Journal of Vegetation Science 6: 449-464, 1995
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A landscape perspective of the Hawaiian rain forest dieback

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Abstract. Throughout the 1960s and 1970s there was a rapid decline and canopy dieback in the *Metrosideros polymorpha* dominated rain forest of Hawai'i. An analysis of air photo sets from 1954, 1965, and 1972, covering the windward slopes of Mauna Kea and Mauna Loa, gave support for an alien disease hypothesis. A total demise of the native forest was predicted for the early 1990s. This prediction as well as the disease hypothesis proved to be wrong. Various searches for a single climatic cause also failed to explain the dieback. The spatial dynamics of the dieback phenomenon were newly analyzed with an additional air photo set from 1977 and by using GIS with spatial statistics. Two juxtaposed and climatically similar landscape matrix samples of ca. 200 km^2, one each on Mauna Loa and Mauna Kea, were subjected to an analysis of landform heterogeneity and superimposed dieback patterns. The Mauna Loa matrix displays up to 15 000 yr old lava flows, while the Mauna Kea matrix displays up to 250 000 yr old substrates. Initiation of dieback occurred simultaneously on both mountains and was highly correlated with poorly-drained sites. The progression of dieback, however, followed a gradient of decreasing soil moisture, which often terminated at clearly recognizable substrate boundaries in the Mauna Loa matrix and moved over well-drained hill sites in the Mauna Kea matrix. *Metrosideros* dieback spread across the entire spectrum of volcanic substrates and habitat moisture regimes and developed from a smaller into a larger patch mosaic. By 1977, ca. 50 % of the forest area in both sample matrices had gone into dieback. Thereafter, the dieback came to a halt. The domino-type collapse, which frequently came to a halt at volcanic substrate boundaries, indicates that stands in better drained sites were also predisposed to die. Stands on adjoining substrates often survived. Substrates with dieback stands displayed no other obvious vigor-reducing stresses. The canopy trees on such substrates may have a common history, such as a major disturbance (including dieback) that synchronized stand development in the past. Subsequent weather disturbances and other abiotic/endogenous stresses associated with stand maturation, such as nutrient limitations and stand-level senescence, may reinforce a rhythmic synchrony over several generations of canopy cohorts.

Keywords: Forest decline; Geographic Information System; Landscape ecology; Spatial dynamics; Succession.

Nomenclature: Wagner et al. (1990).

Introduction

Stand-level dieback of *Metrosideros polymorpha* (*Myrtaceae*), the endemic ōhi'a lehua tree, which dominates the canopy of the Hawai'ian rain forest, became noticeable in the mid-1960s (Mueller-Dombois & Krajina 1968). An air photo analysis in the early 1970s documented a rapid spread of *Metrosideros* tree mortality in an 80 000-ha sample area, covering much of the E to NE-facing windward slopes of the volcanic mountains Mauna Loa and Mauna Kea on Hawai'i (Petteys et al. 1975). Two research efforts were launched. One led by the U.S. Forest Service (Burgan & Nelson 1972) had the premise that this was a new epidemic disease, insect pest or combination of the two. The other led by the University of Hawai'i Botany Department (Mueller-Dombois 1974) assumed that this was a recurring natural phenomenon in the dynamics of an island rain forest.

After a search for biotic agents it became abundantly clear by the end of the 1970s that there was no new disease or pest organism and no anthropogenic cause which could be made responsible for the 'ōhi'a decline or dieback in Hawai'i (Papp et al. 1979). Also, volcanic fuming or air pollution was excluded since the spatial pattern of dieback was completely unrelated to such a cause. Then, the focus turned to climatic stress. For the succession hypothesis, Mueller-Dombois (1980) suggested climatic instability as natural cause of dieback. For instance, extreme rainfall events which affect the soil moisture regime and cause prolonged droughts or floods, could have been particularly stressful in certain stages of stand development and maturation. Despite some efforts to isolate a climatic stress factor (Doty 1981, 1982, 1983; Evenson 1983; Mueller-Dombois 1986; Auclair 1993), no single climatic instability could be made responsible for the forest collapse.

Forest decline and dieback syndrome

Forest dieback, characterized by the gradual but synchronized mortality of mature canopy trees in large groups (Mueller-Dombois 1992a), occurs world-wide in a great diversity of forests (Jane & Green 1983;

Kohyama 1988; Itow & Mueller-Dombois 1988; Hennon et al. 1990; Ammon et al. 1992; Daoust et al. 1992; Houston 1992; Huettl & Mueller-Dombois (1993); Ciesla & Donaubauer 1994). Most commonly, such forests are dominated by one or very few species of pioneer trees. The death of trees cannot be attributed simply to species-specific pathogens, parasites, pollutants or any other single agent of disturbance but must be induced by a combination of biotic and abiotic factors (Manion & Lachance 1992), which have hardly been explained due to the complex patterns of dieback created by the interactions of several inconspicuous factors. Mueller-Dombois et al. (1983) emphasized that the dynamics of tree-population declines and the study of mortality patterns and mechanisms form a new task for vegetation ecology. Not only forest pathology should be taken into consideration.

