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Decline of Ohia *(Metrosideros polymorpha)* in Hawaii: a review

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IN BRIEF

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Portions of the ohia *(Metrosideros polymorpha)* forests on the windward slopes of Mauna Loa and Mauna Kea on the island of Hawaii were noted to be dying during the late 1960's. Aerial photographic evidence, however, showed some mortality occurred as early as 1954, but most took place between 1954 and 1972. Since 1972 little additional mortality has occurred and the problem is still confined to the same general area. Currently, about 50,000 ha are seriously affected by the problem.

Individual trees affected by decline exhibit several kinds of symptoms, from slow progressive dieback accompanied by chlorosis and reduction in leaf size to rapid death of all or part of the crown. Mortality of fine feeder roots is common on affected trees.

Seven types of decline have been identified on the basis of differential response of the associated rainforest vegetation to collapse of the ohia canopy. Two of the types identified, Bog Formation Dieback and Wetland Dieback, make up more than 80 percent of the decline area. Both dieback types occur in an area of high rainfall and are associated for the most part with poorly drained substrates. However, Bog Formation Dieback develops more slowly, ohia regeneration is poor and mostly of vegetative origin, and treeless bogs are widely scattered throughout the area. Ohia trees in the Wetland Dieback type declined rather suddenly, with the most mortality occurring between 1965 and 1972. Impact on associated vegetation was much less than in the Bog Formation Dieback, and ohia regeneration of seedling origin is good.

Loss of the ohia canopy in some areas has resulted in a decrease in population of some native birds and increased numbers of some introduced birds. Endangered plant species in decline areas probably have also been affected. Introduced plant species have invaded some areas.

Although 90 percent or more of the ohia canopy may be killed, subcanopy species and litter provide ground cover for 95 percent or more of the area. For this reason, decline has had no major effect on watershed values, either in amount of runoff or water quality.

Ohia decline appears to be a typical decline disease in which tree mortality results from a sequence of events that starts with tree stress, which in turn predisposes the trees to attack by organisms that eventually kill them. Poor soil drainage is probably the major cause of stress. The ohia borer *(Plagithmysus bilineatus*) and two fungi, *Phytophthora cinnamomi* and *Armillaria mellea,* attack stressed trees. Low soil nutrient levels, aluminum toxicity, and senescence may also play a role in the overall decline syndrome.

Although ohia decline has severely affected the ohia ecosystem in some areas, an ecosystem dominated by native vegetation probably will continue, but this may differ from that present before decline. Except for control of introduced plants and feral animals that spread these plants, little can be done on a practical basis to ameliorate the effects of decline.

INTRODUCTION

Ohia lehua *(Metrosideros polymorpha)* is the dominant forest tree on all the major Hawaiian Islands, comprising about 62 percent of the total forest area *(fig. 1)*. Although the species is little used commercially, it is invaluable from the standpoint of watershed protection, esthetics, and as the only or major habitat for several species of forest birds, some of which are currently listed as threatened or endangered.

During the late 1960's, large areas of dead and dying ohia were noted along the windward slopes of Mauna Loa and Mauna Kea on the island of Hawaii (Mueller-Dombois and Krajina 1968). The problem, commonly referred to as ohia decline or ohia dieback, was extensive and apparently intensifying (Burgan and Nelson 1972). Since 1970, the decline problem has been studied extensively to determine the extent and cause.

This report summarizes what is known about ohia decline, and discusses the implications for managing declining ohia forests. This report also includes new data on the current distribution of decline on the island of Hawaii.

HISTORY

Although concern for decline in the ohia forest on the island of Hawaii dates only from the late 1960's, groups of ohia trees dying in Hawaiian rainforests were reported as early as 1875 (Clarke 1875). Reports of the Committee on Forestry of the Hawaiian Sugar Planters' Association mentioned widespread mortality of both ohia and koa *(Acacia koa)* along the Hamakua Coast on the slopes of Mauna Kea on Hawaii, and on Maui (Horner 1912, Forbes 1918). The mortality was attributed to "bark beetles."

Large areas of dead and dying ohia were observed on Kauai in the early 1900's (Larsen 1910). Fosberg (1961) mentioned the occurrence of dead and dying trees in Hawaiian forests in certain wet areas on comparatively level or gently sloping ground. One particular stand cited was near Hanalei Valley, Kauai. This is probably one of the same areas on Kauai where Petteys and others (1975) found ohia tree death or crown dieback to be abnormally frequent. Similar declining and dead trees were noted on Kohala Mountain along the Kohala Ditch Trail on the island of Hawaii (Donaghho 1971). Native forests on steep slopes were "holding their own," but on broad, plateau-like ridges between the valleys, many trees were dead or dying. In this area the forest continues to decline *(fig. 2)*.

Davis (1947) observed declining forests in several areas in Hawaii Volcanoes National Park on Hawaii. Photographs in the report showed damage similar to that seen today. Some of the trees appeared to be killed by the ohia borer *(Plagithmysus bilineatus)* but other dead and dying trees were found to be free of insect attack.

All the above reports on ohia mortality contain little or no details of locations, symptomatology, site factors, or other observations to indicate their possible similarity to the current decline on the windward slopes of the island of Hawaii. They do, however, indicate that mortality and decline of ohia on a relatively large scale has occurred in the past in Hawaii.

One historical record of large-scale mortality is well documented and may be relevant to the current dieback problem on the island of Hawaii. In 1906, ohia were dying unaccountably in spots of varying size in the Koolau District on Maui (Territory of Hawaii 1907). By 1907, the affected area covered 1,620 to 2,030 ha and was spreading rapidly. The problem extended from the lower edge of the forest to an elevation of 305 to 915 m between Kailua and Nahiku, Maui (Lyon 1909). Up to 95 pct of the trees in the affected area were dead, including associated subcanopy trees as well as ohia.

The striking feature of the problem was the association of tree mortality with topographic features (Lyon 1909). The affected area consisted of a series of sloping ridges separated by gulches of varying depths. Some of these ridges had broad tops, while others were more or less sharp. Mortality was associated with the broad, flattened ridges, and the forest was still healthy on the sharp ridges, or steep slopes of gulches. Such differences can still be seen today.

Tree death was due to killing of the roots that penetrated more than 5 cm of soil (Lyon 1909). Even trees with apparently healthy tops had roots killed back to near the soil surface. The tissues of the dead roots were deep purple or bluish black. Because no pathogenic fungi or potentially harmful insects were found to be associated with affected trees, such organisms were not believed to be the cause of tree mortality. Rather, the cause was believed to be toxic quantities of hydrogen sulfide and ferrous iron compounds produced in soil by bacterial fermentation under conditions of poor drainage. Lyon (1909) suggested that introduced tree species be planted which might be adapted to the wet sites.

Curran, who visited the area in 1911, concluded that the primary cause of the problem was an exceptionally strong storm, which struck the area shortly before the mortality problem was noted in 1906 (Curran 1911). He believed that the exposed flat ridges with their adverse soil conditions and excessive moisture, as well as grazing and ditch construction, reduced vigor of trees and made them more susceptible to the storm damage.

Later, Lyon (1918) indicated that ohia mortality may have been due to clogging of soil interstices in the lower strata with fine leached material under conditions of heavy rainfall. Clogging resulted in gradual changes in the substratum which rendered it less suitable for growth. Lyon (1918) again suggested planting such areas with introduced trees that might be more adaptable.

Guernsey (1965) studied the soils in the dieback area and found that an impervious layer was indeed present. This layer was a dominating soil characteristic on slopes less than 25 pct in areas with annual rainfall above 3,750 mm. Depth of the layer beneath the surface was inversely proportional to amount of rainfall. The layer was dense and impervious to air and water movement. He suggested that it is formed over time by reduction of ferric iron to ferrous iron by hydrogen sulfide, which had been produced by anaerobic fermentation.

The Maui forest dieback area still can be easily identified. It consists primarily of 3.5 to 6.0 m tall ohia, apparently mostly of vegetative origin, with various grasses, sedges, and ferns in the understory. The area is boggy with the water table at or near the soil surface. In spite of the severe conditions, the ohia appear relatively healthy, i.e., crowns show little dieback, although some trees appear somewhat chlorotic. This may indicate that there are genotypes within the species that are adapting to the site. Stumps and snags of the original ohia forest, some more than 1 m in diameter, are still evident *(fig. 3)*.

Following Lyon's recommendations, various introduced tree species were planted on a large scale in the area. Two of these, *Eucalyptus robusta* and *Melaleuca quinquenervia,* have survived and grown well, and the soil beneath has dried considerably in comparison with the unplanted area.

Except for general reports of occurrences of ohia mortality mentioned earlier, records of the decline problem on the island of Hawaii were not available before 1954. At that time, aerial photographs were taken of the entire area now known to be affected. These photographs, along with others from the same area taken in 1965 and 1972, allowed evaluation of the severity and rate of decline between 1954 and 1972 on approximately 71,360 ha (Petteys and others 1975). They found that, in 1954, 42 pct of the study area was classified as healthy, while less than 0.2 pct was classified as having severe decline. Most of the areas of moderate and severe declines were concentrated in the northern part of the study area on Mauna Kea. In 1965, 26 pct was classified as healthy and 22 pct as having severe decline, with most areas of severe decline generally in the northeast and southern parts of the study area. By 1972, only 18 pct of the study area was considered healthy, while 48 pct was in severe decline. No evaluation of the occurrence and severity of decline has been published since 1972.

CURRENT STATUS

In 1982, we reevaluated the extent and severity of ohia decline on the island of Hawaii. Three decline classes were subjectively estimated on the basis of percentage of trees dead or showing obvious symptoms of decline: healthy to slight—10 pct or less trees dead or declining, moderate— 11 to 50 pct of trees dead or declining, and severe—more than 50 pct of trees dead or declining.

General boundaries of the areas in each decline class were delimited on the basis of two separate overflights in a fixed-wing aircraft and outlined on 1:24,000 orthophotoquads. Later, several overflights in a helicopter more precisely defined the boundaries. Additional information was obtained from interpretation of 1977 color infrared and 1978 black and white aerial photographs and from ground checks. Boundaries were delineated on the orthophotoquads, transferred to tracing paper, and each quad was then photographed, printed at approximately one-fourth of actual size and a mosaic made of the photographs. From the mosaic a map of reduced scale was prepared (see foldout map at the back of this report). Acreages in each delineated area were determined with a planimeter, and verified with an area meter (Lambda Instruments Corp.).[1]

Decline areas on Mauna Loa were easily delimited because of the sharp boundaries between adjacent areas of different decline classes, which generally corresponded to well defined lava flows. On Mauna Kea, boundaries between areas of different decline classes were more diffuse.

The area mapped consisted of eight 7½° quads and part of two others (see map). This area is larger than that surveyed earlier (Petteys and others 1975), extending slightly farther north, east, and west, but slightly less on the southern end. The earlier survey also included in the forested area historic lava flows— flows for which the dates are known. We did not study these relatively young forests because the ohia trees were considered immature. Some dieback and mortality occur on portions of these young flows, however. As in the earlier study (Petteys and others 1975), former forest areas that had been disturbed by grazing, logging, agriculture or other activities were not considered in the total forest area. Forest plantations also were not considered, but were generally healthy.

Forests in the 1982 study area not influenced by human activity covered 76,915 ha. Of this area, 35.3 pct was considered healthy or had slight decline, 23.7 pct had moderate decline, and 41.0 pct had severe decline *(table 1)*.

The 1982 evaluation cannot be directly compared with the earlier study (Petteys 1975) because of differences in methodology. However, specific photointerpretation points could

[1]Trade names and commercial enterprises or products are mentioned only for information. No endorsement by the U.S. Department of Agriculture is implied.

Table 1—*Status of ohia decline on the island of Hawaii*

Quad	Healthy to slight decline[1]	Moderate decline[2]	Severe decline[3]	Disturbed areas	Historic lava flows	Forest plantations
			Hectares			
Papaaloa	2,136	0	631	1,375	0	51
Keanakolu	4,791	1,962	1,508	913	0	611
Akaka Falls	28	4,766	8,398	566	0	879
Pua Akala	3,085	2,432	2,585	0	0	0
Piihonua	795	5,336	3,527	6,134	1,593	452
Upper Piihonua	4,523	1,157	5,534	0	4,323	0
Puu Makaala	2,290	1,346	5,066	8,762	0	510
Kulani	6,924	791	1,654	2,224	6,391	335
Volcano	1,853	122	2,624	5,861	0	0
Kilauea Crater	728	279	44	3,115	6,576	0
Total	27,153	18,191	31,571	28,950	18,883	2,838

[1]Less than 10 pct of trees dead or showing decline.
[2]11 to 50 pct of trees dead or showing decline.
[3]More than 50 pct of trees dead or showing decline.

be compared with the earlier map because both were of the same scale. These comparisons lead to the following conclusions:

1. The discrepancy in the area of severe decline between 1972 and 1982 is primarily due to differences in interpretation of degree of decline in the ohia-koa forest type. Petteys and others (1975) reported 6,800 ha of severe decline in ohia-koa forest type, but none of this forest type was characterized as having severe decline in the current evaluation. In fact, most of the upper elevation ohia-koa forests (area 5, map)[2] appear to be relatively healthy with only scattered dead trees. The lower elevation ohia-koa forests along the Hamakua Coast (area 6), although characterized as having moderate decline, are considered to be toward the lower end of that classification.

