

'OHIA' DIEBACK AND PROTECTION MANAGEMENT
OF THE HAWAIIAN RAIN FOREST

Dieter Mueller-Dombois

ABSTRACT

The facts about the 'ohi'a (Metrosideros polymorpha) rain forest dieback are put together in abbreviated form as far as they have been revealed over the past 12 years of intensive research in Hawai'i. They lead to the conclusion that this native rain forest ecosystem is made up of an irregular and dynamic mosaic of 'ohi'a cohort stands occurring side by side. These are in different and similar life stages and successional development. Unlike a multi-species forest with steady-state stand segments, the Hawaiian rain forest appears to break down periodically in larger and smaller stand segments. The primary cause of this breakdown or canopy dieback is considered to be cohort senescence rather than biotic diseases or abiotic environmental fluctuations. The last 2 disturbances are believed to act at secondary levels. The original mosaic, however, is suggested to be largely the result of catastrophic disturbances, which recur rather infrequently on the same site. Recovery following dieback depends largely on the underlying soil-substrate mosaic and the associated species. On nutritionally poor sites, 'ohi'a sapling cohorts following dieback have a better chance of developing a second canopy than on nutritionally rich sites where competition of other species is strong.

This new knowledge has important implications for protection management, particularly with regard to the design of Hawaiian rain forest preserves. For this, ecosystem criteria referring to the considerations of vegetation dynamics given here and the knowledge gained from a one-time survey of current native forest bird refugia by the U.S. Fish and Wildlife Service should be combined. A number of specific management-related research tasks are suggested, such as mapping an already established physical and chemical habitat classification (at 1:24,000) and superimposing on it the

forest vegetation according to structural and compositional criteria in terms of stand life-stage and canopy vigor. A new strategy for alien species control involving soil-site fertility and dieback criteria is suggested for testing. Further monitoring of an established network of permanent plots and experimental sites is considered a continuing source for management-related information.

INTRODUCTION

When driving along the major access routes through the Hawaiian rain forest, one notices 'ohi'a (Metrosideros polymorpha) tree stands in different stages of vigor and stand condition. Some stands are dense with closed canopies, others contain trees with stag-headed (= dead) crowns and leafy branches along their trunks. Some stands consist of scattered 'ohi'a trees with dense treefern (Cibotium spp.) undergrowth, others of mostly dead 'ohi'a trees, while still others are green and healthy looking.

In the early 1970's, the dead and dying 'ohi'a stands were widely thought to be infected by a new and deadly disease (Burgan and Nelson 1972). A prediction was made (Petteys, Burgan, and Nelson 1975) that the entire 'ohi'a forest would soon succumb to this disease. An estimate for the extinction time was given as 15 to 25 years. The estimate was based on an analysis of 3 successively taken sets of aerial photographs (dated 1954, 1965 and 1972) and covering a territory of 80,000 ha on the windward slopes of Mauna Kea and Mauna Loa on the island of Hawai'i.

At the end of almost a decade of intensive disease and insect pest research involving many experts, it was concluded that the 'ohi'a "decline" or "dieback" was not caused directly by any of the discovered biotic disease or pest agents (Papp et al. 1979). Instead, it was considered to be caused by a combination of factors involving abiotic, environmental disturbances or stresses together with biotic agents, with the last playing a secondary role (Hawai'i Department of Land and Natural Resources 1981).

FIVE FACTS FROM VEGETATION RESEARCH

Research on soils and 'ohi'a tree populations throughout the 80,000 ha terrain on the island of Hawai'i was begun in 1975, first by a team consisting of myself and several of my graduate students (Mueller-Dombois et al. 1977, 1980) and then also by the U.S. Forest Service (Adee and Wood 1981). A number of facts were discovered. The most outstanding of these were:

1. That in many cases, 'ohi'a dieback was associated with 'ohi'a reproduction.
2. That the 'ohi'a dieback in each situation sampled was largely restricted to the canopy trees.
3. That the so-called "healthy" stands had usually no 'ohi'a saplings in their undergrowth.
4. That dieback stands were often sharply delineated from non-dieback stands along lava-flow boundaries.
5. That stand-level dieback occurred over the whole spectrum of soil substrates; that is, stands were dead or dying on relatively young and old lava flows; on pahoehoe and 'a'a lava; on well-drained and poorly-drained sites; on deep soils from volcanic ash; and also in young (200 years), recent (1,000 years) and old (over 5,000 years) soils and on permanently water-soaked, boggy soils.

