Soil-Vegetation Relationships in Hawaiian Kipukas[1]

D. MUELLER-DOMBOIS and C. H. LAMOUREUX[2]

KIPUKA, the Hawaiian word for "opening," has come into scientific usage as a term used to designate an older area on the slopes of volcanic mountains that has been surrounded by more recent lava flows. Kipukas are common landscape features on the slopes of Mauna Loa and Kilauea volcanoes on the island of Hawaii, where they can be readily recognized as islands of denser vegetation in the vast, sparsely vegetated areas. They range in size from a few square meters to hundreds of acres.

Kipukas are of special interest for several reasons. As vegetation islands they provide seed-source centers for the invasion of vegetation on new volcanic material. As vegetation islands they represent somewhat simplified ecosystems, analogous to bogs or lakes, that are very suitable for studying internal ecological relationships. The isolation of small populations in kipukas provides unique opportunities for evolutionary studies.

So far, very little ecological work has been done with Hawaiian kipukas. Need for such work has arisen in Hawaii Volcanoes National Park, where the Park Service is confronted with the task of interpreting certain kipuka features to the Park visitors. Kipuka Puaulu, popularly known as "Bird Park," has been accessible to the public for some time and the nearby Kipuka Ki is soon to be opened. For this reason the present study was begun in these two kipukas.

Rock described the flora of both kipukas in an undated manuscript (probably written around 1910) and reported a few general ecological observations. He remarked upon the unique and complex composition of arborescent species from which he judged both kipukas to be "of great age." However, as an approximation he cited the estimate of Professor T. Jaggar (geologist at the Hawaii Volcano Observatory at that time), which placed the kipuka's origin within the Christian era (i.e., less than 2,000 years). Rock recorded 40 arborescent native species forming a complex forest type in Kipuka Puaulu. Only half this number of tree species were found in Kipuka Ki. He also noted the presence of two vegetation types in Kipuka Puaulu, a complex forest type containing many tree species and a *Metrosideros*-dominated type. He believed that soil differences were responsible for the presence of these two types of forest. A general description of the kipuka soils is given in the Soil Survey report for the Territory of Hawaii (Cline et al., 1955), where the soils were classified as Latosolic Brown Forest soils derived from two layers of volcanic ash.

The primary objectives of this present study were to determine the floras of both kipukas, to describe the vegetation types present in each, and to determine what soil-vegetation relationships exist in these places.

DESCRIPTION OF AREA

Both kipukas occur at an elevation of from 1200 to 1300 m on the southeast slope of Mauna Loa approximately 3 km northwest of Kilauea crater (Fig. 1). The central elevation of Kipuka Ki is about 60 m higher than that of Kipuka Puaulu. Both are surrounded and separated by recent beds of rough aa lava. Their boundaries are about 800 m apart. Kipuka Puaulu is about 42 hectares and Kipuka Ki about 18 hectares in size. The climate is characterized by a rather uniform mean annual temperature of 16°C, which is 7°C cooler than that experienced at sea level. The mean variation between the warmest month (August) and the coolest (February) is only 3.5°C. Occasional freezing temperatures can be expected during February nights. Approximate annual rainfall is 1500 mm, varying monthly from about 25 mm in June to 200 mm in January. According to Krajina's (1963) zonal classification, the ki-

---

[1] The study was financed through U.S. Government Contract No. 14-10-0434-1504 to Dr. M. S. Doty, "Bioecological investigations of Hawaii Volcanoes National Park." Manuscript received April 15, 1966.

[2] Department of Botany, University of Hawaii.

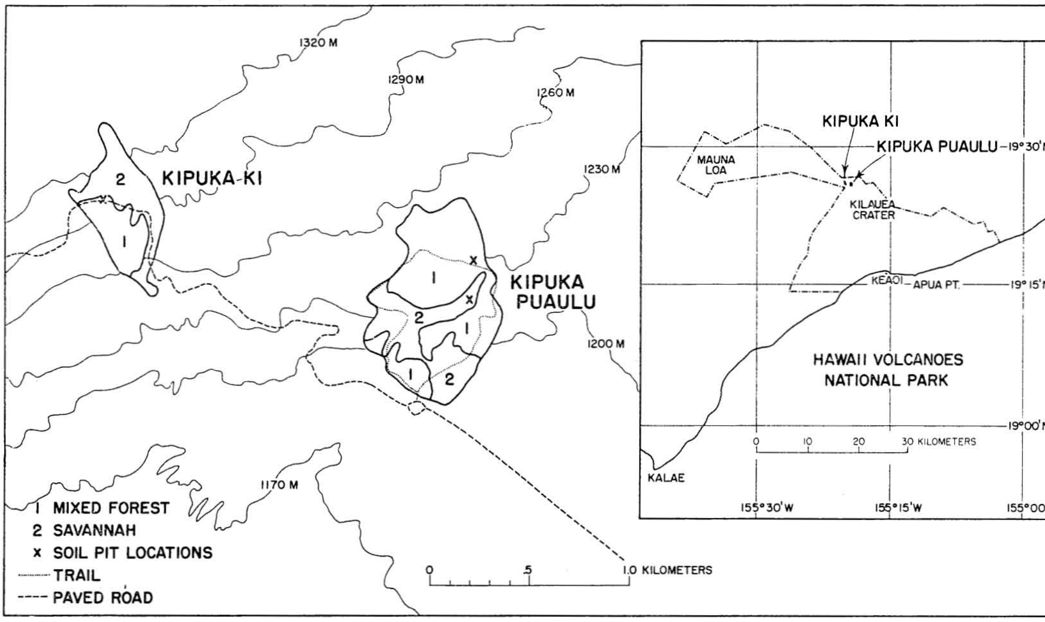

FIG. 1. Map of kipukas showing major vegetation types and soil pit locations. (Drawn from 1:12,000 air photo taken October 1954.)

pukas occur in the lower *Metrosideros* zone, whose climate is described as humid marine tropical (or subtropical) with common clouding. The kipukas are somewhat more sheltered from the windward rains than much of this zone, and Rock (1913) described them as being occupied by dry-mixed forest.

