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TECHNICAL REPORT #20

OHIA RAIN FOREST STUDY

Dieter Mueller-Dombois

1977

FINAL REPORT
IN FULFILLMENT OF
CONTRACT NO. CX 8000 6 0006

Dieter Mueller-Dombois
Principal Investigator

Contribution Number CPSU/UH 010/6

Clifford W. Smith, Unit Director

OHIA RAIN FOREST STUDY:

Ecological Investigations of the Ohia Dieback Problem in Hawaii

by

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FINAL REPORT

In fulfillment of Contract CX 8000 6 0006
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and the National Park Service,
U. S. Department of the Interior

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PREFACE

The study presented in this final report was done in collaboration with three graduate students in vegetation ecology, who were supported on this contract. In addition, a graduate student in plant pathology received partial support, and his results were reported earlier (Hwang 1977).

The funds for this two-year contract (CX 8000 6 0006) were obtained through a proposal directed to the National Park Service Science Center in Mississippi. The funding ($55,000) received for this project is gratefully acknowledged.

Dieter Mueller-Dombois
Principal Investigator
OHIA RAIN FOREST STUDY

ABSTRACT

This final report summarizes the more important results of a two-year study of the ohia (Metrosideros collina subsp. polymorpha) rain forest, extending from within Hawaii Volcanoes National Park north across the east flank of Mauna Kea, Island Hawaii. The study focus was on the ohia dieback which occurs in many areas of this terrain. A 1:48,000 vegetation map was produced, which is included with this report.* In addition, an independent habitat classification was developed from physical soil and moisture regime differences occurring in the area. Over 35 ohia forest stands were sampled in detail for their ohia population structures and 39 relevés were analyzed for their floristic content. Five different forms of dieback were recognized. Two of these, called the Dryland and Wetland Diebacks appear to be the more rapid and dramatic forms. Their causes are not from disease or insect attack, but are presumed to be from climatic triggers, acting through the soil. These diebacks are clearly associated with ohia-stand rejuvenation. A third form of dieback, here called Bog-formation Dieback, appears to be a slower form of stand dieback related to permanent site changes. An Ohia-displacement Dieback occurs in the Olaa Tract area, where tree ferns seem to gradually take over the habitats. Here the dieback cause appears to be overmaturity. Individual tree dieback, the fifth form of dieback, is found as an isolated, but common phenomenon in many non-dieback stands examined. All diebacks appear to have natural causes, which are suggested in detail. A new theory is presented, which proposes that there are a number of dynamic phases, including the dieback, which provide for the perpetuation of the shade-intolerant, dominant tree species (ohia) in this rain forest ecosystem.

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*In selected copies only.

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FINAL REPORT

I. INTRODUCTION AND BACKGROUND

Name of Project: OHIA*RAIN FOREST STUDY

"Ecological Investigations of the Ohia Dieback Problem in the National Parks in Hawaii." Contract No. CX 8000 6 0006

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The project was planned in five integrated subprojects as follows:

Subproject 1: Floristic and Structural Analyses of Ohia Forests in Dieback Areas (D. Mueller-Dombois)

Subproject 2: Soil and Substrate Analyses for a Habitat Type Classification (D. Mueller-Dombois)

Subproject 3: Role of Pathogens in Ohia Dieback (W. H. Ko)

Subproject 4: Vegetation Map of Ohia Forest in Dieback Terrain (D. Mueller-Dombois)

Subproject 5: Experimental Studies to Corroborate Field Observations (D. Mueller-Dombois and W. H. Ko)

Following the original proposal, entitled "The Ohia Dieback Problem in Hawaii" (Univ. Hawaii-CPSU Tech. Report #3, 1974), three progress reports were submitted to the National Park Service in partial fulfillment of our research contract, the first in December 1975, the second in June 1976 and the third in December 1976.

This is the final report, which builds on this background material and summarizes our findings and work-products for the whole contract period, i.e. from September 1975 through September 1977.

The plant-pathological subproject (No. 3) was already completed in February 1977 with the production of UH-CPSU Tech. Report No. 12 by S. C. Hwang. The investigation of S. C. Hwang, which was done under the

*The complete common name and correct pronounciation of this native tree is 'ōhi'a-lehua.

direction of Dr. Ko with partial funding from this contract, was oriented towards the biology of Phytophthora cinnamomi in Hawaiian rain forest soils and specifically toward the relationship of this root pathogen with the ohia decline. It was concluded that the ohia decline is not correlated with the activity patterns of Phytophthora cinnamomi on well-drained soils in the dieback terrain of Hawaii Volcanoes National Park, Mauna Loa and Mauna Kea. Simultaneous disease and insect research focussing on the ohia decline, which was supported by the U. S. Forest Service, has just now come to a similar conclusion. Kliejunas, Papp and Smith (1977) state that: "Results suggest a secondary role for both Phytophthora cinnamomi and Plagithmysus bilineatus in the ohia decline syndrome." Plagithmysus bilineatus, an endemic bark beetle, had been suspected as a possible vector of Phytophthora or other pathogens or as an alternate direct cause in the dieback syndrome of ohia trees.

The research done under this NPS contract was aimed at investigating the dieback phenomenon as a fundamental ecological problem that may have developed in the island's rain forests during their primary succession and evolutionary history (Mueller-Dombois 1974). As a fundamental ecological problem, the dieback was studied for this initial two-year contract period as an important pattern, which was distinguishable among other important patterns in the rain forests on windward Hawaii. For this reason, the other subprojects were included. These were aimed at developing a large-scale vegetation map of the dieback terrain (subproject 4), at a floristic analysis in relation to the major structural variations (subproject 1), at soil and substrate analyses to develop a basic habitat classification for the area (subproject 2) and at experimental studies that would be pursued at a later stage for validating certain working hypotheses that would come forth as the field work progressed (subproject 5).

Accomplishment of these several work-phases during the two-year contract period required a closely coordinated team approach. Three graduate students invested a great deal of their energies and time into this project together with the principal investigator. In the following report sections, their names are listed as authors of the particular project segments for which they assumed major responsibility during the analysis and writing phase.

This report is only a summary-analysis of our findings up-to-date. It is not yet the definitive final product of our efforts. This will come forth in scientific papers on further data processing, analysis and synthesis.

As suggested in the Third Progress Report, this Final Report will give a summary account of the following five work-segments:

- The Vegetation Map and Legend
- Soil Moisture Regimes and Habitat Classification
- Ohia Population Structures in "Healthy" and "Dieback" Situations
- Rain Forest Structure and Floristics
- Evaluation of the Dieback Phenomenon

II. THE VEGETATION MAP AND LEGEND (James D. Jacobi)

1. Introduction

The present study deals with a portion of the native rain forest on the eastern side of the island of Hawaii. This area, roughly between the elevations of 2000 and 6000 feet (610 and 1830 m) stretches from Hawaii Volcanoes National Park, north across the lower saddle area between Mauna Loa and Mauna Kea, and around to the northeastern slope of Mauna Kea above Laupahoehoe (Fig. 1). It lies within the montane rain forest vegetation zone as mapped by Knapp (1965).

A considerable degree of structural and floristic variation can be found throughout this forest zone. Important gradients contributing to the diversity of vegetation types include annual rainfall, temperature, substrate type, and substrate age. Another factor, the past occurrence of ohia decline, has also been important in determining the present vegetation of certain areas.

The vegetation map of Hawaii Volcanoes National Park, produced by Mueller-Dombois and Fosberg (1974), covers a portion of the present study area in Hawaii Volcanoes National Park and the Olaa Tract section of the Park. The vegetation patterns were interpreted from aerial photographs taken in 1954, and were ground-checked in greatest detail in the more accessible areas. The map units on the Mueller-Dombois and Fosberg map were based primarily on dominant species, and structural criteria (such as plant spacing and height) of the vegetation.

The remaining portion of the study area has previously been mapped by Honda and Klingensmith in 1963, as part of the Hawaii Forest Type Map series produced by the U. S. Forest Service and the Hawaii State Division of Forestry. The map units in this case describe a) land use class, b) forest type, c) density of tree cover, d) tree-stand size class. The vegetation types were also interpreted from the aerial photographs taken in 1954, but, unfortunately, they were compiled with only a minimum of ground reconnaissance.

Considerable changes have taken place within the vegetation units of this area since 1954, primary among which has been the spread of ohia decline over the last 20 years (Petteys, Burgan, and Nelson 1975). These recent changes, plus the lack of ground verification, have made the

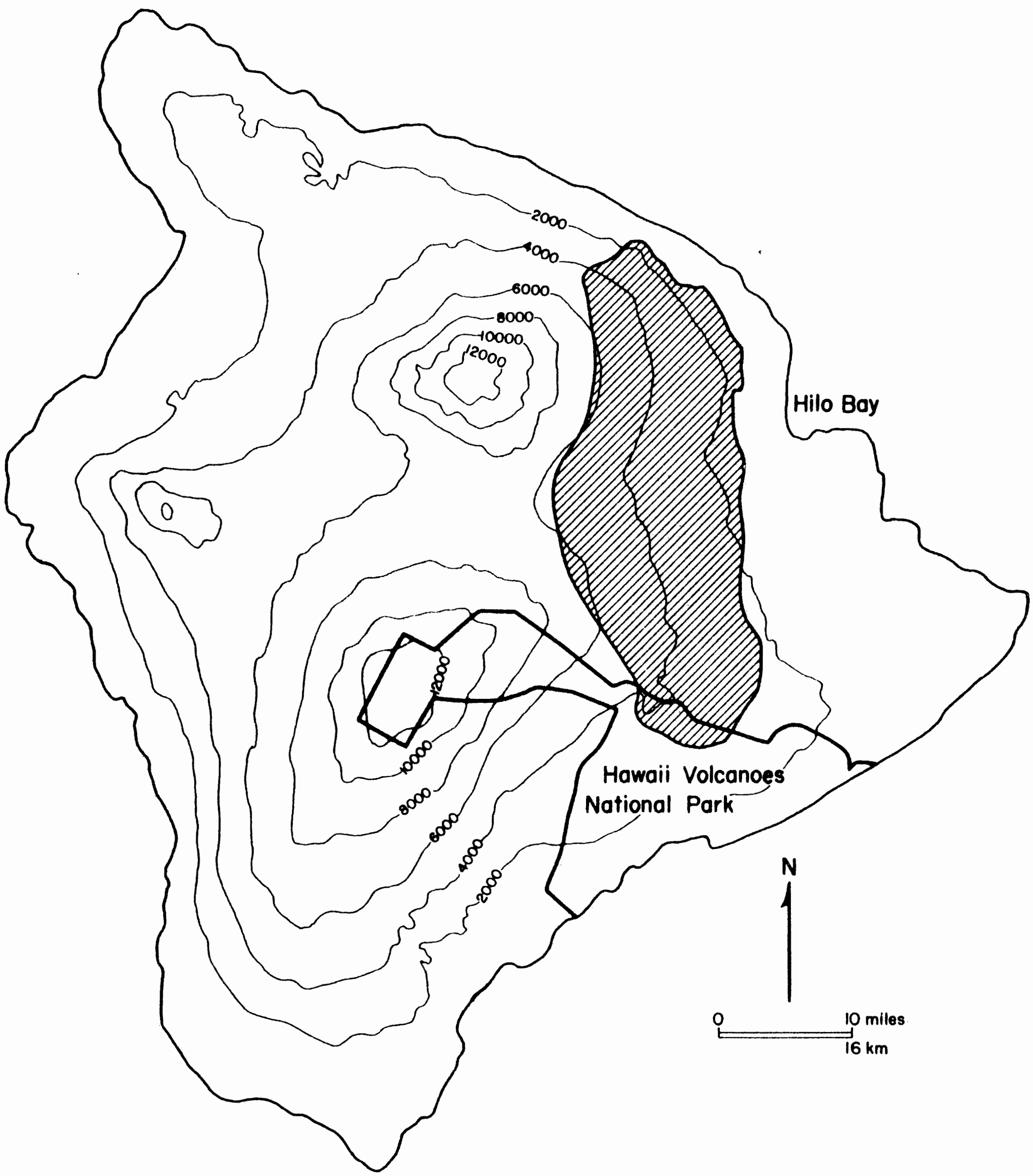

FIG. 1. Island of Hawaii and the Study Area (cross-hatched area). Contour lines at 2000-foot intervals.

Forest Type Maps inadequate for describing the present vegetation of this area.

It was therefore decided that for the present study, a new vegetation map needed to be prepared for the entire study area north of, and including, the Olaa Tract section of Hawaii Volcanoes National Park. This map is being based on more recent aerial photography, and will be ground-checked in great detail.

Included with selected copies of this report is a preliminary version of the new vegetation map. The map unit boundaries, which were interpreted from aerial photographs taken in 1972, 1974, and 1975, are currently being checked, both on the ground and from the air with a light aircraft. This phase of the project is being completed in cooperation with a survey of native forest birds and their habitats, which is being conducted by the U. S. Fish and Wildlife Service. It is expected that the final version of this map will be ready for publication in January 1978.

2. Three Map Sheets

The study area has been divided into four sections. They are, from north to south 1) the Hamakua Forest Section 2) the Waiakea Forest Section 3) the Olaa Forest Section and 4) Hawaii Volcanoes National Park (Fig. 2). Each of these sections represents a discrete geographical area, defined by easily recognizable features of the landscape. Furthermore, each area lies, for the most part, on distinctive substrates.

The first three sections are covered in the new map, while the vegetation in the remainder of Hawaii Volcanoes National Park has been adequately mapped by Mueller-Dombois and Fosberg (1974).

2.1 The Hamakua Forest Section runs from the Wailuku River, north to the boundary between the Laupahoehoe ahupua'a and Kukaiau Ranch. The upper forest boundary corresponds with the Forest Reserve boundary; land above this line is currently in pasture. Downslope, the forest extends to roughly 2000 feet (610 m) elevation, where it abruptly meets the sugar cane fields.

A major portion of this forest lies on deep ash substrates which originated from Mauna Kea. This area is therefore relatively old, as

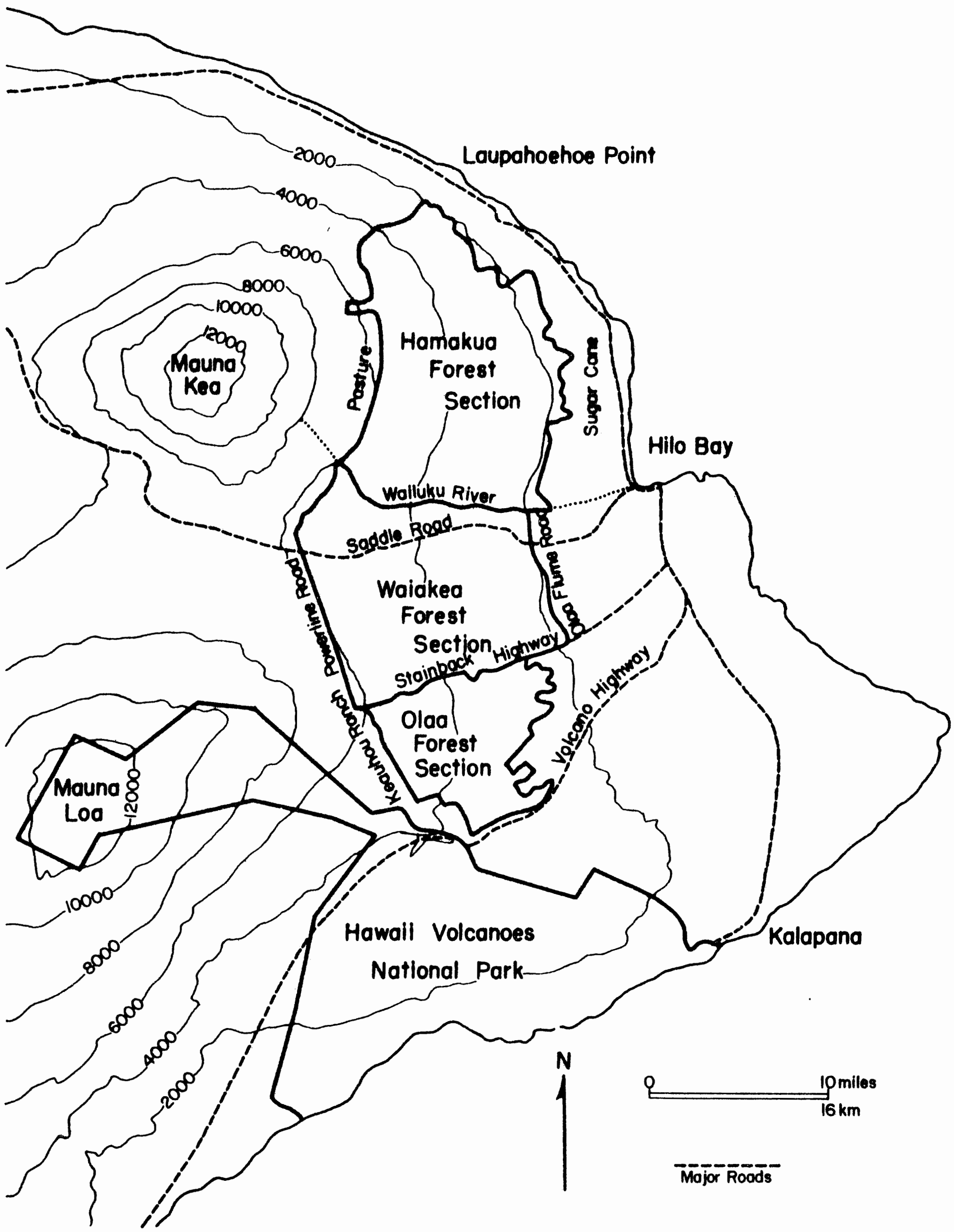

FIG. 2. Eastern Half of the Island of Hawaii Showing the Location of the Three Vegetation Map Sections in Relation to Hawaii Volcanoes National Park. Contour lines at 2000-foot intervals.

compared to the other two forest sections. The most recent eruption which occurred on this side of Mauna Kea took place approximately 3,600 years ago (Macdonald and Abbott 1970).

2.2 The Waiakea Forest Section extends from Stainback Highway, north to the Wailuku River, where it joins with the Hamakua Forest Section. On the preliminary vegetation map, the upper forest boundary follows the Powerline Road, at approximately 5,500 feet (1676 m) elevation, while the lower boundary was drawn along the Olaa Flume Road, at roughly 2,000 feet (610 m).

The substrates in this area all originated from the northeast rift of Mauna Loa, and consist for the most part, of relatively unweathered 'a'a or pahoehoe lavas. The flows range in age from 1942 for the youngest, to probably not much more than 1000 years old for the oldest.

2.3 The Olaa Forest Section map covers the area from the Volcano Highway north to Stainback Highway. This area includes 10,180 acres (4,120 ha) of land known as Olaa Tract, controlled by Hawaii Volcanoes National Park. The western boundary of this map runs along the Kilauea Forest Reserve-Keauhou Ranch boundary, while to the east, the map extends to where the native forest adjoins pasture land and/or exotic tree plantations at about 3,000 feet (914 m) elevation.

The northwestern corner of this forest lies on relatively recent lavas from Mauna Loa, some of which are covered by a shallow ash layer. The southeastern portion is on a deep ash substrate, which Macdonald and Abbott (1970) believe to be "pahala ash", deposited during the late Pleistocene. Recent carbon-14 determinations, however, indicate that at least the upper layer of this ash deposit originated from a violent eruption of Kilauea in 1790 (Jack Lockwood, USGS, pers. comm.).

3. Map Units and Vegetation Type Symbols

The vegetation units recognized in these three map sheets are identical, with some additions, to the units used to map a similar rain forest area on the southeastern side of the island of Hawaii (Jacobi, in prep.). Although the map symbols used here differ somewhat from those used for the map of Hawaii Volcanoes National Park by

Mueller-Dombois and Fosberg (1974), the vegetation units which they describe generally correspond with each other.

The map units are determined by four components of the vegetation: 1) overstory tree cover, 2) overstory tree height, 3) dominant tree species, and 4) species composition of the ground cover. The first three components deal with trees in the T1 and T2 vegetation layers (greater than 10 m and 5 to 10 m, respectively), while the ground vegetation refers to the H (i.e. herbaceous), S1 and S2 (i.e. shrub) layers combined, less than 5 m above the ground.

The symbols used on this map are made up of different combinations of the characters assigned for each of the four recognized components of the vegetation (Table 1).

The first three terms in a symbol refer to tree cover, tree height, and tree species composition, respectively. For example, the symbol "c3M(C)" describes a vegetation unit which has a closed tree canopy ("c" = 60 to 85% cover), composed of tall-statured trees ("3" = trees greater than 10 m tall), dominated by Metrosideros collina, which is abbreviated as "M". The term in parentheses always refers to the ground cover type, which in this case would be dominated by tree ferns, Cibotium spp. In cases where two or more tree species are co-dominant, the abbreviations for each of their names are given, separated by a comma, e.g. "c3M,Ac(C)".

In situations in which trees are entirely absent from a vegetation unit, only the ground cover term, in parentheses, is listed for the symbol. For example, "(b)" refers to an open, treeless bog.

Finally, in two cases, two vegetation types were found to be so closely intermixed at the scale chosen for this map, that they were not separated out on the vegetation map. Both cases occur on the Hamakua map section, and involve bog and forest type mosaics. In these cases, recognition of these mosaics are given in the vegetation symbol, with the predominant vegetation type listed first, followed by a slash, which is then followed by the less prevalent vegetation type. The two symbols in which this occurs are "c3M(C)/(b)" and "(b)/o3M(bs)".

Table 1. Components of the Vegetation Symbols.

1. Overstory tree cover

d = dense canopy; crown cover > 85%, most crowns interlocking
c = closed canopy; crown cover>60-85%, some interlocking crowns
o = open canopy; crown cover 15-60%
s = scattered trees; tree crown cover < 15%, with no distinct canopy

2. Tree stature

1 = very low-statured trees, 2-5 m tall (does not apply to the present map)
2 = low-statured trees,>5-10 m tall
3 = tall-statured trees, > 10 m tall

3. Dominant tree species

Ac = *Acacia koa*
Ch = *Cheirodendron trigynum*
M = *Metrosideros collina*

4. Ground cover type

(b) = open, treeless bog
(bs) = complex of shrubs and herbs on poorly drained substrate; includes *Broussaisia arguta*, *Clermontia* spp., *Pelea clusiaefolia*, *Dicranopteris linearis*, *Cibotium* spp., *Carex alligata*, *Juncus effusus*; epiphytic ferns and mosses abundant

(C) = ground cover dominated by tree ferns (*Cibotium* spp., primarily *C. glaucum*

(Dic) = ground cover dominated by *Dicranopteris linearis*

(mg) = mixed native grass complex; includes primarily *Deschampsia australis*

(ms) = complex of shrubs and ferns growing on a moist, but drained substrate in upper elevation forests; includes *Coprosma* spp., *Styphelia tameiameiae*, *Rubus hawaiiensis*, *Dryopteris paleacea*, and *Cibotium* spp.

(pg) = pasture grass complex; includes *Pennisetum clandestinum*, *Digitaria* spp., *Anthoxanthum odoratum*, *Axonopus affinis*, and *Holcus lanatus*

(pio) = pioneer shrub-fern complex on recent lava flows; includes *Vaccinium* spp., *Dubautia scabra*, *Coprosma ernodeoides*, *Dicranopteris linearis*, *Nephrolepis exaltata*, and *Lycopodium cernuum*

(sh) = mixed shrub-fern complex in mid- to low-elevation forests, on moist, but drained substrates; includes *Broussaisia arguta*, *Styphelia tameiameiae*, *Vaccinium calycinum*, *Coprosma* spp., *Dicranopteris linearis*, and *Cibotium* spp.

4. The Mapped Vegetation Types

Twenty-two vegetation types have been recognized for the study area on the preliminary vegetation map. Twelve of the more important of these units have been examined on the ground in great detail, through the establishment of relevés (vegetation samples) in selected locations. The remaining ten units either cover only a very small part of the total forest area, or do not differ enough from the 12 major units to warrant more detailed sampling.

Table 2 summarizes the 22 vegetation types, with an explanation of the vegetation type symbols and an indication of what map sections each is found on. The relevé numbers are also given for those types which were sampled in detail. The vegetation units in this case are arranged on the basis of overstory tree cover.

Table 3 lists the additional units found on the map which are either a combination of different vegetation types, or units which are not defined in the same manner as the vegetation types.

Table 2. Summary of the 22 Vegetation Types Recognized on the Preliminary Vegetation Map.

Map Symbol	Description of Vegetation Type	Map Segments[1]	Relevé No.
I. Units with a dense overstory tree canopy (canopy cover > 85%)			
d3M(ms)	Dense, tall-statured *Metrosideros* forest with a mixed, upper-elevation forest shrub ground cover	Wai	13,14
d3M(C)	Dense, tall-statured *Metrosideros* forest with a *Cibotium*-dominated ground cover	Olaa, Wai	23,33
II. Units with a closed overstory tree canopy (canopy cover 60-85%)			
c3M(ms)	Closed, tall-statured *Metrosideros* forest with a mixed, upper-elevation forest shrub ground cover	Ham, Wai, Olaa	not sampled
c3M,Ac(ms)	Closed, tall-statured *Metrosideros*-*Acacia* forest with a mixed, upper-elevation forest shrub ground cover	Ham, Wai, Olaa	6,7
c3M(C)	Closed, tall-statured *Metrosideros* forest with a *Cibotium*-dominated ground cover	Ham, Wai, Olaa	4,10,16,20,22,24, 27,32,35,36, 37,43
c3M,Ac(C)	Closed, tall-statured *Metrosideros*-*Acacia* forest with a *Cibotium*-dominated ground cover	Ham, Wai, Olaa	8,41
c3M(sh)	Closed, tall-statured *Metrosideros* forest with a mixed, mid-elevation shrub ground cover	HVNP	30
III. Units with an open overstory tree canopy (canopy cover 15-60%)			
o3M(bs)	Open, tall-statured *Metrosideros* forest with a mixed shrub ground cover, on poorly drained substrate. Many of the areas experiencing moderately fast, wetland dieback were mapped with this unit.	Ham, Wai, Olaa	1,3,5,11,15,19, 25,28,39
o3M(C)	Open, tall-statured *Metrosideros* forest with a *Cibotium*-dominated ground cover	Ham, Wai, Olaa	12,18,21,26,29, 31,34,38,42

Table 2 (Continued).

Map Symbol	Description of Vegetation Type	Map Segments[1]	Relevé No.
III. Units with an open overstory tree canopy (continued)			
o3M,Ac(C)	Open, tall-statured *Metrosideros-Acacia* forest with a *Cibotium*-dominated ground cover	Olaa	not sampled
o3M(mg)	Open, tall-statured *Metrosideros* forest with a mixed, native-grass ground cover	Wai	not sampled
o3M(pg)	Open, tall-statured *Metrosideros* forest with a mixed pasture grass ground cover	Wai	not sampled
o3M(sh)	Open, tall-statured *Metrosideros* forest with a mixed, mid-elevation shrub ground cover	Wai	not sampled
o2M(pio)	Open, low-statured *Metrosideros* forest with a pioneer shrub complex ground cover, on relatively recent lava flows	Wai	9
IV. Units dominated by the ground cover vegetation, with scattered trees			
s3M(bs)	Mixed shrub complex, with scattered tall-statured *Metrosideros* trees, on poorly drained substrate	Wai	not sampled
s3M,Ch(C)	Community dominated by *Cibotium* tree ferns, with scattered, tall-statured *Metrosideros* and *Cheirodendron* trees	Olaa, Wai	not sampled
s3M(Dic)	Community dominated by *Dicranopteris* fern, with scattered, tall-statured *Metrosideros* trees	Olaa, Wai	not sampled
s3M(mg)	Community dominated by native grasses, with scattered, tall-statured *Metrosideros* trees	Wai	not sampled
s3M(pg)	Pasture community, with scattered, tall-statured *Metrosideros* trees	Wai	not sampled

Table 2 (Continued).