Of course, all trees die eventually. However, that so many trees die more or less synchronously is rather unusual. In this context Mueller-Dombois (1992a) pointed out that in forests composed of pioneer species of very low diversity, the establishment, maturation, aging and senescence of trees would occur naturally in groups or cohorts even in the most favorable environments. Also, despite the alarming picture presented by the extensive breakdown of the forest canopy, the death of canopy trees in the dieback phenomenon seldom leads to deforestation. More frequently it promotes rejuvenation of the forest communities by bringing back much-needed sunlight and nutrients into the understory, reducing competition for resources, and encouraging the growth of many sun-loving species including the canopy trees themselves. In fact, Manion (1991) and Manion & Lachance (1992) interpreted forest dieback as a process of natural selection against the more aggressive genotypes or species, a process which balances the losses due to competition of the less aggressive genotypes or species. These authors suggest that forest dieback promotes long-term stability of the forest system.

Research objectives

Dieback often results in large openings in the canopy for considerable time periods. As with all other large-scale disturbances caused by powerful exogenous agents such as fires, hurricanes and insect/disease epidemics, the potential impacts of natural forest dieback on wildlife and ecosystem processes are substantial. To conserve and better manage unique forest ecosystems and their intrinsic dynamics on an individual basis (Noss 1983; Pickett & Thompson 1978), to increase our knowledge and consensus about the mechanisms and the roles of natural forest dieback (Manion & Lachance 1992), and to predict landscape changes imposed by infrequent large-scale disturbances and global change in climate (Mueller-Dombois 1992b), it is very important to understand (1) the reasons why some mature trees lose vigor and die earlier than others in a forest; (2) in which direction the dieback symptoms are likely to spread across a forest landscape; and (3) how extensively a forest can lose the canopy at each dieback event.

We attempted to answer these questions for the *Metrosideros polymorpha* rain forest on the Hawai'ian Islands, where large-scale dieback has been known to occur for more than a century. Major characteristics of stand-level dieback and its consequences have been revealed (Lyon 1919; Kliejunas & Ko 1974; Petteys et al. 1975; Papp et al. 1979; Mueller-Dombois et al. 1980; Stemmermann 1983; Balakrishnan & Mueller-Dombois 1983; Mueller-Dombois 1983; Burton & Mueller-Dombois 1984; Gerrish & Bridges 1984; Hodges et al. 1986; Mueller-Dombois 1986; Jacobi et al. 1988). Dieback was found to occur practically in any habitat of the rain forest from well-drained lava flows to bogs.

In this paper we analyze the development of dieback patterns across the rain forest of Hawai'i over a 23-yr period in relation to several factors of the physical environment, including rainfall, topography and geology. If any part of the dieback behavior was indeed related to physical factors, the spread of dieback across the rain forest could become more predictable. Such a study would also provide a basis for elucidating the reasons why some mature trees die earlier than others.

Study area

The rain forest dominated by *M. polymorpha* is found widely on the larger Hawai'ian Islands where annual rainfall exceeds 2000 mm. Dieback at various scales has occurred here and there in the rain forest, but the recent events on the two adjacent mountains Mauna Loa (4168 m) and Mauna Kea (4205 m) on the island of Hawai'i were particularly extensive. We selected two separate matrices of the rain forest, 193.57 km^2 and 195.33 km^2 in area, for our study on the east-facing slopes of Mauna Loa and Mauna Kea between 580 m and 1710 m a.s.l.

Physical conditions vary within the study area. Median annual rainfall varies from 2000 mm to 5000 mm on Mauna Loa and exceeds 7000 mm on the lower slope of Mauna Kea. The substrates are from three prominent volcanoes, Mauna Loa, Mauna Kea and Kilauea. The surface deposits on the Mauna Loa slope are relatively young, ranging from 35 to ca. 15 000 yr. They consist of ash, spatter, cinder, and basaltic lava flows of two generally recognized types: *pāhoehoe,* having smooth and fragmented surfaces, and *'a'ā*, with rough, boulder-like stony surfaces. They occur in intermixed patches of various sizes forming a complex pattern in space. The surface deposits on the Mauna Kea slope are older. Their estimated age varies from 5000 to 250 000 yr. The deposits consist mostly of lava flows covered by ash to various depths. The spatial pattern appears simple.

Because of the differences in age and type of surface deposits, the topography differs on the two slopes. The young Mauna Loa slope is gently undulating. Steep slopes occur only occasionally in association with small volcanic cones and with gullies of various sizes which cut through the hilly slopes in a few places. Major relief depressions are found frequently between gentle hills, but no distinct valleys and streams are present. In contrast, the older Mauna Kea slope is more deeply dissected than Mauna Loa. Many perennial streams have cut large gullies on the middle slope and deep gulches on the lower slope. The terrain between the grooves is broad and less dissected, but the hill slopes are generally steeper than on Mauna Loa.

The forest on the windward slopes of both mountains is dominated by *Metrosideros polymorpha*, over the elevation range covered by the two sample matrices. Canopy heights vary from < 5 to > 25 m depending on stand age, substrate age and type, and on soil moisture and nutrient regime. In the subcanopy smaller trees of different native species often occur. The more common are *Cheirodendron trigynum* (*Araliaceae*), *Myrsine lessertiana* (*Myrsinaceae*), *Ilex anomala* (*Aquifoliaceae*), *Pelea clusiaefolia* (*Rutaceae*) and *Coprosma ochraceae* (*Rubiaceae*). Dominant in the undergrowth are tree ferns (*Cibotium* spp.) in closed canopy forests and matted ferns (*Dicranopteris* or *Gleichenia* spp.) in open canopy forests. The forest floor contains many herbaceous fern species and bryophytes (see Mueller-Dombois et al. 1980; Jacobi et al. 1983, 1988; Mueller-Dombois 1987; Drake & Mueller-Dombois 1993; Kitayama & Mueller-Dombois 1994).