'OHI'A DIEBACK SHOWS DIFFERENT PATTERNS AND SITE RELATIONSHIPS

We soon discovered that dieback was differently manifested over this site spectrum, and we distinguished 5 forms of stand-level dieback. These we called (Mueller-Dombois 1980, 1981):

1. Wetland dieback
2. Dryland dieback
3. 'Ohi'a displacement dieback
4. Bog-formation dieback
5. Gap-formation dieback.

Both wetland and dryland diebacks refer to 'ohi'a stands dying on lava flows or histosols with soil less than 50 cm deep over lava rock outcrop. The difference is that wetland dieback is associated with poorly-drained and dryland with well-drained substrates. Wetland dieback is more area-extensive, while dryland dieback is currently more restricted. Both forms of dieback are associated with 'ohi'a reproduction, that is, they are "replacement diebacks".

'Ohi'a displacement dieback occurs typically on deep soils from nutritionally rich (= eutrophic) ash, where 'ohi'a sapling development is suppressed (= quantitatively "displaced") by the dense growth of treeferns (Burton and Mueller-Dombois 1984).

Bog-formation dieback occurs also on deep soils from volcanic ash, but on those that are totally and permanently waterlogged. For a general distribution of these sites and dieback types, see Jacobi, Gerrish, and Mueller-Dombois 1983. In the bog-formation dieback, 'ohi'a reproduction appears to be mostly vegetative, often patchy, and of poor growth.

Gap-formation dieback was originally discovered on the knolls, ridges and slopes rising out of the boggy terrain (northwest of Hilo), where koa (Acacia Koa) is sometimes a canopy associate of 'ohi'a (Mueller-Dombois 1981). The term gap-formation dieback refers to small stands dying in patches, where the trees lose their leaves without obvious physical damage to their branch system (like deciduous trees out of season). This feature applies to all 5 types of canopy dieback, but gap-formation dieback typically occurs on well- to moderately well-drained soils from ash (> 50 cm deep) that are not eutrophic, but rather nutritionally poor (= oligotrophic) or intermediate (= mesotrophic). 'Ohi'a reproduction is usually evident in such dieback stands, but undergrowth competition may lead to displacement in some cases.

The U.S. Forest Service vegetation and soil study team, directed by Ken Adee (Adee 1980, Adee and Wood 1981), came to very similar conclusions and discovered independently almost the same 5 dieback types, but Adee and Wood gave them somewhat different names (Hawaii Department of Land and Natural Resources 1981). For example, they recognized a "pubescent structural dieback" type on well-drained soils, which we included in our dryland dieback type. Dieback stands on well-drained soils are indeed often of the pubescent-leaved varieties (M. polymorpha var. polymorpha or var. incana) but also include glabrous forms of 'ohi'a belonging to the varieties glaberrima and/or macrophylla.

During our initial field research, we noticed that in some places dominantly pubescent-leaved 'ohi'a stands seemed to be dying, while the upcoming saplings were dominantly glabrous forms. This led to the hypothesis of successional ecotypes, which we proposed for future study in our first synthesis report (Mueller-Dombois et al. 1977). Another idea put forth in that report was that the 'ohi'a rain forest in Hawaii may consist of stands in different life phases, and we proposed the hypothesis of a forest life cycle, which I will refer to again.

ALTERNATE CAUSE HYPOTHESES

In the initial proposal to the National Park Service for dieback research, which resulted in the needed money in 1975 to do the first basic ecological fieldwork, I proposed as an alternative to the disease hypothesis that the dieback may be "a normal phenomenon, a developmental stage in the primary succession of an isolated rainforest ecosystem" (Mueller-Dombois 1974: 10). This natural-cause hypothesis was based on prior fieldwork (Mueller-Dombois and Krajina 1968) and a literature survey, which revealed that stand-level

dieback in the Hawaiian Islands, particularly in its rain forests, had been noted and discussed by a number of authors (including Clarke 1875; Miller 1900; Lyon 1909, 1918, 1919; Curran 1911; Selling 1948; Fosberg 1972) prior to the discovery of dieback in the early 1970's.

At the conclusion of our basic ecological field survey (Mueller-Dombois et al. 1980), I proposed a new consolidated cause hypothesis for future research on the etiology of the Hawaiian rain forest dieback with the following words: It seems likely "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).

Since then a number of new facts have been accumulated which I can now put together under the 3 points raised in this more recent causal hypothesis.

PUTTING THE FACTS TOGETHER

Climatic Instability Factors

Doty (1982) and Evenson (1983) both studied long-term precipitation records in relation to dieback and independently came to the same conclusion that the year-to-year fluctuations in rainfall bear no clear relationship to 'ohi'a dieback. In an elaboration of the above-stated hypothesis, I suggested (Mueller-Dombois 1980:160) that a sequence of years wetter than normal may result in the drowning of root systems of 'ohi'a stands on poorly-drained sites, and that particularly dry periods may kill stands on well-drained sites. This part of the hypothesis now seems less probable. Moreover, Jacobi (1983) in his air-photo analysis of a 1,600 ha area near the 1,220 m level at the Saddle Road found that the wetland dieback progressed there particularly from 1965 to 1977, when rainfall was excessive only in 1969 and then remained below normal for several years in a row (from 1970 to 1975).