Map Symbol	Description of Vegetation Type	Map Segments[1]	Relevé No.
V.	Units without any trees present		
(b)	Open, treeless bog	Ham, Wai	2,17,40
(mg)	Mixed native grassland	Wai	not sampled
(pg)	Pasture land	Wai	not sampled

[1]Map Segments: Ham = Hamakua Forest Section, Wai = Waiakea Forest Section, Olaa = Olaa Forest Section, HVNP refers to the Vegetation Map of Hawaii Volcanoes National Park (Mueller-Dombois and Fosberg 1974).

Table 3. List of Additional Units Found on the Map which are either Combinations of Different Vegetation Types, or Units which are not Defined in the Same Manner as the Vegetation Types.

Map Symbol	Description	Map Segments[1]
I. Map units which are combinations of different vegetation types		
c3M(C)/(b)	Closed, tall-statured *Metrosideros* forest with a *Cibotium*-dominated ground cover, mixed with treeless bogs	Ham
(b)/o3M(bs)	Predominately treeless bog areas with scattered patches of open, tall-statured *Metrosideros* forest with a mixed shrub ground cover, on poorly drained substrate	Ham
II. Map units which are not defined in the same manner as the vegetation types		
NM	Areas within the mapped segments which are highly disturbed by man's activities, (e.g. cleared areas around buildings)	Wai, Olaa
XP	Areas which have been heavily disturbed by conversion of native forest to exotic tree plantations	Wai, Olaa

[1]Map Segments: Ham = Hamakua Forest Section, Wai = Waiakea Forest Section, Olaa = Olaa Forest Section

III. SOIL MOISTURE REGIMES AND HABITAT CLASSIFICATION (D. Mueller-Dombois)

1. Introduction

The term "soil moisture regime" has a two-fold meaning. It applies to spatial as well as temporal variations in the soil moisture conditions of an area. For the purpose of this study, we were concerned first with the spatial variations, i.e. we evaluated a habitat first according to its normal or average soil moisture status. Seasonal, year-to-year, or other forms of recurring variations in soil moisture are of equal importance in the characterization of a soil moisture regime of a site. But we considered these dynamic variations as superimposed on a given site and thus treated them at a secondary level for the purpose of this initial investigation. Further work needs to be done to assess these temporal variations adequately.

For a useful frame of reference in the spatial-gradient-sense the term soil moisture regime can be related to familiar concepts, such as "well drained" and "poorly drained." To make such a concept or soil moisture status designation useful to others, a given land-area has to be studied for its spatial soil moisture regime variations, and these variations then have to be defined in appropriately descriptive terms.

2. Evaluation of Soil Moisture Regimes

We dug one or two soil pits in each of the 43 relevés. The soil profiles were described by conventional techniques, i.e. by horizontation-depth and kind, soil color, texture, structure, consistency, rooting, and horizon-boundary characteristics. Samples (usually 4 to 6) per profile were taken for further analysis in the laboratory. In addition, special records were taken of soil depths, water table depths, underlying bedrock (pahoehoe or aa) where present, hardpans of different kinds (where present), overall textural profile, rooting depth and abundance pattern, general surface-soil and soil-drainage conditions and vegetation covering the pit. In terms of soil-surface analysis we ran a predetermined 50-point transect through each relevé, whereby a record was kept of the number of points intercepting drained or undrained soil surfaces. Each relevé site was also assessed in terms of its microtopographic position, whether it was level and flat or sloping (to what degree) and whether it was convex (usually associated with some run-off) or depressional (often associated with some run-on during and after heavy showers).

3. Soil Moisture Regime Definitions and Variations within Regimes

Upon analyzing the 43 relevés it became apparent that the soils of the rain forest terrain vary greatly in depth (from about 10 cm to very much over 2 m); slightly in texture (from sandy clays to clays); somewhat in microtopography (most are on flat or gently sloping surfaces); and considerably in drainage conditions.

The following five soil moisture regime types can be recognized based on the drainage conditions of the rain forest sites studied.

3.1 Moderately dry or mesic (8 relevés). Soils belonging to this moisture regime are well-drained and have no boggy depressions. They fall into two groups:

a) Shallow (8-15 cm) organic clay, muck or peat (i.e. histosol) over permeable, relatively recent, pahoehoe lava. Represented by three relevés along the Saddle Road, i.e. #12, 13 and 14, from 4000 to 5000 feet elevation, and by one relevé (#16) at Stainback Highway from lower elevation (1270 feet).
b) Moderately deep (0.5 m) to deep (1.5 m) soil from volcanic ash, of a sandy clay texture with pumice inclusions over permeable, relatively recent, pahoehoe lava. Represented by four relevés in Hawaii Volcanoes National Park, Kilauea Iki area, #18, 20, 26 and 30.

3.2 Moderately moist (7 relevés). Soils are moderately well drained and fall into three groups:

a) Deep soils from volcanic ash consisting of well-aggregated silty clay, deeply permeable without any hardpan. Represented by four relevés in Hawaii Volcanoes National Park, Olaa Tract, #21, 22, 29 and 32.
b) Deep soils from volcanic ash consisting of well-aggregated clay (somewhat finer in texture than above), occurring on knoll or raised ash deposits (probably former ash dunes). Represented by relevé #4 along Wailuku Road on the mauka side of a treeless bog, east slope of Mauna Kea.

c) Shallow to moderately deep soils (30 to 50 cm) of dark-brown silty clay over moderately well drained aa lava. Represented by two relevés in the Puu Makaala area, #23 and 33.

3.3 Moist (16 relevés). Soils in this moisture-regime type are moderately well to poorly drained, which means that under normal conditions there are pocket areas with water standing at or on the soil surface. However, these wet pockets occupy less than 50% of the area. Soils in the moist category show six recognizable variations:

a) Shallow (up to 25 cm deep) very blackish brown muck or silty clay over aa with strongly undulating microtopography, i.e. differences between hummocks and depressions can be 2 m. The depressions are the wet pockets. Represented by two relevés, #6 and 7, at higher elevations (5000-5200 feet) on the east slope of Mauna Kea, near Nauhi and Spring Water Camps, Hamakua Forest Section.

b) Shallow (up to 26 cm) mucky silty clay over aa lava, which forms slightly elevated ridges cutting across poorly drained pahoehoe lava at mid-elevation (2800 to 4500 feet). Represented by relevés #10 (near 42 Lava Flow), #24 and #39 along Tree Planting Road, Waiakea Forest Section.

c) Very shallow and discontinuous (i.e. pocket-like) muck on poorly drained (relatively recent, 120 year-old) pahoehoe lava. Represented by relevé #9, an immature ohia stand on 1855 Lava Flow near Saddle Road.

d) Shallow (up to 25 cm) dark brown mucky silty clay over very undulating, "massive", pahoehoe with limited drainage, but less than 50% undrained. Represented by Tree Planting Road relevés #27, 28 and relevés #34, 35 and 36 at Disappointment Road in Puu Makaala area.

e) Deep, massive, reddish brown "lateritic" clay, well weathered, with bedrock mostly far below rooting zone. Represented by two low-elevation (1800-2000 feet) ohia-koa relevés #8 and 41 and by Wailuku stream-bank relevé #42 at 3620 feet elevation.

f) Deep, silty clay, less weathered soils from layered ash with incipient hardpans in shallow depressions of the habitat. Less than 50% of the surface area poorly drained. Represented by two Olaa Tract relevés #31 and 38.

3.4 Very moist to wet (9 relevés). Soils in this moisture regime class are poorly drained, which means that under normal conditions more than 50% of the surface is either completely water soaked or is slightly under water. Soils of this moisture regime type showed four major variations:

a) Shallow (10-15 cm) black muck over poorly drained aa lava in flat, slightly depressional area. Represented by relevé #43 at Tree Planting Road.
b) Shallow to moderately deep (60 cm) black muck over poorly drained pahoehoe forming large, flat terrains. Represented by relevés #01 and #03 along Wailuku Road, #11 near 42 Lava Flow, #15 Dr. Ko's plot along Saddle Road, #25 along Tree Planting Road from Stainback Highway, and #37 Puu Makaala "hotspot" dieback area.
c) Shallow to moderately deep (40 cm) silty clay over bedrock (probably aa lava). Represented by relevé #19 (stand with some koa), north 100 m from Wailuku Stream at 2800 feet elevation.
d) Deep, well weathered, lateritic reddish brown clay with incipient hardpan at 50 cm. Soil from ash, hardpan probably from decaying rock, can be crushed by hand. Represented by relevé #05, about 1 km north of Wailuku Stream, at 3600 feet elevation, along Carson's trail.

3.5 Extremely wet (3 relevés). These are true swamps or bogs with either sparse stunted shrubby ohia trees or completely treeless. They occur on deep mucky gley soils, soft and soggy, completely water soaked with water tables at or above the surface. Bedrock may be absent or occur in lower profile at 40 cm depth or deeper. Occasional rockoutcrops can be encountered. These swamps appear to have resulted from silting-up of the surface in areas where the laterally-moving drainage water has found no or only limited outflow. Represented by relevés #02 (treeless swamp) at Wailuku Road at 3600 feet, #17 northside of Wailuku Stream at 3780 feet, and #40 near Kapuhe Stream at 1920 feet elevation.

4. Habitat Classification

4.1 Definition of habitat and habitat type. A habitat is here defined conventionally as a place or site in the field with all its important abiotic and biotic factors acting upon this site, although these factors may not all be known at this time. In other words a habitat is considered to be the physical substrate of the plant and animal community and the atmospheric and biotic factors affecting this site. The size or boundaries of a habitat are defined by the relative homogeneity of the substrate itself, but the plant community may be used sometimes as an indicator of habitat boundaries provided that the relationships between plant community and substrate are worked out. This second aspect, the use of the plant community as an indicator of the physical habitat, is of great utility in the interpretation of a vegetation map. This point will be addressed below in Chapter VI, 1. Another problem in the definition of habitat is its relative size. Here, the size-scale concept of habitat is taken to represent the large map-scale range, i.e. spatial habitat variations that are recognized in the field should be mappable at a scale from 1:5000 to 1:50,000. Therefore, they correspond to the degree of detail in variation as recognized for the structural vegetation map-units.

A habitat type, as in all other type concepts, refers to the abstraction made from a number of samples. Thus, a habitat type ideally represents, as a norm, a number of similar habitats in the field.

4.2 Habitat series and their variations. Based on our samples of variations within soil moisture regimes, it is possible to distinguish two major habitat series, and 14 habitat types, i.e. seven habitat types per series.

a) Shallow-soil habitats (soils up to about 50 cm deep overlying pahoehoe or aa lava)

Habitat type 1: Mesic or moderately dry.
Histosol over permeable pahoehoe. (Saddle Road relevés #12, 13, 14 and Lower Stainback Highway relevé #16).

Habitat type 2: Moderately moist.
Dark reddish-brown clay over aa lava. (Puu Makaala relevés #23, 33).

Habitat type 3: Moist.
Shallow mucky clay over imperfectly drained pahoehoe lava. (Disappointment Road relevés #34, 35, 36, and Tree Planting Road relevés #27, 28).

Habitat type 4: Moist.
Discontinuous pocket soil over imperfectly drained pahoehoe. (Immature stand relevé #9 at Saddle Road).

Habitat type 5: Moist.

Shallow mucky clay over aa with silty clay in fissures, upper-slope subtype; (relevés #6, 7); low-ridge subtype, (relevés #10, 24, 39 at Tree Planting Road).

Habitat type 6: Very moist to wet.

Shallow mucky clay over poorly drained pahoehoe. (Relevés #01, 03, 11, 15, 19, 25, 37).

Habitat type 7: Very moist to wet.

Shallow mucky clay over poorly drained aa lava. (Relevé #43).

b) Deep-soil habitats (soils from about 50 cm depth to much greater depths).

Habitat type 8: Mesic or moderately dry.

Well-drained soils of sandy clay texture of 0.5-1.5 m depth overlying permeable bedrock. (Relevés #18, 20, 26, 30 in Kilauea Iki area, Hawaii Volcanoes National Park).

Habitat type 9: Moderately moist.

Over 1 m deep soils of well-aggregated silty clay, deeply permeable without hardpan. (Olaa Tract relevés #21, 22, 29, 32, and Wailuku Road relevé #04).

Habitat type 10: Moist.

Deep silty clay with incipient, discontinuous hardpans. (Olaa Tract relevés #31, 38).

Habitat type 11: Moist.

Deep, soft, well-weathered, massive clay. (Relevés #8, 41 above sugar cane fields on Mauna Kea, and relevé #42 on Wailuku Stream bank).

Habitat type 12: Very moist to wet.

Deep, soft, well-weathered, massive clay with incipient hardpan. (Relevé #05 near Wailuku Stream).

Habitat type 13: Extremely wet.

Deep, mucky, soft clays with water table at or above surface most of the year = treed swamp. (Relevés #17, 40).

Habitat type 14: Extremely wet.

Deep, mucky, soft clay with water table at surface, probably surface completely submerged after heavy shower-activity = treeless swamp. (Relevé #02 at Wailuku Road).

4.3 General distribution of the habitat types. Table 4 gives a summary of the 14 habitat types by location of relevés with reference to the vegetation map sheets, which are enclosed with this report.

From this location analysis, one can see that the deep-soil rain forest habitats are in two general locations of the study area, i.e. in Hawaii Volcanoes National Park in both the Kilauea Iki area and the Olaa Forest Tract, and then again much further north on the east-flank of Mauna Kea, beginning on the north side of Wailuku Stream (Hamakua Forest Section map) and extending beyond the most northern relevé #8, which is downslope of the Piha Forest Reserve, at 1900 feet elevation. There may be a few localized deep-soil habitats in the area in-between, i.e. from Puu Makaala to Wailuku Stream. But these are expected to be small, such as found under relevé #04 at Wailuku Road (N-central on Waiakea Forest Section map), which occurs on a deep-soil knoll, probably representing a former ash-dune. Thus, the vast terrain from the Puu Makaala area on northward (i.e. from the northern half or one-third of the Olaa Forest Section map) across Stainback Highway and the entire Waiakea Forest Section map, including the area northward across the Saddle Road, the rain forest occurs on shallow soils underlain by lava rock. Most of this is pahoehoe, but there are a good number of aa flows also. The latter are usually narrower, i.e. not as widespread laterally along the contours as are the pahoehoe flows.

All of these flows seem to have originated from Mauna Loa. There is, however, another shallow soil habitat at the 5000 foot area on Mauna Kea. This is covered by the rain forest in the lower Piha Forest Reserve, on the Hamakua Forest Section map. Here the outcropping aa flow has undoubtedly originated on Mauna Kea.

Superimposed over the study area is a median annual rainfall gradient, which increases from south to north roughly as shown on Table 5.

This increase from nearly 2 m rainfall to over 7 m coincides with a very gradual decrease in elevation from 4000 to 2000 feet. The change along the contours is not quite as drastic, i.e. at 2000 feet in the rain forest of Hawaii Volcanoes National Park it rains about 3.5 m per year and at 4000 feet on Mauna Kea below Piha the median annual rainfall is about 4.8 m. Therefore, at 4000 feet the increase in rainfall from the Park to below Piha is 2.8 m, at 2000 feet the increase is 3.5 m.

Table 4. Summary of the 14 Habitat Types by Location of Relevés.

Shallow-Soil Habitats	Deep-Soil Habitats
Mesic or moderately dry substrates	
1. Saddle Road relevés #12, 13, 14, Waiakea Forest Section Map, NE area, from 4200' to 5020' elevation. Lower Stainback Highway relevé #16, SE corner off Waiakea Map.	8. Kilauea Iki relevés #18, 20, 26, 30, between 4800-4000' elevation. Mapped on Hawaii Volcanoes National Park Vegetation Map, not on any enclosed map sheet. South of Olaa Forest Section Map.
Moderately moist substrates	
2. Puu Makaala relevés #23, 33 N on Olaa Forest Section Map, 3600-3800' elevation.	9. Olaa Tract relevés #21, 22, 29, 32. S. on Olaa Forest Section Map. 3800-4000' elevation. Wailuku Road relevé #04. N-center on Waiakea map, 3600' elevation.
Moist substrates	
3. Disappointment Road relevés #34, 35, 36 in Puu Makaala area N on Olaa Forest Section Map, 3600-3800' elevation. Tree Planting Road, relevés #27, 28. SE on Waiakea Forest Section Map.	10. Olaa Tract relevés #31, 38 near center on Olaa Forest Section Map. 3900-4000' elevation.
4. Saddle Road relevé #9. Immature stand on 1855 Lava Flow. NE on Waiakea Forest Section Map, 2600' elevation.	11. Mauna Kea relevés #8, 41 at low elevation, 1900', above sugar cane fields. NE and E on Hamakua Forest Section Map. Also Wailuku Stream relevé #42, at 4620' elevation, SW on same map.
5. Mauna Kea relevés #6, 7, on upper slope (5000') in rain forest terrain, Piha Forest Reserve. NE on Hamakua Forest Section Map. Also low-ridge type relevés #10, 39 on Tree Planting Road, SE on Waiakea Forest Section Map (3300-3400'), and #24 NE on Olaa Forest Section Map (3150').	

Table 4 (Continued).

Shallow-Soil Habitats	Deep-Soil Habitats
Very moist to wet substrates	
6. Wailuku Road relevés #01, 03, N-central on Waiakea Forest Section Map, 3600' elevation. Wailuku Stream relevé #19, S on Hamakua Forest Section Map, 2820'. Saddle Road relevé #15 and Tree Planting Road relevés #11, 25, Waiakea Forest Section Map (3200'-3500' elevation). Puu Makaala relevé #37, N on Waiakea Map (3800').	12. Wailuku Stream relevé #5, along Carson's Trail. SE on Hamakua Map, 3600' elevation.
7. Tree Planting Road relevé #43. On Waiakea Map, 3300' elevation.	
Extremely wet	
	13. Treed swamp relevés on Mauna Kea, #17 at 3780', #40 at 1920', both on Hamakua Map.
	14. Treeless swamp relevé #02 on Mauna Kea, N-center on Waiakea Map, 3620' elevation.

Table 5. Median Annual Rainfall Gradient from South to North over the Study Area.*

Area	Median annual rainfall inches	millimeters
Kilauea Iki (northern side, 4000')	80	1960
Olaa Tract (3900')	85	2080
Puu Makaala (3700')	90	2200
Tree Planting Road (south part, 3400')	100	2450
Saddle Road (3200')	150	3670
Wailuku Stream (3000')	200	4900
Honohina Forest Reserve with relevé #8 (2000')	300	7350

* Data extracted from U. S. Weather Bureau map, reproduced on p. 41 in Atlas for Bioecological Studies in Hawaii Volcanoes National Park (Doty and Mueller-Dombois 1966).

This rainfall gradient certainly has an influence on the soil moisture regimes. In the deep-soil habitats there is an increase in the fineness of soil texture, which coincides with the rainfall increase along the spatial gradient as follows:

Area	Soil Texture	Moisture Regime	Annual Rainfall
Kilauea Iki	Sandy clay	Mesic	1960 mm
Olaa Tract	Silty clay	Moderately moist and moist	2080 mm
from Wailuku Stream northward	Massive clay	Moist and very moist to wet and extremely wet (swamps)	~4000 mm to 7350 mm

However, no obvious correlation exists between the rainfall gradient and the soil moisture regimes of the shallow-soil habitats. For example, moderately dry or mesic substrates occur in the relatively high rainfall area at the Saddle Road, from 4000 to 5000 feet elevation. Here the median annual rainfall ranges from about 4.5 m to 3 m over this altitudinal segment. Very moist to wet substrates occur in the Puu Makaala area, where it rains only about 2.2 m per year. Thus, on the shallow-soil habitats, moisture regime is probably related more to the geological recency of the underlying lava and its physical make-up, rather than to the amount of incoming moisture.

A general relationship of soil moisture regime and rainfall exists however with elevation in the rain forest terrain. The mesic sites along the Saddle Road are found only in the area above 4000 feet elevation. Further down, where the rainfall is higher, even rather recent substrates may be of the moist type of water regime, as is exemplified by our relevé on the 1855 lava flow (#9).

Downslope in the Hamakua Forest Section, the soil moisture regimes increase from moist in the lower Piha area (relevés #6 and 7, near 5000 feet elevation) to very moist to wet throughout the mid-slope area (from 4500-3000 feet) to extremely wet (i.e. swampy) in pockets of one acre to 10 hectares (roughly) in size (from 2800-2300 feet). The swamps decrease in size downslope and disappear at about 1900 feet, where the surrounding terrain is mostly in the moist soil-water regime category as exemplified by relevés #8 and 41. The annual rainfall gradient along this downslope transect increases from about 3.5 m to 7.3 m. Thus, the larger swamp areas receive as much or somewhat less rainfall than the smaller swamp areas below. In this area, soil moisture regimes are more closely related to local topography and its lateral drainage as afforded by position relative to streams.

5. Correlation of Habitat Types and Vegetation Map Units

In Table 6, the habitat types are compared to the vegetation units as mapped on the accompanying map sheets.

There appears to be very little correlation between the structural vegetation units and the various habitat types. For example, dense, tall ohia stands (symbol d3M) occur on shallow soils ranging in moisture regime from mesic to wet; likewise closed (c3M) and open, tall ohia forests (o3M) occur on the whole range of moisture regimes on shallow-soil habitats. However, no dense forest stands were found on the deep-soil habitats (no's. 8-14), and closed forests were found only on mesic to moist, deep-soil habitats. On very moist to extremely wet deep-soil habitats, we found only open forests, and it is unlikely that any closed forests will be found on these habitats. On shallow soils (habitat types 1-7), most of the open forests were found on very moist to wet, poorly drained pahoehoe substrates (habitat type 6). On deep soils (habitats 8-14), open forests were equally common on all moisture regimes. Low-stature forests (o2M) were found on moist, shallow soil habitats (no. 4) and on extremely wet habitats (no. 13). In the first case the low-stature stand is a function of the recency of the lava flow, in the second case, the low-stature stands reflect the swamp situation.

One may conclude that it is next to impossible to predict the habitat type from the structure of the rain forest, which formed the basis for the map units in this rain forest terrain. For predicting soil moisture regime and habitat types it is, therefore, necessary to look for other indicators

Table 6. Habitat Types in Relation to the Vegetation Map Units.

Habitat type	Relevé number	Vegetation Map unit
1. Mesic; shallow soil on permeable pahoehoe lava	13,14 16 12	d3M(ms) c3M(C) o3M(C)
2. Moderately moist; shallow soil on moderately well-drained aa lava	23,33	d3M(C)
3. Moist; shallow soil on imperfectly drained pahoehoe	35,36 27 28,34	d3M(C) c3M(C) o3M(bs)
4. Moist; discontinuous pocket soil on imperfectly drained pahoehoe	9	o2M(pio)
5. Moist; shallow soil on imperfectly drained aa:		
upper-slope subtype	6,7	c3Ac,M(C)
low-ridge subtype	10,24 39	c3M(C) o3M(bs)
6. Very moist to wet; shallow soil on poorly drained pahoehoe	37 01,03,11, 15,19,25	d3M(C) o3M(bs)
7. Very moist to wet; shallow soil on poorly drained aa	43	c3M(C)
8. Mesic; moderately deep to deep sandy clay soil, well drained	20,30 18,26	c3M(C) o3M(C)
9. Moderately moist; deep silty clay soil, moderately and evenly drained	04,22,32 21,29	c3M(C) o3M(C)
10. Moist; deep silty clay with incipient, discontinuous hardpans, unevenly drained	31,38	o3M(C)
11. Moist; deep massive clay with moderately lateral drainage	8,41 42	c3M,Ac(C) o3M(bs)

Table 6 (continued).

	Habitat type	Relevé number	Vegetation Map unit
12.	Very moist to wet; deep massive clay with incipient hardpan and poor lateral drainage	05	o3M(bs)
13.	Extremely wet; deep, mucky soft clay with water table at or above surface	17,40	o2M(bs) [too small for correct mapping in areas sampled]
14.	Extremely wet; deep, mucky, soft clay, surface probably submerged for longer periods than in habitat 13	02	b = treeless swamp or bog [too small for correct mapping in area sampled]

than forest structure. On air photos, such indications may be obtained in part by the vegetation-type mosaic of a subarea and in part through closer recognition of the associated vegetation, for example, the presence or absence of *Acacia koa*, the dominance of tree ferns (*Cibotium* spp.), the prevalence of creeping herbaceous ferns (primarily *Dicranopteris* spp.), and other associated vegetation patterns. This aspect will receive further investigation.

IV. OHIA POPULATION STRUCTURES IN "HEALTHY" AND "DIEBACK" SITUATIONS

(Ranjit G. Cooray, James D. Jacobi and D. Mueller-Dombois)

1. Introduction

Structural analyses of ohia forest stands were made using two different methods of sampling. Belt-transects (each 6 m wide) were established in two areas of known forest condition. These transects were run for a considerable distance through whatever variation of forest condition was encountered along the predetermined transect course. The first transect was started in a "severe" ohia decline area at 4200 feet elevation, 3.6 km north of the Saddle Road on Mauna Kea (see First Progress Report, December 75: 8). This transect was run continuously over a distance of 2000 m. The second belt-transect was started in a typically "healthy" or non-decline forest at 3600 feet elevation south of Stainback Highway. This transect was run continuously over a distance of 500 m.

Even though the total belt-transect sample represents a detailed quantification of ohia populations along a distance of 2.5 km, it was felt that some important forest conditions and habitats may not have been encountered in the two transects.

For this reason, structural analyses with similar recording formats were included in the relevé analyses. The guiding factor for locating the relevés was the total variation in pattern noted on the air photographs. Relevés (400 m^2 samples) were placed into as many patterns of air photo and vegetation-structural variations as could be handled in the two-year time frame of this investigation. Thirty-three relevés (no's. 11-43) were analyzed for their ohia population structures. The structural analysis results of these relevés are believed to provide an estimate of the degree of representativeness of the belt-transect analyses. They also were thought to complement the belt-transect results with hitherto unknown structural patterns of ohia stands.

The structural analysis procedures were already given in some detail in previous reports.

2. Ohia Tree Population Structure in a Severe Dieback Stand

For the purpose of quantitatively separating a so-called "dieback" forest from a "healthy" or non-dieback forest, we developed first a vigor classification for individual trees. Two major classes were self-evident, namely dead standing trees (snags) and live trees. Any tree, which had no foliage at all was considered dead. If a tree had only a little foliage left, it was considered alive.

Within the snag category we recognized two classes, namely old snags and recently dead trees. Snags were recognized as old, when most of the thinner branches or branchlets had fallen off and wherever the bark was exfoliated and had dropped off exposing a skeleton tree trunk which resembled a whitish telephone pole. Recently dead trees were recognized as snags with most of their fine branchlets still on the tree, but from which all the foliage had gone. These two separations presented few problems. Most snags were easily identifiable as either old or recent.

Within the live-tree group we recognized three vigor classes as follows:

Class 1 "healthy" trees, which were those with fully foliated crowns;

Class 2 "crown-dying" trees, which were those on which the crown top-half showed obvious signs of deterioration in terms of loss of foliage. Trees in this class had a few barren branches in the upper crown;

Class 3 "trunk-sprouted" trees. Trees in this class were clearly "stag-headed" (i.e. with most crown branches barren), but they also showed a number of lateral branches along the trunk. Trunk-sprouting is found on many trees that appear dead from the air or on air photos. Trunk-sprouting on ohia trees is probably a response to some stress.*

All ohia trees 5 m tall and taller, which were enumerated by diameter at breast height (dbh) along the belt-transects, were classified into either one of the five vigor classes.

From this vigor rating of the individual trees, we classified the forest along the belt-transects into either of two forest condition classes, namely "dieback forest" and non-dieback or "healthy" forest. A dieback forest was recognized where the majority of trees (i.e. >50%) were snags and trunk-sprouted trees with "stagheads."

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*Further research is needed on this tree group to clarify the reasons for lateral sprouting.

The 2 km long Saddle Road transect was started in a typical or severe dieback forest, where the majority of trees were in the lower three vigor classes. This dieback situation continued for 1.3 km, from whereon we encountered "healthy" or non-dieback forest. From hereon, for the remaining 0.7 km, the majority of trees were in vigor class 1 or 2. This 700 m belt-transect segment was therefore classified as "healthy" or non-dieback forest.

