METROSIDEROS DIEBACK IN HAWAI'I: A COMPARISON OF ADJACENT DIEBACK AND NON-DIEBACK RAIN FOREST STANDS

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SUMMARY: Approximately 50,000 ha of native wet *Metrosideros* forest on the island of Hawai'i experienced a drastic reduction (dieback) of the tree canopy between 1954 and 1977. Two general hypotheses have previously been suggested to explain this phenomenon: 1) *Metrosideros* dieback has resulted from recently introduced pathogens, and 2) the dieback has naturally occurred previously in Hawai'i, and is related to plant succession under periodic conditions of climatic instability which effect the soil moisture regime.

Plant species composition, vegetation structure, and general substrate characteristics (lava flow type and soil drainage) were sampled on adjacent dieback and non-dieback rain forest stands. Although the only primary difference identified between these two forest stands was lava flow structure, both the soil drainage conditions and the plant communities which had developed on the two sites were found to be considerably different.

The results of this study lend support to the successional hypothesis of *Metrosideros* dieback.

KEYWORDS: plant ecology; forest ecology; plant succession; rain forest; forest soils; soil drainage; forest composition; dieback; Metrosideros polymorpha; Myrtaceae; Hawai'i.

INTRODUCTION

Between the years 1954 and 1977, large areas of the native montane rain forest on the windward side of the island of Hawai'i experienced death or large-scale defoliation of the tall, canopy-forming individuals belonging to the dominant tree species *Metrosideros polymorpha* Gaud. (Myrtaceae), commonly called 'õhi'a or 'õhi'a-lehua (Mueller-Dombois and Krajina, 1968; Burgan and Nelson, 1972; Mueller-Dombois, 1980). Although standing dead trees are a natural part of any unman aged forest, the appearance of large numbers of dead or dying trees over a relatively short period of time led to the Hawai'ian situation being referred to as a forest decline or dieback (Pettys, Burgan and Nelson, 1975). Initial speculation was that the forests were dying due to introduced diseases, and considerable concern was expressed for the future quality of the forest watershed and the stability of this native ecosystem with its endemic species (Anon., 1974; Clark, 1974; Alton, 1975).

A similar forest dieback occurred on the island of Maui in the early 1900's (Lewton-Brain, 1909; Lyon, 1909). Although fungal pathogens were first suspectted as the cause of the Maui dieback, no conclusive evidence was found to support this hypothesis. Lyon (1918, 1919) surmised that the death of the trees was caused by the inability of the native species of plants to adapt to conditions brought about by weathering of the soil.

Unfortunately, many of the easily accessible areas on Maui which experienced dieback in early 1900 were subsequently replanted with introduced species of trees, and the apparent problem with the native ‘õhi’a forest was generally forgotten. The recent episode of dieback on the island of Hawai'i has fostered a resumption of research on the causes and effects of this phenomenon.

The disease hypothesis

Initial research on what has become known as ‘õhi’a dieback or ‘õhi’a decline on the island of Hawai'i was focused on describing the spread and intensity of the problem (Petteys, Burgan and Nelson, 1975), and searching for fungal pathogens which were believed responsible for the apparent epidemic (Laemmlen and Bega, 1972; Kliejunas and Ko, 1973; Bega, 1974). This disease hypothesis was founded largely on apparent similarities seen between the situation in Hawai'i and the jarrah *(Eucalyptus marginata* Sm.) dieback in Australia. The latter dieback has been reported to be caused by the root-rot fungus *Phytophthora cinnamomi* Rands (Weste and Taylor,

FIGURE 1. *Map of the eastern half of the island of Hawai'i showing the three sections of the windward forest and the Saddle Road study area.*

1971; Podger, 1972). It was also believed that the Hawaiian dieback was aggravated by abnormally high population levels of a native cerambycid beetle *(Plagithmysus bilineatus* Sharp), which has larvae that burrow in the cambium just below the bark of mature 'õhi'a trees. Further studies have shown that although both *Phytophthora cinnamomi* and *Plagithmysus bilineatus* can hasten the death of previously weakened 'õhi'a trees, neither species could be consistently correlated with areas of dieback (Hwang, 1977; Papp *et al.*, 1979).

The successional hypothesis

The lack of supportive evidence for the disease hypothesis of 'õhi'a dieback has lead to a concentration of research on a second hypothesis proposed by Mueller-Dombois (1974), which elaborated on Lyon's (1918, 1919) suggestion that the Hawaiian dieback was a natural process (i.e. not resulting from the recent introduction of a non-native pathogen). Mueller-Dombois' successional hypothesis stated that "the 'õhi'a dieback is a normal developmental stage in primary successon of an isolated island forest ecosystem". He further speculated that "dieback is initiated by a climatic instability which becomes effective through the soil moisture regime under certain conditions of stand maturity" (Mueller-Dombois, 1980). The implications of this hypothesis are that 'õhia' forest dieback has occurred previously in Hawai'i, and under normal circumstances, will recur in the future.

