

'Ōhi'a Dieback in Hawaii: 1984 Synthesis and Evaluation¹

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ABSTRACT: Attention is first drawn to the state of knowledge in 1981 of the Hawaiian *Metrosideros polymorpha* ('ōhi'a) stand dieback. New findings that have largely been developed or published since then are described; these encompass vegetation, soils, hydrology, climatology, and experimental, historical and evolutionary research. A brief comparison of canopy dieback in Hawaii with that in other forest systems is made. New facts on the Hawaiian dieback are summarized within the context of climatic instability, soil, and stand factors. These facts are then related to ideas of environmental disturbance, disease, and cohort senescence. There are strong indications that the primary factor causing 'ōhi'a dieback develops in the dieback population itself due to synchronized aging of cohort stands. External abiotic (environmental) and biotic stress factors (insects and fungal pathogens) appear to play secondary and/or subsidiary roles, respectively. Based on this new knowledge, policy and management considerations are discussed with regard to the role of dieback and its impact on preserve design, forest hydrology, and soil fertility. Finally, a number of recommendations are made for new management-related research and for further research into the etiology of canopy dieback.

PREVIOUS SYNTHESSES AND EVALUATIONS

THE 'ŌHI'A (*Metrosideros polymorpha* Gaud.) dieback on Hawaii (Hawaiian Islands) was initially reported in 1968 as a stand dieback occurring in large patches (Mueller-Dombois and Krajina 1968) and *not* as a forest decline. The forest decline interpretation came 4 yr later, when Burgan and Nelson (1972) referred to the dying or dead 'ōhi'a stands as a rapidly spreading epidemic. They thought then that the dieback was caused by a root pathogen (*Armillaria mellea*) that was considered to be a recent introduction to the islands. In this way, the alien disease hypothesis was born and spawned a decade of thorough disease research in Hawaii, sponsored by the U.S. Forest Service. The initial 'ōhi'a stand dieback observation, on the other

hand, was later formulated into a natural cause hypothesis (Mueller-Dombois 1974), in which dieback was seen as a normal phenomenon, a developmental stage in primary succession of an isolated rain forest ecosystem. This alternate hypothesis similarly spawned a decade of thorough research, sponsored initially by the U.S. Park Service and thereafter by the National Science Foundation and supplemented with McIntire-Stennis funding.

Both research approaches and their findings were synthesized and evaluated in two reports, addressed to the local scientific community and to the people entrusted with land management and policy decision-making in Hawaii. The first was CPSU (Cooperative National Park Resources Studies Unit, University of Hawaii) Technical Report No. 20, published in 1977 at the conclusion of the project sponsored by the U.S. Park Service (Mueller-Dombois et al. 1977). The second was requested by DLNR (Department of Land and Natural Resources, State of Hawaii) and produced by the Pacific Southwest Pest Management Unit of the U.S. Forest Service at the conclusion of its disease research (USDA,

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Forest Service 1981); this report is hereafter referred to as the 1981 DLNR report.

The findings of each report are summarized below, and new research findings since 1981 are presented. The facts are then put together, and considerations for management, policy, and new research are addressed.

*The 1977 CPSU Report*³

The 1977 CPSU report (Mueller-Dombois et al. 1977) explained the ecological research approach taken in 1975 as consisting of five interrelated study components. One dealt with the role of pathogens and the others with vegetation mapping, soil and habitat classification, 'ōhi'a population structure and floristic vegetation studies, and experimental research. Preliminary data from 42 sample plots were presented. Completion of the data analyses was delayed because the analyses formed part of three developing dissertations of the participating collaborators, James D. Jacobi, Ranjit G. Cooray, and N. Balakrishnan. In the synthesis and evaluation, the outcome of the mapping project was presented as consisting at the highest level of hierarchy of three major structural forest types, i.e., dense, closed, and open. Each of these general structural types was further defined by a number of subtypes. Two other major structural types were recognized, i.e., low-growing vegetation with scattered trees and without trees.

In addition to the quantitative structural evaluation of dieback and nondieback stands, the study resulted in the recognition of four tree-group dieback types: (1) wetland, (2) dryland, (3) 'ōhi'a displacement, and (4) bog-formation. Their characteristics were described in terms of spatial patterns, population structural patterns, and habitat relationships.

Two of the four dieback types, dryland and wetland, were associated with adequate 'ōhi'a reproduction in most sample places investi-

gated, while the bog-formation dieback was associated with a deterioration of site capacity for tree growth. 'Ōhi'a displacement dieback occurred on fertile deep ash soils, and resulted in a successional displacement of a closed 'ōhi'a forest by a closed tree fern forest with only scattered 'ōhi'a trees. It was also pointed out that dryland and wetland diebacks, which occurred mostly on lava flow habitats or shallow soils, may display a forest life cycle. Five phases of a forest life cycle were seen as emerging from our population structure data, and a new dieback theory was proposed involving this forest life cycle as a key element.

As to the reproductive strategy of 'ōhi'a, it was suggested that periodic canopy collapse might be the mode of perpetuating the dominance of a pioneer species in the course of primary succession in the Hawaiian rain forest. It was also suggested that 'ōhi'a might have evolved into its own successional replacer by ecotypic segregation into pioneer, seral, and climax races.

In terms of dieback causes, six facts were highlighted: (1) Kleijunas and Ko's (1974) finding that inorganic nutrient deficiency is a factor in 'ōhi'a dieback; (2) Hwang's (1977) finding that *Phytophthora cinnamomi* is not involved as a primary agent, or at least not in the dryland dieback; (3) the findings of Kleijunas, Papp, and Smith (1977) that both *P. cinnamomi* and *Plagithmysus bilineatus* assume only a secondary role in the decline; (4) the demonstration from aerial photographs of Petteys, Burgan, and Nelson (1975) that there was a rapid spread of 'ōhi'a decline (from before 1954 to 1972); (5) our finding that there was stand rejuvenation associated with the wetland and dryland diebacks; and (6) our finding that the Hawaiian rain forest ecosystem is not an environmentally uniform entity and that different forms of dieback are associated with certain major habitat variations.

Each of the four dieback types was thought to be triggered by a different set of causes at a certain stage of stand maturity, and three were said to have abiotic or environmental causes. In a summary paper, based on the synthesis report, the new cause hypothesis was stated: "That the dieback is initiated by a climatic instability which becomes effective through

³The 1977 CPSU report was republished for a wider readership in 1980 as a University of Hawaii Agricultural Publication. It was revised only to include references to two new papers, Mueller-Dombois (1980) and Papp et al. (1979).

the soil moisture regime under certain conditions of stand maturity" (Mueller-Dombois 1980: 159). In this paper a seventh finding was also reemphasized: that dieback is manifested only in canopy trees.

With respect to conservation policy, the 1977 CPSU report pointed to the forest life-cycle concept as providing a new guideline for the size requirement in preserve design. In terms of rain forest-related management problems, the report raised three questions considered important at that time: (1) What is the effect of the dieback on the watershed value of the affected terrain? (2) What effect does dieback have on the rare and endemic species associated with the rain forest ecosystem, including the native birds? (3) Does dieback affect the behavior of exotic plants and animals, including the feral pig? Tentative answers were given to all three questions from our preliminary data base. However, these questions were raised primarily as a guideline for management-related research.

