COMPOSITION OF CERTAIN NATIVE DRY FORESTS: MOKULEIA, OAHU, T.H.

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INTRODUCTION

The richness in tree species of Hawaiian dry forests has attracted the attention of many botanists. Rock (1913) thought it possible to collect more species in dry forests in a single day than in "a week or two" in the rainforests. Selling (1948) stated: "More than half of the many species of trees in these islands belong to this dry forest." He thought, however, that dry forests had mostly disappeared from Oahu, Kauai, Molokai, and West Maui, and that only scattered remnants remained elsewhere. The recent studies of Hosaka (1937) and Egler (1939, 1942, 1947) tended to support this view. Nevertheless, scattered references to "botanical bananzas" in remote areas of Oahu exist in the literature. Thus Judd (1931) reported: "An interesting mine of 42 different species of Hawaiian trees was discovered in a small gulch in Makua Valley, on Oahu." His mention of "Mehamehame" (*Drypetes phyllanthoides* (Rock) Sherff) and "Kalamona" (*Cassia gaudichaudii* Hook. & Arn.) trees leaves little doubt that he was dealing with a dry forest.

In the spring and summer of 1950 the writer accompanied Miss Amy Greenwell, of Captain Cook, Hawaii, and Mr. Otto Degener, of Waialua, Oahu, on several plant-collecting excursions in the Mokuleia region of Oahu, during which many forests rich in reputedly rare, dryland tree species were discovered. The purpose of this paper is to describe certain of these seasonal forests and to mention certain features of the autecology of the more noteworthy species, for it is my opinion that, in addition to the intrinsic interest of these plants, they may have considerable potential importance in the management of Hawaiian watersheds.

ACKNOWLEDGMENTS

The writer wishes to thank Dr. Frank E. Egler, Dr. F. R. Fosberg, Dr. Charles E. Olmsted, and Mr. Otto Degener, who have read portions of the manuscript and offered many helpful suggestions. C. K. Stidd, of the Pineapple Research Institute, Honolulu, has furnished much meteorological data and offered valuable manuscript criticisms. Dr. G. Donald Sherman, of the University of Hawaii Agricultural Experiment Station, very kindly identified soil samples collected by the author. Miss Marie C. Neal and Col. E. H. Bryan, of the staff of the Bernice P. Bishop Museum, Honolulu, have aided me in many ways, especially in the identification of plant specimens. Dr. Earl E. Sherff, Dr. Harold St. John, and Dr. Fosberg have identified many plant specimens belonging to Hawaiian genera in which they have specialized. H. A. Miller and G. Kikudome, of the University of Hawaii, have been pleasant field companions. Mr. Miller collected and determined many moss specimens, while Mr. Kikudome aided in one of the stem counts. I am particularly indebted to Mr. Otto Degener, author of "Flora Hawaiiensis," at whose Mokuleia beach house I was a guest during these investigations. Mr. Degener has an unexcelled knowledge of Hawaiian plants in the field, and he has been most generous in his encouragement, suggestions, and criticisms.

PLACE NAMES

Mokuleia, as defined for the purposes of this study, includes the north-facing side of the Waianae Range of Oahu, from the main crest to the ocean, and extends from East Makaleha Valley to Kealia (Figs. 1 & 2). Other place names used are those of Welch (1938); no new ones are proposed. Elevations and coordinates were taken from U. S. War Department map of Oahu, 1/20,000, 1943.

PLANT NAMES

A list of species found in the Mokuleia dry forests, giving the Latin binomial and the author of the name,

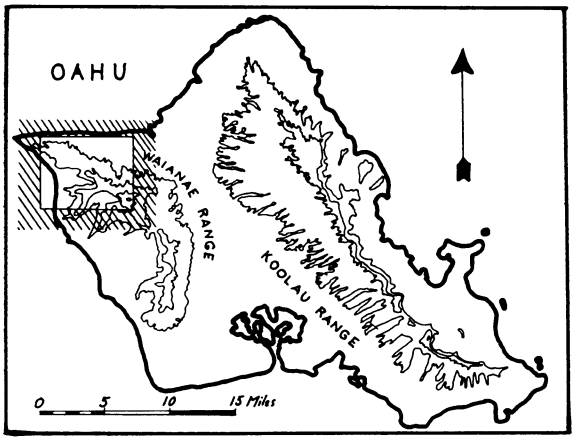

FIG. 1. Island of Oahu, T. H., showing Waianae and Koolau ranges. Contour interval is 1000 feet. Indicated rectangle, shown in detail in Fig. 2, includes area studied.

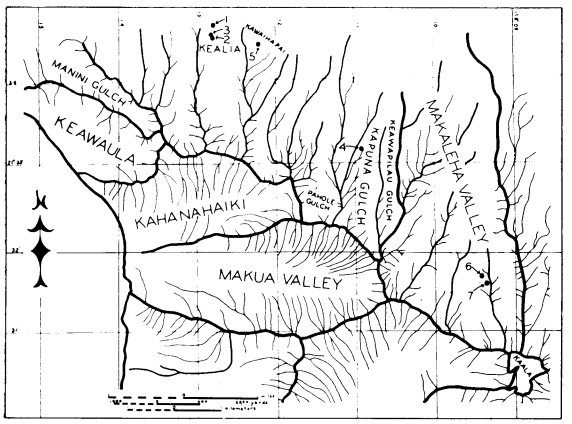

FIG. 2. Mokuleia and adjacent valleys. The solid lines indicate ridges. Numbered dots locate positions of quadrats (cf. Table 2). The elevation of Mt. Kaala, in the southeast corner of the map, is 4,025 feet.

is attached to the end of this paper. No attempt was made thoroughly to collect the flora of the Mokuleia region, and this list is therefore not intended as a check list of that area. Certain species found in these forests, however, appear to be rare or otherwise noteworthy; these have been cited by collection number and place of deposit of specimens.

GENERAL VEGETATIONAL AND ENVIRONMENTAL CONDITIONS

TOPOGRAPHY AND ENDEMISM

The Mokuleia section of the Waianae Range is highly dissected into a series of high ridges and deep valleys ("gulches"), the slopes of the ridges being usually very steep. Plant migration from gulch bottom to gulch bottom or from ridge top to ridge top thus meets with marked topographic barriers, and it is not surprising that local endemism is intense in the Mokuleia flora. Moreover, many, if not most native vegetation types in the Mokuleia region could be considered peculiar to a single gulch, if narrowly interpreted, since trees which are important dominants in certain areas are entirely lacking in others. For example, *Pritchardia kaalae* and *Euphorbia forbesii* in Mokuleia are endemic to a very small area near the head of East Branch of East Makaleha Valley, where they are locally dominant. The possibility that certain other widespread dominants, such as *Sapindus oahuensis,* may exist in several local physiological races, varying significantly in shade tolerance, for example, must also be taken into account.

These considerations lead to obvious difficulties in the classification and naming of forest types. For example, it seems impossible to name the seasonally dry forests of Mokuleia for their dominants—the customary procedure in work in higher latitudes—because the dominants are by no means consistent from valley to valley, or even in different patches of forest within the same valley. The naming of forests for dominants would thus lead to an inordinate number of kinds of forest, each represented by a small number of stands, a treatment which, in the opinion of the author, could hardly be considered conservative. An attempt is made here to give a broad and relatively comprehensive treatment of the native dry forests of Mokuleia. Further field study, however, may make the recognition of subordinate units desirable.

ZONATION AND FOREST TYPES

The seasonally dry forests considered here may be assigned to the "Lower Forest Zone" of Rock (1913). At slightly higher elevations, where much wetter conditions prevail, occurs Rock's "Middle Forest Zone." Here the characteristic vegetation is the montane rainforest, which, in great contrast to the mixed forests of the Lower Forest Zone, is almost always dominated by a single species of tree, *Metrosideros polymorpha.* Montane rainforest, however, is more easily distinguished from the seasonally dry forests by the physiognomy of its ground layer. No contrast could be more striking than the nearly bare ground surface of the seasonally dry forests and the dense undergrowth of the rainforests, with their profusion of ferns, mosses, and shrubs covering the ground. Where the terrain permits, one walks with ease through most seasonally dry forests, while it is often impossible to force oneself through dense rainforest without first clearing a trail.

Below the Lower Forest Zone occurs the "Lowland Zone" of Rock, which was apparently at one time covered with a grassland dominated by *Heteropogon contortus* (L.) Beauv.; perhaps in some places native trees occurred in scattered fashion. This arid country has long since been covered with a vegetation composed largely of species introduced since the discovery of the Hawaiian Islands by Cook, notably *Prosopis chilensis* (Molina) Stuntz and *Leucaena glauca* (Egler 1947). No obvious physiognomic distinction between the Lower Forest Zone and the Lowland Zone still exists, since by the introduction of alien species the latter has been converted from grassland or savanna into closed forest. Indeed, it appears that these introduced species in some places have so modified the

habitats which they have occupied that several native trees of the Lower Forest Zone, finding the new conditions favorable for their growth and development, are actively invading the former Lowland Zone. Consequently, the former marked floristic differences between Lower Forest and Lowland Zones may also be expected to break down. The situation is certainly not yet stable, and it seems premature to suggest any characters by which the two zones of Rock may consistently be distinguished. In fact, Hosaka (1937) and Egler (1939) have judged it necessary to introduce an entirely new scheme of vegetational zonation, based largely on plant communities composed predominantly of exotic species.

This study is concerned only with slope forests composed chiefly of native species (Fig. 3). The steep slopes of the valleys of Mokuleia are covered with a vegetation which differs markedly in flora and physiognomy from that of the ridges and gulch bottoms. Gulch bottoms of the Lower Forest Zone are almost everywhere dominated by the "Kukui" (Candlenut tree), *Aleurites moluccana,* which usually occurs in pure stands. Windswept ridges are often covered with an open vegetation of stunted trees of *Metrosideros polymorpha,* here associated with *Dodonaea eriocarpa* and *Styphelia tameiameiae.*

Two slope forest cover-types are recognized in the Lower Forest Zone of Mokuleia: Evergreen Seasonal Forest and Semi-deciduous Seasonal Forest. Certain stands of these slope forests may be remnants of the original dry forest which once covered much of the Lower Forest Zone of Oahu. In places accessible in the past to feral grazing animals, this vegetation has been largely destroyed, and indeed some species of its flora are apparently extinct. It is only on steep slopes that one can hope to find relatively undisturbed native vegetation in this zone. Gulch bottoms and the tops of secondary ridges form natural routes of travel from the lowlands to the main crests of the mountain ranges, and their vegetation has accordingly suffered severely.