2. Within the area surveyed by Petteys and others (1975), severity of decline apparently has changed little since 1972. The large bog area on Mauna Kea (area 3) was considered to be in severe decline in 1972, with scattered patches of more or less healthy forests. These seem to be deteriorating, however, and there appears to be more open bogs. On Mauna Loa, at least on lava flows covered by thin organic soils (area 8), most of the dieback occurred between 1965 and 1972 and has changed little since then. In the areas most severely affected, up to 90 of the trees died and all remaining trees lost most of their crowns.

Dieback continues on Mauna Loa on the lava flows at the upper elevations above the areas of severe decline. The largest areas with active dieback are just below Kulani Prison (area 11), the area shown as moderate dieback in the northeast corner of the Kilauea Crater quad (area 14), and at the upper margin of the area of severe decline on the lava flow just south of the Saddle Road (area 9).

3. Few areas of active decline occur outside the original 1972 survey area, the major exception being the area currently characterized as moderate decline in Keanakolu quad (area 1). This is an area of large ohia with a few koa. Scattered dead and dying trees occur over the entire area.

Few areas of relatively healthy ohia forests remain on the windward slopes of Mauna Kea and Mauna Loa. The largest is in the Puu Makaala area in the Puu Makaala and Kulani quads (area 12). Another area in the Kulani quad lies just south of the 1942 lava flow (area 10). There is, however, some scattered mortality in this area. A relatively large area of healthy open ohia forest with a dense understory of treefern (*Cibotium* spp.) is located in the Upper Olaa Forest Reserve (area 15). Perhaps the healthiest area is a dense forest of rather small diameter trees located just north of the Saddle Road at about 1,370 to 1,675 m elevation (area 7). On the Hamakua Coast, only one extensive area of relatively healthy forest exists. This extends from the southwest corner of the Papaaloa quad into the lower central portion of the Keanakolu quad (area 2). Some scattered mortality is occurring in this area.

Aerial observation of ohia forests on the western and southern slopes of Mauna Loa showed no significant areas of active dieback, although some mortality and dieback of individual trees occur in all areas.

[2]Numbered areas on map represent the general area occupied by the stand condition or type described in the text, not a specific location.

EFFECTS ON ECOSYSTEM

Dieback of Ohia and Associated Plant Species

The effect of decline on ohia can be described in terms of single trees and of the stand as a whole. Symptomatology on individual declining trees varies considerably, even on different trees in the same general area. Many trees exhibit a slow general dieback, which begins at the branch tips and slowly progresses downward. This progressive dieback is sometimes accompanied by a progressive chlorosis and decrease in leaf size. Sometimes one or more major branches will die suddenly on trees exhibiting symptoms of progressive dieback or even on trees showing no obvious top symptoms. Another common type of symptom is sudden death of whole trees which previously had few or no evident symptoms. Some trees may produce epicormic shoots along the trunk and major branches after loss of all or most of their foliage. Some of these trees eventually die but others remain alive indefinitely.

Mortality of fine rootlets is common on declining trees, but rootlets greater than 5 mm in diameter seldom die until trees are in an advanced stage of decline. Few major roots die before the entire tree crown is dead.

The chronological and spatial development of decline in ohia forests on the island of Hawaii has been studied in considerable detail (Adee and Wood 1982; Mueller-Dombois 1981; Mueller-Dombois and others 1977, 1980). Seven types of decline were identified on the basis of forest structure, habitat and soil types, and regeneration patterns. Three of these decline types were recognized by both Mueller-Dombois and Adee and Wood, but different names were applied. In the following discussion, names used by Mueller-Dombois are shown without parentheses; those of Adee and Wood are enclosed in parentheses.

These types are discussed here only in general terms. Details of stand structure and lists of plant species encountered can be found in the references just mentioned as well as in publications by Jacobi (1983) and Burton and Mueller-Dombois (1984). Details of physical and chemical properties of the soils associated with declining sites are available elsewhere (Wood 1983).

Bog Formation Dieback (Stunted Ohia Wetland)

Bog Formation Dieback covers a large portion of the east flank of Mauna Kea (area 3), extending from the Wailuku River on the south to above Laupahoehoe on the north between about 610 to 1,460 m in elevation. The area most severely affected is circumscribed by the 7,500 mm isohyet, with the annual rainfall decreasing to about 4,375 mm at the upper limit of declining forests. The general topography of the area is a gentle slope broken by small to large hummocks, ridges, knolls, and cinder cones. Several small to large permanent stream channels cut through the area, but there is little or no gully type erosion.

The characteristic feature of this decline type is the large number of treeless bogs *(fig. 4)*. These bogs vary in size from a few hundred square meters to several hectares. They are larger and more numerous at elevations of 730 to 820 m, which probably represents the zone of highest rainfall. Vegetation consists mainly of *Juncus* and *Carex* with some *Sphagnum.* The introduced grass *Andropogon virginicus* is commonly found on both the treeless bogs and more open surrounding areas.

The ohia in the areas surrounding the bogs is generally unhealthy *(fig. 4)*, but amount of dieback varies considerably with elevation and topography. In the central part of the area at about 730 to 820 m elevation, on the gentle slopes, the ohia is usually of low stature and most trees are dead or in an advanced state of decline. Ohia on ridges and knolls are usually of larger stature, and while mortality and degree of decline are somewhat less than in the surrounding areas, most trees have an unthrifty appearance. The stature of the forest upslope and downslope from the central area increases, and the amount of mortality and degree of decline decreases. However, the forest even at the upper limit of the area is still considered to be in severe decline.

With one exception (area 4), the upper limit of the Bog Formation Dieback area merges abruptly at about 1,460 m elevation with the ohia-koa forest (area 5), which generally can be classified as healthy. Of interest is a large area of moderate declining ohia rainforest (area 4) extending downward from the ohia-koa forest into the severely declining area. The margin between these two areas is not clearly defined.

Dense vigorous mats of gleicheniaceous fern (mostly *Dicranopteris linearis*) occur in large patches in the Bog Formation Dieback area. Most of these appear to be rooted on hummocks or piles of debris. Associated woody vegetation is species poor, and generally unthrifty.

Ohia is maintaining itself in this area by vegetative reproduction from larger fallen trees and by limited seed reproduction on downed trees *(fig. 5)*. More than 50 of the young ohia are vegetative in origin. Scarcity of seedlings is probably due in large part to the thick mats of fern. Most young ohia are unthrifty in appearance, and there is some mortality.

Little is known about the soils associated with the Bog Formation Dieback type. Because access is difficult, few detailed soil studies have been attempted. Two soil types were identified in the Bog Formation Dieback type on Mauna Kea (Wood 1983). One was found in the area of highest rainfall on a site covered mainly with *Dicranopteris* spp. and dead and declining ohia. This soil type is characterized by a pan horizon 20 to 30 cm below the surface. The pan is 6 to 12 cm thick, red to grayish-brown, brittle, nonsticky when crushed, and not penetrated by roots *(fig. 6)*. Above the pan are two horizons of muck (undifferentiated whole or decomposed organic matter which is very wet and has little or no structural integrity) which are highly mottled, sticky, gritty, and with a strong hydrogen sulfide smell. The 01 horizon consists of mat-like *Dicranopteris* stems and rhizomes. No abnormal water conditions or mottling were noted below the pan and the horizon is typical of other moderately drained, deep, layered ash soils. The muck horizons were notable for low base saturation, high aluminum, and extremely high iron levels (>3,500 ppm). The pH varied between 4.8 and 5.2. Mueller-Dombois and others (1980) also described a similar hardpan formation at about 30 to 50 cm depth near the edge of the Bog Formation Dieback area in which the soil above the pan was saturated, but below it was drier.

The open bogs on Mauna Kea are characterized by a soil type *(fig. 7)* in which the first horizons are peat, 25 to 60 cm deep, and high in organic carbon, nitrogen, iron, and aluminum. The transition between the peat horizon and the first subsurface horizon is somewhat indefinite. The first subsurface horizon is composed of muck, is slightly darker than the surface, has a hydrogen sulfide smell which increases with depth, and frequently contains large quantities of ohia debris. The peat-muck horizon, which is about 1 m deep, probably sits on a deep, layered ash deposit. The water table persists at or near the surface year-round.

A few scattered wet sites on Mauna Loa were classified by Adee and Wood (1982) as Stunted Ohia Wetland because of the similarity in stand structure to that on Mauna Kea. These sites tended to occupy the lower topographic positions within lava flow complexes. The soils were very poorly drained, rather shallow, and had no restrictive pan horizons but were often underlain by impermeable basalt. At the basalt contact surface was frequently a pronounced gley horizon, indicating poor drainage conditions. The pH of the surface horizon was above 5, and base saturation was very low, but higher than in the bog soils on Mauna Kea.

The chronological development of Bog Formation Dieback is difficult to determine. Photographic records of this area before 1954 are not available. In 1954, a large part of the area now referred to as Bog Formation Dieback was classified as moderate decline (11-40 pct of the canopy dead or dying) with two small areas classified as severe decline (>40 pct dead or dying) (Petteys and others 1975). By 1965, almost the entire area was classified as severe decline.

Current evidence, however, points to a decline process going on for a much longer time. Scattered larger ohia and treefern among the mostly stunted forms now covering the central area are probably relics from a time when the sites were better drained. Numerous dead trees are lying on the soil surface or are partially covered by soil. Perhaps more importantly, considerable ohia debris can be found in the subsurface horizons of the treeless bogs. Although some boggy areas have large numbers of large, dead ohia, which could indicate a relatively rapid transition from closed canopy to bog, most data indicate a more gradual transition over a relatively long period of time. These observations are consistent with the speculation that several bog areas in Hawaii could have developed on level or slightly sloping land in areas of high rainfall after formation of impervious clay layers, above which the soil becomes saturated with water (Fosberg 1961). This pro-cess proceeds slowly with succeeding tree generations becom-ing shorter in stature as the accumulation of water becomes greater, and finally terminates in a low forest, shrub, or sedge bog vegetation. The area of Bog Formation Dieback may eventually evolve into a low stature ohia scrub similar to that described earlier for the Maui dieback area.

Wetland Dieback (Ohia Wetland)

Wetland Dieback is found predominantly on the east flank of Mauna Loa (area 8), between 460 and 1,585 m elevation. The affected area extends from the Wailuku River on the north to just south of the Stainback Highway on the south. Annual rainfall in the area varies from 3,125 to 6,250 mm. Some of the most severely affected areas occur within the lower rainfall limits. The general topography consists of more or less parallel lava flows of various ages. Some of these flows are considered to be "historic," i.e., they occurred within the time frame of recorded history.

The lava flows are generally of two types, pahoehoe and a'a *(fig. 8)*, although integration of the two forms occurs. Pahoehoe flows have a smooth or wrinkled surface and are of more or less the same consistency throughout; however, openings of various diameters and lengths (tubes) occur within the flow. Upon cooling, cracks of various widths and depths form in the surface. A'a flows have a rough, broken surface of lava fragments from a few centimeters to more than a meter in diameter. This broken surface covers a thick, solid interior. A'a flows are generally thicker than pahoehoe flows and the surface topography more uneven.

The consistency of the flows influence greatly the internal drainage through them. On a'a flows, the drainage through the fragmented surface area is rapid. On pahoehoe flows, drainage is limited to the cracks and tubes. On young flows drainage is apparently rapid; however, on older flows, organic material accumulates in the openings and may cause blockage and restrict drainage.

While typical flows of the two types may be readily identified, others may show characteristics of both types. When other factors are added, e.g., ash deposits of various depths, it becomes difficult to draw conclusions about the influence of substrate on drainage and tree growth from casual observations.

A characteristic feature of Wetland Dieback is the relatively rapid dying of high stature, closed ohia forests *(fig. 9)*. Some stands appearing healthy on 1965 photographs were in severe decline by 1972.

Another characteristic feature of Wetland Dieback is its association with the pahoehoe type of lava flow (Mueller-Dombois and Krajina 1968). There are several examples of parallel lava flows of the a'a and pahoehoe types in which the ohia stands on the a'a flows are relatively healthy while those on the pahoehoe flows are in severe decline.

The decline-healthy boundaries between such flows are sharp and apparently static *(fig. 10)*. We observed several cases in which the decline status of the two adjacent flows has remained the same since 1972, and one case in which no change has occurred since 1952, when the ohia stand on the pahoehoe flow was already in severe decline. In all cases we observed, the surface of the a'a flow was 3 to 6 m—and in one case more than 15 m higher than that of the pahoehoe, indicating that the a'a flow occurred later. This is contrary to the flows studied by Jacobi (1983), in which the a'a flow appeared to be partly covered by the pahoehoe. One interesting area involved a portion of an old pahoehoe flow of several hectares in size surrounded by an a'a flow *(fig. 11)*. The ohia stand on the pahoehoe flow was relatively healthy in 1965 but in severe decline in 1972. The surrounding stand on the a'a flow is still healthy.

Not all decline is found on pahoehoe sites, however. Patches of decline may occur on a'a flows (Mueller-Dombois 1980). These appeared to be in small poorly drained areas surrounded by well drained healthy stands.