The 1981 DLNR Report

The 1981 DLNR report (USDA, Forest Service 1981) probably lists all important literature and mimeographed reports that were issued in connection with the 'ōhi'a decline disease research. It also includes some earlier references to rain forest dieback in Hawaii and compares our 1977 CPSU report with the vegetation research of the U.S. Forest Service, which was begun about 2 yr following ours. The U.S. Forest Service's vegetation research was circulated in 1981 as an unpublished manuscript by Adee and Wood (1981).

The DLNR report reviews the disease research under "biotic factors" and all other research under "environmental factors." The biotic factor research is discussed in terms of pathogens, insects, and pest complexes. Four fungi are mentioned as pathogens that at one time were suspected to cause the decline (*Armillaria mellea*, *Pythium vexans*, *Calonecrotia crotolariae*, and *Phytophthora cinnamomi*). Two other pathogen groups were also investigated, plant parasitic nematodes, viruses and/or mycoplasma. Viruses or mycoplasma could not be detected, and nematodes

were not considered dense enough to contribute to the decline. The possible new pathogen on 'ōhi'a, *Endothia metrosideri*, reported recently by Fosberg (1983), was not among those suspected in the decline research.

Among insects, the DLNR report notes that three groups were investigated, psyllids, ambrosia beetles, and the 'ōhi'a borer or bark beetle (*Plagithmysus bilineatus*). Only the last was found to be associated with many, but not all, declining 'ōhi'a trees. The root pathogen *Phytophthora cinnamomi* and the 'ōhi'a bark beetle were later suspected to form a pest complex. It was hypothesized that the fungus could initiate root mortality, which in turn would attract the endemic bark beetle to become epidemic. This hypothesis was thoroughly studied (Papp et al. 1979), with the result that such an interaction could be suspected in some 'ōhi'a decline stands on poorly drained sites but not in all decline stands, i.e., the two agents also acted independently. In the end, it was concluded that neither biotic agent could be considered a primary cause, but that they act in combination with environmental factors to cause 'ōhi'a decline.

Under environmental factors, the DLNR report compares the dieback types recognized in our CPSU report with the "dieback structural" types recognized in the manuscript by Adee and Wood (1981). The DLNR report notices the remarkable similarity of our results with those in the Adee and Wood manuscript, but also points to some differences. For example, the DLNR report emphasizes that Adee and Wood recognized three healthy 'ōhi'a structural vegetation types, namely dense, closed, and open. The CPSU report recognized the same structural categories and presented these together with many finer subvariations on a vegetation map. The DLNR report notes that two of Adee and Wood's dieback types were not recognized in the CPSU report, namely their "pubescent 'ōhi'a structural dieback" type and their "'ōhi'a-koa [*Acacia koa* Gray] structural dieback" type. However, the pubescent structural dieback type of Adee and Wood corresponds in part to our dryland dieback type, except that our dieback type concept is broader in the sense that it includes all dieback

stands on well-drained substrates. These are in many cases stocked by pubescent 'ōhi'a races or varieties but also by stands of mixed pubescent and glabrous varieties and in some cases dominantly by glabrous varieties of 'ōhi'a. It is true that we did not recognize Adee and Wood's 'ōhi'a-koa structural dieback type in our 1977 report, but we recognized a similar dieback type in our subsequent studies, which we reported as "gap-formation dieback" (Mueller-Dombois 1981a). I will refer to its characteristics under new vegetation research below.

The DLNR report points out further that we restricted our concept of 'ōhi'a displacement dieback to stands on deep, rich ash soils, while Adee and Wood's 'ōhi'a-tree fern structural dieback type concept was broader in that it refers also to shallow soils or to any soil capable of supporting a closed tree fern stand. This concept of Adee and Wood should now be considered an improved interpretation of displacement dieback, as will be explained in the next section. However, the interpretation of Adee and Wood that wetland dieback may lead to bog formation needs some qualification to be acceptable as a better interpretation, because of the very different site relationships involved. In our interpretation, wetland dieback relates to poorly drained lava substrates, while bog-formation dieback relates to deep and geologically older soils from ash. One cannot assume that the first leads to the second without more research on the geomorphological aging of this mountain landscape.

In conclusion, then, there are no fundamental differences between the DLNR and CPSU synthesis reports in their interpretation of the dieback causes. Both recognize abiotic factors as primary and biotic factors as secondary or subsidiary in the dieback syndrome.

NEW RESEARCH FINDINGS

Vegetation Research

A National Science Foundation (NSF) grant received in 1979 allowed for continu-

ation of dieback research as part of an ecosystem analysis project. We expanded our sampling base to 62 plots, established four experimental sites, and extended our study to the islands of Maui and Kauai (Mueller-Dombois 1981a). This also allowed for a closer investigation of the remote bog-formation dieback terrain on Mauna Kea, into which we made two expeditions by helicopter in 1980. The broader sampling program resulted in the recognition of a fifth major tree-group dieback, called "gap-formation dieback" (Mueller-Dombois 1981a). Gap-formation dieback is characterized by relatively small patches of 'ōhi'a trees dying or standing dead on knolls and ridges. These landform types are raised several to tens of meters above the boggy and permanently wet depressional habitats of the general bog-formation terrain. We found low-vigor 'ōhi'a stands and tree-group dying currently progressing (in 1980) on some of the forested knolls, while groups of 'ōhi'a trees on other knolls had died long ago. Still other knolls were stocked with healthy 'ōhi'a trees. Some of the knolls, in the 600–1000 m elevation range above the Hamakua coast, had koa trees admixed with 'ōhi'a. Most of these koa trees also displayed low vigor, and some were dying or had fallen down.

At that time we saw no connection to the "gap-phase replacement" that we had described earlier during our IBP (International Biological Program) studies for the Kilauea Forest Reserve on Mauna Loa (Cooray and Mueller-Dombois 1981). The reason was that in the Kilauea Forest, tall koa trees from the senescing canopy population were blown down occasionally during Kona storms. These created gaps by physical damage, which in some cases gave rise to almost pure stands of 'ōhi'a and in others to almost pure stands of tree ferns (Mueller-Dombois, Bridges, and Carson 1981:255). In the IBP study, we saw the wind-throwing of canopy koa in the Kilauea Forest as the cause for gap formation, while now on the knolls of the bog-formation terrain on Mauna Kea we saw canopy collapse of standing 'ōhi'a trees as a cause of gap formation, a process not necessarily involving physical damage. The connection between our gap-formation dieback on Mauna Kea

and our gap-replacement process on Mauna Loa is now apparent; in both cases, we have senescing canopy populations. The concept applies to koa as well as to 'ōhi'a.

In retrospect, we can now also state that our gap-formation dieback type corresponds to the 'ōhi'a-koa structural dieback type of Adee and Wood (1981). One of our observations clearly coincides with theirs, namely that this dieback is not restricted to poorly drained sites. They found low numbers of 'ōhi'a seedlings and healthy 'ōhi'a saplings associated with this dieback type. We found occasional 'ōhi'a seedling gaps but also abundant seedling patches, and in other locations, 'ōhi'a sapling stands associated with the gap-formation dieback, a mosaic structural pattern similar to that described for the Kilauea Forest (Cooray and Mueller-Dombois 1981). Therefore, Adee and Wood's (1981) study and our studies (Mueller-Dombois 1981a, Mueller-Dombois et al. 1980) coincide in their assessment of this dieback type in that 'ōhi'a replacement is clearly evident. Adee and Wood's assessment differs only in the evaluation of the 'ōhi'a reproduction patterns. This, however, is largely a question of sampling scale; i.e., if one averages aggregation patterns of seedlings and saplings with those where they are absent, one may conclude an overall low stocking density.

