

Canopy Dieback and Successional Processes in Pacific Forests¹

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ABSTRACT: Massive tree dieback has occurred periodically in the Hawaiian montane rain forest. The species mainly involved is *Metrosideros polymorpha*, which is the prevailing upper canopy tree species throughout most of this forest on all high Hawaiian islands. The canopy dieback occurs in stands over the entire spectrum of sites, from well-drained lava flows over nutritionally rich volcanic ash to permanently wet bogs with toxic soils. A biotic agent could not be found to cause this dieback. Five main dieback patterns have been recognized, and all are site-specific. These patterns suggest certain causal mechanisms, but they explain only a fraction of the dieback syndrome. A number of additional facts were established which have led to a new dieback theory involving a chain-reaction process: (1) cohort senescing as a predisposing factor; (2) a dieback trigger, which can be either internal (a species characteristic) or external (a fluctuating and recurring site-specific perturbation), and (3) a dieback hastening (biotic agents) or stalling mechanism. It is believed that the dieback phenomenon is not restricted to Hawaii but occurs also in other, functionally similar Pacific forests.

A corollary to the Hawaiian dieback etiology is a new succession theory, which explains the temporally recurring dieback as a pattern and process sequence in primary succession. The larger dieback patterns are considered a consequence of catastrophic disturbances in the past, such as lava flows, ash blanket deposits, or landslides, which gave rise to large cohorts. Canopy dieback of these large cohorts during their senescing stage then gives rise to new cohorts. However, these become successively smaller and more patchy with each dieback cycle. Concomitantly with the dieback cycles a turnover of successional races or ecotypes appears to occur within the *Metrosideros polymorpha* species complex. This may allow us to determine pioneer, seral, and near-climax races within this species complex.

THREE POINTS OF CLARIFICATION

Canopy Dieback Defined

I consider canopy dieback to include all forms of stand-level dieback or forest decline, wherever the canopy and/or subcanopy trees are involved, i.e., the overstory trees. Situations where the undergrowth vegetation is dying and where the overstory remains intact,

are not included. I exclude from canopy dieback all forms of stand-level death that have obvious causes, such as logging, habitat flooding for hydroelectric development, or fire. Canopy dieback should be distinguished from individual tree dieback as stand-level dieback. As such, it principally takes two forms: *tree-to-tree dieback*, i.e., where many adjacent trees are affected; or *salt-and-pepper dieback*, i.e., where dying trees occur repeatedly in a matrix of healthy trees. These two forms of tree dieback may occur over large tracts of land, such as 10 or 100 ha, or they may occur in smaller patches of less than $\frac{1}{2}$ acre. It is only critical that stand-level dieback is manifested as a spatially recurring pattern.

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Symptoms of dieback include both rapid loss of all foliage without recuperation or slow loss from the top downward. The dieback process may also involve the gradual development of "stagheaded" trees.

Canopy Dieback Is More Than a Pathological Problem

Stand-level dieback and individual tree dieback are generally considered to be pathological problems. This is true in the strict sense of the word, since *pathos* is the Greek word for "suffering," and we may think of dieback trees as trees that are suffering. However, I consider tree dieback too important a problem to leave entirely in the hands of forest pathologists—i.e., specialists whose expertise involves the science of tree suffering. As an ecologist, I consider death (or the symptoms leading to death) not merely as a form of suffering but also as an inevitable part of life; that is, death is part of life's program. Moreover, as a community ecologist, I am particularly aware of the fact that tree death or stand-level dieback is not the end of the life of a plant community, unless there is an extreme case of environmental toxification. Instead, succession goes on in spite of stand-level dieback. Moreover, we can expect that stand-level dieback may have a special effect on ecological succession due to the remarkable change in the overstory.

Importance of the Problem

Our symposium on Canopy Dieback and Dynamic Processes in Pacific Forests is one of several in Section A of the 15th Pacific Science Congress. Section A is concerned with conservation and environmental protection. The emphasis in this section is to report on research of high value to conservation management. The canopy dieback phenomenon is common in certain indigenous Pacific forests, particularly in New Zealand, Australia, Papua New Guinea, and Hawaii (Mueller-Dombois 1982a). Natural area and forest managers are under pressure to provide answers concerning dieback, since such poor-

looking and apparently deteriorating indigenous forests are pointed at as examples of poor management by some segments of the public. Because of this public pressure, a conference on beech mortality took place in Tongariro National Park last year. Similar symposia were held in Hawaii (Mueller-Dombois et al. 1980) and Australia (Old, Kile, and Ohmart 1981). For the first time, the theme of forest dieback crosses national boundaries in the Pacific region by means of our present symposium.