Two other important studies were done by the U.S. Forest Service. For 2 years, Doty (1980) monitored water-table fluctuations in adjacent dieback and non-dieback stands in the Waiakea Forest Reserve. He recorded considerable water-table fluctuations in relation to rain showers, but the water-table fluctuations were of similar magnitude in dieback and non-dieback stands, and non-dieback (or "healthy") stands did not become dieback stands when their root systems were temporarily flooded. Doty (1983) also analyzed stream flow data of the Wailuku River, which flows out of the dieback-affected Hilo watershed. He ascertained that

rainfall variations were well reflected in the stream-flow but that the dieback events had no effect on either volume of water or its sediment load and nutrient composition. He explained this with reference to the vegetation research, in which it was found that only the trees were dying while the undergrowth remained stable.

Soil Factors

Even if climatic stresses are involved, they alone can hardly account for the 'ohi'a dieback because of the discontinuous distribution of the dieback stands. Since these stands are often delimited by soil-substrate boundaries, one could think of soil as an important factor.

Kliejunas and Ko's (1974) experiment on fertilizing half-dead 'ohi'a gave strong evidence that nitrogen deficiency plays a role in the dieback syndrome. Since that time, we have completed our soil-nutrient and foliar analyses in relation to the broad spectrum of habitat and dieback types (Balakrishnan and Mueller-Dombois 1983). We found that young volcanic substrates (ash as well as pahoehoe) are particularly deficient in nitrogen; further, that the deep and organically enriched ash soils (about 1,000 years old) of Ola'a Tract are indeed nutritionally rich (= eutrophic), and that the older (over 5,000 years old) substrates exhibit poor nutrient balances, particularly on account of low phosphorus and potentially toxic levels of aluminum, manganese, and iron. Poor drainage and low pH further aggravate metal toxicity. Such soils would not be suitable for crop plants or for nutrient-demanding tree species, and plant nutrient stress is a characteristic of almost all 'ohi'a rain forest sites except the intermediately aged (about 1,000 years old) ash soils.

When we repeated Kliejunas and Ko's (1974) fertilizer experiment in a series of tall-statured dieback stands (Gerrish and Bridges 1984), we found that some dying trees could be revived as measured by diameter increments, but that their crowns did not gain any significant leaf biomass. This placed more emphasis on the third point raised in the 1980 cause-hypothesis, namely on the "certain stage of forest stand maturity", that is, on the life stage of the affected stands.

Stand Factors

Early on we recognized that only the canopy trees of 'ohi'a were dying, while the undergrowth seemed unaffected. This observation argued strongly against the idea of a new killer disease, and also against any violent physical damage (such as feral animals or fire) or severe physiological disturbance (such as air pollution or climatic change) as the cause. That the undergrowth

remains stable during canopy dieback or may even increase in vigor, was indirectly determined also through Doty's (1983) watershed analysis. By not limiting our field research to dieback stands, but including many non-dieback or "healthy" stands in 'ohi'a population samples, we found that the so-called "healthy" stands usually consist of only 2 life-stages of 'ohi'a: mature trees and a scattering of small seedlings on decaying logs. In contrast, dieback stands consisted usually of at least 4 life stages: dieback trees, survivors, seedlings, and, in older dieback stands especially, 'ohi'a saplings. 'Ohi'a saplings often form dense stands, particularly in wetland and dryland dieback areas and along many rights-of-way, even on infrequently driven jeep roads. This is true regardless of location through dieback or non-dieback stands.

A recent reanalysis, after 5 years, of 26 of our permanent plots in dieback stands (Jacobi, Gerrish, and Mueller-Dombois 1983) gave further evidence that 'ohi'a reproduction, in any specific site or stand, occurs in "waves" or restricted periods rather than continuously. Only a disturbance, such as cutting down a stand for a right-of-way or the loss of canopy due to dieback, seems to set the stage for a new 'ohi'a sapling stand to become established. Such a sapling stand when growing on a given site can be called a cohort. The term cohort refers to individuals of the same species or variety when such individuals are members of the same generation occurring together in the same community. Cohort stands can be in different stages of development, such as juvenescence, adolescence, maturity, and late maturity or senescence.

Our earlier finding that dieback stands are often delimited from non-dieback stands along lava-flow boundaries, made us believe that soil is an important factor. But we have since found many dieback stands that are separated from non-dieback stands by no such soil boundaries. A good example is Jacobi's (1983) air photo analysis, where a wetland dieback on poorly drained pahoehoe progressed to an 'a'a flow and then stopped, but where it also stopped in the middle of the same pahoehoe flow and then did not progress after 1977.