Methods

Identification of spatial patterns

For the landscape analysis of *Metrosideros* dieback, the focus was on its distributional dynamics in relation to the spatial patterns of the physical environment. We obtained the spatial patterns of forest dieback from interpreting four sets of stereo air photos from 1954 - 1977 (Table 1). Accommodating the variations in resolution, quality, color and tone among the individual photos, local dieback intensity was defined in three classes based on the following criteria:

20-50 % canopy loss: Defoliated branches scattered among different trees, or defoliated trees scattered among healthy trees. The outline of the original crowns can still be clearly defined.

50-80 % canopy loss: Defoliated branches dominate the forest canopy, occurring more or less evenly among the trees or mixed with a few healthier trees. The original crown outlines of trees are typically defined by the extent of defoliated branches.

80-100 % canopy loss: Most branches are severely defoliated and many trees look literally naked. The undergrowth and, occasionally, fallen trees on the ground can be seen through. The original crown outlines are difficult to trace.

The class boundaries were initially defined on the individual photos, but later redrawn on the planimetrically normal maps at the common scale of 1:24 000 based on the orthographic photos. The dieback map of Mauna Loa representing 1977 was compared with the forest canopy appearance in 1992 in the field. During the 15 elapsed years some progress in dieback had occurred at many locations, but generally the dieback classes on the map indicated the same or less severe stages of defoliation than the 1992 canopy appearance. A number of oblique photos taken from low-flying aircraft between 1976 and 1988 were used to check the dieback regimes at several ground-inaccessible locations. These included particularly areas on the Mauna Kea slope. Temporal recovery of some canopy foliage was observed on the photos. Also, in several early dieback areas that we visited, *Metrosideros* sapling cohorts were forming new low canopies. However, the saplings and foliage recovery were neither clearly visible nor distinguishable from undergrowth vegetation on the photos. In the final maps, the dieback classes and their boundaries were rearranged so that no portion of the patches progressed from a higher to a lower dieback intensity in consecutive years. The post-dieback regeneration based on 26 permanent plots was described by Jacobi et al. (1983, 1988).

Data on spatial patterns of the physical environment were obtained from various sources. The rainfall pattern was adapted from the median annual rainfall map prepared by the Hawai'i State Department of Land and Natural Resources. Digital elevation models (DEM) were produced from the 40-ft contours of the 1:24 000 U.S.G.S. topographic maps. Slope aspect and gradient

Table 1. Four sets of aerial photographs used for the analysis.

Year of dieback map	Photo scale	Photo tone
1954	≈ 1:41 000	Black/white
1965	≈ 1:24 000	Black/white
1972	≈ 1:12 000	Color
1977	≈ 1:48 000	Black/white

patterns were defined based on the DEM, and a number of three dimensional images were generated too. The distribution of various types of volcanic deposits and their estimated ages were obtained from unpublished information provided by John P. Lockwood at the Hawai'i Volcano Observatory and Edward W. Wolfe at the David A. Johnston Cascades Volcano Observatory.

Analysis of pattern association

The patterns of forest dieback and physical environment were integrated into geographic information systems (GIS). Relationships between dieback and physical factors were first examined visually by (1) comparing the relative areas of dieback among the different categories of individual and combined physical factors in graphs, (2) observing the superimposed patterns on maps, and (3) inspecting the three-dimensional images created by stereo photos and computer.

To test the association of dieback with each physical factor and to compare the effects of different physical factors on the development of spatial dieback patterns, logistic regression analysis (Norušis 1990) was applied to the data sets obtained at > 1000 computer-generated random points across each mountain slope each year in the dieback and non-dieback portions of the rain forest, respectively. Multivariate models were built on the data sets (Table 2) for each year to compute the probabilities of individual stands (samples at the computer-generated points) undergoing dieback. In each model, the regression coefficients for the physical variables were estimated based on the maximum-likelihood method and their significance was tested with the Wald statistic (Norušis 1990). The relative contributions of individual physical factors to the logistic regression models were estimated with the R-statistic (Norušis 1990). The goodness of fit of the logistic regression models was assessed by comparing the dieback probabilities of the samples computed by the models and the actual dieback states of the samples for each year. The analysis was done with the SPSS/PC+ Advanced Statistics 4.0 package.

Results

Correlations with rainfall

On Mauna Loa, canopy dieback was overall more extensive and intensive in the higher rainfall zone (Figs. 1 and 3). On Mauna Kea, canopy dieback was most concentrated in the medium rainfall (5000 mm) zone of this slope (Figs. 2 and 3). Except for this zone, the trend was generally similar to that on Mauna Loa. However, the intensity of the dieback-rainfall relationship varied with slope gradient and type of substrate. Dieback increased with annual rainfall more strongly on the flatter surfaces of both mountains and on the substrates containing larger amounts of ash on Mauna Loa.

