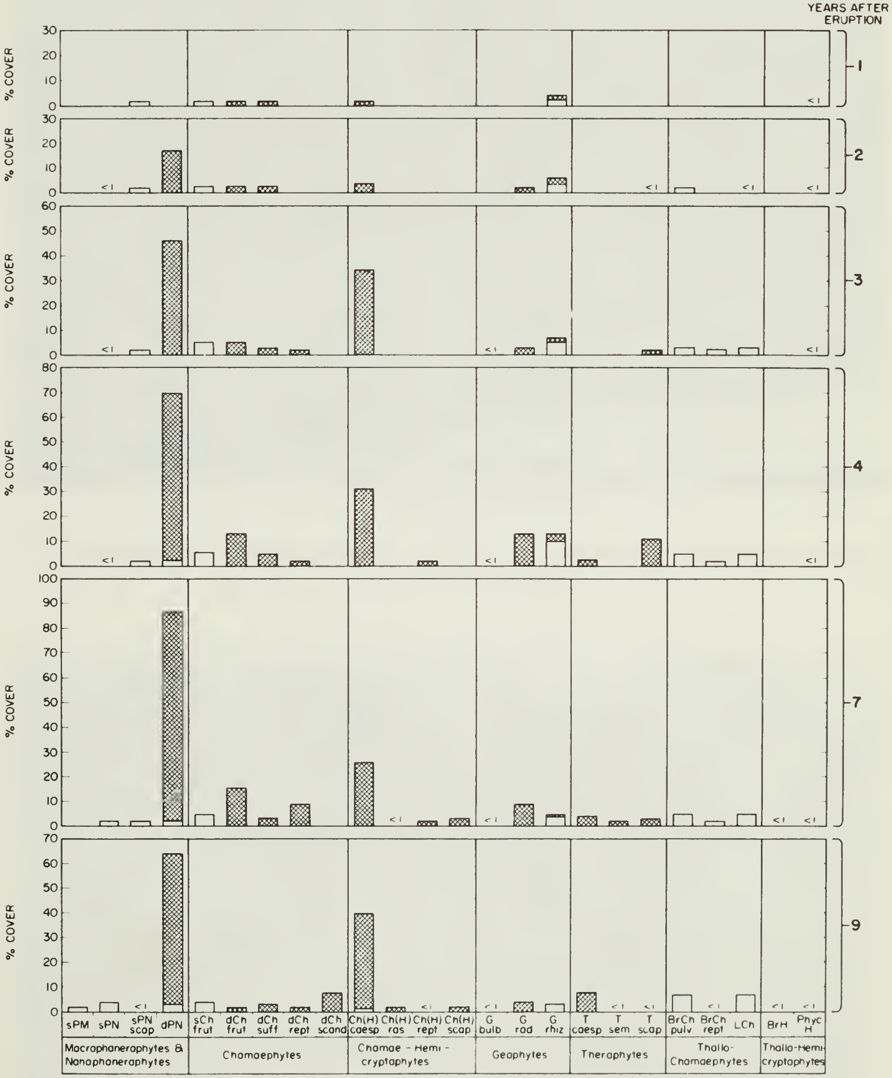

Fig. 8. Life-form spectra chronology—habitat 3. (Symbols explained in Appendix VII).

Fig. 9.1. Segment of habitat 3 photographed in year 1 (1960) after the spatter deposition.

Fig. 9.2. The same habitat segment photographed in year 3 (1962).

Fig. 9.3. The same habitat segment (as shown on Figs. 9.1 and 9.2) photographed in year 4 (1963).

Fig. 9.4. The same habitat segment photographed in year 9 (1968).

Figure 9.3 shows the same place in year 4 (1963); the nanophanerophytes (shrubs) now cover more than 50% of the surface. In addition to the two *Rubus* species, *Buddleja asiatica* is becoming important. Figure 9.4 shows the same place in year 9 (1968). The area is now dominated by *Buddleja asiatica,* but a number of individuals have lost their leaves and are dying. The peak development of *Buddleja* was 2 years earlier, in year 7. Now, in year 9, a few individuals of *Metrosideros* (left-front under the white arrow) and a few resprouts from snag-bases show up (left on Fig. 9.4).

Habitat 4

Figure 10 shows that the plant cover remained rather low throughout the 9-year observation period. Two life-form groups attained more than 5% cover, the soft-leaved evergreen small tree and shrub group (dPN) with *Buddleja asiatica* and *Rubus rosaefolius* and the sclerophyllous woody chamaephyte group (sCH frut) with *Dubautia scabra.* Also of some significance in cover were the rhizome geophyte (G rhiz) *Nephrolepis exaltata* and the chamaephytic lichen (LCh) *Stereocaulon volcani.* Both life forms attained about 3% cover each.

Habitat 5

Figure 11 shows that the greatest cover was produced by the phanerogamic life forms. The sPM column indicates the recovery of the surviving sclerophyllous *Metrosideros* trees. The trees over 2 m in height covered about 50% of the habitat surface in year 7. Their cover did not increase to year 9. The sPN group contained several surviving native shrubs, such as *Dubautia scabra, D. ciliolata, Vaccinium reticulatum, Wikstroemia sandwicensis,* and *Styphelia tameiameiae.* Together with the small *Metrosideros* trees (between 25 and 200 cm height) they covered about 13% of the habitat in year 9. The dPN cross-hatched column shows the cover of the invading *Rubus rosaefolius* and *R. penetrans* shrubs, which increased from about 20% in the year 4 to 30% in year 7. Thereafter, their cover did not increase much. Several native survivors in the dPN category increased in combined cover up to 3% *(W. sandwicensis, Dodonaea viscosa,* and *V. calycinum*). The dPN scand form refers to tree-climbing individuals of *R. penetrans.*

The herbaceous life forms were much less important in habitat 5. The geophytes (G rhiz) covered a little under 10% of the surface. This group included the surviving *Astelia menziesiana, Tritonia crocosmiflora*[1], *Hedychium coronarium*[1], and the fern *Nephrolepis hirsutula*[1]. It also included the native ferns *N. exaltata, Polypodium pellucidum,* and *Pteridium decompositum.* The lichens *Stereocaulon volcani* and *Cladonia skottsbergii* (LCh) together attained a little over 5% cover in year 9. The chamaephytes were fourth in rank of cover importance, with two groups attaining almost 5% cover each in year 9. These were the sclerophyllous, low shrubs (sCh frut) which included *Coprosma ernodeoides* and most of the low-growing (up to 25 cm high) specimens of the species mentioned as the sclerophyllous nanophanerophyte (= sPN) group in habitat 5. The soft-leaved, woody chamaephytes (dCh frut) included *Osteomeles anthyllidifolia* and low growing individuals of *Rubus rosaefolius*[1], *R. Penetrans*[1], *Wikstroemia sandwicensis,* and *Dodonaea viscosa.*

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[1] Exotics

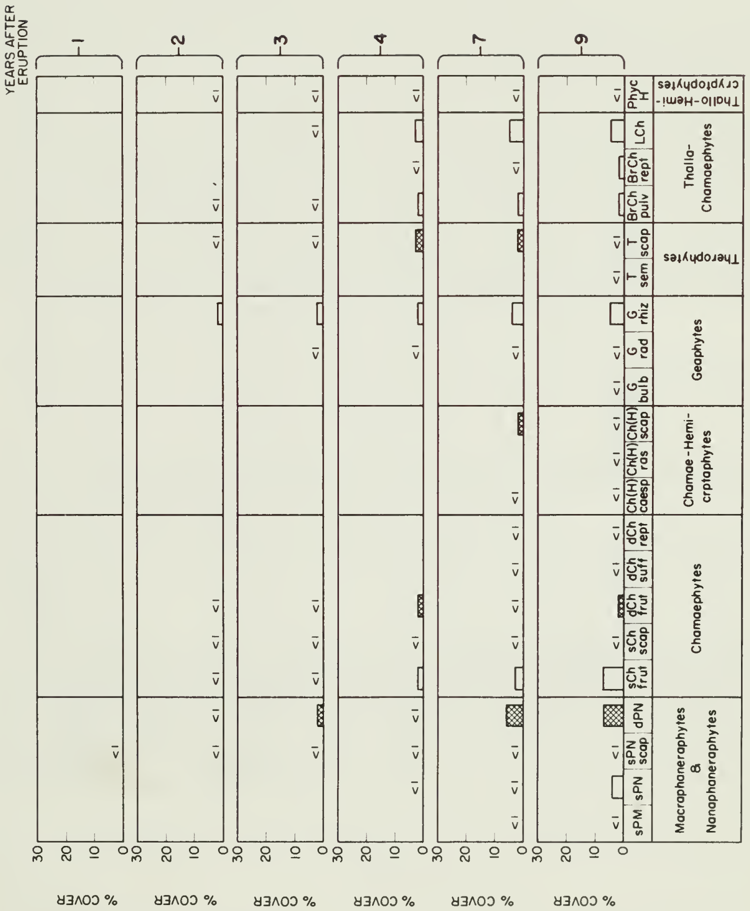

Fig. 10. Life-form spectra chronology—habitat 4. (Symbols explained in Appendix VII).

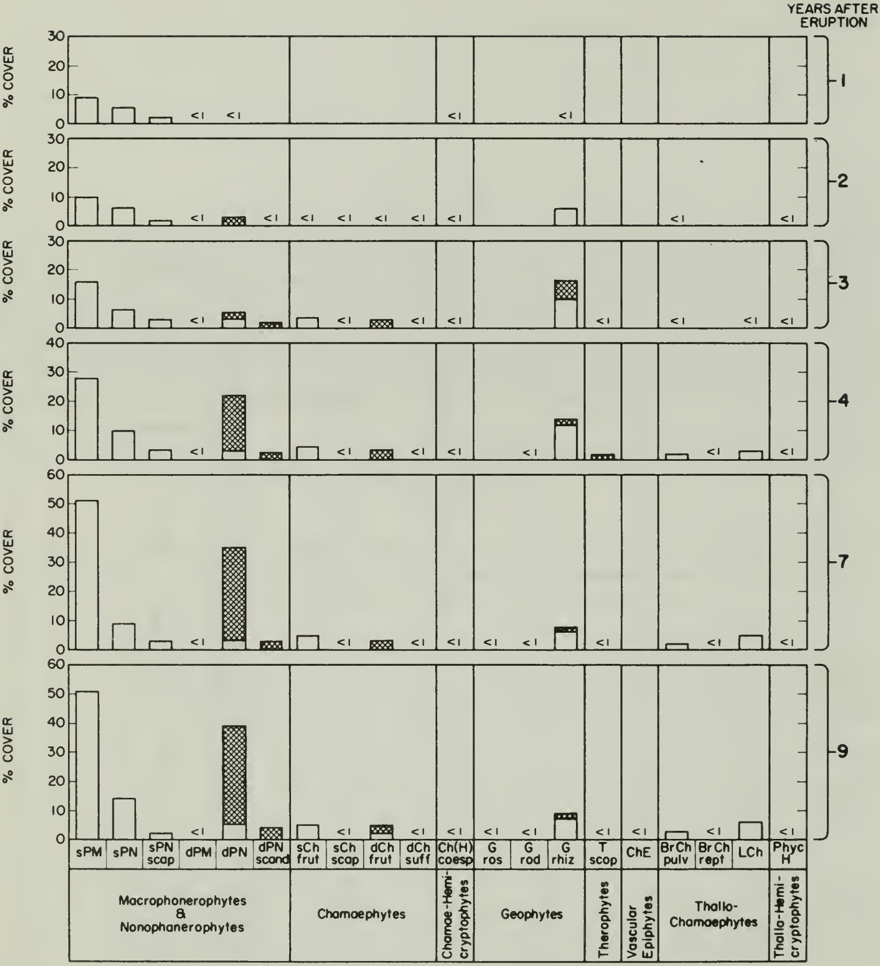

Fig. 11. Life-form spectra chronology—habitat 5. (Symbols explained in Appendix VII).

The recovery of the surviving *Metrosideros* trees in a 1.5 m deep ash deposit in habitat 5 is documented by a sequence of four photographs (Figs. 12.1, 12.2, 12.3, and 12.4). Figure 12.1 shows the trees in year 1 (1960). Nearly all foliage was slashed off, but bark remnants and short branch-stubs were left along the trunks. Figure 12.2 shows the same stand-segment in year 2 (1961). A profusion of new leaves had developed all around the trunks from top to base from adventitious buds formed from the surviving tissue (i.e., bark on branchlets and main stems). Figure 12.3 was photographed in year 4 (1963). The cylindrical crowns still covered less than 30%. Several smaller trees did not recover. Figure 12.4 shows the same stand segment in year 7 (1966). The crowns had expanded radially to about 50% cover, but hardly any significant new plant invasion had occurred on the surface between the trees.

Figure 13.1 shows a cross-section of a *Metrosideros* tree, which stood near the area photographed in Fig. 12. The cross-section was made in year 7 (1966). It exhibits a spontaneous radial increase in diameter from the time of the volcanic explosion. The latter is indicated by the blast injury. Figure 13.2 is a photograph of a similarly sized, uninjured tree that grew in the adjacent forest. The comparison demonstrates that the sudden increase in radial increment of the injured tree was correlated with the volcanic disturbance. The reason for the sudden spurt in diameter growth is probably related to the sudden increase in leaf-area from top to base and the full exposure of the new crowns to light.

Figure 14.1 and 14.2 illustrate a section in habitat 5, where the pumice blanket was only 20-30 cm deep. Here, even a few leaves remained on the trees after the fallout in year 1 (Fig. 14.1). Also the crowns retained a greater number of fine branches. The result was a more uneven, but also thick, refoliation. Figure 14.2 shows the situation in year 3 (1962). Here the trees did not assume the tight cylindrical crown shape shown in Fig. 12. Also many defoliated shrubs were seen under the trees in year 1 in Fig. 14.1. These recovered among the trees (sPN group in Fig. 11). But also many exotic *Rubus rosaefolius* and *R. penetrans* shrubs invaded in this general area (dPN group in Fig. 11). Also some grasses recovered and invaded the area as seen in the foreground in Fig. 14.2. The barren area is a trail that was buried under ash.

Figure 15 shows a section in habitat 5, where the *Metrosideros* trees developed abundant aerial roots that grew like thick, reddish "brooms." Such aerial roots appeared on many of the more vigorous trees standing in 50 cm and deeper pumice deposits. Their function is probably in balancing or replacing the respiration of the buried root system. But this has not yet been studied. Several low-growing roots made contact and grew into the soil, but ground-contact was not very common.

Habitat 6

Figure 16 shows that no life-form group covered much more than 10% in years 7 and 9. The four most important, and about equally abundant, life-form groups were the sclerophyllous nanophanerophytes (sPN), the sclerophyllous woody chamaephytes (sCH frut), the caespitose chamae-hemicryptophytes [Ch(H) caesp], and rhizome-geophytes (G rhiz).

The species in the sPN group were the surviving *Metrosideros polymorpha, Dubautia ciliolata, Styphelia tameiameiae,* and *Vaccinium reticulatum.* Those in the sCh frut group

Fig. 12.1. Segment of habitat 5 in area of 1.5-m-deep pumice deposit photographed in year 1 (1960) after the ash fallout.

Fig. 12.2. The same habitat segment photographed in year 2 (1961).

Fig. 12.3. The same habitat segment (as shown on Figs. 12.1 and 12.2) photographed in year 4 (1963).

Fig. 12.4 The same habitat segment photographed in year 7 (1966).

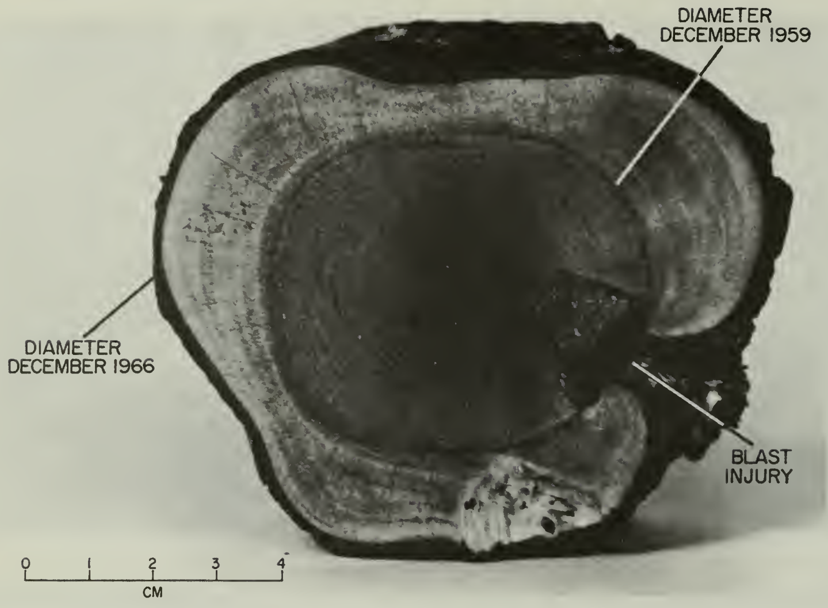

Fig. 13.1 Cross-section of *Metrosideros* stem from surviving stand photographed on Fig. 12, habitat 5.