Lava flow boundaries are not only physical soil boundaries. They are also historical boundaries, and the 'ohi'a stand analyzed by Jacobi (1983), which continued to die progressively from 1965 to 1977 across the poorly drained pahoehoe, was most probably in a senescing life stage. It bordered another 'ohi'a stand in a more vigorous life stage growing on the 'a'a lava, but it bordered also a still rather vigorous 'ohi'a stand on the same poorly drained pahoehoe.

From a synthesis of all the facts so far established, the cohort senescence theory was born (Mueller-Dombois 1982a, 1983a, 1983b, 1983c; Mueller-Dombois et al. 1983), and it serves currently as the most plausible explanation of 'ohi'a dieback.

APPLICATION TO MANAGEMENT

A New Viewpoint

When the previous "biological evaluation of the 'ohi'a decline" (Hawai'i Department of Land and Natural Resources 1981) was prepared as a guide to Hawaiian rain forest management by the U.S. Forest Service San Francisco Pest Management Unit, dieback was still viewed as a disease. However, there has been so far no evidence that 'ohi'a as a species has become subject to a disease of either biotic or abiotic origin, nor to a combination of the two. A disease is usually defined as a physiological or genetic abnormality occurring in an organism or population. Aging is clearly not a disease. It is part of life's program, and the dying of trees, particularly during late maturity or senescence, should not be considered abnormal.

What may strike one as abnormal is that such large tree stands are dying more or less in synchrony. However, we have now learned that the Hawaiian rain forest dieback is not entirely unusual. Similar forest stand diebacks occur also in other biomes, particularly where forests are dominated by one or a few canopy species (Sprugel 1976; Ash 1981; Stewart and Veblen 1982, 1983; Arentz 1983; Mueller-Dombois 1983d). Perhaps Hawai'i may be somewhat more extreme in this respect because of its geographic isolation and associated floristic history (Mueller-Dombois 1983c).

It is important to view the Hawaiian rain forest biome as an ecosystem with broader-scale spatial dynamics with regard to protection management than is usually understood from textbook information. The Hawaiian rain forest is not a climax forest in the conventional sense of Whittaker (1953), in which the canopy species are represented in any given forest stand by all age-classes and sizes or life-stages (such as seedlings, saplings, mature and senescing trees). Instead, sapling stands, mature-tree stands, and senescing stands are seen as occurring in a spatial side-by-side mosaic.

Design of Preserves

How did this spatial side-by-side mosaic originate? One thing is clear. The volcanic history has a lot to do with it on the island of Hawai'i. We witness there large stands of 'ohi'a, that is, cohort stands in different life-stages side by side on differently aged

lava flows and ash deposits. Other large cohort stands may have originated from other catastrophic disturbances, such as hurricanes. On the older islands, smaller cohort stands of 'ohi'a are often associated with landslides (Mueller-Dombois 1982b). On the same site-location, catastrophic disturbances are very infrequent. Therefore, an 'ohi'a stand that originated from a catastrophic disturbance is not likely to be destroyed by a similar disturbance during its life time, unlike other forests, e.g. those with frequent fire-disturbance regimes. Thus, a (given) cohort stand in the Hawaiian rain forest usually has a chance to go from its mature life-stage to its senescing life-stage and to canopy dieback under natural conditions. Following that, there is usually a rebuilding of a new sapling stand as explained before, but this depends in part on the present site conditions and other factors, such as the presence of introduced species.

We know now that it is important for the design of ecological reserves in the Hawaiian rain forest biome to incorporate the cohort mosaic of 'ohi'a stands. For example, it does not appear sufficient to preserve a section of the 1942 lava flow, and to consider it an example of the Hawaiian rain forest. It is only an example, although in itself valuable, of a young life-stage of an 'ohi'a forest. Similarly, it is not sufficient to search for good and healthy looking mature 'ohi'a forests, such as occur in the crater-rim area of Hawai'i Volcanoes National Park or in Pu'u Maka'ala, and to set these aside believing they will remain healthy looking and good stand examples forever. In the next 50 or 100 years these good-looking closed-canopy forests may undergo dieback while other stands may mature. However, if other stands, perhaps now in dieback condition, have been subjected to "enrichment planting" with other species (as was suggested in the 1981 Hawai'i Department of Land and Natural Resources report) or if they have been converted to other uses, we will end up with preserves that represent only fragments of the Hawaiian rain forest biome.

Therefore, new management-oriented research is needed for the proper design of Hawaiian rain forest preserves, with ecosystem criteria based on 'ohi'a dieback research. In order of priority, research can be grouped into 3 work tasks: 1) Mapping of the physical habitat mosaic, which has now been established in the form of a simple and workable classification (Mueller-Dombois 1981; Balakrishnan and Mueller-Dombois 1983); 2) Mapping of 'ohi'a stands by stand condition and vigor state, which requires techniques already developed by Jacobi (1980, 1983); 3) The continuation of permanent plot studies (Jacobi, Gerrish, and Mueller-Dombois 1983) and longer-term research on our

experimental sites (Gerrish and Bridges 1984). Tasks 1 and 2 can be applied from present knowledge as immediate work products for management decisions. Task 3 requires longer-term monitoring, which will yield increasing precision in predictive information for protection management.