In 1973 a research programme was initiated to test this second general hypothesis. Projects completed under this programme have included work on describing and mapping the distribution of vegetation types, the degree of tree canopy loss, the soil moisture regime across a 100,000 ha study area, and detailed studies of the population structure of 'õhi'a in dieback and non-dieback stands on the island of Hawai'i (Mueller-Dombois *et al.,* 1980). Additionally, a project was conducted to determine the sunlight regime under the forest canopy and the response of 'õhi'a seedlings to experimental canopy opening and different levels of light (Burton, 1980).

The present paper reports the results of an investigation of adjacent dieback and non-dieback forest stands in an area of 'typical' 'õhi'a dieback. The focus of this study was on describing the vegetation and dieback structure, the associated floristic composition, and the comparison of vegetation parameters with differences in gross substrate characteristics between the two sites.

DESCRIPTION OF THE STUDY AREA

'Õhi'a die back has been reported from many areas in Hawai'i, including the islands of Kauai, Oahu, Moloka'i, Maui, and Hawai'i. The largest area recently affected has been the rain forest on the northeastern side of the island of Hawai'i. Current research has been focused on this windward forest, specifically in a 100,000 ha area extending from above Laupahoehoe Point, and south to the Volcano Highway, between the elevations of 600 and 1800 m (Fig. 1).

Climate

The climate of the northeastern side of the island of Hawai'i is principally controlled by the northeast trade winds which persist approximately 75% of the year, and the elevational gradient which extends from sea level to over 4000 m at the summits of Mauna Kea and Mauna Loa volcanoes (Blumenstock and Price, 1967). Rainfall is primarily the result of orographic lift of moist trade wind air up the slopes of the mountains. Mean annual rainfall for the study area ranges from greater than 7500 mm per year at 1000 m elevation to approximately 2500 mm at 1800 m (State of Hawai'i, 1970), (Fig. 2). In the forest areas above 1200 m elevation, the total precipitation may be substantially greater than the annual rainfall value due to the addition of fog interception by the vegetation (Juvik and Ekern, 1978).

FIGURE 2. *Distribution of mean annual rainfall (mm) on the island of Hawai'i. Rainfall contours are shown as solid lines; elevational contours are dashed lines. Adapted from State of Hawai'i (1970).*

At the latitude of the island of Hawai'i, mean annual temperature decreases up the elevational gradient from approximately 25°C at sea level to 4.5°C at 4000 m (Doty and Mueller-Dombois, 1966).

Geology

Three basic geological units can be distinguished underlying the vegetation on the windward side of the island of Hawai'i (Fig. I):

(i) The *Mauna Kea section,* which extends from above Laupãhoehoe Point and south to the Wailuku River, contains the oldest lava bedrock. The substrate in this unit is dominated by deep volcanic ash (> 50 cm deep) overlying weathered pãhoehoe or 'a'ã lava, most of which originated from Mauna Kea. The most recent eruption which occurred on the north-eastern slope of this volcano was approximately 3600 years ago. However, the majority of the lava and volcanic ash deposited in this area is believed to be over 10,000 years old (Macdonald and Abbott, 1979).

(ii) The *Waiãkea section,* located in the central part of the windward forest, extends from the Wailuku River to the Stainback Highway. The substrates in this area are for the most part young and unweathered lava flows ranging in age from 1942 for the youngest, to over 4000 years old for the oldest. All of the lava in this section originated from the northeast rift of Mauna Loa. Some of the older flows there are covered by a thin layer of volcanic ash, up to 10 cm thick.

(iii) The *'Õla' a section,* which encompasses the southern portion of the forest; contains a mixture of old and young substrates which were erupted from either Kilauea or Mauna Loa volcanoes. The south-eastern portion of this section has an accumulation of deep volcanic ash, up to 2 m deep. Recent carbon-14 dating of buried charcoal from this area indicates that the ash overburden was deposited in many layers, the most recent of which originated from a violent eruption of Kilauea volcano in 1790 (J. P. Lockwood, pers. comm.).

Soils

Despite the wide variety of lava substrates throughout this windward forest, most of the soil is classified as a Histosol (Sato *et al.,* 1973). Even in the situations where volcanic ash has been deposited, the functional soil, (i.e. where the plant roots are concentrated), is a thin layer of mixed organic material and volcanic ash which lies on top of a more impervious layer of accluded ash with depositions of iron oxide (Jacobi, unpublished data).

Mueller-Dombois *et al.* (1980) recognized five major habitat types with several soil moisture drainage regimes in this forest, including well- to 'poorly-drained lava rock outcrop soils, deep ash soils, and bogs with standing water. The majority of the areas with 'õhi'a die back examined in this study were found on moist and wet sites.