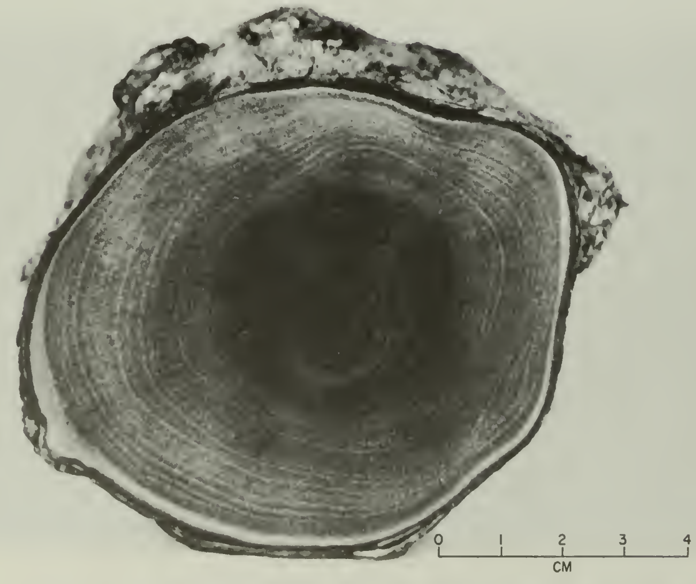

Fig. 13.2. Cross-section of *Metrosideros* stem of uninjured tree in forest adjacent to habitat 5.

Fig. 14.1. Segment of habitat 5 in area of shallow (20-30 cm deep) pumice deposit photographed in year 1 (1960).

Fig. 14.2. The same habitat segment photographed in year 3 (1962).

Fig. 15. Aerial roots on *Metrosideros* trees that survived ash burial of 50-100 cm depth. Photograph taken in year 7 (1966).

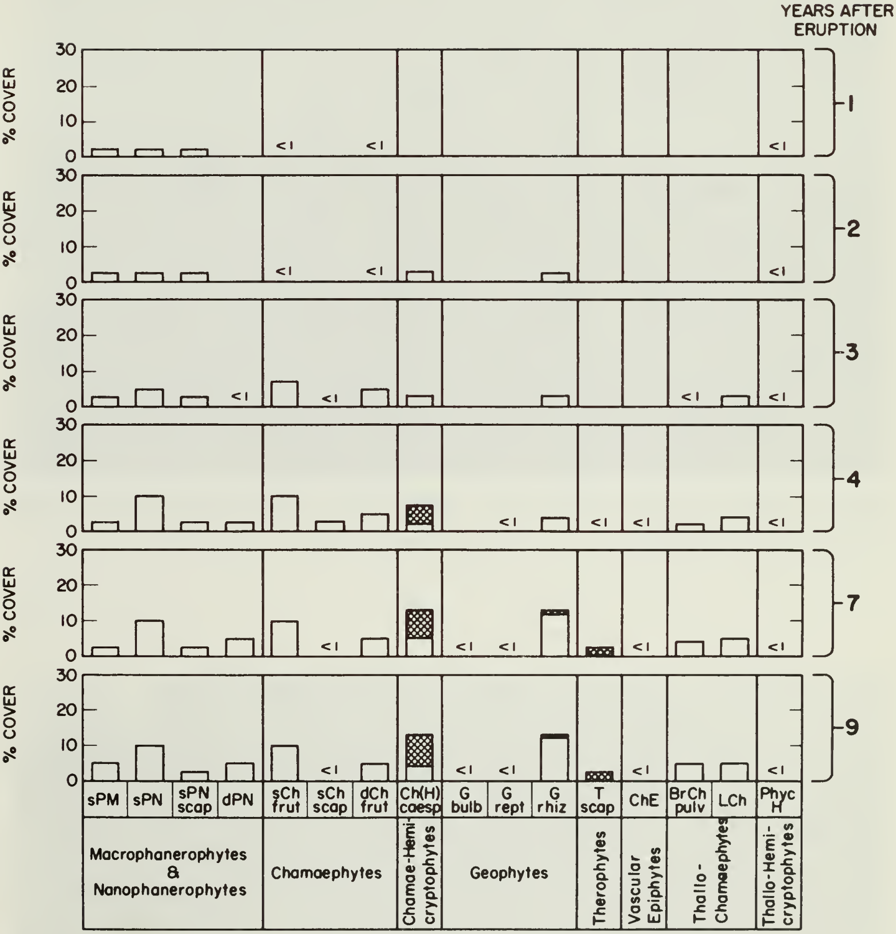

Fig. 16. Life-form spectra chronology—habitat 6. (Symbols explained in Appendix VII).

Fig. 17.1. Segment of habitat 6 photographed in year 1 (1960). Here the pumice blanket was only 10-20 cm deep.

Fig. 17.2. The same habitat segment photographed in year 3 (1963).

Fig. 18.1. Excavated stem of recovered *Vaccinium reticulatum* shrub that was buried under 25-cm-deep ash in habitat 6. Photograph taken in year 4 (1963) after the ash fallout.

Fig. 18.2. Excavated stem of small *Metrosideros polymorpha* tree buried under 25-cm-deep ash in habitat 6, photographed in year 4 (1963).

were mostly the same species of lower (less than 25 cm) stature. The Ch(H) caesp group included primarily sedges (*Machaerina angustifolia, Gahnia gahniaeformis, Cyperus polystachyos*)[1] and grasses (*Andropogon virginicus*[1], *Agrostis avenacea*). The G rhiz group includes mostly ferns such as *Sphenomeris chusana, Polypodium pellucidum, Nephrolepis hirsutula*[1], *Pityrogramma calomelanus*[1], and *Pteris cretica.*

Figure 17.1 shows a section of habitat 6 in year 1 (1960) after the ash fallout. Here the pumice blanket was only 10-20 cm deep. The damage of the woody plants was manifested primarily in sheared-off shoot systems, while remnant crowns survived. Several such remnant crowns are seen in the photograph (Fig. 17.1). Figure 17.2 shows the same section in year 3 (1962). The recovery of sclerophyllous native shrubs (sPN and sCh frut in Fig. 16) was remarkable. The bush in the foreground in Fig. 17.2 is *Dubautia ciliolata.* The taller individuals in the background are shrubby *Metrosideros* trees of about 2-3 m in height. Figure 18.1 shows an excavated main branch of an ash-buried *Vaccinium reticulatum* shrub that was not broken off the root. Several new branches sprouted at the new surface line from the main branch, while the branch itself developed a few lateral roots. A similar resprouting occurred at the new surface line on the main stem of the *Metrosideros* shrub shown in Fig. 18.2. Also, several lateral roots developed from the buried main stem in the new ash layer. These excavations show the development in year 4 (1963) after the disturbance.

[1] Exotics

7

Environmental Conditions

The Climatic Gradient

The climatic gradient over the study area from Kilauea Iki (habitat 1) to the upper Kau Desert (habitat 6) along transect AA′ (Figs. 2 and 3) was already briefly described on page 11. Initially, the existence of this gradient was only assumed from the long-term climatic records of nearby stations at Hawaii Volcanoes National Park headquarters and Halemaumau, respectively. It thus seemed important to test the reality of this gradient and to find out how much of the evolving plant invasion and recovery patterns can be explained by the climatic gradient.

Temperature and relative humidity

A comparison between habitat 1 (Kilauea Iki lava floor) and habitat 6 (upper Kau Desert, at end of transect AA′, Fig. 2) is shown in Fig. 19. The records are from hygrothermograph charts for 2 years of observation (1967 and 1968). Abstracted from these charts were the mean number of hours per day for each month of the year during which the air temperature exceeded 20°C. Similarly, the mean number of hours per month were counted during which the air temperature was below 15°C. The two curves are shown for each habitat on the left side of Fig. 19. Each curve represents the mean trend for the 2 years. The time of a moderately warm growth climate, defined as between 15°C and 20°C air temperature, was of longer duration (by about 1.5 months) in habitat 1 than in habitat 6. The comparison also shows that there were twice as many cool hours under 15°C from November through May in the Kau Desert habitat than on the Kilauea Iki crater floor. Thus, in terms of air temperature, habitat 1 was more moderate than habitat 6. The relative humidity record was similarly abstracted from the charts for the mean hours per day in each month that showed relative humidities over 95% and under 65%, respectively. The right side of Fig. 19 shows that the number of atmospherically humid hours (over 95% relative humidity) was greater for almost every month of the year for habitat 1 than for habitat 6. Also, there were more total hours through the year with relative humidities under 65% in habitat 6. Thus, as expected, the data show that the Kau Desert habitat (6) was consistently drier than the rain-forest habitat (1) of Kilauea Iki.

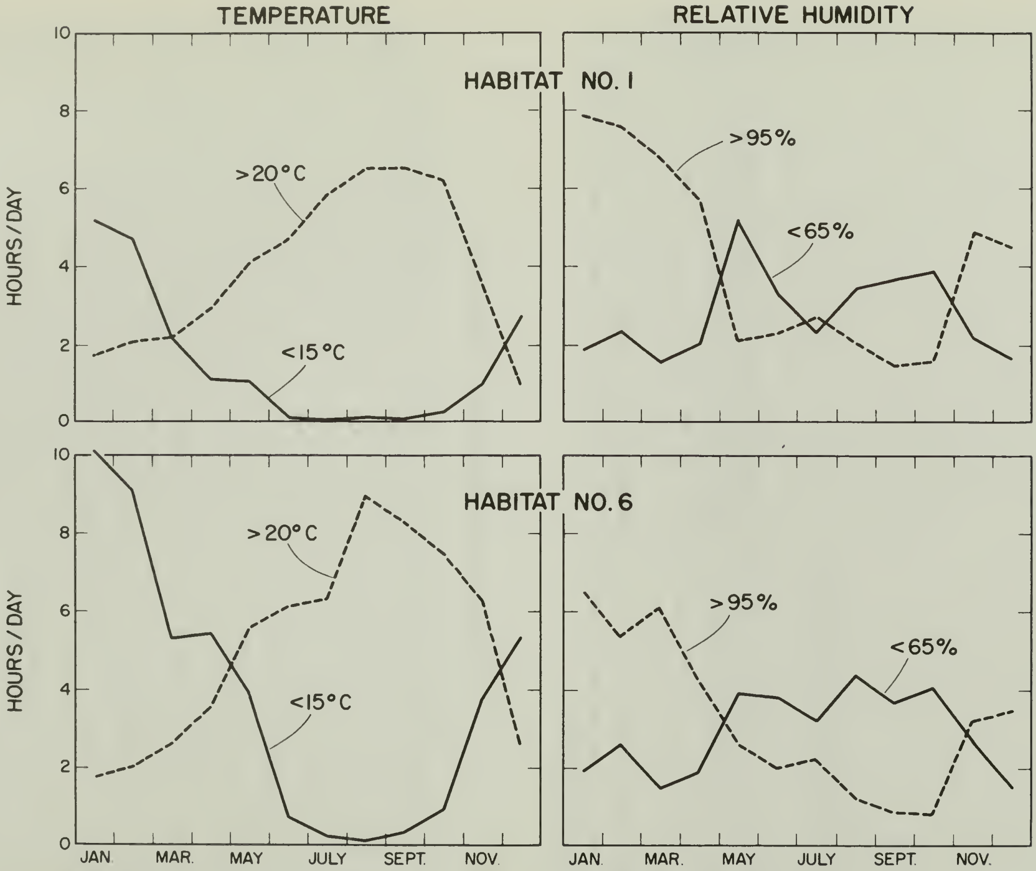

Fig. 19. Comparison of temperature and relative humidity for habitats 1 and 6.

Desiccating power, insolation, and rainfall

Figure 20 shows the relative drying power of the atmosphere for habitats 1, 4, 5, and 6 in relation to the monthly rainfall for a period of 9 months, from May 1968 through January 1969. The relative desiccating power is expressed in terms of mean daily water loss per week from Livingston white and black bulb atmometers. General comparison of the four diagrams shows that the desiccating power in habitats 1 and 4 was quite similar; in habitat 5 it was lowest, and in habitat 6 it was greatest. The same is shown by the 9-month daily mean values (M) stated for the white bulb readings on each diagram. The low readings in habitat 5 relate to the wind protection afforded by the recovered trees. The atmometers were all at 30 cm height above the ground in open places, where they measured the atmospheric environment of low-growing plants. The frequently greater range between white and black bulb values in habitat 6 as compared to 4 (or the other habitats) indicates also the greatest average insolation and thus light intensity for habitat 6. Therefore, the climatic gradient shows only a small difference in terms of desiccating power along the first kilometer from habitat 1 to 4. Both habitats are in the terrain of the original rain forest (Fig. 2). However, there was a distinct decrease in rainfall as can be seen by comparing the equivalent monthly rainfall amounts of habitat 1 with those of habitat 4.

Figure 21 indicates the relationship between mean daily water loss per week (cc) and rainfall per week (mm) for the four habitats. The curves show that if, for example, the weekly rainfall is 125 mm, the daily white bulb evaporation in habitat 6 can be expected to be 16 cc; in habitat 1, it can be expected to be about 7 cc; and in habitats 4 and 5, 3.5 cc. This reemphasizes that the atmospheric drying power of habitat 6 was greatest, but it also shows that the evaporating power in habitat 1 was somewhat greater than in habitat 4. This was not related to a greater direct insolation or greater wind intensity, but probably was an effect of the greater substrate heat radiation on the crater floor (see under substrate temperature, p. 69).

Mean rainfall and dry periods

Figure 22 shows a climate diagram for both habitat 1 and habitat 6, prepared after the method of Walter (1957). These diagrams present the mean monthly rainfall and mean monthly temperature for 1967 and 1968. The rainfall curve is plotted with reference to the right-hand ordinate on each diagram and the temperature curve with reference to the left-hand ordinate. The 12 months of the year, from January to January, are indicated by the dashes on the abscissa, with July indicated by the central dash. The temperature curves show little difference on this basis, but the rainfall curves do. If a dry period is defined as a monthly rainfall of less than 100 mm, then habitat 6 showed two dry periods, one in June and one in September. The September dryness was particularly intense. However, the annual mean rainfall stated as 2203 mm for habitat 6 is as high as recorded for some tropical rain forest areas (Walter and Lieth 1960). Therefore, the upper Kau Desert is certainly not a climatic desert. The mean annual rainfall values in Fig. 22 indicate a rainfall gradient of more than 1000 mm over the study area.

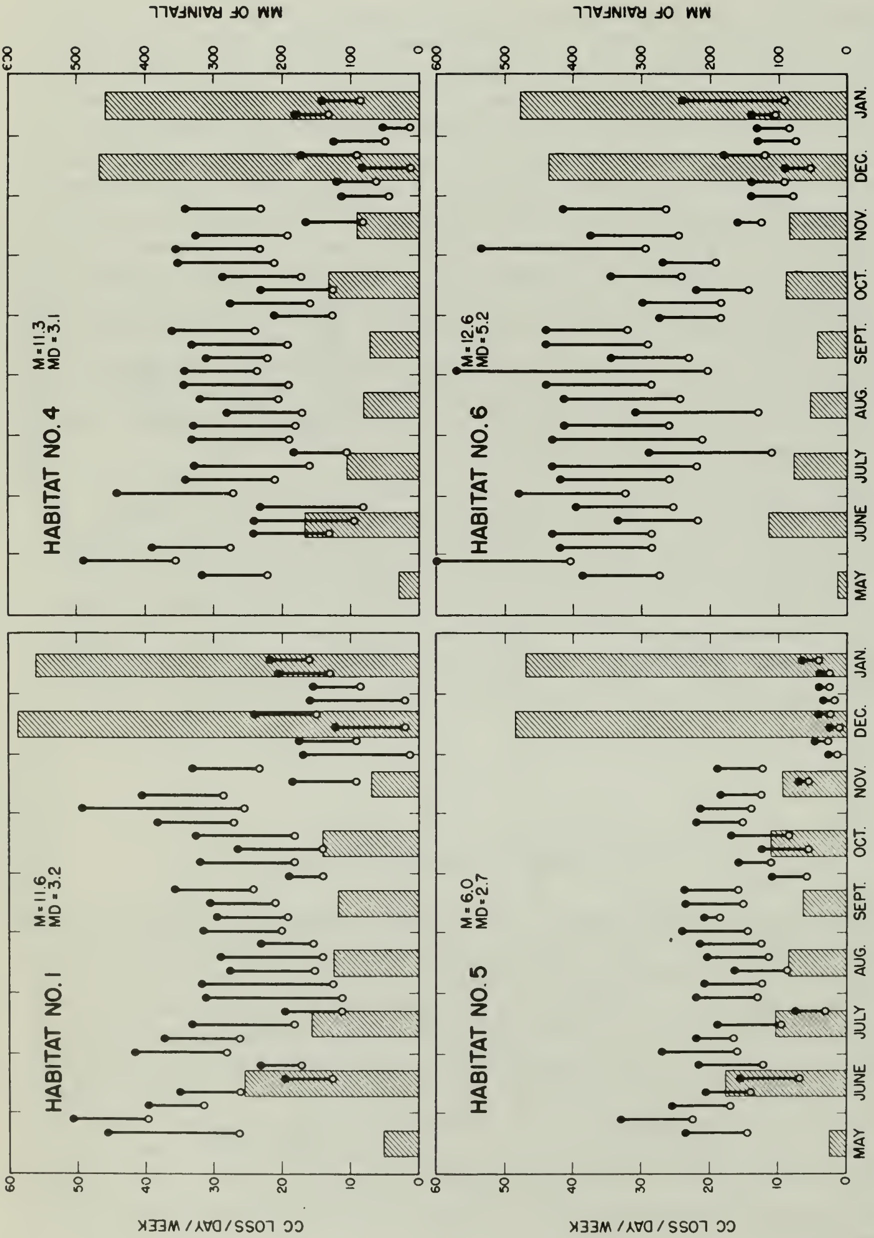

Fig. 20. Mean daily loss of water (cc) per week from white and black Livingston atmometers, and monthly rainfall (mm) in habitats 1, 4, 5, and 6.