With regard to 'ōhi'a reproduction patterns under dieback stands, we can report other significant findings. In a resurvey of 26 permanent plots on dryland and wetland dieback sites after 5 yr (Jacobi, Gerrish, and Mueller-Dombois 1983), we found that in many cases 'ōhi'a reproduction had become more dense. More importantly, several of the original inverse-J-shaped frequency curves for 'ōhi'a seedlings and saplings had shifted to a modal curve trend. This implies that seedling recruitment has ceased in these dieback stands while sapling recruitment has increased. This further implies that the next 'ōhi'a stand replacing the former dieback stand will most likely be a one-generation canopy stand. The idea that 'ōhi'a tends to regenerate in cohorts or regeneration waves had surfaced earlier (Mueller-Dombois et al. 1977), but it had not

been demonstrated before. Now we have a clear indication that this occurs.

The 5-yr resurvey also brought forth new evidence that our concept of 'ōhi'a displacement dieback should be expanded in the direction indicated by Adee and Wood (1981). Moreover, it should be redefined on the basis of competitive relations between 'ōhi'a reproduction following dieback (its density and growth rate) and growth rates of the competing vegetation. Soil fertility is a major factor, but associated plant life forms are also important influences. For example, newly invading exotic tree species, such as strawberry guava (*Psidium cattleianum*), or aggressive vines, such as banana poka (*Passiflora mollissima*), may also cause 'ōhi'a displacement following canopy dieback.

Another significant finding relating to the etiology of 'ōhi'a dieback is that of Jacobi (1983), who studied the progress of dieback over a 1600-ha forest section just north of Saddle Road at 700–1380 m elevation. This area was studied thoroughly on the ground and contains two major habitat types, poorly drained pāhoehoe and moderately to well-drained 'a'ā lava. On the basis of three successively taken aerial photographic sets, Jacobi (1983) mapped nondieback and dieback patterns in 1954, 1965, and 1977. In 1954, there was no dieback in the mapped area. In 1965, dieback became evident in a patch mosaic, which was restricted to the poorly drained pāhoehoe substrate. These dieback patches, which totaled 448 ha in 1965, had largely coalesced into a large dieback area of 1008 ha in 1977. Three points are remarkable in this spread pattern of dieback, which is shown on three published maps (Jacobi 1983: 83–85). First, the dieback stopped exactly along the habitat boundary between pāhoehoe and 'a'ā. Second, the dieback also stopped on the same site in the middle of the poorly drained pāhoehoe. Third, the dieback stopped totally in 1977 and had not spread any further in 1981 (Jacobi 1983). This observation, that dieback stops at certain habitat boundaries but also within uniform sites had been made earlier (Mueller-Dombois et al. 1977), but we did not have such clear evidence for this seemingly puzzling pattern.

It is now possible to explain this pattern. The habitat boundary between pāhoehoe and 'a'ā is not only a physical but also a historical boundary. 'Ōhi'a stands on these historically different habitats are in different life phases; the stand on the pāhoehoe flow is in a senescing life stage and the stand on the 'a'ā flow is in a more vigorous mature growing phase. Moreover, the dieback did not progress further from 1977 to 1981 on the poorly drained pāhoehoe flow. Therefore, on the same site, stands coexist side by side that are in different life phases.

At this time, this explanation is still only a hypothesis, because it is also possible to suggest that the entire forest on pāhoehoe and 'a'ā was in the same mature growing stage, and that the dieback stand was affected differently from the nondieback stand by an environmental disturbance.

Hydrological and Climatological Research

When it became more obvious that biotic agents could not be responsible as the primary cause for 'ōhi'a decline, the U.S. Forest Service started some hydrological research in 1978, the results of which are very revealing. Doty (1980) monitored the groundwater fluctuations in seven sites in the area of the Waiakea wetland dieback for more than 2 yr. Four of his sites were in dieback stands (three on pāhoehoe, one on 'a'ā) and three in nondieback stands (two on pāhoehoe, one on 'a'ā). Wherever he could, Doty established paired dieback and nondieback stands on the same sites. Each site was equipped with several wells in the form of pipes with flotation devices. He found considerable fluctuations in soil water tables. In poorly drained sites, the water table could fluctuate from several centimeters above the soil surface to several decimeters below the surface. In better-drained sites, similar fluctuations occurred from several centimeters below the surface to several decimeters down in the profile. Doty found a fairly close relationship of these soil water fluctuations with rainfall. For example, a 2-cm rainfall could raise the water table by 5 cm in 24 hr due to additional runoff. The greatest fluctuation found over the 2-yr moni-

toring period was 53 cm, from 13 cm above to 40 cm below the surface. In general, there were frequent oscillations in relation to rainfall patterns, but there was no directional change in the water tables up or down over the 2-yr monitoring period. Nor did Doty note differences between paired dieback and nondieback stands in their water table relationships. Water table fluctuations were the same in dieback and nondieback stands.

Doty (1983) published his analysis of stream flow data for the dieback-affected Hilo watershed analyzed over the period 1936–1979. He found a close correlation of stream flow to precipitation amounts but no correlation to the dieback events that occurred in this period. Not only was the water flow unrelated to dieback, but water quality was unaffected. He concludes by referring to Ken Adee (personal communication) that only the trees had died and that the undergrowth remained stable or even increased in vigor and thus prevented the expected loss of watershed values. With this finding, he verified the hypothesis of no loss in watershed values presented in our 1977 CPSU report.

Evenson (1983) analyzed the annual fluctuations in climate across the dieback territory for a recording period of 91 yr (1891–1982). He used monthly precipitation records from 37 stations on the windward side and temperature readings from 36 stations all over the island. From the latter, he developed an estimation scheme for transferring temperature values to those precipitation stations that had no temperature records. He established that high climatic uniformity exists across the area (in the form of a stable gradient) from the Hamakua coast to Hawaii Volcanoes National Park, but found great fluctuations in mean annual rainfall. With a mean precipitation of 3800 mm falling in the approximate center of this area, he found the driest year to be 1963, with 2000 mm, and the wettest year to be 1969, with 5200 mm. Evenson tried to correlate these fluctuations to the big 'ōhi'a dieback periods, the first between 1954 and 1965, and the second between 1965 and 1977. He concluded that unusually wet years in the middle to late 1950s may have contributed to the wetland dieback. However, a similar pat-

tern could not be established for the second dieback period. The years 1969 and 1970 were extremely wet years, but they were followed by 5 yr (1971–75) that were considerably drier than normal. Thus, during the second period (1965–1977) for which Jacobi (1983) showed a great increase in the spread of wetland dieback, rainfall was mostly less than normal. Evenson (1983) concluded that the year-to-year climate fluctuations may contribute to stress, but that they do not explain much about dieback. Instead, he suggested that other parameters, such as storm events, might be more informative.

Doty (1982), who had independently made a similar year-to-year precipitation analysis, also found no relationship to dieback. He noted that precipitation was above normal for prolonged periods in the 1930s and below normal throughout most of the 1970s. However, he found a gradual long-term downward trend of mean annual precipitation on the northern windward side of the island and a similar long-term upward trend on the southeast side. He suggested that further analyses should be made of seasonal variations of rainfall.