The ohia tree population structure of the 1.3 km belt-transect is portrayed on Fig. 3. This is the "dieback" segment. The diagram shows the number of trees in 5 cm diameter classes over the size range encountered, which goes from 5 cm to 70 cm dbh. Over this diameter range the trees ranged in height from over 5 m to about 20 m tall. Each histogram block shows the number of trees of that diameter class in whatever vigor class they were recorded, starting with vigor class 1 (healthy trees) at the bottom, where present, and ending with vigor class 5 (old snags) at the top. It can be seen that old snags occurred in nearly all size classes encountered. The biggest trees (65-70 cm dbh class) were only present as old snags.* From here on down to diameter class 35, there were very few (<5) healthy trees per hectare. In fact the entire ohia tree population of this dieback segment shows only few really healthy, i.e. full-crowned trees. The largest number was 42/ha in the 10 cm dbh class. An interesting aspect is the proportionately large number of trunk-sprouted trees, which are the trees which have mostly dead crowns, but lateral branches, which are foliated. These trees and the snags give the striking dieback appearance to this stand. It should also be noted that these trunk-sprouted trees and the old snags are rather numerous in the 10 to 25 cm dbh class, which gives an indication of the rate of the dieback in this stand. It must have gone on for quite some time, and a large proportion of the trees still hang on to a "marginal" existence (i.e. the trunk-sprouted ones). Also note that the proportion of recently dead trees and that of crown-dying trees is relatively smaller, which supports the idea that the dieback is not occurring at a very fast rate, i.e. probably not under 10 years, but rather over a 20 to 40 year period. However, a 20 to 40 year period is still relatively fast for a generation of ohia trees, which may be guessed at about 200 to 300 years. Unfortunately, we cannot determine

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* Diameter measurements uncorrected for bark loss.

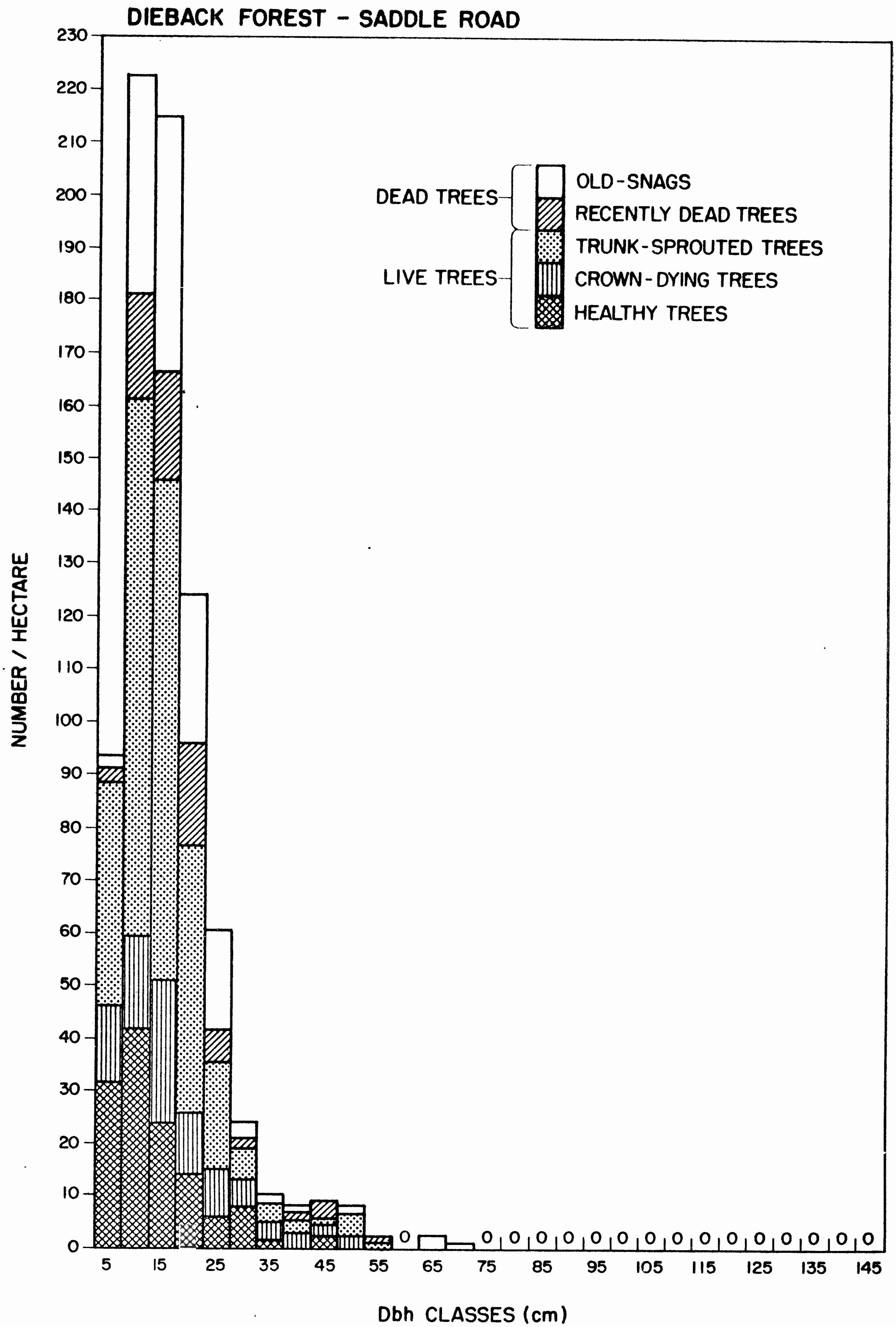

FIG. 3. Ohia Tree Population Structure in 1.3 km Dieback Segment of

tree ages from increment borings in this environment, and there are no studies as yet that give a reliable estimate of the rate of growth of ohia trees in these rain forest habitats.

The histogram blocks show a modal curve, which is strongly skewed to the left. This curve-shape is evident, whether one connects the total blocks giving all trees per size class or whether one connects only the "healthy" trees at the bottom of the diagram. This curve-shape indicates a one-generation ohia stand, because it has a single, steep mode combined with a relatively narrow size range. Such a curve-shape is characteristic for pioneer-tree species in general. However, the skewed modal curve in this stand has an important additional meaning, which should be emphasized. The dieback has occurred in a one-generation stand, where it has reduced this tree generation to a small remnant population of healthy trees. The dieback has resulted in a drastic opening-up of the canopy. Whether the remnant healthy population will also die with the other members of this generation is an interesting question which cannot be answered at this time.

3. Ohia Tree Population Structures in Healthy Stands

Figure 4 shows population structures of the taller (>5 m) ohia trees in two healthy stands; A: along the remaining 700 m segment of the Saddle Road transect and B: along the 500 m Stainback Highway transect. Both stands have more than 70% of their ohia populations in vigor class 1 (healthy trees).

The Saddle Road stand has trees distributed over a wide range of diameter classes, from 5 cm to 140 cm dbh. There are only few big-diameter trees present, but it is remarkable that these still show maximum vigor. Here it seems unlikely that the trees are all of the same generation as in the previously discussed dieback stand. When one connects the tops of the histogram blocks by a curve, it will be seen that the population curve for this stand is bimodal. One population mode occurs at 70 cm dbh, another at 20 cm dbh. Although the mode at 70 cm dbh is not pronounced, there is a much greater size range on Figure 4A as compared to Figure 3. Conservatively, one may speak of a two-generation stand on Figure 4A, whereby the older generation, here the bigger trees, have become reduced to a very small number of remnant trees. The smaller-diameter tree population, which presumably represents the younger generation, may extend over a diameter range from 5 to 55 cm, which correlates well with the diameter range of the neighboring dieback stand on Figure 3. The number of healthy

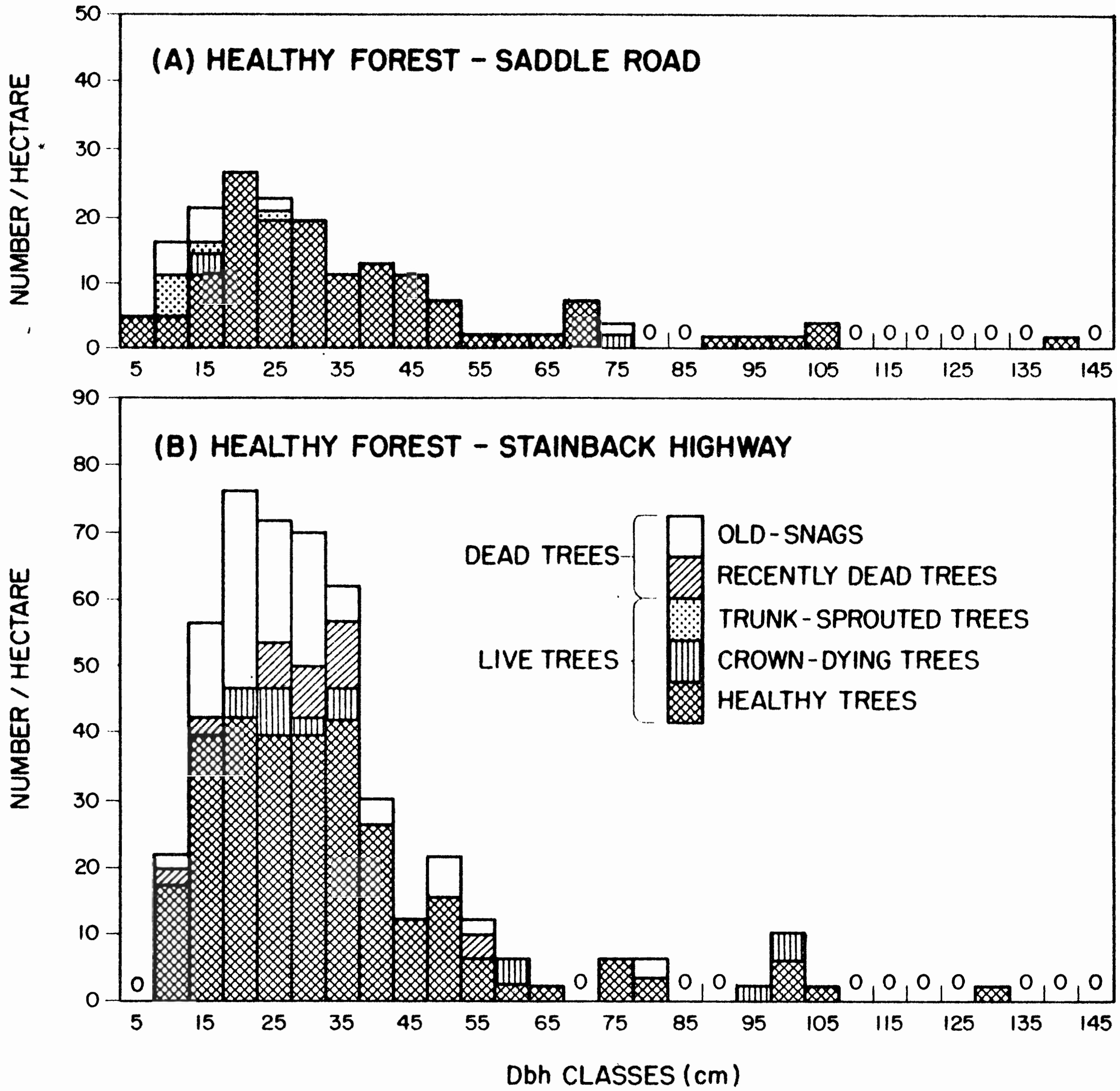

FIG. 4. Ohia Tree Population Structures in Two "Healthy" Forest Segments:

A the 700 m Belt-Transect Segment at Saddle Road
B the 500 m Belt-Transect Segment at Stainback Highway

trees in this non-dieback forest is not much greater than the number of healthy trees in the neighboring dieback forest. It might appear that this openly stocked stand may have gone through a dieback phase and that we are witnessing a remnant adult tree population. However, this is unlikely, since we found not many more dead trees lying on the ground than in the neighboring dieback stand. What seems more probable is that the few widely scattered big-diameter trees of the earlier generation represent a remnant population, which has gone through a dieback phase some time ago, and then gave rise to this second generation stand of lower density. The two stand segments along the Saddle Road transect occur on two different moisture regimes and habitats. The dieback segment occurred largely on habitat type 6 (very moist to wet, shallow soil over poorly drained pahoehoe), and the healthy forest segment occurred largely on habitat type 5 (moist, shallow soil over aa, the low-ridge subtype). There is therefore a habitat correlation with the dieback pattern along the Saddle Road belt-transect, and it would not be correct--without further knowledge--to relate the two forest conditions to the same dynamic phenomenon.

The second healthy forest B on Figure 4, which was sampled along Stainback Highway, was a closed-canopy forest. It has much greater ohia-tree density per unit area than the healthy forest A. However, in common with stand A, the Stainback Highway stand also seems to be comprised of two generations. A bigger-diameter (probably older) tree population with a modal diameter of about 100 cm dbh and a smaller-diameter (probably younger) tree population with a broad-modal diameter centering near 20 cm dbh like stand A. The broad mode of this second-generation stand currently has tapered off by dieback.

This stand B, although it is currently classified as healthy, appears to be in a breakdown stage, which has started some time ago. Interestingly, there are no trunk-sprouted trees in this stand. Instead we find a certain proportion of old snags, a somewhat smaller proportion of recently dead trees and a few crown-dying trees. The stand appears to be opening up in the form of a relatively rapid dieback, since no trunk-sprouted trees are present.

4. Reproduction Patterns in Dieback and Healthy Forests

The reproduction of ohia is analyzed for the same three stands on Figure 5. Small ohia trees were enumerated in 1-m height or stem-length classes, from <0.1 m to 5 m. The reproduction data for each stand is shown on two diagrams. The right-hand diagram of each stand gives the density pattern in the five one-meter stem-length classes and the left-hand diagram details the 1-m stem-length class for each stand.

In comparing the right-hand diagrams of each stand, it becomes apparent that the most advanced small-tree growth occurred in the severe dieback stand at the Saddle Road, i.e the stand has a good representation of advanced tree growth up to 5 m tall. All five one-meter stem-length classes are numerically well represented. They show an inverse J-shaped distribution indicating the development of a second-generation stand under the dieback canopy. The separation of the first one-meter stem-length class into three seedling classes, up to 0.1 m, >0.1-0.5 m and >0.5-1 m height, show a similarly healthy trend. The dieback stand is reproducing well.

The healthy forest segment at Saddle Road shows only a sparse representation of small ohia trees from 1 m to 5 m tall, while seedlings up to 1 m tall are even more abundant than in the dieback forest segment. However, among the <1 m seedlings, individuals are most numerous as germinants only, i.e. <0.1 m tall seedlings. There appears to be considerable mortality as seedlings grow from <0.1 m to 0.5 m and then from 0.5 m to 1 m in size. This reproduction pattern indicates that something is interfering with the establishment of sapling trees and seedlings in this openly stocked healthy forest. Most likely this is shade near the ground caused by the more luxurious undergrowth vegetation of ferns in this forest.

The second healthy forest at Stainback Highway shows yet another reproduction pattern. This is a closed ohia forest, which appears to be entering a dieback stage. Reproduction is very little advanced. In fact there were no small ohia trees >1 m present. However, reproduction in the <1 m stem-length class was quite well represented.

Shading of the forest floor in the closed-canopy forest was still quite pronounced, very much more so than in the advanced, severe dieback forest and somewhat more so than in the openly-stocked healthy forest along Saddle Road. Thus the reproduction patterns appear to be related

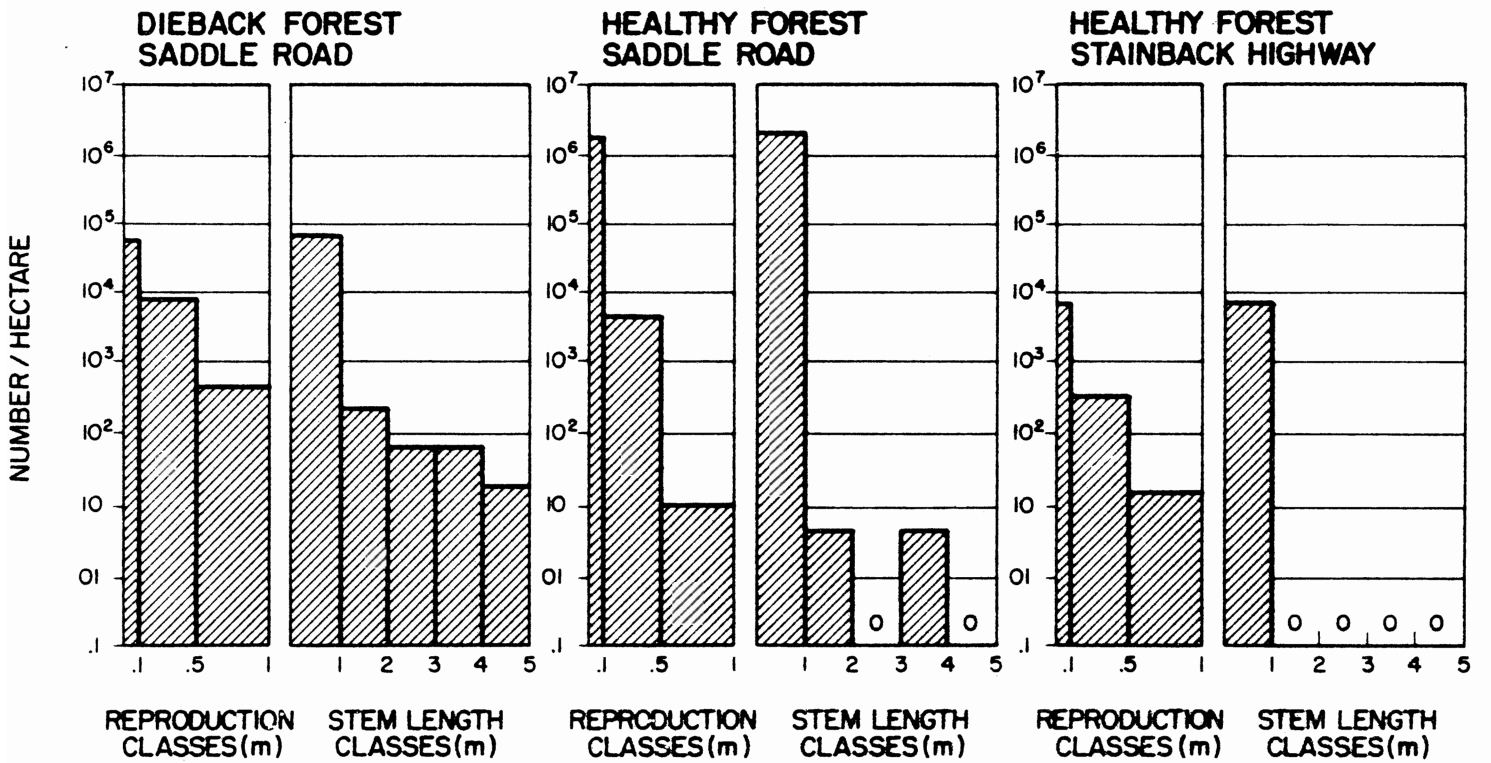

FIG. 5. Reproduction of Ohia Trees up to 5 m Tall in the Three Different Stands, i.e. Dieback Forest, Open "Healthy" Forest and Closed "Healthy" Forest.

primarily to the availability of light on the forest floor. In our search for ohia seedlings in natural rain forests elsewhere we found germinants (< 0.1 m tall seedlings) in each stand so far examined. But in dark, closed-canopy forests, we found no taller seedlings or intermediate-sized trees in the 1 to 5 m stem-length classes.

5. Quantification of Ohia Dieback on a Stand Basis

After having analyzed the two belt-transects and the 33 relevés in which we made very similar quantitative records, we found a method to quantify ohia dieback on a stand basis.

The method involves relating the number of dieback trees to the total number of trees in a stand sample. This ratio gives us a dieback index, which we express in percent. As dieback trees we consider the old snags, the recently dead trees and the stag-headed trees with live branches on the trunk, i.e. the sum of trees in vigor classes 5, 4 and 3.

Table 7 gives the dieback indices for the three belt-transects and the 33 relevés. Based on these dieback indices for each of the 36 sample stands, we developed a stand-dieback classification of five classes, which are as follows:

Stand Dieback Class	Percent Range	Meaning
1	< 10%	normal for open ohia stands
2	10-25%	normal for closed and dense ohia stands or slight dieback for open stands
3	>25-50%	slight to moderate breakdown or dieback
4	>50-75%	heavy dieback
5	> 75%	very heavy dieback

It should be pointed out that many of the individual stand indices are not yet reliably established. The reason for this is that our tree sample was not yet large enough in most of the open stands, where we enumerated less than 30 trees in the 400 m^2 relevé. We may consider a dieback index reliably established wherever we enumerated more than

Table 7. Dieback Indices for all Sample Stands Analyzed in this Project.

Sample Stand or Relevé No.		Dieback Index (%)	Dieback Class
Saddle Road Transect:			
• Dieback segment		70.2**	4 (heavy)
• Healthy segment		13.6**	2 (normal for closed stand)
Stainback Highway Belt Transect		29.4**	3 (slight dieback)
Open forest relevés:			
on mesic sites	12 (1)*	100.0	5 (very heavy)
	18 (8)	100.0	5
	26 (8)	91.7	5
mod. moist sites	29 (9)	33.3	3 (moderate)
	21 (9)	0.0	1 (normal)
moist sites	39 (5)	71.4	4 (heavy)
	28 (3)	87.5	5
	34 (3)	91.9	5
	31 (10)	80.0	5
	38 (10)	83.3	5
	42 (11)	89.4	5
very moist to wet sites	11 (6)	94.6**	5
	15 (6)	92.9	5
	19 (6)	47.4	3 (moderate)
	25 (6)	35.7	3
extremely wet sites	17 (13)	--	no trees > 5 m tall
	40 (13)	--	
Closed forest relevés:			
on mesic sites	16 (1)	25.8**	3 (slight)
	20 (8)	61.1**	4
	30 (8)	19.4**	2 (normal for closed stand)
mod. moist sites	22 (9)	0.0	1
	32 (9)	20.0	2

Table 7 (Continued).

Sample Stand or Relevé No.		Dieback Index (%)	Dieback Class
Closed forest relevés (continued):			
moist sites	24 (5)	85.7	5 (very heavy)
	27 (3)	29.4**	3 (slight)
	41 (11)	10.0	2 (normal for closed stand)
very moist to wet	43 (7)	58.1	4 (heavy)
Dense forest relevés:			
on mesic sites	13 (1)	72.7**	4
	14 (1)	11.3**	2
mod. moist sites	23 (2)	18.2**	2
	33 (2)	25.8**	3 (slight)
moist sites	35 (3)	29.8**	3
	36 (3)	14.8	2
very moist to wet	37 (6)	93.9	5

* Number in brackets after relevé number refers to habitat type number (Chapter III).

** Indices based on a count of at least 30 trees over 5 m tall.

30 trees in all five vigor classes per stand. These indices are marked with a double asterisk on Table 7. Since we got a few reliably established dieback indices over the whole spectrum of site and forest structural variation it appeared justified to set the threshold ranges for the five stand-dieback classes as tabulated above. This classification appears to fit the concept of an intuitive classification, which one may establish on mere estimation of the percentage of dieback/total trees in any ohia rain forest stand.

6. Ohia Tree Population Structures in Selected Relevés

We have selected 22 relevés for showing their ohia-tree population structures diagrammatically. The selection was based on sample stand condition. We wanted to include a variety of cover types, soil moisture regimes and dieback situations. The structural diagrams are shown in Figures 6, 7 and 8.

The relevés on the figures are identified by their number. These can be checked against Table 7 for their forest condition (structure, habitat, dieback index and dieback class). In addition, the ratio of dieback trees/total trees is listed on each relevé diagram from which the dieback index can be calculated.

Relevé 13 on Figure 6 is the densest stand encountered in our samples. Its dieback index is 72.7%, i.e. a heavy dieback stand. It represents dieback that occurred on a mesic shallow-soil habitat in a dense forest. It is interesting that the proportion of dieback trees (individual tree classes 3, 4 and 5) to healthy trees (classes 1 and 2) is quite similar to that found in the heavy or severe dieback stand along the 1.3 km long belt-transect (Fig. 3). Thus, the pattern of dieback occurring on a very moist to wet shallow-soil habitat (the belt-transect dieback) and that occurring on a mesic, well-drained shallow-soil habitat, does not appear to be different on first view. However, an important difference is the density of trees. On the mesic site, tree density was greater by approximately one order of magnitude. In both cases, we are obviously dealing with a one-generation stand, a pioneer stand. This is shown by the limited

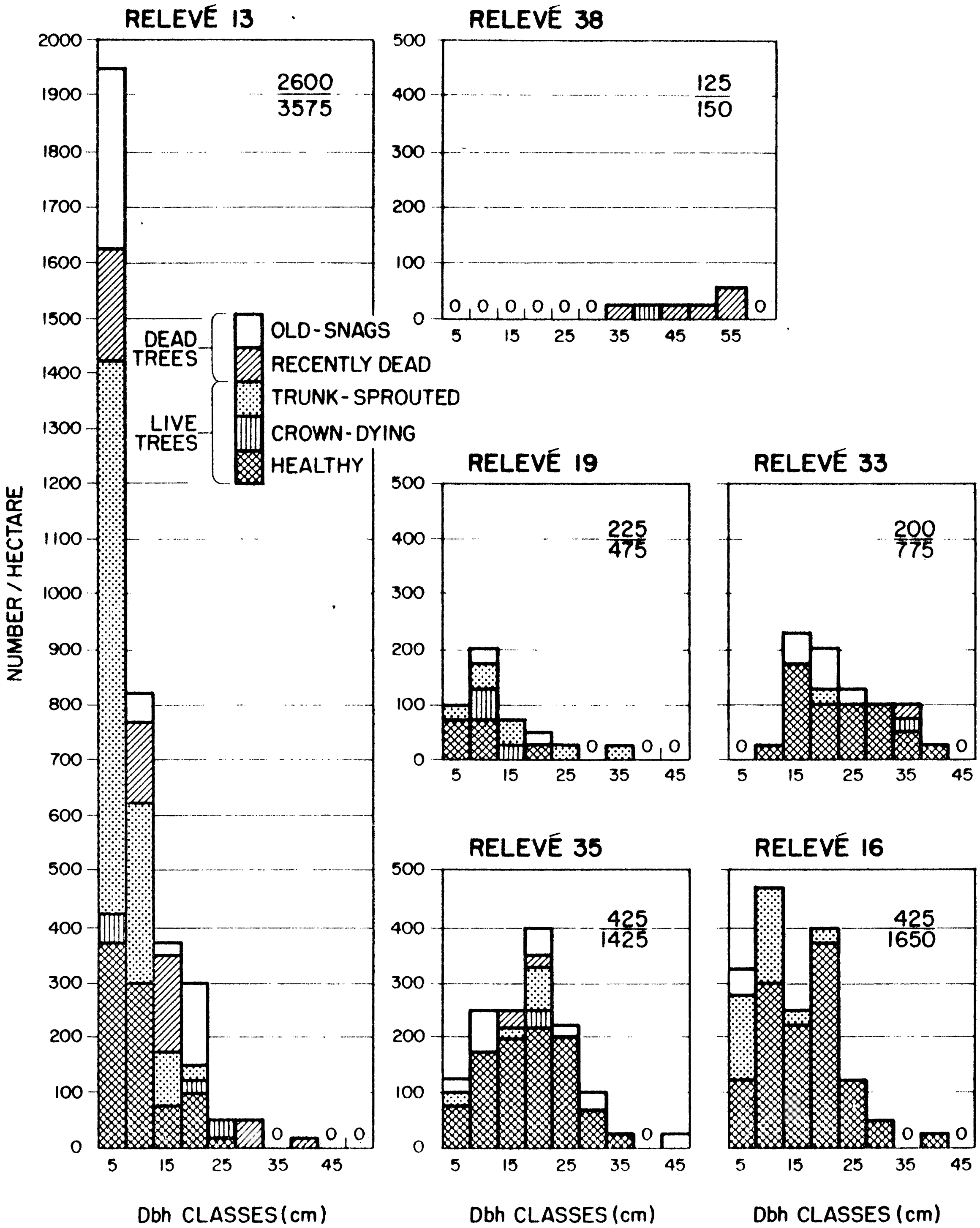

FIG. 6. Ohia Population Structures of Six Selected Relevés. The ratios relate the number of dieback trees (i.e. the dead + trunk-sprouted) to all trees per hectare.

size-range of diameters for both situations. In the mesic site relevé (#13) the size-range of over 5 m tall trees is even narrower (from 5 to 40 cm dbh), and the curve is not a normal curve skewed to the left, but an inverse J-shaped curve. However, in the mesic-site stand (relevé 13) the skew occurred below the 5 cm diameter class among the trees under 5 m tall, i.e. there were very few present. This will be explained further in the next section.