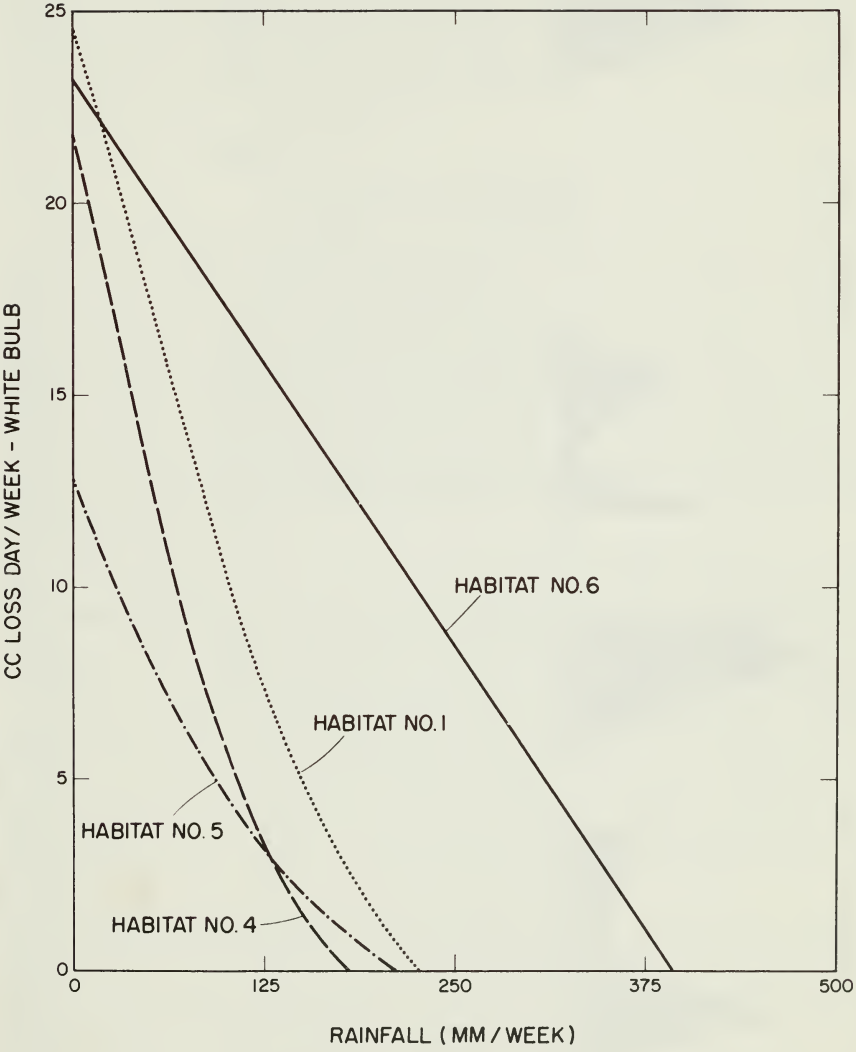

Fig. 21. Relationships between evaporation rate of white bulb atmometers (mean daily water loss in cc/week) and monthly rainfall (mm) in habitats 1, 4, 5, and 6. Data from May 1968 through January 1969.

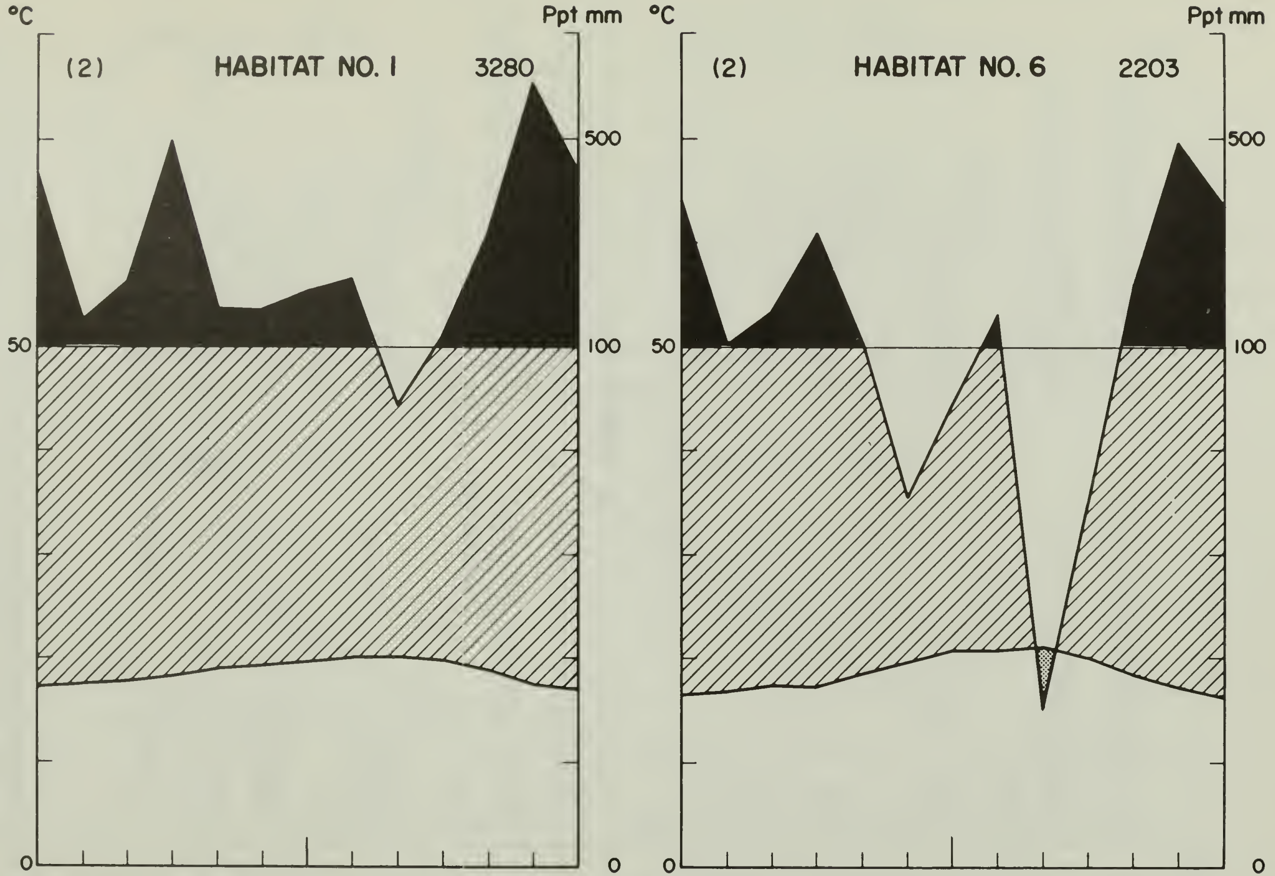

Fig. 22. Climate diagrams for habitats 1 and 6. Mean monthly air temperatures (°C) and precipitation (ppt mm) for 2 years (1967 and 1968). Mean annual rainfall stated under ppt mm.

Substrate Differences

The gross substrate differences have already been emphasized under the section describing the new volcanic habitats (pages 13-19). They are summarized briefly on the habitat map (Fig. 2) and the profile diagrams (Figs. 3 and 4) in that section.

Additionally, a few analyses of substrate temperature, moisture, and chemical and mineralogical properties were made.

Substrate temperature

Substrate temperatures of habitats 1 and 2 have changed considerably over the study period. After the eruption stopped, the thin crust of the crater floor in habitat 1 was very hot. The floor steamed heavily during and after a rainfall. Nine years later, most of the steaming was concentrated toward the center of the lake, but a few areas of steaming cracks radiated toward the edge of the crater. In March 1960, two holes were drilled into the crust over the deepest portion of the lake (115 m) to gain information on the rate of cooling (Ault et al. 1961). At this time the lake crust was about 4 m thick and the melt beneath was over 1000 °C. This melt temperature compared with that of 1060-1190 °C measured in the lava fountain during the eruption. Continued drillings and temperature measurements have been made over several years, and, by 1968, the crust was about 30 m thick and the melt beneath was 1065-1090 °C (Fig. 3).

Generally, there has been a continued crustal temperature increase toward the center of the lake. Surface temperature measurements made in September 1968 at the warmest period of the day, and across the lake toward the center (from east to west), gave the following results: at 3 m from edge, 43 °C; at 30 m, 52 °C; at 300 m, 54 °C; at 500 m, 60 °C. Earlier, still higher surface temperatures (70-74 °C) were recorded during the same summer season at 300 m and 500 m points. These higher temperatures prevailed at midday during a dry spell when the black, glassy surface of the massive pahoehoe lava had been exposed to intense sunshine in the morning. This temperature gradient corresponded to the invasional pattern of plants observed. In year 9 (1968), algae and lichens had penetrated to 250 m (54 °C) on the crater floor, while ferns and mosses followed closely. Native woody plants were established up to 114 m (52-53 °C), but the exotic grasses and forbs had penetrated less than 20 m (43 °C).

Temperature measurements were also made in joint cracks where *Nephrolepis exaltata* was established. During the warmest part of the day, the temperature at the places of rhizome attachment were up to 13 °C below the surface temperatures. The exposed joint faces, which consisted of dark red and greenish black strata, varied in surface temperature. When equally exposed to the sun, the black, glassy, and red surfaces became much warmer (39.0 °C) than the greenish-black surfaces (35.5 °C).

The cinder-cone summit of habitat 3 took a long time to cool off. During the first 3 to 4 years after the eruption, the summit steamed vigorously after each rainfall. Steam rising through the hot mound of cinders and buried forest caused considerable hydrothermal alteration in the pyroclastic material. In the first 2 years, large deposits of whitish to orange sublimates were deposited around the steaming fissures on the summit. The summit and slope temperatures remained high for several years. In July 1963, Fox (1964) made several temperature measurements along the east slope. He reported a surface temperature of 20 °C at the lower slope of the cone. Further up, the temperature began to increase steeply, and at about one-fourth of the distance from the summit, temperatures of 150-160 °C were recorded within 10 cm of the surface in year 4. In this area of the summit, native woody plants *(Vaccinium reticulatum, Dubautia scabra,* and *Metrosideros polymorpha)* were noted only in year 9 (1968). At that time only a few fissures continued to emit steam.

Thus, in habitats 1 and 2 substrate surface temperatures—controlled primarily by the slow cooling pattern of the interior of the new volcanic habitats—were correlated with the observed plant invasion pattern. In habitat 1 this explains in part the concentric progression of plant life toward the center. In habitat 2 the still slower cooling of the surface partly explains the delay till year 3 (1962) of the first algal appearance (Appendix II).

Substrate moisture

The properties tested were simulated field capacity and permanent wilting percentage of the pyroclastic materials. Unexpectedly, there were no significant differences in the soil moisture constants between spatter and pumice materials. Their simulated field capacities (FC) varied from 33% to 46% (by weight), their permanent wilting percentages (PWP at 15 atm) varied from 31% to 43%. Thus, available water (defined as the difference between FC and PWP) ranged only from 2% to 3%. Small cinder blocks from the summit of the cinder cone (habitat 2) had a field capacity of only 15%, but available water was even slightly greater with 3.7%. However, this difference was probably not significant. Thus, there is less water available in these new volcanic materials than in most soils including sands, and plants will have water for growth only for short periods after showers.

This is further corroborated by the substrate moisture values shown in Table 7. Even 48 hours after a prolonged shower in excess of 100 mm, the moisture downward in several ash profiles was barely in the range available to plants. The values in Table 7 may show two things: first, that a 2-day evaporation had dried up the upper 5 cm considerably below the wilting percentages; second, that even a prolonged shower may not wet the ash particles to capacity. A plant rooted in the upper 25 cm therefore would grow actively only for a short period following profile wetting. This may also explain the greater success of more deeply rooted woody plants and of herbaceous plants with thick rhizomes (ferns) or bulbs.

TABLE 7. Substrate moisture (% weight) in volcanic ash profiles 48 hours following a rain shower in excess of 100 mm. Each value represents the mean of 10 samples.

Depth of sample	Habitat				
	2	3	4	5	6
1-3 cm	8.5	12.4	16.2	22.6	3.5
3-5 cm	10.0	14.4	18.0	—	11.0
8-12 cm	14.0	20.5	20.5	33.0[a]	—
15-25 cm	20.0	—	45.6	40.0	—

[a] Only the blocked-out values are in the available range.

Plant nutrients in soil and rain water

The volcanic substrates of all six habitats originated more or less simultaneously from the same source. The rock source is described as olivine basalt (Macdonald and Hubbard 1966). The basic chemical constituents in these physically different materials is known to differ little. However, the question of concern here was whether this is true also for the exchangeable and available plant nutrients.

Nutrient analyses were made from chipped off lava rock material of habitat 1 and for ash material of habitat 2. The values are shown in Table 8. Both the lava rock (habitat 1) and the volcanic ash (habitat 2) have some nutrient capability as indicated by the chemical analysis.

TABLE 8. Exchangeable cations and available phosphorus and nitrate in two volcanic substrates 8 years after deposition. All values in ppm.

	Lava	Volcanic ash	
Nutrients	depth 0-2 cm	0-2 cm	8-12 cm
Exchangeable			
Ca	4.4	7.4	3.0
Mg	1.0	3.6	1.5
K	1.4	5.6	2.8
Na	2.0	5.0	3.0
Available			
P	5.3	0.8	1.2
NO_3	6.7	59.9	14.7

The surface values of exchangeable cations for the ash are higher than for the lava. However, these were single determinations only. It appears conceivable that the greater surface area associated with the finer particle size of the ash is consistently correlated with higher values for exchangeable cations. The higher NO_3 values of the ash samples in comparison to the lava are rather striking. In Hawaiian agricultural soils, NO_3 values of between 5 ppm to 40 ppm are considered normal (Dr. Y. Kanehiro, pers. comm.). Thus, the value for the surface 3 cm of the volcanic ash on the cinder-cone habitat is extremely high and may have been a local unconformity. Nevertheless, the subsurface ash value is more than twice as high as that on the lava. Moreover, it is interesting that even the NO_3 value on the lava rock falls into the range of what is considered a ''normal'' NO_3 amount for mature soils.

A number of pH determinations were made for the surface and subsurface material in August 1967. These are shown in Table 9.

TABLE 9. Substrate pH values at surface and subsurface in six new volcanic habitats. Values stated are the most frequent out of 10 determinations each.

	Surface	Subsurface	
Habitat	0-2 cm	at 10 cm	at 20 cm
1	6.4	—	—
2	5.0	6.2	—
3	4.5	5.0	—
4	5.0	6.3	6.3
5	5.4	6.3	6.6
6	4.9	5.8	—

The pH values show a range from 4.5 to 6.4 for the surface of the ash substrates. They were more acid than the lava rock surface. Downward in the ash profiles, the pH values increased consistently. The increase of pH values with profile depth is quite normal for soils that have a higher organic content at the surface. In the ash substrates the organic content was not tested because it appeared negligible. The lower pH values at the surface were somewhat surprising. They could have been related to the surface nitrogen present. If the N were originally present in NH_4^+ form, an acid condition could result from the following reaction:

$$NH_4^+ + 2O_2 \rightarrow 2H^+ + NO_3^- + H_2O.$$

Two rainwater analyses were made to see if there could have been any nutrient contribution through this source. The results are stated in Table 10. Both analyses were made at a time when volcanic fumes were blown from other active volcanic vents (Halemaumau and Aloi-Alae) toward the park headquarters and the study areas. This may account for the high amount of SO_4 in each sample. It appears likely that the SO_4 may contribute even more strongly than the N to the acidification of new volcanic surfaces discussed above.

It is interesting also that small amounts of NO_3 were present in the rainwater. This quantity may have been sufficient to provide a basis for establishment of plant life on raw volcanic substrates that were initially devoid of organic nitrogen. Of course, also the NO_3 in the rainwater must have an organic origin.

TABLE 10. Plant nutrients in rainwater (ppm) near the study area (Park Headquarters).[a]

Nutrients	Feb. 68	Feb. 70
NO_3	0.01	0.07
Ca	0.9	3.2
Mg	0.5	0
K	0.5	0
SO_4	2.5	3.7

[a] Both samples were taken during volcanic fuming.

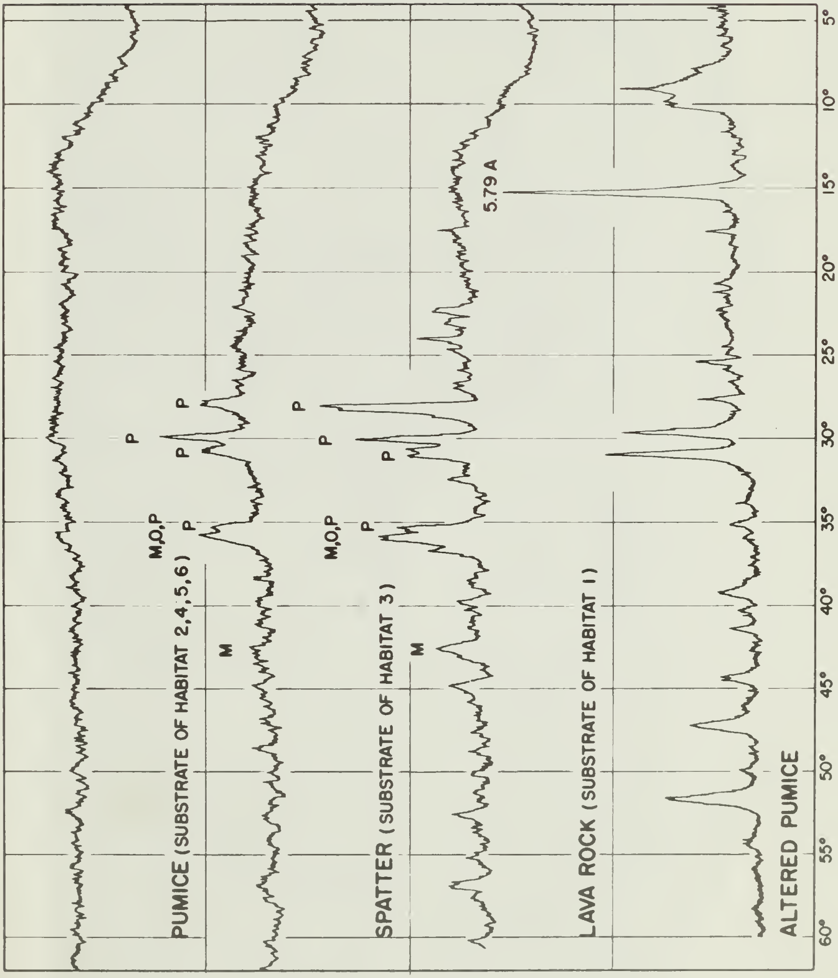

Fig. 23. X-ray diffraction tracings for habitat substrates showing gross mineralogy.