Soils Research

In the 1977 CPSU report we proposed a soil habitat classification of 14 types. These were separated into two broad classes, shallow-soil types (<50 cm deep) and deep-soil types (>50 cm deep). The two groups were broken down further by drainage into five moisture regime classes (mesic, moderately moist, moist, wet, and extremely wet). With further research (Mueller-Dombois 1981a), this habitat classification was simplified into ten types by reducing the earlier recognized five moisture regimes to two for the lava types (i.e., well-drained and poorly drained) and by emphasizing chemical and landform criteria for the deeper ash soils. The first breakdown into shallow-soil and deep-soil habitat types was maintained. At the second level, five main habitat types were recognized: (1) pāhoehoe and (2) 'a'ā lava among the shallow soil types; and (3) eutrophic ash, (4) oligotrophic ash, and (5) bogs among the deep-soil types. Each

of these five main types was broken down further into two subtypes, the lava substrate types into well-drained and poorly drained and the deep-soil types by easily recognizable nutrient regime, soil texture, and landform criteria.

Eight of the ten soil habitat types have now been analyzed for their chemical properties (Balakrishnan and Mueller-Dombois 1983). Severe nitrogen deficiency was found to occur in habitats of well-drained pāhoehoe and in coarse-textured (relatively young) ash soils. The two, however, differed in that the well-drained pāhoehoe sites were overlain by extremely acid histosols ($\text{pH} < 4.0$) while the coarse-textured ash soils were only weakly acid ($\text{pH} > 5.5$). Poorly drained pāhoehoe sites also had very acid organic overlays but showed moderate nitrogen availability, while they tended to have potentially toxic levels of Al and heavy metals (Fe, Mn). The same was true for moderately well-drained soils from geologically older, heavily leached ash, as found on the east flank of Mauna Kea. These had still higher levels of nitrogen, but were deficient in phosphorus. The bog soils from the same ash were chemically similar but with occasionally very high levels of potentially toxic Fe and Mn. The 'a'ā substrates showed weakly acid organic overlays, moderate levels of available nitrogen and phosphorus, and low levels of potentially toxic metals. The habitats with dense growth of tree ferns were the richest in nutrients. These are what we had called eutrophic fine-textured deep-ash soils (Mueller-Dombois et al. 1977, 1980). They showed only weakly acid surface layers associated with high levels of mineral mixed organic carbon, moderate levels of available cations and nitrogen, and almost no soluble metals.

Thus, both the 'a'ā substrates and eutrophic fine-textured deep-ash soils can be considered nutritionally balanced, while all other habitats can be termed imbalanced (i.e., the young ash and well-drained pāhoehoe sites because of their nitrogen limitation; the old ash, bog, and poorly drained pāhoehoe sites because of their potentially high levels of toxic metals). Moreover, phosphorus may be limiting in all sites. It was highest in the eutrophic

ash sites, but not as available as desired for garden soils.

We concluded that nutrient limitations, such as here described, may contribute to stress during ‘ōhi‘a stand development except on the eutrophic ash and ‘a‘ā sites. Such stress may predispose stands to dieback by lowering their vigor gradually as trees reach maturity. However, the soil nutrient study does not offer a satisfactory explanation for the suddenness and the synchrony of the ‘ōhi‘a dieback.

Experimental Research

A tree fern canopy removal experiment was done by Burton (1980a, Burton and Mueller-Dombois 1984) in the area of the ‘ōhi‘a displacement dieback, on eutrophic, fine-textured deep-ash soil. Numerous small ‘ōhi‘a seedlings were recorded on the forest floor and on tree fern trunks before artificial canopy opening. Their response was monitored for 15 months. Many new ‘ōhi‘a seedlings became established following canopy opening. The new sun-born seedlings grew almost twice as fast as the shade-born seedlings. Most of the shade-born seedlings died in the 100% canopy removal treatment, and many died in the control treatment (i.e., where the canopy was left intact).

This experiment has shown that the ‘ōhi‘a displacement dieback results in a quantitative (but not total) displacement of the next generation ‘ōhi‘a. The displacement here is largely due to shade limitation and associated environmental factors (e.g., temperature and soil moisture of the seedbed) as caused by competition through a vigorous undergrowth species. The displacement can be called successional but it may not be permanent. Storms may open the tree fern canopy occasionally and allow ‘ōhi‘a to regain a certain local dominance. Moreover, when soil fertility declines through leaching in the course of soil aging, the tree fern component probably becomes less vigorous and more scattered. Under these conditions, ‘ōhi‘a may regain its dominance in the course of primary succession. The differential response of shade-born and light-born ‘ōhi‘a seedlings provided new ideas for future research.

Three permanent experimental areas varying in size from 4000 m² to 6000 m² were established in partial dieback stands on moderately well-drained soils. In each area, 60 trees with partial foliage loss were selected for continued monitoring. We devised three treatments for each subgroup of 15 subject trees growing together on subplots: (1) thinning of neighboring trees, (2) fertilizing, and (3) thinning and fertilizing. In addition, 15 untreated subject trees were used as a control group at each site. Results after almost 3 yr of monitoring showed that a small proportion of subject trees died in each area regardless of whether they were treated or not. The Saddle Road site had higher losses than the Puu Makaala and Thurston sites. The trees that died were generally those that showed the highest loss of leaves (> 50%) before the experiment was started. The thinning treatment had generally no effect on releasing the subject trees. Therefore, the trees were not under any significant intraspecific competition pressure as had been assumed earlier. Fertilizing and the combined treatment had an effect on the surviving subject trees in most cases by increasing their diameters (Gerrish and Bridges 1984). However, foliar resprouting or an increase in leaf biomass could not be detected as in the earlier fertilizing experiment of Kliejunas and Ko (1974). The recovery with the same rate and type of NPK fertilizer in our three experimental sites was not as dramatic as that reported by Kliejunas and Ko.

Historical Research

Holt (1983) made a detailed study of the file records, reports, and publications issued in connection with the so-called “Maui forest disease” or “Maui forest trouble,” which was researched by Lyon (1909, 1918, 1919) and others earlier in this century. When Lyon and collaborating entomologists could not find any biotic agent to be responsible for the ‘ōhi‘a dieback on Maui, he concluded that the forest had died due to soil toxification brought about by soil aging. He did not believe in another opinion raised at that time (Curran 1911) that the forest had collapsed because of a devastating storm. Neither did he consider

Selling's (1948) suggestion that the forest had died from a change in climate a valid explanation. Instead, Lyon went on in concluding that 'ōhi'a, being a pioneer species, could not adapt to the changes that come about with soil aging. He believed this to apply to the Hawaiian vegetation in general and advocated replanting the Maui dieback area with nonnative tree species adapted to older soils.

Lyon's management recommendations were adopted by Hawaii Territorial Forestry, and about half of the "Maui forest trouble" area was later replanted with *Eucalyptus robusta* and *Melaleuca leucadendra* (Holt 1983). The replanting was done to save the watershed which, according to Lyon, was deteriorating because of the 'ōhi'a dieback. However, the Maui sugar planters did not agree with Lyon. They voiced their opinion in memoranda saying that the watershed had not deteriorated and that whatever native vegetation cover was in the dieback area, it was doing its job in regulating the water flow.