Rare Endemic and Introduced Species

A number of rare endemic species are distributed throughout the 80,000 ha dieback and non-dieback territory across the eastern slopes of Mauna Kea and Mauna Loa (Mueller-Dombois et al. 1980). What happens to these species following canopy dieback has not yet been established. If species are shade-adapted, they may become locally extinct not only because of the increased exposure to light, but also because of the increased competition by heliophytes, such as the mat-forming native fern Dicranopteris linearis. Do these rare endemics return during canopy closure of the forest, or do they find refuge during the recovery process in the changing matrix of the dominant plant species?

One thing is clear already. Most native Hawaiian rain forest birds use non-dieback forests as refugia (Scott et al., in press) and seem to disappear from dieback stands. Do bird populations return when 'ohi'a cohort stands form closed canopies or regain maturity? And do they migrate in relation to their dynamic rain forest habitat? Such questions are important, if we want to find out how to manage the Hawaiian rain forest for the preservation of rare and endemic species. It is dangerous to use knowledge about bird refugia determined in one survey as a basis for permanent reserves. The reserves may collapse in the not too distant future while in the meantime other potential refugia have been given to other uses.

Senescing stands are a "weak" life-stage. Penetration by alien species during and after canopy dieback is a reality (Jacobi, Gerrish, and Mueller-Dombois 1983) in some cases, and a strong probability in others. Closed or "saturated" native communities are not as prone to alien species invasion as are dieback stands (Mueller-Dombois, Bridges, and Carson 1981). Of course, this depends in part on the life-form of the alien species. Feral pigs (Sus scrofa) may aggravate the effects of canopy dieback and thus aid in converting such stands into alien replacement communities. Little is known about this as yet. However, greater control efforts near dieback stands appear to be prudent (Mueller-Dombois et al. 1980), and the patterns of canopy dieback and recovery may be usefully incorporated into the strategies of protection management.

Soil Fertility

Because of Kliejunas and Ko's (1974) finding that inorganic nitrogen was involved in the 'ohi'a decline, it was suggested in the 1981 Hawai'i Department of Land and Natural Resources report that fertilizing dying 'ohi'a stands is a management option. Primarily because of the high costs of such undertaking, however, this option was not considered viable.

We can now say that fertilizing 'ohi'a dieback stands on an operational scale would probably be one of the worst mistakes in protection management. The reason for this is that dieback on infertile or nutritionally imbalanced soil-substrates guarantees a much better chance of 'ohi'a stand recovery than dieback on nutritionally improved or fertile sites. On fertile sites, we discovered the 'ohi'a displacement dieback. It comes about through the slow growth rates of 'ohi'a seedlings relative to those of the tree fern undergrowth (Burton and Mueller-Dombois 1984). The good 'ohi'a sapling recovery in the wetland and dryland diebacks is clearly a function of the high tolerance of 'ohi'a for nutritionally poor soils and the inhibited growth rate of competitors under such conditions. 'Ohi'a manages to achieve reasonable growth on such oligotrophic sites, while its competitors are kept in check. Moreover, oligotrophic habitats may be considered "natural exclosures" for many aggressive introduced plant species (Gerrish and Mueller-Dombois 1980). Most of the aggressive alien plants are adapted to nutritionally rich soils. They have a hard time competing with the tough and tolerant 'ohi'a on poor native soils in the montane rain forests of Hawai'i (Balakrishnan and Mueller-Dombois 1983).

The suggestion to map already classified physical habitats as a first priority management task, as stated before, would therefore serve at least 2 purposes: 1) the design of viable rain forest preserves, and 2) an improved strategy for alien species control.

Forest Hydrology

Doty's (1983) recent analysis of the Hilo watershed, in which large stands of 'ohi'a were subject to dieback, clearly shows that there is no need to replant trees in order to save the watershed. The native communities, in spite of obvious canopy disturbances, apparently stabilize the water flow primarily through their undergrowth.

Holt (1983) recently established, through historical file and literature research, that fear of losing the forest-watershed cover in connection with the "Maui Forest Trouble" caused a major replanting program with Australian tree species in the 1930's. However, in

this case the sugarcane planters felt no need for this program in spite of the huge 'ohi'a dieback throughout their watershed. Their newly dug Maui ditch system was apparently operating just fine. It was Lyon (1918, 1919) who insisted on replanting with alien species, since he felt that the Hawaiian vegetation consisted primarily of pioneer species that could not adapt to changes such as toxification that come about with aging of tropical soils.