Vegetiton

The vegetation in most of the central windward area can be classified as montane rain forest, having no extended periods of negative moisture stress throughout the year. 'Õhi'a is the dominant tree species. However, above 1520 m elevation and below 900 m in portions of the Mauna Kea section, it is found in mixed stands with koa *(Acacia koa* Gray). Additionally, the Waiãkea forest section includes 'õhi'a scrub vegetation on the more recent lava flows.

The understory vegetation in the rain forest is dominated by hãpu'u treefern *(Cibotium glaucum* (Sm.) Hook. & Arn.) with admixed native shrub and ground-fern species. In the central, very wet portions of the Mauna Kea section, the lower layers of the vegetation (< 2 m tall) are composed of a mixture of native sedges, shrubs, matted ferns (Gleicheniaceae), :and introduced grasses and forbs.

Introduced plant species have invaded most of these forest areas. Although many of these species are widely distributed, they are uncommon and appear to have little potential to dominate or drastically alter the structure or composition of the native vegetation. However, some species are considered to

FIGURE 3. *Map of the eastern half of the island of Hawai'i showing the distribution of the three major dieback types described by Mueller-Dombois* et al. (1982).

be extremely invasive. The understory along the lower edge of the forest below 600 m elevation is highly disturbed, and is dominated by *Psidium cattleianum* Sabine (Myrtaceae) in the 'Õla'ã and Waiãkea sections, and additionally by *Melastoma* spp. (Melastomataceae) in the Mauna Kea section. Several other plants including *Passiflora mollissima* (HBK.) Bailey (Passifloraceae), *Rubus penetrans* Bailey, R. *ellipticus* Sm. (Rosaceae), and *Setaria palmaefolia* (Koen.) Stapf. (Gramineae) have become well established in other portions of the study area. The distribution of the introduced plants in the wet forest zone has been fostered by disturbance of the native forest habitats resulting from direct land use changes (urbanization, agriculture, logging and grazing) and degradation by introduced mammalan herbivores (primarily feral pigs *(Sus scofa)* and cattle *(Bos Taurus))*. It has been suggested that the distribution and abundance of introduced plant species may increase in the native forests following a large-scale opening-up of the tree canopy by 'õhi'a dieback (Pettys *et al.*, 1975).

Types of 'õhi'a dieback

Mueller-Dombois *et al*. (1980) classified 'õhi'a dieback for this windward forest into four different types based on a combination of habitat features and dynamics of the vegetation following canopy defoliation (Appendix 1). The most widespread type identified was *wetland die back*. Less common were the *bog-formation* and *'õhi'a displacement* types. A fourth type of die back, called *dryland* or *hotspot die back,* was found to be of very limited distribution in only the Waiãkea section.

An analysis of aerial photographs taken in 1977 showed that approximately 50,000 ha (50%) of this windward forest area could be considered to have been in heavy to severe dieback condition at that time (i.e. > 50 % of the mature trees in an area were either standing dead or had lost most of their leaves) (Fig. 3). Most of the affected forests were found in areas where the mean annual rainfall exceeds 4000 mm. However, in the Waiãkea forest section, dieback was also found in somewhat drier sites.

The Saddle Road study area

One site in the Waiãkea section of the forest was selected for a detailed comparison of the vegetation and substrate characteristics of adjacent dieback and non-dieback forest stands in an area of wetland dieback. This study site was located approximately 1.5 km north of Saddle Road, adjacent to the 1855 lava flow, between the elevations of 1150 and 1450 m (Figs. 1, 4A). The study area encompassed two different lava flows: a dense, smooth-surfaced pãhoehoe flow; and a rough, clinkery 'a'ã lava flow. The pahoehoe flow has been determined to be between 3000 and 4000 years old through carbon-14 dating of buried charcoal at its margin (J. P. Lockwood, pers. comm.). The 'a'ã flow appears to be partly covered by the pãhoehoe flow, indicating the former to be the older of the two substrates.

METHODS

Sampling design

Vegetation and substrate sampling were conducted along a 2000 m belt-transect established through the Saddle Road study site in 1974-1976. A segment of this transect (735 m) was located in the 'õhi'a forest growing on 'a'ã lava, while the remaining 1265 m ran through the stand on pãhoehoe lava (Fig. 5).

The 2000 m transect was divided into ten 100 m plot segments which alternated with ten 100 m interplot segments. Additionally, twenty 3 *x* 5 m subplots were established on either side of the 100 m transect segments, for a total of 40 subplots per 100 m of transect. This sampling design was adapted from similar studies conducted by Maka (1973) and Coo ray (1974) in another Hawaiian rain forest area (see also Mueller-Dombois, Bridges and Carson, 1981: 222).

FIGURE 4(A).

FIGURE 4. *Map of the Saddle Road study area showing the location of the 2000* m *transect, lava flows, and vegetation as interpreted from aerial photographs taken in (A) 1954, (B) 1965, and (C) 1977.*

FIGURE 5. *Sampling design along the 2000* m *transect in the Saddle Road study site.*

Data were collected on the distribution and abundance of all vascular plant species, substrate drainage, and soil depth along selected portions of the transect. Additionally, aerial photographs taken in 1954, 1965, and 1977 were examined to determine the spread of 'õhi'a dieback in the Saddle Road study area over this 23 year period (Fig. 4 A, B, C).