Later, Selling (1948) published his work on pollen statistics recorded in Hawaiian rain forest bogs (on Maui, Molokai, and Kauai). He found fluctuating amounts of 'ōhi'a pollen, tree fern spores, and other tree pollen in his bog profiles. Selling believed these fluctuations to reflect climatic changes but he had no dates to back up his conclusions. Through recent historical research by Takeuchi (1985) and efforts of Jim Juvik (personal communication), Selling's work will be newly interpreted. The 325-cm-deep Molokai bog profile of Selling appears to have started to form about 8000–10,000 yr ago, according to Juvik. If one portrays Selling's pollen diagram of 'ōhi'a over the time interval of 10,000 yr (Mueller-Dombois, Vitousek, and Bridges 1984: 80), many of the fluctuations appear at approximately 300–400 yr intervals. The latter time span may coincide with the generation time or average life span of 'ōhi'a tree populations as estimated by Porter (1973). This is a tentative but very important historical finding. One thing is very clear from Selling's work: 'ōhi'a has not declined over the past 10,000 yr. Instead, it can be characterized as an "oscillating persister" in primary succession. I have described the concept oscillat-

ing persister, for *Canavalia kauensis*, the endemic vine that undergoes periodic dieback in the coastal lowland ecosystem of Hawaii Volcanoes National Park (Mueller-Dombois 1981b).

Evolutionary Research

Adee and Wood (1981) focused on what they called the "adaptive strategy of 'ōhi'a" as part of their dieback impact and response research. Part of our future research, likewise, was going to be devoted to the successional adaptation of 'ōhi'a as explained under the rain forest life-cycle concept described in the 1977 CPSU report (Mueller-Dombois et al. 1980: 44–45).

With the new funding base obtained from the NSF in 1979 for ecosystem analysis research, Lani Stemmermann began to explore our earlier indications that the 'ōhi'a species (*Metrosideros polymorpha*) may contain "successional ecotypes," i.e., races or varieties that follow each other or overlap along successional gradients. We were concerned mainly with the primary successional gradient associated with soil aging, but we also studied the secondary successional gradient associated with the recovery phases following dieback.

Stemmermann (1983) used three approaches. The first was to collect seeds from 'ōhi'a populations growing on a range of young-to-old volcanic substrates. She recognized these populations as different varieties and asked as the first question if these would maintain their varietal characteristics when grown in a common transplant garden. For the latter she used two large tanks with sloping surfaces and controlled water tables. Each tank was filled with a different volcanic soil. Second, she carried out field surveys of 'ōhi'a varieties to determine their quantitative overlap or sympatric relationships on substrates of different ages. Third, she investigated spatially overlapping varieties as to their physiological adaptation relative to the habitats in which they grow. The latter approach is also currently being used by Joan Canfield for two 'ōhi'a taxa growing sympatrically in Alakai Swamp. The physiological properties investigated in both

cases are plant water potential and stomatal behavior (Robichaux et al. 1984).

Some of Stemmermann's (1983) results have been published. They show first of all that the varietal characteristics are indeed genetically controlled, since the seed lots maintained their own recognizable characteristics when grown as seedlings under uniform conditions. Moreover, Stemmermann found that the pubescent varieties grow much faster than the glabrous varieties in their early stages of growth. A faster early growth rate is typical for pioneer trees such as represented by certain pine species on the mainland. A slower growth rate is typical for seral tree species such as represented by spruces and firs or certain late-successional hardwoods in eastern North America. These follow each other in succession in several continental forests in the northern hemisphere. Pines, like pubescent 'ōhi'a, are also more xerophytically adapted than spruces and firs, which show more mesophytic tendencies, like the glabrous 'ōhi'a varieties.

One of the exciting new aspects of this dieback-related evolutionary research is that it has added a new dimension to the concept of "adaptive radiation" in Hawaii. This is the evolutionary adaptation of species in a successional or chronosequential sense rather than in a spatial or geographic sense only. It implies that Hawaiian plant species may have segregated genetically into successional functional roles. This latter possibility was not considered by Lyon (1918, 1919), who thought that Hawaiian species were outliers of an impoverished continental flora representing only one successional role, namely that of pioneer species.

Dieback Research Elsewhere

Stand-level diebacks similar to those found in Hawaii occur in other indigenous Pacific forests. Stand-level or canopy diebacks are common in monodominant *Eucalyptus*, *Nothofagus*, and *Metrosideros* forests, and also in forests dominated by other genera. During the last 2 yr, I have written several papers about these similarities (Mueller-Dombois 1982a, b, 1983a, b, c). They include similarities in types

of dieback, such as found in our bog-formation, displacement, and replacement (wetland and dryland) diebacks, and similarities in research approaches and findings (Mueller-Dombois 1983d).

For example, the *Nothofagus pullei* dieback in montane Papua New Guinea was also once thought to be caused by *Phytophthora cinnamomi* (Arentz 1983). Lack of clear associations of this root pathogen with dieback stands resulted in an abiotic-biotic factor complex theory (Ash 1982). A symposium was recently published for the various forms of *Eucalyptus* dieback in Australia (Old, Kile, and Ohmart 1981). Here, the pathological viewpoint is dominant, but several authors seriously doubt the primary influence of biotic agents for certain types of *Eucalyptus* dieback.

In New Zealand, the *Nothofagus* and *Metrosideros* forest diebacks have been attributed largely to introduced animals as the principal killer agents (i.e., the European red deer in *Nothofagus* forests and the Australian opossum in *Metrosideros* forests). More recent research has changed emphasis to abiotic factors such as climatic stress (Jane and Green 1983, Skipworth 1983, Wardle and Allen 1983). A special symposium was held 2 yr ago in Tongariro National Park (Silvester and Watt 1983), where the problem of deterioration of the park's indigenous *Nothofagus* forest was of prime concern to the New Zealand Park Service. Our 'ōhi'a dieback research was presented there by Gerrish (1983) and created some interest. New thought was given to the question of how trees die without external stress under natural conditions (Benecke 1983). Several papers have since been published by Stewart and Veblen (1982, 1983; Veblen and Stewart 1982) on the *Metrosideros* dieback in New Zealand. These authors blame the species *M. umbellata* itself for much of its dieback, as I have done for 'ōhi'a in the cohort senescence theory (Mueller-Dombois 1982a, b, 1983a, b, c).

Mueller-Dombois et al. (1983) reviewed several of the so-called forest-decline diseases (Manion 1981) that have been reported during the last few decades on the United States mainland. These include the little-leaf disease of southern pines, western white pine pole

blight, oak decline, and maple and birch diebacks in the northeastern United States. We found that they can largely be explained by the cohort senescence theory.

Currently, much is made of acid rain killing forests in the Atlantic region of Europe (Forstwissenschaftliches Centralblatt 1981, Landesanstalt für Oekologie 1982, Ulrich 1982) and North America (Smith 1981, Vogelmann 1982). There is little doubt that a new abiotic stress complex has been added to the Atlantic forest systems, but few clear-cut relationships have been established thus far that tie forest canopy dieback directly to acid rain.