Both kipukas are situated on moderate south slopes and have an irregularly undulating topography with a few short, steep slopes, several level areas, a few larger somewhat inclined areas, and scattered small pocket-like depressions.

Two distinct vegetation formations were found in Kipuka Puaulu: a closed to semi-open forest type (Fig. 1, type 1), and a savannah type with a dense grass cover and scattered trees of *Metrosideros* and *Acacia koa* (Fig. 1, type 2). Kipuka Ki is dominated by a moderately stocked forest vegetation type, which in places is also semi-open (Fig. 1, type 1), but it lacks the very dense or closed forest stand segments found in Kipuka Puaulu: a closed to semi-open also in Kipuka Ki, representing there, however, mainly a transition zone in which occasional lava rocks protrude to the surface (Fig. 1, type 2). Characteristically, no rocks are found near the surface in either kipuka with the exception of the transitory savannah in Kipuka Ki. Within the forest formation of both kipukas several smaller plant communities can be recognized. One of the more obvious associations, common to both kipukas, is characterized by a ground cover of *Microlepia setosa*, a lush fern up to 1 m tall. The tree layer is dominated by *Acacia koa* and *Sapindus saponaria*. This plant association occurs on level to moderately sloping ground.

METHODS

For the purpose of comparing the soils of the two kipukas, soil pits were dug in each kipuka in the *Microlepia* community near a tall *Acacia koa* tree in a level place. A level place near a tall koa tree was also chosen for a soil pit in the savannah for making a comparison between the soils of the forest and the savannah formation within Kipuka Puaulu (Fig. 1). The reason for choosing a level place was that the soils there were presumably not influenced by lateral seepage.

Each pit was dug to a depth of 2 m. The soil horizons were described as to depth, material, and color, and samples were collected for laboratory analysis. The soil samples included three sets, one for microbiological analyses (now being conducted), one for current soil moisture analysis, and one for other soil tests. In addition, the three soil profiles were prepared as soil monoliths after the method of Smith and Moodie (1947) for further mega- and microscopic inspection and as permanent records.

Subsequent soil tests carried out included determination of moisture equivalents (by the centrifuge method), permanent wilting percentages (by the sunflower method), organic carbon (by the Walkley-Black wet-combustion method), and pH (by electric pH meter).

Herbarium specimens were prepared. One set has been deposited in the herbarium of the University of Hawaii, and a second set in the herbarium of Hawaii Volcanoes National Park.

RESULTS AND DISCUSSION

A. Soils

The soils give convincing evidence that they have been derived from volcanic ash and not from old, disintegrated lava as has been assumed by the authors who published the nature trail guide for Kipuka Puaulu (1961 edition). Ash strata were found to the depth of 2 m to which all soil pits were dug and there was no sign of parent material change at this depth. Rock (undated) indicated that the soil in Kipuka Puaulu was nearly 6 m deep. The maximum soil depth in Kipuka Ki is not known.

Ash was deposited not at one time but in several stages, probably extending over many hundreds of years. Corresponding ash layers that appear to have originated from the same eruptions can be found in all soils we examined. Noteworthy are two thin red pumice layers that occur in each soil. One occurs in the lower profile at 100 cm depth in the soil of Kipuka Ki, at 140 cm in the forest soil of Kipuka Puaulu, and at 145 cm in the savannah soil (Fig. 2). A second red pumice layer is found in all soils nearer the surface, at 60 cm in Kipuka Ki, at 70 cm in the forest soil of Kipuka Puaulu, and at 85 cm in the savannah soil.

Ash deposits were composed of at least five different materials: a fine, dusty gray ash with scattered pebbles up to 5 mm in diameter, a gravelly ash with basaltic and variously vesicular pebbles up to 1 cm in diameter, a black vitreous ash, a yellow-olive pumice, and the red pumice mentioned above.

The fine, dusty gray ash occurs at a depth of 15–20 cm from the surface in all profiles. It is most pronounced in the savannah soil and least so in the soil of Kipuka Ki. This layer looks like the leached layer of a podzolic soil. However, there are three arguments against this interpretation. First, the layer is brightest under savannah, which has the least acid surface layer (Table 1). Second, it was horizontally continuous only in Kipuka Puaulu, whereas it occurred in local pockets in Kipuka Ki. Third, Wentworth (1938), in his study of ash formations around Kilauea Crater, described a "gray-lavender, fine sand-size ash" near the surface in several places which seems to fit this layer.

The gravelly ash was described by Wentworth as "basalt in glass" and is well shown in the savannah soil, where it recurs as a thin layer (usually $\pm$ 5 cm thick) at depths of 30, 50, and 70 cm.

Black vitreous ash appears as a layer 20 cm deep in all three soils, from 50–70 cm depth in Kipuka Ki, from 60–80 cm in the forest soil of Kipuka Puaulu, and from 75–95 cm in the savannah soil. It recurs at three places above this layer (at 65 cm, 45 cm, and 25 cm) in the savannah soil. These black layers are black not only from ash but also, perhaps more dominantly so, from an extremely high incorporation of organic carbon (between 10.1 and 15.7%, Table 1).

A yellow-olive pumice layer (called "reticulite" by Wentworth) is found in the savannah soil incorporated into the black layer at 25 cm depth. Some of this pumice occurs also in both forest soils beneath the fine gray ash layer (C1), but here it is less abundant and less well stratified (Fig. 2).

The lower ash deposits, from the thick black layer (Alb) down, in both soils of Kipuka Puaulu are not stratified horizontally, whereas the upper ones are more or less horizontally stratified (see Fig. 2, P_1 and P_2). Angles of departure were between 20 and 30°. This fact indicates that there have been some relief changes throughout the build-up of the soil to its present surface level. This suggests something about the origin of Kipuka Puaulu, which may apply to Kipuka Ki as well. It appears probable that lateral translocation of ash has occurred after deposition as a result of wind or water erosion, especially during the early stages when the kipuka was only sparsely vegetated.