The following key will serve to distinguish the two chief native slope cover-types recognized:

1. Canopy usually somewhat open; trees never more than 50 feet and usually less than 30 feet tall; certain species summer-deciduous; *Lantana* usually abundant; dominants: *Sapindus, Erythrina, Diospyros sandwicensis, Rauvolfia, Osmanthus,* or variously mixed.....1. Semi-deciduous Seasonal Forest.

1. Canopy usually closed, although a few of the taller species may project far above the closed layer; certain species to 70 or more feet tall, and most over 30 feet in height; all species evergreen; *Lantana* usually not abundant; dominants: *Diospyros sandwicensis, Drypetes, Acacia, Syzygium, Metrosideros, Pterotropia,* or variously mixed.....2. Evergreen Seasonal Forest.

PRECIPITATION

Stidd & Leopold (MS) have made the interesting empirical discovery that, where adequate data are available (as in the Koolau range of Oahu), isohyets tend to be logarithmically spaced around the main mountain masses of the Hawaiian Islands. Thus, if each value of a series of isohyets is a constant multiple of the next lower, the isohyets will tend to be equally spaced. Extrapolating these observations to certain areas where very few data are available, Stidd (1950) has been able to draw a mean annual rainfall map of Oahu, which is reproduced here. (Fig. 4). The Mokuleia values are still rather uncertain, since, although Waialua precipitation values are well known, long-term observations on the summit of Mt. Kaala, the rainiest place in our area, are lacking. Moreover, abrupt variations in rainfall over very short horizontal distances are commonplace in Hawaii (cf. Leopold & Stidd 1949). Consequently, estimates of rain-

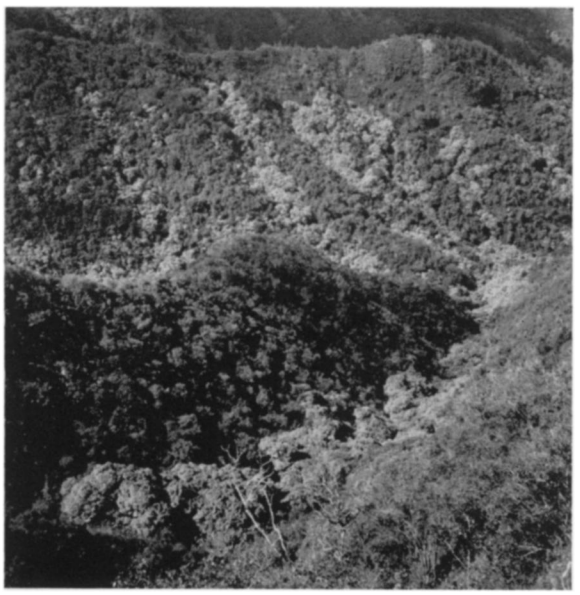

FIG. 3. Vegetation of the Lower Forest Zone in East Makaleha Valley. 43 species of native trees were found in the small gulch in the foreground. The light-colored foliage in the gulch bottoms is that of *Aleurites moluccana.*

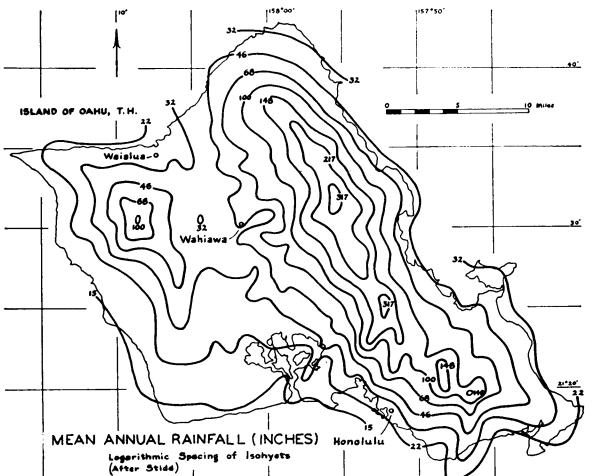

FIG. 4. Mean annual rainfall map of Oahu (after Stidd). Note that a place receiving over 300 inches of rainfall annually is located only 7 miles from the 15-inch isohyet.

fall received by certain of these forests are not considered very accurate. Median monthly rainfall estimates, derived from an earlier publication of Halstead & Leopold (1948), are mentioned below. These are also to be considered the best available at present, but certainly subject to revision.

The forests here considered occur in regions subject to marked seasonal drought, as shown in Table 1, in strong contrast to the montane rainforest of higher elevations, the precipitation of which is nearly evenly distributed throughout the year. The dry season generally occurs from May through October, and reaches its height in June or July.

TABLE 1. Drought and Precipitation Data.

Forest Type	Number of Dry Months*	Mean Annual Rainfall (inches)
I. Semi-deciduous seasonal		
1. Kawaihapai.....	12	30
2. Kapuna Gulch.....	7	40
3. Makaleha Valley.....	4	65
II. Evergreen Seasonal		
1. Makaleha Valley.....	4	75

*A "dry month" is defined for the purposes of this study as one receiving less than 4 inches of rainfall. Data from Halstead & Leopold (1948).

SOILS

Dr. G. Donald Sherman, of the University of Hawaii Agricultural Experiment Station, has very kindly analyzed soil samples collected by the author in both forest types. He considered the soils immature stages of the Humic Latosol (Cline, *et al* MS). This great soil group, which develops under an annual rainfall of from 50 to 150 inches, is characterized by a low silica-sesquioxide ratio, an organic matter content of 10-15%, a very low base saturation, but a high cation exchange capacity (cf. Matsusaka & Sherman 1950). The Humic Latosols are clay soils possessing a granular structure which is highly waterstable.

DESCRIPTIONS OF FOREST TYPES

To amplify the verbal descriptions which follow, sample plot data were obtained in certain carefully selected stands of native forest. It must be emphasized that these plots were not random samples of the Mokuleia vegetation and therefore cannot be considered average in any statistical sense. In the opinion of the author, random samples are of value in the study of large areas covered by approximately uniform types of vegetation. It would seem difficult, however, to apply random methods to the vegetation considered here, for it consists mostly of isolated patches of forest which are rare in distribution and small in area.

TABLE 2. Location of Quadrats.

Quadrat Number	Vegetation type	Place	Latitude	Longitude	Elevation
1.	Secondary succession	Kealia	21° 34.62′N	158 12.78′W	260 feet
2.	Secondary succession	Kealia	34.47′	12.76′	1020
3.	Secondary succession	Kealia	34.49′	12.82′	940
4.	Semi-deciduous forest	Kapuna Gulch	33.16′	10.96′	1180
5.	Semi-deciduous forest	Kawai-hapai	34.40′	12.23′	300
6.	Semi-deciduous forest	Makaleha Valley	31.76′	9.48′	1280
7.	Evergreen forest	Makaleha Valley	31.59′	9.40′	1820

To enable future workers readily to examine the sites of the quadrats, Table 2, giving the precise location of each plot, is presented.

SEMI-DECIDUOUS SEASONAL FOREST

Forests composed of large numbers of native dryland tree species in which no single species can be said consistently to dominate the vegetation occur in East Makaleha Valley and Kapuna Gulch at elevations of 1100 to 1500 feet. Over thirty species of native trees occur in these semi-deciduous forests, but many are very rare in Mokuleia or have very local distributions. Consequently, the composition of this mixed forest varies considerably from place to place. Although a few species, such as *Erythrina sandwicensis, Dracaena aurea, Sapindus oahuensis, Reynoldsia sandwicensis,* and *Canthium odoratum,* are relatively constant and impart a certain homogeneity to an otherwise floristically and physiognomically heterogeneous group of stands, the outstanding floristic characteristic of well developed semi-deciduous forest is the occurrence together in relatively small areas of many species of trees, most of which are rare. Indeed, many, if not most of the rare tree species found in semi-deciduous forest appear to be virtually restricted to such "bonanzas." It seems possible that they require primeval forest conditions for proper development.

The species of trees comprising semi-deciduous forest are in general small, seldom exceeding 30 feet in height. One of the most common trees, *Canthium odoratum,* has a stem diameter rarely greater than 4 inches and is generally only 12 to 15 feet tall. Some individuals, indeed, can best be described as giant shrubs. A single tree of *Osmanthus sandwicensis,* for example, may consist of as many as ten stems, each over 2 inches in diameter at breast height (d.b.h.), originating from a common base at ground level. Nor are these small trees closely spaced; the canopy is usually somewhat open, although in no sense could this forest be considered parkland or savanna. Locally one of the larger species may occur in large numbers and dominate the vegetation. Osmanthus, Erythrina, Sapindus, *Rauvolfia sandwicensis,* and *Diospyros sandwicensis* in such cases may form closed communities. Perhaps the sandalwood (*Santalum freycinetianum*) groves mentioned by early explorers (cf. St. John 1947) were another example of single-species dominance. From a distance semi-deciduous forest presents a somewhat somber aspect of gray-green, roundish crowns, in which the light-green leaves of *Reynoldsia sandwicensis* and *Bobea sandwicensis* are easily distinguished. Occasionally the tops of trees of *Hibiscus arnottianus* and *Ery-*

thrina sandwicensis may be covered with large bright flowers; in such cases one can identify these trees at a distance of nearly a mile. Although these forests experience a pronounced dry season, only Erythrina and Reynoldsia (Fig. 5) are deciduous,* and the white trunks and branches of the latter are then very conspicuous in the forest.

FIG. 5. Semi-deciduous forest at Kawaihapai. Showing summer-deciduous habit of *Reynoldsia sandwicensis.*

Possibly because of the relatively open nature of these forests, certain somewhat shade-intolerant exotic species are common, but usually not dominant, in apparently undisturbed semi-deciduous forest. Thus the Java plum, *Syzygium cumini,* is thoroughly at home here, being a nearly constant associate of the rare native trees, *Mezoneuron kavaiensis* and *Colubrina oppositifolia. Lantana camara,* a noxious prickly weed, is the most common member of the shrubby layer of the forest and in open places usually occurs in pure stands. *Leucaena glauca, Schinus terebinthefolius,* and *Psidium guayava* are occasional.