By combining our research experience on the Hawaiian 'ōhi'a dieback with the information gained from the first Pacific International Dieback Symposium held in Dunedin, New Zealand, in the spring of 1983, I was able to present a new Pacific perspective on the Atlantic region dieback (Mueller-Dombois 1984). This new perspective gives rise to a third factor complex in the dieback syndrome that has rarely been emphasized. This factor complex is comprised of the demographic life stage, physiological behavior, and population dynamics of the dieback species itself. In the 1981 DLNR report only two factor complexes were considered, biotic factors and environmental factors. Our more recent findings in combination with the earlier ones lead to the inescapable conclusion that the third factor complex, i.e., the internal or autogenic stresses in the dieback populations themselves, should receive much more attention. This is particularly true for 'ōhi'a dieback, where the third factor complex seems to operate at the primary level of causation.

PUTTING THE FACTS TOGETHER

The disease research report of the U.S. Forest Service (Papp et al. 1979) concluded that pathogens, including insects, play a secondary role in dieback. Instead, environmental factors were considered to play a more important role than pathogens. This hypothesis was followed up with the hydrological and climatological research of Doty (1980,

1982, 1983) and the vegetation research of Adee (1980, Adee and Wood 1981).

Our earlier conclusions were similar (Mueller-Dombois 1980, Mueller-Dombois et al. 1980). Further research was seen to be useful in studying climatic instabilities, soil factors, and stand factors according to our 1980 research hypothesis, which said "that the dieback is initiated by a climatic instability which becomes effective through the soil moisture regime under certain conditions of forest stand maturity" (Mueller-Dombois 1980: 159).

Climatic Instability

Doty's (1982) and Evenson's (1983) analyses of long-term precipitation records were very important and revealing about the causes of dieback. Both authors independently agree in their conclusions that the year-to-year precipitation fluctuations show no correlation to 'ōhi'a dieback. The idea (Mueller-Dombois 1980: 160) that a series of years with greater than normal rainfall may have resulted in the drowning of root systems of 'ōhi'a stands in poorly drained sites or that particularly dry years may kill stands on well-drained sites seems now much less probable.

Furthermore, the findings of Doty (1983) that year-to-year variations in stream flow from the Hilo watershed show no relationship to the dieback events in the Hilo Forest Reserve (Petteys, Burgan, and Nelson 1975) are further evidence for the nonrelationship concluded from the rainfall analyses.

This does not mean, however, that there may not be still other climatic instabilities (e.g., in connection with El Niño) that could have caused dieback. Two other possibilities were mentioned, storm events (by Evenson 1983) and seasonality (by Doty 1982). Storm events, if very strong, may act like hurricanes in breaking off tree crowns or branch systems or in leveling whole forest stands. However, this sort of violent disturbance is not reflected in the typical 'ōhi'a dieback stands. Storm events of a lesser nature, such as the regularly recurring Kona storms (with gusts up to 50–80 km/hr), can only be considered as secondary causes from our field and experi-

mental research. But as such they may be at least as important as the pathogens investigated. Seasonality, i.e., the number of consecutive months (rather than years) with either excessive or very low rainfall, should be investigated particularly in connection with El Niño. A high number of consecutive months with low rainfall could conceivably kill a vigorous forest stand. Thus, there are other important climatic parameters that have not yet been fully investigated. However, the non-homogeneous distribution of the dieback stands or their patchiness in the dieback territory as a whole suggests that a climatic instability alone cannot account for the dieback patterns. Soil factors were considered to play another important role.

Soil Factors

Soil factors could only be considered as killing vigorous forest stands if they occurred in a drastically fluctuating manner. Doty's (1980) monitoring of water table fluctuations in adjacent dieback and nondieback stands revealed no difference between the two. He had studied both stand conditions on a range of poorly to moderately drained soils and concluded that the fluctuations do not explain much about the dieback. One may go a step further and hypothesize that dieback was not caused by poor drainage at all. Longer-term monitoring of Doty's stations may have been more revealing. But the presence of many dieback stands on well-drained sites can serve as an additional support for this hypothesis.

Conversely, we have monitored soil-surface moisture fluctuations over 2 yr in experimental plots covered with dieback stands on well-drained to moderately drained sites (Gerrish and Bridges 1984) and found that soil moisture never dried up beyond the wilting percentage even during prolonged dry periods.

Jacobi's (1983) aerial photographic analysis of the spread pattern of dieback incorporated known soil factor variations. Dieback on the poorly drained pāhoehoe site continued to spread (from 1965 to 1977) in spite of the fact that annual rainfall was well below normal for several years in a row. The dieback stopped in 1977 in the middle of the same

poorly drained pāhoehoe site when rainfall was slightly wetter than normal. In this case, dieback seems to have little to do with the interaction of precipitation and soil moisture regime.

We have no evidence that soil chemical factors are acting in a drastically fluctuating manner. This also seems unlikely, although Ulrich (1981*a, b, c*) has suggested a fluctuating chemical mechanism in connection with the Atlantic forest-stand dieback. Kliejunas and Ko's (1974) findings that low-vigor 'ōhi'a trees could be revived by additions of NPK fertilizer indicated that nutrient deficiency acted as a gradual stress rather than sudden disturbance triggering synchronized mortality. Gradually increasing rather than fluctuating stresses were also concluded from our findings of nutrient imbalances (Balakrishnan and Mueller-Dombois 1983). These gradual stresses are seen as of two kinds, i.e., nitrogen deficiency in well-drained young volcanic soils and potential metal toxicity in older soils, particularly when poorly drained. However, another nutrient relationship points to the life stage of the tree stand as a factor. This is the less vigorous recovery of the tall-stature stands at our three experimental sites (Gerrish and Bridges 1984) as opposed to the more vigorous recovery of the low-stature stands of Kliejunas and Ko (1974).

Stand Factors

Early on, we recognized that only the canopy trees were dying in the dieback stands and not the undergrowth. This important fact was supported independently by Adee's (1980) work. Doty's (1983) stream flow analysis gave further indirect evidence in that stream flow was not affected by 'ōhi'a dieback events in the Hilo watershed. In other words, dieback over large areas did not cause any deterioration of watershed values, a finding also revealed for the former "Maui forest trouble" by Holt's (1983) historical research.

The generally uniform morphological structure of 'ōhi'a stands has impressed other researchers in the past, e.g., Vogl (1969), who regarded them as even-aged. Our recent re-analysis of dieback stands in permanent plots

(Jacobi, Gerrish, and Mueller-Dombois 1983) brought further evidence that 'ōhi'a reproduces in cohorts. The term *cohort* is defined in *Webster's New Collegiate Dictionary* as "a group of individuals having a statistical factor (as age or class membership) in common." Thus, it is reasonable to speak of canopy cohorts when stands comprised of individuals of the same species exhibit uniform canopy structure. The canopy may be closed, open or sparse, but the individual trees belonging to the canopy cohort must be relatively uniform in height, branching pattern, and bark characteristics. Such a canopy cohort may contain trees with a wide range of diameters. Although tree age would be an invaluable parameter in the detection of cohorts, according to the above definition, one can consider trees as members of a cohort stand even if their ages are not known. Moreover, demographic research has established that morphological or architectural parameters in plant populations are often better predictors for their life stages than are their actual ages (Silvertown 1982).

Our as yet unpublished tree population data reveal that most of our closed, non-dieback 'ōhi'a stands contain two cohorts, a canopy cohort and a cohort of small seedlings. They lack a sapling cohort. However, many of the older dieback stands have a sapling cohort. Moreover, dieback stands sometimes contain a numerically small cohort of larger-diameter survivors. This indicates that not all canopy trees have died synchronously in those stands and that the few surviving trees may grow beyond the general dieback phase to sometimes twice the diameter of the dieback trees. This puzzling pattern needs further study.