Similar ideas proved to have such a profound effect on forest watershed management in Hawai'i that some foresters believe that native tree species have to be replaced by introduced species. It will be necessary to put more management-related research efforts into finding out just how native species become adapted or decline in relation to soil aging and toxicity. It is of similar importance to find out in what way today's native rain forest vegetation has evolved from pioneer or colonizing ancestors. How far is successional adaptation developed or completed? Or is there a real difference between the isolated Hawaiian biomes and less isolated montane rain forest biomes elsewhere?

Apart from these fundamental questions, there is a real need for more pragmatic forest-hydrology research. Many foresters and biologists will probably agree that water and the native biota are the most important resources of the Hawaiian mountains. Their functioning and conservation management is very compatible with recreational and some forms of agricultural land use.

The U.S. Forest Service should play a more important role in forest hydrological research in Hawai'i. There is a real need to establish more sophisticated and multidisciplinary research on Hawaiian watersheds similar to research at Hubbard Brook and Coweeta in the eastern United States. There are at least 2 good reasons for having such studies in the State of Hawai'i: 1) Hawai'i supports the only large tropical montane rain forest in the United States. Results from Hawai'i are more applicable to other tropical areas than results from temperate forests. 2) Hawai'i can serve as a biological control for forests in the Atlantic region which are now impacted by new industrial stresses from air pollution (Smith 1981) and acid rain (Vogelman 1982; Ulrich 1982). Hawai'i could serve as a biological control for the biogeochemical cycling of nutrients in forest watersheds and the phenomenon of canopy dieback (Mueller-Dombois, Vitousek, and Bridges 1984) in more artificially stressed situations elsewhere.

CONCLUSIONS

Our 'ohi'a dieback research began with an ecological study of the problem as it presented itself during the 1970's. Since dieback did not turn out to be a new disease as most people had expected, agency support for further research was withdrawn. For this reason, we had to turn to the National Science Foundation (NSF) for further support. However, as a basic research supporting institution, NSF was not interested in management-oriented research. As a consequence we had to concentrate our efforts on fundamental research relating to the etiology of the Hawaiian forest canopy dieback and to the long-term ecosystem dynamics and development.

Questions raised in this paper under the section concerned with management application could not be included in our NSF-sponsored research. Therefore, clear-cut recommendations for specific management options or alternatives cannot be given here. Instead, a framework for new management related research is offered. This research should be carried out with agency funding (e.g. from the Hawai'i State Department of Land and Natural Resources, the U.S. Forest Service, the U.S. Fish and Wildlife Service, and the National Park Service).

In summary, management-related research tasks are here restated as:

1. The habitat types should be mapped on a large map scale, such as 1:24,000.
2. Cohort stands should be mapped according to stand condition and life stages on the same scale and superimposed on the physical habitat map.
3. This will form a basic tool for proper "minimal area" design of preserves from the viewpoint of ecosystem dynamics using plant ecological criteria.
4. These criteria should be integrated with those from the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey.
5. New studies should be initiated focusing specifically on the effect of dieback on rare endemic forest species.
6. New studies should be initiated focusing on the effect of dieback on alien species invasion.
7. Alien species control efforts should make use of and test the newly provided physical and chemical habitat classification once it is mapped (see item 1 above).
8. Monitoring vegetation changes in an established network of permanent plots (Jacobi, Gerrish, and Mueller-Dombois 1983) and experimental sites (Gerrish and Bridges 1984) should be continued.

In general, there is a need for a new view of the Hawaiian rain forest as an ecosystem composed of forest life stages which occur side by side in the form of an irregular mosaic. The Hawaiian rain forest should no longer be viewed as an ecosystem that is sick and doomed for extinction. In terms of watershed values, more confidence should be placed on the native vegetation as providing an inexpensive and functionally reliable plant cover. At the same time, there is an outstanding opportunity in Hawai'i for modern forest hydrological research to be done by the U.S. Forest Service as a service to the State, the Nation and the international community of tropical countries. Management efforts to preserve integrated units of the life-stage mosaic of the Hawaiian rain forest are definitely worthwhile. Such efforts should be incorporated as a high priority into Hawai'i Department of Land and Natural Resources management policy.

ACKNOWLEDGEMENTS

The work here presented could not have been done without an initial contract from the National Park Service provided through former Chief Scientist G.A. Smaathers and without the help of Hawai'i County Councilwoman M.K. Lai. Moreover, the writer is indebted to the research efforts of his collaborators including particularly J.D. Jacobi, R.G. Cooray, N. Balakrishnan, G. Gerrish, P.J. Burton, and K.W. Bridges. The draft manuscript was typed by J. Hokama.

Later research efforts were financed through the National Science Foundation, through an East-West Center/University of Hawai'i collaborative grant and a sustaining grant provided by the McIntire-Stennis Foundation. This paper is contribution 25 from NSF Grant 79-10933 and McIntire-Stennis Grant HAW-00684.