The ground in these forests is essentially bare. Occasional individuals of *Carex brunnea, Doryopteris decipiens* and *Peperomia leptostachya* occur, often on bare rock, but tree seedlings make up by far the largest proportion of the ground layer. The tough lianas, *Breweria menziesii* and *Canavalia galeata,* are occasional annoying impediments to the explorer, but the weak-stemmed *Cocculus ferrandianus* is comparatively innocuous in this respect.

Semi-deciduous forest in which *Sapindus oahuensis* emerges into dominance is physiognomically rather distinct from the more open mixed phase described above. Sapindus forest in Kapuna Gulch (Fig. 6), for example, is characterized by a closed canopy 40 or more feet above the ground, and by an understory of Sapindus saplings, *Ochrosia sandwicensis, Nototrichium viride,* and *Leucaena glauca.* Lantana occurs only occasionally. The dominant trees—Sapin-

* The species of *Kokia* native to Oahu was probably summer-deciduous, but it is now apparently extinct. The closely related *K. drynarioides,* which grows in the semi-deciduous forests of PuuWaawaa, Hawaii, is summer-deciduous.

TABLE 3. Quadrat no. 6. Semi-deciduous seasonal forest. West branch of East Makaleha Valley. Area of quadrat: 400 square meters. Trees over 1 inch d.b.h.

Species	Diameter Classes (inches)												Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9	over 9.9	Total	Percent	Total	Percent
Canthium odoratum	66	9	2	1							78	53.79	1.28	16.44
Diospyros sandwicensis	14	3	1			3	1				22	15.17	1.23	15.91
Reynoldsia sandwicensis	1									1	2	1.38	1.22	15.70
Syzygium cumini	4	5	1	1	3						14	9.66	0.93	11.89
Colubrina oppositifolia										1	1	0.69	0.71	9.12
Osmanthus sandwicensis							1	1			2	1.38	0.64	8.22
Diospyros hillebrandii	5	3	2			1					11	7.59	0.47	6.04
Erythrina sandwicensis								1			1	0.69	0.42	5.37
Dracaena aurea	1		1			1					3	2.07	0.34	4.33
Jossinia reinwardtiana		1				1					2	1.38	0.24	3.06
Mezoneuron kavaiensis	3	2	1								6	4.14	0.21	2.66
Ochrosia sandwicensis	2			1							3	2.07	0.18	1.38
Total	96	23	8	3	3	6	2	2	..	2	145	100.01	7.87	100.12

dus, Reynoldsia, Dracaena, Osmanthus, and Erythrina —attain a greater size than in the more typical mixed phase of semi-deciduous forest. One Sapindus tree in Kapuna Gulch, for example, was 45 feet tall and 28 inches d.b.h. Except for tree seedlings and occasional ferns and carices, the ground layer is again virtually barren.

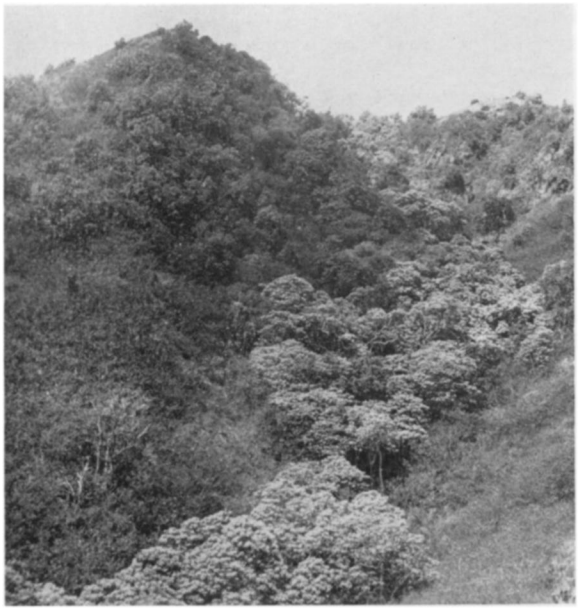

FIG. 6. Semi-deciduous seasonal forest in Kapuna Gulch. 21 species of native trees were counted in this unpromising-looking place, growing on the slopes of the hill in the left center. The prominent light-colored foliage is that of *Aleurites moluccana*, which is predominant in the bottom of the gulch. The adjacent scrub consists of thickets of *Leucaena glauca* and *Lantana camara*.

An interesting phase of Sapindus-dominated semi-deciduous forest occurs on talus below the cliffs of Kawaihapai (Fig 7). The forest here is composed essentially of only two species, *Sapindus oahuensis* and *Reynoldsia sandwicensis*, which here attain their greatest size on Oahu. One Sapindus tree (Fig. 8) was 50 feet tall and 40 inches d.b.h.; Reynoldsia reaches a height of 44 feet and a d.b.h. of 25 inches. The forest is characterized by an open canopy and an almost park-like appearance and, where best developed, consists of virtually only one layer. Occasional plants of *Peperomia leptostachya, Doryopteris decipiens,* and *Plumbago zeylanica* grow on the large angular boulders that are the substrate of this forest, and Sapindus seedlings are common. Other characteristic trees of semi-deciduous forest, such as Erythrina, Rauvolfia, Dracaena, Canthium, Osmanthus, and *Myoporum sandwicense,* are practically restricted to small ledges on the cliffs overlooking the talus slopes. Large openings in the forest, apparently caused by rock slides, are dominated by Lantana or Leucaena. *Aleurites moluccana* occurs commonly along muddy rivulets issuing from small springs at the base of the cliffs above.

There is thus evident much physiognomic heterogeneity among the semi-deciduous forest stands studied. Correlated with this are striking differences in precipitation values (see Table 1). In general, forests dominated by *Sapindus oahuensis* are drier than the more open mixed phase. Thus, in spite of the essential floristic homogeneity of the Mokuleia semi-deciduous forests, there exists some justification for naming more than one type. If more relatively undisturbed forests were available for study in the Mokuleia region, such a procedure might be conservative, but to do so at present would be to describe in-

TABLE 4. Quadrat no. 4. Semi-deciduous seasonal forest. Kapuna Gulch. Area of quadrat: 400 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)											Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–4.9	5.0–6.9	7.0–8.9	9.0–10.9	11.0–12.9	13.0–14.9	over 14.9	Total	Percent	Total	Percent
Sapindus oahuensis	1	1		3	1	3	3		1	13	17.1	9.20	52.34
Dracaena aurea			3	2	3		1	1		10	13.2	3.52	20.04
Osmanthus sandwicensis					2		1		1	4	5.3	2.81	15.98
Erythrina sandwicensis							1			1	1.3	0.75	4.29
Leucaena glauca	21	11	2							34	44.7	0.75	4.26
Syzygium cumini	6	1			1					8	10.5	0.40	2.31
Charpentiera ovata		2								2	2.6	0.07	0.42
Neraudia angulata	1	1								2	2.6	0.04	0.25
Nototrichium viride	1									1	1.3	0.02	0.10
Reynoldsia sandwicensis	1									1	1.3	0.01	0.03
Total	31	16	5	5	7	3	6	1	2	76	99.9	17.57	100.02

FIG. 7. Semi-deciduous seasonal forest on the talus slopes of Kawaihapai. In the center and right are trees of *Reynoldsia sandwicensis,* bare of leaves during the summer dry season.

FIG. 8. Semi-deciduous forest. The largest known tree of *Sapindus oahuensis* (50 ft. tall and 40 in. d.b.h.), growing on the arid talus slopes of Kawaihapai.

dividual stands in isolated places as representatives of types possibly much more widespread in the past. It seems quite possible, on the other hand, that in a forest composed of many species of trees, certain components should emerge into dominance in relatively wetter areas and others, such as Sapindus and Erythrina, in relatively drier areas. Associated species, except for local endemics, are nearly constant throughout semi-deciduous forest and probably constitute the best index of its homogeneity.

Well developed semi-deciduous forest is at present restricted to the steep slopes of small gulches and to talus slopes covered with coarse boulders. The angle of slope in these places commonly exceeds 30 degrees, and consequently it is not surprising that soils are seldom more than 3 inches deep. In the laboratory water runs through these clay soils as if through coarse sand, and the result is that, because of the steep slopes and the excessive internal drainage of these soils, the ground is usually very dry in summer, although never dusty. Another consequence of the difficult terrain upon which these forests are found is that it is nearly impossible for the explorer to walk or even to stand upright in most of these places without supporting himself against tree stems. Avalanching is probably not uncommon; particularly devastating landslides may be the cause in some cases of destruction of native forest and subsequent replacement of it by pure stands of Lantana or Leucaena.