Correlations with topography

Generally, canopy dieback was not associated with a particular orientation of slope. The Wald statistic indicated no correlation between dieback and slope aspect at the significance level of 0.05 (Table 3).

Canopy dieback was correlated with slope gradient. It was more extensive and intensive on the flatter surfaces (Fig. 4). The trend was clear on Mauna Loa only in the early years, but very significant on Mauna Kea for all years. This difference in the intensity of the trend between the two mountains appears to be largely attributable to the difference in annual rainfall. This trend was substantially strong in the high-rainfall (> 6000 mm) zones on Mauna Kea (Fig. 5). In the low-rainfall zones of both mountains, dieback was not strongly associated with slope gradient. There, dieback occurred more frequently on the steeper surfaces of gullies. The turning point of these trends occurred at an annual rainfall of ca. 4000 - 5000 mm. This agrees with an earlier observation that mesic habitats were only found in the areas of the rain forest receiving < 4500 mm rainfall annually, whereas, in the higher rainfall zones located at lower elevations, habitats were moist to wet even on young substrates, which were considered to be more permeable

Table 2. Variables included in the logistic regression models. Models were constructed for four separate years from 1954 to 1972 for each of the Mauna Loa and Mauna Kea slopes based on data extracted from numerous computer-generated random sample points on the maps.

Variable	Parameter coding and description
Dependent	
Dieback	0 = Non-dieback (< 20% canopy loss), 1 = Dieback (> 20% canopy loss)
Independent	
Annual rainfall	2 = 2000-3000 mm, 3 = 3000-4000 mm, 4 = 4000-5000 mm, 5 = 5000-6000 mm, 6 = 6000-7000 mm, 7 = >7000 mm
Slope aspect	0=S/SW/SE, 1=N/NW/NE
Slope gradient	Actual % grade calculated from DEM
Mean slope	Actual mean % grade of the terrain obtained from DEM by 100 m-interval elevation zone
Substrate age	The mid-point of the estimated range in 1000 years (e.g. 6 = a deposit which is 5000-7000 years old)
Substrate type	1 = Ash/mixed ash-lava/ash-covered lava (fine-textured) 2 = Pāhoehoe (medium-textured deposits) 3 = 'A'ā / mixed 'a'ā - pāhoehoe / cinder-spatter (coarse-textured)
Substrate patch	Each patch was assigned a contrast value calculated based on the deviations from the overall effect

than older and weathered substrates (Mueller-Dombois et al. 1980). Thus, soils were probably continuously supplied with moisture in the high-rainfall zones. This could have been a major problem for the development of tree root systems particularly on the flatter slopes, while the steeper surfaces provided better-drained habitats. In the low-rainfall zones, in comparison, prolonged floodings of soils were rare even on very flat surfaces. However, the gullies collected surface runoff water from the surrounding ground and provided wetter habitats, which could have resulted in poor development of tree root systems.

The high concentration of dieback in the 5000 mm rainfall zone on Mauna Kea could be partly related to the general shape of the slope profile and the relative proportions of flat and steep surfaces of the terrain. The proportion of the flatter (< 10 %) surfaces on Mauna Kea is largest in the 5000 mm rainfall zone, whereas that of the steeper (> 10 %) surfaces is smallest there (Fig. 6). The mean slope gradient of the terrain between 900 m and 1100 m on Mauna Kea, where the 5000 mm rainfall zone is situated, is ca. 8.6 %, reaching the lowest along the elevational gradient. Hence, the general profile of the Mauna Kea slope is most gentle in this zone. On Mauna Loa, in comparison, the proportions of flat versus steep surfaces change systematically with annual rainfall (i.e. flatter surfaces increase with rainfall) and the mean slope increases with elevation. Therefore, the dieback-rainfall relationship was less complicated.

Examination of the stereo pairs and the graphical reproduction of the landscapes in three dimensional images detected another characteristic of dieback being associated with topography. Dieback frequently initiated on concave surfaces at hill bottoms or relatively flat areas just below steep slopes, and then slowly spread uphill, along the valley and gully lines, over the gentle hill slopes, and eventually on the hill tops. Despite the differences of the sites in general landform, annual rainfall, and the type and age of substrate this trend was apparent on both Mauna Loa and Mauna Kea at the local scales where the expansion of dieback patches could be examined on an individual basis through time (Fig. 7). At the landscape level the progression stage of dieback varied greatly among the individual dieback initiation areas each year.

Correlations with substrate

The association between dieback and the type of substrate was only examined for Mauna Loa. Overall, dieback was most extensive and intensive on the deep ash and the mixed ash-lava deposits (Fig. 8). This trend was particularly pronounced in the higher rainfall zone but unaffected by slope gradient. Among the substrates containing relatively low amounts of ash deposits, the *pāhoehoe* type suffered more dieback than the *'a'ā* or the cinder/spatter types. Also, a comparison of the patterns of dieback with those of substrate type indicated that dieback was spatially more continuous over the deposits of ash, ash-lava and *pāhoehoe* than the deposits of *'a'ā*, cinder and spatter. Ashes consist of pyroclastic fragments < 2 mm average diameters. *Pāhoehoe* lava flows provide smoother and more homogeneously-textured surfaces than *'a'ā* flows do. Furthermore, in a habitat survey conducted in the past, an increase in fineness of soil texture with annual rainfall was noted for relatively well-developed soils of various parental materials (Mueller-Dombois et al. 1980). Therefore, although the dieback concentrations could have been affected partly by the distribution of deposits in relation to the annual rainfall (particularly so for the mixed *'a'ā / pāhoehoe* type, which was present only in the low-rainfall zone of the study area), the general pattern appears to be a larger and more continuous dieback on the substrates of finer texture.