Foliage cover

Foliage cover for all vascular plant species was estimated using the line-intercept method (see Mueller-Dombois and Ellenberg, 1974). A meter tape was stretched along each of the ten 100 m plot segments on the transect. The distance of the meter tape which each species covered was recorded for six vegetation layers: H (0 - 0.5 m), S3 (> 0.5 - 1m), S2 (> 1 - 2m), S1 (>2-5m), T2 (>5-10m) and T1 (> 10 m).

Measurements of 'õhi'a trees greater than 5 m tall

The number of, diameter at breast height (DBH), and vigour of all 'õhi'a trees> 5 m tall were recorded in the 3 x 5 m subplots along the entire transect. Tree vigour was recognized in five classes, based on the degree of crown defoliation for live trees and the relative age of dead trees, following the classification system described by Mueller-Dombois *et al*. (1980).

Class 1: trees with fully foliated crowns.
Class 2: trees which had some defoliated branches; < 25 % of the total crown dead.
Class 3: trees which had most of the upper crown branches defoliated but with many lateral branches along the trunk.
Class 4: recently dead trees with some fine branches (< 5 cm in diameter) and most of the bark remaining.
Class 5: old dead trees which had only major branches remaining and most of the trunk without bark.

Substrate depth, drainage, and lava flow type

Data for the substrate were recorded at 50 cm intervals along the transect in each 100 m plot segment. At these points, a steel rod was lowered from the meter tape, and the substrate depth, lava flow type, and drainage condition were recorded. Two categories of soil drainage were recognized:

(i) *saturated soil,* which included soil with water standing over it, or soil which emitted free water at the surface when very slight pressure was applied on it with a finger, and

(ii) *drained or unsaturated soil,* which required considerable pressure to show free water on its surface.

Although this method of saturation determination was crude, it allowed for a rapid field assessment of truly saturated soil conditions. Since sampling along the transect was conducted during the dry summer months, the results represent a conservative estimate of the percentage of poorly drained substrate.

Mapping the spread of 'õhi'a die back in the Saddle Road study site

The spread of 'õhi'a dieback in the Saddle Road study site was assessed by mapping the tree canopy foliage cover from aerial photographs taken in 1954, 1965, and 1977. The photos used had approximate scales of 1: 50,000 (1954), 1: 24,000 (1965), and 1: 40,000 (1977). Areas were considered to be in a dieback condition in 1965 and 1977 if the tree canopy foliage cover had been reduced >50% from what it was mapped as using the 1954 photographs. This die back classification corresponds to the heavy to severe dieback stand class described by Mueller-Dombois *et al*. (1980).

Data analyses

For analysis, the data from each of the 100 m plot segments were grouped into five 20 m subplot segments. The species cover values from the line-intercept sampling were converted to percent cover for each subplot.

Basic comparisons of variables between the dieback and non-dieback portions of the transect were conducted using a two-tailed t-test. For data collected as percent cover, an arcsine transformation was made on the cover values before the t-test was applied Similarly, a square-root transformation was used for variables involving counts per subplot (Sokal and Rohlf, 1969).

Analyzing species associations along the transect

Species association patterns along the 2000 m transect were analyzed using a dendrograph plotting program (McCammon, 1968; McCammon and Wenniger, 1970) and a two-way synthesis table program (Ceska and Roemer, 1971). In both of these analyses, the cover values for all plant species in all vegetation layers were utilized.

The dendrograph technique is used to display vegetation samples clustered at different levels of similarity (Mueller-Dombois and Ellenberg, 1974). The generated dendrograph is based on a similarity-dissimilarity matrix calculated for each pair of vegetation samples. Two similarity indices were used for this analysis: Sørensen's index, based only on species presence or absence in the samples; and Spatz's index, which combines both species presence-absence, and species abundance values. Both indices are described in detail by Mueller-Dombois and Ellenberg (1974).

The two-way synthesis table technique isolates groups of species which have a common distribution among the sample plots. The Ceska and Roemer program close]y simulates the Braun-Blanquet synthesis table technique, described by Mueller-Dombois and Ellenberg (1974). Using this program, the rows (sample plots) and the columns (species) of the raw data matrix are re-ordered so that groups of species with similar distributions in sample plots are listed together.

The dendrograph and two-way synthesis table techniques complement each other in that together they yield information on the similarities between the sample plots, and identify groups of species which have a common distribution.

RESULTS

Spread of 'õhi'a die back in the Saddle Road study site between 1954 and 1977

There is little question that a die back event (i.e. a relatively simultaneous death or defoliation of most of the tall ‘õhi’a trees) occurred in the study area sometime between 1954 and 1977. The reason these years are most often referred to in discussions of die-back in this forest is because they are when aerial photographs were taken for the entire area. However, local residents who have hunted in these windward forests indicated that dieback first became noticeable in the early 1960's, and had reached its greatest extent by 1974.