Because aerial photographs of the wetland dieback are available for only a few years, the exact pattern of symptom progression cannot be determined with certainty. However, a more or less synchronous dieback apparently occurred over large areas, sometimes of several hundred hectares. And there is no evidence of advancing fronts—except possibly at the upper and lower limits of decline—or expanding centers that might be associated with diseases. In one area, what appeared to be a wide ancient pahoehoe flow has been dissected by two later flows (one historic, one prehistoric). The ohia forests on all identifiable segments of the old pahoehoe flow, including isolated kipukas (islands), declined more or less simultaneously *(fig. 9)*.

In the areas of most severe decline, mortality of ohia approached 100 pct over large areas. In other areas, however, mortality ranged from 60 to 90 pct, with the remaining living trees having significant crown loss *(fig. 12)*. In 1976, six transects were established on separate pahoehoe flows that had been in severe decline since 1965 or 1972. All trees that were alive at the time the plots were established were still alive in 1982, and a few appeared to be recovering. Similar observations were reported by Jacobi and others (1983), who found that plots established in 1976 showed no marked increase in decline in 1982.

In contrast to Bog Formation Dieback, the subcanopy vegetation is more diverse in Wetland Dieback, and much healthier. In some areas dense fern mats (mainly *Dicranopteris linearis)* are developing, but these are not so large or numerous as in the Bog Formation Dieback. Some of these mats appear to be declining in patches under developing ohia reproduction. Koa is invading Wetland Dieback areas on well drained microsites and appears to be quite vigorous.

Regeneration of ohia in the Wetland Dieback area is generally very good, and the seedlings and advanced reproduction are healthy *(fig. 13)*. Mueller-Dombois and others (1980) found adequate regeneration (>3,500 seedlings/ ha) in all nine releves sampled in this dieback type, with numbers of seedlings per hectare ranging from 3,834 to 26,792. Jacobi and others (1983) reported similar findings. Jacobi (1983) found that 79.4 pct of the subplots measured in one dieback area had ohia saplings 2 to 5 m tall, with a mean cover of 7.6 pct. Ohia reproduction dominates many of the ohia wetland stands but is variable and appears to be limited by dense fern mats and poor drainage on a few sites (Adee and Wood 1982). These factors may prevent the recurrence of a closed ohia forest on such areas, but the general prognosis for the wetland dieback area in this regard is good.

Some introduced plants are invading the Wetland Dieback area. In one study site (dieback and healthy) 20 pct of the plant species recorded were introduced and most of these were recorded only in the dieback stand (Jacobi 1983). However, none of those species encountered were considered a serious threat to native species. Mueller-Dombois and others (1980) found 2 to 12 species of introduced plants in releves sampled in dieback forests. Only *Psidium cattleianum,* which was found mainly at lower elevation sites, was considered to have the capacity to displace ohia.

Wood (1983) recognized two soil types in the Wetland Dieback, both of which were poorly drained. On both soils the surface horizon is generally muck situated in concave pockets of varying surface areas and depths. Both types are usually underlain by pahoehoe lava at various depths, usually at 50 cm or less. The irregular surface topography of the pahoehoe results in considerable variation in soil depth and drainage characteristics of the soils.

One soil has two or more distinct subsurface ash horizons which are high in organic matter, mottled, and have a weak to strong hydrogen sulfide smell. The other soil is always shallower with less ash (if any) in the profile, and has a strong gley horizon at the pahoehoe contact surface *(fig. 14)*. Both soil types are strongly acid, with very low base saturations, very high surface aluminum content, and often extraordinarily high aluminum values (>4,000 ppm) in the lower horizons.

Ohia Displacement Dieback (Ohia-Treefern Forest)

Ohia Displacement Dieback occurs in the Olaa Forest Reserve area on the east flank of Mauna Loa, at about 790 to 1,310 m elevation (area 13). Rainfall in the area varies from 2,500 to 3,750 mm. For the most part the topography consists of gentle slopes and the soils are relatively deep and moderately well drained. The area was previously covered by scattered, large-canopied trees with a dense subcanopy of treefern (*Cibotium* spp.), which still persists.

In 1954, most of the area was considered to be in slight decline, with a few scattered areas in moderate decline (Petteys and others 1975). By 1965, most of the area was in severe decline. Currently, a small strip between about 1,220 and 1,310 m elevation appears to be actively declining (area 14). In contrast to the Wetland Dieback, which occurs on lava flows oriented with the slope, this area of active dieback follows the contours, and is sharply delimited from the healthy ohia-treefern forest above. The name Ohia Displacement Dieback describes a dieback forest in which regeneration of ohia was prevented by the dense treefern subcanopy (Mueller-Dombois 1977). Unlike treeferns on Wetland Dieback and Bog Formation Dieback, the treeferns— as well as other subcanopy species— on this area were unaffected by the factor or factors responsible for decline of the ohia, and form an almost continuous closed canopy *(fig. 15)*.

Adee and Wood (1982) found that germination and establishment of ohia seedlings is not limiting under such conditions. Data of Burton and Mueller-Dombois (1984) also show that a significant number of ohia germinants (86/ 100 m^2) occur under dense treefern cover, although removal of various amounts of canopy increased the number. Both the above observations agree with Friend's (1980) laboratory study, which suggested that ohia seedlings will survive and grow under even lower radiation levels than those found in the rainforest. However, a closed treefern canopy apparently does constrain the developing ohia population by affecting

Figure 1—Stand of mature healthy ohia, island of Hawaii.

Figure 2—Severely declining stand of ohia on gentle slopes of Kohala Mountain, island of Hawaii. (Photo by Ed Petteys, Hawaii Division of Forestry and Wildlife.)

Figure 3—Short-stature ohia in Maui forest dieback area. Snags of trees that died in the early 1900's can be seen.

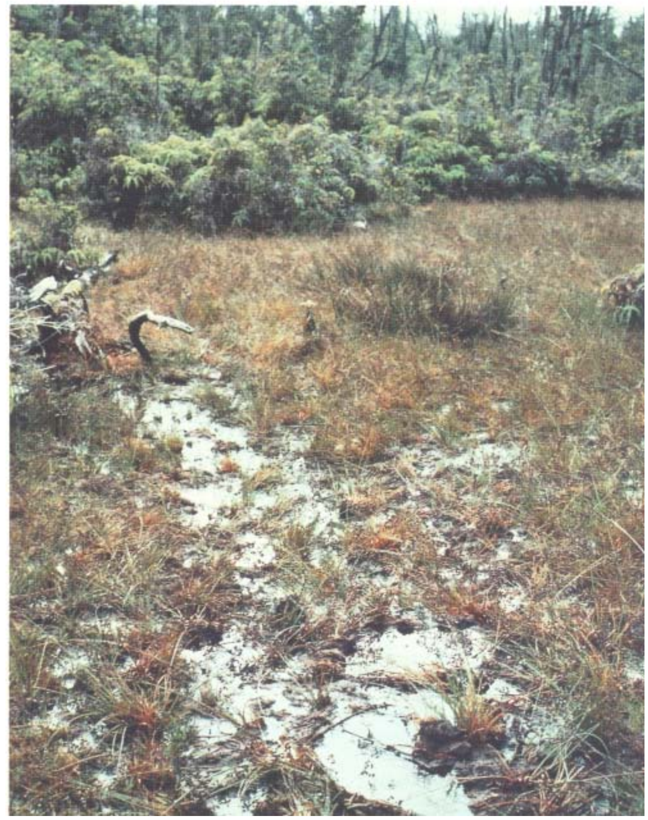

Figure 4—Treeless bogs are characteristic of Bog Formation Dieback. Note poor condition of the surrounding forest and heavy cover of *Dicranopteris linearis* in the understory.

Figure 5—Ohia reproduction is mainly vegetative in Bog Formation Dieback.

Figure 6—Water restrictive pan horizons are commonly associated with Bog Formation Dieback. A muck horizon less than 50 cm thick is seen above the hardpan, while below is a moderately drained horizon, typical of deep, layered ash soils.

Figure 7—Soil in open bog areas is characterized by a surface layer of peat 20-30 cm thick, above a muck horizon containing wood debris, which is above a relatively thin sticky gley horizon.

Figure 8—New lava flows of the pahoehoe (dark) and a'a (light) types differ in physical characteristics.

Figure 9—Large pahoehoe flow on Mauna Loa supports massive Wetland Dieback. This flow is bordered on both sides by a younger flow. Small kipukas (islands) showing similar damage are segments of the older larger flow, which were surrounded by the younger flow.

Figure 10—The boundary between declining ohia forest on pahoehoe flow (foreground) and healthy forest on a'a flow (background) is distinct.

survival to the sapling class (Burton and Mueller-Dombois 1984).

Two soil types were encountered in the Ohia Displacement Dieback area (Wood 1983). These deep soils are derived from volcanic ash and are highly leached. In the profiles examined, the lower boundaries were not reached at 1 m depth. Drainage was moderately good, although some indications of pan formation (fractured) were found in the lower horizons. The soils are strongly acid with low base saturation. Aluminum concentration is very high in the surface horizon and even higher (>3,000 ppm) in the lower horizons. A variant soil recognized in one plot has slightly poorer drainage with some mottling and presence of organic pockets in the surface horizons. Iron and aluminum concentrations are very high in the surface horizons.

The long-term outlook for ohia in the Ohia Displacement Dieback type is difficult to assess. Only a severe disturbance to the treefern canopy would result in the ohia size distributions characteristic of a closed ohia forest. Lacking that, some ohia probably will emerge from the more or less persistent bank of seedlings in treefern-dominated stands in openings created by falling ohia snags or treeferns. Young ohia saplings, apparently healthy, can already be seen scattered through the area. Eventually, an open ohia-treefern forest similar to the one above the current dieback forest should develop, but perhaps with fewer ohia.

Dryland Dieback

Dryland Dieback occurs on well drained shallow or deep soil habitats in pocket-like distributions or areas usually less than 0.5 ha in size in Hawaii Volcanoes National Park (Mueller-Dombois and others 1977). This type of dieback appears to be associated with dense stands. Annual rainfall in the area is less than 3,125 mm.

We also recognized a similar type of dieback, which we informally call "hotspots." These also occur in small pockets of 0.1 to 0.3 ha in otherwise healthy dense stands on well drained sites *(fig. 16)*. The boundaries between declining and healthy trees are sharp, but with few exceptions, no changes in topography or soil characteristics are discernible at these boundaries. All the trees within the area apparently died at about the same time and the areas have not increased in size in the 12 to 15 years since they were first noted on aerial photographs.

Variable amounts of advanced ohia regeneration occur in many of the Dryland Dieback and hotspot areas (Gerrish and Bridges 1984, Mueller-Dombois and others 1980). Ohia probably will eventually become reestablished on such sites.

Gap Formation Dieback

Gap Formation Dieback occurs on a number of ridges and knolls in the general area of the Bog Formation Dieback (Mueller-Dombois 1981). Such sites are generally elevated above the bogs and usually are covered with relatively tall-stature (over 15 m high) closed or open ohia forests. Formerly vigorous trees usually died in groups and showed no evidence of physical damage. Unlike the Bog Formation Dieback, ohia reproduction is often abundant in the gaps. Mueller-Dombois (1984) suggested Gap Formation Dieback may be equivalent to the Ohia-Koa Dieback type of Adee and Wood (1982).

(Ohia-Koa Dieback)

Ohia-Koa Dieback occurs on the lower slopes of Mauna Kea and extends from the Bog Formation Dieback down to the cane fields (area 6) (Adee and Wood 1982). The transition from Ohia-Koa Dieback to Bog Formation Dieback is rather broad and poorly defined. This is in contrast to the rather sharp transition between the upper limit of the Bog Formation Dieback area and the upper elevation ohia-koa forests, which are relatively healthy. Annual rainfall in the area ranges from 5,000 to 7,500 mm. Drainage varies considerably, but most of the area is considered to be moderately well drained to somewhat poorly drained, with scattered poorly drained areas of variable sizes scattered throughout.

The stands consist of a more or less equal mixture of ohia and koa, with ohia dominating in some areas and koa in others. Dieback in the area is quite variable and affects both ohia and koa. The entire area is currently classified as moderate decline but in reality the area consists of a mosaic of small groups of dead trees interspersed with trees in various vigor classes. Subjectively rating an area of this type is difficult, but it is generally in fairly good health and should be considered on the lower end of the moderate decline scale. Development of decline in the area has been slow, and except for small localized areas, has changed little since 1954.

The subcanopy tree species are typical of other moderately well drained sites and are little affected by loss of the canopy. However, the area has a high population of feral pigs whose rooting activity is seriously affecting the area. Disturbed areas are being invaded by grasses, especially *Setaria palmifolia,* which may limit development of both ohia and koa seedlings. Regeneration is limited in some areas almost entirely to downed trees and hummocks of organic debris. Pig activity may also directly disturb the root systems of both large and small ohia and koa. In the areas just above the cane fields, *Psidium cattleianum* forms extremely dense thickets, which exclude ohia and koa regeneration.

The two soils identified in the Ohia-Koa Dieback are the same as those found in Ohia Displacement Dieback. The soils in the two areas probably were derived from different ash deposits, but no major differences between the two areas were apparent with the limited sampling done.