As to the association of dieback with substrate on Mauna Loa, dieback generally increased with age of substrate and peaked on 3000 - 10 000 yr old deposits. However, the range of ages represented by the different substrate types varied. In addition, the trend appears to

Table 3. The Wald statistic (with a χ^2 distribution) for the coefficients of various physical factors included in the logistic regression models; coefficients were estimated by the maximum-likelihood method applied to the sampled data sets (see Methods). * = highly significant; # = < 0.05; these values can be considered to be correlated with dieback; other values not significant.

Physical factor	Mauna Loa				Mauna Kea			
Year/	1954	1965	1972	1977	1954	1965	1972	1977
Annual rainfall	43.8*	105.2*	102.6*	130.0*	214.7*	206.6*	234.7*	202.9*
Slope aspect	1.0	5.0#	0.8	0.1	2.5	6.3#	0.0	1.0
Slope gradient	4.7#	2.7	11.4*	8.0*	64.6*	18.9*	11.5*	9.8*
Substrate type	439.0*	251.5*	133.5*	150.4*				
Substrate age	31.5*	27.8*	2.9	13.8*				
Mean slope gradient by 100 m-interval elevation zone					184.7*	172.6*	223.4*	244.0*

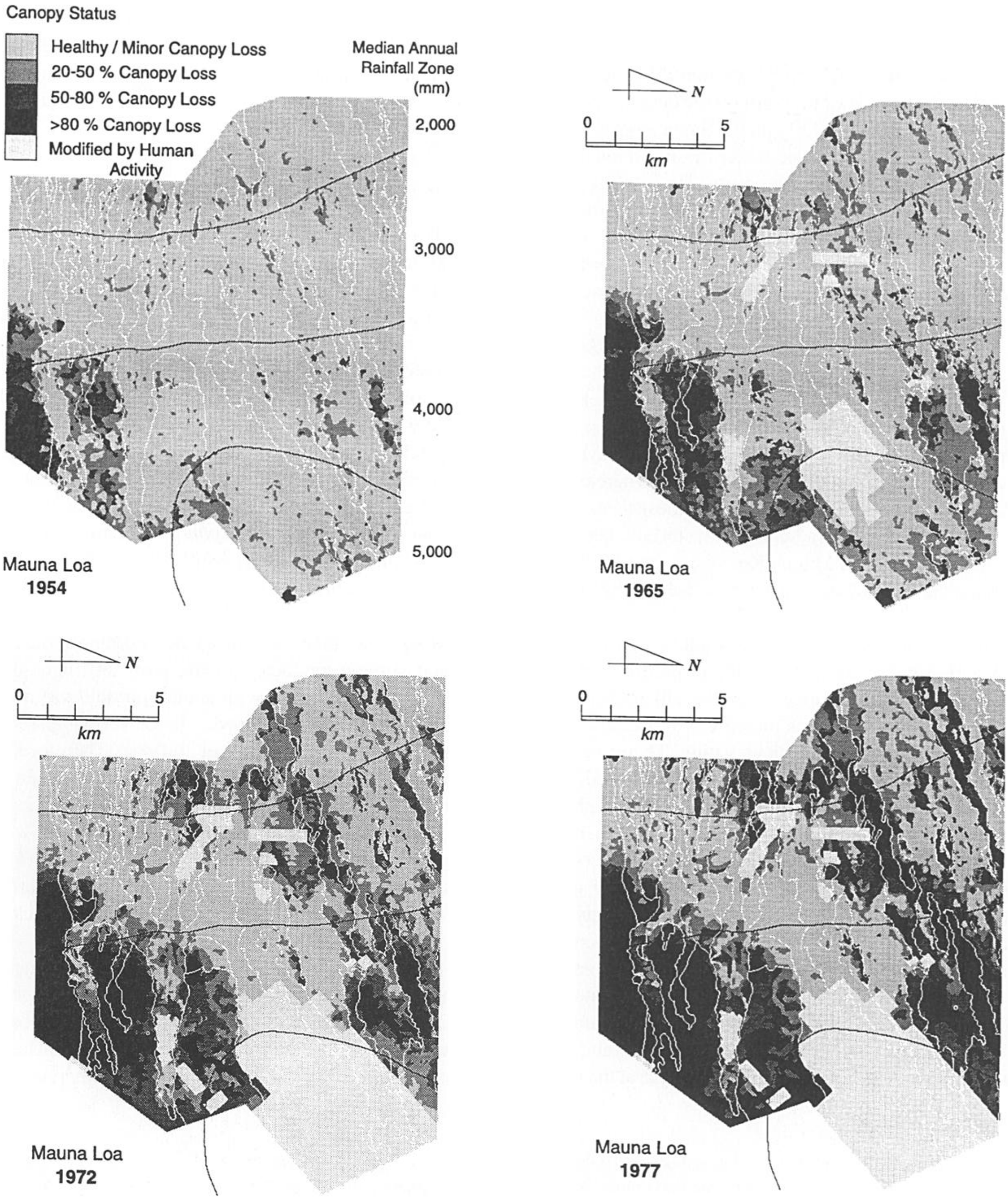

Fig. 1. Development of forest canopy dieback patterns on Mauna Loa during the period 1954-1977 in relation to median annual rainfall zones (separated by dark lines) and underlying substrates (white lines). Four images: 1954, 1965, 1972, 1977.

have been affected strongly by the concentrations of dieback on particular substrate types as well as by annual rainfall. The Wald statistic indicated only weak correlations between dieback and substrate age (Table 3).