Relevé 38 represents another form of heavy dieback on a moist deep-soil habitat. In contrast to relevé 13, this relevé is from a very open ohia stand in Olaa Tract, where tree ferns (Cibotium glaucum) form a dense understory. The dieback index of 83.3% for this relevé is not yet established reliably, but the dieback class (namely 5) is not expected to change with further sampling of a more adequate number of trees.

Relevé 19 represents another open forest, but one occurring on a very moist to wet shallow-soil habitat. Its dieback index (47.4%) places this stand into the moderate breakdown or dieback class 3. The relevé can be considered as showing beginning dieback on a wetland habitat in contrast to the advanced dieback on a wetland site shown by the 1.3 km belt-transect stand on Figure 3. However, there are no recently dead trees in relevé 19.

Relevé 33 represents a dense forest on a moderately moist shallow-soil habitat in the Puu Makaala area. The stand shows slight dieback with an index of 25.8%. There are a few recently dead trees in the 35 cm diameter class, which may indicate beginning dieback.

Relevé 35 is very similar to relevé 33. It also occurs in the Puu Makaala area, but its habitat is one category moister. Its dieback class is the same (namely 3, slight to moderate), its dieback index is only a little greater (29.8%), and there are also a few recently dead trees.

Relevé 16 is in the same dieback class again, namely 3 (25.8%). It is a stand occurring on habitat type 1: mesic, shallow soil. It is thus on the same habitat as relevé 13. However, in contrast to the latter it occurs at low elevation (1270 feet) on Stainback Highway.* Relevé 16

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*S. C. Hwang and Dr. Ko sampled this stand for Phytophthora cinnamomi as a "healthy" forest sample on well-drained soil, and they found no difference in the population of this root-fungus to a neighboring "dieback" stand.

shows no recently dead tree and most of the few dieback trees are trunk-sprouting stagheads.

Thus, the only heavy dieback stands on Figure 6 are relevés 13 and 38. These show very different dieback patterns. Relevés 19, 33, 35 and 16 are in the same dieback class, i.e. slight to moderate. Among these only the two Puu Makaala stands (33, 35) show recently dead trees.

Figure 7 shows the structural diagrams of another 10 selected relevés. Relevé 42 represents an open forest on a moist deep-soil habitat, north of Wailuku Stream. Its dieback index is 89.4%, which puts it into the very heavy dieback class 5. Because of the openness of this stand the tree sample was only small on 400 m^2. There was no really healthy tree in the sample, and the dieback looks somewhat like that in relevé 38 (Fig. 6). In common with that relevé, there are a few recently dead (class 4) and thinly foliated (class 2) trees in relevé 42, but relevé 42 differs in having also several stagheads (class 3) and old snags (class 5). The reason for the absence of the latter two tree vigor classes in relevé 38 is perhaps only a reflection of the fewer trees enumerated in relevé 38.

Looking over the remaining nine diagrams on Figure 7, we may now group them into population-structure types. The next six relevés (no's. 11, 15, 24, 37, 26, 12) all show very heavy dieback, while the bottom-three relevés (no's. 14, 23, 27) show only normal to slight dieback. Most of the heavy dieback relevés were mapped as open forests (no's. 11, 15, 26, 12). Only two were mapped as closed or dense, respectively, namely 24 and 37. Relevé 37, however, was an open "pocket stand" in an otherwise dense forest. The dieback pocket was too small for mapping it as an open forest at the chosen map-scale. Interestingly, there are a large number of recently dead standing trees, but no old snags. This stand must have died very suddenly and recently. There are a few recently dead trees in all of these heavy dieback stands except in relevé 12. This relevé is one of the "classical" dieback stands adjacent to the Saddle Road (north of its junction with the Tree Planting Road).

Figure 8 shows another set of six relevés. Three of these are healthy forests, relevés 30, 32 and 36. Relevé 30 was sampled in Hawaii

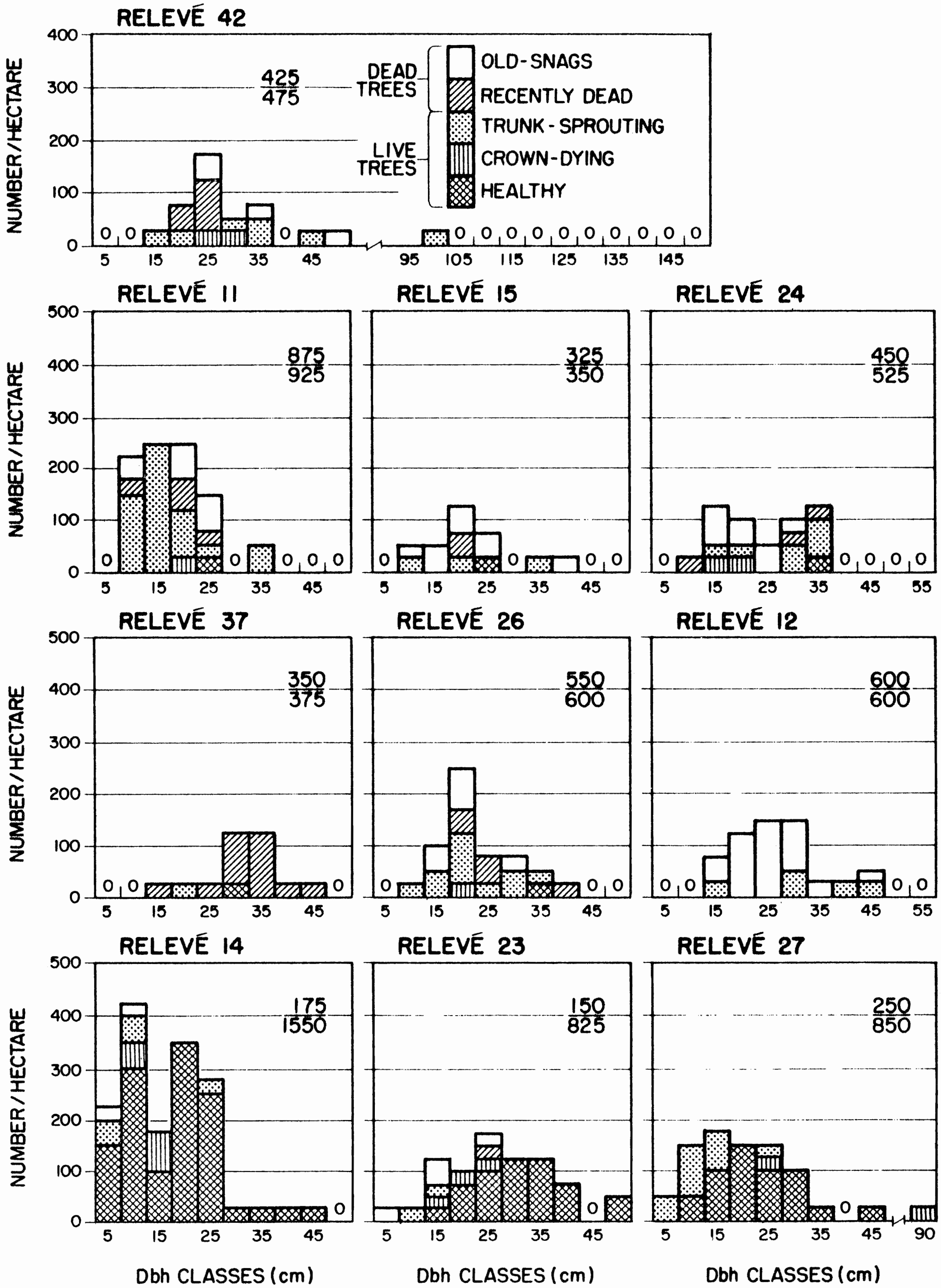

FIG. 7. Ohia Population Structures of Ten Selected Relevés. The ratios relate the number of dieback trees (i.e. the dead + trunk-sprouted) to all trees per hectare.

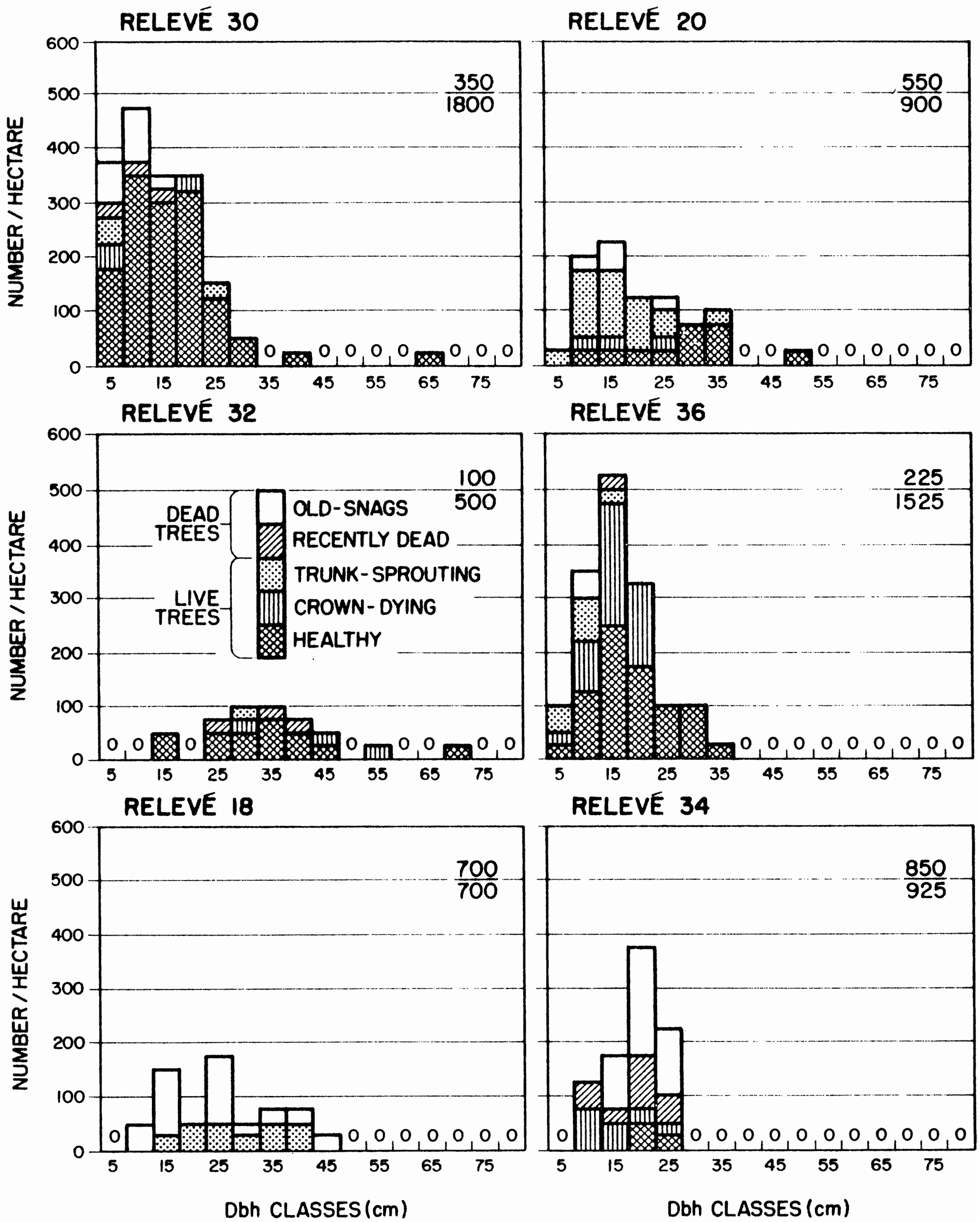

FIG. 8. Ohia Population Structures of another Six Selected Relevés. The ratios relate the number of dieback trees (i.e. the dead + trunk-sprouted) to all trees per hectare.

Volcanoes National Park. It is a closed forest on a mesic, moderately deep-soil habitat. Its dieback index is 19.4%, which we consider normal for a healthy, closed forest. It may be noted also that the snags in this stand are in the smaller diameter classes. This indicates that the snags are probably from suppressed trees which died under competitive pressure of the bigger-diameter trees.

Relevé 32 is in a healthy, closed forest on Olaa Tract, where it occurs on a moderately moist, deep-soil habitat. Note, that the diameter mode in this stand is near 35 cm dbh, which implies that the trees on this site are much bigger than those in relevé 30. In this Olaa Tract relevé (no. 32) they are probably also greater in height (a parameter not yet analyzed), which would explain, in part, the lower density (i.e. number of trees) in this relevé as compared to the other two healthy-stand relevés (no's. 30 and 36).

The third healthy stand (no. 36) on Figure 8 shows greater similarity in tree structure to relevé 30. Relevé 36 is a dense, tall forest sample from Puu Makaala, where the stand occurs on a shallow, moist soil. There are a relatively large proportion of crown-dying trees in this stand. This may indicate that this stand is entering a dieback phase.

The remaining three relevés, 20, 18 and 34, are stands with heavy to very heavy dieback. Both relevés 20 and 18 were sampled in Hawaii Volcanoes National Park along the Crater Rim Road. Relevé 18 was formerly sampled as a "disease center" (personal communication with Dr. Ko) by other researchers but without recovery of Phytophthora cinnamomi. The only live trees are trunk-sprouts, but there are no recently dead trees. In contrast, relevé 20 has a good number of healthy and trunk-sprouting trees. There are not so many old snags, but a few recently dead trees are present. Therefore, one may conclude that although both stands are in the same dieback class, they are in a somewhat different stage of dieback. Relevé 20 got hit by dieback at a more recent date and now its dieback is progressing further; whereas relevé 18 has come to a very advanced stage of dieback some time ago, and may now have ceased to progress further. The few trunk-sprouted trees may possibly survive. The present dieback pattern of relevé 18 looks very similar to the "classical" dieback pattern of relevé 12 (Fig. 7). All these (i.e. relevés

12, 18, and 20) represent dieback on mesic, well-drained habitats.

Relevé 34 (Fig. 6) represents an open forest with very heavy dieback on a moist, shallow-soil habitat in the Puu Makaala area. It is thus not very far in location from the other Puu Makaala dieback relevé 37 (on Fig. 5). However, relevé 34 shows a good number of old snags and not as many recently dead trees as does relevé 37. Thus, these two dieback relevés may also be considered as showing dieback phases. Relevé 34 appears to have entered a dieback phase some time ago and now has progressed to a more slowly advancing end-point. In contrast, the ohia population of relevé 37 has died recently and rather suddenly as if it had collapsed. Both Puu Makaala stands are on moist and very moist to wet habitats, respectively.

7. Ohia Regeneration Patterns in the Relevés

All 33 relevés in which we recorded small ohia trees from 0.1 m to 5 m tall, were analyzed in detail and diagrammed in the same manner as the previously described reproduction trends along the belt transects (Section IV-4 and Fig. 5). In the relevé analyses, however, we omitted the very small ohia seedlings <0.1 m tall because we do not consider these as "established". These very small seedlings may also be referred to as "germinants", which implies that they merely give an indication of the availability of viable seeds in the stand. The behavior of such germinants may as yet be "phenological" in the sense that they can be expected to form an abundant crop in one year which may largely disappear in the next year. Or they may even die within the same year when, for example, their as yet shallow rooting substrate temporarily drops below the permanent wilting percentage.

Using the 33 relevés, it was possible to establish certain criteria for classifying the regeneration trends for each stand which we analyzed in the field. The criteria are stated in Table 8. A somewhat arbitrary decision had to be made on the "adequacy" of stocking density for small ohia trees. The concept of adequacy here relates to the probability of the currently regenerating small-tree population to form a new mature tree generation on the same site. For this, we set the standard at 3500 small trees per hectare, which is roughly equivalent to

Table 8. Regeneration Classes for Small Ohia Trees from 0.1 to 5 m Tall.

A = Adequate number, i.e. > 3500 per hectare*	
A I	Present, but only under 0.5 m tall
A II	Recent, ohia regeneration up to 1 m tall
A III	Moderately advanced, ohia regeneration up to 2 m tall
A IV	Advanced, ohia regeneration up to 3 or 4 m tall
A V	Very advanced, ohia regeneration up to 5 m tall
Inadequate to maintain a forest: number of small trees under 3500 per hectare; classes as above.	

* Pacific Coast Forestry Standard for adequate stocking is > 1625 to 3750 seedlings or small trees per hectare (Forestry Handbook for British Columbia 1953: 70). Further research into an adequate restocking standard for Hawaiian rain forests is underway.

one small ohia tree per three square meters. In comparison to established restocking standards for natural regeneration in cut-over Pacific Coast forests, the lower limit of 3500 small trees per hectare is quite conservative. This is particularly true if one considers that we are here dealing with a natural forest and not with a forest which is managed for timber production. For the latter, the stocking density requirement could be expected to be greater than for a self-maintaining natural forest. However, the dispersal pattern or the clumping pattern of small trees should also be taken into consideration. For this reason, we set the adequacy of stocking standard rather high for the accepted minimum range as applied to Pacific Coast forests. We have information on the dispersal pattern, which will be analyzed at a later date.

It was possible to classify the regeneration patterns of all relevés into either adequate or inadequate and further into any one of the five height classes (Table 8). These height classes, backed up by the tree-density standard, give a clear indication of the status of a regeneration trend in the sense of whether it is advanced or recent. Some other aspects, namely site productivity and degree of shading, also enter into the assessment of the regeneration status of a stand. These aspects will be pointed out below, where applicable.

Figure 9 shows an example of each regeneration trend as classified by the criteria given on Table 8.

Table 9 tabulates the basic data for all 33 relevés and the three formerly described belt-transect segments. The latter were classifiable into regeneration trends only after analysis of the additional sample stands.

From Table 9 it becomes apparent that the ohia regeneration trends are closely correlated with the mapped forest-canopy units (open, closed, dense). Most of the open forest stands sampled had adequate ohia regeneration. The exceptions are relevés 21 and 29, both from Olaa Tract, and relevés 17 and 14, which are the bog relevés with shrubby ohia-tree growth not exceeding 5 m in height. The two Olaa Tract relevés (no's. 21 and 29) occur in an area of vigorous tree fern (Cibotium glaucum) growth, where the tree ferns form a dense undergrowth canopy at about 4 to 5 m height. Here, ohia appears to be displaced from the site.

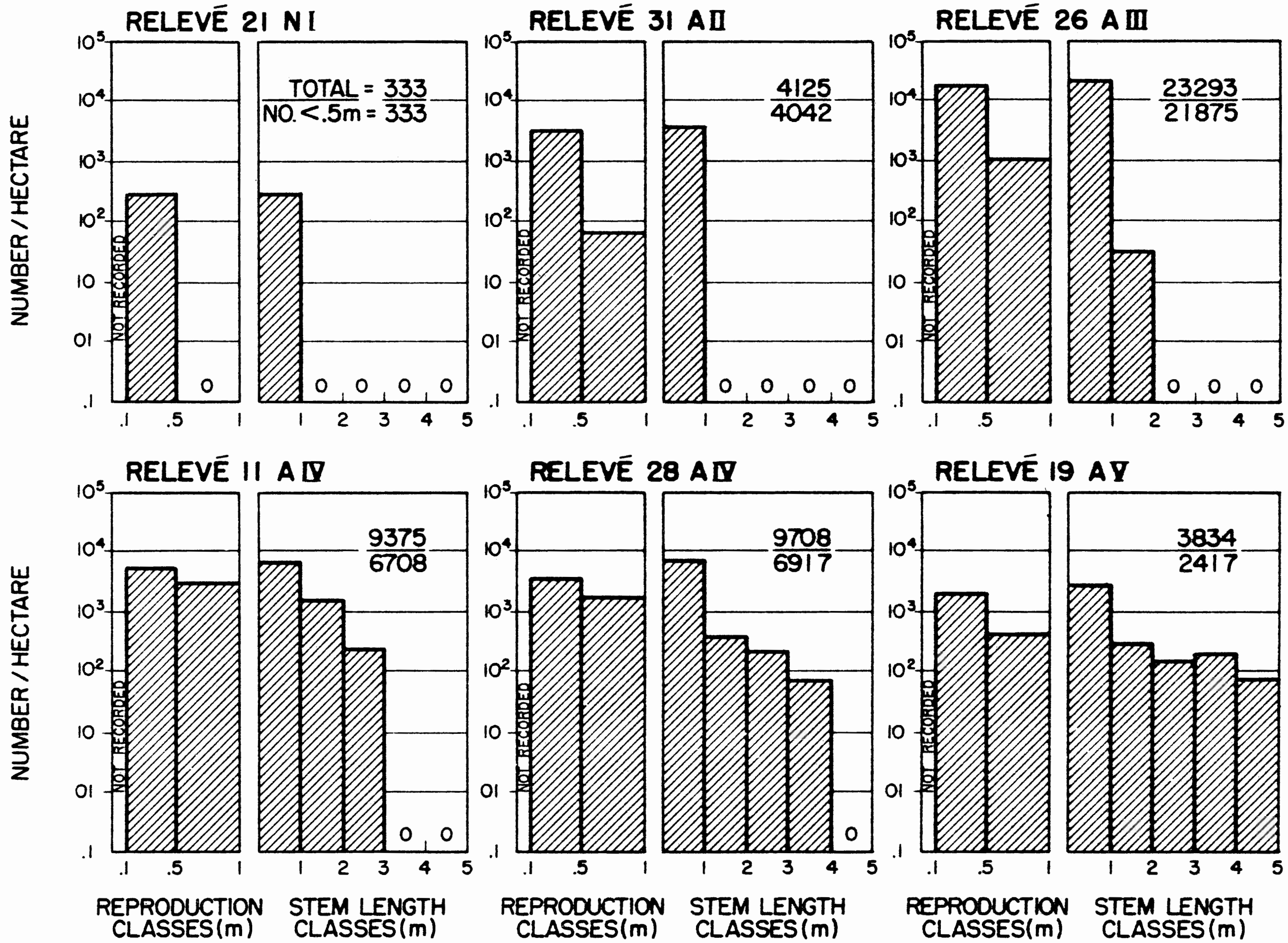

FIG. 9. Example Data for Each of the Regeneration Classes Recognized in Table 2. N I = Not adequate, only under .5 m tall, A II = adequate, recent, ohia regeneration up to 1 m tall, A III = adequate, moderately advanced, A III = advanced, regeneration up to 3 or 4 m tall, A V = adequate, very advanced. The ratio on each diagram relates the total number of small trees to those under .5 m tall.

Table 9. Ohia Regeneration Trends for All Sample Stands Analyzed in this Project.

Sample Stand or Relevé No.		Number of Trees/ha from 0.1-5 m tall	Regeneration Class
Saddle Road Belt Transect:			
• Dieback segment		9898	**A V (very advanced)
• Healthy segment		6600	A IV (advanced)
Stainback Highway Belt Transect		461	Inadequate II (recent)
Open forest relevés:			
on mesic sites	12 (1)*	33249	A IV
	18 (8)	7416	A IV
	26 (8)	23293	A III (mod. advanced)
mod. moist sites	29 (9)	125	Inadequate I
	21 (9)	333	Inadequate I (present, but only < 0.5 m tall)
moist sites	39 (5)	7000	A V
	28 (3)	9708	A IV
	34 (3)	26792	A III
	31 (10)	4125	A II (recent)
	38 (10)	3875	A II
	42 (11)	17458	A III
very moist to wet sites	11 (6)	9375	A IV (advanced)
	15 (6)	41875	A IV
	19 (6)	3834	A V (very advanced)
	25 (6)	4083	A V
extremely wet sites	17 (13)	1542	Inadequate III
	40 (13)	3041	Inadequate IV
Closed forest relevés:			
mesic sites	16 (1)	291	Inadequate II
	20 (8)	5251	A III (mod. advanced)
	30 (8)	9417	A IV
mod. moist sites	22 (9)	83	Inadequate I
	32 (9)	167	Inadequate I

Table 9 (Continued).

Sample Stand or Relevé No.		Number of Trees/ha from 0.1-5 m tall	Regeneration Class
Closed forest relevés: (continued)			
moist sites	24 (5)	12833	A III
	27 (3)	6000	A III
	41 (11)	2250	Inadequate IV
very moist to wet	43 (7)	10458	A III
Dense forest relevés:			
mesic sites	13 (1)	1000	Inadequate III
	14 (1)	458	Inadequate V
mod. moist sites	23 (2)	2083	Inadequate II
	33 (2)	292	Inadequate II
moist sites	35 (3)	1333	Inadequate III
	36 (3)	792	Inadequate I
very moist to wet	37 (6)	17750	A II (recent)

* Number in brackets after relevé number refers to habitat type number (Chapter III)

** A = adequate regeneration, i.e. number > 3500/ha

On the other extreme, all dense forest relevés show inadequate ohia regeneration. The exception is relevé 37 which is the recent dieback pocket stand in the Puu Makaala area. The regeneration in this is clearly adequate with more than two established seedlings per square meter. The size of the ohia seedlings (up to 1 m tall) indicates that the dieback here occurred recently, perhaps within the past five years. Thus, in addition to the many recently dead trees shown for this stand on Figure 7, its regeneration trend provides a second supporting index for the recency of the dieback in this stand. The inadequate regeneration trends for the other six dense forest stand samples analyzed simply show that ohia regenerates poorly in shade. Therefore, we may consider their regeneration patterns as being retarded by shade.

Among the nine closed forest relevés analyzed, there are four with inadequate and five with adequate regeneration trends. Those with inadequate regeneration trends are all "healthy" forests. Only relevé 16 of this group has a dieback index of 25.8%, which just exceeds the 25% considered normal for closed ohia forests. Of the five closed forest relevés with adequate regeneration trends, three show heavy dieback (no's. 20, 24, 43); the two others (no's. 27, 30) have low dieback indices (29.4% and 19.4%, respectively). In these stands, for some other reasons not apparent from the displayed data, regeneration has progressed without a major canopy opening.

V RAIN FOREST STRUCTURE AND FLORISTICS

(N. Balakrishnan and D. Mueller-Dombois)

1. Introduction

This subproject was set up to record the floristic composition of each forest stand sample or relevé and to study the distribution of the ohia-associated plant species throughout the study area. The more immediate objectives were to determine the native and exotic species diversity as related to forest structure, location, moisture regime and habitat. Another related objective was to clarify whether the dieback has anything to do with the invasion of exotic species. We also wanted to study the distribution of the rare endemic species and to find out if undergrowth species can be used to identify habitat types for mapping purposes.

For the proper assessment, these study objectives require an analysis of all the plant species encountered in at least 80 to 120 relevés. Thus far, we have only 39 relevés analyzed.* Moreover, the relevés and species have to be treated by multivariate analysis techniques to produce reliably definitive statements. This work is still in progress, and we need about two more years of fieldwork to obtain the desired number of relevés. Therefore, this work should be continued under a new project.

2. Species Richness in Different Rain Forest Stands

The concept of species richness relates to the number of species found in a given area. It differs a little from the concept of species diversity, which is usually interpreted by combining species number and species or population quantity into an index. We intend to do that at a later stage of data analysis.

In the number of plant species recorded for each relevé on Table 10, we excluded the mosses, liverworts and lichens. These non-vascular plants still require special attention. Thus, the species numbers refer to all vascular plants recorded, including the epiphytes. A checklist of all species is given as Appendix I on p. 101.