EVERGREEN SEASONAL FOREST

In Mokuleia forests dominated by *Diospyros sandwicensis* occur at elevations of from 1500 to 1800 feet. Greater size of trees, closed canopy, and differences in floristic composition are the chief characters distinguishing this evergreen forest from the drier semi-deciduous forest occurring at lower elevations. *Myrsine lessertiana* and *Bobea elatior,* for example, are rainforest elements which are common in evergreen seasonal forest but not found in semi-deciduous forest, while such strictly dryland trees as *Nesoluma polynesicum, Colubrina oppositifolia, Mezoneuron kavaiensis, Bobea sandwicensis,* and *Erythrina sandwicensis* do not occur in evergreen forest. In addition, several dominant tree species are restricted to evergreen forest. Among these are *Alectryon macrococcus, Pteralyxia macrocarpa, Drypetes phyllanthoides,* and *Straussia (Psychotria) oncocarpa.*

The physiognomy of evergreen seasonal forest in

TABLE 5. Quadrat no. 5. Semi-deciduous seasonal forest. Kawaihapai. Area of quadrat: 1000 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)											Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–5.9	6.0–8.9	9.0–11.9	12.0–14.9	15.0–17.9	18.0–20.9	over 20.9	Total	Percent	Total	Percent
Sapindus oahuensis	16	2	4	3	6	8	8	3	2	52	92.85	35.40	87.90
Reynoldsia sandwicensis					2		1	1		4	7.15	4.87	12.10
Total	16	2	4	3	8	8	9	4	2	56	100.00	40.27	100.00

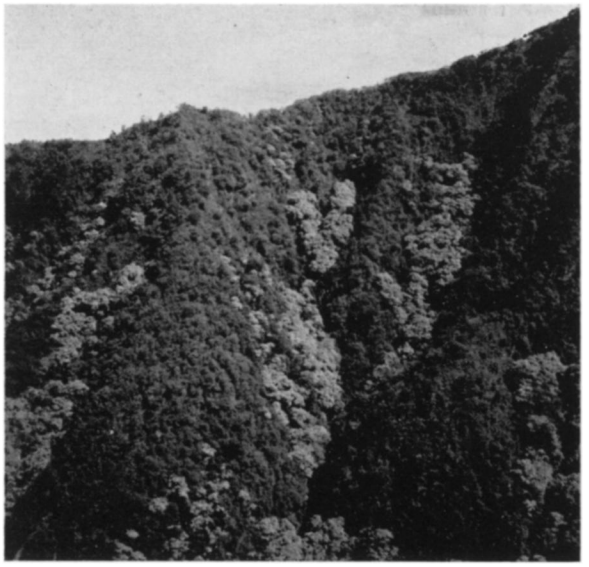

FIG. 9. Evergreen seasonal forests in East Makaleha Valley. Note the precipitous slopes on which these forests occur. The light-colored vegetation consists of trees of *Aleurites moluccana,* mostly restricted to gulch bottoms.

Mokuleia is somewhat variable. In many places the trees are of nearly uniform size and appearance. Viewed from above, as from a point of vantage on a ridge (Fig. 9), such forests present a rather somber, monotonous aspect. The grayish-green crowns of the predominant species, *Diospyros sandwicensis,* extend in seemingly endless fashion, being overtopped only occasionally by the brightly flowering trees of *Metrosideros polymorpha* or by the sharply contrasting light-green crowns of *Tetraplasandra kaalae.* The canopy in such cases is completely closed, so that tree trunks are invisible from outside.

In places where certain larger trees occur, however, the aspect of evergreen forest is strikingly different. In such cases gigantic individuals of the rare tree, *Drypetes phyllanthoides* (Fig. 10), may project far above the closed canopy of smaller trees. In Keawapilau Gulch huge trees of *Syzygium* sp. behave in much the same fashion. Elsewhere the handsome crowns of *Pterotropia* sp. or *Acacia koa* may overtop their smaller neighbors. Thus the physiognomy of evergreen forest is determined by the geographical distribution of the members of its dominant flora, and certain of these species are very rare or local.

The interiors of evergreen forest are, however, much the same from place to place. Ground cover is exceedingly sparse; only occasional clumps of carices and ferns obscure the shallow black clay soil and outcropping basaltic rock. Vines are not uncommon, especially *Alyxia oliviformis* and *Canavalia galeata.* A very striking plant is the ropy liana, *Strongylodon lucidus,* the brilliant flowers of which sometimes festoon the tops of the larger trees. Except for the bird's nest fern, *Asplenium nidus,* conspicuous epiphytes are not common. The canopy of evergreen

FIG. 10. Evergreen seasonal forest. A young tree of *Drypetes phyllanthoides* 50 ft. tall and 25 in. d.b.h. Dead trunks of this species over 4 ft. in diameter abound in the gulches of Makaleha Valley.

forest is usually at a height of about 35 feet, and since it is completely closed, very little light reaches the forest floor. Thus the interiors of evergreen forest present a somber aspect. Indeed, there is little color other than the dark-green canopy overhead, the black soil underfoot, and the many erect black and brown trunks of the smaller trees.

Yet evergreen seasonal forests are of exceptional floristic interest, for they often harbor a great many rare plants. Thus, members of three genera rare and endemic in the Hawaiian Islands (*Isodendrion, Neraudia, Diellia*) were collected in a single 1000-square-meter quadrat (No. 7), and thirty-three species of native trees were found within a radius of 150 yards of the center of this plot. In other places, however, evergreen forests may consist of nearly pure stands of *Diospyros sandwicensis* and consequently are of little interest to the plant collector.

DEVELOPMENTAL TENDENCIES

Egler (1942) has well described the pessimistic attitude of many contemporary botanists in the Hawaiian Islands with respect to the status of native forest. It is still a common opinion that native forest, if once destroyed, is unable to replace the alien weedy species that invade nearly all newly opened land surfaces. Egler found, on the contrary, that "the evidence strongly favors the view that most aliens will be destroyed by the indigenes, such aliens surviving only in greatly reduced numbers and as very sub-

TABLE 6. Quadrat no. 7. Evergreen seasonal forest. West branch of East Makaleha Valley. Area of quadrat: 1000 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)													Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9	10.0–10.9	over 10.9	Total	Percent	Total	Percent
Diospyros sandwicensis	11	31	17	27	10	7	9	4	2	3	1	122	45.87	13.19	40.42
Metrosideros polymorpha		2		1			2	3	1		5	14	5.27	7.72	23.62
Straussia oncocarpa	4	9	4	7	6	2	3	1				36	13.55	3.25	9.97
Pisonia umbellifera		1	2	1		1			2	2	1	10	3.76	3.23	9.89
Canthium odoratum	10	17	3	3	1	1						35	13.15	1.15	3.52
Pouteria sandwicensis							1			1		2	0.75	0.83	2.54
Tetraplasandra kaalae	1						1		1			3	1.13	0.75	2.29
Myrsine lessertiana	3	6	1		2	1						13	4.90	0.75	2.29
Santalum freycinetianum						1			1			2	0.75	0.64	1.98
Bobea elatior			2	2	1							5	1.88	0.47	1.45
Osmanthus sandwicensis	1	4	2									7	2.64	0.18	0.55
Xylosma hawaiiensis	1				1							2	0.75	0.17	0.51
Dracaena aurea	3			1								4	1.50	0.09	0.27
Dodonaea sandwicensis	1	2										3	1.13	0.06	0.18
Jossinia reinwardtiana		2										2	0.75	0.04	0.12
Charpentiera ovata		2										2	0.75	0.04	0.11
Pelea wawraeana			1									1	0.38	0.04	0.11
Rauvolfia sandwicensis			1									1	0.38	0.04	0.11
Syzygium cumini	1	1										2	0.75	0.02	0.07
Total	36	77	33	42	21	13	16	8	7	6	7	266	100.04	32.66	99.96

ordinate members of the resulting ecosystem." He thought that many native species were very shade-tolerant "climax" forms, ill fit directly to colonize barren, wind-swept and sun-baked slopes, but well adapted to grow in the shade of alien "nurse crops," such as mature stands of *Leucaena glauca* or *Psidium* sp.* This suggested that it should be possible to find cases of secondary succession leading from stands of alien species back to native forest.

My field observations repeatedly confirmed Egler's hypothesis. Because his views on this matter have not been generally accepted in Hawaii and because, if true, they could be of importance in the proper management of seasonally dry vegetation in the Hawaiian Islands, I undertook three minor quadrat studies in places where native woody species appeared to be replacing aliens. Of course, the fact that native species, such as *Sapindus oahuensis, Erythrina sandwicensis, Canthium odoratum, Dracaena aurea,* and *Reynoldsia sandwicensis,* appear to be replacing aliens in a few carefully selected plots by no means implies that the same process is taking place to the same degree throughout the Mokuleia region. It is not. The plots do suggest, however, that under certain conditions native forest can "come back." Furthermore, there seems to be little if any evidence that alien species are actively displacing rare endemics in the well developed native forests described above. Thus, in my opinion, there is little doubt that native seasonal forest represents a later stage of development than the scrub of Leucaena, *Psidium guayava,* and Lantana which covers so many of the dry forehills of Oahu.

Quadrat No. 1 (Table 7), located on an arid talus slope near Kawaihapai, suggests the fate of many stands of *Leucaena glauca* when seed trees of certain larger native species are nearby. A middle-aged thicket of Leucaena, the average height of which was 15 feet (maximum: 19 ft.; minimum: 10 ft.), had

* Dr. Fosberg informs me that he no longer is of the opinion that *Psidium littorale* Raddi var. *lucidum* (Hort.) Fosb. is the correct name for the common "Waiawi" guava. He thinks it may be a variety of *P. catteianum,* the "strawberry" guava, which is only a small shrub, while the "Waiawi" is a large tree. The two p'ants differ further in color, size, shape, and taste of fruit.

been invaded by Sapindus, Reynoldsia, Erythrina, and Canthium. The average height of the invading species was 9 feet, the largest sapling (Sapindus) being 12 feet tall. All appeared vigorous. A small grove of 30-foot Sapindus trees stood less than 50 yards away and had not been invaded by Leucaena. It seems likely that the native species will soon overtop the alien Leucaena in this place. Succession would then lead back to a stand similar to the nearby Sapindus-Reynoldsia phase of semi-deciduous seasonal forest of Kawaihapai, described above.

A second quadrat (Table 8) was laid out near the summit of the Kealia cliffs in a thicket of *Lantana camara* and *Tricholaena repens* (Willd.) Hitchc. This arid, windswept locality was being invaded *en masse* by the small indigenous tree *Canthium odoratum* (Fig. 11). The data of this plot indicate that replacement of Lantana-Tricholaena scrub by a mixed forest of several species will be chiefly a question of time and availability of seeds.

A third plot (Table 9), illustrates the ability of *Erythrina sandwicensis* to effect mass invasion of Tricholaena grassland, providing a few seed trees are present. The stand is at present very dense, and during the wet season very little light penetrates the canopy (Erythrina is summer-deciduous). From this and other centers on the Kealia trail seeds of Erythrina and other native dryland trees are rolling down the steep hillsides. Numerous young individuals of these species are at present appearing in open Tricholaena grassland and under Leucaena, and eventual reestablishment of semi-deciduous forest in which native species will predominate appears certain.