Comparisons of the aerial photographs taken in 1954, 1965, and 1977 show a consistent increase in the extent of ‘õhi’a dieback in the 1600 ha of mature native forest mapped in the Saddle Road study site over that 23 year period (compare Figs. 4 A, B, and C). In 1954, the vegetation across the entire area was considered to be in non-dieback condition. The 1965 photos show 450 ha of the forest had experienced a major reduction in tree canopy cover. By 1977, the area of dieback had increased to 1000 ha. It is important to note that all of the affected forest in this area was found growing on pãhoehoe lava. Additionally, the distribution of die back seen on the 1977 photos is essentially identical to its distribution in 1981. For the Saddle Road study area specifically, die back has remained restricted to the ‘õhi’a forest growing on pãhoehoe lava.

The 1965 photographs show a patchy pattern of die back distribution. By 1977, most of the 1965 die-back patches had merged, resulting in a consistent band of dieback up to 1380 m elevation on the pãhoehoe lava. None of the forest growing on the ‘a’ã lava flow shows any reduction of the tree canopy in the photos.

Along the transect, 70.6 % of trees recorded in the die back stand were considered unhealthy (vigour class 3, 4, or 5), while only 14.8 % of trees on the ‘a’ã flow had lost most of their crown foliage. Some sections of the transect on pãhoehoe lava had less than 5 % healthy trees (vigour class 1 or 2).

Substrate characteristics along the transect

Mean soil depth on the pãhoehoe lava was slightly greater than on the ‘a’ã flow; however this difference was not highly significant (Tabbe 1). It is suspected that more soil filtered down between the ‘a’ã lava blocks than could be detected with the soil probe, so this implied difference in soil accumulation may not be real.

The greatest difference found in the substrate of the two stands was in soil drainage. All but three of the subplots on ‘a’ã lava had greater than the median frequency of drained soil, calculated for all of the plots (Fig. 6). The distinction between the two sites was even more complete for the saturated soil condition where all of the subplots sampled on ‘a’ã lava

TABLE 1. *Comparison of substrate depth and percent cover for the two drainage classes between the non-dieback and dieback forest stands.*

	Non-dieback Stand		Dieback Stand		Comparison		
Drainage Class	$\bar{x}$	n	$\bar{x}$	n	t	df	p<
Drained	62.2%	17	38.6%	33	4.37	48	.001
Saturated	12.1 %	17	49.9%	33	6.89	48	.001
Soil Depth	13 . 7 cm	17	15.1 cm	33	1.83	48	.04

FIGURE 6. *Percent frequency of drained soil in the plots sampled along the 2000* m *transect*.

had less than the median frequency value for all of the plots (Fig. 7). However 79 % of the subplots on pãhoehoe lava had greater than the median frequency of saturated soil.

Results of the dendrograph and two-way synthesis table analyses

The dendrograph cluster analysis showed a consistent separation of the subplots with non-dieback forest growing on 'aa lava from the subplots with dieback forest. Two major clusters were identified on each dendrograph (Figs. 8 A, B). Both similarity indices used in the calculations yielded comparable results, although the similarity level at which the major groups were separated was lower using Spatz's index (9% similarity), than when Sørensen's index was used (43 % similarity). This difference in separation level is simply a function of the type of similarity index used (Mueller-Dombois and Ellenberg, 1974).

The two-way synthesis table analysis also separated the non-die back from the dieback forest plots. In addition four species groups were identified, all pertaining to the dieback stand (Table 2). Species group 1 consisted primarily of weedy, introduced herbaceous plants which normally grow in wet, open situations. This group included the rush *Juncus effusus* L., and two herbs, *Cuphea carthagensis* (Jacq.) Macbride, and *polygonum glabrum* Willd. Species group 2 also included species which grow in wet, open locations, however three of the four plants in the group, *Styphelia tameiameiae* (Cham.) F. Muell., *Carex alligata* F. Boott and the moss *Sphagnum vitianum* Schimp. are native. Groups 3 and 4 were composed principally of native shrubs and small trees. Most of these species, such as *Sticherus owhyensis* (Hook.) Ching, *Lycopodium cernuum* L., *Myrsine sandwicensis* A. DC., *Sadie ria pallida* Hook. & Am., and larger individuals of *Styphelia tameiameiae,* are generally early woody colonizers of recent lava flows or disturbed areas in wet and moist habitats.

Species richness

The two-way synthesis table analysis was useful for identifying groups of two or more species which were similarly distributed along the study transect. However when the distributions of all plant species were analyzed individually, the floristic differences between the non-dieback and dieback stands were even more distinct.