Another stand factor mitigates against strong abiotic disturbances causing 'ōhi'a dieback. This is the presence of small 'ōhi'a seedlings in dieback and nondieback stands. Evidently, not all seedlings become established after canopy dieback, but many do (Burton and Mueller-Dombois 1984). It is quite certain that the factor causing death of the canopy trees is not operating in the undergrowth or the seedlings of the dieback species. Therefore, the primary dieback cause can

hardly be a violent physiological or physical disturbance such as a drought, flood, or strong storm.

DISTURBANCE, DISEASE, OR SENESCENCE?

Papp et al. (1979) concluded that pathogens may accelerate 'ōhi'a decline when trees have lost vigor from another cause. This other cause then was believed to be an abiotic environmental factor or a disturbance. As indicated in our 1980 research hypothesis, we believed this disturbance to be modified by habitat factors such as fluctuations in soil moisture regime. In other words, we thought that each major dieback type (wetland, dryland, bog-formation, and displacement) had a somewhat different cause. We recognized the wetland and dryland diebacks as fast and the bog-formation and displacement diebacks as slow processes of stand breakdown (Mueller-Dombois et al. 1980).

Yet, in addition to climatic instability we suggested another factor common to all dieback types in our 1980 research hypothesis, namely that dieback occurs "under certain conditions of stand maturity" (Mueller-Dombois 1980: 160). This observation, relating to canopy dieback rather than simultaneous undergrowth dieback provided for an additional focus on stand factors in the etiology of 'ōhi'a dieback.

What are the conditions at stand maturity that must be met before the 'ōhi'a canopy collapses more or less in synchrony? External or environmental disturbances can hardly be considered alone. The decline in vigor at a certain stage of stand maturity must also be controlled by internal factors or stresses, at least in part.

What internal stresses then could be involved? Biotic disease certainly does not play a role. In the case of 'ōhi'a dieback, stand vigor has declined before pathogens play any role. Internal stresses may be associated with the advancing life stage (senescence) of an 'ōhi'a stand regardless of habitat. Earlier, we thought senescence to be the primary cause only in the 'ōhi'a displacement dieback, which we described for the externally least stressful environment, the eutrophic deep-soil habitats

(Mueller-Dombois et al. 1980). Now we believe cohort senescence to be the underlying primary cause for all dieback types recognized (Mueller-Dombois et al. 1983).

Senescence for plants is defined in *Webster's New Collegiate Dictionary* as "the plant growth phase from full maturity to death that is characterized by an accumulation of metabolic products, increase in respiratory rate and a loss in dry weight especially in leaves and fruit." Senescence in plants therefore is associated with physiological changes, which may, for example, provide for a breakdown of the plant's biochemical defenses which in turn allow disease-causing organisms to take hold. But senescence is not a physiological abnormality; it is not a disease. A disease by definition is a physiological or genetic abnormality in an organism or population. Senescence instead is a normal part of life, just as are birth, juvenescence, adolescence, maturity, and death. Different forms or manifestations and lengths of senescing periods may be programmed into the life of certain species (and also subspecies, races, and/or varieties). Some may have short periods, others longer ones. Senescing life stages may be differently manifested in the same species when it grows on different habitats and under different environmental stresses. Under nutrient stress the senescing period may be prolonged. Under eutrophic conditions it may be very short.

According to Harper and White (1974), senescence is not identical to old age, since under certain conditions senescence is partially reversible to a more vigorous life stage, while old age is not reversible. Under certain marginal habitat conditions a cohort stand may progress from an adolescent stage directly into a senescing stage without ever coming to full reproductive maturity. Such situations may apply to the so-called "toothpick" stands, which I have observed on Vancouver Island for western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) and in central Canada for black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). In these stands, the natural thinning process that functions under normal conditions in stand development did not operate. Such situations may thus be considered abnormal senescing.

In the cohort senescence theory (Mueller-Dombois 1982*a, b*, 1983*a, b, c*, Mueller-Dombois et al. 1983), the cohort concept (as defined earlier in this paper) provides in part for the synchrony of dieback among the individuals of the stand in its breakdown phase. Disturbance plays another important part in the theory at two levels. A violent disturbance is postulated as giving rise to a cohort of 'ōhi'a under certain conditions, e.g., following a new lava flow, ash blanket deposit, hurricane, or landslide. Such violent disturbances can be of large or small areal extent, but if 'ōhi'a is present in neighboring stands as a seed source it usually responds by wave regeneration. A good example of this is in some of the forest roads and right-of-ways that go through dieback and nondieback stands. Where jeep traffic is low or along the road sides (e.g., along the upper part of Stainback Highway), 'ōhi'a seedling and/or sapling cohort stands are common. 'Ōhi'a "toothpick" stands have developed on some infrequently driven jeep trails in the center between the tracks. These stands remain dwarfed by periodic physical abrasion of their apical meristems, and may become old and die without ever reaching the flowering stage.

The second level of disturbance in the cohort senescence theory is postulated to occur any time after the senescing life stage has begun. It relates to a fluctuating site factor, such as a Kona storm or a temporary flooding or soil drought, that may not seriously affect a vigorously growing stand of 'ōhi'a but may upset a senescing stand by triggering a dieback. This second-level less violent disturbance may also act as an additional synchronizing factor. After the second level of disturbance the stand may partially recover and the following dieback may be very slow or staggered, particularly if the secondary pathogens (such as *Plagithmysus bilineatus*, *Phytophthora cinnamomi*, or others) fail to infect such stands. This concept of senescence is consistent with that of Harper and White (1974) and other ecologists.

It should be realized that senescence is a natural and normal phenomenon in tree stands. This applies to all forest systems in true nature reserves, where tree cutting is

prohibited or where periodic fire is not used as a management tool to rejuvenate a forest stand. However, not all forest systems or plant communities are made up of a mosaic of cohort stands, as appears to be the case in the Hawaiian 'ōhi'a rain forest ecosystem.

To answer the question posed in the heading of this section: The 'ōhi'a dieback phenomenon is now evaluated as caused primarily by cohort senescence in combination with different kinds of disturbances that vary between sites and islands. It should no longer be evaluated as a disease or physiological abnormality, because enough facts have now been accumulated that speak against such an interpretation. However, disease may enter into the etiology of dieback at a secondary or tertiary level. In this context it would be important also to pay attention to the possible new pathogen on 'ōhi'a recognized recently by Fosberg (1983). A biotic hastening function in canopy dieback may be of co-evolutionary significance in the rejuvenation process of 'ōhi'a stands.

POLICY AND MANAGEMENT CONSIDERATIONS

In our 1977 CPSU report (Mueller-Dombois et al. 1977, 1980) we raised three management-related questions which I repeated earlier in this paper. However, since our research results pointed to a natural cause of the dieback, the National Park Service felt that further research funding should be obtained elsewhere. The U.S. Forest Service was even more pragmatic in its outlook; it terminated its own mycological, entomological, climatological, hydrological, soils, and vegetation research because 'ōhi'a dieback turned out not to be a disease. As such, 'ōhi'a dieback lost its urgency as a management-related problem, because it was felt that nothing could be done if dieback is a natural phenomenon.