Our results show that the total number of these species varies on areas of 400 m^2 from under 10 to over 60 species. A low total number of

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* Relevés 6, 7, 8, 9 were omitted from this analysis because three of these are _Acacia koa_ stands and one is an immature ohia stand.

Table 10. Species Richness of Native and Exotic Vascular Plants in the 400 m^2 Sample Stands.

Sample Stand or Relevé No.		# Native plant species	# Exotic plant species	Location
<u>Open forest relevés</u>:				
on mesic sites	12 (1)*D	45	2	Saddle Road
	18 (8) D	24	14	HVNP
	26 (8) D	24	14	HVNP
mod. moist sites	29 (9)	43	0	Olaa Tract
	21 (9)	46	1	Olaa Tract
moist sites	39 (5) D	24	12	Tree Planting Road
	28 (3) D	48	12	Tree Planting Road
	34 (3) D	54	2	Puu Makaala
	31 (10) D	43	4	Olaa
	38 (10) D	54	2	Olaa
	42 (10) D	40	7	Wailuku Stream area
very moist to wet sites	01 (6) D	25	9	Wailuku Stream area
	03 (6) D	21	8	Wailuku Stream area
	11 (6) D	40	8	Tree Planting Road
	15 (6) D	43	11	Saddle Road
	19 (6)	42	10	Wailuku Stream area
	25 (6)	33	10	Tree Planting Road
extremely wet sites	17 (13)	19	6	Wailuku Stream area } bogs
	40 (13)	30	8	Hamakua Coast } bogs
<u>treeless</u> bog	02 (14)	4	4	Wailuku Stream area
<u>Closed forest relevés</u>:				
on mesic sites	16 (1)	25	8	Lower Stainback Hwy.
	20 (8) D	26	18	HVNP
	30 (8)	23	10	HVNP
mod. moist sites	04 (9)	38	3	Wailuku Stream area
	22 (9)	47	0	Olaa Tract
	32 (9)	40	1	Olaa Tract
moist sites	10 (5)	57	1	Tree Planting Road
	24 (5) D	54	4	Puu Makaala
	27 (3)	57	9	Tree Planting Road
	41 (11)	30	7	Hamakua Coast

Table 10 (Continued).

Sample Stand or Relevé No.		# Native plant species	# Exotic plant species	Location
Closed forest relevés (continued):				
very moist	43 (7) D	47	2	Tree Planting Road
to wet	05 (12)	41	6	Wailuku Stream area
Dense forest relevés:				
on mesic	13 (1) D	37	0	Saddle Road
sites	14 (1)	35	1	Saddle Road
mod. moist	23 (2)	55	1	Puu Makaala
sites	33 (2)	58	0	Puu Makaala
moist	35 (3)	53	0	Puu Makaala
sites	36 (3)	48	1	Puu Makaala
very moist to wet	37 (6) D	53	3	Puu Makaala

* Number in brackets refers to habitat type number
D = stand with heavy or very heavy dieback

only eight species was found in the treeless bog relevé (no. 2). Here, only four species dominated the site, the other four were of minor occurrence. The most dominant species was the endemic sedge Rhynchospora lavarum (with about 60% shoot cover). The other three dominants were exotics, a rush (Juncus planifolius), a grass (Sacciolepis indica) and a forb (Cuphea carthagenensis). This treeless bog, no doubt is an environmentally extreme habitat. The next lowest total number of species, 25, was recorded also in a bog site (relevé 17), which however was occupied with stunted ohia trees < 5 m tall. The presence of ohia here is associated with an increase in native species, some of which occurred as epiphytes. The third bog relevé (no. 40) had 38 species, and thus compared well in richness with the other forest stands sampled in this study. Their total species number varied mostly from 30 to 60. Therefore, species richness is not related to soil moisture regime or habitat type, except in some extremely wet sites.

Stands rich in native species, i.e. containing over 50/400 m^2, were found in open, closed and dense forests. Conversely, stands poor in native species, i.e. under 30/400 m^2, were found in open and closed but not in dense forests. If one relates the number of relevés rich in native species (> 50 species) to all relevés in each major structural category (and omitting the three bog relevés), the following relationship is indicated, 12% (2/17) for open forests, 25% (3/12) for closed forests and 57% (4/7) for dense forest. If one relates the number of relevés with low numbers of native species (< 30) to all relevés in each major forest structural category, the relationship is reversed, namely 29% (5/17) for open forests, 25% (3/12) for closed forests and none for dense forests. This indicates that there is a general relationship of dense ohia forests being associated with a greater number of native plant species than closed forests and these in turn appear to be richer in native species than open forests. It may also be noted that the dense forest samples contained the fewest numbers of exotic species.

However, a still closer correlation of native species richness and exotic species invasion exists with location. The four relevés in Hawaii Volcanoes National Park all showed low native species numbers (< 30/400 m^2) and high numbers of exotics (from 10-18/400 m^2). In Olaa Tract, native species richness was greater (between 40-55 species/400 m^2) and exotic species invasion was much less (from 0 to 4/400 m^2). However, here some of the exotics, particularly the vine Passiflora mixta, appears to have the potential for rapid spreading (Jacobi and Warshauer 1975). The Puu Makaala area shows a still greater richness in native species. Except for one stand (no. 36, with 48 native species) all other stands sampled in this area had native species numbering > 50/400 m^2. None of these stands contained more than four exotic species, and Passiflora mixta was not found in this area.

Other areas with relatively high numbers of exotic species, i.e. eight or more, were found at the Tree Planting Road, at the lower Stainback Highway, in the Wailuku Stream area (not far from a forest-access road), at certain areas along the Saddle Road and in the Hamakua Coast area above the planted eucalyptus belt near 2000 feet elevation. In these areas, exotic species seem to have followed inroads created by past management activities.

3. Dieback and Exotic Species Invasion

From the overview of species richness given in Table 10, it is possible to relate the number of exotic species to the stands with and without heavy (class 4) or very heavy (class 5) ohia dieback. The dieback stands are indicated as such on the table. The non-dieback stands (those with dieback class 1-3) are the others. The three bog samples are omitted from this analysis. The following tabulation brings out the relationship:

No. Exotic Species	No. of Dieback Stands Sampled	No. of Non-Dieback Stands Sampled
> 10	6	-
5-10	4	7
< 5	8	11

As shown by the tabulation, high numbers of exotic species (> 10, i.e. from 11-18) were found only in stands with heavy dieback. However, moderately high numbers of exotic species (from 5-10) were found in both dieback and non-dieback stands, and low numbers, under five exotic species, were also found in both types of stands. This may give the impression that ohia dieback is associated with exotic species invasion.

Inspection of the locations of the first six relevés on the tabulation shows three of them to occur in Hawaii Volcanoes National Park. Two are from the Tree Planting Road and one is from the Saddle Road. This indicates that dieback invites exotic species invasion in areas where there are already relatively large numbers of exotic species present. However, the dieback as such can hardly be considered the cause of exotic species invasion in general. The tabulation shows that the number of dieback stands with a small number of exotics (< 5 species) is greater than those in which we found over 10 exotics. In fact, the number of dieback stands with moderate (5-10) and low (< 5) numbers of exotic species is less than the number of non-dieback stands in these categories. This indicates that dieback has no particular influence on exotic species invasion in other areas, where the exotic species pressure is not as great.

However, species numbers alone bring out only general tendencies. What really goes on can only be clarified by an examination of the species themselves. We did a preliminary analysis of distribution groups of exotic plant species in the study terrain and found that they can be divided into two major groups:

1. Exotic species more or less restricted to certain geographic areas
2. Exotic species occurring throughout the study terrain

It must be emphasized, however, that this study was not designed to study the distribution of exotic species in the rain forests. Its objective was to study the dieback and intervening "healthy" forest stands. Therefore, we did not look for areas with high exotic species numbers or stands containing certain exotics. Instead our record of exotics can be considered a small random sample of the forest dieback terrain as a whole.

3.1 <u>Exotic Species mostly Restricted to Certain Geographic Areas</u>.-- This group was dividable into five subgroups as follows:

a) Exotics found only in our Hawaii Volcanoes National Park relevés: Shrub: <u>Rubus penetrans</u>; Grasses: <u>Holcus lanatus</u>, <u>Setaria geniculata</u>, <u>Aira caryophylla</u>, Forbs: <u>Anemone hupehensis</u>, <u>Phajus tankervilliae</u>, Youngia japonica, Hypochoeris radicata, Fragaria alba, Anagallis arvensis.

b) Exotics found only in our Olaa Tract relevés:
Vine: Passiflora mixta, Forb: Epilobium cinereum.

c) Exotics encountered only in our relevés in the Wailuku River area:
Grass: Axonopus affinis, Forbs: Veronica plebeia, Ageratum conyzoides, Polygonum glabrum.

d) Exotics found only in our relevés at lower elevation (< 2000 feet) at Hamakua Coast and Stainback Highway:
Tree: Spathodea campanulata, Shrub: Melastoma malabathricum.

e) Exotics encountered only in our relevés along the Tree Planting Road:
Vines: Passiflora edulis, Passiflora ligularis, Tall Grass: Setaria palmifolia, Forb: Arundina bambusifolia.

3.2 Exotic Species Occurring Throughout the Study Terrain.--This group could be divided into two subgroups:

a) Exotic species found mostly in poorly drained situations in our relevés:
Rushes: Juncus effusus, J. bufonius, J. tenuifolius, J. planifolius, Grass: Sacciolepis indica, Forbs: Ludwigia octivalvis, Cuphea carthagenensis, Commelina diffusa, Drymeria cordata.

b) Exotic species found in openings and locally disturbed places in our relevés:
Trees: Psidium cattleianum, Buddleja asiatica, Shrub: Rubus rosaefolius, Grasses: Andropogon virginicus, Paspalum conjugatum, P. orbiculare, Digitaria sp., Sedge: Cyperus brevifolius,
Forbs: Eupatorium riparium, Erechtites valerianaefolia, Hypericum degeneri.

In the first group of the more or less locality-restricted exotics, we encountered only two potentially damaging exotic plants. By potentially damaging is meant a plant that may interfere significantly with the reproduction cycle of the native forest plants if allowed to become abundant. One was the shrub Rubus penetrans in Hawaii Volcanoes National Park, the other the vine Passiflora mixta in the Olaa Tract. The woody plants, Spathodea campanulata and Melastoma malabathricum, which we found restricted to lower elevations, may also be considered potentially damaging. The same may apply to the other Passiflora vine species found in the Tree Planting Road area. The remaining species in the locally restricted group appear to be of little influence on the rest of the vegetation.

Among the second group of exotics, i.e. those spread throughout the rain forest terrain, only one woody plant seems of concern. This is the tree Psidium cattleianum, which is well represented at several lower-elevation sites. It may have the capacity to displace ohia in such places where it has become abundant. Among the other widespread species, Andropogon virginicus is locally common in open and poorly drained places. However, it does not seem to interfere with the reproduction cycle of native woody plants. Eupatorium riparium is common in Hawaii Volcanoes National Park and in the Tree Planting Road area. It is rare in Olaa Tract and the other rain forest areas. Since it is a shade-tolerant weed, it may interfere with the development of native undergrowth species in those areas where it is common.

4. Rare Endemic Species

For the purpose of identifying the rare endemic species in the study area, we transferred all our plant records into a preliminary synthesis table (Mueller-Dombois and Ellenberg 1974). From this table, we then determined the frequencies of all species throughout the set of the 39 vegetation samples analyzed in this project. An endemic species found in less than 15% of our relevés (i.e. < 6/39) was considered rare (i.e. infrequent) in the study area. In addition, we have records on the quantity of each species in each relevé. These records provide for an estimate of the local abundance of each species.

The rare or infrequent rain forest endemics are listed in Table 11. We included a few species, which were considered rare or of uncertain status in the list of rare and endangered species by Fosberg and Herbst (1975), but which exceeded our standard of rareness as defined above. The degree of rareness or infrequency can be determined from Table 11 by counting the number of relevé entries given for each species and by dividing this number by the total number of relevés studied. Our local abundance symbols for these species ranged from r to 2. The meaning of these symbols is given in the following tabulation:

Abundance Symbol	Quantitative Meaning
r	locally rare, i.e. only one individual/ 400 m^2
+	few individuals, i.e. 2-5 individuals for woody plants or any number of individuals in forbs or other life forms, but with small shoot or foliage cover
1	more than 5 individuals for woody plants, or cover up to 5%
2	many individuals, their combined foliage cover from 5-25% of the relevé area

Table 11 lists the 24 rare endemic species, which we located in our survey. The list includes five trees, 13 shrubs, two vines, three ferns and one forb. In the remarks taken from the Fosberg-Herbst list, the comment "uncertain status" relates to the question of whether the species or variety is endangered. It does not relate to any taxonomic uncertainty. However, we have not been able in some cases to determine the varietal status of some of our rare species entries. This work is still in progress. It should also be reemphasized that our sample of 39 relevés is not nearly enough to make definitive statements in all cases. When we have sampled 80 to 120 relevés, it may be possible that some species now considered rare or infrequent will become less rare. Several others will undoubtedly remain rare in the study area. Trees in this group are, for example, Xylosma hawaiiense var. hillebrandii, Bobea timonioides, Tetraplasandra meiandra and Labordia sp. Among the shrubs, we can now consider the status "certain" for Cyanea longipedunculata. This species was listed as uncertain, i.e. possibly endangered, by Fosberg and Herbst. We found it in nine of our relevés, i.e. with 23% frequency in the study area. Locally, this species is mostly represented by only one or a few individuals. But it is present in scattered occurrence throughout certain areas of the study area. Other shrub species not so rare are Cyrtandra lysiosepala and C. platyphylla. However, these seem to be represented with different genetic races or

Table 11. Rare Endemic Plant Species Recorded in this Relevé Survey.

Species by Life-form Categories	General Assessment Our Survey Local Abundance	Relevé No.	Other Remarks from Fosberg-Herbst List (FH) and St. John's Checklist (STJ)
TALL TREE (> 10 m tall when mature)			
1. Xylosma hawaiiense var. hillebrandii	r	(21)*	STJ: One variety FH: In cultivation; depleted
LOW-STATURE TREES (< 10 m tall)			
2. Bobea timonioides	r +	33 (33)	FH: Very local and rare
3. Tetraplasandra meiandra	r r	24,33 (24),(16)	STJ: 10 varieties FH: Eight of them of uncertain status and two rare
4. Nothocestrum longifolium	r r + +	10,23 24 16,33 (29)	STJ: One variety FH: Status uncertain
PALM TREE (with fan-shaped fronds)			
5. Pritchardia spp.	r r	22,24 27,28	STJ: 10 varieties FH: Most of them of uncertain status
TALL SHRUBS (> 2 m tall when mature)			
6. Urera sandwicensis	+ r	33 23	STJ: Two varieties FH: Both rare or uncertain
7. Touchardia latifolia	r	(32)	
SHRUBS (< 2 m tall)			
8. Trematolobelia grandifolia	r r	24,(24) 33,(16)	
9. Platydesma spathulata	+	(38)	STJ: One variety

Table 11 (Continued).

Species by Life-form Categories	General Assessment: Our Survey Local Abundance	Relevé No.	Other Remarks from Fosberg-Herbst List (FH) and St. John's Checklist (STJ)
SHRUBS (< 2 m tall) (continued)			
10. Clermontia	r	11,12	STJ: Two varieties
montis-loa	r	36	FH: One of uncertain status
11. Phyllostegia vestita	2	37	FH: Status uncertain
12. Phyllostegia	+	(43)	STJ: Two varieties
floribunda			FH: One is very rare
13. Labordia	+	11,12	STJ: Seven varieties
hedyosmifolia	+	14,15	FH: Four of them rare
	+	22,37	
14. Cyanea	r	23	STJ: Two varieties
tritomantha			FH: Both rare
15. Cyanea	+	10,23	FH: Status uncertain
longipedunculata	+	35,43	
	r	33,34	
	r	35,36	
	r	37	
16. Cyrtandra	+	10,34	STJ: Two varieties
paludosa	+	35,36	FH: One of uncertain status
17. Cyrtandra	+	23,30	STJ: Three varieties
lysiosepala	+	32,34	FH: Two of uncertain status
	+	35,36	
	+	43	
	r	22,37	
18. Cyrtandra	+	23,24	STJ: Six varieties
platyphylla	+	26,27	FH: All six of uncertain status
	+	29,30	
	+	34	
FORB			
19. Plantago muscicola	r	13	FH: Status uncertain

Table 11 (Continued).

Species by Life-form Categories	General Assessment: Our Survey: Local Abundance	Relevé No.	Other Remarks from Fosberg-Herbst List (FH) and St. John's Checklist (STJ)
VINES			
20. Stenogyne rugosa	r	16,29	STJ: Two varieties
	r	31	FH: One of uncertain status
21. Stenogyne calminthoides	r	33,35	STJ: Four varieties
	r	37,43	FH: Three of uncertain status
TALL FERNS (> 1.5 m tall)			
22. Sadleria souleyetianum	+	35,39	
	r	34,36	
23. Dryopteris paleacea var. fusco-atra	r	38,42	
SMALLER GROUND-ROOTED FERN			
24. Asplenium rhipidoneuron	r	22,23	

* Species found outside relevé 21. All outside records are shown in brackets.

varieties in the area, and thus these may be rare and endangered. Most of the other species listed will probably remain rare with even more intensive searches for their distribution.

It would be easy now to map the distribution records of the 24 rare and endemic species listed on Table 11. However, this was not our objective at this time.

VI. SYNTHESIS AND EVALUATION OF THE DIEBACK PROBLEM (D. Mueller-Dombois)

1. Relationship of the Study Components

The vegetation map resulted in three major forest structural types:

I Dense ohia forests (with 2 subtypes)

II Closed ohia forests (with 5 subtypes)

III Open ohia forests (with 7 subtypes)

These three structural types were based on tree canopy cover (i.e. I > 85%, II >60-85%, III 15-60%). In addition, two other major structural types were recognized:

IV Low-growing vegetation with scattered trees (5 subtypes, tree cover < 15%)

V Low-growing vegetation without trees > 5 m tall (3 subtypes)

Most of our samples were concentrated in units I, II and III. We had no sample yet in unit IV, and we sampled only one of the subtypes in unit V, the bogs, with three relevés.

It was pointed out that there was very little correlation between the four soil moisture regime types (mesic, moderately moist, moist, very moist to wet) and the three major forest structural units. In other words, one can expect dense, closed or open ohia rain forests to occur on any one of these four soil-moisture regimes. However, extremely wet habitats, the swamp or bog types, show a low-growing vegetation cover with or without very low-stature (< 5 m tall) ohia trees. Since nearly the same vegetation structure can occur on relatively recent lava flows, recognition of physical habitat type from air photographs is not easy. Therefore, ground-reconnaissance is extremely important for mapping habitat types in this rain forest terrain.

Some aspects of habitat mapping have already been incorporated into the present preliminary version of the enclosed three vegetation map-sheets. These relate to three ground-cover types identified by the following symbols:

bs = bog shrub and herb complex

ms = shrub-fern complex on well-drained sites at upper elevations

sh = shrub-fern complex on well-drained sites at lower elevations

Thus, here, two soil moisture indicator groups of undergrowth species have been employed, a group for poorly drained, wet sites and a group for well-drained sites. The latter has been split by elevation into a sub-group more related to cooler temperatures (prevailing at higher elevations) and another sub-group related to warmer temperatures (prevailing at lower elevations).

Other undergrowth vegetation types recognized relate primarily to forest structure, namely:

C = Cibotium (tree fern) undergrowth, and

Dic = Dicranopteris (creeping fern) undergrowth.

However, also the cover-degree of these major fern undergrowth types may be utilizable as an indicator of habitat type (e.g. Becker 1976).

Another undergrowth type recognized on the present vegetation map indicates a time relationship in terms of geological recency:

pio = pioneer shrub-fern complex on recent lava flows.

It may also be possible to separate this species complex into moisture regime-related species with further research. This multi-variate analysis will form part of another project.

Once worked out, the use of indicator species for mapping habitat types can be very useful. Plant species may be employed to specify the boundaries between habitat types and to predict the temporal pattern from a few well located sample locations. Such a habitat type map will then reveal the physical site-mosaic in detail which underlies this rain forest, extending across the east flanks of Mauna Loa and Mauna Kea.

Superimposed on this physical site-mosaic is a dynamic forest pattern. This is strongly indicated by the fact that different forest-structural types are found on the same basic habitat type.

The analysis of ohia population structures has given independent, additional evidence for this dynamic pattern. It also has given evidence for the ohia dieback as being part of this dynamic pattern. However, the moisture regime and habitat type analyses have brought forth basic physical site variations and restrictions, which set certain limits to the extrapolation of any one dynamic pattern across the whole rain forest study area. There is no question anymore that the dynamic patterns which occur across the area, differ in major environmental sections of this broad rain forest ecosystem. This will be further explained in the following sections.

2. Five Kinds of Dieback

Table 13 gives a summary of the major components analyzed in this project. From this and the analyses given in the preceding chapters, it is now possible to recognize five kinds of dieback. These can be called:

1) Wetland dieback (symbol W on Table 13)
2) Dryland dieback (symbol D)
3) Ohia-displacement dieback (symbol O-d)
4) Bog-formation dieback (symbol B)
5) Individual-tree dieback (no symbol)

Their characterization is as follows.

2.1 The Wetland Dieback.--This dieback type is most prevalent on very moist to wet, shallow-soil habitats, where it occurs most commonly on poorly drained pahoehoe lava (habitat type 6). However, the wetland dieback is not restricted to pahoehoe. It may occur also on poorly drained aa lava (relevé 43, habitat type 7) and on moist, imperfectly drained, shallow soil habitats (no. 3 and 5). We also find it on moist deep-soil habitats (no. 10, 11). The wetland dieback is characterized primarily on air photographs as a large-area dieback, varying in size from less than a hectare to several hectares over uniform sites. It seems to stop wherever there is a major change in habitat. Canopy density may vary from dense (relevé 37) to open (many examples). This relationship indicates that the wetland dieback is not necessarily density-related. A probable cause could be temporary or prolonged inundation (or flooding) of the root system of the ohia trees. Inundation of some sites may be the result of unusually heavy rainfall, which may occur in certain segments of the study area in some years and not to the same extent in others. The inundation patterns are certainly not uniformly distributed through this terrain, which extends from Olaa Forest Tract across the Waiakea Forest Section to a considerable distance north of Wailuku Stream. Over the moist to wet site mosaic to which this dieback type is generally related, there appears to be a temporal pattern, about which we have only indirect information in our data. Certain wetland diebacks have occurred only recently (e.g. that in relevé 37),

Table 12. Interrelationships of Forest Structure, Habitat Type, Dieback Class and Type and Ohia Regeneration Patterns among the Sample Stands Studied in the Project.

Sample Stand or Relevé No.		Dieback Class and Type	Regeneration Pattern
Saddle Road Belt Transect:			
• Dieback segment		4 (heavy) W	**A V (very advanced)
• Healthy segment		2 (normal for open forest)	A IV (advanced)
Stainback Highway Belt Transect		3 (slight to moderate)	Inadequate II (recent)
<u>Open forest relevés</u>:			
on mesic sites	12 (1)*	5 (very heavy) D	A IV
	18 (8)	5 D	A IV
	26 (8)	5 D	A III (mod. advanced)
mod. moist sites	29 (9)	3 O-d	Inadequate I
	21 (9)	1 O-d	Inadequate I (present, but only < 0.5 m tall)
moist sites	39 (5)	4 W	A V
	28 (3)	5 W	A IV
	34 (3)	5 W	A III
	31 (10)	5 W	A II
	38 (10)	5 W	A II
	42 (11)	5 W	A III
very moist to wet sites	11 (6)	5 W	A IV
	15 (6)	5 W	A IV
	19 (6)	3 W	A V
	25 (6)	3 W	A V
extremely wet sites	17 (13)	-- B	Inadequate III
	40 (13)	-- B	Inadequate IV
<u>Closed forest relevés</u>:			
on mesic sites	16 (1)	3 D	Inadequate II
	20 (8)	4 D	A III
	30 (8)	2 (slight for closed forest)	A IV
	22 (9)	1 (normal for closed forest)	Inadequate I
	32 (9)	2	Inadequate I

Table 12 (Continued).

Sample Stand or Relevé No.		Dieback Class and Type	Regeneration Pattern
Closed forest relevés (continued):			
moist sites	24 (5)	5 W	A III
	27 (3)	3 W	A III
	41 (11)	2	Inadequate IV
very moist to wet	43 (7)	4 W	A III
Dense forest relevé:			
on mesic sites	13 (1)	4 D	Inadequate III
	14 (1)	2	Inadequate V
mod. moist sites	23 (2)	3	Inadequate II
	33 (2)	3	Inadequate II
moist sites	35 (3)	3	Inadequate III
	36 (3)	2	Inadequate I
very moist to wet	37 (6)	5 W	A II (recent)

* Number in brackets after relevé number refers to habitat type (Chapter III)

** A = Adequate regeneration, i.e. > 3500 small ohia trees per hectare

Dieback Type Symbols: W = Wetland Dieback
D = Dryland Dieback
O-d = Ohia-displacement Dieback
B = Bog-formation Dieback

others have occurred a much longer time ago (e.g. the one in the 1.3 km belt-transect along the Saddle Road). The indices we obtained for the timing of dieback are the number of old snags, recently dead trees and the relative advancement of the ohia regeneration.

It is of considerable importance to note that all wetland dieback areas, which we analyzed in this project, showed adequate reproduction (i.e. 13 relevés plus the 1.3 km belt-transect).

2.2 The Dryland Dieback.--This dieback type appears to be restricted to mesic or well-drained sites, where it occurs on both shallow-soil and deep-soil habitats. On air photographs this dieback type shows a "pocket"-like distribution. These pockets are usually less than an acre to rarely more than an acre in size. In the population structure analysis there appears to be little difference between the dryland and wetland diebacks, except that some dryland diebacks appear to be associated with dense ohia stocking (e.g. relevé 16) or with higher stocking density before most of the dead standing trees had fallen down (e.g. relevé 12). Thus, it appears probable that the dryland dieback is a response to a plant-crowding phenomenon on these mesic sites.

It is quite conceivable to imagine that ohia stand-development on these mesic habitats proceeds to a point, when a temporary soil-drought may trigger a dieback. The ohia seedlings become established in a restricted time-period (probably in less than a decade), and they form a one-generation stand. As the initially small trees increase in size, they require more nutrients and water per individual. Depending on their stocking density, they will begin to diminish each other's nutrient and water supply sooner or later. Nutrient- and water-withdrawal is further aggravated by the developing undergrowth vegetation. The mesic sites in this rain forest area have nearly unweathered substrates. Because of their recent volcanic origin, they are loaded with nutrients, but these nutrients may not become available from weathering as fast as the demand of the plant cover increases in ohia stand development. As a result, the ohia trees when having reached a certain size may be on a "starvation diet." Then, a soil-drought could trigger a stand-dieback. This dieback would extend over that stand-segment on the mesic site where the trees are dense or otherwise in intense competition with the associated vegetation. For this reason, the dryland dieback may have the "pocket" pattern as mentioned before. This hypothesis involves plant competition and then soil-drought as a trigger. It would explain Dr. Ko and Kliejunas' earlier experimental results (Kliejunas and Ko 1974) in which these authors demonstrated that declining ohia trees respond positively to fertilization.

With only two exceptions, we found adequate ohia regeneration on the mesic-site stands which were struck by dieback (Table 13). In relevé 16, which was one of the exceptions, the dieback index was only 25.8%. It thus represents an almost "healthy" closed forest, and for this reason probably--namely the shaded forest-floor conditions--the regeneration is inadequate. The second exception is relevé 13, which showed heavy dieback. But here, the remnant "healthy" stand was still so dense that ohia regeneration had not progressed very far. In this stand, one may expect adequate ohia regeneration to occur within the next decade.

It may be noted that in all but one of the dense forests sampled in this study, ohia regeneration was inadequate. The one exception is the before discussed wetland dieback relevé 37. This clearly demonstrates that ohia regeneration is present, but inadequate in ohia forests with >.85% crown closure. Moreover, in all closed forests (with crown closures ranging from >60-85%), ohia regeneration was inadequate, wherever there was no significant dieback (Table 13).