Fig. 24. The summit of the cinder cone photographed in year 3 (1962) after formation.

Mineralogical properties

Examination of the lava rock and pyroclastics by X-ray diffraction analysis revealed that there were some differences in their mineral composition. Although all of these substrates have the same chemical composition, the minerals varied from the noncrystalline material in fresh pumice to the crystalline magnetite, olivine, and plagioclase feldspar in the spatter and lava rock. The X-ray tracings of these substrates are presented in Fig. 23.

These tracings reveal that pumice, a pyroclastic material which has cooled sufficiently fast, is composed primarily of glass. Under these conditions, it is not possible to detect crystallinity by X-ray diffraction analysis. However, the spatter and lava rock, which have cooled much more slowly than the pumice, show the presence of the crystalline minerals mentioned above.

Although the materials have been subjected to 9 years of soil-forming processes, based on X-ray techniques there is no noticeable alteration in the primary minerals except in the hydrothermally altered lava rock in habitat 1. Here, the petrographic microscope revealed some slight alteration of the iron bearing minerals to hematite.

Finally, Fig. 23 shows that the altered pumice, which contained sublimates deposited around fumaroles, was quite different in mineral composition when compared to the spatter and the lava rock. It was not possible to identify these sublimates. The same difficulty was encountered previously by Murata (1966), who collected deep orange pseudomorphs from the pumice that had been exposed to acid gases coming through fissures on the cinder cone. He concluded that the deep orange color was brought about by highly porous pseudomorphs absorbing large quantities of ferric chloride. An analysis of the pseudomorphic material showed that it contained 79.2% SiO_2, 17.0% H_2O, and other minor constituents commonly found in basalts. The composition corresponded to that of a hydrous silica, and the X-ray diffraction pattern of the same material showed a single diffuse maximum band typical of amorphous silica. Murata (1966) concluded that the steaming hydrochloric and sulfuric acids had decomposed the superficial pumice into the siliceous pseudomorphs. Yellowish nodules of pumice fragments cemented by crystallization of various salts (mostly chlorides) were also examined by Murata through X-ray diffraction analysis. Most of this material was amorphous, although small amounts of halite and anatase were present. A solution prepared of this material gave a strong test for Cl^-, Fe^{+2}, Fe^{+3}, Mg^{+2}, Al^{+3}, and Na^+ Thus, based on the results of Murata, there is strong suggestion that the secondary materials found on the cinder cone consist primarily of opal, a hydrous noncrystalline silica (a whitish deposit), gypsum (also a whitish deposit), hematite (a dark red material), and limonite (a yellow to orange material). Figure 24 shows a photograph of the cinder cone, which indicates the discoloration by these secondary materials.

8

Discussion

Obviously, the patterns of plant invasion and recovery observed depended on a number of specific factors and combinations of factors of which only some can be explained by the environmental measurements made. However, the breakdown of the total area into the six habitats and the study of associated features provided a basis for isolating the most probable causes or limiting factors from the total matrix of factors involved in the plant establishment on these new volcanic materials.

The recorded plant invasion and recovery patterns may be summarized as follows:

- A directional progression of invasion was recorded on Kilauea Iki crater floor (habitat 1) and the spatter-with-tree-snags area (habitat 3). A directional recovery was also noted in habitats 3 and 5.
- Differences in rate of invasion were observed in the same climate on different substrates of the same age.
- Distinct sequences in arrival of plant life forms were recorded in different habitats.
- Primary community formation was observed through development of synusiae and aggregation.
- Survival capacity was seen to be a combination of degree of destruction effects and plant life-form characteristics.
- Observations were made on the relative contribution of native and exotic species to plant recovery.

Factors Related to Directional Invasion and Recovery

At the onset of the study, it was assumed that the climatic gradient may have some influence on the direction of plant invasion. However, edaphic differences along this gradient exerted a much stronger control. Moreover, directional invasion patterns were not influenced by one factor only.

Substrate heat gradient

The concentric inward advance of plant life on the Kilauea crater floor was closely related to the substrate heat gradient that showed initial cooling at the crater floor margin. As shown by the substrate temperature measurements, the temperature increased toward the center of the crater. The temperature measurements made were too general to assign any threshold values that limited the advance of the different life forms. But the algae were found in the first advancing front and here maxima measured on the lava surface ranged from 54°C to 70°C during the warmest part of the day in summer 1968. Apparently, the same surface maxima were tolerated by the lichens which appeared only 2 years after the algae, but then occurred in the advancing front together with the algae. The probable cause of delay in arrival of the lichens will be discussed later. All other life forms advanced behind the algae. Thus, their establishment was possible only at lower temperature maxima. Moreover, they occurred at their advancing front only in lava cracks where surface temperatures were moderated by shade. Direct temperatures of the vapor steam were as high as 98°C and ferns and mosses would grow next to such hot vapor in the same cracks. But the substrate temperatures at the points of plant attachment were quite moderate, always under 45°C. The lava surface temperatures were probably a combination of two heat sources: one coming from the glowing magma below, the other from the sun. W. P. Hasbrouck (U.S. Environmental Science Service Administration) made several subsurface temperature measurements in shallow bore holes of the lava rock near the center of the crater floor in 1967. He recorded the following temperatures (Table 11).

Table 11 shows that the heat increased downward as expected. However, a 50°C (122°F) surface temperature can easily be generated on any black surface during periods of sun exposure in temperate climates. Thus, it can be said with certainty that the pioneer mosses, ferns, and seed plants did not invade the crater floor until the lava surface heat was down to a temperature level that could be found in the cracks of any paved road in that climate. It is probable even that purely sun-generated heat kept these plants from entering the lava surface, while this was evidently not so for the lichens and algae. Therefore, the progress of plant life toward the center of the crater floor was related to a decrease in the volcanic heat from below, and plant life invaded only when the heat level had arrived at a temperature range found on nonvolcanic surfaces.

A subsurface heat-related invasion was also observed on the cinder cone habitat. However, here the invasion pattern was not as clearly directional as on the crater floor. Instead, the invasion delay of 2-3 years (Appendix II) was most probably caused by the slow cooling of the cinder cone surface.

The directional invasion recorded in the spatter-with-tree-snags habitat (3) had nothing to do with substrate temperatures. Here, the direction was related to two factors: the nearness of a seed source, and a snag-density gradient.

TABLE 11. Temperatures in shallow bore holes measured in a 2-ft circle on the Kilauea lava floor (near center) in 1967. (Unpublished data courtesy of W. P. Hasbrouck.)

Depth	Temperatures			
6.4 cm	50°C	—	—	59°C
7.5 cm	—	59°C	—	—
11.4 cm	—	—	50°C	69°C
14.0 cm	54°C	62°C	60°C	—

Nearness of seed source

As shown on the map (Fig. 2), a relatively undisturbed rain forest bordered habitat 3 on the east side. The invasion began at this border and progressed across the board walk toward the cinder cone habitat in an easterly direction. The disseminule abundance was probably great right at this border and decreased away from it.

The important invaders here were the exotic woody plants, *Rubus rosaefolius, R. penetrans,* and *Buddleja asiatica.* All three were of minor quantitative importance in the undisturbed rain forest next to habitat 3. A major factor for their success was an explosive fruit and seed production of the surviving individuals at the margin of the relatively undisturbed forest. This was undoubtedly caused by the sudden openness and increased light availability right after the ash fallout.

Snag-density gradient

The advance of seed plants onto the new volcanic surface was facilitated by the presence of the *Metrosideros* tree snags. They caused microhabitats around the stem that showed better moisture relations than existed in the ash between the snags. Many of the new invaders became established at the base of such snags. Such an establishment is shown in Fig. 25 for *Buddleja asiatica.* This establishment pattern was typical also in the pumice-with-tree-snags habitat (4). A number of substrate moisture samples were collected at tree-snag bases and in intervening spaces. The values shown in Table 12 are indicative for the differences recorded.

The greater moisture at the snag bases is easily explained. Rainfall occurred usually in association with strong winds from the northeast. During such driving rains, the tree snags acted as interceptors and more water would run to their bases than was normally distributed over the surface. This precipitation moisture concentration effect on objects elevated above the surface occurred over the entire study area. The effect was borne out by the comparison of moisture caught in paired rain gauges, one of which was equipped with a Grunow fog interceptor. Table 13 shows the amounts of monthly rain water caught in such paired rain gauges in habitat 6. The precipitation water caught in the gauge with fog interceptor was consistently higher. The excess quantity ranged from 1.2 to 1.8. The Grunow fog interceptor is a 20-cm-high wire cylinder of 9.6 cm diameter. A 2-m-tall snag of similar diameter would have probably supplied 12-18 times the amount of normally distributed rainfall. This indicates that the moisture concentration at the bases of snags must have been an important factor in plant establishment. This moisture concentration effect is particularly important when viewed in relation to the low capacity of the ash substrates to store water in available form for plant growth.

The density of snags was higher near the border of the undisturbed forest in habitat 3 (Fig. 9) and decreased to the border of the cinder cone (Fig. 25). This snag-density gradient, therefore, was a supporting factor in the directional invasion from east to west in habitat 3.

TABLE 12. Substrate moisture (% by weight)[a] recorded at the base of tree snags and in the open ash surface 48 hours following rain in excess of 100 mm.

Habitat	Depth (cm)	At snag base	>1 m away
No. 3	1-3	14.1	12.4
	3-5	17.2	14.4
No. 4	1-3	18.4	16.2
	3-5	20.9	18.0

[a] Each value represents the mean of 10 samples.

Fig. 25.1. Eastern boundary of spatter-with-tree-snags habitat (3) where it joins the cinder cone habitat (2). Photograph taken in year 4 (1963).

Fig. 25.2. The same location photographed in year 7 (1966). Several *Buddleja asiatica* individuals had become established at the bases of tree snags.

Fig. 25.3. The same location photographed in year 9 (1968). More *Buddleja* individuals had become established but several were dying where the snags had fallen.

TABLE 13. Monthly precipitation water (mm) received in a standard rain gauge and an adjacent one equipped with a Grunow fog interceptor in habitat 6 during 1968.

Month	Standard gauge	Gauge with fog interceptor	Fraction of standard
March	87.4	148.1	1.7
April	462.5	703.1	1.5
May	78.3	123.1	1.6
June	115.1	201.5	1.8
July	82.9	127.0	1.5
August	55.4	96.7	1.7
September	48.4	70.3	1.5
October	93.4	122.2	1.3
November	90.9	104.6	1.2
December	436.9	612.2	1.4
Totals	1551.2	2308.8	—
Mean	—	—	1.5

Ash-depth gradient

A directional recovery of surviving plants was observed only in two habitats: in the spatter-with-tree-snags habitat (3) and in the pumice-with-surviving-trees habitat (5). The obvious cause was the ash-depth gradient which in both habitats started at their outer margins with less than 10 cm depth and increased in direction of the cinder cone habitat (2) to more than 2 m depth (Fig. 2).

In habitat 3 this directional recovery was manifested in basal sprouting of *Metrosideros* snags that were initially believed killed. Basal sprouting started at the habitat border, where the spatter was less than 10 cm deep, and continued eastward to the middle of habitat 3 (near the board walk) where the spatter was about 50 cm deep (Fig. 9.4). The basal sprouting was unique to the spatter habitat and must have been related to the nature of this pyroclastic deposit. The material immediately became welded or cemented into coarser fragments upon deposition. The fallout stripped off nearly all small branches and bark. However, at the base of the stems, molds were formed through a sudden chilling of the glowing ash. A small space was usually left between the scored stem base and the mold. This space must have provided for precipitation moisture penetration and accumulation around the stem and for gaseous exchange which encouraged the basal sprouting from still living tissue at the stem base. A tree mold in habitat 3 is shown in Fig. 26, where the original *Metrosideros* tree was burned at the base. It is probable that only the older trees with rough bark and a thick epiphytic moss layer surrounding their tree base survived the spatter deposition.

The *Metrosideros* trees in habitat 5 recovered more or less simultaneously along the ash-depth gradient, and their resprouting was rarely from the base, but instead from the remaining aerial stem part. A directional recovery was observed only for the surviving undergrowth species, the shrubs and herbs. Here a rough relationship of size and pumice depth was noted. The surviving shrubs reappeared generally up to a pumice depth of 50 cm and the herbs up to depths of 25 cm. However, these life-form boundaries of surviving undergrowth plants were not so clearly defined. A directional invasion pattern similar to that of habitat 3, with *Rubus rosaefolius* and *R. penetrans* advancing from the undisturbed stand, was also seen in habitat 5. However, this area was not included in the transect system. The invasion at this side was not nearly as vigorous as that observed in habitat 3. The two *Rubus* species were much more scattered and very few *Buddleja* seedlings advanced from the east side of habitat 5. This difference in habitat 5 was probably related to the much rarer occurrence of these species in the neighboring, undisturbed seasonal forest (Fig. 2). Also, the somewhat reduced rainfall along this border of habitat 5 may have been a contributing factor.

Fig. 26. Tree mold in habitat 3 with *Sadleria cyatheoides* seedling. Tree molds were preferred microhabitats for invasion of pioneer mosses and ferns.

Factors Related to Differences in Invasion Rate

Rate of invasion was defined previously in three ways: (1) the quantitative spread of plants over the new volcanic surfaces in terms of increasing frequencies; (2) the increase in number of species; and (3) the increase in plant cover.

The results can be briefly summarized as follows:

Habitat 1 (crater floor) showed a moderately fast rate of invasion but no significant increase in cover. Its species diversity was moderate, with 30 species in year 9.

Habitat 2 (cinder cone) showed a delay of invasion by 2-3 years and no significant cover increase. Its species diversity was low, with only 18 species in year 9.

Habitat 3 (spatter with snags) showed a fast rate of invasion that was supported by a high rate of plant cover increase. Species diversity was highest, with 64 species established in year 9.

Habitat 4 (pumice with snags) showed an earlier invasion but otherwise the same rate as occurred in habitat 2. Its species diversity was moderate with 34 species, and the cover was small in year 9.

Habitat 5 (pumice with surviving trees) showed a somewhat faster invasion rate than habitat 4. The cover of the invading species was also greater than in habitat 4, but species diversity was even less, with 28 species in year 9.

Habitat 6 (thin fallout area) showed an invasion rate similar to habitat 5, but there were some significant differences in floristic composition. The cover of the invaders was a little greater than in habitat 4, but less than in 5, and the species diversity was relatively low, with 23 species in year 9.

These differences in rate of invasion can be explained by almost the same factors that were discussed for the directional influence of invasion patterns observed.

Substrate cooling, disseminule supply, and life form

The 2-3 year delay in plant invasion in habitat 2 was already explained as being primarily the result of the slow cooling of the cinder cone. The low species diversity in year 9 was also related to the late start of plant invasion. In time, species diversity will probably increase and become similar to that of habitats 1 and 3. The fast rate of invasion in habitat 3 was related to the absence of such a limiting factor as volcanic heating from below. But this was also true for habitats 4, 5, and 6. A major factor in habitat 3 was the nearby seed source and the favorable microhabitats provided by the tree snags. The fast cover increase was a function of the rapidly growing, exotic woody seed plants and grasses that covered more surface area than the other pioneer life forms, such as the algae, mosses, ferns, and seedlings of *Metrosideros* trees and native shrubs. The somewhat faster invasion rates in habitats 5 and 6 as compared to 4 and 2 are also related to invasion of exotics and their growth characteristics.

This brings up the question of disseminule supply. This factor was not measured in this study because of technical difficulties and lack of time. It was somewhat equalized, however, by layout of the transect system (Fig. 2). As mentioned above, in habitat 3, disseminule supply was undoubtedly an important factor. Also, habitat 1 adjoined an intact rain forest that surrounded the crater rim. However, because of the substrate-heat gradient on the crater floor, a disseminule-supply gradient from the margin inward was probably only a minor contributory factor here.

An approximate equalization of the disseminule-supply factor existed among habitats 2, 4, 5, and 6 that were cut by transect AA' (Fig. 2). This equalization is supported by the observation that there was no directional invasion noted in the transect quadrats. Transect AA' is about equidistant from the undisturbed rain and seasonal forests to the east of the study area. An additional disseminule supply developed later in habitats 5 and 6 through sexual reproduction of surviving native trees and shrubs. The lateral transects BB' in habitat 2 and DD' and CC' in habitat 4, which were closer to a surviving seed source, can be considered to have counterbalanced the disseminule-supply factor among the habitats. Therefore, we may assume that this factor did not enter significantly into the invasion differences noted among habitats 2,4,5, and 6. However, there is another factor that needs special consideration. This is the availability of microhabitats favorable for invasion.