CANOPY DIEBACK IN THE HAWAIIAN RAIN FOREST—A BRIEF OVERVIEW

Historic Accounts

Groups of dead standing trees have always been part of the normal physiognomy of indigenous Hawaiian forests. More than a hundred years ago, Clarke (1875) gave a brief account on the decadence of Hawaiian forests. He noticed recurring groves of dead standing *Acacia koa* in the midst of vigorous forests of similar stature and remarked on the absence of any obvious disturbance there. *Acacia koa* is the second most abundant native Hawaiian canopy tree species. Twenty-five years later, Miller (1900) referred to stands of dying *Metrosideros polymorpha* in an area that is now part of Hawaii Volcanoes National Park on the island of Hawaii. He described these stands as giving the impression of an "autumn woods" as in eastern North America. The normally evergreen *M. polymorpha* is the most abundant and most widely occurring native canopy species in Hawaii, particularly in the montane rain forest. However, a good number of other native tree species grow as lower-stature trees or arborescent shrubs in association with *Metrosideros*. Among the most abundant rain forest associates on the island of Hawaii are the tree ferns (several species of *Cibotium*), which often form an important second stratum in the undergrowth.

Further accounts of stand-level dieback were given earlier in this century for the island of Maui by Lyon (1909, 1918, 1919),

in the 1960s for the island of Kauai by Fosberg (1961) and for the island of Hawaii by Mueller-Dombois and Krajina (1968), and more recently for the island of Oahu by Gerrish and Mueller-Dombois (1980). Lyon had studied the Maui forest dieback as a pathogenic disease problem, but later came to a different conclusion, which I will discuss in the section titled "Environmental Stress Hypotheses."

Disease Research During the 1970s

Two foresters, Burgan and Nelson (1972), drew attention to the widely occurring forest dieback on the island of Hawaii and suggested the possibility of a new disease. Subsequently, Petteys, Burgan, and Nelson (1975) published a paper on a very rapid decline of the native *Metrosideros* rain forest on the windward slopes of Mauna Kea and Mauna Loa. These authors had analyzed three successive sets of aerial photographs. For an area of 80,000 ha of native rain forest, they recorded 120 ha of severe decline for 1954, 16,000 ha cumulative for 1965, and 34,500 ha cumulative for 1972. From this they concluded that the forest would be totally destroyed in another 15–25 yr if that rate of damage continued. This analysis spurred an intensive search for the cause of the decline. Introduced animals (such as cattle and feral pigs) and/or air pollution were soon dismissed as possible causes, but fungal pathogens were strongly suspected.

A number of expert pathologists and entomologists worked for almost 10 yr to find the biotic agent that presumably was killing the forest. A complete summary of this effort is given by the USDA Forest Service (1981). Initially, it was thought that a disease had been introduced to the islands, to which the island vegetation was not adapted. The fungus *Phytophthora cinnamomi* was isolated and was believed for a while to be the most likely killer. However, dieback stands were found without traces of this fungus (Hwang 1977, Hwang and Ko 1978), while several nondieback stands were infected with the fungus. Then, for a while, it was thought that the native, host-specific

Metrosideros bark beetle, *Plagithmysus bilineatus*, could be the killer. However, this wood borer, which is indeed associated with dying stands, was found to become more abundant when trees had started dying from loss of vigor (Papp et al. 1979). Experimental inoculations with *Plagithmysus* gave further evidence that the beetle could not be implicated as the primary cause in dieback.

Ecological Research Since 1975

In 1975, we began ecological research of the dieback phenomenon (Mueller-Dombois et al. 1980). One of the first things noted was that *Metrosideros* seedlings and saplings were growing up in most dieback stands. Moreover, we found that the dieback was restricted to the canopy trees. Petteys, Burgan, and Nelson (1975) had stated that trees of all ages were affected by the decline, but we found that the dieback was restricted to the overstory trees, and mostly to *M. polymorpha*. We also found that in relation to site differences, very low stature trees as well as tall trees were affected by dieback, but we never found the two contrasting tree-stature types (low and tall) dying on the same site and/or in the same stand.