So, where do we stand now with regard to input for policy and management considerations? Since we obtained new funding from the NSF, our focus has not been to follow up on management-related problems, but instead to concentrate on dieback etiology in an ecosystem context. Therefore, we do not have all the answers to the problems concerned, for

example, with regard to the impact of dieback on rare endemics or introduced species. Questions of such relationships have only recently become important to native ecosystem management in Hawaii. However, it is possible to address some general policy and management concerns. These are discussed below.

Dieback and Preserve Design

Because of all the research findings discussed above, we cannot consider the Hawaiian rain forest to represent a climax forest in the pattern sense of Whittaker (1953). A climax forest in this sense is a forest in dynamic equilibrium with its environmental factors in which the species composition remains constant over long periods of time. One visualizes a closed-canopy forest, certainly without large-scale canopy dieback, but with a few dead or dying trees or tree groups here and there. Following their collapse or breakdown, new vegetation fills these gaps so that the structure of the forest remains essentially constant. Moreover, the important canopy species are considered to reproduce more or less continuously, and their populations are represented numerically in larger numbers in the undergrowth and subcanopy than in the canopy.

This concept does not apply to the Hawaiian rain forest. Instead, we see this forest as made up of a spatial mosaic of cohort stands, almost like a plantation forest under sustained yield management. The natural mosaic of cohort stands is not in such a neat array of differently aged or differently sized cohort or plantation stands as is a man-made forest, so the natural mosaic can be conceived as in disarray, and we do not know if its yield is sustained. Yield in this case refers to the forest's different life stages or growth phases. This becomes critical if we believe that we can reduce the Hawaiian native rain forest into smaller and smaller fragments (Mueller-Dombois 1982c). For example, large segments or cohort stands may be at approximately the same life stage, while other smaller and more randomly distributed segments may be in different life stages. Moreover, the underlying habitat mosaic provides for still greater restrictions.

For a proper approach to preserve design,

this rain forest life cycle should receive priority attention in management-related research. The underlying habitat mosaic should be mapped independently of the overlying forest vegetation pattern. The latter should be re-studied and reevaluated spatially so that we know how to design a preserve in which a sufficient number of all forest life stages are preserved. At this point we can only say that a closed, healthy-looking 'ōhi'a forest is certainly not a good guide for preserve design. This forest may go into dieback in the next 50–100 yr. At that time, environmental conditions will change for all associated species in that forest, and competitive relationships between species will change.

At this time, we should consider including in a proper native rain forest preserve not only the good-looking closed-canopy forest, but also all its other important structural variations. We can expect these structural variations to move laterally through the whole ecosystem given enough time. In this case, time relates to the mean life span of 'ōhi'a cohorts and to the frequency and size of catastrophic disturbances in different locations of the whole rain forest ecosystem.

Dieback and Hydrology

Since watershed values have evidently not deteriorated under 'ōhi'a dieback in the Hilo watershed (Doty 1983) nor on Maui earlier in this century (Holt 1983), more confidence should be placed in native Hawaiian vegetation as a watershed cover. It should therefore not be necessary to plant exotic tree species, such as *Eucalyptus robusta* or *Melaleuca leucadendra*, as was done in the Maui dieback area following Lyon's recommendation. Even "enrichment planting," as suggested in the management alternatives of the 1981 DLNR report, should not be advocated. The Hawaiian vegetation apparently can cope with the changes during and after dieback in the sense that disturbances such as are imposed by loss of 'ōhi'a canopy are balanced by the undergrowth.

Management-related research is needed to find out how deterioration of watershed hydrology is prevented by the vegetation that remains after canopy dieback. Only if we

understand how Hawaiian watersheds work under native and introduced vegetation, can we really begin to make wise management decisions.

Dieback and Soil Fertility

The 1981 DLNR report considered fertilizing 'ōhi'a stands as a management option to prevent dieback. However, it recognized correctly that this would merely prolong the life of existing stands, which eventually would die anyway. Moreover, fertilization was considered too costly as a viable management technique.

We predict that fertilizing dieback stands on an operational scale would be a mistake in forest management. This observation is based on the fact that nutritionally imbalanced or even potentially toxic soils—as are found under native 'ōhi'a forest stands—are among the best "exlosures" for many alien plant species (Gerrish and Mueller-Dombois 1980). 'Ōhi'a reproduction in association with canopy dieback is most successful on nutritionally poor substrates, because aggressive exotic species are generally prevented from becoming serious competitors on these substrates. 'Ōhi'a seedlings and saplings are tolerant of poor nutrient substrates. They grow slowly on these substrates and form a second canopy only if they are not overwhelmed by competing species in their seedling and sapling stages.

'Ōhi'a displacement dieback was originally considered only for the nutritionally richest habitats, the deep eutrophic ash soils. Here, native tree ferns outcompete 'ōhi'a following dieback. The idea of removing tree ferns to allow 'ōhi'a reproduction to take advantage of the nutrients does not work, because these nutrient-rich sites are immediately invaded by a large host of exotic species (Burton 1980*b*). The stabilizing position of tree ferns on nutrient-rich soils was also recognized by Becker (1976).

NEW RESEARCH NEEDS

While the relationship of dieback to preserve design, hydrology, and soil fertility provides new background for management-related

research, more basic research is needed on dieback etiology in Hawaii. Senescence has received little attention in ecosystem research and management in general. Considerable research has been done on monocarpic senescence (Thiman 1980), but little on polycarpic senescence (Molisch 1938, Ward 1982). Moreover, senescence has rarely been studied at the population level, and much less so in the context of community and ecosystem analysis.

For example, we need to know the biochemical changes that take place during stand-level senescence. Furthermore, we need to know how spatial patterns of dieback are related to spatial patterns of the original seedling and sapling cohorts. Moreover, we need to know how 'ōhi'a stands grow and develop over their life-span. Long-term permanent plot studies are extremely important for this purpose, particularly if they are selected in stands of the same major habitat type but in different stages of cohort development. It will be important to put new research effort into studies of aging 'ōhi'a trees and cohorts. It will also be important to separate gradually increasing internal stresses from gradually increasing external stresses. This may be done by studying 'ōhi'a stands experimentally on stressful nutrient-poor soils and on nonstressful nutrient-rich soils. Physiological, anatomical, and morphological methodology at the individual, population, and ecosystem levels of organization should be utilized.

Further historical research is needed to find out how 'ōhi'a and its major associated community members have behaved in relation to real time scales. This can be accomplished by carbon dating of bog profiles. To interpret the pollen history of a bog, it will be necessary to determine how far pollen travels from healthy stands. Similarly, research should be done on the distribution and viability of 'ōhi'a seeds and seedlings in relation to dieback and other disturbed areas that have been disturbed at different size scales and by different factors (such as lava flows, hurricanes, landslides, and fires).

A new integrated and interdisciplinary research program should be developed that focuses on modeling the Hawaiian dieback for predictive purposes. This program should

include not only ecologists, but geneticists, specialists in nutrient cycling, hydrologists, mycologists, and entomologists. It is important that we find out as much as we can about how the native Hawaiian forest ecosystem functions. Some of this knowledge will become important in the near future when we may want to compare Pacific forest ecosystems with those in the acid-rain-impacted and industrially polluted Atlantic region. Initial steps for such comparisons, using the Hawaiian rain forest as a biological control, are now underway (Mueller-Dombois 1984, Mueller-Dombois, Vitousek, and Bridges 1984).

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