A small kipuka of about 1 hectare in the Kau Desert south of Kilauea crater, which is just "in-the-making," shows that it has originated as a small dune ecosystem. Gray-black sandy ash was deposited here in a thin layer on a large flat area of smooth pahoehoe lava. Wind has swept

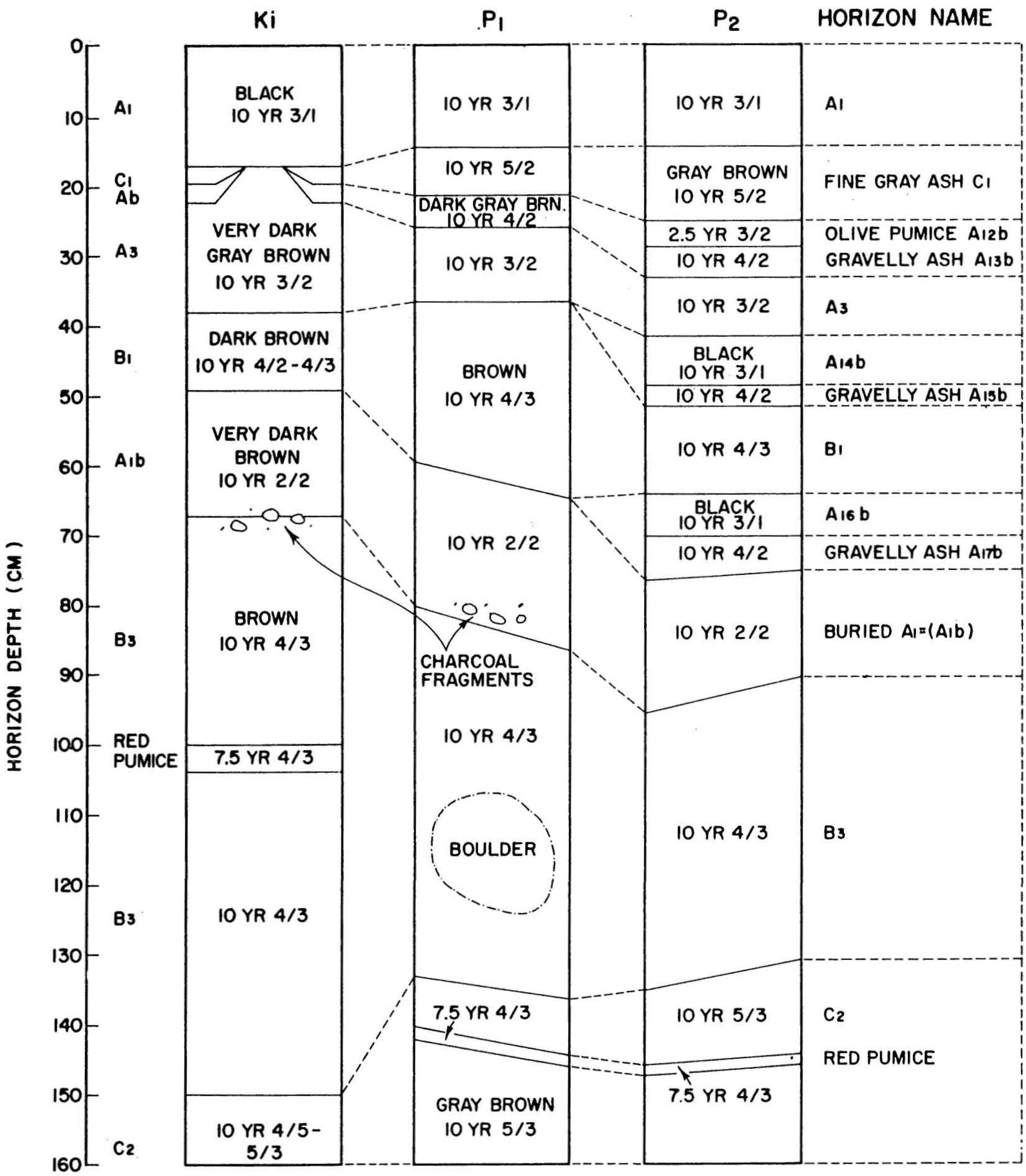

FIG. 2. Comparison of horizons of kipuka soils (*Ki*, forest soil of Kipuka Ki; P_1, forest soil of Kipuka Puaulu; P_2, savannah soil of Kipuka Puaulu). Color symbols from Munsell charts refer to air-dry soil. Nomenclature of horizons after the 1962 Supplement to the Agriculture Handbook No. 18, Soil Survey Manual.

TABLE 1

SOME PARAMETERS OF THE KIPUKA SOILS

HORIZON	CURRENT MOISTURE CONTENT (%)[1]			AVAILABLE WATER (%)[2]			ORGANIC CARBON (%)[3]			pH[4]		
	Ki[5]	P_1[6]	P_2[7]	Ki	P_1	P_2	Ki	P_1	P_2	Ki	P_1	P_2
A1	67	56	106	23	23	30	11.1	10.4	14.3	5.2	4.8	5.7
Fine gray ash C1	21	27	30	13	13	10	4.2	3.3	1.1	5.7	5.5	5.4
Olive pumice A12b			55			34			15.7			6.4
	23	16		–	–		9.6	12.6		5.9	5.8	
Gravelly ash A13b			17			7			15.4			5.9
A3	24	44	28	18	13	10	9.9	10.5	7.2	6.2	5.6	6.4
A14b			58			–			12.0			5.7
gravelly ash A15b			19			5			3.0			6.5
B1	29	44	44	15	16	15	7.7	7.8	5.7	5.9	5.6	5.7
A16b			48			–			13.5			6.1
gravelly ash A17b			10			3			7.8			6.3
Buried A1 (= A1b)	40	75	60	23	20	20	12.7	12.1	10.1	5.7	5.7	5.7
B3	47	42	37	9	10	5	9.0	6.9	5.4	6.0	5.7	5.9
Red pumice	53	31	16	–	–	–	3.8	3.6	1.8	5.8	5.7	7.0
C2	90	36	21	11	12	5	9.0	7.6	1.9	6.0	5.7	6.0