LITERATURE CITED

- Adee, K. 1980. Canopy structure in the ohia decline zone of Mauna Kea and Mauna Loa, Hawaii. [Abstract] Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 1. Honolulu: Univ. Hawaii.
- Adee, K., and H. Wood. 1981. Regeneration and succession following canopy dieback in an ohia (Metrosideros polymorpha) rainforest on the island of Hawaii. U.S. For. Serv., Honolulu. Mimeo.
- Arentz, F. 1983. Nothofagus dieback on Mt. Giluwe, Papua New Guinea. Pac. Sci. 37(4):453-458.
- Ash, J.E. 1981. The Nothofagus Blume (Fagaceae) of New Guinea. In Biogeography and ecology of New Guinea, ed. G.L. Gressitt, Vol. 42, Biologica, 355-363. The Hague, Netherlands: Dr. W. Junk Pub.
- Balakrishnan, N., and D. Mueller-Dombois. 1983. Nutrient studies in relation to habitat types and canopy dieback in the montane rain forest ecosystem, island of Hawaii. Pac. Sci. 37(4):339-359.
- Burgan, R. E. and R. E. Nelson. 1972. Decline of ohia lehua forests in Hawaii. U.S. For. Serv. Pac. Southwest For. Range Exp. Stn. Gen. Tech. Rep. PSW-3.
- Burton, P.J., and D. Mueller-Dombois. 1984. Response of Metrosideros polymorpha seedlings to experimental canopy opening. Ecology 65(3):779-791.
- Clarke, F.L. 1875. Decadence of Hawaiian forests. All about Hawaii (Thrum's Hawaiian Annual) 1:19-20. Honolulu: Thos. G. Thrum.
- Curran, H.M. 1911. The Maui forests. Hawaii. For. Agric. 8:185-187.
- Doty, R.D. 1980. Groundwater conditions in the ohia rain forest near Hilo. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 101-111. Honolulu: Univ. Hawaii.
- Doty, R.D. 1982. Annual precipitation on the island of Hawaii between 1890 and 1977. Pac. Sci. 36(4): 421-425.
- Doty, R.D. 1983. Stream flow in relation to ohia forest decline on the island of Hawaii. Am. Water Resour. Assn. Water Resour. Bull. 19(2):217-221.

- Evenson, W.E. 1983. Climate analysis in ohia dieback area on the island of Hawaii. Pac. Sci. 37(4): 375-384.
- Fosberg, F.R. 1972. Guide to Excursion III. In Tenth Pacific Science Congress, rev. ed. Honolulu: Univ. Hawaii.
- Gerrish, G., and K.W. Bridges. 1984. A thinning and fertilizing experiment in Metrosideros dieback stands in Hawaii. Hawaii Bot. Sci. Pap. 43.
- Gerrish, G., and D. Mueller-Dombois. 1980. Behavior of native and non-native plants in two tropical rain forests on Oahu, Hawaiian Islands. Phytocoenologia 8(2):237-295.
- Hawaii Department of Land and Natural Resources. 1981. A biological evaluation of ohia decline on the island of Hawaii. U.S. For. Serv., Pac. Southwest. Region, San Francisco Pest Manage. Unit and Hawaii Dep. Land Nat. Resour. Div. For. Wildl. Mimeo.
- Holt, R.A. 1983. The Maui forest trouble: a literature review and proposal for research. Hawaii Bot. Sci. Pap. 42.
- Jacobi, J.D. 1980. The vegetation map and legend. In Ohia rainforest study: ecological investigations of the ohia dieback problem in Hawaii, ed. D. Mueller-Dombois, J.D. Jacobi, R.G. Cooray, and N. Balakrishnan, 6-12. Hawaii Agric. Exp. Stn. Misc. Pub. 183.
- Jacobi, J.D. 1983. Metrosideros dieback in Hawaii: a comparison of adjacent dieback and non-dieback rain forest stands. New Zealand J. Ecol. 6:79-97.
- Jacobi, J.D., G. Gerrish, and D. Mueller-Dombois. 1983. Ohia dieback in Hawaii: vegetation changes in permanent plots. Pac. Sci. 37(4):327-337.
- Kliejunas, J.T., and W.H. Ko. 1974. Deficiency of inorganic nutrients as a contributing factor to ohia decline. Phytopathology 64:891-896.
- Lyon, H.L. 1909. The forest disease on Maui. Hawaii Planter's Rec. 1:151-159.
- Lyon, H.L. 1918. The forests of Hawaii. Hawaii Planter's Rec. 20:276-281.