Of the total of 117 vascular plant species noted in the Saddle Road study site, 63 were ,recorded in the sample plots along the 2000 m transect (Appendix 2). Of this number, 25 were found in both forest situations, 28 exclusively in the dieback plots, and 10 only in the non-dieback stand. AU of the plants in the latter group, *Nertera granadensis* (L.f.) Druce,

FIGURE 7. *Percent frequency of undrained (saturated with water) soil in the plots sampled along the 2000* m *transect*.

FIGURE 8. *Dendrograph generated from vegetation samples along the 2000* m *transect using (a) Sørensen's and (b) Spatz's index of similarity.*

TABLE 2. *Distribution of species groups along the* 2000 *m transect, generated by the* two-way synthesis table analysis.

Species groups and vegetation layers for each species

Species group 1: *Cuphea carthagenensis* (H), *Juncus effusus* (H), *Polygonum glabrum* (H)

Species group 2: *Carex alligata* (H), *Juncus tenuis* (H), *Sphagnum* vitianum (H), *Styphelia tameiameiae* (S3)

Species group 3: *Sticherus owhyensis* (S2), *Styphelia tameiameiae* (S1,S3), *Vaccinium calycinum* (S2)

Species group 4: *Cheirodendron trigynum* (H), *Ilex anomala* (S3), *Lycopodium cernuum* (H,S2,S3) *Myrsine lessertiana* (S2), M. *sandwichianum* (SI,S2), *Pelea clusiaefolia* (S2), *Polygonum glabrum* (S3), *Sadleria pallid a* (H), *Sticherus owhyensis* (H)

TABLE 3. *Comparison of the number of species per vegetation layer between plots in the non-dieback and dieback forest stands.*

	Non-dieback Stand		Dieback Stand		Comparison		
Vegetation Layer	$\overline{X}$	n	$\overline{X}$	n	t	df	P<
H (>0.5m)	3.50	17	7.59	33	4.67	48	.001
S3 (>0.5-1 m)	2.46	17	4.75	33	4.20	48	.001
S2 (> 1-2 m)	2.32	17	5.39	33	6.30	48	.001
S1 (>2-5 m)	3.43	17	5.31	33	2.92	48	.01
T2 (> 5-10 m)	1.99	17	1.01	33	3.37	48	.01
Tl (>10m)	0.56	17	0.20	33	3.61	48	.001

Freycinetia arborea Gaud., *Psychotria* sp., and several epiphytic terns, were recorded in only one of the 17 subplots sampled in the non-dieback stand. In that they were so rarely encountered, these species cannot be considered to be indicative of just the non-dieback forest type. Of the 28 species found only in the dieback stand, 10 had a frequency> 20%. These species included those isolated in the two-way synthesis-table analysis, plus an additional four introduced and native species including *Juncus planuifolus* R. Br., *Dicranopteris linearis* (Burm.) Underw., and *Machaerina angustifolia* (Gaud.) Koyama.

A total of 24 (20%) of the plants recorded for the entire study site were introduced species. Most of these were found only in the dieback stand. Although this forest contained a large number of introduced plants, none of those encountered are considered to pose a serious threat by replacing native species at this elevation.

An examination of the number of species per layer in each forest type further revealed that the dieback stand contained an additional complement of species, particularly in the vegetation layers > 5 m tall (Table 3).

Distribution and abundance of hãpu'u tree fern and 'õhi'a.

The distribution and abundance of two dominant wet forest species, the hãpu'u treefern and 'õhi'a

TABLE 4. *Comparison of frequency and mean cover for Cibotium glaucum and Metrosideros polymorpha in the S1 (<2-5 m) and S2 (<1-2 m) vegetation layers between the non-dieback and dieback forest stands.*

	Non-dieback Stand			Dieback Stand			Comparison		
	Freq.	$\overline{X}$	n	Freq.	$\overline{X}$	n	t	df	P<
S1 Layer									
C. glaucum	100	82.8	17	73.5	9.7	33	12.22	48	.001
M. polymorpha	0	-	17	79.4	7.6	33	-	-	-
S2 Layer									
C. glaucum	100	13.1	17	97.0	17.0	33	1.40	48	.04
M. polymorpha	12.5	-	17	32.0	-	33			

TABLE 5. *Comparison of 'õhi'a canopy, tree stocking, percent of unhealthy trees (Vigour class 3-5), mean dbh, and basal area/ha between the non-die back and dieback forest stands.*

	Non-dieback Stand		Dieback Stand		Comparison		
	$\overline{X}$	n	$\overline{X}$	n	t	df	P<
Canopy cover	60.7%	17	17.6%	33	4.66	48	.001
No. trees/ha	123.2	34	727.7	66	9.39	98	.001
Percent unhealthy trees	14.8%		70.6%				
Mean dbh (cm)	37.4	81	16.2	608	13.90	687	.001
Total basal area (m^2)/ha	30.9	34	21.6	66	1.60	98	.02

were examined in more detail along the transect. Each of these species was found in both of the forest types sampled.