[1] Moisture content at date of sampling, November 23, 1963.
[2] Available water = moisture equivalent (%) – permanent wilting percentage.
[3] Walkley-Black values.
[4] Measured electrometrically.
[5] Ki = Kipuka Ki, forest soil.
[6] P_1 = Kipuka Puaulu, forest soil.
[7] P_2 = Kipuka Puaulu, savannah soil

up much of this ash and redeposited it as a dune at a place where the smooth lava was intercepted by a rough aa flow. The ash-dune now represents an island supporting pioneer vegetation. This process is accumulative since the vegetation, once established, catches more eolian deposits and in turn contributes organic matter, soon forming a moisture- and nutrient-improved habitat that also differs in elevation from its surroundings. It is quite conceivable that such elevated dune ecosystems can be surrounded by subsequent lava flows. Such an occurrence, on a much larger scale, could account for the origin of the kipukas discussed here, although additional evidence to support this hypothesis must be obtained. Also, many, if not most, of the Hawaiian kipukas, such as Kipuka Nene, undoubtedly have developed merely by the disintegration *in situ* of older lavas, the kipuka area being subsequently surrounded by newer flows.

The upper ash deposits in the kipuka soils are more or less horizontal with respect to the present soil surface, a form of deposition which Powers (1948) calls "blanket deposits." The "blanket deposits" in the savannah soil show that there have been at least 9 ash deposits in Kipuka Puaulu since establishment of the thick black horizon (Alb). Not all of these may have been derived from different explosions, but Powers has discovered ash from at least 26 eruptions in the area that occurred later than the big Kilauea ash explosion of 1790. The latest recorded near Kipuka Puaulu was from the 1924 eruption. This shows that the soil is not of one (old) age, but is of several ages from older to younger, and the surface soil may even be much younger than the surrounding rough aa flow, rather than older as indicated by Rock. The surrounding flow is prehistoric, thus at least pre-1778.

Fragments of charcoal were found in both kipukas in the forest soils. They occurred at 70 cm depth in Kipuka Ki and at 80 cm in Kipuka Puaulu. This indicates two facts. First, there was fire in both kipukas at an earlier date in their development; and second, both had woody vegetation growing on them at that time. Although charcoal was not found in the savannah soil, fire may explain its origin. It is interesting that the savannah soil looks quite different from the forest soils which, in spite of being in two separate kipukas, show much similarity in appearance. Both forest soils are deeply melanized, dark brown in color, and are rather uniformly enriched with organic carbon (Table 1). The savannah soil shows more clearly the parent material, because of less uniform melanization. Here organic carbon content fluctuates greatly between soil horizons. These two patterns, that is, the more uniform color and organic carbon distribution in the forest soils and the greater variation in color and organic carbon distribution in the savannah soil, are undoubtedly associated with past rooting zones. One may assume that a mixed, well-stocked forest occupies the soil volume more uniformly than does a dominantly grass-covered savannah. The grass and ground vegetation roots may have been more restricted to the black horizon zones. Such a concentration in rooting depth was also found at present at the soil surface of the savannah soil. This pattern supports the assumption that the savannah originated after a fire. It is probable that the fire occurred when the 20 cm-thick, black layer, the buried Al horizon (Alb), was at the surface supporting actively growing vegetation, because the charcoal was found right at the lower boundary of this layer in both forest soils (Fig. 2). Therefore, the savannah may be quite old. The C-14 date of the 70 cm-deep charcoal in Kipuka Ki came to 2,170 $\pm$ 200 years, *i.e.*, about 220 years B.C.[3]

Analyses of potentially available water, organic carbon, and pH show no significant differences between savannah soil and forest soil in Kipuka Puaulu, so that neither soil water nor nutrient differences can be assumed to be responsible for the difference in vegetation. Moreover, there is no distinctive topographic pattern associated with either type, so that the savannah's origin is not attributable to environmental differences related to topography.

B. *Flora*

Between November 1963 and March 1965 botanical surveys were made of both kipukas. Voucher specimens have been deposited in the herbarium of the Department of Botany, University of Hawaii, and duplicate specimens in

[3] Sample GX0394, Geochron Laboratories, Inc.

the herbarium of Hawaii Volcanoes National Park. At the end of this article will be found a check list of the plants found in the two kipukas. It includes also records from Rock (undated, and 1913), and Fagerlund and Mitchell (1944), as well as specimens in the herbaria of Hawaii Volcanoes National Park and the Bernice P. Bishop Museum, Honolulu, Hawaii.

Table 2 summarizes the information provided in the check list. It shows that Kipuka Puaulu now contains, and has contained, significantly more species of vascular plants than has Kipuka Ki. Table 3 provides an analysis of the numbers of species common to both kipukas and of those found only in Kipuka Puaulu or Kipuka Ki. This indicates that, while each kipuka contains species which the other does not, Kipuka Puaulu has a significantly greater number of unique species than does Kipuka Ki.

Thus, the observations recorded in Tables 2 and 3 and in the check list agree with Rock's (1913) observation that there are more species

TABLE 2

NUMBERS OF SPECIES, VARIETIES, AND FORMS OF VASCULAR PLANTS RECORDED FROM KIPUKA PUAULU AND KIPUKA KI

PLANTS	ALL DATA	KIPUKA PUAULU	KIPUKA KI
Total number of spp.	158 (104)*	145 (92)	73 (63)
Native spp.	86 (52)	81 (48)	36 (30)
Native trees	42 (21)	42 (21)	15 (11)
Introduced spp.	72 (52)	64 (44)	37 (33)

* Figures outside parentheses include all spp. ever recorded. Figures within parentheses include all spp. growing naturally in 1963–65.