2.3 The Ohia-Displacement Dieback.--This third kind of dieback was found only on moderately moist deep-soil habitats in Olaa Forest Tract, where much of the area is covered by mono-dominant tree-fern (*Cibotium* spp.) forests. Here, it seems old, big-diameter ohia trees are dying out slowly without adequate replacement by reproduction. Examples for this kind of dieback are relevés 21 and 29 (Table 13). The trees are tall and limby, often heavily laden with epiphytes. Their foliar biomass and leaf-area seems small relative to their woody biomass in trunks and branches. Many of these trees appear to have transgressed the CO_2 compensation point and now seem to be dying slowly from overmaturity.

The moderately moist deep-soil habitats of Olaa Tract (including the lower part of the Kilauea Forest Reserve) obviously represent the ecological optimum for tree ferns in the entire study area. Here tree ferns are effectively crowding out ohia as a successional tree species. An occasional ohia sapling can be found to grow epiphytically on tree fern trunks, but this phenomenon is too rare to be quantitatively of significance as a mechanism for ohia stand rejuvenation.

Under the tree fern canopy, the associated undergrowth plants do not appear to be negatively affected by the gradual disappearance of the tall ohia trees. The displacement of ohia may not be permanent. A heavy windstorm, which can blow down part of a tree fern forest may result in a reappearance of ohia. However, so far we have seen little evidence for this.

2.4 The Bog-Formation Dieback.--This form of dieback occurs only on very moist to extremely wet deep-soil habitats, which cover a large area on the Hamakua Forest Section map. This area extends from north of Wailuku Stream to near Laupahoehoe and is altitudinally confined between about 2000 and 4500 feet elevation. Like the wetland dieback, the bog-formation dieback appears to be associated with habitat inundation, except that the inundation can be considered permanent instead of periodically fluctuating. The bog-formation dieback can be related to a gradual site-change as the result of geomorphological development and landscape-aging.

There is a spatial pattern related to this dieback, which shows some altitudinal banding on the aerial photographs. Going altitudinally upwards in this part of the Hamakua Forest section, there occurs first a band of closed forest at about 2000 feet elevation, which is interspersed with small (> 0.1 ha to 0.5 ha) bogs occupied with sparse, stunted ohia-tree growth. Going up higher to about 2600 feet elevation, the bogs increase in size to a maximum of approximately 10 ha. Here, the forest-covered area occurs interspersed among the bogs in form of narrow strips, which are low ridges covered with decadent forests. Going up further to 3700 feet elevation, the bog-openings become again smaller, their size being about 0.5 ha to 1 ha, and the forest-covered area becomes correspondingly larger. The bogs disappear at about 4200 feet elevation. Here the forest is more or less closed throughout, but it shows heavy dieback. Still higher, above 4800 feet the forest is dominantly "healthy" to its upper limit near 5500 feet, where the rain forest merges into a climatically drier forest belt dominated by Acacia koa.

This altitudinal banding and the bog-mosaic within each elevational band or belt is also indicated on the enclosed vegetation map sheet (Hamakua Forest Section). Here, the combination of vegetation symbols reflects this bog-mosaic. A larger-scale map (at about 1:5000) would be needed to truly portray the outlines of the numerous bogs in this mid-slope terrain. Throughout the bog area there is more or less heavy dieback in the interspersed forest-covered areas, and much of this forest, particularly between 3000 and 4000 feet elevation is structurally open (crown cover < 60%).

What really goes on in this area is still a mystery. The area is difficult to reach on foot. We managed to get into some of the smaller bogs in the lowest bog-belt near 2200 feet elevation (relevé 40) and at mid-elevation (3500 feet) from the Wailuku Stream side (relevés 2 and 17). Except for relevé 2, which represents a totally treeless bog, the other two had stunted (< 5 m tall), but mature and flowering, ohia trees. These grew very sparse among sedges, rushes, other bog plants (including Sphagnum vitianum), some broomsedge (Andropogon virginicus) and the creeping uluhe fern (Dicranopteris linearis). Ohia regeneration was "inadequate", but "advanced" (Table 13) according to our before described standards. Only few snags were recorded.

We lack as yet samples of the open forest and dieback stands surrounding the bogs nearer the center of the bog mosaic. One of our relevés (no. 5), which occurred near a bog north of Wailuku Stream, showed a hardpan at about 30 to 50 cm depth in the soil profile (at several places in the relevé), which resembled a weakly cemented clay layer. The layer was easily cut by a knife. But the soil above was watersoaked, and it was drier below the hardpan.

It is too early to predict clay hardpan formation as a cause for the bog-formation dieback on Mauna Kea. Many more samples in this area are needed for that. However, Fosberg (1961) concluded many years ago from his observations of ohia dieback in montane wetland forests on Kauai and Maui that clay hardpan formation may be involved in this dieback and the formation of Hawaiian bogs. Since Dr. Fosberg's conclusions appeared in a publication of limited distribution and since his conclusions are very appropriate to recall at this place, they are quoted here in full:

> For years it has been noticed that certain Hawaiian forests are in very poor condition, with many dead or dying trees. In some areas these are accounted for by the activities of grazing animals. This is especially true in dry areas and on cliffs and rough steep slopes. However, decadence of forest is also observed in very wet areas where there is no particular grazing; these areas are on comparatively level or gently sloping ground. The larger trees are dead or almost so, but usually there is a well developed stand of smaller trees or shrubs, including some or all of the same species as in the original forest. The stands are of varied statures, but within a stand the height is fairly uniform. These low forests do not seem to be simply young forests, as some of the taller ones, 4-6 m, have an abundance of old dead or partially dead taller trees, while in some lower stands, 1-2 m, standing dead trees are uncommon or rare. The lowest of these forests have been referred to as incipient bogs, and have well developed basal clay layers (Patterson, personal communication, 1961). One such stand east of Hanalei Valley, Kauai, where traversed by a road, shows a striking white clay substratum.
>
> It is suggested that these decadent forests are stages in the process leading to the formation of bogs. Weathering of the basalt under cool, very wet, conditions that permit an accumulation of humus and thus percolation of humic acid solutions yields clay (Wentworth et al. 1939). Formation of clay on level or gently sloping ground gradually impedes drainage, and brings about the accumulation of perched water on top of the clay. This drowns the root-systems of the large trees, causing them to die slowly, as is seen in the decadent forests. They are replaced by smaller trees, more shallowly rooted. As the clay layer becomes more impervious and perhaps more extensive, the accumulation of water may become greater and may even drown the shallow root systems of the small trees. This process repeats itself, until the low forest, the shrub bog, and finally the very low sedge bog vegetation, are formed.
>
> This theory would account for the present distribution of bogs in the Hawaiian Islands, for the correlation of decadent forest with flat very wet terrain, and for the correlation of clay layers on the basalt with decadent forest and bogs. It would also account for the decadence of the forest on flat ground immediately adjacent to healthy forest of tall stature on steeper slopes. This gradual dwarfing process might also have brought about the evolution of dwarf races of such forest trees as <u>Metrosideros</u> that are in full flower when only a few centimeters tall.

Undoubtedly, Dr. Fosberg was talking about what we here have identified as the bog-formation dieback in yet another area.

Nevertheless, it seems hard to believe that one may witness stand-dieback as caused by a pedogenic or geomorphological phenomenon. Such processes are considered to proceed on a much longer time-scale than a tree generation. However, when flying over this boggy slope-terrain on Mauna Kea, one can observe many dead trees on the ground, which are heavily overgrown with other vegetation. Here the dieback does not appear to be a phenomenon that has occurred suddenly and recently. Instead it gives a strong indication of having gone on for a very long time. The dieback appears to be occurring in stages more or less continuously distributed over the habitat mosaic of this terrain. Several ohia tree generations seem to be involved in this process. Undoubtedly, the site capacity for tree-growth is changing more rapidly in some (now depressional topographic positions), and less rapidly, if at all perceptibly, in others (the raised topographic positions). Not all of the area will end in bogs. Dieback in less inundated but wet positions may merely result in a less tall and more open forest to follow, like the dieback which occurred around the turn of the century on East Maui (see Literature Review in First Progress Report). Site stability may then prevail for several centuries in certain habitats, while others undergo further changes.

2.5 <u>The Individual-Tree Dieback</u>. In all "healthy" closed forest samples we have observed a few isolated dead, standing trees. This "individual-tree dieback" is therefore a common phenomenon in natural ohia rain forest stands. Some of these individuals had died recently, with brown leaves still hanging on; others had died a longer time ago. Commonly these trees were of lower diameter classes and subcanopy position. Their death may be explained as a normal event of natural thinning of the physiologically weaker individuals. Death may be the result of intraspecific competition or a combination of factors including a pathogen or a wood borer, such as <u>Plagithmysus</u> <u>billineatus</u> (the endemic ohia borer).

The main difference to the previously discussed diebacks is that this form of dieback strikes only individual trees which are scattered throughout an otherwise "healthy" forest. It is thus not to be confused with a stand-dieback, where groups of neighboring trees are dying more or less simultaneously. Of course, a stand-dieback may begin with one or two individuals dying and a chain-reaction of tree-deaths may follow. Thus, it is not always easy to distinguish individual-tree dieback from initial stand-dieback. Here, monitoring of large-scale air photos and permanent plots in mature, healthy forests should provide a clear understanding. An on-site indication is given when a dominant, canopy tree dies or when a smaller subcanopy dies. In the first instance, a stand-dieback may follow.

3. Dynamic Phases: A Rain Forest Life Cycle

The study has given conclusive evidence that there are several associated dieback and regeneration patterns occurring simultaneously within the study area. However, these relate only to the Dryland and Wetland Diebacks. The other two forms of stand-dieback result in different vegetation structures.

It is now possible to suggest that the Wetland as well as the Dryland Dieback initiate each a series of dynamic phases, which can be named and characterized as follows.

3.1 Incipient Breakdown or Dieback Phase.--This phase would be indicated by ohia stands with slight to moderate (class 3) dieback. Ohia regeneration in this condition may still be inadequate (< 3500/ha). But in some cases regeneration is just starting to become abundant and well established (Regeneration class AI - AIII).

3.2 Full Breakdown Phase Accompanied by Stand Rejuvenation.--This phase would be indicated by ohia stands with heavy (class 4) or very heavy (class 5) dieback. Ohia regeneration would be adequate (> 3500/ha) and recent (AII) to moderately advanced (AIII).

3.3 Advanced Reproduction Phase with Snags Still Standing.--This phase would also be indicated by dieback classes 4 or 5, but with advanced ohia reproduction occurring among the snags, i.e. reproduction classes AIV (advanced) and AV (very advanced).

3.4 Full Production Phase.--In this phase most new-generation ohia trees have exceeded 5 m in height, they have become dominant in height and outnumber all other woody plant species in the stand. Only a few snags are still standing (which may still be taller than the taller new-generation ohia trees). Ingrowth of ohia has considerably slowed down.

3.5 Mature Phase.--In this phase the ohia forests have reached their height limits as determined by the capacity of the site on which they are growing. Most of the trees are full-crowned and vigorous, but a few snags may be encountered, which are members of the current generation. Stands are in what we have called "healthy" condition, i.e. dieback class 1 (= normal for open forests) or 2 (= normal for closed forests). New ohia regeneration in this stage is present, but usually retarded (i.e. inadequate or AI or AII).

3.6 A New Dieback Theory.--It is important to reemphasize that these dynamic phases can only be associated with the Dryland and Wetland Diebacks and not with the others. Moreover, we may recognize somewhat different tendencies in the dynamic phases initiated by these two dieback types. The Dryland Dieback may be more commonly associated with full restocking, which results in closed forests, while the Wetland Dieback may often result in less-densely stocked, or more open forests. The reverse is also possible, but to be expected less commonly.

The described dynamic phasing pattern, which is seen as being initiated by both the Wetland or Dryland Dieback, is a new theory, which proposes a rain forest life cycle as related to the successional behavior of the stand-structure forming dominant tree species, ohia. This theory was concluded from a factual and properly documented series of stand-dieback and reproduction patterns currently occurring side-by-side in the ohia rain forest terrain studied. Thus, the patterns are spatial in fact and dynamic only in this theory. However, this dynamic phasing theory is testable, and testing of this theory will form a new research project.

There are two further elements to this theory, which relate to the following.

Firstly, ohia is known to be a pioneer tree species. Its occurrence as the first major stand-forming tree on new volcanic substrates has been amply documented (Atkinson 1970, Smathers and Mueller-Dombois 1974, among others). From all observations at hand, ohia seems to be a shade-intolerant species. This implies that the species requires a good amount of light to grow successfully from seedling to maturity. In closed ohia forests there is only reduced light available on the forest floor. Ohia seedlings germinate, but their mortality is very high, probably from light starvation. In order to reproduce successfully there must be a mechanism that removes the shade. There is no doubt, based on our data, that the dieback (both wetland and dryland type) provides this mechanism.

Other forests with perpetuating pioneer species are maintained by long-term or erratically recurring perturbations. For example, the Douglas-fir forests in the Pacific Northwest are known to be maintained naturally by periodic fires (Schmidt 1960). Tropical rain forests elsewhere with permanent pioneer species are known to be maintained in some cases by periodically recurring hurricanes (Whitmore 1975). Neither fire, nor hurricanes are important perturbations in the Hawaiian montane rain forests. Thus, a drastic canopy collapse, as resulting from the ohia dieback, may be seen as a recurring mechanism that became successful in maintaining ohia dominance in the Hawaiian rain forests. It also explains the peculiar one-generation structure of many ohia stands, which made Vogl (1969: 35) believe that such ohia stands had a fire-origin.

Secondly, ohia is known to be a polymorphic species as is indicated by its scientific name, *Metrosideros collina* subsp. *polymorpha*. The two authors (Rock 1917 and Skottsberg 1944), who monographed this species taxonomically, agreed that there are many varieties, but they disagreed considerably in detail. Occasionally, more than one ohia variety has been reported from the same site. This phenomenon coupled with the fact that ohia is found on a wide range of soil moisture regimes, from excessively drained (on new lava flows) to extremely and permanently wet (in bogs), makes it likely that the ohia species is comprised of successional races or ecotypes. With further knowledge about the validity of this successional ecotype theory, it may be possible to recognize pioneer, seral and climax races within the ohia species complex. These races may differ little in their light requirement, but may exhibit different substrate adaptations and tolerances, from an almost xerophytic existence (on alternately wet and dry substrates) to an almost hydrophytic existence (in permanently water-soaked substrates with little oxygen supply).

A research proposal has been submitted to the National Science Foundation to study the successional ecotype theory for ohia. This work, coupled with intensive field sampling, should provide an answer also to the Bog-formation Dieback.

4. Conclusions and Applications

4.1 The Current Status of Ohia Dieback Research.--The researchers concerned with the dieback problem gathered for a day-long seminar on October 25, 1977 (see Appendix II, Ohia Decline Seminar).

All insect and disease research so far has given negative evidence so that the idea of the ohia dieback as a "creeping epidemic" is in serious doubt.

The root pathogen *Phytophthora cinnamomi*, which was once strongly suspected as the killer of ohia (see Appendix 2 in UH/CPSU TR 3) was clearly dismissed as a primary cause. Dr. Kliejunas, who has studied the relationship of *Phytophthora cinnamomi* with ohia decline for the past five years, stated that there was only a correlation of this root pathogen with soil moisture regime, but not with the decline. He also said that he had dismissed *Phytophthora cinnamomi* as a primary cause already "in 1972". The pathogen's secondary involvement, however, in the Wetland Dieback, is still considered a possibility. Yet, the pathogen is clearly not the trigger of the dieback. Investigations into other possible pathogens are being continued.

The ohia wood borer (*Plagithmysus bilineatus*) has also been investigated for its involvement in the dieback for the past several years. Dr. Papp presented evidence that this endemic beetle increases in population numbers on physiologically weakened ohia trees. He showed a perfect correlation of ohia crown-loss and borer population density. Yet, he concluded that the borer can be considered both a cause and an effect of the ohia decline. His data, however, showed that the role of the borer as an effect is significant while his data showed little evidence for the borer's role as a cause. In other words, if this borer does attack an occasional "healthy" ohia tree, this form of attack has not yet been shown to be quantitatively significant.

Post decline effects on soils and plants were presented as another research emphasis of the U. S. Forest Service. So far, no evidence could be given for the decline affecting a change in soil water relations.

Our studies have shown conclusive evidence for the dieback being associated with vigorous ohia reproduction. If nothing else, this is perhaps the most important single result of our investigations. It also should clarify the notion of ohia "decline". There is indeed no significant lateral decline of ohia forests in the study area. The only true decline (in the lateral sense) occurs as a result of the Ohia-displacement Dieback in the Olaa Tract of Hawaii Volcanoes National Park. The Bog-formation Dieback may also be considered a form of ohia decline, where, in a few places, treeless bogs are formed. As a decline or retreat of ohia from the rain forest terrain as a whole, however, the few treeless bogs are insignificant.

Another important result of our studies is the sorting out of the vegetation, moisture regime and habitat patterns occurring within the montane rain forest ecosystem studied. Pettys, Burgan and Nelson (1975), who predicted the rapid decline of ohia forests from an analysis of three successive sets of air photos, refer to the area as if it were one big uniform entity. They obviously suspected the cause of the epidemic, whatever it was, not to be restricted by any habitat boundary. Our studies have shown that habitat boundaries are important. The Wetland Dieback is clearly related to habitat characteristics. However, since not all wetland areas (e.g. very moist to wet shallow soil over pahoehoe habitats) are in the same stage of dieback, the habitat correlation of this dieback is not an obvious one. It could only be established through careful ground sampling. The Dryland Dieback appears to be not merely habitat related, but also density related. The density and competition relationships will be an aspect of further research.

From our results it also becomes important to reevaluate the air photo prediction of the rapid decline made by Pettys, Burgan and Nelson (1975). There is little doubt that some areas have had a rapid dieback. This is clear also from the ohia regeneration response in these areas. However, the Bog-formation Dieback is probably not a rapid dieback, and it appears now, in view of our findings, untenable to consider the ohia dieback as caused by a single trigger.

4.2 The Size Requirement for Conservation Purposes.--Our investigations have clearly shown that the ohia rain forest is not an endangered ecosystem. We can now predict with a high degree of confidence that the ohia species will maintain itself as the major stand-forming dominant tree throughout the rain forest territory except in some locally restricted areas, which are naturally converting to pure tree fern forest or to treeless bogs. However, ohia maintenance is predictable in this sense only if reasonably large areas of its ecosystem are left intact. There is a good possibility that exotic tree species, such as the strawberry guava (*Psidium cattleianum*) may displace ohia in certain areas, if the natural rain forest is allowed to be converted to exotic tree plantations or other commercial uses over larger tracts of land than have been converted at this stage in time.

In this regard, it is very important to emphasize that none of the forest samples or relevés, which we analyzed in this study, can be considered to be in climax condition. A climax as here understood, refers to a vegetation which is in dynamic equilibrium with its environment and which over a longer span of time (say from 200 to 500 years) shows essentially the same species composition. Although there is much confusion about the climax concept, this definition is generally accepted. There is, however, an important corollary to this definition of a forest vegetation being in dynamic equilibrium. This is the size-scale which one applies to the climax.

Recent studies in natural rain forests on Oahu have shown (Gerrish, unpublished) that one can recognize the before discussed five life-cycle phases of ohia stands on relatively small tracts of land. In Pupukea (north-end of Koolau Mountains on Oahu) these phases can be seen and are documented to occur on areas of one hectare or less in size. Here, dieback is restricted to scattered individuals or groups of individuals. In association with old ohia snags, one commonly finds advanced ohia regeneration. More recently dead or dying ohia trees are usually associated with smaller-sized ohia reproduction, while closed and full-crown forest patches show only sparse seedling occurrences. In some localities of this area, the strawberry guava (Psidium cattleianum) is now involved in the forest reproduction cycle, and there are sites where this exotic tree has displaced ohia in competition. However, except for the disturbances in natural forest composition caused locally by the success of some exotics, the Pupukea rain forest can be said to be in dynamic equilibrium with itself and its environment. In this case one can speak of a near-climax or disclimax vegetation.

In the rain forest study area on the Island of Hawaii, we have only found one forest that can be considered a disclimax, in the sense of showing some disturbance by exotic organisms, but having all dynamic phases occurring side-by-side on a relatively small tract of land. This is the Kilauea Forest Reserve (Cooray 1974), which supports Acacia koa as an important second tall-growing tree. Here, the 25-30 m tall, often overmature Acacia koa trees, cause relatively big gaps upon their being thrown-over by an occasional tropical storm. In this forest, one can recognize and map gap phases relating to different reproduction patterns of the major tree species and associated plants (IBP Synthesis Volume, in preparation). Cooray's (1974) analysis has shown that this forest is in a dynamic equilibrium, i.e. perpetuating itself with essentially the same species composition. In this forest, the dynamic equilibrium operates on a somewhat larger size-scale than at Pupukea, Oahu. The size needed for long-term perpetuation of this rain forest with Acacia koa as a second dominant can be estimated to require a minimum-area of approximately 100 to 200 hectares.

In addition, one would have to consider a sizable buffer area to minimize the invasion of exotic plant species. Further size-considerations may enter into the question of perpetuating the necessary minimum range or critical habitat for native bird life.

In the ohia dieback terrain studied in this project, we found hardly a stand that could be considered in dynamic equilibrium with itself and its environment. The only exceptions appear to be the upper and lower elevation belts containing Acacia koa as second dominant. In these forests we found no significant ohia dieback. Another special case is the area with the Bog-formation Dieback.

Thus, in the areas with Dryland Dieback (Hawaii Volcanoes National Park, lower Stainback Highway and upper Saddle Road), Wetland Dieback (from Puu Makaala north across Wailuku Stream) and Ohia-displacement Dieback (mostly in Olaa Tract), there is no single ohia forest that can be considered a climax or disclimax stand. It is necessary, therefore, to draw a much larger boundary around the vegetation that can be considered to be in dynamic equilibrium with the environment and with itself, which in other words, may remain relatively stable over longer periods of time. For example, the Puu Makaala area is considered a prime area for conservation purposes at this time, because of its fine examples of closed ohia forest with a diverse association of other native undergrowth species. However, much of the Puu Makaala forest shows signs of incipient Wetland Dieback. It is possible that this forest will soon enter into an advanced breakdown phase and with this, it may lose some of its associated endemics during the rejuvenation phase. Therefore, it appears necessary to draw the conservation boundary around a much larger tract of land, which includes in addition to the closed "healthy" forest a sufficient area in various stages of dieback and rejuvenation. Specific areas would have to be mapped out to assemble in one unit a self-perpetuating natural unit of ohia rain forest for conservation purposes. With only little additional work, this could be done on the basis of this study.

4.3 Implications for Rain Forest-Associated Management Problems.--The more important practical considerations related to the dieback phenomenon may be phrased in three questions:

1) What is the effect of the dieback on the watershed value of this rain forest terrain?
2) What effect does the dieback have on the rare and endemic species associated with this rain forest ecosystem, including the native birds?

3) Does the dieback affect the behavior of exotic plants and animals, including the feral pig?

Although our study was not oriented towards answering these questions directly, we now can evaluate them to some extent from our familiarity with the area and the dieback problem.

To question 1: The watershed values can certainly be expected to deteriorate when large segments of a montane rain forest are struck by dieback. In this particular area, excess water is the problem, and forest dieback could result in excessive runoff. The excessive runoff could have a negative impact on the sugar cane growing areas downslope of the rain forest along the Hamakua Coast. This deduction appears reasonable.

However, from our current knowledge of the forest, two observations point against this deduction. The sugar cane fields north of Wailuku Stream are below the area where much of the Bog-formation Dieback occurs. Bogs act like "collecting pans" or like "sponges". The difference depends on their vegetation cover. Surface runoff water accumulates in them. There can be a considerable lag-effect after water is released from these boggy areas following heavy shower activity. Thus, the bogs have a regulatory effect on the surface-water flow. The bog-mosaic in this dieback area can be considered an effective watershed, perhaps even superior to a closed forest cover.

The second factor reducing runoff-impact can be attributed to the loss of forest itself. Clouds are seen to persist in the Hamakua montane rain forest belt for much of the time. Fully foliated, densely standing trees collect a large quantity of condensation water by acting as fog interceptors. Open forests and snags add less condensation water to the ground than closed, "healthy" forests in such a fog-belt, and treeless vegetation intercepts even less. A study of fog-interception was done by Juvik and Perreira (1973) on the east flank of Mauna Loa, which lends considerable weight to the suggestion made here, that the quantity of condensation water obtained from interceptors is very substantial, perhaps approaching a value equal to the annual rainfall.

In spite of this hypothesis that the ohia dieback in the Hamakua forest section is not impairing the watershed value of the area, the watershed relationship to the dieback should be studied for obtaining hard evidence for either of the two arguments.

On the poorly drained, shallow-soil habitats, where the Wetland Dieback was said to occur, the watershed situation is again different. This area is largely south of Wailuku Stream, occurring in areas along and across the Saddle Road, mostly on the Waiakea map sheet. Here, the dieback may well result in an increase of the surface water level. However, also here, fog interception is no doubt reduced under dieback as compared to non-dieback stands, a factor working against great changes in the soil water regime following dieback. Also, here the undergrowth vegetation is vigorous and ohia regeneration is developing well, which indicates that water absorption from the soil surface layers is functioning adequately. In addition, downslope from this Wetland Dieback area occur still many recent volcanic substrates, which are quite permeable to the incoming water. Therefore, the downslope section will hardly be affected by excess water as a result of the Wetland Dieback.

Again, what is said here is merely a hypothesis. The effect of the Wetland Dieback on the soil water regime is well worth investigating.

The Dryland Dieback occurs on well-drained habitats. The watershed problem does not apply to this type of dieback. The same can be said for the Ohia-displacement Dieback, which occurs mostly on moderately moist to moist, rather permeable deep-soil habitats.

To question 2: The effect of the Wetland and Dryland Diebacks on the rare and endemic plant species is not yet clear from our data. There are indications, however, that dense mature forests contain a greater number of rare endemics than do open forests. Whether or not such species are displaced during a dieback depends on their response to the changed light conditions. Many of them appear to be shade-adapted plants (i.e. sciophytes). In that case they can be expected to be negatively affected or to be displaced by heliophytes, such as the uluhe fern (*Dicranopteris linearis*).

As a working hypothesis, it is now possible to suggest that these two forms of dieback (Wetland and Dryland) affect the associated vegetation as in a succession. The dieback initiates a secondary pioneer stage*, which in some cases may be drastic enough to displace the rare endemics.

The same can be said also for the endemic forest birds. Dieback areas seem to be very poor in birdlife. The birds will probably return during the advanced rejuvenation phase of the forest or during a later phase. Also, the rare endemic plant species may behave similarly.

To question 3: Our data indicates that exotic plant species behavior is affected by the dieback. In some of the Wetland and Dryland Dieback stands the number of exotic species was greater than in the surrounding non-dieback stands. In these cases, an important factor is the richness of exotic species in the area. Conversely, in areas where the number of exotic species is low, the dieback appears not to be associated with exotic species invasion.

Another important factor is the eco-physiological preadaptation of the exotic species in question. Many exotic species, such as Erechtites valerianaefolia, Andropogon virginicus and Buddleja asiatica, are pioneer species. These require a good amount of light for successful propagation. Such exotics can be expected to disappear in the course of the stand-recovery after a dieback.

Our data with regard to feral pig activity is not yet conclusive. But pig activity appears to be generally low on shallow-soil habitats, where much of the Wetland Dieback occurs. Pig activity appears to be low also in dense forests, but higher in open forests on deep-soil habitats. In Hawaii Volcanoes National Park, where some of the Dryland Dieback occurs,pigs seem to be particularly active in those areas. There is little doubt that the habitat distribution of the area is a primary influence on the home ranges of the feral pig. Forest structure and the dieback appear to play a secondary role.

For a pig activity and home range study in the rain forest ecosystem, it would therefore be useful to generate a habitat map based on the criteria developed in Chapter III.