Individual deposits, or substrate patches, are recognized by the spatial contacts of different ages and/or substrate types, whose surface boundaries are indicated by white lines on Fig. 1.The 53 deposits on Mauna Loa which are > 10 ha in exposed surface area, were compared for their dieback concentrations in 1977 (Fig. 9). The concentration varied among the individual deposits of the same substrate type (A) and age group (B). It

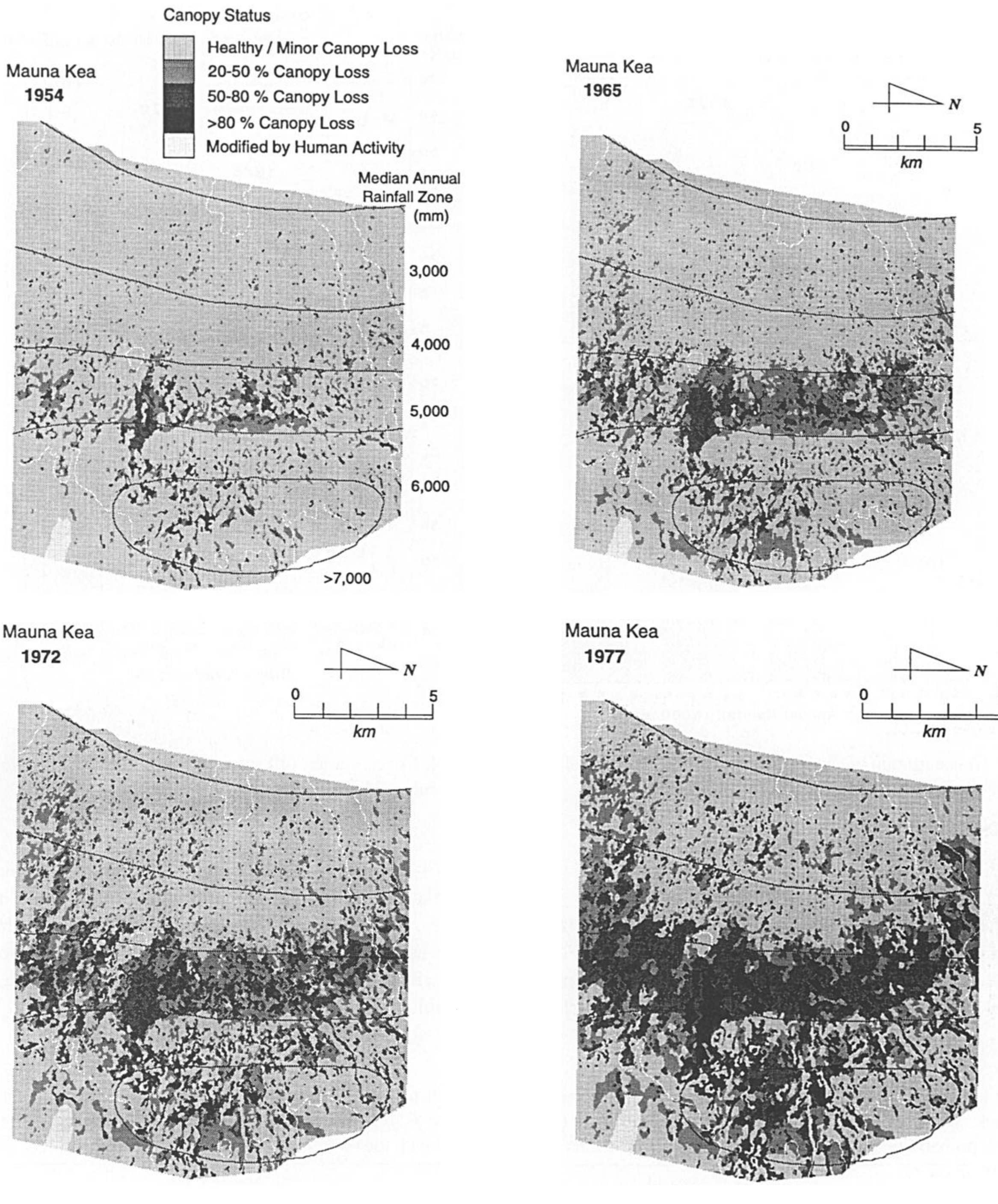

Fig. 2. Development of forest canopy dieback patterns on Mauna Kea during the period 1954-1977 in relation to median annual rainfall zones (separated by dark lines) and underlying substrates (white lines). Four images: 1954, 1965, 1972, 1977.

appears that, although overall dieback concentration may have been associated with substrate type, individual substrate patches or deposits have affected the spatial patterns of dieback more directly. However, the effect of these deposits on dieback pattern was not constant through time. Dieback occurred more or less randomly with respect to the substrate patches in the early years, but became increasingly associated with them as time passed by (Fig. 1). Frequently, the expansion of dieback stopped at the substrate patch boundaries.