TABLE 3

DISTRIBUTION OF SPECIES, VARIETIES, AND FORMS OF VASCULAR PLANTS BETWEEN KIPUKA PUAULU AND KIPUKA KI

PLANTS	COMMON TO BOTH KIPUKAS	KIPUKA PUAULU ONLY	KIPUKA KI ONLY
Total number of spp.	60 (51)*	85 (41)	13 (12)
Native spp.	31 (26)	50 (22)	5 (4)
Native trees	15 (11)	27 (10)	— (—)
Introduced spp.	29 (25)	35 (19)	8 (8)

* Figures outside parentheses include all spp. ever recorded. Figures within parentheses include all spp. growing naturally in 1963–65.

in Kipuka Puaulu. The number of native trees now growing in Kipuka Puaulu (21) is almost twice as large as that in Kipuka Ki (11). However, Rock reported in 1913 that there were at least 40 native tree species growing in Kipuka Puaulu. Even allowing for differences of taxonomic opinion, the decrease in number of tree species during the last 50 years appears quite remarkable. In his book, "Indigenous Trees of the Hawaiian Islands," Rock (1913) included 19 photographs of tree species in Kipuka Puaulu. Fifteen of these photographs show bits of landscapes and ground vegetation, which at that time appeared badly abused by cattle grazing. Many areas appear barren or show trampled ground vegetation, and several pictures show broken-down trees. From the photographic record one could assume that the present savannah formation is caused entirely by cattle grazing. However, two photographs show what appear to be sections of the present savannah formation. One of these shows a dense cover of *Pteridium,* which today is also well established in the savannah. Inasmuch as fire has definitely occurred in both kipukas, it is believed that fire may have created openings in the forest that were aggravated and maintained by subsequent cattle grazing. It seems probable that cattle were guided in their grazing habits by this fire-conditioned vegetation pattern, since a denser ground vegetation would be found in the open, coupled with fewer obstacles for the movement of cattle. Increased cloud interception and fog drip in the forest (Ekern, 1964) may also have contributed to maintaining the pattern. This is indicated by the greater current moisture content in the lower profile of the forest soil (Table 1) and the location of the kipukas in a zone of common cloud occurrence (Krajina, 1963).

There are several possible explanations for the larger number of both native and introduced species in Kipuka Puaulu.

1. The larger number of native species in Kipuka Puaulu may be related to:

(a) LARGER AREA. Both kipukas are so much larger than the "minimal" area-size of forest stand communities cited in the literature (Ellenberg [1956] gives 500 m^2; Cain and Castro [1959], $< 20{,}000\ m^2$ for tropical rain forest), that one may think that size is not a factor.

However, such minimal area calculations are based on the more common species. From the records it is quite clear that the now extinct species were extremely rare. The smaller size of Kipuka Ki can be used, therefore, as one explanation for its smaller number of indigenous species.

(b) GREATER AGE. Rock (1913) believed that Kipuka Ki was more recent in origin than Puaulu, because of the common assumption that an older area would have more species. His idea cannot be disproved from current evidence, but one observation points in the opposite direction. The amount of organic carbon did not decrease in the lower profile of Kipuka Ki, whereas it did so in both soils of Kipuka Puaulu (Table 1). This may indicate vegetative activity at an earlier date in Kipuka Ki as compared with Puaulu.

(c) GREATER DIVERSIFICATION IN HABITATS. This factor in Kipuka Puaulu is not expected from observations made so far. Both kipukas have similar topographic variations and deep, rich soils. Also, the distribution of tree species is not as likely to be affected by small-scale environmental variations as is that of herbaceous plants.

(d) DIFFERENT HISTORY OF DISTURBANCE. Little definite information is available on differences in disturbance-history. We know only that three important disturbance factors operated in both kipukas: fire, cattle grazing, and pig damage. Current pig damage appears to be less in Kipuka Ki. Past cattle grazing also was probably less devastating here. It is possible, however, that fire eliminated a few trees, either directly, or indirectly by competition of more aggressive plants that followed the fire in both kipukas. In this connection, the chance of the smaller, isolated kipuka to be restocked with rare species would be less than that of the larger one, which also may have provided a greater chance of survival of rare tree species simply because of its larger size.

(e) DIFFERENCES IN RAINFALL AND PRODUCTIVITY. It was interesting to find that the current moisture distribution downward in the soils differed between the kipukas. The current soil water content increased considerably in the bottom part of the profile in Kipuka Ki and was higher than in the soils of Kipuka Puaulu, whereas the upper part of the profile was drier than that of the soils in Kipuka Puaulu. This indicates a different rain shower pattern between the kipukas. This may be a random pattern, however, which then would have no bearing on the total amount received. Except for the lower profile parts (B3 and C2), there was little difference in the amount of organic carbon in the two forest soils, indicating a similar productivity in both kipukas. Thus, the differences in number of species cannot be related to differences in productivity.

2. The larger number of introduced weed species in Kipuka Puaulu may be caused by (a) its greater exposure to man and cattle, and (b) its larger sun-exposed area, which favors the establishment of shade-intolerant weeds. It is interesting that the fewer weed species in Kipuka Ki occupy more ground. Some of them have formed dominant communities.

C. Vegetation

Several obvious plant communities occur under the forest cover. They are represented by native and introduced plants as follows:

NATIVE

Microlepia association
Nephrolepis association
Peperomia patches
Pipturus shrub strata
Coprosma thickets

INTRODUCED

Commelina association
Rubus penetrans association
Solanum association
Dactylis patches
Commelina-Nephrolepis mixed community

Nephrolepis communities and *Dactylis* patches are common also in open areas. *Coprosma* thickets are characteristic only for Kipuka Puaulu. The *Rubus penetrans* and *Solanum* associations are characteristic for Kipuka Ki. Only one small *Solanum* patch was observed in Kipuka Puaulu. All other associations occur in both kipukas. *Peperomia* patches seem to be established on ground that has been rather recently scarified by pigs, and form there a pioneer community in shaded habitats. Similarly, *Coprosma* thickets are associated with pig scarification, which is particularly pronounced under larger *Sapindus* trees where the pigs seem to search for their fruits.