TABLE 7. Quadrat no. 1. Kealia. Area of quadrat: 30 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)				Basal Area (sq. ft.)
	1.0–1.5	1.6–2.0	2.1–2.6	Total	
Leucaena glauca	9	17	5	31	0.501
Sapindus oahuensis	4	4		8	0.084
Reynoldsia sandwicensis		1		1	0.015
Total	13	22	5	40	0.609

TABLE 8. Quadrat no. 2. Kealia. Area: 1000 square meters.

Species	Individuals
Canthium odoratum	149
Leucaena glauca	12
Psidium guayava	2
Erythrina sandwicensis	1
Dodonaea eriocarpa	1

FIG. 11. *Canthium odoratum* invading a thicket of *Lantana camara* and *Tricholaena repens*. Kealia trail, looking north toward the Pacific Ocean.

TABLE 9. Quadrat no. 3. Kealia. Area: 200 square meters. Trees over 1 inch d.b.h.

Species	Diameter Classes (inches)						Basal Area (sq. ft.)
	1.0–2.9	3.0–4.9	5.0–6.9	7.0–8.9	over 8.9	Total	
Erythrina sandwicensis	31	22	15	3	4	75	10.48
Canthium odoratum	7			2		9	0.95
Total	38	22	15	5	4	84	11.43

Indeed, Erythrina appears likely to become a pasture weed of some importance in certain Mokuleia localities. On the northwest slope of Keawapilau Gulch a pure stand of vigorous young trees is located in the middle of an over-aged stand of Leucaena in a cattle pasture near the forest reserve line. It appears that Leucaena has been overtopped and eliminated by Erythrina. Since Leucaena is generally regarded as a valuable wild forage crop, while Erythrina appears unpalatable to stock, the aggressiveness of the latter species may become a matter of concern to ranchers. At present, however, the tree is rather local in its distribution.

Similar situations obtain in the moister evergreen belt. In these places it is possible to find nearly pure stands of *Acacia koa* or *Metrosideros polymorpha*, the ground cover of which is composed largely of such weedy species as *Oplismenus hirtellus* and *Nephrolepis exaltata*. Development of such stands proceeds by the invasion of *Diospyros sandwicensis* and a host of other very shade-tolerant species. It seems possible, for example, that the forest studied in Quadrat No. 7 (Table 6) is the result of a similar series of events; the five large Metrosideros trees may be relics of a previous invasion of an open grassy slope by that species. A few large *Acacia koa* trees occur in the same forest outside the sample plot. The ultimate composition of these secondary forests depends to a great extent on the proximity of seed trees. Mixed forests, of course, indicate the previous availability of seeds of many species. Pure, uneven-aged stands of *Diospyros sandwicensis* probably show that seeds of other species are locally lacking. It is important not to underestimate the relative rarity of many of these interesting plants. Because of this

and the difficult topographic barriers to migration, they may be highly localized and indeed in danger of extinction in case of any profound changes in their habitats. Appreciable extensions of their ranges in general cannot be accomplished by natural agencies alone. As Egler (1942) pointed out, "Artificial introduction [of these endemic species] therefore should be part of any forest management plan."

DISTRIBUTION OF NATIVE DRY FOREST IN THE PAST

Ripperton & Hosaka (1942) have constructed a vegetation map of Oahu in which the system of zonation employed is based on the predominant vegetation existing at the present time. It would be interesting to construct a map of the former distribution of native dry forest on Oahu, and a plausible point of departure would be the map of Ripperton & Hosaka. There are two reasons, however, why this does not seem to be possible. The correspondence between the vegetation zones proposed by Ripperton & Hosaka and the forest types of the present author is not exact.* Semi-deciduous forest for the most part coincides with Zone C_2, but in some cases, as at Kawaihapai and Kapuna Gulch, extends into the C_1 zone. Similarly, evergreen seasonal forest occurs chiefly in Zone D_1, but also extends into Zone C_2. Fig. 12 will clarify these relationships.

A second major difficulty lies in the possible former influence of the native forest on local climates. Historical records of native forest exist in areas which today seem much too dry to support such a vegetation. There are also reports (Egler 1947) of native villages and springs in places which are quite lacking in water sufficient to supply the needs of human populations. Egler (1942, 1947) has emphasized the role of individual plants of *Schinus terebinthefolius,* an exotic shrub or small tree, in the conservation of soil and moisture on arid slopes and ridges; the influence of a continuous forest cover in such places would have been considerable. A contemporary example is the destruction of the famous dry forest between PuuWaawaa and Huehue, Hawaii Island, which was described by Rock (1913). The present author made studies of remnants of this forest in 1950 (unpublished). Rock's description of the composition of this rich forest corresponds well with that

<table>
<tr><th>RIPPERTON AND HOSAKA</th><th>THE SYSTEM HERE PROPOSED</th><th>ROCK</th></tr>
<tr><td>ZONE D_2</td><td>MIDDLE FOREST ZONE</td><td>MIDDLE FOREST ZONE</td></tr>
<tr><td>ZONE D_1</td><td>EVERGREEN SEASONAL FOREST</td><td rowspan="3">LOWER FOREST ZONE</td></tr>
<tr><td>ZONE C_2</td><td>SEMI-DECIDUOUS SEASONAL FOREST</td></tr>
<tr><td>ZONE C_1</td><td rowspan="3">LOWLAND ZONE</td></tr>
<tr><td>ZONE B</td><td rowspan="2">LOWLAND ZONE</td></tr>
<tr><td>ZONE A</td></tr>
</table>

FIG. 12. Comparison of systems of zonation proposed by Rock (1913), Ripperton & Hosaka (1942), and the present author.

of the Mokuleia semi-deciduous forests. Within the past 30 years this land has been opened to grazing by cattle and much of the native forest has been destroyed. The vegetation succeeding the native dry forest is variously dominated by *Opuntia megacantha* Salm-Dyck, *Pennisetum ruppelii* Steud., or *Leucaena glauca,* and has been mapped by Ripperton & Hosaka as lying in Zone B and Zone C_1, although the native forest would appear to correspond more accurately to Zone C_2. Destruction of the native forest has thus resulted in an apparently much drier type of vegetation.

There exist, however, two methods of arriving at very satisfactory estimates of the past distribution of native dry forest. Historical accounts of native forests are to be found in the journals of the early explorers. In some cases it is possible to locate such stands precisely. Thus St. John (1947) has demonstrated the existence in 1821 of *Santalum freycinetianum, Diospyros hillebrandii, Elaeocarpus bifidus, Aleurites moluccana, Styphelia tameiameiae, Dianella sandwicensis,* and other species of the Lower Forest Zone at Pouhala, on the Leilehua (Schofield) Plain, between the Waianae and Koolau ranges. The list of species is highly suggestive of evergreen seasonal forest, although ridge-top and ravine-bottom species are present as well.

A second method of estimating the former distribution of native dry forest is the plotting of records of distributions of "indicator species." It was the opinion of Egler (1942) that many of the rare indigenous trees of the Hawaiian Islands are "highly tolerant 'climax' species." These are in general successional in the absence of fire or grazing to the weedy scrub now covering most of the dry forehills of Oahu. According to this view, the rarest species are possibly those requiring for their proper growth and development conditions found in nature only in the primeval dry forest. Indeed, the native forests described in this paper were discovered by an application of this concept. From herbarium records the writer plotted the known distributions of several very rare, native dryland tree species, such as *Mezoneuron kavaiensis, Colubrina oppositifolia, and Drypetes phyllanthoides.*

* It is possible that I have misinterpreted the system of vegetational zonation of Ripperton & Hosaka. My concept of the Lower Forest Zone has been based chiefly on observations of vegetation in which native species predominate. I interpret it to include the semi-deciduous and evergreen seasonal forests of the slopes, as described above, and to coincide almost exactly with the distribution of forests of *Aleurites moluccana,* which occupy the bottoms of gulches. The zones of Ripperton & Hosaka, although adapted in part from Hosaka's earlier paper (1937), are based on cultivated crops, pastures, and the most common existing vegetation, which is chiefly alien in flora and youthful in development. Indeed, it would be remarkable if schemes of zonation based on such widely divergent factual data should agree precisely. I recommend the system of Ripperton & Hosaka for application in agriculture and range management, where the system of Rock (1913), based as it is today on a decimated native vegetation, would be quite impracticable. For general work in natural history the system of Rock has in my opinion decided advantages, not the least of which is priority of publication.

Explorations were conducted chiefly in those areas in which these species appeared to be concentrated. The fact that well developed native dry forests were discovered argues strongly for the validity of the method.

This procedure must be applied with considerable caution. Certain species which are common in native dry forest are aggressive in the secondary succession following the cessation of disturbance, as discussed above. This is especially true of *Canthium odoratum, Sapindus oahuensis, Erythrina sandwicensis,* and *Dracaena aurea.* The presence of these species in a given place does not necessarily demonstrate the former existence there of well developed native dry forest. In general, a careful field survey of areas suggested by herbarium records is highly desirable.

Large, weatherbeaten veterans of *Reynoldsia sandwicensis* are occasionally encountered in the middle of thickets of *Lantana camara* and other introduced scrub. If it could be shown that these trees are more than 160 years old, as seems possible in some cases, they would clearly antedate the disturbing effects of grazing and hence perhaps indicate the former sites of forests (cattle were introduced in the Hawaiian Islands by Vancouver in 1793). The rates of growth of native species are generally unknown, however, and annual rings are usually absent. It thus seems impossible to determine the ages of these trees.

A map showing the distributions of certain indicator species is included (Fig. 13). It would appear that the area of greatest concentration of native dry forest was in the region of Mt. Kaala, in the Waianae range.

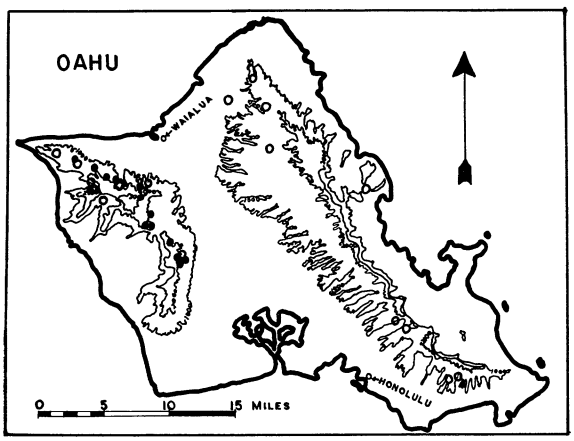

FIG. 13. Distribution of certain species indicating probable former extent of native dry forest. Solid black dots: *Alectryon macrococcus* (after St. John & Frederick 1947); circles: *Pteralyxia macrocarpa* (after Caum 1933); solid triangles: *Mezoneuron kavaiensis* (data from herbarium specimens and Hillebrand 1888).