4.4 Hypotheses, Facts and Theories.--As a final point, it may be useful to summarize the more relevant hypotheses, facts and theories that so far were developed in connection with the ohia dieback or decline.

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* In contrast to primary, which would be the pioneer stage on new volcanic substrates.

1) <u>Hypotheses</u>: Webster's dictionary defines a hypothesis as "a tentative assumption made in order to draw out or test its logical or empirical consequences." Implicit in this definition is the "tentativeness" of an idea and the purpose to "test its consequences."

There were only two important general ohia decline or dieback hypotheses that started serious research efforts in the Hawaiian rain forest. These were:

A. The disease or insect-damage hypothesis proposed by the U. S. Forest Service and promoted as a research approach particularly by R. E. Nelson (i.e. Burgan and Nelson 1972; Petteys, Burgan and Nelson 1975).

B. The succession or natural phenomenon hypothesis proposed and promoted as a research approach by the writer (Mueller-Dombois 1974).

It should be noted that other authors (Lyon 1909, Fosberg 1961, Stoner 1976) presented similar ideas as the writer. But these ideas were not yet tested. They also differ in detail, and will be referred to once more below under "theories".

It is useful to distinguish between general hypotheses and so-called working hypotheses. The latter relate to the testing of more specific ideas that evolve during the course of an investigation. A number of such working hypotheses are suggested in this report, but they will not be summarized at this place.

A general research hypothesis is a powerful tool insofar as it gives direction to the kind of research which follows. This was and still is the case in both of the two general hypotheses involved in the ohia decline problem. However, it should also be made clear that a general hypothesis is merely an "educated guess" about a phenomenon. If properly approached in research, the author or proponent of a general hypothesis, should truly verify the hypothesis. This means that he should give equal weight to disproving his own hypothesis as he does to proving it.

2) <u>Facts</u>: Webster's dictionary gives several definitions of the concept "fact". The most applicable for biological research is, "a piece of information presented as having objective reality." On this basis,

the more important facts brought to light in the ohia dieback research so far are:

(1) The finding of Kliejunas and Ko (1974) that deficiency of inorganic nutrients is a factor in ohia decline.

(2) The study of Hwang (1977), which demonstrates clearly that the root fungus Phytophthora cinnamomi is not involved in the dieback, which in this report is referred to as the Dryland Dieback.

(3) The demonstration from aerial photographs of a rapid spread of ohia decline by Petteys, Burgan and Nelson (1975), which undoubtedly applies to what is in this report referred to as the Dryland and the Wetland Dieback.

(4) The findings published by Kliejunas, Papp and Smith (1977) that Phytophthora cinnamomi and the endemic ohia borer (Plagithmysus billineatus) assume only a secondary role in the ohia decline.

(5) Our ohia reproduction analysis, which shows that ohia stand rejuvenation is associated with both the Wetland and the Dryland Dieback.

(6) Our soil moisture regime and habitat analysis, which clarifies that the rain forest ecosystem is not an environmentally uniform entity and that different forms of ohia dieback are associated with certain habitats.

3) Theories: There is confusion on this concept, which is also apparent from the interpretations found in Webster's dictionary. Here one finds theory defined first as "the analysis of a set of facts in their relation to one another." In an alternative way, theory is defined as "a hypothesis assumed for the sake of argument or investigation."

Clearly, Webster's alternate definition is that of a hypothesis. If one wants to distinguish between the concepts of hypothesis and theory, as is customary in science, then the two concepts cannot be the same. A scientific theory, therefore, requires a set of facts in their relation to one another.

So far, the disease hypothesis has not resulted in a theory. At least the writer is not aware of any organismic agent theory, which brings a series of facts together into a comprehensive "epidemic ohia decline" theory.

On the other side, the succession or natural phenomenon hypothesis has been supported by several theories.

(1) Lyon (1909) having worked intensely on the so-called Maui forest disease, which clearly was a form of ohia dieback, concluded that it was definitely not caused by a fungal pathogen. He found that the dead and dying trees occurred on the more gentle slopes with poor drainage, whereas trees on steep slopes or well-drained soils remained healthy. He observed that not only ohia trees die in the poor drainage areas, but that several associated tree species also die in these situations. He made numerous root isolations and always found them to be of a deep purple or bluish black coloration. He noted what looked like "oil slicks" on the standing water in pools of poorly-drained areas and concluded that hydrogen sulfide was produced by bacteria in the stagnating surface water, which would be toxic to tree growth. Moreover, he said that the free hydrogen sulfide changes harmless ferric (iron) compounds to poisonous ferrous (iron) compounds. He buried a heavily rusted axe head among dying ohia tree roots for 21 days and found after that period that the rust was easily removed by washing, which exposed the bluish black steel beneath. He concluded that hydrogen sulfide in the soil had reduced the rust to ferrosoferric hydrate and possibly iron sulfide. He also noted that the soil had very little calcium, resulting in an unusually high magnesium/calcium ratio.

Although Lyon's findings on the ohia decline on East Maui in the first decade of this century were circumstantial rather than direct, they provide an important working hypothesis that has not been fully investigated. Lyon's working hypothesis may be called a theory, since his explanation is based on a number of facts synthesized into a logical relationship.

(2) Fosberg's (1961) theory, which was restated on p. 79. It is based on a few factual records of hardpan formation on very moist to wet deep-soil habitats. Fosberg's theory would explain the Bog-formation Dieback as discussed in this report.

(3) Stoner's (1976) theory, which was only published in form of an abstract. The abstract is here retyped in full for the sake of clarification.

"According to this theory, the decline of ohia forests (Metrosideros and other genera) is basically a natural phenomenon most pronounced on original surfaces of youthful shield volcanoes. The precipitant nature of decline is attributed to a situation wherein an environmentally tolerant flora allows the forest to survive largely intact for a time, while the soil becomes progressively more adverse to root growth and ecosystem stability decreases. Fragility, particularly in the rhizosphere, predisposes the forest ecosystem to decline, which may be precipitated by one or more agents. Once initiated, decline spreads rapidly as a chain reaction in the fragile ecosystem. Local patterns of decline vary due to site factors. Vegetational changes during and following decline promote substrate alterations contributing to the geomorphic cycle. Later, structurally and genetically different forests develop on steeper slopes or other surfaces. Factors underlying fragility include edaphic changes related to the rapid growth of dense forests on some young soils in wet areas; fungus-poor soils; and processes or agents impeding the drainage or evaporation of water from soils. Elements such as insects, pathogenic fungi, and climatic changes can act as precipitators or accelerators of decline. This theory is supported by the characteristics of decline; many features of the islands, including climate, geology, soil-vegetation relationships, and microbiology; and analyses of wild-land soil ecosystems on Hawaii."

Stoner's theory coincides closely with the general hypothesis proposed earlier by the writer (Mueller-Dombois 1974). However, Stoner's theory is so general that the trigger for the dieback is not any more an issue. He merely proposes that there is fragility in the rhizosphere, which predisposes the forest ecosystem to decline. This decline according to Stoner, can be precipitated by one or more agents. It is not clear, however, how the rhizosphere can become fragile. Stoner proposes that the soil may become adverse to root growth, but he doesn't say in what way.

Both Lyon and Fosberg give an explanation for soil deterioration, i.e. toxicity (Lyon), hardpan formation (Fosberg). If Stoner refers to these situations, then he does not really address the important forms of dieback, namely the Dryland and Wetland Diebacks. Stoner supports the idea, that the dieback is a natural phenomenon, but his explanation is so general and based on so little study that it can hardly be called a scientific theory.

(4) The new theory proposed in this report by the writer, which integrates the six important facts or findings mentioned before. This theory is related to the five forms of dieback and to the dynamic phases, which are recognized as a forest life cycle for ohia stands on relatively recent volcanic substrates. As proposed in this theory, the dynamic phases become reduced in size-scale on geologically older substrates, which are represented on the older Hawaiian islands. The triggers for the dieback are important concerns in this theory, which are formulated into new working hypotheses. Intra- and interspecific competition are proposed as factors in the Dryland Dieback. Soil-drought is suggested as the trigger. Temporary flooding or inundation and drowning out of the root system of the canopy trees is suggested as the trigger in the Wetland Dieback. The Bog-formation Dieback may be related to hardpan formation as proposed by Fosberg or to soil toxicity as suggested by Lyon or to a combination of both factors.

Related to this theory of the dieback is a still unexplored general hypothesis of the writer, which would explain the maintenance of ohia as a dominant woody plant in the rain forests for millions of years as is demonstrated by the presence of ohia rain forests on all high Hawaiian islands. This is the idea of the existence of successional races or ecotypes in the ohia species.

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IX APPENDICES

APPENDIX I. Provisional Checklist of Plants, Ohia Rain Forest Study.

Names of the flowering plants are based on the checklist of St. John (1973). Ferns and fern allies are named in accordance with a checklist of Lane (undated). Mosses were named by W. H. Hoe and checked against his list (Hoe 1974). Liverworts and lichens were identified by C. W. Smith and algae by Isabella Abbott.

On the list, in front of a name E stands for endemic species, I for indigenous species, and X for exotic or introduced plants.

Note: See end of the checklist for further explanation of the names of ferns.

	Family and Scientific Name	Common Name	Voucher Number
	Flowering Plants		
	APOCYNACEAE		
E	*Alyxia olivaeformis* Gaud.	Maile, maile kuahiwi	
	AQUIFOLIACEAE		
E	*Ilex anomala* H. & A.	Kāwa'u, ka'awa'u	
	ARALIACEAE		
E	*Cheirodendron trigynum* (Gaud.) Heller	'Ōlapalapa, māhu	
E	*Tetraplasandra meiandra* (Hbd.) Harms	'Ohe, 'ohe mauka	
	BIGNONIACEAE		
X	*Spathodea campanulata* Beauv.	African tulip tree, fire bell	895
	CARYOPHYLLACEAE		
X	*Cerastium vulgatum* L.	Larger mouseear chickweed, nehine-hāuli	
X	*Drymaria cordata* (L.) Willd. ex R. & S.	Pipili	
	CELASTRACEAE		
E	*Perrottetia sandwicensis* Gray	Pua'a olomea	2030
	COMMELINACEAE		
X	*Commelina diffusa* Burm. f.	Honohono, honohonowai	

APPENDIX I (Continued).

	Family and Scientific Name	Common Name	Voucher Number
	COMPOSITAE		
X	*Ageratum conyzoides* L.	Maile-honohono	
E	*Dubautia scabra* (DC.) Keck	Kūpaoa	913
X	*Erechtites valerianaefolia* (Wolf) DC.		
X	*Eupatorium riparium* Regel	Spreading mist flower	
E	*Gnaphalium sandwicensium* Gaud.	'Ena'ena, Hawaiian cudweed	
X	*Hypochoeris radicata* L.	Gosmore, hairy cats-ear	
X	*Youngia japonica* (L). DC.	Oriental hawksbeard	
	CYPERACEAE		
E	*Carex alligata* F. Boott		
X	*Cyperus brevifolius* (Rottb.) Hassk.	Kili'o'opu, manu'nēnē	884
X	*Cyperus haspan* L.		750
X	*Cyperus polystachyus* Rottb.		751,916
E	*Cyperus* sp.		752
I?	*Eleocharis obtusa* (Willd.) Schult.	Pīpī wai, kohekohe	115,745,885
E	*Machaerina angustifolia* (Gaud.) Koyama	'Uki	
I	*Machaerina mariscoides* (Gaud.)	'Uki, 'aha'niu	753
E	*Oreobolus furcatus* Mann		875
E	*Rhynchospora lavarum* Gaud.	Kuolohia, pu'uko'a	113,906
I	*Uncinia uncinata* (L.f.) Kuek.		2014
	EPACRIDACEAE		
E	*Styphelia tameiameiae* (Cham.)	Pūkiawe, maiele, kāwa'u	
	ERICACEAE		
E	*Vaccinium berberifolium* (Gray) Skottsb.	'Ōhelo, barberry-leaved 'ōhelo	
E	*Vaccinium calycinum* Sm.	'Ōhelo-kau-lā'au	106
E?	*Vaccinium* sp.	'Ōhelo-'ai	755
	EUPHORBIACEAE		
E	*Antidesma platyphyllum* Mann	Mehame, ha'ā	893
	FLACOURTIACEAE		
E	*Xylosma hawaiiense* Seem. var. *hillebrandii* (Wawra) Sleumer	Maua	756

APPENDIX I (Continued).

Family and Scientific Name	Common Name	Voucher Number
GESNERIACEAE		
E *Cyrtandra lysiosepala* (Gray) C. B. Clarke		933,757
E *Cyrtandra paludosa* Gaud.		2047
E *Cyrtandra platyphylla* Gray		2042
E *Cyrtandra* spp.	Ha'i wale, ulunahele	835,933
GRAMINEAE		
X *Aira caryophyllea* L.		
X *Agrostis avenacea* Gmel.	He'u-pueo	819,914
X *Andropogon virginicus* L.	Broomsedge, yellow bluestem	
X *Axonopus affinis* Chase	Narrow-leaved carpet grass	761,909
E *Deschampsia australis* Nees ex Steud.		
X *Digitaria* spp.		
X *Holcus lanatus* L.	Velvet grass, Yorkshire fog	
E *Isachne distichophylla* Munro ex HBD.		
X *Microlaena stipoides* (Labill.) R. Br.	Pu'u-lehua, meadow rice grass	760
X *Paspalum conjugatum* Berg.	Hilo grass, manu'u-malihini	
X *Paspalum orbiculare* Forst. f.	Rice grass, mau'u-laiki	
X *Paspalum urvillei* Steud.	Vaseygrass	889
X *Sacciolepis indica* (L.) Chase	Glenwood grass	759
X *Setaria geniculata* (Poir.) Beauv.	Perennial foxtail	
X *Setaria palmaefolia* (Koen.) Stapf		
GUTTIFERAE		
X *Hypericum degeneri* Fosb.		
X *Hypericum mutilum* L.	St. Johnwort	764,865
JUNCACEAE		
X *Juncus bufonius* L.	Common toad rush	765
X *Juncus effusus* L.	Bog rush, Japanese mat rush	905
X *Juncus planifolius* R. Br.		109,864
X *Juncus tenuis* Willd.		771
E *Luzula hawaiiensis* Buch.		108

APPENDIX I (Continued).

	Family and Scientific Name	Common Name	Voucher Number
	LABIATAE		
E	*Phyllostegia floribunda* Benth.	Kāpana	
E	*Phyllostegia vestita* Benth.	Kāpana	774
E	*Stenogyne calaminthoides* Gray		1010,2039
E	*Stenogyne rugosa* Benth. f. *rugosa*		118
E	*Stenogyne* spp.	Mā'ohi'ohi, māhihi	843,931
	LEGUMINOSAE		
E	*Acacia koa* Gray	Koa, koaka	
	LILIACEAE		
E	*Astelia menziesiana* Sm.		846,2028
E	*Smilax sandwicensis* Kunth	Hoi-kuahiwi, aka'awa	
	LOBELIACEAE		
E	*Clermontia montis-loa* Rock		
E	*Clermontia parviflora* Gaud. ex Gray		891,2025
E	*Clermontia* spp.		976
E	*Cyanea longipedunculata* Rock		838
E	*Cyanea pilosa* Gray		2045
E	*Cyanea tritomantha* Gray		1015
E	*Trematolobelia grandifolia* (Rock?) Deg.		
	LOGANIACEAE		
X	*Buddleja asiatica* Lour.	Dogtail, huelo-'īlio	
E	*Labordia hedyosmifolia* Baill.		
E	*Labordia* sp.	Kāmakahala	847
	LORANTHACEAE		
E	*Korthalsella complanata* (v. Tiegh) Engler	Hulumoa	777
	LYTHRACEAE		
X	*Cuphea carthagenensis* (Jacq.) Macbride	Tarweed, puakamoli	778,780

APPENDIX I (Continued).

Family and Scientific Name	Common Name	Voucher Number
MELASTOMATACEAE		
X Heterocentron subtriplinervium (Link & Otto) A. Br. & Bouché	Pearl flower	780
X Melastoma malabathricum L.	Malabar melastome, Indian rhododendron	
MYOPORACEAE		
E Myoporum sandwicense Gray	Naio, bastard sandalwood	
MYRSINACEAE		
E Myrsine lessertiana A. DC.	Kōlea-lau-nui	
E Myrsine sandwicensis A. DC.	Kōlea-lau-li'i	
MYRTACEAE		
E Metrosideros collina subspp. polymorpha (Gaud.) Rock	'Ōhi'a-lehua, lehua	806,808
X Psidium cattleianum Sabine	Strawberry guava, waiawī-'ulu'ula	
ONAGRACEAE		
X Epilobium cinereum A. Rich.	Pūkāmole, willow herb	
X Ludwigia octivalvis (Jacq.) Raven	Primrose willow	
ORCHIDACEAE		
X Arundina bambusaefolia (Roxb.) Lindl.		
X Phaius tankervilliae (Banks ex L'Hér.) Bl.		
PALMAE		
E Pritchardia? beccariana Rock		
PANDANACEAE		
E Freycinetia arborea Gaud.		
PASSIFLORACEAE		
X Passiflora edulis Sims	Purple water lemon	
X Passiflora ligularis Juss.	Sweet granadilla, lili-wai	
X Passiflora mixta L.	Banana poka	

APPENDIX I (Continued).

Family and Scientific Name		Common Name	Voucher Number
PHYTOLACCACEAE			
E	Phytolacca sandwicensis Endl.	Pōpolo-ku-mai	
PIPERACEAE			
E	Peperomia hypoleuca Miq.	'Ala'ala-wai-nui	941,2052
E	Peperomia leptostachya H. & A.		922,2009
E	Peperomia sp.	'Ala'ala-wai-nui kāne	787,896
PITTOSPORACEAE			
X	Pittosporum undulatum Vent.	Orange Pittosporum	892
PLANTAGINACEAE			
E	Plantago muscicola (Rock) Pilger	Lau-kāhi kuahiwi	878
POLYGONACEAE			
X	Muehlenbeckia axillaris (Hook. f.) Walp	Wire plant	790
X	Polygonum glabrum Willd.	Kāmole, knotweed	107,119
E	Rumex giganteus Ait.	Pāwale, uhauha-kō	
PRIMULACEAE			
X	Anagallis arvensis L.	Scarlet pimpernel	
RANUNCULACEAE			
X	Anemone hupehensis (Lem. & Lem. f.) Lem. & Lem. f.	Hupeh anemone	
ROSACEAE			
X	Fragaria vesca f. alba (Ehrh.) Rydb.	'Ōhelo-papa	910
E	Rubus hawaiiensis Gray	'Ākala, 'ākalakala	
X	Rubus penetrans Bailey	Prickly Florida blackberry, 'ōhelo 'ele'ele	
X	Rubus rosaefolius	Roseleaf raspberry, 'ōla'a	
RUBIACEAE			
E	Bobea timonioides (Hook. f.) HBD.	'Ahakea, 'akupa	
E	Coprosma ernodeoides Gray	Leponēnē, 'ai-a-ka-nēnē	
E	Coprosma ochracea Oliver	Pilo, kopa	1027,2049
E	Coprosma rhynchocarpa	Pilo	911,912

APPENDIX I (Continued).

	Family and Scientific Name	Common Name	Voucher Number
	RUBIACEAE (continued)		
E	Coprosma sp.?	Pilo	791,871
E	Gouldia hillebrandii Fosb.		793
E	Gouldia terminalis (H. & A.) Hbd.	Manono	841,1016
	Gouldia sp.	Manono	894
E	Hedyotis centranthoides (H. & A.) Steud.	Kīlauea hedytis	
E	Nertera granadensis (L. f.) Druce		
E	Psychotria hawaiiensis (Gray) Fosb.	Kōpiko-'ula	792
E	Psychotria sp.	Kōpiko, 'ōpiko	842,940
	RUTACEAE		
E	Pelea clusiaefolia Gray	Alani, Clusia-leaved pelea	103,863
E	Pelea sp.	'Alani	795,2041
E	Platydesma spathulata (Gray) Stone	Pilo-kea	
	SAPINDACEAE		
E	Dodonaea sandwicensis Sherff	Hawaiian hopseed bush	
	SAXIFRAGACEAE		
E	Broussaisia arguta Gaud.	Kanawao, pū'aha-nui	
	SCROPHULARIACEAE		
X	Veronica plebeia R. Br.	Common speedwell	
X	Veronica serpyllifolia L.	Thyme-leaved speedwell	796
	SOLANACEAE		
E	Nothocestrum longifolium Gray	'Aiea, hālena	
	THEACEAE		
E	Eurya sandwicensis Gray	Anini, wanini	
	THYMELIACEAE		
E	Wikstroemia phillyroefolia Gray	'Ākia, false 'ōhelo	
	Wikstroemia sp.	'Ākea	845

APPENDIX I (Continued).

	Family and Scientific Name	Common Name	Voucher Number
URTICACEAE			
E	*Pipturus albidus* (H. & A.) Gray		798
E	*Pipturus* sp.	Māmaki, māmake	2048
E	*Touchardia latifolia* Gaud.	Olonā	
E	*Urera sandvicensis* Wedd.	Ōpuhe, hona	749,2026
ZINGIBERACEAE			
X	*Hedychium coronarium* Koenig		
	Ferns and Fern Allies		
ADIANTACEAE			
E	*Coniogramme pilosa* (Brack.) Hieron	Lo'ulu	830,2035
I	*Pteris excelsa* Gaud.	Waimaka-nui	938,715
X	*Pteris irregularis* Kaulf.	Mānā, 'iwa-puakea	2038
ASPIDIACEAE			
X	*Athyrium japonicum* (Thunb.) Copel.	Hō'i'o	761,822
E	*Athyrium microphyllum* (Sw.)	'Akōlea	110,839
E	*Athyrium sandwichianum* Presl	Hō'i'o	924
	Ctenitis rubiginosa (Brack.) Copel.	Pauoa, paunoa	721,848
E	*Cyclosorus cyatheoides* (Kaulf.) Farewell [=*Christella cyatheoides* (Kaulf.) Holtt.]	Kikawaiō, pakikawaiō	923,2033
I	*Cyclosorus dentatus* (Forssk.) Ching [=*Christella dentata* (Forssk.) Brownsey & Jermy]		718,898
E	*Cyclosorus sandwicensis* (Brack.) Copel. [=*Pneumatopteris sandwicensis* (Brackenridge) Holtt.]	Hō'i'o-kula	844,899
I	*Dryopteris glabra* (Brack.) Kuntze	Kīlau	720,721
E	*Dryopteris*? *hawaiiensis* (Hlbd.) Robinson		710,711
E	*Dryopteris keraudreniana* (Gaud.) C. Chr. [=*Pseudophegopteris keraudreniana* (Gaud.) Holtt.]	Waimaka-nui, 'ala'alai	828,703
I	*Dryopteris paleacea* (Sw.) Robinson	Lau-kāhi	707
I?	*Dryopteris paleacea* var. *fusco-atra* (Hlbd.) C. Chr.		708
E	*Dryopteris sandwicensis* (Brack.) Copel.	Hō'i'o-Kula	722

APPENDIX I (Continued).

	Family and Scientific Name	Common Name	Voucher Number
	ASPIDIACEAE (continued)		
E	Dryopteris unidentata (Hook. & Arn.) C. Chr.	'Akole	939
	Dryopteris spp.	Olua, 'opeha	
E	Elaphoglossum alatum Gaud.		828,1005
E	Elaphoglossum crassifolium (Gaud.) Anderson & Crosby		740,829
E	Elaphoglossum hirtum var. micans (Mett.) C. Chr.		121,735
	Elaphoglossum pellucidum Gaud.		736,135
	Elaphoglossum wawre (Luerss.)		738,867
	Elaphoglossum sp.	'Ēkaha	827
E	Tectaria gaudichaudii (Mett.) Maxon	'Iwa'iwa-lau-nui	701
E	Thelypteris globulifera Brack. [=Amauropelta globulifera (Brackenridge) Holtt.]	Palapalai-a-kama-pua'a	2051
	ASPLENIACEAE		
E	Asplenium contiguum Klf.		125,729
I	Asplenium lobulatum Mett.	'Anali'i, pi'ipi'i-lau	927,730
E	Asplenium macraei Hk. & Grev.		766
I	Asplenium normale Don		727
	Asplenium schizophyllum C. Chr.		134
E	Asplenium? sphenotomum Hlbd.		134A,728
I	Asplenium trichomanes L.	Spleenwart, 'owāli'i	724
I	Asplenium unilaterale Lam.	Pāmoho	2019
	Asplenium sp.	'Iwa-lau-li'i	818
	BLECHNACEAE		
E	Sadleria cyatheoides Klf.	'Ama'u, 'ama'uma'u	
E	Sadleria pallida Hk. & Arn.	'Ama'u, ama'u-'i'i	717
E	Sadleria souleyetiana (Gaud.) Moore	'Ama'uma'u	
	DAVALLIACEAE		
I	Nephrolepis cordifolia (L.) Presl		712,883
I	Nephrolepis exaltata (L.) Schott	Pāmoho, sword fern	713,900

APPENDIX I (Continued).

	Family and Scientific Name	Common Name	Voucher Number
	DENNSTAEDTIACEAE		
I	*Microlepia strigosa* (Thbg.) Presl	Palai, palai-'ula	731,938
E	*Pteridium aquilinum* var. *decompositum* (Gaud.) Tryon	Kīlau, bracken	732
	DICKSONIACEAE		
E	*Cibotium chamissoi* Klf.	Hāpu'u 'i'i, 'i'i	
E	*Cibotium glaucum* (Sm.) Hk. & Arn.	Hāpu'u	
E	*Cibotium hawaiense* Nakai & Ogura	meu	
	GLEICHENIACEAE		
E	*Dicranopteris emarginata* (Brack.) Robinson	Uluhe, unuhe	860,809
I	*Dicranopteris linearis* (Burm.) Und.	Uluhe, unuhi	112,861
E	*Hicriopteris pinnata* (Ktze.) St. John	Uluhe-lau-nui	
	Sticheris owhyhensis (Hook.) St. John		111,862
	GRAMMITIDACEAE		
E	*Adenophorus hymenophylloides* (Klf.) Hk. & Grev.	Pai, palai-lā'au	757,821
E	*Adenophorus sarmentosus* (Brack.) K. A. Wilson		755,756
E	*Adenophorus tamariscinus* (Klf.) Hk. & Grev.	Wahine-noho-mauna	758,820
E	*Grammitis hookeri* (Brack.)Copel.	Māku'e-lau-li'i	745,869
E	*Grammitis tenella* Klf.	Kolokolo, mahina-lua	741,1009
E	*Xiphopteris saffordii* (Maxon) Copel.	Kihi, kihe	
	HYMENOPHYLLACEAE		
E	*Callistopteris baldwinii* (Eaton) Copel.		831,2013
I	*Gonocormus minutus* (Bl.) V. D. Bosh		765
E	*Mecodium recurvum* (Gaud.) Copel.	'Ōhi'a ku	752,764

APPENDIX I (Continued).

	Family and Scientific Name	Common Name	Voucher Number
	HYMENOPHYLLACEAE (continued)		
E	Sphaerocionium lanceolatum (Hk. & Arn.) Copel.	Palai-lau-li'i	748,751
E	Sphaerocionium obtusum (Hk. & Arn.) Copel.	Palai hinahina	753
E	Vandenboschia davallioides (Gaud.) Copel.	Kīlau, palai-hihi	132,2015
	LINDSAEACEAE		
I	Sphenomeris chinensis (L.) Maxon	Pala'ā, palapala'ā	
	LYCOPODIACEAE		
I	Lycopodium cernum L.	Wawae-iole, club moss	746
I	Lycopodium phyllanthum Hk. & Arn. Lycopodium serratum Thunb.	Wawae-iole, club moss	901
	MARATTIACEAE		
E	Marattia douglasii (Presl) Bak.	Pala, kapua'i lio	
	OPHIOGLOSSACEAE		
I	Ophioglossum pendulum L.	Lau-kāhi, puapua-moa	906A
	POLYPODIACEAE		
I	Pleopeltis thunbergiana Klf.	Laua'e, auwa'e	734
E	Polypodium pellucidum Klf.	'Ae, 'ae-lau-nui	2027
	PSILOTACEAE		
I	Psilotum complanatum Sw.	Moa, pipi	747
	SELAGINELLACEAE		
E	Selaginella arbuscula (Klf.)	Lepelepe-a-moa	2042A

APPENDIX I (Continued).