SUMMARY AND CONCLUSIONS

1. The soil of both kipukas is derived from several ash deposits. The lower, sloping ones in Kipuka Puaulu differ from the upper ones, which are stratified horizontally.

2. Charcoal was found in both kipukas under forest in association with a buried, black surface horizon, at 70 cm depth in Kipuka Ki and at 80 cm in Puaulu.

3. The C-14 analysis of the 70 cm-deep charcoal in Kipuka Ki indicates that a fire occurred at about 220 B.C.

4. The forest soils of both kipukas are uniformly melanized, showing considerable megascopic similarity, and differ markedly from the savannah soil, which showed melanization restricted to narrow layers and which exposed a clear parent material stratification.

5. The soil parameters tested indicated no significant differences between the forest soil and the savannah soil of Kipuka Puaulu in terms of soil water, organic carbon, and pH.

6. The forest soils of the kipukas differ only in current soil moisture distribution and organic carbon content of the lower horizons (B3 and C2).

The work so far is only an introduction to the plant ecology of Hawaiian kipukas and points to the need for the following further research:

1. Analysis of photographs. It would be profitable to examine all photographs Rock made of Kipuka Puaulu and, if possible, to identify some spots for rephotographing. This could reveal certain interesting successional changes over the last 50 years.

2. Current observation indicates reoccupation of the savannah by forest. This appears to be accomplished by sucker growth of *Acacia koa*. Invasion of trees by seed seems practically impossible. It would be interesting to study the rate of reinvasion, now, when there is no more interference by cattle.

3. Studies of cloud interception. Differences in soil water supply as a result of fog drip should be investigated, to determine the role this environmental factor plays in influencing the rate of reinvasion of forest into the savannah.

4. Measuring pig damage. Current observation indicates that pigs affect the forest vegetation in two ways. (a) By scarifying the surface, they eliminate ground vegetation and provide ideal seed beds for tree seed germination of that which is left. Many formerly pig-scarified areas seem to come back in thickets of tree seedlings of *Sapindus* and *Coprosma*. (b) During periods of food scarcity or over-population pigs seem to gnaw away the bark of trees, particularly of *Coprosma,* thus damaging them severely, e.g., by providing entrance avenues for pathogens. The food habits of pigs should be studied in connection with population counts to explain their influence on vegetation patterns.

5. Quadrat studies of vegetation patterns. These should be done in particular with *Peperomia*, as a probable native pioneer on pig-scarified ground; with *Commelina* and *Nephrolepis* mixed associations, to determine whether *Commelina* takes over the habitats occupied by the native fern, *Nephrolepis*; and with the two weed communities formed by *Rubus penetrans* and *Solanum pseudocapsicum*, to determine their effect on the native *Microlepia* association.

6. An ecological survey of all kipukas and their surroundings should be made in an attempt to assess their development in succession and their influence on the vegetation of the surrounding more recent volcanic material.

CHECK LIST OF PLANTS IN THE KIPUKAS

This check list includes all of the vascular plant species of Kipuka Puaulu and Kipuka Ki as of May 1965. The symbols used are: * = native Hawaiian species; # = native tree; + = growing, apparently naturally, in kipuka in 1963–65; a = growing in kipuka in 1963–65 only as individuals recently planted by National Park Service; b = specimens, collected between 1930 and 1960, in herbaria at Hawaii Volcanoes National Park or B. P. Bishop Museum, but species not found growing in kipuka in 1963–65; c = reported by Fagerlund and Mitchell (1944), but no specimens available; d = reported by Rock (undated, and 1913), but no more recent specimens available.

SPECIES	KIPUKA PUAULU	KIPUKA KI
PTERIDOPHYTA		
ASPIDIACEAE		
* *Athyrium sandwichianum* Presl.	+	
Cyclosorus dentatus (Forsk.) Ching	+	
C. parasiticus (L.) Farwell		+
* *Cyrtomium caryotideum* (Wall.) Presl.	+	
* *Dryopteris glabra* (Brack.) Kuntze	b	
* *D. hawaiiensis* (Hillebr.) Christ	+	+
* *D. latifrons* (Brack.) Kuntze	+	
* *D. paleacea* (Swartz) Christensen	+	+
* *Elaphoglossum conforme* (Swartz) Schott		b
ASPLENIACEAE		
* *Asplenium adiantum-nigrum* L.	+	
* *A.* cf. *caudatum* Forst. f.	+	+
* *A. macraei* Hook. et Grev.	c	b
BLECHNACEAE		
* *Sadleria cyatheoides* Kaulf.	+	+
DAVALLIACEAE		
* *Nephrolepis exaltata* (L.) Schott	+	+
POLYPODIACEAE		
* *Pleopeltis thunbergiana* Kaulf.	+	+
PSILOTACEAE		
* *Psilotum nudum* (L.) Griseb.	+	
PTERIDACEAE		
* *Cibotium chamissoi* Kaulf.	d	
* *C. glaucum* (Smith) Hook. et Arn.	+	+
* *Coniogramme pilosa* (Brack.) Hieron.		+
* *Microlepia setosa* (Smith) Alston	+	+
* *Pellaea ternifolia* (Cav.) Link	b	
* *Pteridium aquilinum* (L.) Kuhn		+
* *Pteris cretica* L.	+	+
* *P. excelsa* Gaud.	+	
MONOCOTYLEDONAE		
COMMELINACEAE		
Commelina diffusa Burm.	+	+
CYPERACEAE		
* *Carex macloviana* D'Urv. var. *subfusca* (Boott) Kükenth.	+	+
* *C. wahuensis* C. A. Meyer var. *rubiginosa* R. W. Krauss	+	
Cyperus brevifolius (Rottb.) Hassk.	+	+
* *C. hillebrandii* Boeck.	b	
* *C. polystachyus* Rottb.		+
GRAMINEAE		
Agrostis retrofracta Willd.		+
Anthoxanthum odoratum L.	+	+
Briza minor L.	b	
Bromus commutatus Schrad.	c	
B. rigidus Roth	c	+
B. secalinus L.	b	
B. unioloides (Willd.) H.B.K.	+	+
Cynodon dactylon (L.) Pers.	+	+
Dactylis glomerata L.	+	+
Digitaria pruriens (Trin.) Buese	d	
Festuca dertonensis (All.) Asch. et Graebn.	b	
Holcus lanatus L.	+	
* *Panicum tenuifolium* Hook. et Arn.	b	
Paspalum conjugatum Berg.	+	
P. dilitatum Poir.	+	+
P. urvillei Steud.		+
Poa annua L.	+	
P. pratensis L.		+
Setaria geniculata (Lam.) Beauv.	+	