The prognosis for the Ohia-Koa Dieback area is not clear. Decline in the past has proceeded somewhat slowly and may continue to do so in the future. Not enough information on soil development is available to allow speculation on why impervious hardpans are forming in the Bog Formation Dieback area and not in the Ohia-Koa Dieback area. Formation of impervious pans in the future with the subsequent bog formation in these areas of high rainfall could lead to successional characteristics similar to those of Bog Formation Dieback. A continued high level of pig activity in the area will severely impact ohia and koa regeneration even in the absence of dieback. Continued encroachment of *P. cattleianum* from downslope will also impact ohia and koa regeneration.

(Pubescent Ohia Dieback)

Pubescent Ohia Dieback occurs on a single lava flow just south of the Saddle Road between 1,220 and 1,370 m elevation (area 9) (Adee and Wood 1982). Rainfall in the area varies from 3,500 to 4,500 mm annually. The lava flow is of the. a'a type overlaid by a shallow organic muck, which is apparently well drained throughout the area of dieback.

This particular stand is characterized by a canopy of ohia with pubescent leaves rather than one with glabrous leaves that occurs in other dieback types. Mueller-Dombois and others (1980) suggest that ohia, which is one of the original colonizing species on new lava flows as well as the climax species, occurs as successional races or ecotypes that occupy the roles of pioneer, seral, and late seral dominants, and that Pubescent Ohia Dieback may represent the changeover from one seral type to another. Stemmerman (1983) found that pubescent ohia may represent the colonizing form. The observations of Adee and Wood (1982) support this theory. Trees in the Pubescent Ohia Dieback area are of relatively small stature with a small range of diameters. Floristic remnants of pioneer vegetation of young lava flows, e.g., *Heyotis centrathoides, Dubautia scabra*, and *Styphelia tameiameiae* occur in the subcanopy, indicating that the stand is still going through its primary successional phase. Many of the surviving canopy trees and the majority of the abundant smaller ohia are quite vigorous. If the canopy trees surviving continue to develop normally, they may come to dominate and form a healthy open stand.

Mueller-Dombois (1984) suggested that Pubescent Ohia Dieback may correspond to his Dryland Dieback because of its occurrence on well drained sites. Pubescent Ohia Dieback differs, however, in not being confined to small, more or less circular areas.

Wood (1983) characterized the soil in the Pubescent Ohia Dieback area as having 0.0 to 7.5 cm of organic muck over fragmental a'a lava *(fig. 17)*. The surface horizon is strongly acid with low base saturation. Aluminum is high, but generally lower than for other dieback soils. Iron is also high, and calcium levels are among the highest recorded on any of the soils studied. Although the surface horizon is shallow, the effective rooting depth is somewhat greater. Roots may penetrate 0.5 m or more into the fractured a'a lava, which also contains some organic material in the voids between the fragments. No significant differences between physical and chemical soil characteristics could be found between dieback areas and nearby healthy areas.

Watershed Values

In areas of severe decline, 90 pct or more of the ohia canopy may be dead. Such areas are not denuded of vegetation, however. Subcanopy species and litter provide ground cover for perhaps 95 pct of the area (Adee and Wood 1982). Loss of a major portion of the canopy may be expected to reduce evapotranspiration and thereby increase runoff, which in turn might increase sedimentation and reduce water quality. The limited long-term water quantity and quality records for streams draining the area of severe decline, however, preclude determining whether ohia decline has had a significant adverse impact on watershed values.

Limited data on precipitation, streamflow, and sedimentation are available from 1929 to 1980 for the Wailuku River, which drains a portion of the decline area. Before 1954, ohia forests on the Wailuku River watershed showed only slight to moderate decline, but by 1972 they had deteriorated significantly (Petteys and others 1975). Doty (1983) compared annual streamflow relative to precipitation before decline (between 1939 and 1955) and after decline (between 1956 and 1978), floodflow before and after decline, and evaluated current water quality in terms of suspended sediments and certain chemical constituents.

The ratio between precipitation and runoff did not differ before and after decline. Analysis of the precipitation-runoff relationships after storms showed that the percentage of precipitation occurring as runoff was higher for the period before decline than it was after decline. However, even with the lower absolute volume after decline, runoff occurred at a faster rate with a higher peak per unit precipitation. Any changes in flooding could not be related to presence of decline.

No data were available for suspended sediments in downstream water before the advent of forest decline. However, the amount of suspended sediments in the Wailuku River and Honolii Stream, which also drains a decline area, was well within the range of the sediment load of six healthy forested watersheds studied on Oahu (Doty and others 1981). Chemical components of the Wailuku River and Honolii Stream between 1976 and 1979 remained well within acceptable levels. Although the Wailuku River and Honolii Stream watersheds represent only a relatively small part of the affected area on the windward slopes of Mauna Kea, decline of the ohia forests apparently has had little, if any, adverse effect on streamflow and water quality. Reduced evapotranspiration and fog drip resulting from loss of the ohia canopy may have been offset by increased growth of subcanopy species.

Few permanent streams are in the decline area on the slopes of Mauna Loa, and none reach the ocean by surface flow. Although some of the decline sites show evidence of impeded drainage, excess runoff—if any—can rapidly infiltrate the porous substrates downslope from the decline area and reach the ocean through underground channels.

Rare and Endangered Plant Species

Mueller-Dombois and others (1980) recorded several rare and endangered plant species included in the list of Fosberg and Herbst (1975) from various dieback areas. However, their relative abundance was not compared with that in healthy stands. Although no data are available on predecline populations of these species, decreases in the amounts of closed forest habitat, especially within Bog Formation Dieback and Wetland Dieback, may have resulted in the loss of some taxa.

Populations of Forest Birds

Ohia decline, at least in the large area of Bog Formation Dieback on the east flank of Mauna Kea, significantly affected populations of native and introduced bird species. When compared with adjacent tall closed ohia forests, decline sites had 70 pct fewer 'Apapane *(Himatione sanguinea sanguinea),* 77 pct fewer 'I'iwi *(Vestiaria coccinea)*, 47 pct fewer Hawaiian Thrush *(Phaeornis obscurus obscurus)*, and 93 pct fewer 'Elepaio *(Chasiempis sandwichensis sandwichensis)* (Scott and others, in press). On the other hand, the populations were larger in decline areas for two introduced species, the Red-billed Leiothrix *(Leiothrix lutea)* (30 pct higher) and the Japanese White-eye *(Zosterops japonicus)* (34 pct higher). Such changes in bird populations undoubtedly were caused by loss of the ohia canopy.

No mention was made of influence on bird populations on the Mauna Loa decline area so presumably no significant differences were noted.

ETIOLOGY

Research on the possible causes of ohia decline has generally followed two lines: (1) decline may be due to attack by insects, pathogenic organisms, or both; and (2) decline may be related to certain ecological and environmental factors within the normal developmental phases of the ecosystem.

Insects and Pathogenic Organisms

Several insects and pathogenic fungi have been investigated as possible causes of ohia decline. Among the insects considered, only the two-lined ohia borer *(Plagithmysus bilineatus)* received significant attention. The ohia psyllids (*Trioza* spp.) and two scolytids *(Xyleborus similis* and *X. saxeseni)* were dismissed early from possible involvement in the decline syndrome (Samuelson and Gressitt 1976).

Several fungi, *Phytophthora cinnamomi, Armillaria mellea, Pythium vexans,* and *Endothia metrosideri* have been suggested as possibly being implicated in ohia decline, but only *P. cinnamomi* has been studied in detail.

Plagithmysus bilineatus

Plagithmysus is a genus of endemic Hawaiian cerambycid wood borers believed to have evolved from a single immigrant ancestor species from the southwest United States or Mexico (Gressitt 1978). Currently, 136 species are recognized. Hosts are known for more than 90 pct of the species, and over 93 pct of these are recorded from a single genus of host plant. Although closely related species occur on different islands and often have the same host association, no one species occurs on more than one island.

Plagithmysus spp. are associated primarily with living plants, and females may lay eggs on the bark of apparently healthy trees. Little is known, however, about the relationship of tree vitality to success of attack.

The two-lined ohia borer *(fig. 18)*, is commonly associated with declining trees (Papp and Samuelson 1981). It is 1 of 10 *Plagithmysus* spp. believed to be associated with *Metrosideros* spp. in the Hawaiian Islands, and 1 of 2 on the island of Hawaii. Its only host is *M. polymorpha*, but the insect is widely distributed on the island (Stein 1983) *(fig. 19)*. *Plagithmysus abnormis* was also reported from *Metrosideros* on Hawaii (Gressitt and Davis 1969), but its biology is unknown. It was not encountered during studies on ohia decline.

Papp and others (1979) studied the association of *P. bilineatus* and the root fungus *Phytophthora cinnamomi* with ohia trees on 100-tree transects on several sites, both within and outside the area of intensive decline. The roots of 40 trees on each transect were examined to determine the degree of necrosis, and sections were cultured for the presence of *P. cinnamomi*.

Larvae of *P. bilineatus* were found on declining trees at each site. The percentage of trees infested as well as frequency of attack was greater on trees with the poorest crown conditions. However, 14 pct of the apparently healthy trees were attacked, and 25 pct of severely declining trees were not attacked by *P. bilineatus*.

Most galleries of *P. bilineatus* in standing trees were abortive, containing only dead larvae or pupae (Papp and Samuelson 1981). Percentages of galleries with living larvae or pupae in standing trees varied from 4.3 to 30.0 pct and averaged 11.4 pct. In slash of previously felled trees, on the other hand, 89 pct of galleries contained living larvae or pupae. Successful attack (those in which larvae pupated) was much higher in severely declining trees (31.1-35.3 pct) than in apparently healthy trees (2.0-4.8 pct).

The results of the transect study indicate that *P. bilineatus* apparently prefers declining trees as oviposition sites. Other studies support this conclusion. Papp and Samuelson (1981) found that *P. bilineatus* adults are rapidly attracted to felled trees, sometimes within a few hours of felling, even in healthy forests. Nagata and Stein (1982) used guy wires to brace several healthy trees in an upright position before severing them at the base. The saw kerf was sealed and all traces of sawdust were removed. The severed trees as well as adjacent uncut trees were sprayed with tanglefoot adhesive to trap any adult beetles attracted to the trees. Beetles were attracted to all cut trees before the trees showed any visual symptoms of stress. Beetles were not attracted to adjacent control trees. Survival of larvae increased from 10 pct in healthy trees to 83 pct in severed trees (Stein and Nagata 1985). The attraction of beetles to severed trees apparently was a specific response to chemical stimuli produced by physiological changes taking place after severing. Similar changes presumably occur in declining trees as well. Beetle preference for oviposition on stressed trees may provide a mechanism whereby larvae have a greater chance of survival.

Plagithmysus bilineatus is probably not the primary incitant of ohia decline. This insect may, however, hasten the death of stressed trees or cause the death of stressed trees that otherwise might have recovered. Galleries of beetle larvae are confined to the cambium-phloem tissue or to the outermost sapwood. These galleries typically spiral around the tree trunk or branches in barber-pole fashion and commonly reach lengths of 2 m or more *(fig. 20)*. Such galleries effectively girdle the stem or branch, which may result in the death of some trees or portions of trees. The number of declining trees that might have survived in the absence of attack by the ohia borer has not been determined, however.

The ecological niche of *P. bilineatus* in the ohia forests on the island of Hawaii includes the spectrum from apparently healthy trees to living trees under some kind of stress (Papp and others 1979). In forests without decline, the insect attacks apparently healthy, overmature, or suppressed trees, or individual trees weakened by adverse localized conditions. However, a preferential attraction to stressed host material is evidenced by the rapid appearance of adult beetles on cut trees in healthy forests (Nagata and Stein 1982, Papp and Samuelson 1981). The same behavior may be shown in the initial or latent phases of ohia decline. As decline intensifies, attacks become more numerous in the progressively weakened trees. Where trees decline somewhat rapidly and synchronously over an extensive area, the available opportunet substrates for oviposition may exceed the resident female population, and a certain proportion of declining trees will escape attack.

Phytophthora cinnamomi

The fungus *P. cinnamomi* is widely distributed and reportedly is pathogenic to a large and diverse variety of plant species (Zentmeyer 1980). Of particular relevance to ohia decline is the implication of *P. cinnamomi* in several dieback and decline type diseases, including these: littleleaf disease of shortleaf pine in the southeastern United States (Zak 1961), jarrah dieback in western Australia (Podger 1972), dieback of *Eucalyptus* spp. in eastern Australia (Weste and Taylor 1971), and rainforest dieback in Queensland, Australia (Brown 1976).

Phytophthora cinnamomi was first reported from Hawaii in pineapple fields on Oahu (Sideros and Paxton 1930). The fungus subsequently was found on a wide variety of hosts on the other major Hawaiian Islands. Before its possible implication in ohia decline, only Mehrlich (1936) had reported it in the forests of Hawaii.

Kliejunas and Ko (1973) were the first to recover *P. cinnamomi* from roots of ohia. The fungus was isolated from necrotic rootlets from declining ohia on wet sites but not from healthy or declining ohia on dry sites. Bega (1974) also recovered *P. cinnamomi* from roots of declining ohia as well as those of several associated species. Kliejunas and Ko (1976a) found the fungus in roots of declining trees in 32 of 35 decline areas sampled and occasionally from healthy trees in declining and healthy forests. It was also recovered from soil in 72 of the 75 decline sites sampled and from 13 of 15 sites on which trees were apparently healthy.