Availability of microhabitats

The relatively fast rate of invasion of mosses, ferns, and seed plants on the Kilauea crater floor, which seemed to be limited only by the cooling rate of the lava surface, was undoubtedly related to the large number of favorable microhabitats. These were primarily the joint cracks and crevices disrupting the smooth and solid pavement-like rock surfaces on the lava floor.

There are several factors involved in rendering the lava floor fissures as favorable microhabitats. The more moderate surface temperature as compared to the flat surfaces has already been emphasized. Another factor was the added precipitation moisture. As mentioned earlier, after rain showers, vapor steaming was vigorous from most cracks. A certain amount of this vapor was thought to condense directly at the fissure-sides where the mosses and ferns became established. This factor is extremely difficult to measure directly, but a certain idea of the added quantity of both, vapor steaming and rain falling at an angle during high winds, was obtained by the paired rain gauges placed on the crater floor during 1967 and 1968. The values shown in Table 14 are for 1968 only in order to save space and to allow for ready comparison with the Kau Desert (habitat 6) values in Table 13.

By comparing the two tables, it can be seen that the relative amounts of added precipitation in the interceptor gauges were not very different in habitats 1 and 6. However, the actual amounts of precipitation per month were about 50-80 mm more in habitat 1. The interceptor-gauge results do not separate the amounts contributed by driving rain and vapor steaming. However, from general observations, the amount added in habitat 6 was entirely from driving rain. In habitat 1, which was in a deep wind-sheltered depression where rains would descend more vertically, the amount added was probably mostly from vapor steaming. Thus, vapor-steam precipitation may have added some moisture to those joint cracks where the sides of the rock sheets jutted higher from the ground. Doty (1967b) also believed that vapor steam was a major factor in maintaining pioneer plant populations on new lava flows. However, a particular concentration pattern of plants at such cracks was not observed. Another moisture-concentration effect was probably much more important on the lava floor habitat. This was the lateral runoff of precipitation water following its fall on the solid pavement pieces of the lava. These pavement pieces must have acted like inverted

TABLE 14. Monthly precipitation received in two sets of paired rain gauges on the Kilauea crater floor in 1968 (transects a and b). One gauge equipped with Grunow fog interceptor (f).

	Gauge labels identifying transects on Fig. 2					
Month	a (mm)	af (mm)	af/a	c (mm)	cf (mm)	cf/c
March	134.2	199.1	1.5	124.8	185.1	1.5
April	623.2	745.8	1.2	570.5	699.5	1.2
May	139.6	258.5	1.9	130.7	245.0	1.9
June	226.3	348.3	1.5	196.6	285.9	1.5
July	140.7	209.2	1.5	130.2	182.5	1.4
August	97.7	165.8	1.7	92.8	150.1	1.6
September	97.0	139.4	1.4	93.8	140.0	1.5
October	151.8	169.1	1.1	143.8	172.3	1.2
November	111.7	122.4	1.1	101.4	108.3	1.1
December	523.9	646.5	1.2	457.1	575.1	1.3
Totals	2246.1	3004.1	—	2041.7	2743.8	—
Means	—	—	1.4	—	—	1.4

funnels, causing a greater water supply in the fissures. Since there was no significant water storage capacity for plant growth in the lava rock itself, the added lateral seepage after rains and its temporary trapping in sealed joints and where chipped-off wind- or water-moved rock flakes had become trapped was probably the most important environmental factor in filling these fissures with plants. Yet, after a relatively fast advance of the ferns and native woody seed plants toward the crater center, the cover of these plants was still rather insignificant in year 9. The reason for this was that they remained confined to the fissures throughout this observational period. The invasion of plants with root systems onto the lava rock surface will probably take a very long time. It requires some accumulation of particulate material and probably a reduction in surface temperature maxima.

The cinder cone habitat was also criss-crossed by surficial fissures. Here, lateral seepage was probably less important. However, many fissure-profiles showed a cemented layer within 50 cm beneath the upper loose rubble of cinder and ash. This cemented sublayer may have acted similarly to the lava rock by channelling rain water laterally to the fissures, because most mosses, ferns, and seed plants became established in the fissures.

Tree molds, such as are shown in Fig. 26, were characteristic microhabitats in the spatter-with-snags habitat (3). These were also preferentially invaded where the snags had fallen right after spatter deposition. Such tree molds did not receive added moisture by either seepage or interception. In most tree molds, ferns and mosses became established on the side of the walls below the general surface of the habitat or even on the bottom of the mold. Shading and wind protection and thus conservation of moisture as well as lower surface temperature maxima were probably the main factors that made these microhabitats favorable for fern and moss invasion. Seed plants were found mostly at the molds with standing snags, or where the snags had fallen long after the seedlings had become established. In several such cases where the snags had fallen, the taller *Buddleja* individuals died back. This die-back phenomenon is shown in Fig. 25.3. It was probably related to edaphic drought.

Depressional microhabitats, such as cracks and molds, were found only in the first three habitats. Habitats 4, 5, and 6 had generally smooth, even surfaces covered with pumice. In the pumice-with-snags habitat (4), seed plant and fern invasion was decidedly associated with the standing snags. Here, the added precipitation moisture from interception was the main factor. The invasion pattern in habitat 5 (pumice with surviving trees) seemed more haphazard than in any of the other habitats. Some *Rubus* shrubs became established at tree bases, but others invaded the spaces between the trees. Accumulation of leaf litter was noted under the larger surviving trees in year 7 and 9 (Fig. 12.4), but this did not seem to have any specific influence on plant invasion in year 9. In habitat 6, invasion of new plants was concentrated somewhat around surviving shrubs but the open barren surface was invaded also by a few scattered sedges (*Bulbostylis capillaris*) and grasses (*Andropogon virginicus* and *Rhynchelytrum repens*). Thus, in general, invasion patterns associated with recognizable microhabitats decreased with the severity of the volcanic disturbance.

Climatic gradient

Contrary to an initial hypothesis, the climatic gradient had very little influence on the invasion patterns in the "Devastation Area." If there had not been an edaphic heat gradient on the Kilauea crater floor, the establishment of mosses, ferns, and seed plants in the joint cracks and fissues would probably have been haphazard over the entire floor to begin with. Then also, the invasion rate may have been considerably faster than at the drier end of the climatic gradient. The same cannot be said for the cinder cone (habitat 2). Elimination of the invasion delay caused by the prolonged volcanic heating showed that the invasion rate on the cone after cooling was not faster than in habitat 4. The invasion rates in habitat 5 and 6 were also not slower than those in habitat 4. Therefore, the effect of decreasing rainfall and increasing desiccating power along transect AA′ (NW to SE) was counterbalanced by the influence of the microhabitats described previously.

However, a certain floristic variation was correlated with the climatic gradient. This was the appearance of a few pioneer seed plants in the upper Kau Desert habitat (6) which did not appear in the moister zone. These were *Rumex giganteus, Rhynchelytrum repens,* and *Bulbostylis capillaris.* Moreover, a few rain forest associated pioneers did not enter habitat 6, such as *Hedyotis centranthoides, Pipturus albidus, Vaccinium calycinum,* and the exotics *Eupatorium riparium* and *Paspalum dilatatum*. From an island-wide distribution study of grasses on Oahu, *Rhynchelytrum repens* is known to be associated with seasonal climates (Kartawinata and Mueller-Dombois 1972).

Probable Reasons for Observed Life-Form Establishment Sequences

The recorded establishment sequences of eight life-form groups are summarized by habitat in Table 15. The term "establishment" rather than "arrival" is used here because there were two cases when a herbaceous seed plant species arrived and then disappeared. Such transient colonizers are not included in Table 15 and the following discussion.

TABLE 15. Summary of establishment sequences of plant life forms in the six habitats. Consistent patterns are blocked out.

	Habitat					
Life form	1	2	3	4	5	6
Algae	1st	1st	1st	1st	1st	1st
Mosses	1st	2nd	2nd	1st	1st	2nd
Lichens	2nd	2nd	2nd	2nd	2nd	2nd
Ferns	1st	2nd	1st	1st	1st	2nd
Native woody seed plants	3rd	3rd	2nd	1st	2nd[a]	1st[a]
Exotic woody seed plants	4th	4th	1st	1st	1st	3rd
Grasses or sedges	5th	4th	1st	3rd	1st	2nd
Forbs	4th	—	1st	1st	1st	3rd

[a] Seedlings of surviving woody plants.

Algae were always the first to become established on the new volcanic surfaces. Lichens were never the first; they arrived consistently as the second life form. Mosses and ferns became established either first, along with the algae, or they arrived as the second cryptogamic life-form group together with the lichens. On the two habitats with no remains of an earlier vegetation (i.e., on the crater floor, 1 and the cinder cone, 2), native woody seed plants were the third life form to arrive and exotic woody and herbaceous plants were the last. On habitats 3, 4, and 5, which showed remains of the former *Metrosideros* forests, exotic woody and herbaceous plants were among the first life forms to become established.

The consistent early arrival of algae supports Doty's (1967b) previous observation on the 1955 Puna lava flow. On the Kilauea crater floor, algae colonies were observed to occupy both the crevices and surfaces of the pahoehoe lava sheets. On the latter, there was no other macroscopic plant life form until arrival of the lichens During the entire observational period, the lava rock surfaces were occupied only by these two life forms and there was no obvious interaction with any of the other plant life forms.

The reason for the early arrival of algae was not investigated. But, as suggested already by other investigators (Treub 1888; Doty 1961, 1967b), they can probably grow on the volcanic surfaces when organic nitrogen levels are still too low for other plant life forms. As indicated on the crater floor, the algae also seem to have a greater tolerance to high temperatures than the other life forms, except the lichens.

The reasons for the consistently later arrival of lichens is worth a thorough investigation. The explosive, nondirectional invasion pattern of the lichen *Stereocaulon volcani* suggests that this lichen may be formed on the new lava surfaces *in situ* by the joining of an alga and fungus. Observations on a number of recent lava flows show a generally uniform distribution pattern of *Stereocaulon*. If this lichen was established from small wind-carried pieces of lichen thalli, one would expect some indication of a directional invasion pattern related to the location of a major disseminule source. Moreover, of the lichen-initials observed under the microscope, all had the same tiny (1-2 mm) globose thallus. One would not expect wind-transported thallus fragments to be of such uniform structure. Since lichens are known to be extremely sensitive to toxic substances, their delayed arrival may also be linked to the removal by rain water of lichen inhibitors from new, raw volcanic materials. Such materials could, for example, be traces of sulfurous precipitates. In contrast to algae, mosses, and ferns, lichens were never found at fumaroles or in the pathway of vapor-steam.

The generally subsequent arrival of mosses and ferns after the algae may be only an artifact, insofar as both mosses and ferns develop from gametophytes. The protonema of mosses look like algae and thus were not separately recognized. The fern gametophytes are also easily overlooked. Only the sporophyte generations of mosses and ferns were recorded in this study.

It is interesting that native woody seed plants were the third life-form group to arrive on the totally new primary habitats (1 and 2). They are typically sclerophyllous plants (i.e., *Metrosideros, Dubautia,* etc.) that indicate a xerophytic adaptation. These native woody plants can probably survive under more severe water stress conditions than the exotic woody plants that appeared as the main pioneers *(Buddleja* and *Rubus* species) in habitats 3, 4, and 5. This applies also to the herbaceous plants (grasses and forbs) that were among the last major life forms to arrive on these totally new materials. Somewhat more mesic conditions develop slowly on the new lava flows by entrapments of chipped-off rock flakes, dust, and litter in the crevices. This observation was stressed particularly by Eggler (1941, 1971).

In contrast, the exotic woody and herbaceous plants were among the first invaders on the habitats that contained remnants of the former *Metrosideros* forests. As explained before, here the snags provided locally more favorable moisture conditions that made it possible for these aliens to arrive on the otherwise xeric substrates.

The sequence of life-form establishment, as shown in Table 15, does not comply with Clements' (1916) records of life-form invasion sequences. His observations have dominated textbooks for many years. Clements gave his own observations and quoted those of several other investigators, stating that lichens were the first life forms on xeric rock substrates. These were to be followed by mosses and these, in turn, by herbaceous plants. Woody plants were not recognized in the early pioneer sequence. Moreover, Clements recognized these life-form sequences as real vegetation types or seral stages. However, he also stated (1916:84) that, on sedimentary rocks in climates with moist growing seasons, the pioneers are mostly mosses and liverworts that are often preceded by algae. Yet, he maintained that plant life begins with crustose lichens on igneous rocks. It must be remembered that all of Clements' observations relate to the temperate zone, and differences are to be expected. For example, the presence of a fern stage seems to be uniquely tropical (see also Keay 1959). Ferns and lichens dominate the cryptogamic stage in Hawaii.

Table 15 shows that an algal stage may be recognized, but thereafter, there is no single life-form stage. One may speak merely of a cryptogamic stage. It is also significant that on materials without remnants of a former vegetation, woody plants appear definitely before herbaceous plants. This correlates with the pattern of evolution of these life forms, although there may be no logical relationship between present-day primary invasion and plant life-form evolution in the phylogenetic sense.

On new volcanic surfaces in Hawaii, one may, therefore, recognize four stages:

1. An algal stage, which may form the sole stage for 1 year in the humid climate.
2. A cryptogamic stage, which may remain as such for 2 additional years.
3. A native woody seed plant stage, which includes the former life forms, and which may last 1 more year.
4. A stage in which exotic woody and herbaceous plants become associated.

This applies only to new volcanic surfaces of lava or ash without remnants of a former vegetation and to humid climates. No such stages could be observed on the volcanic materials with former vegetation remnants. Here exotic seed plants were among the first pioneer life forms.

Factors Influencing Plant Survival

Depth and nature of pyroclastic deposit

As expected, the survival of original plants decreased with increasing depth of the pyroclastic deposits. But there were great differences in survival with respect to the kind of pyroclastic deposit. *Metrosideros* trees survived under a pumice blanket slightly deeper than 2.5 m in habitat 5. In habitat 3, all *Metrosideros* trees were severely damaged by the glowing-hot spatter that became welded upon deposition. Where the original surface was covered with less than 10 cm of spatter, trees recovered fast, but only few survived of those buried under spatter deeper than 10 cm. In this habitat, surviving trees resprouted from the base only and recovery occurred merely up to a spatter-depth of about 50 cm. As mentioned previously, the basal sprouting was probably possible because of small spaces that developed at the contact zone between the spatter and the damaged basal stem. This permitted water penetration from stem runoff into the tree molds and gaseous exchange. In habitat 3, none of the surviving trees showed aerial roots.

Instead, aerial root development was seen only on survival trees in habitat 5 that were buried under pumice deeper than 20 cm. The significance of this aerial rooting is as yet unknown. If it were really essential for survival, one could expect it to have occurred on all reflushing *Metrosideros* trees that were buried under ash deeper than 50 cm, particularly on those surviving under the deepest deposits $>$ 2.5 m.

Size of plant

Trees that survived in the spatter area had relatively large basal diameters of 20 cm or more. An important survival factor associated with size was probably an epiphytic moss layer surrounding the stem base. Also, under the pumice only the larger trees survived the deeper deposit as seen in Figs. 12.1-12.4. Smaller diameter *Metrosideros* trees survived under the shallower pumice blanket. In habitat 6, all individuals were small and all survived. Eggler (1948) found on El Parícutin that pine trees of intermediate size survived best under an ash blanket. This observation does not necessarily contrast with the one here where the largest trees were seen to be the better survivors. Very large and old *Metrosideros* trees did not occur in the study area. Such individuals may have a decreased survival capacity. However, no prediction can be made from the present observations.

Vegetative regrowth capacity

The observation that all surviving trees in the area recovered only when their trunks were buried to less than half their height stands in contrast to the survival capacity of the other plant life forms—the shrubs and herbs that survived the burial.

Several of the native shrubs and herbs survived under the pumice layer even where their entire shoot system had been broken off or buried. This was particularly true for the native shrubs *Vaccinium reticulatum, Dubautia scabra, Styphelia tameiameiae,* and *Coprosma ernodeoides*. But this included also a few shrub-like individuals of *Metrosideros polymorpha* in the upper Kau Desert (habitat 6). Vegetative regeneration from a basal remnant or root system is probably a characteristic for most shrubs. But in the Hawaiian forms mentioned, it may also be an evolutionary adaptation to this kind of volcanic damage. Among the herbaceous life forms, most of the survivors were plants with underground storage organs. These plants were defined as geophytes although they do not necessarily reduce their shoot systems in a seasonal rhythm as do the typical temperate- and arid-zone geophytes. This group of damage-adapted geophytes included native species, such as *Astelia menziesiana* (which grows usually as an epiphyte in older rain forests), *Dianella sandwicensis, Polypodium pellucidum, Pteridium decompositum,* as well as several exotics, *Spathoglottis plicata, Hedychium coronarium,* and *Tritonia crocosmiflora*. Among the herbaceous survivors were also a few chamae-hemicryptophytes, such as the native sedges *Machaerina angustifolia* and *Gahnia gahniaeformis*. These plants survived usually by regrowth from remnant shoot systems.

Primary Community Formation

According to Poore (1964), most ecologists agree that to qualify as a community a stand of plants must show some form of integration. The kinds of developing integration observed on the new volcanic habitats may be discussed under two subheadings: plant aggregation, and complementation and competition.