With regard to site relationships, we soon found that dieback is often strongly correlated with substrate boundaries. For example, a nondieback forest on an 'a'ā lava flow (a clinkerlike rock outcrop substrate) may extend in the form of tongues into a dieback forest that grows on a pāhoehoe lava flow (a smooth pavementlike rock outcrop substrate). A similar observation was made for the *Metrosideros umbellata*—*Weinmannia racemosa* stand dieback in Westland National Park, New Zealand, on substrates exposed following a dated deglaciation event (Mueller-Dombois 1982a).

Initially, we thought that the dieback was restricted to poorly drained pāhoehoe flows, but then we found that it occurred also on deep, fine soils from old, very leached volcanic ash. Moreover, we found stand-level dieback to occur on well-drained pāhoehoe flows as well as on moderately drained deep soils from recent, nutritionally rich, volcanic ash.

The Five Dieback Types

After examining 60 detailed soil profile and vegetation samples taken throughout the study area (on the windward slopes of Mauna Kea and Mauna Loa, island of Hawaii), five dieback types were recognized (Mueller-Dombois 1981):

(1) **WETLAND DIEBACK**: Usually a radical tree-to-tree dieback on poorly drained shallow lava rock outcrop soils, which includes both lava types, pāhoehoe and 'a'ā. In terms of area, this is currently one of the most dominant dieback types.

(2) **DRYLAND DIEBACK**: Usually a salt-and-pepper dieback or patchy dieback on well-drained shallow lava rock outcrop soils of both lava types.

(3) **DISPLACEMENT DIEBACK**: Found on moderately to well-drained deep soils of organically enriched and therefore fertile volcanic ash. Here, tree ferns are so vigorous that they displace the canopy *Metrosideros* trees when these undergo stand-level dieback. *Metrosideros* seedlings may be abundant on the forest floor, but the tree ferns shade out a significant number (Burton and Mueller-Dombois 1984).

(4) **BOG-FORMATION DIEBACK**: Occurs also on deep soils from volcanic ash, but here the ash is relatively old, nutritionally poor, and permanently soggy or water-soaked. This is a salt-and-pepper dieback involving groves of dead trees and nondieback trees in various patterns.

(5) **GAP-FORMATION DIEBACK**: Found on the moderately well-drained ridges dissecting the bog-formation terrain in the northern half of the dieback territory. It involves small tree groves or tree patches as in the dryland dieback. However, gap-formation dieback occurs on older, nutritionally depleted ash soils, some of which are suspected to show aluminum toxicity.

Further information on the nutrient aspects is presented in Balakrishnan and Mueller-Dombois (this issue).

With regard to nutrient relations, an important fertilization experiment should be mentioned. A low-stature incipient dieback stand on an 1855 pāhoehoe flow was treated

by Kliejunas and Ko (1974) with NPK fertilizer (784 kg/ha). This resulted in full recovery of half-dead trees, that is, in "dieback reversal." In contrast, three tall-statured stands of similar dieback status (with a significant number of half-dead trees, i.e., 25–50% crown loss), treated in the same way with NPK fertilizer did not result in dieback reversal (Mueller-Dombois 1981, Gerrish and Bridges 1984).

Successional Implications

The different dieback types also exhibit differences in succession patterns. Four types (displacement dieback is the exception) show replacement with either seedlings or clones of the dying canopy species, *Metrosideros polymorpha*. However, replacement is not in all cases to be expected to result in closed forests. There are obvious quantitative variations due to undergrowth competition and site (Jacobi, Gerrish, and Mueller-Dombois, this issue). Moreover, we have reasons to believe that the replacement crop of *M. polymorpha* is not always genetically of the same composition as the dying stand. For example, a pubescent type of *Metrosideros* (var. *incana*) may be replaced with a certain percentage of seedlings of a glabrous type of *Metrosideros* (var. *glaberrima*). This and other observations have led to the hypothesis of successional ecotypes or races (Mueller-Dombois et al. 1980). If these exist in *M. polymorpha*, they may have roles similar to those of pioneer and seral species in floristically more diverse regions. This aspect is further treated by Stemmermann (this issue).

Environmental Stress Hypotheses

FLUCTUATING SITE FACTORS: Earlier in our studies of the Hawaiian rain forest dieback we thought (Mueller-Dombois et al. 1980) that a plausible alternative to the disease or biotic agent hypothesis would be a "natural environmental stress" hypothesis. We thought that perhaps a period of three or more abnormally wet years may have resulted in drowning of the root systems of stands in such habitats as associated with the wetland

and bog-formation diebacks, and alternatively that a drought period in a recent year may have triggered dieback in the dryland dieback sites. We further thought that dryland dieback in particular could be associated with nutrient limitation, perhaps aggravated through intraspecific competition. Thus, we assumed that climatic stress acting in a site-specific manner might explain the dieback phenomenon (Mueller-Dombois 1980). The results of a climatic perturbation analysis are presented by Evenson (this issue).