Further studies (Kliejunas and others 1977) showed *P. cinnamomi* to be widely distributed in the native forests on the other major Hawaiian Islands *(fig. 21).* The presence of the fungus was correlated with wet soils but not with health of the forest canopy, or subcanopy density or composition. It was isolated from 97 pct of the poorly drained sites on all the islands, regardless of the presence of decline, but not from excessively drained sites. The fungus was commonly recovered on Maui (Kliejunas and others 1977) from the area where severe decline occurred in the early 1900's (Lyon 1909). Currently, this area supports a sparse, low stature ohia forest in a relatively good state of health.

In areas where sharp boundaries exist between adjacent declining and healthy forests, such as those described in the section on Wetland Dieback *(figs. 8 and 9),* little difference can be found in populations of *P. cinnamomi* between healthy and declining sites (Hwang and Ko 1978b, Kliejunas and Ko 1976a).

Papp and others (1979) analyzed trees on each of eight sites with varying degrees of decline for rootlet mortality and the presence of *P. cinnamomi.* They found that *P. cinnamomi* was present on 80 pct or more of the trees on the two sites with the greatest decline and the highest percentage of rootlet mortality. These two sites were also the most poorly drained. On the sites with less decline, rootlet mortality was less but was not related to presence or absence of *P. cinnamomi.*

In addition to ohia, *P. cinnamomi* has been isolated from roots of a large number of indigenous, endemic, and introduced species associated with ohia (Bega 1974, Kliejunas and Ko 1976b). The health of these associated species was not detailed, although some species had decline symptoms (Kliejunas and Ko 1976b).

Seedlings and small plants of some species are susceptible to *P. cinnamomi* when artificially inoculated. Kliejunas (1979) compared the relative susceptibility to *P cinnamomi* of ohia and several other endemic and introduced species. In this study ohia was judged to be moderately susceptible to the fungus while the other endemic species tested were highly to moderately tolerant. *Eucalyptus sieberi, E. baxteri,* and *E. marginata,* reported to be highly susceptible in Australia (Podger 1972, Weste and Taylor 1971) were also susceptible in Hawaii.

Current knowledge on the relationship of *P. cinnamomi* to ohia decline can be summarized as follows:

- The fungus has wide distribution in the native rainforests on all the major Hawaiian Islands. Although it has been recorded in Hawaii only since 1925, it probably has been present for much longer. The fungus may be indigenous to the islands because of the relative tolerance of most of the endemic plant populations (Kliejunas 1979). It is found in remote roadless areas but could have easily been spread there by the activity of feral pigs, which are numerous in the

Hawaiian rainforests. The fungus has been recovered from the feet of feral pigs (Kliejunas and Ko 1976b). Surface movement of water during heavy rains also could result in rapid spread.

• Although *P. cinnamomi is* commonly associated with declining ohia on the island of Hawaii, it is also present in apparently healthy ohia forests on Hawaii and other islands. Thus, there is no constant association between the presence of *P. cinnamomi* and ohia decline. Rootlet mortality on declining ohia is usually high and *P. cinnamomi* can be isolated from dead and dying rootlets. However, rootlet mortality could also result directly from poor drainage and subsequent low soil aeration characteristic of most decline sites, as well as from other factors. *Phytophthora cinnamomi* can colonize pieces of ohia shoot tissue (2 mm in diameter) placed in infested soil, so rootlets killed as a result of poor soil aeration or other factors possibly could later be colonized by the fungus (Hwang and Ko 1978a). The fungus was also isolated after 1 year from 50 pct of the artificially inoculated ohia root pieces buried in the soil, demonstrating its saprophytic competitiveness.

• *Phytophthora cinnamomi* has been isolated from a wide variety of native and introduced plant species in Hawaii. In inoculation studies that used seedlings or small plants, ohia was determined to be "moderately susceptible" to the fungus when levels of inoculum were high. Seedlings grown in soils from decline areas with lower natural levels of inoculum had less root necrosis and no significant growth loss. Associated native plants were found to be even less susceptible. Large numbers of ohia seedlings and saplings are present on many sites where mortality of the ohia overstory was 75 pct or more and where *P. cinnamomi* was present in relatively high populations. These seedlings and saplings are growing vigorously and display no crown symptoms.

The exact role of *P. cinnamomi* in the ohia decline syndrome is difficult to determine. It appears unlikely, however, to be a primary factor in initiation of the problem. The fungus probably plays a secondary role, attacking rootlets of trees already under stress, and contributes to a greater or lesser degree to the overall decline sequence.

Armillaria mellea

The root fungus *Armillaria mellea is* distributed worldwide in temperate and tropical regions and attacks a wide range of hosts. The fungus has been known to occur in Hawaii since 1963 (Rabbe and Trujillo 1963), when it was reported to have attacked several *Pinus* spp. on land cleared of native forest. The fungus later was reported to occur on ohia and other native and introduced tree species (Burgan and Nelson 1972, Laemmlen and Bega 1974).

We have observed *A. mellea* to be widely distributed throughout the decline area in areas above approximately 1,200 m elevation, on both dead ohia trees and those exhibiting symptoms of decline. However, it was not consistently associated with declining trees. In some areas, as many as 80 pct of dead and declining trees had typical mycelial mats of the fungus, while in nearby areas severely affected by decline, the fungus could not be found. These observations indicate that *A. mellea* cannot be considered a primary cause of decline, but almost certainly contributes to mortality of declining trees in areas where it is present. A similar role for *A. mellea* has been proposed in several dieback and decline diseases in the Eastern United States (Houston 1973).

Pythium vexans

Pythium vexans is widely distributed on the island of Hawaii, and has been isolated from roots of declining ohia trees (Kliejunas and Ko 1975). The fungus was pathogenic to ohia in greenhouse inoculation studies, causing root necrosis or seedling death or both. However, the fungus also occurs in areas supporting healthy ohia forests, and could not be recovered from all areas exhibiting severe decline. *Pythium vexans* probably plays no major role in ohia decline, but some minor root necrosis and contribution to the overall decline syndrome cannot be discounted.

Endothia metrosideri

Roane and Fosberg (1983) described a new fungus, *Diaporthopsis metrosideri*—later changed to *Endothia metrosideri* (Barr 1983)—from recently dead ohia trees in Hawaii Volcanoes National Park. Later, Fosberg (1983) speculated that the fungus was pathogenic to ohia and suggested that it posed a serious threat to this species. However, no inoculation studies to confirm pathogenicity have been carried out thus far. Even if *D. metrosideri is* pathogenic, any connection with ohia decline is doubtful. Fruiting bodies of the fungus are fairly conspicuous, and we have not observed them. on dead or declining trees in the major decline areas.

Climatic, Edaphic, and Environmental Factors

Rainfall

Petteys and others (1975), in their initial survey for ohia decline, found a correlation between rainfall and ohia decline index in each of 3 years (1954, 1965, and 1972) for which estimates were made. Decline index, on the basis of canopy loss, increased as precipitation increased. A similar correlation was found between increase in elevation and increase in decline index. This correlation is consistent with the occurrence of generally higher rainfall at the midelevations, where decline is most severe; however, regressions of decline index on precipitation and elevation for each of the 3 years showed that they explained only 4 to 9 pct of the variation. Precipitation and elevation are probably not the limiting factors in the decline problem.

Doty (1982) studied the precipitation records from the southeastern and windward sides of the island of Hawaii between 1890 and 1977. Although a consistent long-term downward trend in precipitation was noted for the windward side of the island where ohia is declining, relationships between patterns of precipitation and occurrence of decline were not significant.

Analysis of climatic data from the ohia decline area by Evenson (1983) for the period 1891-1982 showed a large fluctuation in relative water availability, compared with that during the median year. Such fluctuations could produce either flooding or drought conditions across the decline area, depending on soil conditions. While the unusually wet years in the middle to late 1950's and the dry years 1958-59 and 1962 could have contributed to development of Wetland Dieback and Dryland Dieback, respectively, Evenson concluded that much more information is necessary before the exact role of climate can be determined.

Nutrition and Toxicity

Kliejunas and Ko (1974) applied various combinations of fertilizer treatments to single trees in intermediate or advanced stages of decline and to plots containing trees in various stages of decline. Treatment of individual trees with complete fertilizer resulted in production of numerous new leaf buds after 6 weeks, and new vigorous healthy leaves after 3 months. Foliar applications of nitrogen, phosphorus, and potassium (NPK) plus a micronutrient solution also resulted in new buds and leaves, but fewer than resulted from ground application. The new growth produced in response to the fertilizer applications remained vigorous after 1 year.

In a separate study, declining trees responded to both complete fertilizer and NPK with micronutrients, but not to N, P, K, or micronutrients alone (Kliejunas and Ko 1974). Trees showed some response to NP but not to NK or PK.

In plot studies with small trees, application of complete fertilizer resulted in development of numerous new buds on trees in all stages of decline, and fertilized trees were still producing new buds 11 months later. When larger trees were fertilized, only a few new buds were visible after 3 months. However, 4 months after a second application, a definite response was evident.

When fertilizer was applied in combination with various nematicides and fungicides (Nemagon, Difolitan, Benlate, or Dexon)[3] (Kliejunas and Ko 1976a), response of declining trees to fertilizer alone was similar to that in a previous study (Kliejunas and Ko 1974); but no response was obtained with any of the nematicides or fungicides. However, fertilizer plus fungicides resulted in greater response than did fertilizer alone.

Most of the trees used in the above-mentioned experiments were small (less than 2.5 m high) and were growing on relatively young historic lava flows. Whether the response of these young trees to fertilization can be extrapolated to trees in high stature ohia forests suffering severe decline is uncertain at best.

Gerrish and Bridges (1984) established in 1979 a combination thinning-fertilization treatment in three closed mature ohia forests on well drained sites (two on pahoehoe substrates and one on eutrophic ash). At each site, trees with partial foliage loss (10-60 pct) were selected for fertilization or release from competitors or both. Fertilized trees received NPK fertilizer of 16-16-16 composition at the rate of 784 kg/ha in 1979 and three additional applications of 392 kg/ha of Keaau 19 (approximately 12-27-7 plus micronutrients) in 1981 and 1982. The mortality rate of treated trees $2^1/_2$ years after the first application of fertilizer was no lower than that of the untreated trees. However, application of fertilizer at two sites and fertilizer plus thinning at the third site significantly increased mean annual diameter growth. These increases, however, were small—less than 2 mm over the controls.

Little information is available on the nutrient status of soils in the ohia decline area. Wood (1983) did not find any consistent differences between declining and healthy sites. In general, the levels of all nutrients were low in all soils examined. Nitrogen levels varied from 1.2 to 2.1 pct in the surface horizons but generally were less than 0.5 pct in lower horizons. Phosphorus varied from 3 to 28 ppm in the surface horizons but was seldom more than 8 ppm in the lower horizons. Potassium levels ranged from 64 to 488 ppm in the surface horizons but were generally less than 200 ppm. Levels in lower horizons were usually less than 70 ppm. Levels of calcium (284-3,011 ppm) and magnesium (67-497 ppm) were variable in the surface horizons. Manganese levels were generally low (6-30 ppm) but occasionally were high (78-232 ppm). Aluminum—extracted at pH 4.8—also varied, with the surface horizons containing from 272 to 1,578 ppm. Unlike other elements, however, aluminum levels increased dramatically in the lower horizons, sometimes reaching levels of more than 4,000 ppm.

All of the soils studied had relatively high cation exchange capacities, but low base saturation percentages. Organic carbon contents in surface horizons were high (16-68 pct), suggesting limited microbial activity on most sites. Most of the soils had very low bulk densities (0.1-0.2 g/cm^3) and high water-holding capacities (80-90 pct by volume), regardless of the parent material (ash, basalt, or organic). Upon drying, soil shrinkage can be more than 70 pct of its original volume.

Foliar nutrient levels in healthy ohia differed little among sites and soil types (Mueller-Dombois 1981, Wood 1983). Levels generally were 5,600 to 7,500 ppm for nitrogen, 800 to 1,200 ppm for phosphorus, 4,500 to 7,500 ppm for potassium, 3,500 to 3,800 ppm for calcium, 1,200 to 1,500 ppm for magnesium, and 19 to 23 ppm for aluminum. Differences in foliar nutrient levels between healthy and declining trees were not consistent, although aluminum levels from selected declining and dead trees were up to three times higher than those in healthy trees. Preliminary data of Mueller-Dombois (1981) indicate that concentrations of most elements tend to decrease in leaves of declining trees but that aluminum and manganese increase.

Wood (1983) found that aluminum concentrations in ohia roots were up to 20 times greater than levels in leaf tissue. Smaller roots (<5 mm in diameter) contained greater amounts of aluminum than did larger 5- to 10-mm roots. Roots of one declining tree had an aluminum concentration of 977 ppm, but concentrations in some healthy trees

[3]This report neither recommends the pesticide uses reported, nor implies that they have been registered by the appropriate governmental agencies.

exceeded 700 ppm, and no consistent pattern between aluminum concentration and health of tree was evident.

The high levels of aluminum found in the roots of ohia trees could affect the uptake of other nutrients by the tree and further aggravate the poor nutritional status of the tree due to low levels of nutrients in the soil. The levels encountered also could be potentially toxic to fine feeder roots. Death and blackening of such roots commonly associated with declining trees are similar to symptoms associated with aluminum toxicity in other plants (Foy 1971).