- Lyon, H.L. 1919. Some observations on the forest problems of Hawaii. Hawaii Planter's Rec. 21:289-300.
- Miller, L.H. 1900. Collecting trips. Verbatim copy of journal, the original of which was donated to Bancroft Library, Univ. Calif., Berkeley. Xeroxed copy in Sinclair Library, Univ. Hawaii.
- Mueller-Dombois, D. 1974. The ohia dieback problem in Hawaii: a proposal for integrated research. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 3. Honolulu: Univ. Hawaii.
- Mueller-Dombois, D. 1980. The ohia dieback phenomenon in the Hawaiian rain forest. In The recovery process in damaged ecosystems, ed. J. Cairns, Jr., 153-161., Ann Arbor, Mich.: Ann Arbor Sci. Pub., Inc.
- Mueller-Dombois, D. 1981. Spatial variation and succession in tropical island rain forests: a progress report. Hawaii Bot. Sci. Pap. 41.
- Mueller-Dombois, D. 1982a. Canopy dieback in indigenous forests of Pacific Islands. Hawaii Bot. Soc. Newsl. 21:2-6.
- Mueller-Dombois, D. 1982b. Island ecosystem stability and Metrosideros dieback. Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 138-146. Honolulu: Univ. Hawaii.
- Mueller-Dombois, D. 1983a. Canopy dieback and successional processes in Pacific forests. Pac. Sci. 37(4):317-325.
- Mueller-Dombois, D. 1983b. Stand-level dieback in New Zealand forests and the theory of cohort senescence. Hawaii Bot. Soc. Newsl. 22:33-42.
- Mueller-Dombois, D. 1983c. Population death in Hawaiian plant communities: a new causal theory and its successional significance. Tuexenia (Festschrift H. Ellenberg) 3:117-130.
- Mueller-Dombois, D. 1983d. Canopy dieback and dynamic processes in Pacific forests: introductory statement and concluding synthesis. Pac. Sci. 37(4): 313-316, 483-488.
- Mueller-Dombois, D., and V.J. Krajina. 1968. Comparison of east-flank vegetations on Mauna Loa and Mauna Kea, Hawaii. Rec. Adv. Trop. Ecol. 2:508-520.

- Mueller-Dombois, D., K.W. Bridges, and H.L. Carson, eds. 1981. Island ecosystems: biological organization of selected Hawaiian communities. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.
- Mueller-Dombois, D., P.M. Vitousek, and K.W. Bridges. 1984. Canopy dieback and ecosystem processes in Pacific forests: a progress report and research proposal. Hawaii Bot. Sci. Pap. 44.
- Mueller-Dombois, D., J.E. Canfield, R.A. Holt, and G.P. Buelow. 1983. Tree-group death in North American and Hawaiian forests: a pathological problem or a new problem for vegetation ecology? Phytocoenologia 11(1):117-137.
- Mueller-Dombois, D., J.D. Jacobi, R.G. Cooray, and N. Balakrishnan. 1977. Ohia rain forest study: final report. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 20. Honolulu: Univ. Hawaii.
- Mueller-Dombois, D., J.D. Jacobi, R.G. Cooray, and N. Balakrishnan. 1980. Ohia rain forest study: ecological investigations of the ohia dieback problem in Hawaii. Hawaii Agric. Exp. Stn. Misc. Pub. 183.
- Papp, R.P., J.T. Kliejunas, R.S. Smith, Jr. and R.F. Scharpf. 1979. Association of Plagithmysus bilineatus (Coleoptera: Cerambycidae) and Phytophthora cinnamomi with the decline of ohia-lehua forests on the island of Hawaii. For. Sci. 25: 187-196.
- Petteys, E.Q.P., R.E. Burgan, and R.E. Nelson. 1975. Ohia forest decline: its spread and severity in Hawaii. U.S. For. Serv. Pac. Southwest For. Range Exp. Stn. Res. Pap. PSW-105.
- Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol.
- Selling, O.H. 1948. Studies in Hawaiian pollen statistics. Part III. On the late Quarternary history of the Hawaiian vegetation. B.P. Bishop Mus. Spec. Pub. 39.
- Smith, W.H. 1981. Air pollution and forests. Heidelberg, Berlin: Springer-Verlag.
- Sprugel, D.G. 1976. Dynamic structure of wave-regenerated Abies balsamea forests in the northeastern United States. J. Ecol. 64:889-911.

- Stewart, G.H., and T.T. Veblen. 1982. Regeneration patterns in southern rata (Metrosideros umbellata)-kamahi (Weinmannia racemosa) forest in central Westland. New Zealand J. Bot. 20:55-72.
- Stewart, G.H. and T.T. Veblen. 1983. Forest instability and canopy tree mortality in Westland, New Zealand. Pac. Sci. 37(4):427-431.
- Ulrich, B. 1982. Gefahren für das Waldkosystem durch saure Niederschläge. In Sonderheft: Immissionsbelastungen von Waldkosystemen, 9-25. Landesanstalt für Ökologie. Münster, Fed. Rep. Germany: Schutzgemeinschaft Deutscher Wald e.v., Landwirtschaftsverlag GmbH.
- Vogelmann, H.W. 1982. Catastrophe on Camel's Hump. Nat. Hist. 91(11):8-14.
- Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23:41-78.