While climatic stress or perturbations are not ruled out as being involved, it is realized that they can provide only a partial explanation of wetland and dryland diebacks. It is more difficult to link displacement and bog-formation diebacks to climatic stress.

Of course, it is also possible that the different dieback types have little more in common than dead standing trees.

CHANGE IN SOIL CHEMISTRY: In this connection it is of interest to refer to an earlier, significant forest dieback that was discovered after the turn of the century on the island of Maui. Harold Lyon, a researcher for the Hawaiian Sugar Planters Association, searched for more than 6 yr for a biotic agent responsible for the Maui forest dieback. He finally concluded (Lyon 1918, 1919) that the Hawaiian rain forest trees, particularly *Metrosideros polymorpha*, were dying because of a change in soil chemistry involving toxicity (development of large amounts of H_2S and an abundance of reducing iron) under conditions of poor drainage. Further literature and historic file research by Holt (1983) revealed that Lyon thought that the Hawaiian forest vegetation was largely comprised of pioneer species which could not adapt to changes in the soil chemistry as brought about in the course of Hawaiian soil formation. He then promoted the introduction of exotic tree species as plantation stock to save the Hawaiian watersheds from deteriorating under the "decadent" native vegetation. About one-third of the Maui forest dieback terrain was later planted to two Australian tree species, *Eucalyptus robusta* and *Melaleuca leucadendra*.

CLIMATIC CHANGE: Selling (1948), a Swedish palynologist, analyzed bog soil profiles in Hawaii. Selling argued with Lyon that climatic stress might be a better explanation for the dieback. Some of Selling's bog soil profiles show *Metrosideros* pollen periodically decreasing and increasing. Although no time scale has as yet been established that can be related to the retreat and comeback phases of *Metrosideros* pollen in the bog soil profiles, they indicate that *M. polymorpha* can be described as an "oscillating persister" in primary succession. A time scale in relation to the oscillations might establish whether the oscillations can be conceived as climatic fluctuations or whether they simply represent *Metrosideros* stand generations.

FORMATION OF CLAY HARDPAN: A fourth environmental stress hypothesis was presented by Fosberg (1961), who suggested that the decadent *Metrosideros* stands on poorly drained, level or gently sloping soils in Maui and Kauai were dying because of formation of a clay hardpan that would restrict oxygen in the root zone. He noted that dying taller stands under these conditions were successively replaced by lower-growing stands until shrub bogs and finally sedge bogs were developed.

THE COHORT SENEESCENCE THEORY

A Four-Level Causal Chain

The absence of a biotic disease agent as primary cause and the different site factor correlations established for the five Hawaiian dieback types suggest a complex of abiotic causes. However, the spatial importance, frequency, and temporal recurrence of stand-level dieback in the Hawaiian rain forest indicate that the dieback has something to do with the physiology and population dynamics of the leading canopy species, *Metrosideros polymorpha*. This implies that there is a common basis to the different dieback types recognized. This communality is seen as a four-level chain reaction as follows:

(1) A catastrophic disturbance, such as a lava flow, ash blanket deposit, landslide, hurricane, or fire, may set the stage for a wave of regeneration; that is, a relatively large cohort becomes established, provided there is a species that is capable of such opportunistic invasion of disturbed habitat. *Metrosideros polymorpha* is such a species.

(2) The cohort consists of individuals of similar age and physiological constitution, particularly when growing on uniform habitats. During stand development, some individuals become suppressed or are thinned out, but many trees develop uniformly into maturity and then also enter the senescing life stage together. On nutritionally poor habitats, senescing cohorts will be of low stature; on nutritionally rich habitats, they will achieve tall stature. It is also possible that a cohort growing on a nutritionally imbalanced habitat may be forced into an earlier than normal senescence. Thus, environmental stress may contribute to senescence.

(3) During the senescing life stage, the cohort stand decreases in vigor. A fluctuating site factor, such as a transient soil drought in the root zone or temporary flooding, may trigger stand-level dieback in this life stage. For example, an otherwise noncatastrophic perturbation, such as a storm, may tear off a large amount of leaf biomass that cannot be replaced due to the senescing life stage of a stand.