Family and Scientific Name	Common Name	Voucher Number
	Mosses (Bryophytes)	
AMBLYSTEGIACEAE		
Platyhypnidium muelleri (Jaeg.) Fleisch.		950,958
BARTRAMIACEAE		
E Philonotis hawaica (C. Müll.) Broth.		955A
BRACHYTHECIACEAE		
Brachythecium sp.		203
Eurhynchium vagans (Jaeg.) Bartr.		956
CALYMPERACEAE		
E Syrrhopodon hawaiicus C. Müll.		853
DICRANACEAE		
E Campylopus densifolius var. purpureo-flavescens (Hampe ex C. Müll.) Mill		212
Campylopus spp.		210,2022
E Dicranum speirophyllum var. breviflagellare (C. Müll.) Bartr.		907
E Dicranum speirophyllum Mont.		871,874
Dicranella sp.		201
E Holomitrium seticalycinum C. Müll.		880B,2006
FUNARIACEAE		
E Funaria subintegra Broth.		202
GRIMMIACEAE		
E Grimmia haleakalae Reichardt.		977
HOOKERIACEAE		
E Distichophyllum freycinetii (Schwaegr.) Mitt. var. freycinetii		812,921
E Distichophyllum paradoxum (Mont.) Mitt.		206,920
Hookeria acutifolia Hook. & Grev.		955

APPENDIX I (Continued).

Family and Scientific Name	Common Name	Voucher Number
SEMATOPHYLLACEAE		
E *Acroporium fusco-flavum* (Par.) Broth. var. *fusco-flavum*		804,873B
Trichosteleum hamatum (Dozy & Molk.) Jaeg.		961,2001
SPHAGNACEAE		
Sphagnum vitianum Schimp. ex Warnst.		209
THUIDIACEAE		
E *Thuidium hawaiense* Reichardt.		205
E *Thuidium plicatum* Mitt var. *plicatum*		213,2016
Liverworts (Bryophytes)		
ANEURACEAE		
Riccardia attenuata (Steph.) Miller		932
Riccardia sp.		891
CEPHALOZIACEAE		
Cephalozia sp.		1040
Odontoschisma sandvicense (Angtr.) Evans		858
DILAENACEAE		
Pallavicinia laceratus		1046
Pallavicinia sp.		1037,1042
Symphyogyna sp.		810
FRULLANIACEAE		
Frullania sp.		1031A
HERBERTACEAE		
Herberta helleri (Steph.) Nicholas		1034
Herberta sp.		873,852

APPENDIX I (Continued).

Family and Scientific Name	Common Name	Voucher Number
JUNGERMANNIACEAE		
Jamesoniella robusta (Aust.) Steph.		1036
Plectocolea sp.		1038
LEPIDOZIACEAE		
Bazzania cordistipula (Mont.) Trev.		803
Bazzania spp.		856,1045
Lepidozia sp.		873,1044
MARCHANTIACEAE		
Dumortiera hirsuta (Sw.) Nees		204,918
PLAGIOCHILACEAE		
Plagiochila sp.		1039,1041
Plagiochilion sp.		1035,2052A
RADULACEAE		
Radula sp.		815,1043
Hornworts (Bryophytes)		
ANTHOCEROTACEAE		
Dendroceros crispus (Sw.) Nees		917
Algae (Thallophytes)		
ZYGNEMACEAE		
Zygnema sp.		150
Fungi (Thallophytes)		
Agaricales		231

APPENDIX I (Continued).

Family and Scientific Name	Common Name	Voucher Number
Lichens (Lichenes)		
CLADONIACEAE		
Cladonia farinacea (Vain.) Evans		
Cladonia scabriuscula (Del. ex Duby) Nyl.		854
Cladonia skottsbergii Magn.		802,879
PANNARIACEAE		
Pannaria mariana (Fr.) Muell. Arg.		1032
PELTIGERACEAE		
Peltigera sp.		
Sticta plumbicolor Zahlbr.		1033
PHYSCIACEAE		
Anaptychia leucomeleana (L.) Mass.		1031
Anaptychia sp.		603
LICHENES IMPERFECTI		
Lepraria sp.		817,877

Revisions of the fern genus *Elaphoglossum* by Anderson and Crosby (1966) and of the fern genus *Adenophorus* by Bishop (1974) have been incorporated in our list. These revisions supercede Lane's list. Fern names recently revised by Holttum (1977) are given in brackets where applicable, since Holttum's publication was obtained only after preparation of this manuscript. Porter's (1972) list has been followed for the common names of ferns.

APPENDIX II.

OHIA DECLINE SEMINAR

Room 322-A
Kalanimoku Building
1151 Punchbowl Street
Honolulu, Hawaii

October 25, 1977

0930 Opening Remarks, Introduction of Participants
C. S. Hodges, U. S. Forest Service

0945 Ohia Dieback: Is it a Creeping Epidemic or a Natural Phenomenon?
Dieter Mueller-Dombois, University of Hawaii

1040 Quantification of the Dieback
Jim Jacobi, University of Hawaii

1105 Ohia Population Structures in Dieback and Non-Dieback Areas
R. G. Cooray, University of Hawaii

1130 An Ohia Climax Forest on Oahu
Grant Gerrish, University of Hawaii

1200 Lunch

1330 Ohia Decline: A Working Hypothesis
W. H. Ko, Beaumont Agricultural Experiment Station, Hilo, HI

1350 Post Decline Effects
Soils - H. B. Wood, U. S. Forest Service
Plants - B. R. McConnell, U. S. Forest Service

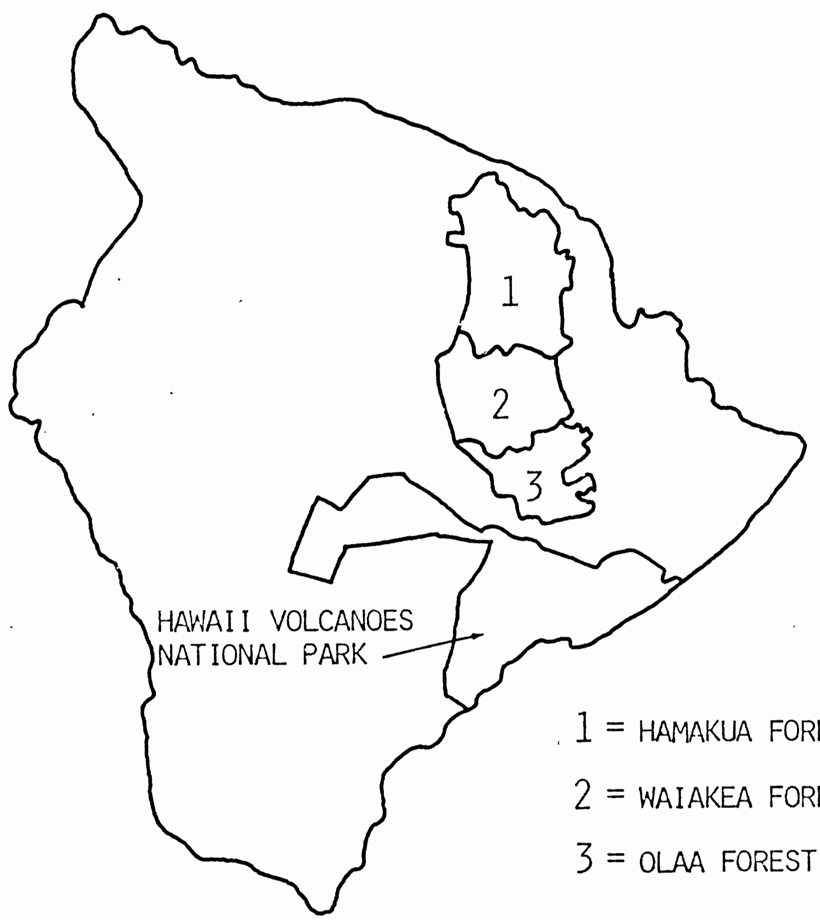
1420 Studies on the Role of _Plagithmysus bilineatus_ in the Epidemic Decline of Ohia Forests
R. P. Papp, Bishop Museum

1450 Studies on the Role of _Phytophthora cinnamomi_ in the Epidemic Decline of Ohia Forests
J. T. Kliejunas, Beaumont Agricultural Experiment Station, Hilo, HI

1520 Site and Other Factors Related to Ohia Decline
C. S. Hodges, U. S. Forest Service

1540 General Discussion

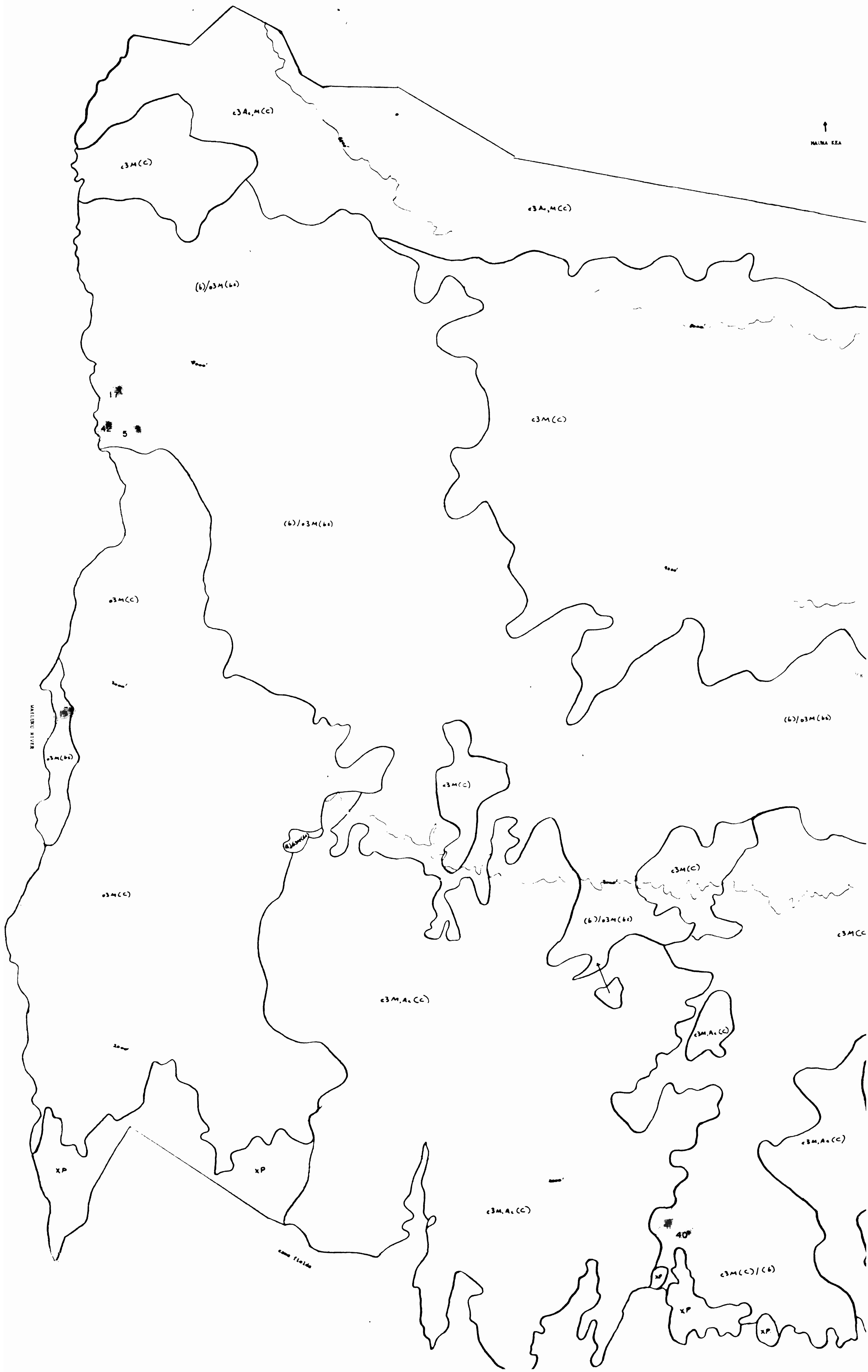
INDEX TO VEGETATION MAP SECTIONS



1 = HAMAKUA FOREST SECTION

2 = WAIAKEA FOREST SECTION

3 = OLAA FOREST SECTION



MAUNA KEA
c3A₀,M(C)
c3M(C)
c3A₀,M(C)
(6)/o3M(60)
c3M(C)
17
42
5
(6)/o3M(60)
o3M(C)
WAILUKU RIVER
o3M(60)
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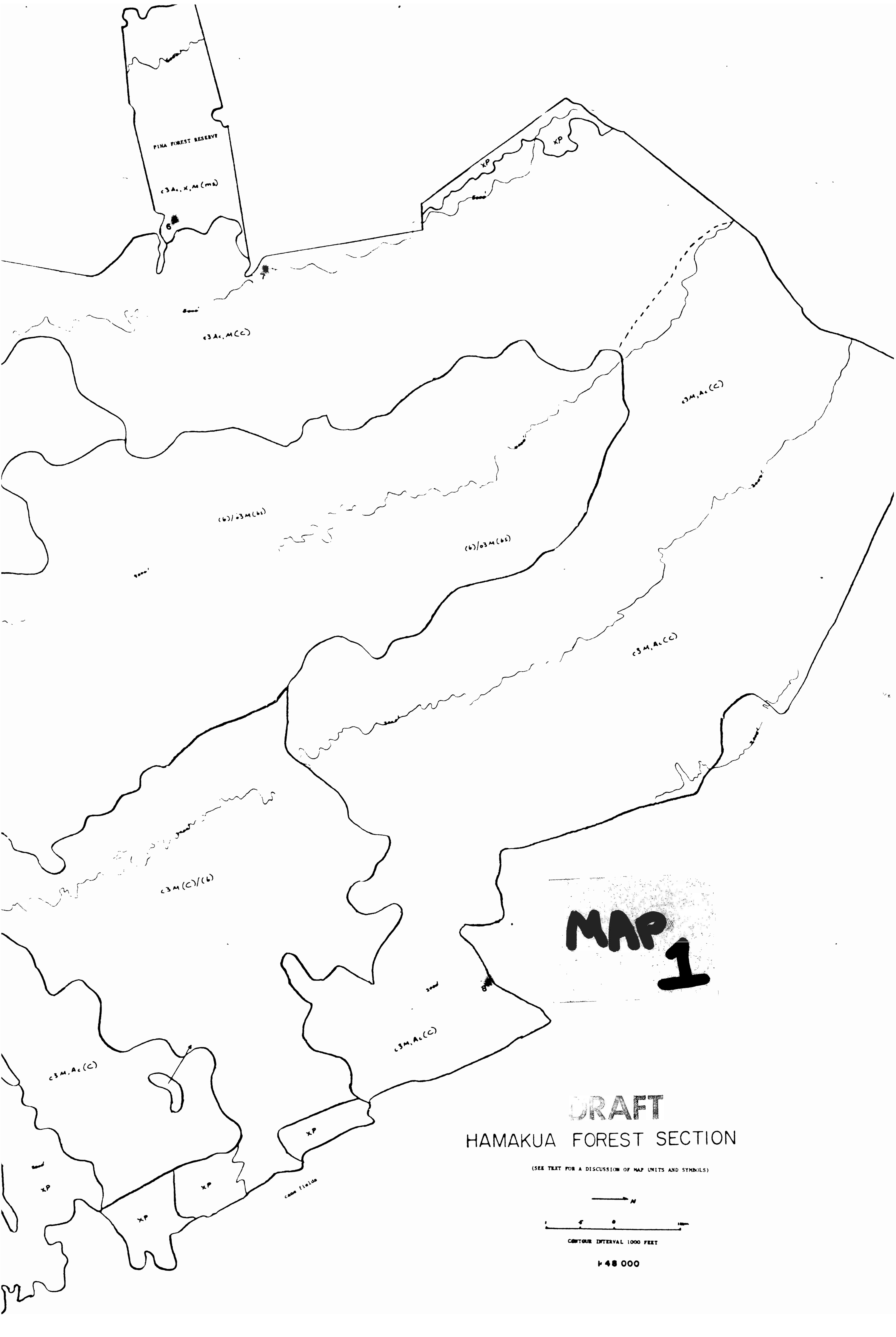

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HAMAKUA FOREST SECTION

(SEE TEXT FOR A DISCUSSION OF MAP UNITS AND SYMBOLS)

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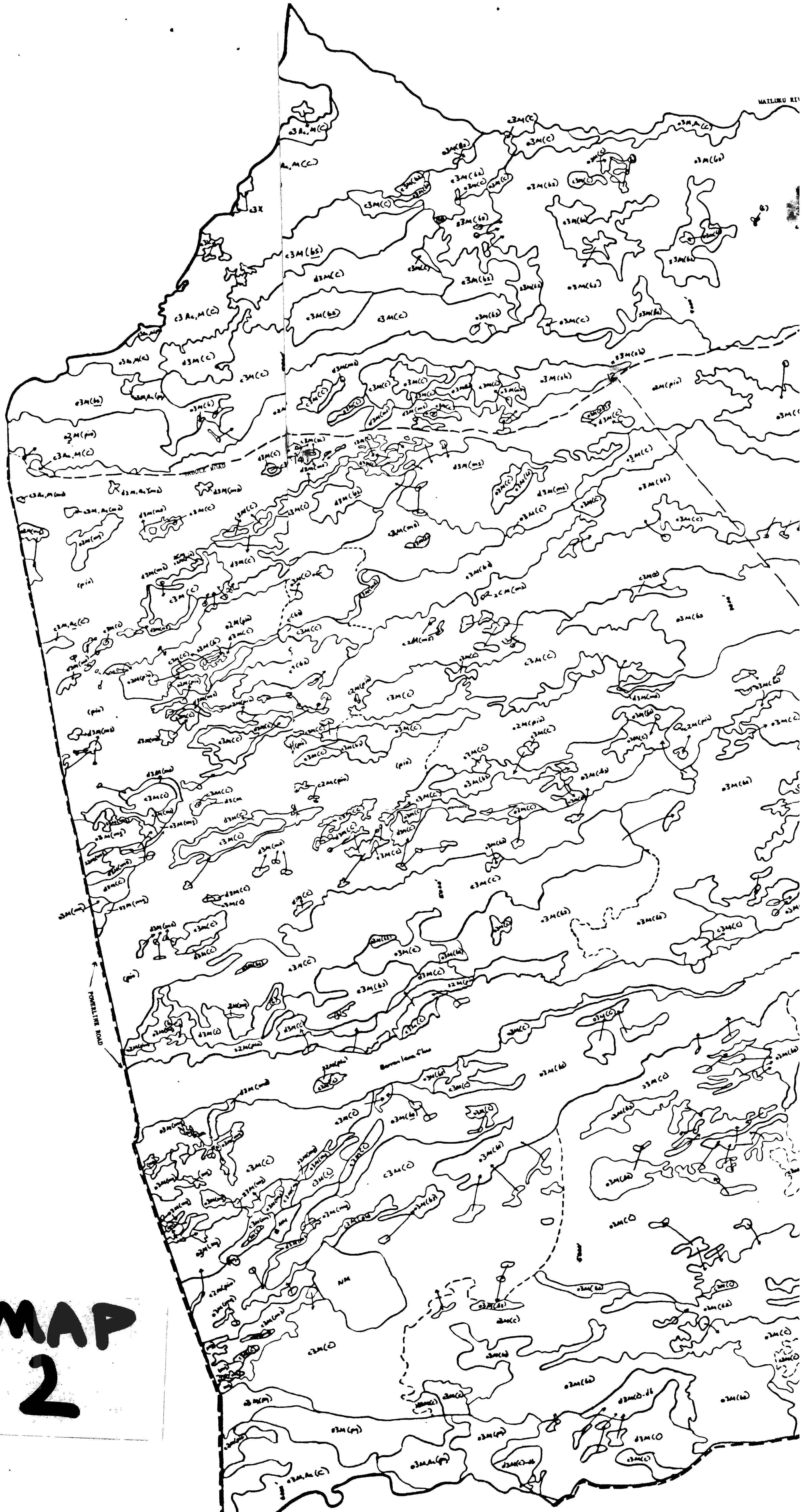
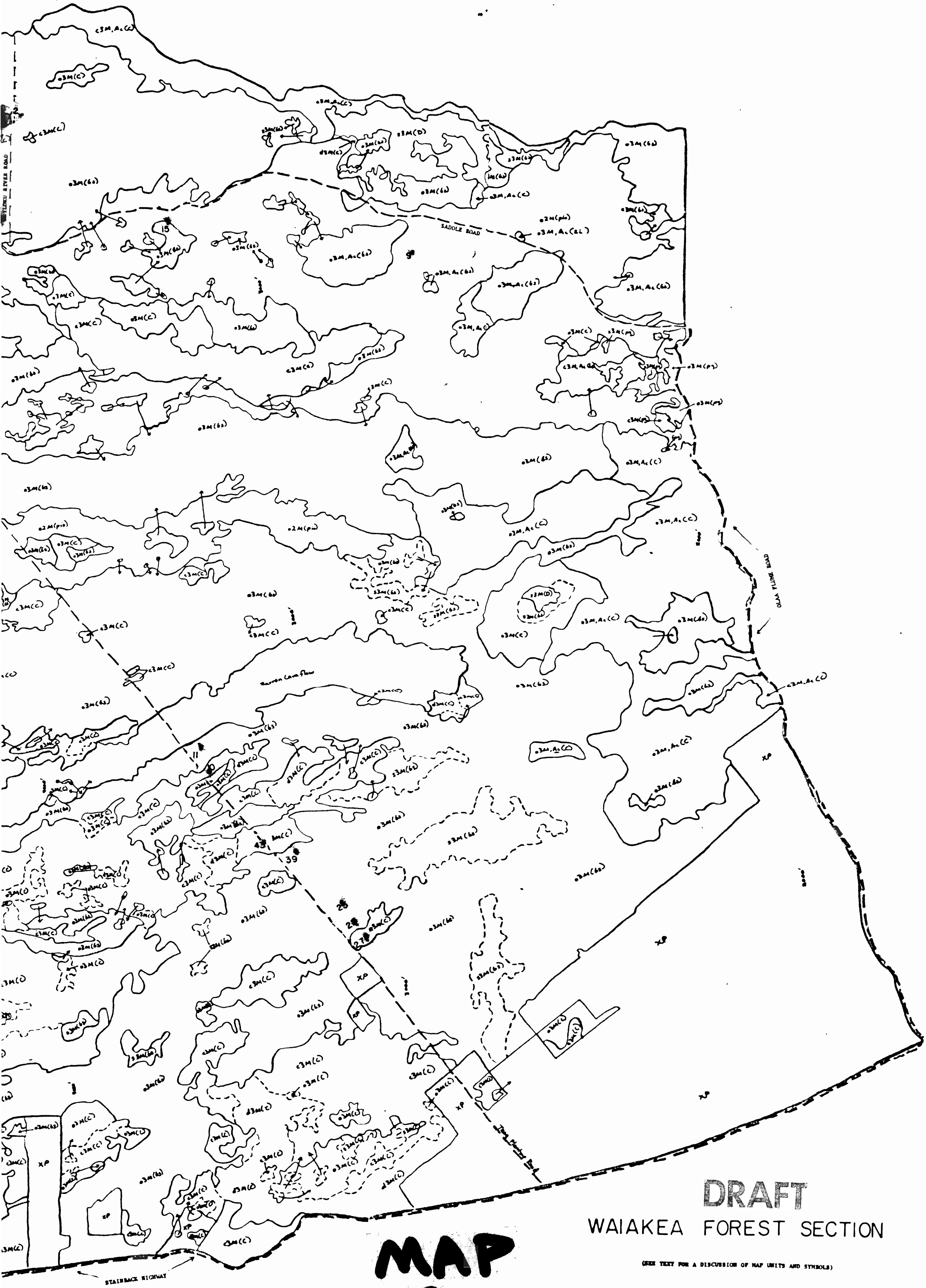
MAP 2





MAP 2

DRAFT

WAIAKEA FOREST SECTION

(SEE TEXT FOR A DISCUSSION OF MAP UNITS AND SYMBOLS)

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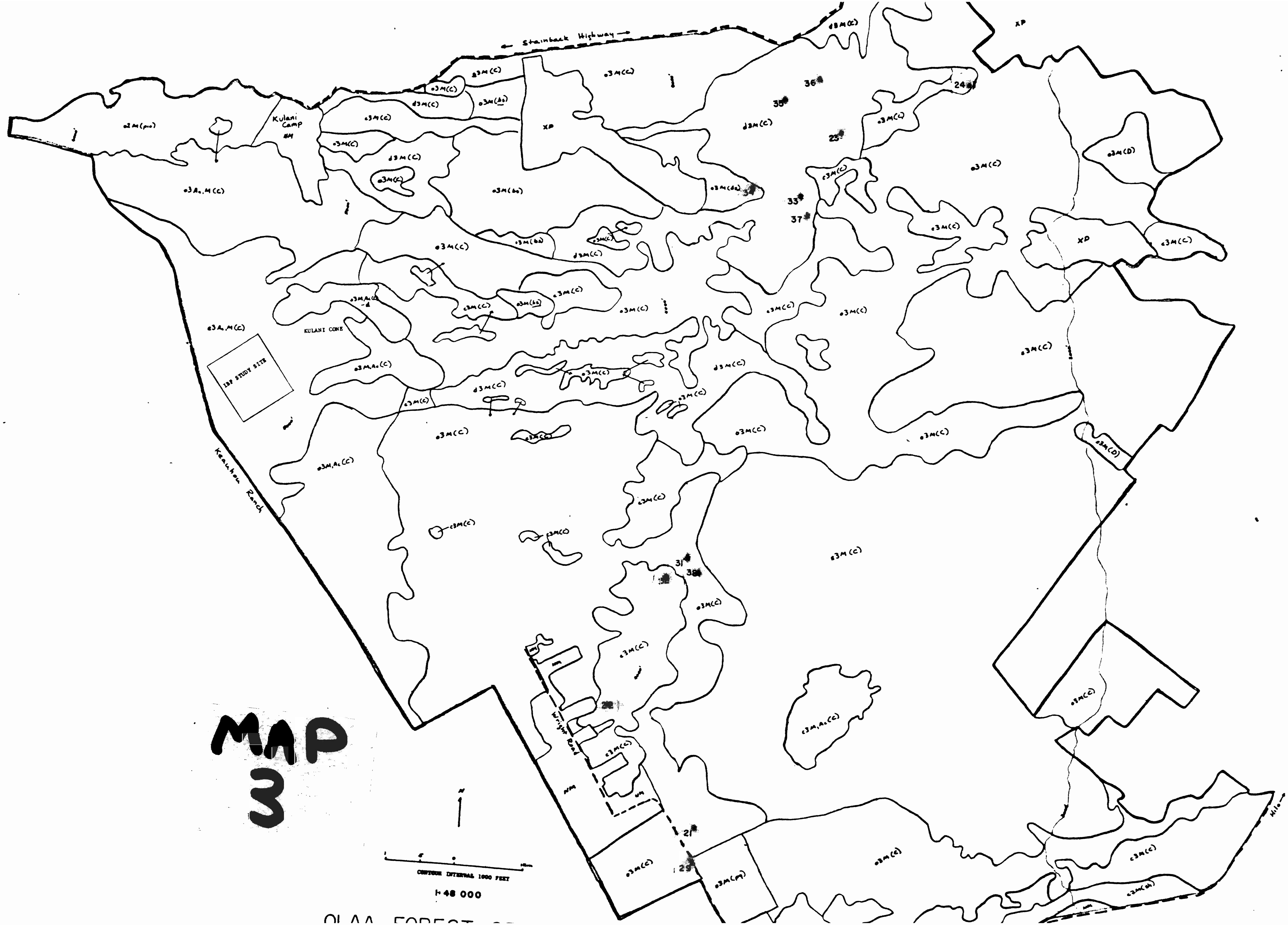

MAP 3

OLAA FOREST