The richness of this region is probably due to factors other than the present comparatively undisturbed state of its natural vegetation. The Waianae range is geologically one of the oldest areas in the Hawaiian Islands. Sufficient time has elapsed since the emergence of these mountains above the ocean to allow the immigration and development of a richer flora than may be found elsewhere on Oahu. In the opinion of the author, the imperfectly explored area which includes the summit of Mt. Kaala and the valleys of Makaleha, Makua, and Makaha is possibly the richest collecting area in the Hawaiian Islands. In addition to this concentration in northwest Oahu, native dry forest also occurred in most of the Waianae range, in the Pupukea region of northern Oaku (Koolau range), and in leeward southeast Oahu, mostly between elevations of 1000 and 2000 feet.

This estimate is conservative. According to St. John (1947), "on Oahu, the forest did not stop at the 1000- or 1,500-foot line, but came in places right to the sea. . . . The Leilehua or Schofield plains between the two mountain forests were densely and continuously forested. On the lowest, driest slopes, an open forest or savanna doubtless spread, largely of wiliwili (*Erythrina sandwicensis*) but also containing the ohe (*Reynoldsia sandwicensis*)."

GROWTH AND DEVELOPMENT OF NATIVE WOODY SPECIES

Native trees have not been used to any great extent in Hawaiian forestry. In fact, virtually nothing is known regarding rates of growth or suitable planting sites. Although several native dryland trees are distinctly ornamental (e.g., *Kokia* spp., *Hibiscus brackenridgei, Mezoneuron kavaiensis, Erythrina sandwicensis, Reynoldsia sandwicensis, Metrosideros polymorpha, Gardenia brighamii*), it is rare indeed to find a native street tree in Honolulu. It is a commonly held view that Hawaiian trees are "difficult" or grow too slowly to be of benefit in reforestation of barren hillsides. Since the majority of these trees appear to be restricted to late stages of development under semi-natural conditions, this opinion is easy to understand. Plantings of *Eucalyptus* spp., *Grevillea robusta, Casuarina* spp., and other exotics show quick and impressive growth on the poorest sites and are undoubtedly of much benefit in prevention of soil erosion in such places.

Nevertheless, it seems likely that native species could be of service in programs of afforestation in certain situations. It scarcely needs to be demonstrated that native dry forest in the Hawaiian Islands, if once established and if not subjected to disturbance by introduced grazing animals or fire, will maintain itself indefinitely. On the other hand, many planted stands of Eucalyptus and Grevillea in Hawaii appear unlikely to persist beyond a single generation. As a permanent, slope-cover type which requires little if any attention once established, native dry forest would seem to merit more consideration than it has hitherto received.

Because it is felt that any information on the autecology of these trees may be of some service to future workers in basic and applied fields, a list (Table 10) of the more common native species, arranged in order of apparent shade tolerance, is presented. This list is purely provisional, to be revised when experimental data concerning these species are

available. Obviously, what is needed is a set of long-term experimental observations on the growth and development of important native woody species. It is an unfortunate fact that virtually no studies on the physiology of native Hawaiian trees have been published. The deplorable condition in which Egler (1947) found arid southeast Oahu vegetation is, in the opinion of the present author, a direct result of ignorance of the autecology of the woody species of the available flora. This situation is surprising in a community which has well developed scientific resources and an active appreciation of the importance of watershed values.

TABLE 10. Scale of Shade Tolerance.

Very tolerant species	Tolerant species	Intolerant species
Diospyros hillebrandii	*Pisonia umbellifera*	*Myrsine lanaiensis*
Pittosporum flocculosum	*Erythrina sandwicensis*	*Metrosideros polymorpha*
Pteralyxia macrocarpa	*Pouteria sandwicensis*	*Acacia koa*
Canthium odoratum	*Osmanthus sandwicensis*	*Styphelia tameiameiae*
Diospyros sandwicensis	*Dracaena aurea*	*Dodonaea sandwicensis*
Sapindus oahuensis	*Alectryon macrococcus*	*Dodonaea eriocarpa*
Ochrosia sandwicensis	*Reynoldsia sandwicensis*	
Myrsine lessertiana	*Mezoneuron kavaiensis*	
Straussia oncocarpa	*Rauvolfia sandwicensis*	

SUMMARY

Most native vegetation in the Hawaiian Islands has been sadly disturbed in the past 160 years. Destruction has been most severe in the lowest, driest regions, but on Oahu the wetter areas of the mountains—especially the rainforest belt—still exist in their primeval state.

Between the Lowland Zone and the rainforest is a belt of forest—the Lower Forest Zone—in which disturbance has been severe. Nevertheless, in the Mokuleia region of Oahu it has been possible to find isolated stands in which native trees are predominant.

Two broadly defined slope-cover types are described in the Lower Forest Zone of Mokuleia: semi-deciduous seasonal forest and evergreen seasonal forest. Composition of these forests is extremely variable. Examples of single-species dominance and mixtures of over 20 native species of trees can be found in both types.

Because of the rugged topographic barriers to plant migration, many of the 50-odd species of native trees of the Mokuleia Lower Forest Zone have very local distributions. Some of these trees may be important constituents of the vegetation where they occur.

Sapindus oahuensis, Erythrina sandwicensis, Canthium odoratum, Dracaena aurea, Osmanthus sandwicensis, and *Reynoldsia sandwicensis* are among the more widespread trees of semi-deciduous forest. This type is usually rather open, and most species are less than 30 feet tall. Sapindus sometimes forms closed forests, however, in which the canopy is over 40 feet above the ground.

Evergreen seasonal forest is commonly dominated by *Diospyros sandwicensis,* which forms a closed canopy 30 to 40 feet high. Over 30 other native species may be associated with it in some stands, however, and certain of these at irregular intervals may project far above the prevailing level of the crowns of the smaller trees.

Precipitation in semi-deciduous forest ranges from 30 to 65 inches annually, and the dry season averages about 7 months in length. Evergreen seasonal forest receives about 70 inches of annual rainfall, the dry season lasting about 4 months. The slopes on which these forests occur are very steep, and internal drainage is excessive.

Both types appear to be successional to the scrub of exotic species which covers most of the dry forehills of Oahu. A large proportion of Hawaiian trees seems to be very tolerant of shade but unable to cope with the conditions caused by large grazing animals. In some cases establishment of alien "nurse crops," such as stands of *Leucaena glauca,* may be necessary for the establishment of native forest in denuded places.

As a protection forest on the drier Hawaiian watersheds, native dry forest might have certain advantages over plantations of *Eucalyptus* spp., *Grevillea robusta,* etc., which in many cases seem unable to reproduce themselves naturally. There is every reason to believe that the native forest, once established, would perpetuate itself indefinitely in the absence of disturbance.

There can be little doubt that Hawaiian dry forests were once much more extensive than they are today. Observations by 19th-century explorers are often valuable in determining former locations of native forest. Certain native species of trees may be used as indicators of former forests. Isolated mature specimens persisting but not reproducing in thickets of *Lantana camara* probably are witnesses of former forested conditions. Herbarium records of localities of species most severely affected by changed conditions also serve to place former forest. On Oahu native dry forests probably were generally distributed in the Waianae range at elevations of 1000 to 2000 feet and occurred in the northwestern and southeastern extremities of the Koolau range at similar elevations.

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LIST OF SPECIES

Plant names are arranged alphabetically under separate life-form headings: trees; treelets, shrubs, and woody climbers; herbs; and mosses. The list of tree species is believed to be complete; only those plants in the remaining categories which are considered to be of vegetational or floristic significance are included. The abbreviations in parentheses have been used in the citation of specimens to designate the institutions in which the specimens are housed: Bernice P. Bishop Museum (Ho), Chicago Natural History Museum (F), herbarium of F. R. Fosberg (FRF). All moss specimens are in the herbarium of Harvey Alfred Miller. A second set of abbreviations has been used to indicate the forest types of the Lower Forest Zone of Mokuleia in which the plants occur: semi-deciduous seasonal forest (SDF) and evergreen seasonal forest (EF). Collection numbers are those of the author unless otherwise noted.

TREES

Acacia koa A. Gray. SDF, EF. A large tree. Often a pioneer on open grassy slopes, but commonly persisting as scattered tall individuals in later stages of development.

Alectryon macrococcus Radl. (102, F, Ho). EF. Not uncommon in rich, dark forests, where it is often associated with Pteralyxia.

Aleurites moluccana (L.) Willd. SDF, EF. A consistent dominant in gulch bottoms, but only occasional on the slopes. Probably of aboriginal introduction.

Antidesma pulvinatum Hillebr. (283, 399, Ho). EF. Observed only three times in the Kaala region, where single trees occurred in dark forests.

Bobea elatior Gaud. (351, 388, FRF). EF. A wide-ranging, somewhat polymorphic species, most common in the lower rainforest.

Bobea hookeri Hillebr. (155, FRF). SDF. Rather rare, in the very dry, mixed forests of Kapuna Gulch. Perhaps not specifically distinct from the following.

Bobea sandwicensis Hillebr. (191, 285, 400, FRF). SDF. Occurs sporadically in the very dry forests of East Makaleha Valley, where it is one of the larger trees.

Canthium odoratum (Forst.) Seem. SDF, EF. Abundant small tree of wide ecological amplitude.

Charpentiera ovata Gaud. (174, F). SDF, EF. A characteristic understory tree, occurring singly or in small groups. No attempt has been made to distinguish this species from *C. obovata* Gaud.

Cassia gaudichaudii Hook. et Arn. SDF, EF. Common, usually a shrub, but a 25-ft. tree was observed in East Makaleha Valley. Judd (1931) reported a 38-ft. tree of this species in Makua Valley.