Plant aggregation

Initially, invading plants tended to occur as scattered individuals. However, as soon as these first individuals were established, other plant individuals tended to become established next to them. Therefore, aggregation was noticed as an early pattern of plant invasion. This is quite understandable in view of the presence of favorable microhabitats that occurred in all but perhaps habitat 5. On the crater floor (habitat 1), the joint cracks and crevices were occupied by algae, mosses, and ferns. Soon after one fern individual was noticed, others were seen in the same crevices. Often it was difficult to distinguish fern individuals of *Nephrolepis exaltata,* because new fronds developed relatively quickly from the extending rhizomes. It seemed peculiar in many instances that one crevice was crowded with algae, mosses, ferns, and native woody seed plants, while another adjacent crevice, which looked identical in all aspects, remained vacant. Such vacant crevices were still found in year 9, while others were crowded with individuals of all the above-mentioned life forms. This phenomenon seems to indicate that a favorable event must have facilitated the establishment of a pioneer individual or group. These, in turn, through their own establishment, must have improved the moisture relations in the crevice so that other plant individuals, particularly seed plants, found an easier entrance to the microhabitat. However, *Metrosideros* seedlings were observed to grow without other plant life forms in certain crevices where rock-flakes had accumulated. This showed that the presence of cryptogams was not necessary for seed plants to become established. What was necessary was merely a somewhat improved retention of precipitation water in the crevices to satisfy the minimum water requirements for establishment of native seed plants.

Plant aggregations developed in habitat 3 at the tree molds, and larger-sized aggregations developed around the snags and surviving trees. A similar snag-associated aggregation pattern developed in habitat 4. In habitat 6 (Kau Desert) plant aggregation was also quite pronounced around surviving *Metrosideros* trees and shrubs. The environmental relations in these tree- and snag-associated microhabitats have already been discussed.

Incipient plant aggregations began to develop in some of the cinder cone crevices, although here and in habitat 5 (pumice-with-survival-trees), aggregation patterns were least clearly defined during the period of observation. Nevertheless, it can be said that plant aggregations are typical for the invasion of plants on new volcanic surfaces. This statement is in accord with the observations of Millener (1953) in New Zealand. In all cases, the cause for this early community formation through aggregation seemed to be associated with locally improved edaphic moisture relations. These became effective either through improved retention of soil water, shading, fine particle accumulation, or plant material itself or through locally higher input of water (interception at snags or accumulation of runoff water) or both.

Complementation and competition

The accommodation of seed plants in crevices densely occupied with cryptogams may be viewed as a form of complementation. This form of complementation probably was brought about by an improved runoff-water retention in the established moss mats and among the fern rhizomes. Another form of complementation was observed under *Buddleja* trees and other shrubs in habitat 3, where several species of rain forest mosses invaded the shaded areas beneath these bushes. Moss invasion in the shade of trees occurred also in some places in habitat 5, under the surviving *Metrosideros trees.* A third form of complementation was observed in habitat 1 and 3. Here, a herbaceous seed-plant synusia, consisting of grasses and forbs, was spreading under established scattered woody seed plants. This occurred in habitat 1 only at the first 10-15 m inward on the crater floor of transect a. This was also the only place where seed plants had invaded the flat surface of the massive pahoehoe lava. The area was as yet very small in terms of the total crater floor area. The main reason for this form of invasion was probably not the partial shade provided by the scattered woody plants, but rather the morning shade provided by the crater slope rising steeply behind this location. A more advanced development of synusial layering occurred in the spatter-with-snags habitat

(3) where the grasses, such as *Paspalum dilatatum* and *Holcus lanatus*, advanced in the partial shade of woody plants.

Here also the first signs of competition were noted among the grasses and forbs. *Paspalum dilatatum* and *Setaria geniculata* seemed to decline because of the advancing *Holcus lanatus*, *Cyperus polystachyos*, and *Pennisetum clandestinum*. *Eupatorium riparium* and *Lythrum maritimum* seemed to be replaced in part by *Commelina diffusa*. Similar replacement patterns were noted with basally resprouting *Metrosideros* and *Buddleja asiatica*. A decline of *Rubus rosaefolius* and *R. penetrans* was observed in habitats 3 and 5, while *Vaccinium reticulatum* and *Dubautia scabra* increased in spread. It could not be ascertained in all cases whether this replacement pattern was in fact competition. But in habitat 5, several cases were observed where the native *Coprosma ernodeoides* clearly had invaded patches occupied by the exotic *Rubus penetrans*, with the result that the latter declined in vigor and then died.

Relationship Between Native and Exotic Invaders

The study has shown that both native and exotic seed plants and ferns participated in the invasion on new volcanic surfaces in Hawaii. New volcanic surfaces without remains of former vegetation were clearly dominated by native species in the early stages of primary invasion. In contrast, pyroclastic fallout habitats with forest remnants (such as habitats 3 and 5) were dominated initially by exotic invaders. However, even in these habitats, native woody seed plants and ferns were in no way affected by competition from exotics, but there were definite indications that exotic seed plants were replaced by competition from native seed plants of similar life form. This was observed in the case of the exotic small-tree *Buddleja asiatica*, which seemed to be affected by competition from *Metrosideros polymorpha* snag-resprouts. It was also observed in the case of *Rubus penetrans* that was replaced in several locations by the native woody creeper *Coprosma ernodeoides*, which had a life form similar to *R. penetrans* on these pumice substrates.

The majority of exotic species were herbaceous seed plants and grasses and forbs. Only very

The majority of exotic species were herbaceous seed plants, grasses and forbs. Only very few native species are in this life-form group. Thus, the herbaceous exotics fill a practically vacant niche. It is expected that these herbaceous exotics will become even more abundant in time in the continuing process of invasion. However, they do not appear to interfere with the development of native plants, because both are complementary life forms. An early succession was recorded in this group, some of which seemed to be caused by competitive replacement. This form of interaction is expected to increase as the new surfaces become filled more and more with plant life.

Appendix I

SPECIES FREQUENCY (%) OF INVADERS DURING YEARS FOLLOWING ERUPTION IN HABITAT 1. DATA FOR THE TOTAL 1445 SQUARE METER PLOTS ALONG THE FOUR BELT-TRANSECTS ON KILAUEA IKI CRATER FLOOR.

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
ALGAE							
Stigonema panniforme Phyc H[1]		0.8	0.9	3.0	7.2	25.6	40.5
Scytonema myochrous Phyc H		—	0.9	3.3	8.4	26.0	40.5
Anacystis montana Phyc H		—	—	2.3	5.7	20.8	40.5
Hapalosiphon laminosus Phyc H		—	—	0.2	1.4	9.7	20.0
Stichococcus subtilis Phyc H		—	—	—	—	0.1	0.1
MOSSES							
Campylopus densifolius Br Ch pulv		0.1	0.3	1.4	1.9	5.3	8.5
Campylopus exasperatus Br Ch pulv		0.1	0.3	1.7	2.1	4.9	7.0
Campylopus purpureoflavescens Br Ch pulv		—	—	—	—	0.1	0.2
Rhacomitrium lanuginosum var. *pruinosum* Br Ch rept		—	—	0.4	1.1	2.9	5.1
Bryum crassicostatum Br Ch pulv		—	—	—	—	—	0.2
LICHENS							
Stereocaulon volcani L Ch		—	—	2.0	4.9	24.0	32.5
Cladonia skottsbergii L Ch		—	—	—	1.1	8.6	13.5
FERNS							
Nephrolepis exaltata G rhiz		0.2	0.5	0.8	1.6	6.0	7.7
Sadleria cyatheoides sCh scap		—	0.1	0.1	0.3	0.5	0.6
Pityrogramma calomelanos G rhiz		—	—	—	0.1	0.2	0.5
Polypodium pellucidum G rhiz		—	—	—	—	1.1	1.9
Cibotium glaucum sCh scap		—	—	—	—	—	0.1

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
SEED PLANTS							
Woody							
Metrosideros polymorpha sCh frut		—	—	—	0.4	1.5	2.7
Vaccinium reticulatum sCh frut		—	—	—	0.2	1.3	2.3
Dubautia scabra sCh frut		—	—	—	0.4	1.5	2.0
Hedyotis centranthoides sCh frut		—	—	—	0.3	0.6	0.6
Cyrtandra sp. dCh frut		—	—	—	—	0.1	0.1
Coprosma ochracea dCh frut		—	—	—	—	—	0.1
Buddleja asiatica[2] dCh frut		—	—	—	—	0.1	0.3
Cuphea carthaginensis[2] dCh frut		—	—	—	—	—	0.1
Grasses							
Andropogon virginicus[2] Ch (H) caesp		—	—	—	—	—	0.1
Setaria geniculata[2] Ch (H) caesp		—	—	—	—	—	0.1
Paspalum dilatatum[2] Ch (H) caesp		—	—	—	—	—	0.2
Paspalum conjugatum[2] Ch (H) caesp		—	—	—	—	0.1	—
Forbs							
Anemone japonica[2] Ch (H) ros		—	—	—	—	0.2	0.2
Fragaria vesca var. *alba*[2] Ch(H) ros		—	—	—	—	—	0.2
Lythrum maritimum[2] dCh rept		—	—	—	0.1	—	—

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[1] Life-form symbol explained in Appendix VII.

[2] Exotic species.

Appendix II

SPECIES FREQUENCY (%) OF INVADERS DURING YEARS FOLLOWING ERUPTION IN HABITAT 2 (CINDER CONE). DATA FROM 85 QUADRATS OF 10 x 10-m SIZE.

Species	Year	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968
ALGAE							
Scytonema myochrous Phyc H[1]		—	—	9	20	35	59
Stigonema panniforme Phyc H		—	—	—	20	35	61
Anacystis montana Phyc H		—	—	—	20	25	61
MOSSES							
Campylopus exasperatus Br Ch pulv		—	—	—	6	12	19
Campylopus densifolius Br Ch pulv		—	—	—	1	6	15
Rhacomitrium lanuginosum var. *pruinosum* Br Ch rept		—	—	—	5	12	21
LICHENS							
Stereocaulon volcani L Ch		—	—	—	20	42	82
Cladonia skottsbergii L Ch		—	—	—	—	9	30
FERNS							
Nephrolepis exaltata G rhiz		—	—	—	11	26	40
Pityrogramma calomelanus G rhiz		—	—	—	—	5	8
Polypodium pellucidum G rhiz		—	—	—	—	7	13
Sadleria cyatheoides sCh scap		—	—	—	—	8	12

Species	Year	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968
SEED PLANTS							
Woody							
Dubautia scabra sCh frut		—	—	—	—	8	17
Vaccinium reticulatum sCh frut		—	—	—	—	8	19
Buddleja asiatica[2] dCh frut		—	—	—	—	—	11
Metrosideros polymorpha sCh frut		—	—	—	—	7	18
Styphelia tameiameiae sCh frut		—	—	—	—	—	6
HERBACEOUS							
Agrostis avenacea[2] Ch (H) caesp		—	—	—	—	—	1

[1] Life-form symbols explained in Appendix VII.

[2] Exotic species.

Appendix III

SPECIES FREQUENCY (%) OF INVADERS DURING YEARS FOLLOWING ERUPTION IN HABITAT 3 (SPATTER AREA WITH SNAGS). DATA FROM 21 QUADRATS OF 10 x 10-m SIZE.

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
ALGAE							
Stigonema panniforme Phyc H[1]		52	67	67	100	100	100
Scytonema myochrous Phyc H		—	67	67	100	100	100
Anacystis montana Phyc H		—	—	—	100	100	100
MOSSES							
Campylopus densifolius Br Ch pulv		—	19	19	29	95	10
Campylopus exasperatus Br Ch pulv		—	5	24	33	100	100
Rhacomitrium lanuginosum var. *pruinosum* Br Ch rept		—	—	5	19	67	86
Ceratodon purpureus Br Ch pulv		—	—	—	—	10	10
Bryum crassicostatum Br Ch pulv		—	—	—	10	5	5
Brachymenium exile Br Ch pulv		—	—	—	—	14	14
Ctenidium decurrens Br Ch rept		—	—	—	—	5	5
Rhizogonium spiniforme Br Ch rept		—	—	—	—	5	5
Trichosteleum lamatum Br Ch rept		—	—	—	—	5	5
Hypnum plumaeforme[2] Br Ch rept		—	—	—	—	—	19
Thuidium plicatum Br Ch rept		—	—	—	—	—	10
Macromitrium owaihense Br H		—	—	—	10	29	48
Ectropothecium sandwicense Br H		—	—	—	—	—	5
Isopterygium albescens Br H		—	—	—	—	—	5
Racopilum cuspidigerum Br H		—	—	—	—	—	10

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
LICHENS							
Stereocaulon volcani L Ch		—	53	53	95	95	100
Cladonia skottsbergii L Ch		—	—	—	48	100	100
FERNS							
Nephrolepis exaltata G rhiz		10	19	38	72	53	95
SEED PLANTS							
Woody							
Rubus rosaefolius[2] dCh frut		5	19	29	43	14	14
Rubus penetrans[2] dCh frut		—	10	24	48	14	5
Pluchea odorata[2] dPN		—	—	5	10	14	14
Buddleja asiatica[2] dPN		—	—	24	33	86	76
Pipturus albidus dPN		—	—	—	10	10	10
Metrosideros polymorpha sPN		—	—	14	24	86	95
Vaccinium calycinum dCh frut		—	—	—	5	10	10
Vaccinium reticulatum sCh frut		—	—	—	14	38	57
Dubautia scabra sCh frut		—	10	29	43	29	43
Dubautia ciliolata sCh frut		—	—	—	—	—	5
Hedyotis centranthoides sCh frut		—	—	—	—	—	10
Grasses							
Holcus lanatus[2] Ch(H) caesp		—	—	19	33	53	62
Paspalum dilatatum[2] Ch(H) caesp		10	19	33	57	5	5
Andropogon virginicus[2] Ch(H) caesp		—	—	5	5	10	14
Agrostis avenacea[2] Ch(H) caesp		—	—	—	—	—	5
Setaria geniculata[2] G rhiz		5	19	29	29	5	5

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
SEED PLANTS							
Grasses (continued)							
Pennisetum clandestinum[2] Ch(H) rhiz		—	—	14	14	19	24
Sacciolepis indica[2] T caesp		—	—	—	14	10	5
Cynodon dactylon[2] Ch(H) rept		—	—	—	10	—	—
Sporobolus africanus[2] Ch(H) caesp		14	19	29	43	—	—
Sedges							
Cyperus polystachyos[2] Ch(H) caesp		—	—	—	24	24	24
Cyperus brevifolius[2] Ch(H) caesp		—	—	24	29	10	5
Cyperus rotundus[2] Ch(H) caesp		—	—	19	19	5	5
Carex wahuensis Ch(H) caesp		—	—	—	—	—	10
Forbs							
Eupatorium riparium[2] dCh suff		14	19	24	43	5	5
Cuphea carthaginensis[2] dCh suff		—	—	—	10	5	5
Commelina diffusa[2] dCh rept		—	—	14	24	29	38
Lythrum maritimum[2] dCh rept		—	—	19	10	10	10
Epilobium cinereum[2] Ch(H) rept		—	—	—	14	19	24
Hypericum japonicum[2] Ch(H) scap		—	—	—	—	14	14
Epilobium adenocaulon[2] Ch(H) scap		—	—	—	—	—	14
Gnaphalium purpureum[2] Ch(H) scap		—	—	—	—	—	5
Fragaria vesca var. *alba*[2] Ch(H) ros		—	—	—	—	—	19
Anemone japonica[2] Ch(H) ros		—	—	—	—	5	10
Geranium carolinianum[2] T caesp		—	—	—	14	5	5
Physalis peruviana[2] T caesp		—	—	—	5	5	5

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
Forbs (continued)							
Bidens pilosa[2] T caesp		—	—	—	—	5	5
Sonchus oleraceus[2] T scap		—	14	29	62	10	5
Erechtites valerianaefolia[2] T scap		—	—	24	62	10	5
Conyza canadensis[2] T sem		—	—	—	—	14	5
Astelia menziesiana G rhiz		5	5	10	10	10	10
Hypochoeris radicata[2] G rad		—	19	29	62	43	71
Oxalis corniculata[2] G rad		—	—	—	5	5	5
Oxalis martiana[2] G rad		—	—	—	5	5	5
Cirsium vulgare[2] G rad		—	—	—	5	5	5

[1] Life-form symbols explained in Appendix VII.

[2] Exotic species.

Appendix IV

SPECIES FREQUENCY (%) OF INVADERS DURING YEARS FOLLOWING ERUPTION IN HABITAT 4 (PUMICE AREA WITH SNAGS). DATA FROM 72 QUADRATS OF 10 x 10-m SIZE.