Hãpu'u is the dominant understory species in most of the mature wet forests on the island of Hawai'i. However, in situations where the tree cover is less than 25 %, the treefern cover is often reduced. Hãpu'u is generally confined to the H, SI, and S2 vegetation layers (< 5 m tall), although individuals of this and the other two *Cibotium* species on the island can exceed 5 m in height (Becker, 1976).

Hãpu'u was found in all plots sampled along the 2000 m transect. For the Silayer, there was a marked difference in this species' cover in the non-dieback forest (mean cover 82.8%), as compared with the dieback stand (mean cover 9.7%) (Table 4). Additionally, most of the hãpu'u plants in the dieback stand had a tapered apex and few large fronds, indicating that they had recently decreased in vigour (Becker, 1976).

'Qhi'a was also found in all plots sampled along the transect. Major differences in foliage cover, stand density, mean tree diameter, and tree vigour were recorded in the two stands.

The greatest difference in 'õhi'a foliage cover between the two stands was found in the S1 and T1 vegetation layers. The tall tree canopy (T1 layer) in the non-dieback forest had an average 'õhi'a cover of 60.7%, whereas in the die back forest it was 17.6% (Table 5). This difference in cover is directly the result of the 'õhi'a canopy dieback between 1954 and 1977 since on the 1954 photographs the tree canopy in this area is estimated to have been> 60%.

A similar but opposite pattern was found in the tall shrub (S1) layer (Table 4). No 'õhi'a saplings were recorded in this layer for the non-dieback forest. However, 79.4% of the subplots in the dieback stand had saplings, with a mean cover of 7.6%.

Significant differences were also found in the density of trees and in the mean diameter of 'õhi'a trees greater than 5 m tall in the two stands (Table 5). For this comparison all trees, dead, dying, or healthy were used in the analysis. This allowed for a comparison of the tree densities in each stand prior to the dieback event on the pãhoehoe lava flow.

Although the density of trees on pãhoehoe lava was nearly six times the density of trees on the 'a'ã flow, the mean diameter of trees on 'a'ã lava was much larger than for trees on the pãhoehoe flow. When both of these variables were combined into basal area per hectare, the values for the two forest stands did not differ significantly.

Discussion

Similarities and differences between the die back and non-dieback stands

The two forest stands sampled in the Saddle Road study site were found to have many features in common. Since they are adjacent to each other, factors such as rainfall, temperature, and availability of species for colonization are essentially identical. Additionally, both lava flows are at least 3000 years old. Although little information is available on vegetation development over time in moderate-aged Hawaiian wet forest habitats, 3000 years appears adequate for the vegetation structure and species composition to attain a relatively stable state on both pãhoehoe and 'a'ã lava (Atkinson, 1970; Eggler, 1971).

Despite the simlarities in these primary community development factors, the two forest stands were found to differ considerably in plant species composition and abundance, soil drainage, and in the occurrence of canopy dieback. However, most of the features which were found to differ between the two sites are considered to be secondary characteristics i.e. features which have resulted from the development of the vegetation and soil over time.

The only primary factor believed to differ between the two forest stands is lava flow structure. Pãhoehoe and a'ã lavas are very similar in their chemical compositions. The basic difference between them is their physical structure which is determined by the viscosity of the magma and the amount of gas which remains in the lava as it flows (Macdonald and Abbot, 1970). Pãhoehoe flows are relatively fluid, cooling to a smooth or slightly undulated surface with shallow cracks between the adjoining plates. 'a'ã lava flows have a rough, broken surface consisting of a layer of clinkery blocks of lava, generally 10-50 cm in diameter, riding on top of a thick, pasty flow interior. When a 'a'ã lava cools, its surface retains a clinkery crust up to 1.5 m thick, and has a dense interior.

The structure of each of these lava flow types can result in different soil development and drainage conditions in' the wet forest habitats, which may be an important factor in causing 'õhi'a dieback. Due to the broken, porous structure and resulting relatively large surface area of 'a'ã lava, chemical weathering proceeds at a much greater rate on this flow type, than on the denser and smoother pãhoehoe lava (Sherman, 1972).

With regards to drainage, on 'a'ã lava there is initially almost unrestricted downward movement of excess water through the spaces between the lava blocks until it reaches the flow's massive center. As organic material is accumulated on the surface of the flow, it also gets distributed downward. This results in a deep zone above the center of the flow which is both fertile and well-drained. On pãhoehoe lava, rapid percolation of water is limited to shallow cracks between the lava plates. As organic material accumulates, movement of water is further restricted, and localized ponding may occur. Additionally, organic material which is deposited in the cracks between the lava plates further slows the downward movement of water, yielding even larger areas of poorly drained substrate.

In wet habitats, the rooting zone on pãhoehoe lava is restricted to the shallow layer of organic material which sits on top of the lava surface (Jacobi, *in prep.)*. This shallow organic soil is subject to occasional flooding when excess water accumulates on the surface of the flow.