More data on both soil and foliar nutrient levels are needed before any definitive conclusions can be reached concerning the relationship between nutrition and ohia decline. Even though both soil and foliar nutrient levels are low in most cases, they are not low enough to have caused the massive death and decline of the ohia forest. Except possibly for certain metals like aluminum, a sudden change in nutrient status that would account for the relatively rapid decline is not likely. However, the generally low nutrient status of the ohia forests possibly could make the trees more vulnerable to other stresses and thus play a secondary role in the decline syndrome.

Soil Drainage

The association of some types of ohia decline with poor soil drainage is well documented. Bog Formation Dieback and Wetland Dieback, which make up more than 80 pct of the area in severe decline (map, *table 1*), are both characterized as being on poorly to very poorly drained sites (Adee and Wood 1982, Mueller-Dombois and others 1980). These decline types also generally occur in areas of the highest rainfall on the island, although portions of the Wetland Dieback occur on more mesic sites. Most of the mortality in the Ohia-Koa and Dieback Gap Formation Dieback types is also associated with poorly drained sites. Ohia Displacement Dieback and Pubescent Ohia Dieback, which also contain areas classified as being in severe decline, occur on moderately to well drained substrates. However, these two types make up only a small percentage of the total area in decline.

The drainage characteristics of the various soils that support healthy and declining ohia forests—for the most part—have been subjectively estimated on the basis of such visual parameters as soil color, structure, vegetation, and topographic position. Doty (1981), however, established wells consisting of 2.5-cm diameter tubing to study the relationship of groundwater levels to ohia decline. The wells were installed at seven locations, each of which contained two to nine individual wells. These locations represented a wide range of soil conditions and vegetation, and included both healthy and declining ohia forests. Ground water levels in the wells were observed weekly, and the weekly high level was determined by the adherence of finely ground cork on a wooden dowel placed in the well.

One year after installation of the wells, water levels in the individual wells fluctuated considerably, sometimes even among wells in the same location. In general, however, the organic muck soils that supported severely declining trees were saturated to within 5 to 10 cm of the surface more than 50 pct of the time. Some wells had water levels at this depth more than 90 pct of the time. On healthy sites over pahoehoe lava, water levels were lower than 22 cm 90 pct of the time. On a'a lava sites, the water level was never less than 36 cm below the soil surface, regardless of whether the site supported healthy or declining forests.

Wood (1983) continued to monitor the wells installed by Doty for an additional 1½ years. These new data generally confirmed the high variability previously reported by Doty (1981). The wells were excavated at the end of 2½ years to enable better characterization of the microsite conditions at each well. Water levels were charted for four wells on soils that were representative of those on which the major types of decline are found *(fig. 22)*.

Water levels on the very poorly drained bog soils, where all the Bog Formation Dieback sites are located, were at or above the surface 90 pct of the time *(fig. 22A)*. Little difference was apparent between the highest and average weekly water levels.

The mean water level typical of Wetland Dieback was only 7.6 cm below the soil surface and above-surface water levels, which occurred during storm periods, were common *(fig. 22B)*.

On the deep ash, moderately well drained soils typical of the Ohia-Koa and Ohia Displacement Diebacks, ground water levels rarely stayed near the soil surface for long periods of time. An example from one of the shallower ash soils *(fig. 22C)* shows that ground water levels remained more than 30 cm below the soil surface 90 pct of the time.

Most of the healthy sites sampled were on better drained sites; however, both Pubescent Dieback and Dryland Dieback also occur on well drained soils. The ground water levels in these well drained soils were usually well below the soil surface *(fig. 22D)*, although the highest water level attained during any weekly period occasionally reached the surface or exceeded it. Even during storm events, these periods of high ground water periods were brief, never lasting beyond the duration of the storm.

Within the scope of the study established by Doty (1981), no healthy ohia forests were sampled on the more poorly drained sites, and certain dieback types were associated only with continuously high ground water levels. While the exact role of drainage or high water levels has not yet been clarified, the poor drainage conditions associated with declining ohia on most areas could severely affect root functions and subsequent tree vigor and health.

Synchronous Cohort Senescence Theory

Early in the course of research on ohia decline, Mueller-Dombois (1974, p. 10) suggested that pathogens were not the primary cause of the problem, even though they may be involved as secondary agents that operate after tree vigor is reduced by some other cause. Instead, he proposed ". . . that the ohia dieback is a normal phenomenon, a developmental stage in primary succession of an isolated rainforest ecosystem." This hypothesis developed in succeeding years (Mueller-

Dombois 1980, 1981; Mueller-Dombois and others 1977, 1980) and recently culminated (Mueller-Dombois 1982, 1983, 1984; Mueller-Dombois and others 1983) in a theory termed "synchronous cohort senescence." In this theory, a generally even-age or even-stature stand of ohia (cohort) results from a catastropic disturbance such as a lava flow, ash deposit, or hurricane. Seed for regeneration comes from adjacent stands. The stands develop and eventually reach maturity, after which senescence begins. Different forms or manifestations and lengths of senescing periods may be programmed into the life of certain species or may be manifested differently in the same species when it grows on different habitats and under different environmental stresses (Mueller-Dombois 1984). Inherent in this concept is the possibility that environmental factors may affect the initiation of senescence (Mueller-Dombois 1983), which in some cases may be reversible (Mueller-Dombois and others 1983).

For synchronous dieback of the ohia cohort to occur, a second disturbance is necessary after the onset of senescence. This disturbance could be a fluctuating site factor such as a storm, temporary flooding, or soil drought, which might not seriously affect a vigorously growing stand but might trigger decline in a senescing stand. Such a disturbance may also act as an additional synchronizing factor. After decline is triggered, secondary pathogens or insects may attack the weakened trees. The severity of the second disturbance and of the attack (if any) of secondary organisms may influence the amount of damage the stand (canopy) sustains, the speed and pattern of tree mortality, and whether there is partial recovery.

In summary, the dieback mechanism proposed for ohia decline involves (1) cohort senescence as the primary or predisposing cause, (2) a sudden perturbation as a second and additionally synchronizing cause, acting as a trigger in the senescing life-stage, and (3) biotic agents as tertiary or contributing and dieback hastening causes (Mueller-Dombois and others 1983). This concept has been broadened to include diebacks and declines of other forest trees (Mueller-Dombois and others 1983) and even of certain grasses, shrubs, and vines (Mueller-Dombois 1983), in which the dieback populations themselves occur in cohort communities of low species diversity.

Decline Concept

Manion (1981) characterized declines as diseases caused by the interaction of a number of interchangeable, specifically ordered abiotic and biotic factors to produce a gradual general deterioration, often ending in the death of trees. A similar definition has been proposed by Houston (1973, 1982, 1984), who indicated that declines are diseases initiated by predisposing effects of biotic or abiotic environmental stresses which culminate in attacks, often lethal, by organisms of secondary action. In the absence of stress, the secondary organisms are unable to attack the trees successfully. Conversely, trees under stress may recover after removal of the stress factor were it not for attack by the secondary organisms. This is not to say that severe stress, if repeated or prolonged, cannot result in tree death.

Houston (1982) recognized two phases of the decline complex—dieback and decline. He conceived dieback to be a progressive development of symptoms beginning with the dying back of buds, twigs, and branches, which often results from the effect of the stress factor(s) alone. Trees often recover once the stress abates. Decline refers to the phase in which the vitality of the entire tree lessens and often culminates in death. This phase usually results from attack by secondary organisms on stress-altered trees. Recovery from this phase is less likely to occur after stress abatement. The terms dieback and decline are often used interchangeably, as in the case of the ohia problem.

Decline diseases are difficult to diagnose. The symptomatology of most decline-type diseases is remarkably similar—rootlet mortality and general crown dieback—and can be caused by a large number of biotic and abiotic factors, either alone or in combination. Such symptomatology offers little explanation of the cause of the problem, especially where several causal factors are involved and where primary injury occurs in the root system. This symptomatology makes it difficult to determine whether all declines with similar symptoms have similar etiologies.

Also, diagnosis is difficult because decline-type diseases usually involve a sequence of events triggered by some environmental, site, or biotic factor or factors resulting in stress. Often, these "triggers" or "incitants" are ephemeral, and their occurrence may not be known at the time diagnosis is attempted. The degree of decline depends on the severity and continuity of the initial stress factor; presence of disease organisms and insects capable of attacking the stressed trees; and interrelationships of these organisms, such as their sequence of occurrence and how they are influenced by environmental and site factors.

Another difficulty in diagnosing decline-type diseases is that they generally occur in mature forest ecosystems involving large trees. Conducting controlled experiments is difficult under such conditions, especially when two or more variables are studied. On the other hand, conducting experiments using seedlings in a greenhouse or environmental chambers in which one or a few factors are easily controlled, and extrapolating the results to the forest can often be misleading.

Several factors that may be involved to some degree in the ohia decline syndrome include poor soil drainage, drought, nutrition, toxic elements or compounds, intraspecific competition, senescence, insects, and pathogens. Site conditions or environmental factors may be the primary factors in the initiation of ohia decline (Papp and others 1979). This would support Houston's (1973) concept of decline diseases—tree mortality results from a sequence of events that starts with stress, which predisposes trees to attack by organisms, which eventually kill them. In the case of ohia decline, the organisms involved are primarily *P. bilineatus* and *P. cinnamomi.* A biological evaluation of ohia decline generally supports this assessment (U.S. Dep. Agric., Forest Serv. 1981).

Mueller-Dombois (1983), however, disagreed with the above conclusions as well as with the decline disease concept of Manion (1981). Instead, he proposed that senescence is the

Figure 11—Severely declining ohia forest on pahoehoe flow sur-rounded by healthy forest on a'a flow.

Figure 12—Severely declining ohia forest showing some surviving trees at least 15 years after estimated onset of decline.

Figure 13—Healthy ohia reproduction under stand of ohia in severe decline of Wetland Dieback type.

Figure 14—Soil typically associated with some Wetland Dieback stands shows a thin gley horizon at the pahoehoe lava subsurface contact and an overlying layer of rhizomes and organic muck.

Figure 15—Ohia Displacement Dieback is characterized by an almost continuous understory of healthy treefern.

Figure 16—Small area of dead ohia ("hotspot") in otherwise dense, healthy ohia forest. Trees died synchronously over a relatively short time and the original affected area has not expanded.

Figure 17—Profile of rugged surface jumble of a'a lava shows organic material and small basalt clinkers. Such soils are well drained and usually support healthy ohia but also are found in Pubescent Dieback.

Figure 18—Adult female two-lined ohia borer *(Plagithmysus bilineatus)* depositing eggs in bark crevices of ohia.

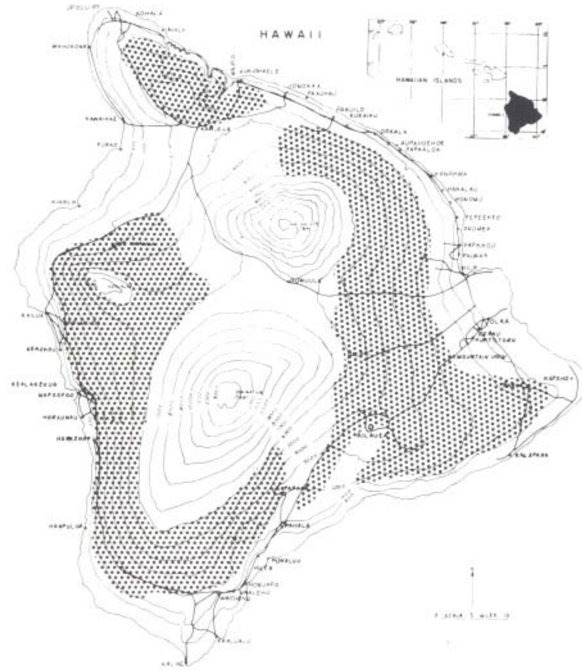

Figure 19—The two-line ohia borer *(Plagithmysus bilineatus)* is widely distributed on the island of Hawaii.

Figure 20—Spiraling larval gallery of *Plagithmysus bilineatus* on ohia effectively girdles the trunk.