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
ALGAE							
Stigonema panniforme Phyc H[1]		—	—	13	16	47	82
Scytonema myochrous Phyc H		—	2	13	16	47	82
Anacystis montana Phyc H		—	—	13	16	47	82
MOSSES							
Campylopus exasperatus Br Ch pulv		—	1	2	4	8	12
Campylopus densifolius Br Ch pulv		—	—	—	5	12	15
Rhacomitrium lanuginosum var. *pruinosum* Br Ch rept		—	—	—	8	14	19
Ceratodon purpureus Br Ch pulv		—	—	—	—	1	1
LICHENS							
Stereocaulon volcani L Ch		—	—	13	16	47	82
Cladonia skottsbergii L Ch		—	—	—	9	17	38
FERNS							
Nephrolepis exaltata G rhiz		—	3	6	12	17	22
Polypodium pellucidum G rhiz		—	—	—	4	6	6
Pleopeltis thunbergiana Ch E		—	—	—	2	9	10
Sadleria cyatheoides sCh scap		—	1	1	4	8	5
SEED PLANTS							
Woody							
Rubus rosaefolius[2] dPN		—	3	3	3	6	8
Rubus penetrans[2] dPN		—	—	1	2	5	5

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
SEED PLANTS							
Woody (continued)							
Buddleja asiatica[2] dPN		—	—	2	4	14	17
Metrosideros polymorpha sPN		—	2	1	9	14	23
Dubautia scabra sCh frut		—	—	2	9	14	16
Dubautia ciliolata sCh frut		—	—	—	—	—	1
Pluchea odorata[2] dPN		—	—	—	—	—	1
Grasses							
Andropogon virginicus[2] Ch(H) caesp		—	—	—	—	1	3
Holcus lanatus[2] Ch(H) caesp		—	—	—	—	—	3
Forbs							
Rumex giganteus dCh frut		—	—	—	—	1	5
Eupatorium riparium[2] dCh suff		—	—	—	—	3	4
Epilobium cinerium[2] dCh rept		—	—	—	1	5	4
Lythrum maritimum[2] dCh rept		—	—	—	—	1	2
Epilobium adenocaulon[2] Ch(H) scap		—	—	—	—	3	3
Fragaria vesca var. *alba*[2] Ch(H) ros		—	—	—	—	—	1
Anemone japonica[2] Ch(H) ros		—	—	—	—	—	3
Conyza canadensis[2] T sem		—	—	—	—	—	1
Erechtites valerianaefolia[2] T scap		—	2	3	10	8	3
Sonchus oleraceus[2] T scap		—	—	1	8	13	9
Hypochoeris radicata[2] G rad		—	—	3	9	12	15
Arundina bambusaefolia[2] G bulb		—	—	—	1	2	5

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[1] Life-form symbols explained in Appendix VII.

[2] Exotic species.

Appendix V

SPECIES FREQUENCY (%) OF INVADERS DURING YEARS FOLLOWING ERUPTION IN HABITAT 5 (PUMICE AREA WITH SURVIVNG TREES). DATA FROM 32 PLOTS OF 10 x 10-m SIZE.

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
ALGAE							
Stigonema panniforme[1] Phyc H		—	100	100	100	100	100
Scytonema myochrous Phyc H		—	—	—	100	100	100
Anacystis montana Phyc H		—	—	100	100	100	100
MOSSES							
Campylopus densifolius Br Ch pulv		—	13	13	13	66	84
Campylopus exasperatus Br Ch pulv		—	—	6	9	63	94
Campylopus purpureoflavescens Br Ch pulv		—	—	—	—	—	3
Rhacomitrium lanuginosum var. *pruinosum* Br Ch rept		—	—	6	19	47	78
Bryum argentum var. *lanatum* Br Ch pulv		—	—	—	—	—	6
Dicranum speirophyllum Br Ch pulv		—	—	—	—	—	6
Thuidium plicatum Br Ch rept		—	—	—	—	—	6
LICHENS							
Stereocaulon volcani L Ch		—	—	100	100	100	100
Cladonia skottsbergii L Ch		—	—	6	25	94	100
FERNS AND FERN ALLIES							
Nephrolepis exaltata G rhiz		—	28	44	59	31	19
Polypodium pellucidum G rhiz		—	—	6	13	16	31
Psilotum nudum Ch ep		—	—	—	—	—	3

Species	Year	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968
SEED PLANTS							
Woody							
Rubus rosaefolius[2] dPN		—	—	16	25	6	6
Rubus penetrans[2] dPN		—	—	6	19	9	25
Grasses							
Andropogon virginicus[2] Ch(H) caesp		—	—	—	9	16	22
Paspalum dilatatum[2] Ch(H) caesp		—	—	13	16	3	3
Sedges							
Cyperus brevifolius[2] Ch(H) caesp		—	16	16	16	3	3
Cyperus polystachyos[2] Ch(H) caesp		—	—	—	—	—	9
Gahnia gahniaeformis[2] Ch(H) caesp		—	—	—	6	16	22
Forbs							
Hypochoeris radicata[2] G rad		—	—	25	34	19	16
Fragaria vesca var. *alba*[2] G ros		—	—	—	—	—	3
Cirsium vulgare[2] G ros		—	—	—	—	—	3
Anemone japonica[2] G ros		—	—	—	—	3	6
Erechtites valerianaefolia[2] T scap		—	—	13	22	3	3
Eupatorium riparium[2] dCh suff		—	3	19	22	16	3

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[1] Life-form symbols explained in Appendix VII.

[2] Exotic species.

Appendix VI

SPECIES FREQUENCY (%) OF INVADERS DURING YEARS FOLLOWING ERUPTION IN HABITAT 6 (THIN FALLOUT AREA, UPPER KAU DESERT). DATA FROM 5 PLOTS 10 x 10-m SIZE.

		1	2	3	4	7	9
Species	Year	1960	1961	1962	1963	1966	1968
ALGAE							
Stigonema panniforme Phyc H[1]		100	100	100	100	100	100
Scytonema myochrous Phyc H		—	100	100	100	100	100
Anacystis montana Phyc H		—	—	—	100	100	100
Coccochloris stagnima Phyc H		—	—	—	—	—	100
MOSSES							
Campylopus densifolius Br Ch pulv		—	—	40	60	60	80
Campylopus exasperatus Br Ch pulv		—	—	—	60	60	80
Weisia viridula Br Ch pulv		—	—	40	40	40	40
Anthoceros sp. Br Ch pulv		—	—	40	—	40	40
LICHENS							
Stereocaulon volcani L Ch		—	—	100	100	100	100
Cladonia skottsbergii L Ch		—	—	40	60	100	100
FERNS AND FERN ALLIES							
Sphenomeris chusana G rhiz		—	—	—	40	60	20
Psilotum nudum Ch ep		—	—	—	40	40	40
Pleopeltis thunbergiana Ch ep		—	—	40	60	80	80
SEED PLANTS							
Woody							
Psidium cattleianum[2] sPN		—	—	—	—	20	20
Buddleja asiatica[2] dCh frut		—	—	—	—	—	40

Species	Year	1 1960	2 1961	3 1962	4 1963	7 1966	9 1968
Grasses							
Andropogon virginicus[2] Ch(H) caesp		—	—	—	—	60	60
Agrostis avenacea[2] Ch(H) caesp		—	—	—	20	40	40
Rhynchelytrum repens[2] G rept		—	—	—	40	40	60
Digitaria pseudoischaemum[2] G rept		—	—	—	—	20	20
Sedges							
Cyperus polystachyos[2] Ch(H) caesp		—	—	—	40	40	40
Bulbostylis capillaris[2] Ch(H) caesp		—	—	60	80	80	80
Forbs							
Arundina bambusaefolia[2] G bulb		—	—	—	—	20	40
Conyza canadensis[2] T scap		—	—	—	20	20	40

[1] Life-form symbols explained in Appendix VII.

[2] Exotic species.

Appendix VII

EXPLANATION OF SYMBOLS USED ON LIFE-FORM DIAGRAM (Figs. 8, 10, 11, 16).

PM = "Macrophanerophyte"; i.e., tall woody plant, here defined as trees over 2 m tall (example, surviving *Metrosideros polymorpha*)

PN = "Nanophanerophyte"; i.e., small woody plant, here defined as from 25 cm to 200 cm tall (example, surviving *Vaccinium reticulatum)*

Ch = "Chamaephyte"; here defined as low shrubs or woody plant seedlings that were up to 25 cm tall at the time of observation (example, *Vaccinium reticulatum*)

Ch(H) = "Chamae-hemicryptophyte"; here defined as herbaceous perennials whose shoot system remained alive above the surface also when part of it died or dried up. This is a new term combination used for this paper, because the typical hemicryptophytes of temperate- and arid-zones have a shoot system that dries down in its entirety to a remnant shoot system that remains above the ground, while the plants here designated as chamae-hemicryptophytes showed only partial die-back. A part of the shoot system remained green through the year (example, *Machaerina angustifolia)*

G = "Geophyte"; here defined as herbaceous perennials that can reproduce vegetatively from underground storage organs after shoot die-back. In contrast to the typical temperate and arid-zone geophytes, regular seasonal shoot die-back was not observed. The plants here called geophytes could be designated as "mechanical geophytes" meaning that they were plants (other than grasses) that could regenerate their entire shoot system after it had been removed from the surface by mechanical means (example, *Spathoglottis plicata*)

T = "Therophytes"; defined as herbaceous plants lacking the capacity of vegetative shoot reproduction

BrCh = "Thallo-chamaephytes"; i.e., cushion-forming bryophytes (example, *Rhacomitrium lanuginosum* var. *pruinosum*)

LCh = "Thallo-chamaephytes"; i.e., fruticose lichens (example, *Stereocaulon volcani)*

BrH = "Thallo-hemicryptophytes"; i.e., flat-appressed mosses (*Macromitrium owaihense*)

PhycH = "Thallo-hemicryptophytes"; i.e., macroscopic algae (example, *Stigonema panniforme*)

s = "sclerophyllous"; i.e., leathery leaved woody plants (example, *Metrosideros polymorpha*)

d = "daphnous"; i.e., soft-leaved woody plants (example, *Buddleja asiatica*)

bulb = "bulbous" geophytes that arise from bulbs or corms (example, *Tritonia crocosmiflora*)

caesp = "branched from near the base"; i.e., bunch habit (example, *Andropogon virginicus*)

frut = "frutescent"; meaning woodiness completed into branch tips (example, *Vaccinium reticulatum*)

ep = "epiphytic"; growing on other plant (example, *Psilotum nudum)*

pulv = "pulvinate"; refers here to cushion-forming mosses (example, *Campylopus exasperatus*)

rad = "radicigema"; refers to root-budding geophytes (example, *Hypochoeris radicata*)

rept = "reptant"; meaning the plant has a creeping habit; usually stoloniferous (example, *Commelina diffusa*)

rhiz = "rhizome"-geophytes that arise from rhizomes of various length (example, *Nephrolepis exaltata*)

ros = "rosette-forming" plant (example, *Anemone japonica*)

scand = "scandent"; refers to plants that have a tendency to climb (example, *Rubus penetrans*)

scap = "scapose" or single-stemmed (example, *Erechtites valerianaefolia*)

sem = "semi-rosette" plants (example, *Conyza canadensis*) as opposed to those that have completed rosettes (ros)

suff = "suffrutescent"; i.e., semi-woody (example, *Eupatorium riparium*)

Appendix VIII

SCIENTIFIC AND COMMON NAMES OF PLANTS

(E = endemic, I = indigenous, X = exotic species. Citation of seed plant names follows the recent checklist of St. John 1973; citation of fern names according to the revised park checklist of Fosberg 1972.)

	Scientific name	Common name
X	*Acacia farnesiana* (L.) Willd. [Leguminosae]	kolū, klu, aroma, popinac
X	*Agrostis avenacea* Gmel. [Gramineae]	he'u-pueo
	Anacystis montana (Kütz) Drouet and Daily [Chroococcaceae]	blue-green algae
X	*Andropogon glomeratus* (Walt.) BSP [Gramineae]	bush beardgrass
X	*Andropogon virginicus* L. [Gramineae]	broom sedge
X	*Anemone japonica*[1] S. and Z. [Ranunculaceae]	Japanese anemone
E	*Astelia menziesiana* SM. [Liliaceae]	pa'iniu
X	*Briza minor* L. [Gramineae]	little quakinggrass
E	*Bryum crassicostatum* Broth. [Bryaceae]	moss
I	*Bryum argentum* var. *lanatum* (P. Beauv.) Hampe [Bryaceae]	moss
X	*Buddleja asiatica* Lour. [Loganiaceae]	butterfly bush, dogtail
X	*Bulbostylis capillaris* (L.) C.B. Clarke [Cyperaceae]	annual sedge
I	*Campylopus densifolius* Angstr. [Dicranaceae]	moss
I	*Campylopus exasperatus* (Nees and Blume) Brid. [Dicranaceae]	moss
E	*Carex wahuensis* C. A. Mey. [Cyperaceae]	perennial sedge
I	*Ceratodon purpureus* (Hedw.) Brid. [Ditrichaceae]	moss
E	*Cibotium glaucum* H. and A. [Dicksoniaceae]	hapu, tree fern
X	*Cirsium vulgare* (Savi) Tenore [Compositae]	puākala, bull thistle, spear thistle

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[1] Now recognized as *Anemone hupehensis* (Lem. and Lem.) Lem. and Lem. f. by St. John (1973)

	Scientific name	Common name
E	*Cladonia skottsbergii* H. Magn. [Cladoniaceae]	lichen
X	*Commelina diffusa* Burm. f. [Commelinaceae]	honohono
E	*Coprosma ernodeoides* Gray [Rubiaceae]	kukae-nene, leponene, black-fruited coprosma
E	*Coprosma ochracea* var. *rockiana* Oliver [Rubiaceae]	pilo, kopa
X	*Cuphea carthagenesis* (Jacq.) Macbride [Lythraceae]	tarweed, puakamoli
	[Cyanophyceae]	blue-green algae
I	*Cyperus polystachyus* Rottb. [Cyperaceae]	kulukulua
X	*Cyperus brevifolius* (Rottb.) Hassk. [Cyperaceae]	kili'o'opu, manu-nene
X	*Cyperus rotundus* [Cyperaceae]	kili'o'opu, nut grass
E	*Cyrtandra* sp. [Gesneriaceae]	ha'i wale
E	*Deschampsia australis* Nees ex Steud. [Gramineae]	—
E	*Dianella sandwicensis* H. and A. [Liliaceae]	uki, Hawaiian dianella
E	*Dicranum speirophyllum* Mont. [Dicranaceae]	moss
E	*Diospyros ferrea* (Willd.) Bakh. [Ebenaceae]	lama
I	*Dodonaea viscosa*[2] [Sapindaceae]	a'ali'i, Hawaiian hopseed bush
E	*Dubautia ciliolata*[3] D.C. [Compositae]	kupaua, kupaoa, hana-paoa
E	*Dubautia scabra*[4] [Compositae]	kupaoa
X	*Epilobium cinereum* A. Rich. [Onagraceae]	willow herb, pukamole
	Equisetum arvense L. [Equisetaceae]	common horsetail
X	*Erechtites valerianaefolia* (Wolf) DC. [Compositae]	hino-hana
X	*Eupatorium riparium* Regel [Compositae]	Hilo pamakani, spreading mistflower
X	*Ficus* sp. [Moraceae]	fig

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[2] Now recognized as *Dodonaea sandwicensis* var. *sandwicensis* D. by St. John (1973), an endemic.

[3] Now recognized as *Raillardia ciliolata* DC. by St. John (1973)

[4] Now recognized as *Raillardia scabra* DC. by St. John (1973)

	Scientific Name	Common Name
X	*Fragaria vesca* var. *alba* (Ehrh.) Rydb. [Rosaceae]	ohelo papa, white strawberry
X	*Fuchsia magellanica* var. *discolor* Bailey [Onagraceae]	kula pepeiao, fuchsia
E	*Gahnia gahniaeformis*[5] (Gaud.) Heller [Cyperaceae]	—
X	*Geranium carolinianum* L. [Geraniaceae]	Carolina crane's bill
E	*Gouldia terminalis* (H. and A.) Hld. [Rubiaceae]	manono
	Hapalosiphon sp. [Stigonemataceae]	blue-green algae
X	*Hedychium coronarium* Koenig in Retz [Zingiberacae]	white ginger
E	*Hedyotis centranthoides* (H. and A.) Steud. [Rubiaceae]	pilo
X	*Holcus lanatus* L. [Gramineae]	velvet grass, Yorkshire fog
X	*Hypochoeris radicata* L. [Compositae]	gosmore, hairy cat's ear
E	*Ilex anomala* (H. and A.) [Aquifoliaceae]	kawa'u, ka'awa'u
E	*Isachne distichophylla* Munro ex Hbd. [Gramineae]	ohe, ma ohe ohe
	[Jungermanniaceae]	liverwort family
	Lythrum maritimum HBK. [Lythraceae]	pua kamoli, pukamole
I	*Machaerina angustifolia* (Gaud.) Koyama [Cyperaceae]	'uki
I	*Macromitrium owaihense*[6] C. Muell. [Orthotrichaceae]	moss
X	*Metrosideros excelsa* Soland. ex Gaerth. [Myrtaceae]	pohutukawa, New Zealand Christmas tree
E	*Metrosideros polymorpha*[7] Gaud. [Myrtaceae]	ohia, ohia-lehua, lehua
E	*Myrsine lessertiana* A. DC. [Myrsinaceae]	kolea-lau-nui
	[Myxophyceae]	slime algae, blue-green algae
I	*Nephrolepsis exaltata* (L.) Schott [Polypodiaceae]	ni'ani'au, okupukupu, sword fern
X	*Nephrolepsis hirsutula* (Forst. filius) Presl. [Polypodiaceae]	hairy sword fern

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[5] Now recognized as *Machaerina gahniaeformis* (Gaud.) Kern by St. John (1973)

[6] Now better called *Macromitrium reinwardtii* Schwaegr.