SPECIES	KIPUKA PUAULU	KIPUKA KI
Sporobolus africanus (Poir.) Robyns et Tournay	+	
Stenotaphrum secundatum (Walt.) Kuntze	b	
Unidentified grass	+	+
IRIDACEAE		
X *Tritonia crocosmaeflora* Lemoine	+	
LILIACEAE		
Cordyline terminalis (L.) Kunth	+	
* *Smilax sandwicensis* Kunth	d	
ZINGIBERACEAE		
Hedychium coronarium Koenig	+	
DICOTYLEDONAE		
AMARANTHACEAE		
* # *Charpentiera obovata* Gaud.	+	a
APOCYNACEAE		
* *Alyxia olivaeformis* Gaud.	+	
* # *Ochrosia sandwicensis* A. Gray	a	
ARALIACEAE		
Brassaia actinophylla F. Muell.	b	
* # *Cheirodendron trigynum* (Gaud.) Heller	+	
CELASTRACEAE		
* # *Perrottetia sandwicensis* A. Gray	+	
COMPOSITAE		
Achillea millefolium L.	b	
Bidens pilosa L.	+	+
Cirsium lanceolatum (L.) Hill.	+	
Erigeron albidus (Willd.) A. Gray	b	
E. canadensis L.	b	
Hypochaeris radicata L.	+	+
Senecio sylvaticus L.		c
Sonchus asper L.	+	+
S. oleraceus L.	c	

SPECIES	KIPUKA PUAULU	KIPUKA KI
CONVOLVULACEAE		
* *Ipomoea indica* (Burm.) Merr.	+	+
CRUCIFERAE		
Lepidium virginicum L.	b	
Sisymbrium officinale (L.) Scop.		b
EPACRIDACEAE		
* *Styphelia tameiameiae* (Cham.) F. Muell.	+	+
EUPHORBIACEAE		
Aleurites moluccana (L.) Willd.	a	
FLACOURTIACEAE		
* # *Xylosma hawaiiensis* Seem. var. *hillebrandii* (Wawra) Sleumer	b	
GENTIANACEAE		
Centaurium umbellatum Gilib.	b	
GERANIACEAE		
Geranium carolinianum L. var. *australe* (Benth.) Fosb.	+	+
HYPERICACEAE		
Hypericum mutilum L.	+	
LABIATAE		
Mentha sp.	+	
LAURACEAE		
Persea americana Mill.	+	
LEGUMINOSAE		
* # *Acacia koa* A. Gray	+	+
Desmodium uncinatum (Jacq.) DC.	+	+
* # *Sophora chrysophylla* (Salisb.) Seem.	+	+
LOBELIACEAE		
* # *Clermontia hawaiiensis* (Hillebr.) Rock	d	
* # *Clermontia* sp.	a	
LORANTHACEAE		
* *Korthalsella complanata* (Van Tiegh.) Engl.	+	
LYTHRACEAE		
Cuphea carthaginensis (Jacq.) Macbride	b	
Lythrum maritimum H. B. K.	+	+

SPECIES	KIPUKA PUAULU	KIPUKA KI
MALVACEAE		
* # *Hibiscadelphus giffardianus* Rock	a	a
* # *H. hualalaiensis* Rock	a	
* # *Kokia rockii* Lewt.	a	
Modiola caroliniana (L.) G. Don	+	+
MENISPERMACEAE		
* *Cocculus ferrandianus* Gaud.	+	
MORACEAE		
Ficus carica L.	b	
MYOPORACEAE		
* # *Myoporum sandwicense* A. Gray var. *fauriei* (Lev.) Kraenzl.	+	+
MYRSINACEAE		
* *Embelia pacifica* Hillebr.	+	
* # *Myrsine lessertiana* A. DC.	+	+
MYRTACEAE		
* # *Metrosideros polymorpha* Gaud.	+	+
Psidium cattleianum Sabine	+	
P. guajava L.		+
NYCTAGINACEAE		
* # *Heimerliodendron brunonianum* (Endl.) Skottsb.	+	a
OLEACEAE		
* # *Osmanthus sandwicensis* (A. Gray) Knobl.	+	+
ONAGRACEAE		
Oenothera stricta Ledeb.		+
OXALIDACEAE		
Oxalis corniculata L.	+	+
PAPAVERACEAE		
* *Argemone glauca* L. ex Pope	b	
PASSIFLORACEAE		
Passiflora ligularis Juss.	+	
PHYTOLACCACEAE		
* *Phytolacca sandwicensis* Endl.		+