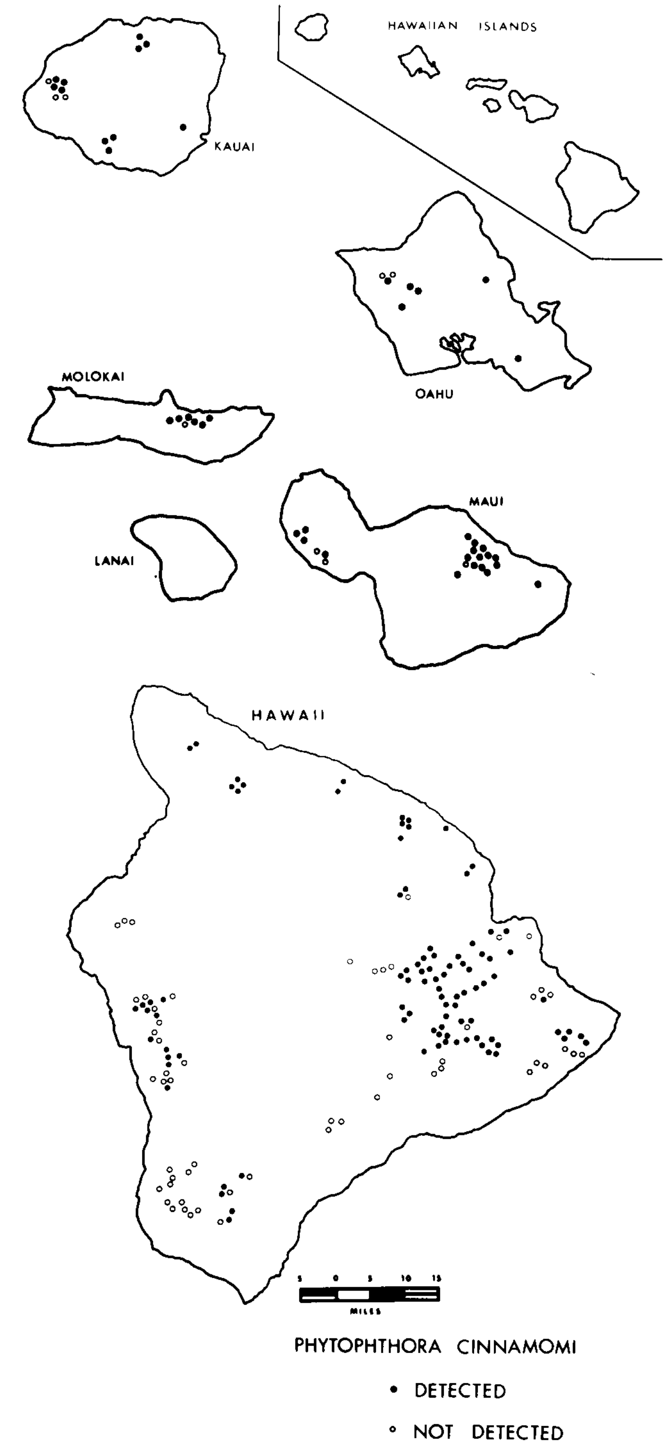

Figure 21—The fungus *Phytophthora cinnamomi* is widely distributed in the Hawaiian Islands.

predisposing factor, and—because senescence in plants is a natural phenomenon—conditions such as ohia decline can not accurately be termed diseases. Senescence is indeed a natural phenomenon, and all plants surviving to the end of their biological age potential go through such a period in their life cycle. However, even if all ohia trees suffering from decline were in senescence before the onset of decline (and there is no experimental evidence to support this), the fact that they are declining is due primarily to external stress factors and not to senescence *per se.* Innate tree vigor (= senescence?) at the time stress starts undoubtedly is an important factor in the typical decline syndrome, but the severity of the resulting decline is equally or perhaps more influenced by the strength and duration of the predisposing stress factors. The theory of Mueller-Dombois and others (1983) further deviates somewhat from the usual definition of senescence by including those cohorts whose life stage has not yet reached the normal biological age of senescence, but may have been induced into physiological senescence by environmental stresses. In our view such a broad definition of senescence in relation to declines in general helps little to identify the real precipitating causes of a particular decline problem and the term "synchronous cohort senescence" does not appear to describe in a meaningful way the etiology of ohia decline.

MANAGEMENT OF DECLINE AREAS

Because of the generally poor form of most trees and wood characteristics that make it unsuitable for most commercial purposes, ohia has little commercial value. For this reason, commercialization is not an important factor to be considered in managing areas affected by ohia decline. The ohia forests are, however, important for watershed protection, as a unique ecosystem valued for esthetic purposes, and as a habitat for large numbers of endemic flora and fauna—some of which are rare and endangered. The following comments concern-ing management needs are addressed to these functions.

Watershed Protection

The watershed characteristics of ohia decline areas on Mauna Loa and Mauna Kea differ significantly. On Mauna Loa, sites vary from bare recent lava flows, to shallow organic soils overlying older flows, to deep soils derived from ash. Even though most of the soils in the decline area are poorly drained, all the precipitation the area receives eventually percolates into a subsurface water system. There are no established stream channels, although during periods of high rainfall surface flow is considerable. Even though the ohia canopy has been reduced over much of the area, subcanopy cover remains high. Following decline, dense stands of young ohia have developed in many areas. Because of this dense cover and the drainage characteristics of the site, ohia decline has

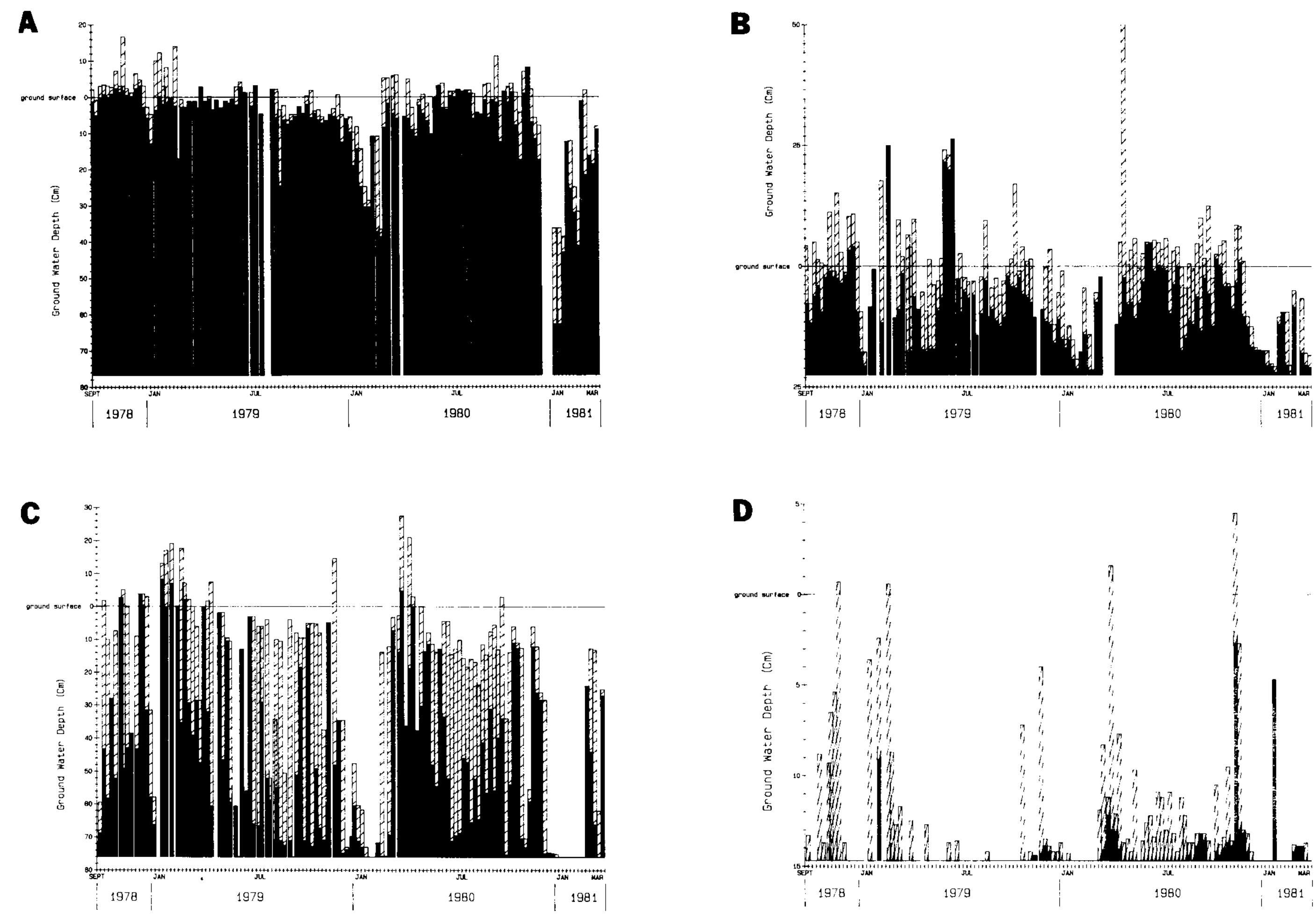

Figure 22—Ground water levels of four major drainage categories as related to ohia decline structural types: (A) very poorly drained—Bog Formation Dieback, some Wetland Dieback; (B) poorly drained—Wetland Dieback; (C) moderately well drained—Ohia-Koa Dieback, some Ohia Displacement Dieback; and (D) well drained—healthy stands, Pubescent Ohia Dieback, Dryland Dieback. Shaded bars represent weekly high water levels, and solid bars represent observed water levels.

had no adverse effect on the watershed values of this area, and none are foreseen. From this standpoint, therefore, no remedial action is necessary.

The situation on Mauna Kea is different. Soils are older and—for the most part—derived from ash deposits. Several permanent stream channels traverse the area and carry runoff water to the ocean a few miles away. The ohia canopy as well as the subcanopy species have been greatly reduced. Treeless bogs of various sizes covered with grasses, sedges, and sphagnum are being formed. Drainage has been greatly impeded in some areas through the formation of hardpans in the soil, and surface flow is considerable, which sometimes results in sheet erosion. Even with these deleterious effects of decline, there has been no major impact on amount of stream runoff or increase in stream sediment load, mostly because lost vegetation has been replaced by dense cover of *Dicranopteris* ferns and bog vegetation. Areas bare of plant cover are rare. Measurements of runoff and sediment loads from streams drain-ing the Mauna Kea decline areas should be continued. However, unless these measurements indicate a significant deterioration of the watershed, no remedial steps need be taken.

Parts of the similar Maui decline area were replanted to *Eucalyptus robusta* and *Melaleuca quinquenervia* in the early 1900's. Current survival and growth of these two species are excellent. Soil moisture levels in the plantings are also much lower than in the adjacent nonplanted areas. Skolmen (1984) has also obtained good survival and growth of these two species, as well as of *Alnus nepalensis,* on a bog area on Hawaii after 2 years. If it is deemed necessary to replant the Mauna Kea decline area in the future because of further deteriorating conditions, these species should do well. Some concern exists, however, that *M. quinquenervia* might spread by natural seeding into other areas. This has occurred in the Maui decline area to a limited extent. Because of the value of Hawaiian forests as laboratories for the study of speciation and natural history in general, we recommend the use of introduced and potentially disruptive species only if danger of watershed deterioration is significant.

Ecosystem Values

Unquestionably, decline has severely affected the ohia canopy over a large area on the island of Hawaii. Impact on the subcanopy vegetation has been variable but generally less. Although predecline data are not available, some rare plant species may have been completely lost. Native bird populations in some areas have been significantly reduced, followed by an increase in some introduced species.

Extensive studies of post-decline succession clearly show, however, that most of the vegetation now covering decline areas is composed of native species. Although several introduced species have invaded some areas, these species apparently have had surprisingly little impact on recuperation of native species, including ohia. Many of the shade-intolerant introduced species will probably disappear with canopy closure. The major exception is the rapid invasion of some areas by *Psidium cattleianum,* especially along peripheral areas such as those adjacent to cane fields, roads, and other areas of human disturbance. No feasible means of controlling this plant is available. Further spread could be slowed, however, by reducing the population of feral pigs in the forest, which are important in seed distribution.

Feral pigs also are responsible for the establishment of other introduced plants. Grasses such as *Setaria palmifolia* colonize bare areas formed by the pigs' rooting activities, which also directly destroy seedlings of many native species. For these reasons, reduction of feral pig populations in decline areas would probably result in more rapid recuperation of native vegetation.

The future course of successional events in ohia decline areas on the island of Hawaii is uncertain. The evidence presented in this report, however, points to continuation of an ecosystem dominated by native plants, but one that will differ—radically in some places—from that present before decline. With the exception of attempts to control invasion and spread of introduced plants and to reduce the population of feral pigs, little can be done on a practical basis to speed the recovery process.