Colubrina oppositifolia Brongn. (124, Ho, F; 382, Ho). SDF. Very few Oahu collections known, but not uncommon in East Makaleha Valley. Small tree.

Diospyros hillebrandii (Seem.) Fosb. Very shade-tolerant small tree, with dense foliage. Ground usually completely bare underneath.

Diospyros sandwicensis (A. DC.) Fosb. SDF, EF. Exists in many morphological forms and probably as many physiological races, both in wet and dry forests. Unquestionably the most common species in the native dry forests of Makaleha and Makua Valleys, but elsewhere in my experience unimportant on Oahu. In Niu and Wailupe Valleys, southeast Oahu, however, it appears to be successional to stands of the Waiawi (*Psidium* sp.) (cf. Egler 1942). One of the two or three most important native trees in any reforestation program in dry areas.

Dodonaea eriocarpa Smith. SDF. Dr. Sherff has referred my Mokuleia collections to the following varieties: var. *glabrescens* Sherff (164, F) and var. *degeneri* Sherff (229, F). They appear to be ecologically equivalent, mostly pioneering on ridges, but sometimes extending down the slopes into semi-deciduous forest.

Dodonaea sandwicensis Sherff. EF. Uncommon, in rich forests.

Dracaena aurea H. Mann. SDF, EF. One of the most common and striking of the trees of the Mokuleia dry forests.

Drypetes phyllanthoides (Rock) Sherff. (98, F; 395, Ho). According to the field labels quoted by Sherff (1939), most collectors would regard this species as rapidly approaching extinction and probably much more abundant in the past. Certainly most of the living trees recently observed have been "half dead" or "dying," and before the discovery of several living trees in Makaleha Valley during the course of these investigations Mr. Degener told me he believed the species to be extinct. Yet had Drypetes been common, it surely would have been discovered by Hillebrand, Wawra, or Forbes, all of whom collected vigorously in the Kaala region. The species was first collected on Oahu by G. W. Russ, in 1929 (reported by Judd 1930). My collections, made from two splendid trees in East Makaleha Valley (cf. Fig. 10), are apparently the first reported in Mokuleia. It is my opinion that Drypetes has always been rare, and that the species is long-lived and slow-growing. Its great size—to 11.3 ft. d.b.h. (Judd 1931)—extremely hard and heavy wood, and attractive foliage recommend it for further study and cultivation. I doubt that it is in immediate danger of extinction in Makaleha Valley.

Elaeocarpus bifidus Hook. et Arn. EF. Most common at the lower margin of the rainforest but attains its greatest size in the Lower Forest Zone.

Erythrina sandwicensis Deg. SDF. One of the most widely distributed and common species of the Hawaiian dry forests, both as a pioneer and in late stages of development.

Euphorbia celastroides Boiss. var. *hathewayi* Sherff (223, 228, 374, all F). SDF. Often shrubby, but occurs as a 15-ft. tree in Makaleha Valley, growing with *Myrsine lanaiensis*, Ochrosia, Colubrina, and Tetraplasandra.

Euphorbia forbesii Sherff (125, F). EF. Sherff (1950) has commented on the rediscovery of the type locality of this species.
Hibiscus arnottianus A. Gray. SDF, EF. A very common tree; to 30 ft. tall.
Hibiscus brackenridgei A. Gray (71, F). SDF. Mr. Degener informed me that he found this species at Kawaihapai. I have collected it only at Puu Pane, 3 mi. east of Makaleha Valley, where it is a large tree, occurring in pure stands or in association with Erythrina.
Jossinia (Eugenia) reinwardtiana (Blume) Blume. (35, F). SDF. This species, morphologically a shrub, is often as tall as the dominant trees in some semi-deciduous forests and is hence listed in the "tree" category. Although it has the reputation of being rather rare, I found it not uncommon in all Oahu dry forests.
Leucaena glauca (L.) Benth. Egler (1947) has discussed the occurrence of this small tree in detail. Exotic.
Metrosideros polymorpha Gaud. (420, Ho). SDF, EF. Until the taxonomy of this truly polymorphic assemblage is better understood, I shall refer all the forms of Metrosideros found in Mokuleia to this species. It seems incredible, however, that a single species should have such a wide ecological amplitude, for the "Ohia Lehua" is abundant in all stations from the driest open ridges to the wettest rainforests. In the seasonally dry forests it occurs chiefly as a pioneer.
Mezoneuron kavaiensis (H. Mann) Hillebr. (108, Ho; 129, Ho, F). SDF. The last previous Oahu collection of this ornamental species appears to have been in 1931 (G. W. Russ, Makua Valley, 6-1931, Ho). This is the first modern record of Mezoneuron in Mokuleia, where it was observed in four Makaleha stations. Mezoneuron on Oahu rarely exceeds 15 ft. in height and seems partial to sunny slopes. Yet many thrifty seedlings and saplings were observed growing in shade.
Morinda trimera Hillebr. (412, Ho, sterile). EF. A small tree occurring rarely in the darkest forests.
Myoporum sandwicense (A. DC.) A. Gray. SDF, EF. A 20-ft. tree, occurring occasionally in most dry forests, but never abundant in Mokuleia.
Myrsine lanaiensis Hillebr. (116, F).SDF. A medium-sized tree, frequent, especially in Kapuna Gulch.
Myrsine lessertiana A. DC. (326, F). EF. Several authors (cf. Rock 1913) have remarked on the polymorphic nature of this species. Its autecology is no less variable, for it occurs in dry, wet, and very wet forests.
Nesoluma polynesicum (Hillebr.) Baill. (318, Ho). SDF. Very rare. Its attractive, shiny, dark-green, evergreen foliage and full, round crown recommend this species as an ornamental shade tree in very dry places.
Ochrosia sandwicensis A. Gray (172, Ho; 181, F; 213, Ho). SDF, EF. Small tree, most frequent in dark forests. Rarity overestimated by many.
Osmanthus sandwicensis (A. Gray) Benth. & Hook. SDF, EF. One of most common and characteristic trees of the seasonally dry forests of Oahu. Osmanthus also extends into the lower rainforest.
Pelea wawraeana Rock (353, 393, Ho). EF. A small tree, occasional in Makaleha Valley.
Pipturus skottsbergii Krajina. SDF, EF. A small tree, rather common in small openings in the forest.
Pisonia umbellifera Seem. (281, F). SDF, EF. A very common and characteristic species of all Oahu dry forests, both on open slopes and in dark gulch bottoms.
Pittosporum flocculosum (Hillebr.) Sherff (234, F; 383, F). SDF, EF. Occurring singly or in small groups in the understories of the darkest forests. A tree to 35 ft. tall.
Pittosporum sulcatum Sherff var. *remyi* Sherff (160, F). SDF. Almost invariably as widely scattered individuals in open dry forests.
Pritchardia kaalae Rock. EF. Observed at the type locality in East Makaleha Valley, where there is a pure stand of these interesting palms. Other Pritchardias, possibly referable to this species, are growing on inaccessible cliffs on the slopes of Mt. Kaala.
Pseudomorus pendulina (Endl.) Stearn var. *sandwicensis* (Deg.) Stearn. (411, Ho). EF. Rather rare small tree occurring at the upper margin of the Lower Forest Zone.
Psidium guayava L. SDF, EF. Frequent invader of cattle pastures and open slopes, and common in gulch bottoms. "Lemon guava" is a shade-intolerant pioneer weed tree, rarely persisting in later stages of development. Exotic.
Pouteria sandwicensis (A. Gray) Baehni & Deg. (386, Ho). SDF, EF. Common tree, occurring chiefly as scattered individuals.
Pteralyxia macrocarpa (Hillebr.) Schum. (415, Ho). EF. Judd (1932) corrected stated that the rarity of this large, handsome tree has been greatly overestimated. Common and characteristic in rich evergreen season forest.
Pterotropia sp. EF. Large tree, with handsome pinnate foliage, overtopping most of its neighbors. Locally abundant at the upper margin of the Lower Forest Zone.
Rauvolfia sandwicensis A. DC. (158, F; 169, F; 421, Ho). SDF, EF. One of the larger and more common trees in the very dry forests. Occasionally in pure stands.
Reynoldsia sandwicensis A. Gray. SDF. Very common in all Oahu dry forests, where it is one of the larger trees; nearly always as scattered individuals.
Sapindus oahuensis Hillebr. SDF. Large tree, abundant in the Mokuleia dry forests; a common dominant.
Santalum ellipticum Gaud. (185, F). Usually a shrub, this species becomes a 15-ft. tree in some dry forests.
Santalum freycinetianum Gaud. (184, F). SDF, EF. St. John (1947) discussed the history and occurrence of this interesting species in detail. One of the larger trees in the dry forests, where it is common. I suspect that reproduction is chiefly vegetative, from root sprouts, and I have seen no evidence that it is ever a root parasite.
Straussia (Psychotria) oncocarpa Hillebr. (389, F, Ho). EF. A well marked species, very common in the moister forests of the Lower Forest Zone of Makaleha Valley.
Syzygium (Eugenia) cumini (L.) Skeels. SDF, EF. Exotic tree, now very common in well developed semi-deciduous forest in Mokuleia.
Syzygium (Eugenia) sp. (Trees sterile, no specimens collected). EF. This very interesting tree is dominant in a small patch of moist forest in Keawapilau Gulch, where it attains enormous size. The taxonomy of Syzygium in Hawaii is in a very confused state; careful monographic study may show that this is a new species.
Tetraplasandra kaalae (Hillebr.) Harms. (106, F; 209, F; 405, Ho). SDF, EF. Rock (1913) stated that Hillebrand collected this species on the summit of Mt. Kaala, while Hillebrand (1888) wrote merely "Kaala." Degener (1938, Fam. 281) called *T. kaalae* "a very rare plant." It is abundant in Makaleha Valley, however, and occurs even in the driest forests. I doubt that it grows on the summit of Mt. Kaala, which is a rainy swamp. *Tetraplasandra kaalae* is a medium-sized tree, with handsome pinnate foliage and striking umbels.
Urera glabra Hook & Arn. (324, F; 401, Ho). EF. Occurs mostly in clearings, but a few large trees were observed in Keawapilau Gulch, growing in deep shade.
Xylosma hawaiiensis Seem. (418, Ho). Uncommon, mostly in dark forests.