[7] Syn. to *M. collina* (J. R. and G. Forst.) Gray subsp. *polymorpha* (Gaud.) Rock

	Scientific Name	Common Name
E	*Osteomeles anthyllidifolia* Lindl. [Rosaceae]	ulei, uulei, Hawaiian hawthorn
I	*Pandanus tectorius* Warb. [Pandanaceae]	hala, puhala, lauhala, screw pine
X	*Paspalum conjugatum* Berg. [Gramineae]	Hilo grass, manu’u-malihini
X	*Paspalum dilatatum* Poir [Gramineae]	dallis grass, Australian watergrass
X	*Pennisetum clandestinum* Hochst. ex Chiov. [Gramineae]	kikuyu grass
	Persea americana Mill. [Lauraceae]	avocado alligator pear
X	*Physalis peruviana* L. [Solanaceae]	poha, cape gooseberry, ground cherry
E	*Pipturus albidus* (H. and A.) Gray [Urticaceae]	mamaki, mamake
X	*Pityrogramma calomelanus* (L.) Link [Polypodiaceae]	colomelanos, silver fern, gold fern
X	*Pluchea odorata* (L.) Cass. [Compositae]	shrubby fleabane, sour bush
E	*Polypodium pellucidum* Kaulf. [Polypodiaceae]	ae
X	*Psidium cattleianum* [Myrtaceae]	strawberry guava, waiawi-’ulu’ula
	Psidium guajava L. [Myrtaceae]	guava
E	*Pteridium aquilinum* var. *decompositum* (Gaud.) Tyron [Polypodiaceae]	kilau, kilauapueo
I	*Pteris cretica* L. [Polypodiaceae]	owalii
I	*Rhacomitrium lanuginosum* var. *pruinosum* Wils. [Grimmiaceae]	moss
X	*Rhynchelytrum repens* (Willd.) G. E. Hubb [Gramineae]	Natal redtop
X	*Rosa* sp. [Rosaceae]	rose
X	*Rubus rosaefolius* Sm. [Roseceae]	ola’a, akala, thimbleberry, roseleaf raspberry
X	*Rubus penetrans* Bailey [Rosaceae]	blackberry
E	*Rumex giganteus* Ait. [Polygonaceae]	pawale, uhaohako
E	*Sadleria cyatheoides* Kaulf. [Polypodiaceae]	amaumau
	Scytonema myochrous (Dillw.) Ag. ex Born. et Flah. [Scytohomataceae]	blue-green algae (with false branching)
X	*Setaria geniculata* (Poir.) Beauv. [Gramineae]	yellow foxtail

	Scientific Name	Common Name
X	*Sonchus oleraceus* L. [Compositae]	sow thistle, yellow pua-lele
X	*Spathoglottis plicata* Bl. [Orchidaceae]	Philippine ground orchid
I	*Sphenomeris chusana*[8] (L.) Copel. [Polypodiaceae]	palapalaa, palaa
X	*Sporobolus africanus* (Poir.) Robyns and Tournay [Gramineae]	rattail grass, smutgrass
	Stereocaulon volcani (Bory) Ach. [Cladoniaceae]	lichen
	Stigonema panniforme (Ag.) Kirchner [Stigonemataceae]	blue-green algae (with true branching)
E	*Styphelia douglasii* (Gray) F. Muell. and Scottsb. [Epacridaceae]	pukiawe
I	*Styphelia tameiameiae* (Cham.) F. Muell. and Scotsb. [Epacridaceae]	pukiawe, maieli, kawaiu
E	*Thuidium plicatum* Mitt. [Thuidiaceae]	moss
X	*Tritonia crocosmiflora* Nichols. [Iridaceae]	tritonia
E	*Vaccinium peleanum* Scottsb. [Ericaceae]	ohelo
E	*Vaccinium reticulatum* Sm. [Ericaceae]	ohelo
E	*Vaccinium calycinum* Sm. [Ericaceae]	ohelo-kau-la'au
E	*Wikstroemia sandwicensis* Meisn. [Thymeliaceae]	akia, false ohelo

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[8] Recently renamed *Sphenomeris chinensis* (L.) Maxon according to F. R. Fosberg

Literature Cited

ASTON, B. C. 1916. The vegetation of the Tarawera Mountain, New Zealand. *J. Ecol.* **4**:18-26.

ATKINSON, I. A. E. 1969. *Ecosystem development on some Hawaiian lava flows.* Ph.D. Thesis. University of Hawaii, Honolulu. 191 p.

———. 1970. Successional trends in the coastal and lowland forest of Mauna Loa and Kilauea volcanoes, Hawaii. *Pac. Sci.* **23**:387-400.

AULT, W. V., J. P. EATON, and D. H. RICHTER. 1961. Lava temperatures in the 1959 Kilauea eruption and cooling lake. *Geol. Soc. Am. Bull.* **72**:791-794.

BEHRE, K., and G. H. SCHWABE. 1969. *Algenbefunde in den Kraterräumen auf Surtsey Island.* Vorlaufige Mitt. aus dem MPI fur Limnologie, Plon. 6 p.

BOOTH, W. E. 1941. Algae as pioneers in plant succession and their importance in erosion control. *Ecology* **22**:38-46.

BRAUN-BLANQUET, J. 1965. *Plant sociology: The study of plant communities.* (Transl., rev., and ed. by C. D. Fuller and H. S. Conrad.) Hafner Publishing Co., London. 439 p.

BRAY, R. H., and L. T. KURTZ. 1959. Determination of total organic and available forms of phosphorus in soils. *Soil Sci.* **59**:39-45.

BROWN, W. H., E. D. MERRILL, and H. S. YATES. 1917. Revegetation of Volcano Island, Luzon, Philippine Islands, since eruption of Taal Volcano in 1911. *Philipp. J. Sci.* **12**(4):Sect. C. 177-248.

CAMPBELL, D. H. 1909. The new flora of Krakatoa. *Am. Nat.* (43):449-460.

CLEMENTS, F. E. 1916. *Plant succession and analysis of the development of vegetation.* Carnegie Inst. Washington Publ. No. 242. 512 p.

———. 1928. *Plant succession and indicators.* H. W. Wilson Co., New York. 453 p.

DILMY, A. 1965. Pioneer plants found one year after the 1963 eruption of Agung in Bali. *Pac. Sci.* **19**:498-501.

DOTY, M. S. 1957. *Natural populations of the 1955 Puna lava flows.* Abstract. Reprint from Proc. Hawaiian Acad. Sci. 32 Ann. Meeting, published by University of Hawaii.

———. 1961. Lava flow pioneer populations. Pages 139-144 *in* F. R. Fosberg. *Guide to excursion III.* Tenth Pac. Sci. Congr.

———. 1967a. Pioneer intertidal population and the related general vertical distribution of marine algae in Hawaii. *Blumea* **25**(1):95-105.

———. 1967b. Contrasts between the pioneer populating process on land and shore. *Bull. S. Calif. Acad. Sci.* **66**(3):175-194.

———, and D. MUELLER-DOMBOIS. 1966. *Atlas for bioecology studies in Hawaii Volcanoes National Park.* University of Hawaii, Hawaii Bot. Sci. Paper No. 2. 507 p.

EGGLER, W. A. 1941. Primary succession on volcanic deposits in southern Idaho. *Ecol. Monogr.* **11**:277-298.

———. 1948. Plant communities in the vicinity of the volcano El Paricutin, Mexico, after two and a half years of eruption. *Ecology* **29**(4):415-436.

———. 1963. Plant life of Paricutin Volcano, Mexico, eight years after activity ceased. *Am. Midl. Nat.* **69**(1):38-68.

———. 1967. Influence of volcanic eruptions on xylem growth patterns. *Ecology* **48**(4):644-647.

———. 1971. Quantitative studies of vegetation on sixteen young lava flows on the island of Hawaii. *Trop. Ecol.* **12**(1):66-100.

EGLER, F. E. 1939. Vegetation zones of Oahu. *Hawaii Empire For. J.* **18**:44-57.

———. 1947. Arid southeast Oahu vegetation, Hawaii. *Ecol. Monogr.* **17**:383-435.

Ellenberg, H. 1956. *Grundlagen der Vegetationsgliederung.* Verlag Eugen Ulmer, Stuttgart, Germany. 136 p.

———, and D. Mueller-Dombois. 1967. A key to Raunkiaer plant life forms with revised subdivisions. *Ber. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rubel Zür.* **37**:56-73.

Ernst, A. 1908. *The new flora of the volcanic islands of Krakatoa.* (Transl. A. C. Seward.) Cambridge University Press. 74 p.

Forbes, C. N. 1912. Preliminary observations concerning the plant invasion of some of the lava flows of Mauna Loa, Hawaii. *Occas. Pap. B. P. Bishop Mus.* **5**(1):15-23.

Fosberg, F. R. 1959. Upper limits of vegetation on Mauna Loa, Hawaii. *Ecology* **40**:144-146.

———. 1961. *Guide to excursion III.* Tenth Pac. Sci. Congr. and Univ. of Hawaii. 204 p. (Revised ed. 1972, 249 p.)

———. 1972. *Checklist of vascular plants and ferns of Hawaii Volcanoes National Park.* Based on pages 153-238 *in* Hawaii Botanical Science Paper No. 2. Revised 1972. (Computer print-out obtainable from Dept. of Botany, University of Hawaii, Honolulu).

Fox, S. W. 1964. Thermal polymerization of amino-acids and production of formed microparticles on lava. *Nature* **201**(4917):336-337.

Gates, F. C. 1914. The pioneer vegetation of Taal Volcano. *Philipp. J. Sci.* **9**:Sect. C. 391-434. Pl. 3-10.

Griggs, R. F. 1918. The recovery of vegetation at Kodiak. *Ohio J. Sci.* **19**(1):1-57.

———. 1922. *Climatic effects of the eruption and recovery of vegetation at Kodiak.* Pages 33-56 *in* The valley of ten thousand smokes. Natl. Geogr. Soc.

———. 1933. The colonization of the Katmai ash, a new and inorganic "soil." *J. Bot.* **20**:92-113.

Harper, H. J. 1924. The determination of ammonia in soils. *Soil Sci.* **18**:409-418.

Hart, C. G., and M. C. Neal. 1940. The plant ecology of Mauna Kea, Hawaii. *Ecology* **21**:237-266.

Hasselo, H. N., and J. T. Swarbrick. 1960. The eruption of the Cameroons Mountain in 1950. *West Afr. Sci. Assoc.* **6**(2):96-101.

Hatheway, W. H. 1952. Composition of certain dry forests: Mokuleia, Oahu. *Ecol. Monogr.* **22**(4):153-168.

Hillebrand, W. 1888. Die Vegetationsformationen der Sandwich Inseln. *Bot. Jahrb.* **9**:305-314.

Hosaka, E. Y. 1937. Ecological and floristic studies in Kipapa Gulch, Oahu. *Occas. Pap.B. P. Bishop Mus.* **13**:175-232.

Jackson, M. L. 1958. *Soil chemical analysis.* Prentice Hall, Inc., Englewood Cliffs, N. J. 498 p.

Jackson, T. A. 1969. *The role of pioneer lichens in the chemical weathering of recent volcanic rocks on the island of Hawaii.* Ph.D. Thesis. University of Missouri, Columbia. 211 p.

Kartawinata, K., and D. Mueller-Dombois. 1972. Phytosociology and ecology of the natural dry-grass communities on Oahu, Hawaii. *Reinwardtia* **8**(3):369-494.

Keay, R. W. J. 1959. Lowland vegetation on the 1922 lava flow, Cameroons Mountain, *J. Ecol.* **47**:25-29.

Krajina, V. J. 1963. Biogeoclimatic zones on the Hawaiian Island. *Newsletter Hawaii Bot. Soc.* **2**(7):93-98.

Knapp, R. 1965. *Die Vegetation von Nord-und Mittelamerika und der Hawaii Inseln.* Gustav Fischer Verlag, Stuttgart, Germany. 373 p.

MacCaughey, V. 1917. Vegetation of Hawaiian lava flows. *Bot. Gaz.* **64**:386-420.

MacDonald, G. A. 1962. The 1959 and 1960 eruptions of Kilauea Volcano, Hawaii, and the construction of walls to restrict the spread of the lava flows. *Bull. Volcanologique* **24**:249-294.

———, and T. Katsura. 1961. Variation in the lava of 1959 eruption in Kilauea Iki. *Pac. Sci.* **15**:358-369.

———, and D. H. Hubbard. 1966. *Volcanoes of the national parks in Hawaii.* Hawaii Natural History Association. 52 p.

Millener, L. H. 1953. How old is the vegetation on Rangitoto Island? *N. Z. Ecol. Soc.* May:17-18.

———. 1965. Forest, scrub, and fresh-water communities. *Science in Aukland.* 11th New Zealand Sci. Congr.:1-13.

MILLER, H. A. 1960. Remarks on the succession of bryophytes on Hawaiian lava flows. *Pac. Sci.* **14**(3):246-247.

MUELLER-DOMBOIS, D. 1967. Ecological relations in the alpine and subalpine vegetation on Mauna Loa, Hawaii. *J. Indian Bot. Sci.* **96**(4):403-411.

———, and H. P. SIMS. 1966. Response of three grasses to two soils and a water table depth gradient. *Ecology* **47**(4):644-648.

———, and V. J. KRAJINA. 1968. *Comparison of east-flank vegetations on Mauna Loa and Mauna Kea, Hawaii.* Proc. Symp. Rec. Adv. Trop. Ecol., Varanasi, India. 16-21 January 1967.

MURATA, K. J. 1966. *An acid fumarolic gas from Kilauea Iki, Hawaii.* U.S. Geol. Surv. Prof. Pap. 537-C. U.S. Government Printing Office, Washington, D.C.

NEWELL, C. L. 1968. *A phytosociological study of the major vegetation types in Hawaii Volcanoes National Park, Hawaii.* M.S. Thesis. University of Hawaii, Honolulu. 191 p.

OLSEN, C. 1929. On the analytical determination of ammonia in soil, and the absorption power of soil for ammonia. *C. R. Trav. Lab. Carlsberg* **27**(15).

POORE, M. E. D. 1964. Integration in the plant community. *J. Ecol.* **52**(Suppl):213-226.

POWERS, H. A. 1948. Chronology of the explosive eruptions of Kilauea. *Pac. Sci.* **2**(4):278-292.

RAJPUT, M. A. 1968. *Tree stand analysis and soil characteristics of the major vegetation cover types in Hawaii Volcanoes National Park.* M.S. Thesis. University of Hawaii, Honolulu. 236 p.

RAUNKIAER, C. 1918. Recherches statistiques sur les formations végétales. Det Kgl. *Danske Vidensk. Selsk. Biol. Medd.* **1**:3-80.

RIGG, B. G. 1914. The effects of the Katmai eruption on marine vegetation. *Science* N.A. **40**(1032):509-513.

RIPPERTON, J. C. and E. Y. HOSAKA. 1942. Vegetation zones of Hawaii. *Hawaii Agric. Exp. Stn. Bull.* **89**:1-60.

ROBYNS, W., and S. H. LAMB. 1939. Preliminary ecological survey of the island of Hawaii. *Bull. Jard. Bot. Etat Brux.* **15**:241-293.

ROCK, J. F. 1913. *The indigenous trees of the Hawaiian Islands.* Honolulu, Hawaii. 518 p. (Book published under patronage.)

SANDS, W. N. 1912. An account of the return of vegetation and the revival of agriculture in the area devastated by the Soufriere of St. Vincent in 1902/3. *West Indian Bull.* **12**:22-23.

SCHWABE, G. H. 1969. Pioniere der Bediedlung auf Surtsey. *Umsch. Wiss. Tech.* **2**(69):51-52.

SKOTTSBERG, C. 1941. Plant succession on recent lava flows in the island of Hawaii. Goteborgs Kungl. *Vetenskap-och Vitterhetssamhalles Handlinger Sjatte Fojden.* Ser. B. Bd. 1. **8**:32 p.

SØRENSON, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Det. Kong. Danske Vidensk. Selsk. Biol. Skr.* **5**(4):1-34.

ST. JOHN, H. 1973. *List and summary of the flowering plants in the Hawaiian Islands.* Pac. Trop. Bot. Garden Memoir No. 1. (Lawai, Kauai, Hawaii). 519 p.

STONE, J. B. 1926. *The products and structure of Kilauea.* Bull. B. P. Bishop Mus. 32. 59 p.

TAGAWA, H. 1964. A study of the volcanic vegetation in Sakurajima, southeast Japan. I. Dynamics of vegetation. *Mem. Fac. Sci. Kyushu Univ. Ser. E. (Biology)* **3**(3-4):165-228.

———. 1966. *A study of the volcanic vegetation in Sakurajima, southwest Japan.* III. Trap samplings of disseminules on the lava flow and the culture experiment of some pioneer mosses, Sci. Rep. of Kagoshima Univ. No. 15.

———. 1968. *A study of the volcanic vegetation in Sakurajima, southwest Japan.* IV. Monthly fluctuation of disseminule fall on the lava and viability of seeds. Sci. Rep. of Kagoshima Univ. No. 15.

TAYLOR, B. W. 1957. Plant succession on recent volcanoes in Papua. *J. Ecol.* **45**:233-243.

TEZUKA, Y. 1961. Development of vegetation in relation to soil formation in the volcanic island of Oshima, Izu, Japan. *Jap. J. Bot.* **17**(3):371-496.

TREUB, M. 1888. Notice sur le nouvelle flora de Krakatoa. *Ann. Jard. Bot. Buitenzorg* **7**:213-223.

UHE, G., JR. 1972. *A contribution to the ecology of vegetation on recent volcanic deposits.* Ph.D. Thesis. University of Auckland, New Zealand. 250 p.

WALTER, H. 1957. Wie kann man den Klimtypus anschaulich darstellen? Umsch. Wiss. Tech. **24**:751-753.

———, and H. LIETH. 1960. *Klimadiagramm-Weltatlas.* VEB Fisher Verlag Jena.

WENTWORTH, C. K. 1966. The eruption and the original population. Pages 330-334 *in* M. S. Doty and D. Mueller-Dombois. *Atlas for bioecology studies in Hawaii Volcanoes National Park.* Hawaii Bot. Sci. Pap. 2.

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