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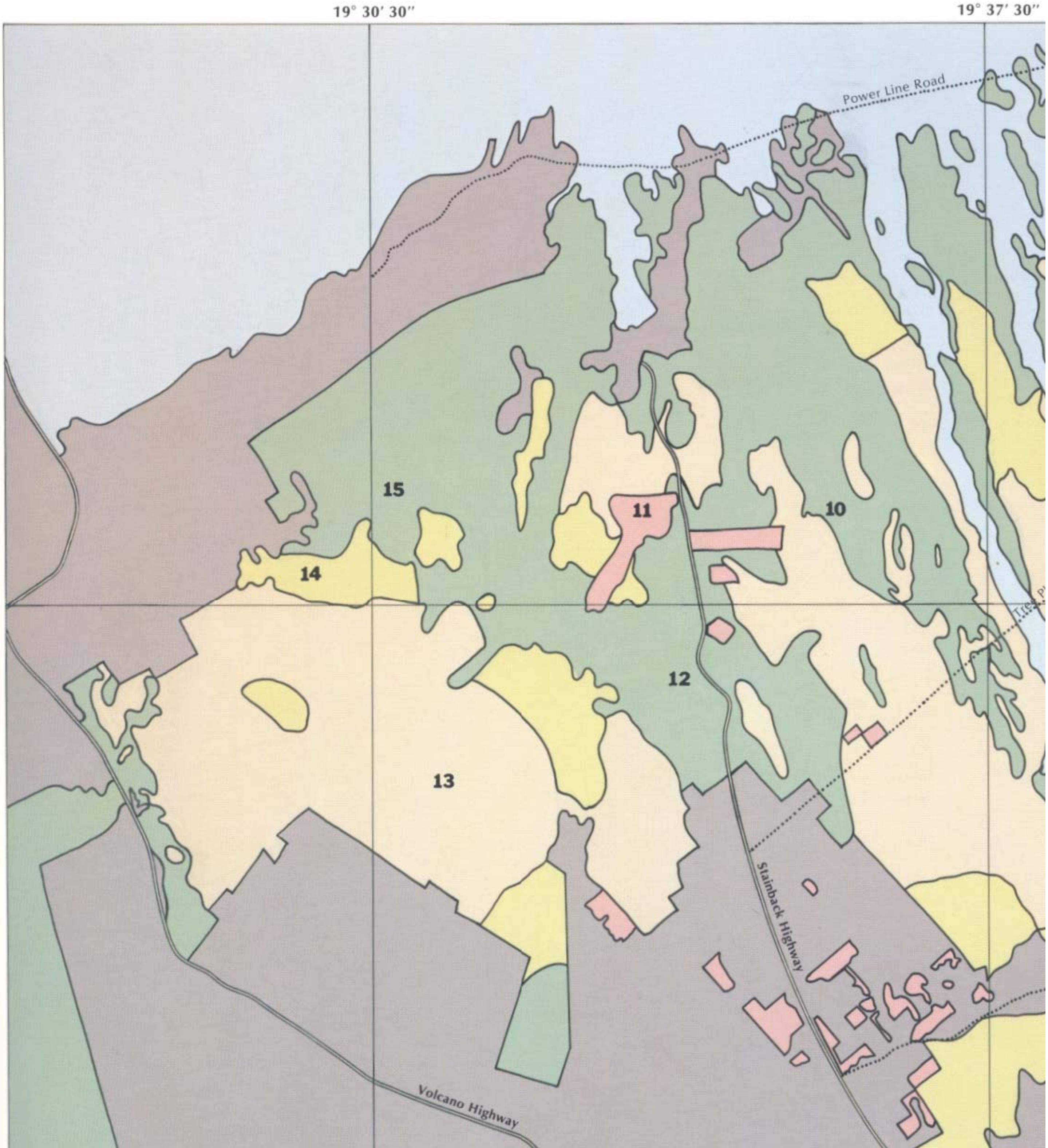
19° 30′ 30″
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Power Line Road
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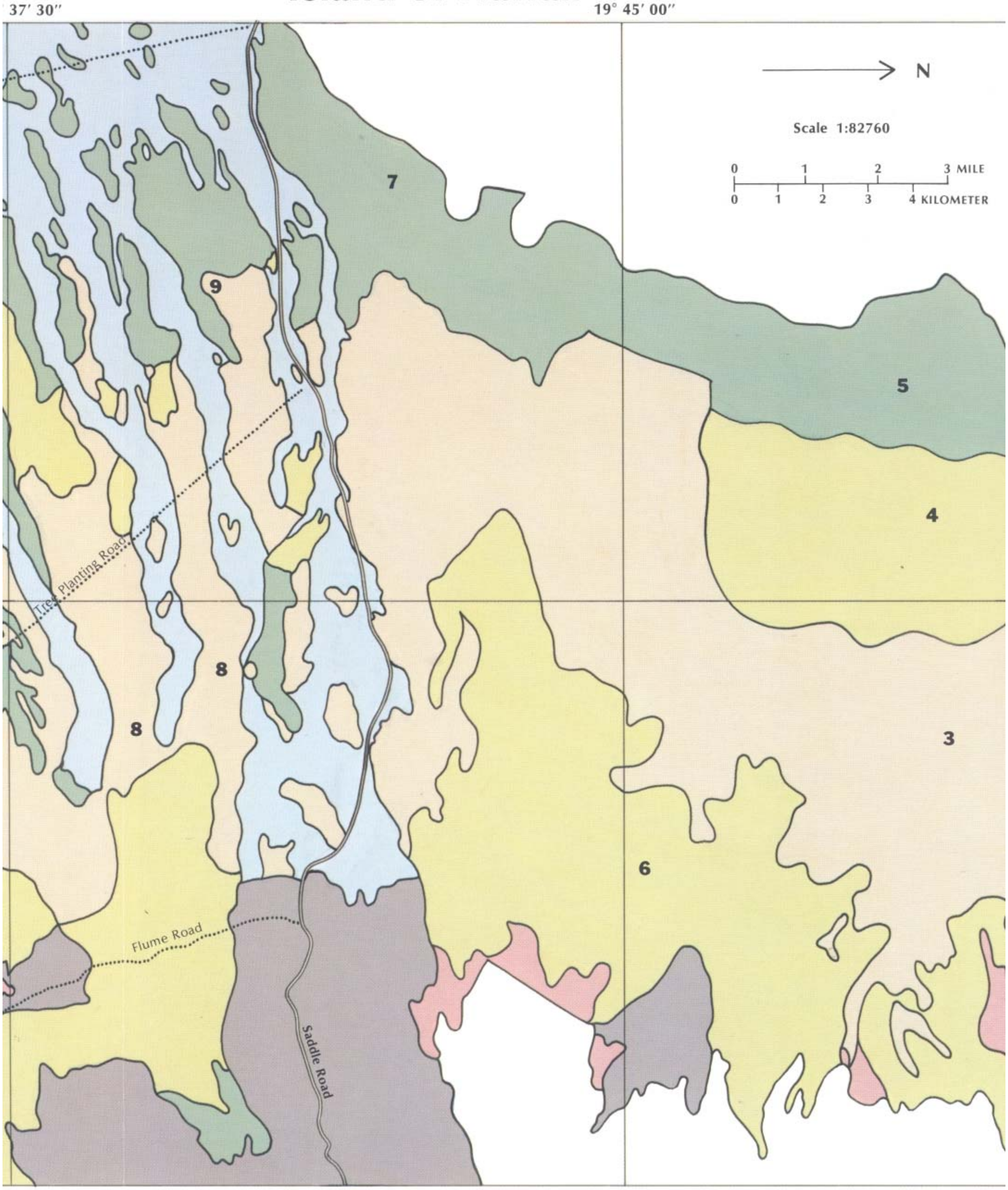
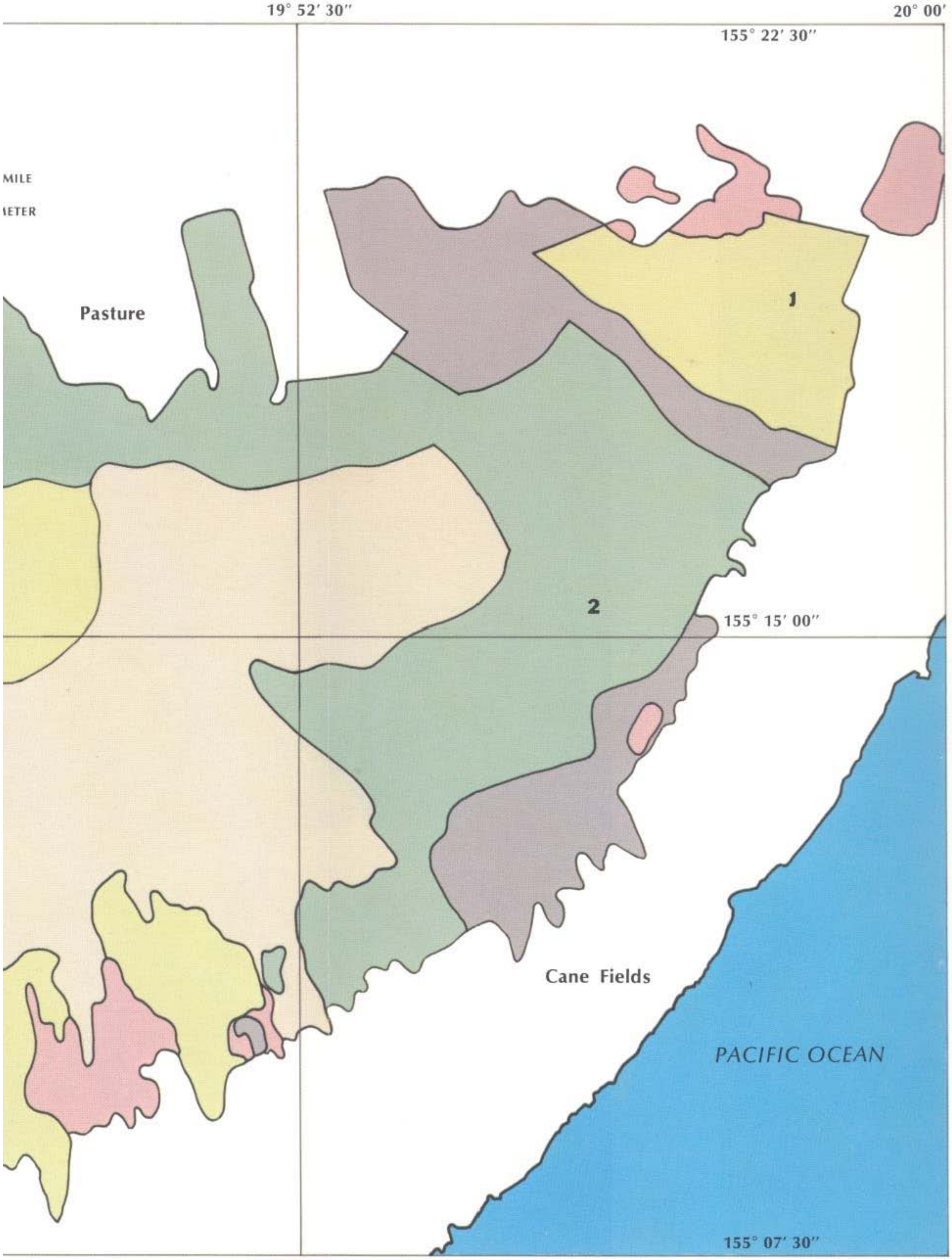
Stainback Highway
Volcano Highway

Distribution and Severity of
OHIA FOREST DECLINE
Island of Hawaii





19° 52′ 30″
20° 00′
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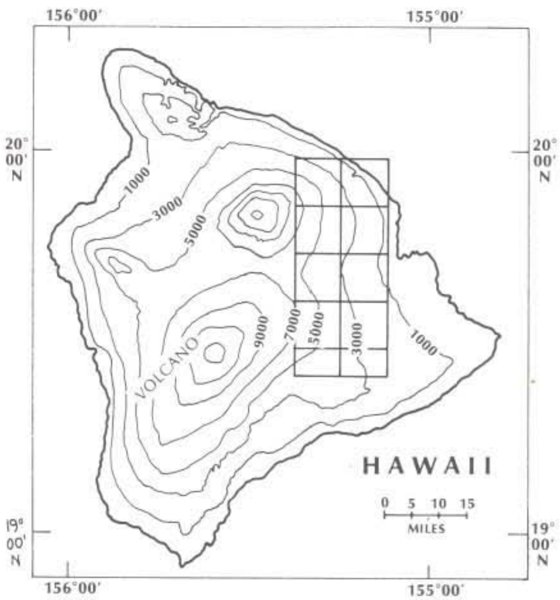

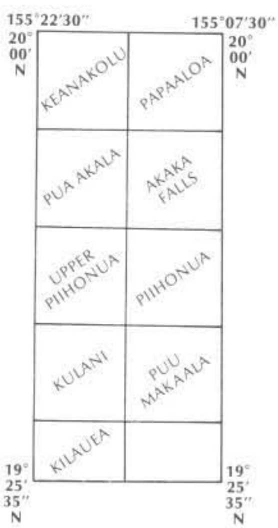

LEGEND

Severe Decline

Moderate Decline

Healthy - Slight Decline

Historic Lava Flow

Disturbed Land

Tree Plantation

Highway

Jeep Road

Hodges, Charles S.; Adee, Ken T.; Stein, John D.; Wood, Hulton B.; Doty, Robert D. **Decline of ohia *(Metrosideros polymorpha)* in Hawaii: a review.** Gen. Tech. Rep. PSW-86. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986. 22 p.

Portions of the ohia *(Metrosideros polymorpha)* forests on the windward slopes of Mauna Loa and Mauna Kea on the island of Hawaii began dying in 1952. Little mortality has occurred since 1972. About 50,000 ha are affected by the decline. Individual trees exhibit several symptoms, from slow progressive dieback to rapid death. Seven types of decline have been identified on the basis of differential response of the associated rainforest vegetation. Two of the types, Bog Formation Dieback and Wetland Dieback, make up more than 80 percent of the decline area. The decline has affected bird populations and plant species in some areas, but has had no major effect on runoff or water quality. Ohia decline appears to be a typical decline disease caused by a sequence of events. Poor drainage is probably the major cause of stress and is followed by attack of the ohia borer *(Plagithmysus bilineatus)* and two fungi *(Phytophthora cinnamomi* and *Armillaria mellea),* which kill the trees. Except for controlling introduced plants and feral animals that spread them, little can be done to ameliorate the effects of the decline.

Retrieval Terms: Armillaria mellea, Metrosideros polymorpha, Plagithmysus bilineatus, Phytophthora cinnamomi, decline, rainforest, Hawaii