(4) Upon breakdown of the canopy, hastening factors, such as a bark beetle population buildup or increased fungal attack by weak pathogens, may contribute to a rapid decline. However, temporary recovery may also occur after a fluctuating stress factor, such as root flooding or soil drought, has subsided. The first situation would cause rapid dieback; the second, a lingering dieback.

Successional Consequences

The theory of cohort senescence requires the meeting of environments with catastrophic disturbances and species that can take

advantage of such habitat disturbances by rapid invasion. Moreover, it requires that catastrophic disturbances on the same site are less frequent than the life-span or generation turnover of the dieback species. For example, fire environments (as in some pine and/or eucalypt regions) are not conducive to stand-level dieback, because the fire frequency may be so high that stands are killed before they break down naturally from senescence. However, where actively protected from fire, such stand-level senescence may also be expected, particularly in environments where fires give rise to cohort stands. Ecosystems in which one may not expect cohort senescence to be important are multi-species tropical rain forests (Mueller-Dombois 1983).

Canopy breakdown as a consequence of cohort senescence may stimulate development of a new cohort. Intraspecific competition is suddenly relaxed, and the decaying roots of the dying cohort may provide more favorable nutrient relations for regrowth of the next generation. However, with each generation turnover, the cohort sizes become smaller, more disjunct, and/or irregular. Also, the undergrowth will change, and because of ongoing soil development, certain species in the undergrowth may become more competitive as their growth rates increase relative to those of the seedlings of the dieback species. Thus, one can expect successive senescing cohorts to be spatially reduced or patchy and out of phase with one another. This change in pattern fits the array of stand-level dieback configurations observed in the Hawaiian rain forest (Mueller-Dombois 1982b). Only a new catastrophic disturbance may again enlarge and homogenize the subsequently developing dieback pattern.

I have already mentioned the theory of successional ecotypes in *Metrosideros polymorpha*, which is expected to resolve some formerly puzzling questions of taxonomic *Metrosideros* diversity occurring on the same habitat. It is expected that successional races in *M. polymorpha* have similar successional functions as have pioneer and successional canopy species in floristically more diverse regions.

CONCLUSIONS: STAND DYNAMICS—A
RELATIVELY UNEXPLORED ASPECT

Mueller-Dombois et al. (1983) review several of the so-called decline diseases reported for North America. In a forest pathology text, Manion (1981) makes a distinction between biotic, abiotic, and decline diseases. Biotic diseases are obvious diseases such as western white pine blister rust, Dutch elm disease, and chestnut blight. Abiotic diseases are described as caused by environmental stresses such as air pollution, imbalanced nutrient inputs, or soil toxification. Decline diseases are considered the result of complex causes involving a combination of abiotic and biotic stresses and sometimes the genotype or old age of the host species. Manion presents a three-step chain reaction model for decline diseases that involves predisposing stresses, inciting factors, and contributing causes. It is similar to our four-level model, but does not emphasize cohort senescence and omits consideration of successional implications. This is understandable, because a disease is a disorder, and cohort senescence would not be considered a disorder.

In reviewing the literature on five of the so-called North American decline diseases (birch dieback, maple and oak decline, western white pine pole blight, and little-leaf disease of southern pines), it became clear that almost no information is available on stand dynamics or on the succession patterns following stand-level breakdown. Our studies in Hawaii have shown that stand and/or population dynamics of the dieback species must receive greater attention in the etiology of stand-level breakdown. Understanding the causes of canopy dieback will also permit a substantially improved prediction of its successional consequences. A similar conclusion was reached simultaneously but independently, by Stewart and Veblen (1982, Veblen and Stewart 1982) with regard to certain New Zealand forests. Their work is summarized in this issue.

Apart from cohort detection research in the field, new research should include studies on the biochemistry of stand-level senescence.

Such work appears particularly timely now, because many forest dieback reports come from the industrialized regions of eastern North America and central Europe. Industrial pollution (in the form of SO₂ emission, acid rain, heavy metal contamination, and other factors) is considered an important form of environmental toxification resulting in large-scale forest dieback (Smith 1981, Ulrich 1981, Vogelmann 1982). There is little doubt that some of these factors provide environmental stresses, but without an understanding of the underlying stand dynamics, the causal relationships of stand-level dieback will not be resolved.

Studies on canopy dieback in Pacific forests, particularly in Hawaii, New Zealand, Australia, and Papua New Guinea, may contribute important information to the whole question, since they come from areas that are practically free of heavy industries and thus from industrial pollution stresses.

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