The following trees have been observed by the author in seasonally dry forests elsewhere in the Hawaiian Islands and have been reported on Oahu. None was encountered in these studies, although certain of them are known from earlier collections in Makaleha Valley.

Alphitonia ponderosa Hillebr.
Cryptocarya oahuensis (Deg.) Fosb. Three or four seedlings possibly referable to this species were observed by Dr. Fosberg and the author in the evergreen seasonal forests of Makaleha Valley. No large trees were observed, however, so that the tree cannot definitely be assigned to the forests here studied.
Gardenia brighamii H. Mann.
Kokia sp. Probably extinct on Oahu.
Sophora chrysophylla Seem.
Trema amboinensis Blume.

TREELETS, SHRUBS, AND WOODY CLIMBERS

Alyxia oliviformis Gaud. SDF, EF. Abundant woody climber, especially in evergreen forests.
Bidens amplectens Sherff (224, F). SDF.
Bidens torta Sherff (233, F). EF.
Bidens waianensis Sherff (227, F). SDF, EF.
Breweria menziesii Benth. & Hook. (156, F, Ho). SDF. Very local, but a serious impediment to travel where it occurs. *Breweria* is a woody vine capable of overgrowing the tops of 50 ft.-trees.
Canavalia galeata Gaud. SDF, EF. Vine common in all seasonally dry forests.
Cassia gaudichaudii Hook. & Arn. SDF, EF.
Caesalpinia crista L. (291, F). SDF. Large prickly climber, common in the drier forests.
Chenopodium oahuense Meyen. SDF.
Cibotium splendens (Gaud.) Krajina. EF. Most common tree fern of the Lower Forest Zone, but more abundant in the rainforest.
Claoxylon sandwicense Muell. Arg. var. *glabrescens* Sherff (Degener & Hatheway 21,165, F). EF. Observed only twice, growing in deep shade.
Cordyline terminalis Kunth. SDF, EF. Aboriginally introduced.
Euphorbia celastroides Boiss. var. *hathewayi* Sherff. SDF.
Euphorbia hillebrandii Levl. (99, F). SDF, EF.
Hedyotis acuminata (Cham. & Schlecht.) Fosb. (385, FRF). EF.

Ipomoea alba L. SDF. Local in the Kawaihapai region, where it sometimes covers the crowns of the larger trees. Flowers nocturnal.

Isodendrion laurifolium A. Gray (398, F, Ho). A small tree about 9 ft. tall, encountered in quadrat No. 7. The last previous Oahu collection appears to have been that of William Hillebrand, and his specimens in the Bishop Museum bear no date (Hillebrand left the Hawaiian Islands in 1871). Hillebrand's collection is labeled "Wailupe Valley," a station in the Koolau Range 30 mi. from our area. Isodendrion is a violaceus genus endemic in the Hawaiian Islands.

Lantana camara L. SDF, EF. Abundant and troublesome exotic, mostly in semi-deciduous forest.

Neraudia angulata Cowan var. *dentata* Deg. & Cowan (34, F). SDF. This urticaceous genus is endemic in the Hawaiian Islands, and all species are usually considered rather rare. I find this and the following species fairly common in rich dry forests.

Neraudia melastomifolia Gaud. var *parvifolia* Cowan (391, Ho). EF.

Nototrichium viride Hillebr. var *subtruncatum* Sherff (157, 168, F). This amaranthaceous genus is endemic in the Hawaiian Islands; *N. viride* appears to be rather rare.

Osteomyles anthellidifolia Lindley. SDF. Very common native shrub, sometimes forming nearly impenetrable thickets.

Psidium cattleianum Sabine. SDF, EF. The common "strawberry guava." Exotic.

Schinus terebinthefolius Raddi. SDF. Exotic.

Sicyos sp. (171, Ho). SDF. Abundant in the Mokuleia dry forests, where it is usually an annual, dying with the onset of the summer dry season. In Kapuna Gulch, however, I collected a Sicyos growing as a woody liana to the top of a 40-ft. tree of *Sapindus oahuensis*. The stem was nearly an inch in diameter, and the plant was deciduous.

Sida fallax Walp. SDF.

Sida meyeniana Walp. SDF. This species is common in the forests, whereas *S. fallax* usually occurs in open places, especially at Kealia.

Smilax sandwicensis Kunth. EF. Rare and local in the seasonally dry forests, but sometimes forming dense tangles in the rainforests.

Strongylodon lucidus (Forst.) Seem. (397, F). EF. Locally abundant in East Makaleha Valley, growing over the tops of trees and shrubs.

Styphelia tameiameiae (Cham. & Schlecht.) F. Muell. SDF, EF. Abundant on open windswept ridges, but not very common in well developed slope forests.

Viola tracheliifolia Ging. (360, Ho). EF. Most common of the Hawaiian woody violets, resembling in habit a miniature palm tree. Usually in open forests on ridge tops, but also encountered in Quadrat No. 7.

Wikstroemia oahuensis (A. Gray) Rock. (175, Ho). SDF.

HERBS

Asplenium enatum Brack. (287, F). EF.

Asplenium horridum Kaulf. EF.

Asplenium nidus L. SDF, EF.

Carex brunnea Thunb. (38, F). SDF, EF.

Carex wahuensis Mey. EF.

Cocculus ferrandianus Gaud. SDF, EF. Very common weak-stemmed trailer.

Cyrtomium caryotideum (Wall.) Presl. (115, F). EF.

Dianella sandwicensis Hook & Arn. SDF, EF.

Diellia falcata Brack. (104, F, Ho). EF. This genus of ferns is endemic in the Hawaiian Islands, and most species are rare. *D. falcata*, however, is common in well-developed evergreen forest, where it often occurs in the crevices of outcropping rocks, in deep shade.

Diplazium fenzlianum (Luerss.) C. Chr. (295, F, Ho). EF.

Doodia kunthiana Gaud. SDF, EF.

Doryopteris decipiens (Hook.) J. Sm. SDF, EF.

Dryopteris dentatus (Forsk.) C. Chr. SDF, EF.

Dryopteris goggilodus (Schk.) Kuntze emend. Fosb. (146, F) SDF.

Eragrostis grandis Hillebr. EF.

Eragrostis variabilis (Gaud.) Steud. SDF.

Gahnia globosa H. Mann. (286, F; 422, Ho). EF.

Korthalsella platycaula (v. Tiegh.) Engl. (173, F, Ho). On *Sapindus oahuensis*.

Korthalsella remyi A. Gray. On *Diospyros sandwicensis*.

Microlepia setosa (Sm.) Alston (329, F). SDF, EF.

Mirabilis jalapa L. SDF. Exotic.

Nephrolepis exaltata (L.) Schott. SDF, EF.

Oplismenus hirtellus (L.) Beauv. SDF, EF.

Panicum kaalense Hitchc. EF.

Peperomia leptostachya Hook. & Arn. SDF.

Peperomia reflexa A. Dietr. var. *parvifolia* C. DC. (362, F). EF. Epiphytic.

Peperomia sandwicensis Miq. (105, F). SDF, EF.

Phyllanthus sandwicensis Muell, Arg. (97, F). EF.

Plectranthus parviflorus Willd. (114, F). SDF, EF.

Plumbago zeylanica L. SDF.

Polypodium atropunctatum Gaud. SDF, EF.

Psilotum nudum (L.) Beauv. SDF, EF.

Pteridium aquilinum (L.) Kuhn var *decompositum* (Gaud.) Tryon. (328, F). SDF.

Pteris cretica L. var. *decurrens* Hillebr. (394, F). EF.

Selaginella sp.

Schiedea hookeri A. Gray var. *acrisepala* Sherff (162, F). SDF.

Schiedea kealiae Caum & Hosaka. SDF.

Schiedea ligustrina Cham. & Schlecht. (230, F) and var. *nematopoda* Deg. & Sherff (133), F), both SDF.

Tectaria gaudichaudii (Mett.) Maxon. (284, F). EF.

MOSSES

Anoectangium euchloron (Schwaeg.) Mitt. (H. A. Miller 1635, 2207). Not previously reported on Oahu.

Bryum megalostegium Sulliv. (H. A. Miller 1648). SDF. Not previously reported in the Waianae range.

Campylopus introflexus (Hedw.) Bridel. (H. A. Miller 1524). EF. Not previously reported on Oahu.

Fissidens delicatulus Angstr. (H. A. Miller 1523, 1599, 1646, 2208). SDF, EF. Not previously reported in the Waianae range.

Fissidens hawaiicus Bartr. (H. A. Miller 2052a). Not previously reported in the Waianae range.

Haplohymenium triste (Cesati) Kindb. (H. A. Miller 1531). EF. Not previously reported on Oahu.

Homaliodendron flabellatum (Dicks. & Sm.) Fleissh. SDF. EF.

Hyophila dozy-molkenboeri Fleisch. (H. A. Miller 1598). SDF. Not previously reported in the Waianae range.

Leucobryum gracile Sulliv. EF.

Macromitrium emersulum C. Müll. (H. A. Miller 1543). EF. Not previously reported on Oahu.

Macromitrium intricatum C. Müll. (H. A. Miller 2038, 2039). SDF. Not previously reported in the Waianae range.

Pseudosymblepharis mauiensis (C. Müll.) Broth. SDF, EF.

Rhacopilum cuspidigerum (Schwaeg.) Mitt. SDF, EF.

Rhizogonium spiniforme (Hedw.) Bruch. EF.

Sematophyllum hawaiiense (Broth.) Broth. SDF.

Taxithelium mundulum (Sulliv.) Bartr. SDF, EF.

Thuidium crenulatum Mitt. (H. A. Miller 1600, 1642, 2200). Not previously reported on Oahu.

Thuidium hawaiiense Reich. SDF, EF.

Trichostomum mauiense Broth. (H. A. Miller 1633, 1650, 1651). SDF. Not previously reported on Oahu.

Trichostomum oblongifolium Bartr. (H. A. Miller 1630, 1634). SDF. Not previously reported on Oahu.

Weisia ovalis (R. S. Williams) Bartr. (H. A. Miller 2060). Not previously reported in the Waianae range.