A working hypothesis for 'õhi'a die back presented by Mueller-Dombois (1980) stated that "dieback is initiated by a climatic instability which becomes effective through the soil moisture regime under certain conditions of forest stand maturity". The soil drainage patterns seen in the dieback and non-dieback stands in the Saddle Road study site show a strong correspondence between dieback and poorly drained substrate. It can be argued that the loss of the tree canopy on this flow would result in less moisture removed by transpiration and therefore yielding poorer soil drainage. Certainly this may be part of what has happened, but the poor drainage characteristics of pãhoehoe lava in the first place causes the shallow root zone to be less bufferred against rapid increases of excess moisture. If flooding and subsequent anaerobic conditions persist in the soil, enough of the fine plant roots may be killed, which could lead to a rapid die back of the trees. On a'ã flows, the clinkery crust allows for better drainage, so less flooding of the root zone will occur during long periods of high rainfall.

Secondary effects of 'õhi'a dieback

One of the most interesting differences found between the two forest stands examined was the large number of 'õhi'a saplings which had become established on the pãhoehoe flow following the canopy dieback. 'õhi'a shows many characteristics of being a pioneer species. It has small seeds which are easily dispersed over long distances, and seedlings require well-lighted conditions to grow to maturity (Burton, 1980). The abundance of 'õhi'a saplings in the dieback: forest stand was most likely in response to the better light conditions near the ground following the loss of the tall-tree canopy. In this forest type, the 'õhi'a regrowth phase is just as dramatic as the initial canopy dieback. It is possible to speculate that after some period of time 'õhi'a saplings will grow to maturity, resulting in a forest which will again develop a dosed canopy, and be heavily stocked with a relatively even-aged stand of 'õhi'a. The mean dbh and dense tree stocking for 'õhi'a on the pãhoehoe flow suggest the previous generation of trees found there also developed following an earlier episode of dieback.

Hãpu'u treeferns appear to have responded negatively to the opening of the canopy, as indicated by their reduced state of vigour on the pãhoehoe flow. Several other species of plants appear to have increased in abundance as a result of the canopy dieback. These include *Dicranopteris linearis* and several of the herbaceous species which were found growing in wet, open sites.

Conclusions

The 'õhi'a rain forest serves two very important functions; it reguiates the flow of water through this habitat, and it provides a habitat for a largely endemic biota, including many species of both plants and animals which are now considered to be endangered (Berger,]972; Fosberg and Herbst,]975). There is little doubt that a rapid defoliation or death of the tall canopy-forming trees over a large area could, at least temporarily, alter the composition, structure, and function of this community.

Although it appears now that 'õhi'a dieback has not resulted directly *from* the introduction of a pathogen, further research is still needed to test various aspects of Mueller-Dombois' successional hypothesis. Specifically, more information is needed on rooting patterns and soil and plant nutrient status on both lava flow types in different habitats, and information on climatic fluctuations across the study area, which may have served to trigger the dieback. Only with a clearer understanding of both the mechanism and consequences of 'õhi'a dieback will we be able to properly manage what remains of the Hawaiian rain forest ecosystem.

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APPENDIX 1

Description of the four major dieback types found in *the windward forests on the island of Hawai'i. Adapted from Mueller-Dombois* et al. *(1980).*

1. *Wetland dieback*. This dieback type is most prevalent in very moist to wet, shallow-soil habitats, where it occurs most commonly on poorly drained pãhoehoe lava. Wetland dieback is what has become known as 'typical' 'õhi'a dieback as it is most easily visible from Saddle Road in the Waiãkea forest section. It is charact. erized as having large areas of forest with most of the standing trees either dead or defoliated, and a very poorly drained substrate. There appears to be adequate

regeneration of small ‘õhi’a trees (> 3500 saplings per ha), in response to the opening of the tree canopy.

2. *Bog-formation dieback*. This type has been found in extremely wet, deep-soil habitats in the central portion of the Mauna Kea forest section. Mean annual rainfall for this area exceeds 4000 mm. In this dieback situation, there does not appear to be adequate establishment of new ‘õhi’a saplings when the older trees die. Typically bog-formation dieback *is* characterized as having scattered standing snags, or trees with a few leaves in an area where the substrate is continually poorly drained. Most of the living trees are found growing on top of old fallen logs.

3. *‘õhi’a-displacement dieback*. This type has been found only in moderately moist deep-soil habitats in the Õla’ã forest section, where the understory is dominated by hãpu’u treeferns. In this situation it appears that as the mature ‘õhi’a trees die, the dense treefern canopy is maintained, restricting light necessary for the establishment of new saplings.

4. *Dryland or hotspot dieback*. This type appears to be restricted to mesic or well-drained sites where it occurs on shallow soil habitats. Typically hotspot dieback is found as small clumps of dead trees across an area approximately 50-75 m in diameter, in forests with a very dense tree canopy. It has been noted to occur in both the Waiãkea and Õla’ã forest sections, as well as in the upper portion of the Ka'ü Forest Reserve on the south-eastern slope of Mauna Loa.