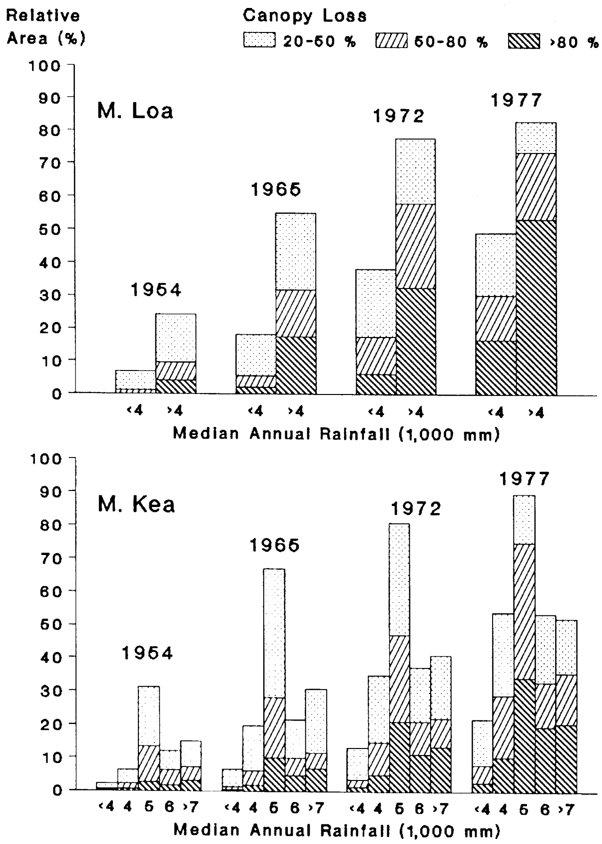

Fig. 3. Concentration of canopy dieback in relation to median annual rainfall on Mauna Loa and Mauna Kea.

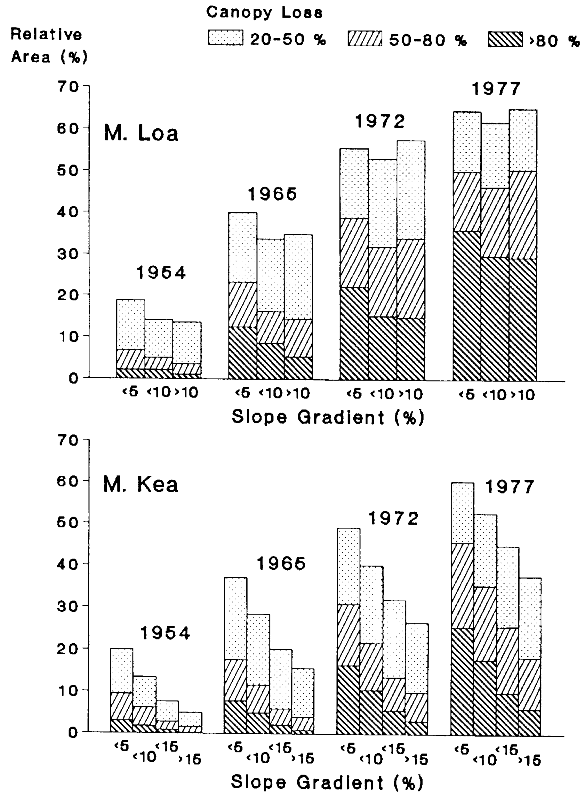

Fig. 4. Concentration of canopy dieback in relation to slope gradient on Mauna Loa and Mauna Kea.

Relative effects of factors

The contributions of individual physical factors (R) to the logistic regression models are compared in Fig. 10. Because the variable substrate patch is a combination of substrate type and age, it showed high correlations (40-60 %) with the latter two variables. A high correlation between independent variables affects R-values, leading to misinterpretation. Thus, two models were used: one with and one without substrate patch. The within-group correlations of the other independent variables were relatively low, between 1 and 28 %.

Table 4. Goodness of fit of the logistic regression models based on mappable physical parameters. The samples were classified into 'dieback' when their dieback probabilities computed by the models were > 50 % and into 'non-dieback' when their computed dieback probabilities were < 50 %. The model predictions were compared with the observed canopy states of the samples.

		Mauna Loa			Mauna Kea		
Year	Canopy status	Observed	Correctly predicted	% correct	Observed	Correctly predicted	% correct
1954	Dieback	1361	942	69	1098	811	74
	Non-dieback	1178	970	82	1209	812	67
	Overall	2539	1912	75	2307	1623	70
1965	Dieback	1076	725	67	1030	736	72
	Non-dieback	1095	845	79	1109	732	66
	Overall	2171	1570	72	2139	1468	69
1972	Dieback	1018	611	60	1017	701	69
	Non-dieback	1000	723	72	1170	788	67
	Overall	2018	1334	66	2187	1489	68
1977	Dieback	1296	901	70	1099	790	72
	Non-dieback	1105	716	65	1120	696	62
	Overall	2401	1617	67	2219	1486	67