SPECIES	KIPUKA PUAULU	KIPUKA KI
PIPERACEAE		
* *Peperomia cookiana* C. DC.	+	+
* *P. hypoleuca* Miq.		+
* *P. leptostachya* Hook. et Arn.	b	
* *P. reflexa* Dietr. var. *reflexa*	c	
* *P. reflexa* Dietr. var. *parvifolia* C. DC.	+	+
PITTOSPORACEAE		
* # *Pittosporum hosmeri* Rock var. *longifolium* Rock	a	
* # *P. hosmeri* Rock var. *saint-johnii* Sherff	a	
PLANTAGINACEAE		
Plantago lanceolata L.	+	+
POLYGONACEAE		
Rumex acetosella L.	+	+
PRIMULACEAE		
Anagallis arvensis L.	c	+
RANUNCULACEAE		
Ranunculus muricatus L.	c	b
RHAMNACEAE		
* # *Alphitonia ponderosa* Hillebr.	a	
ROSACEAE		
Fragaria vesca L. forma *alba* (Ehrh.) Rydb.	+	+
Prunus persica (L.) Batsch	+	c
* *Rubus hawaiiensis* A. Gray	+	
* *R. macraei* A. Gray	d	
R. penetrans L. H. Bailey	+	+
R. rosaefolius Smith	+	+
RUBIACEAE		
* # *Coprosma cymosa* Hillebr.	c	
* # *C. rhynchocarpa* A. Gray	+	+
* # *Gouldia terminalis* (Hook. et Arn.) Hillebr. var. *antiqua* Fosb. forma *antiqua*	c	

SPECIES	KIPUKA PUAULU	KIPUKA KI
* # *G. terminalis* (Hook. et Arn.) Hillebr. var. *antiqua* Fosb. forma *acuta* Fosb.	+	
* # *G. terminalis* (Hook. et Arn.) Hillebr. var. *konaensis* Fosb. forma *konaensis*	b	
* # *Psychotria hawaiiensis* (A. Gray) Fosb. var. *hillebrandii* (Rock) Fosb.	+	+
RUTACEAE		
* # *Fagara dipetala* (Mann) Engl. var. *geminicarpa* (Rock) St. John	+	
* # *F. mauiense* (Mann) Engl. var. *anceps* (Rock) St. John	b	
* # *F. mauiense* (Mann) Engl. var. *anceps* (Rock) St. John forma *petiolulatum* (Rock) St. John	b	
* # *Fagara* sp.	d	
* # *Pelea hawaiiensis* Wawra var. *gaudichaudii* (St. John) Stone	+	
* # *P. puauluensis* St. John	+	
* # *P. zahlbruckneri* Rock	+	
* # *Pelea* sp.	d	
* # *Pelea* sp.	d	
* # *Pelea* sp.	d	
SAPINDACEAE		
* # *Dodonaea viscosa* (L.) Jacq. var. *spathulata* (Sm.) Benth.	+	+
* # *Sapindus saponaria* L.	+	+
SCROPHULARIACEAE		
Linaria canadensis (L.) Dumont	b	
Veronica plebeia R. Br.	+	+
V. serpyllifolia L.	+	
SOLANACEAE		
* # *Nothocestrum breviflorum* A. Gray	b	b
* # *N. longifolium* A. Gray	d	
Physalis peruviana L.	+	+
Solanum pseudocapsicum L.	+	+
THYMELAEACEAE		
* *Wilkstroemia phillyreaefolia* A. Gray	b	
TROPAEOLACEAE		
Tropaeolum majus L.	+	
UMBELLIFERAE		
Hydrocotyle sibthorpioides Lam. var. *oedipoda* Deg. et Greenwell	+	
URTICACEAE		
* # *Pipturus hawaiiensis* Lev.	+	+
* # *Urera sandwicensis* Wedd.	+	
VERBENACEAE		
Verbena litoralis H. B. K.	+	+

REFERENCES

BUCK, P. H. 1953. Explorers of the Pacific. Bernice P. Bishop Museum, Special Publ. 43.

CAIN, S. A., and G. M. DE OLIVEIRA CASTRO. 1959. Manual of Vegetation Analysis. Harper and Brothers, New York. 325 pp.

CLINE, M. G., et al. 1955. Soil Survey of the Territory of Hawaii. Soil Survey Series 1939, No. 25. 644 pp.

EKERN, P. C. 1964. Direct interception of cloud water on Lanaihale, Hawaii. Soil Sci. of Am. Proc. 28(3):419–421.

ELLENBERG, H. 1956. Grundlagen der Vegetationsgliederung. I. Aufgaben und Methoden der Vegetationskunde. Eugen Ulmer Verlag, Stuttgart. 136 pp.

FAGERLUND, G. O., and A. L. MITCHELL. 1944. A check list of the plants, Hawaii National Park, Kilauea–Mauna Loa Section. Natural History Bull. No. 9. Hawaii National Park (mimeographed).

HAWAII NATURAL HISTORY ASSOCIATION. 1961. Kipuka Puaulu, Self-guiding Nature Trail. Hawaii Volcanoes National Park, National Park Service. Unnumbered pamphlet. 10 pp.

KRAJINA, V. J. 1963. Biogeoclimatic zones on the Hawaiian Islands. Newsletter of the Hawaiian Botanical Society 2(7):93–98.

POWERS, H. A. 1948. A chronology of the explosive eruptions of Kilauea. Pacif. Sci. 2(4):278–292.

ROCK, J. F. 1913. The Indigenous Trees of the Hawaiian Islands. Published under patronage, Hawaii. 518 pp.

ROCK, J. F. undated. Kipuka Puaulu near the Volcano of Kilauea, Hawaii. Extract of unpublished manuscript (typescript). Botany Department, University of Hawaii. 5 pp.

SMITH, W. H., and C. D. MOODIE. 1947. Collection and preservation of soil profiles. Soil Sci. 64:61–69.

WENTWORTH, C. K. 1938. Ash Formations on the Island of Hawaii. 3rd Spec. Rept. Hawaii Volcano Observatory. Honolulu. 183 pp.