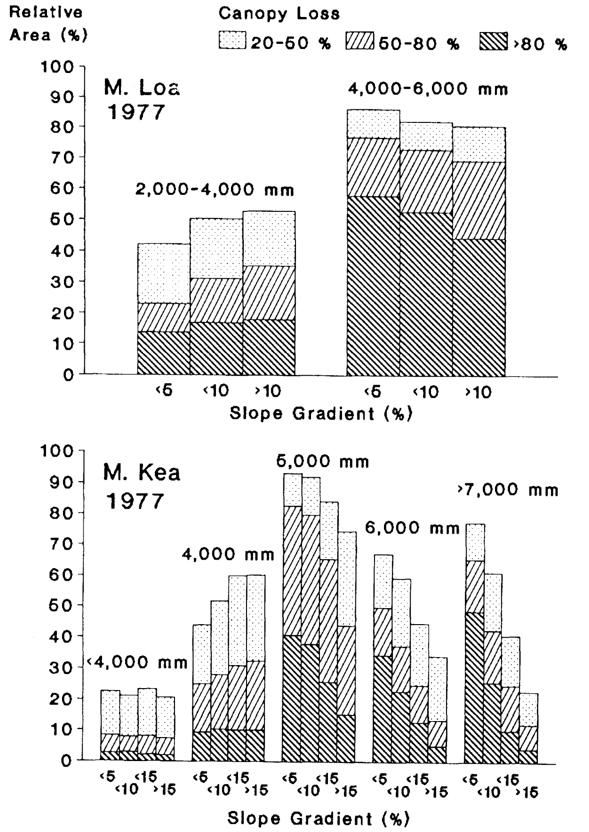

Fig. 5. Concentration of canopy dieback in relation to slope gradient and median annual rainfall on Mauna Loa and Mauna Kea.

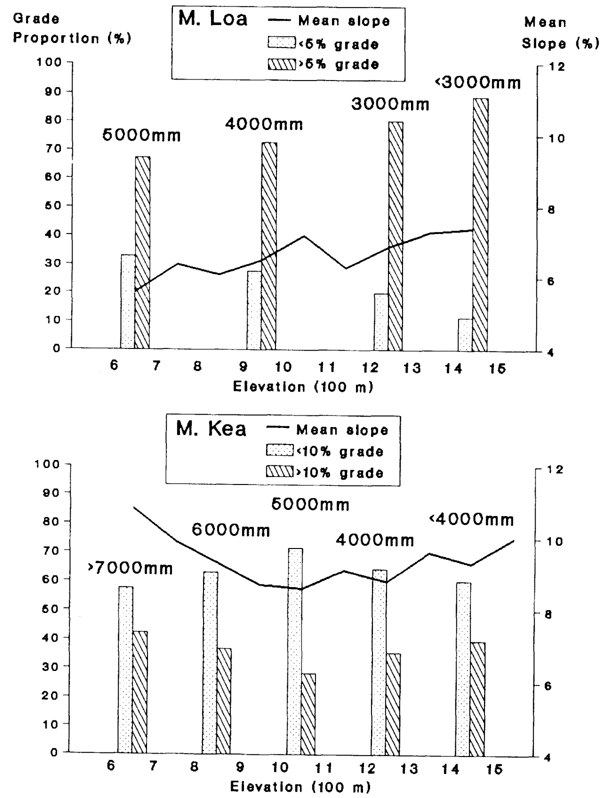

Fig. 6. Proportions of flatter and steeper surfaces at median annual rainfall zones (indicated by patterned bars) and mean slope gradients by elevation zone (indicated by lines) on Mauna Loa and Mauna Kea. On both mountains annual rainfall decreases with increasing elevation.

On Mauna Loa, the canopy dieback was most strongly correlated with substrate type during the early years and substrate patch in the late years. This strong early-year correlation of dieback with substrate type, particularly in 1954, was affected obviously by the dieback on the ash and the mixed ash-lava substrates at the SE corner of the study area, which had started earlier than in the rest of the forest and was already in the advanced stages by that time (Fig. 1). Nonetheless, the influence of substrate type on dieback was still comparatively strong in more recent years after dieback became very common and extensive across the forest. Annual rainfall also had relatively high and persistent correlations with dieback after 1954. The correlation of substrate age fluctuated in the more recent years, and as noted previously, substrate age does not seem to be a reliable parameter. In comparison, on Mauna Kea, where the substrates are all mixed ash-lava type, the canopy dieback was most strongly correlated with annual rainfall and the mean slope of the terrain by elevation zone. Slope gradient at individual sites had higher correlations with dieback than on Mauna Loa, particularly in the early years. The correlation of dieback with substrate patch increased in the more recent years, but it was not as high as on Mauna Loa. This seemed to be largely due to a very extensive ash deposit present in the Mauna Kea study area.

The dieback probabilities of the samples estimated by the models, excluding the variable substrate patch, are compared with the actual dieback states of the samples. Classifying the samples into dieback and non-dieback at the estimated dieback probability of 50 %, the goodness of fit of the logistic regression models based on the mappable physical parameters alone was fairly high (Table 4). The fit of the models, however, decreased with time as dieback expanded in space. This could be attributed to the decreases in the correlation of dieback with substrate type on Mauna Loa, and the slope gradient at individual sites on Mauna Kea (Fig. 9). When the factor substrate patch was included in the models, the goodness of fit of the models were maintained at the 75 % level for Mauna Loa and the 68 % level for Mauna Kea up to the more recent years.

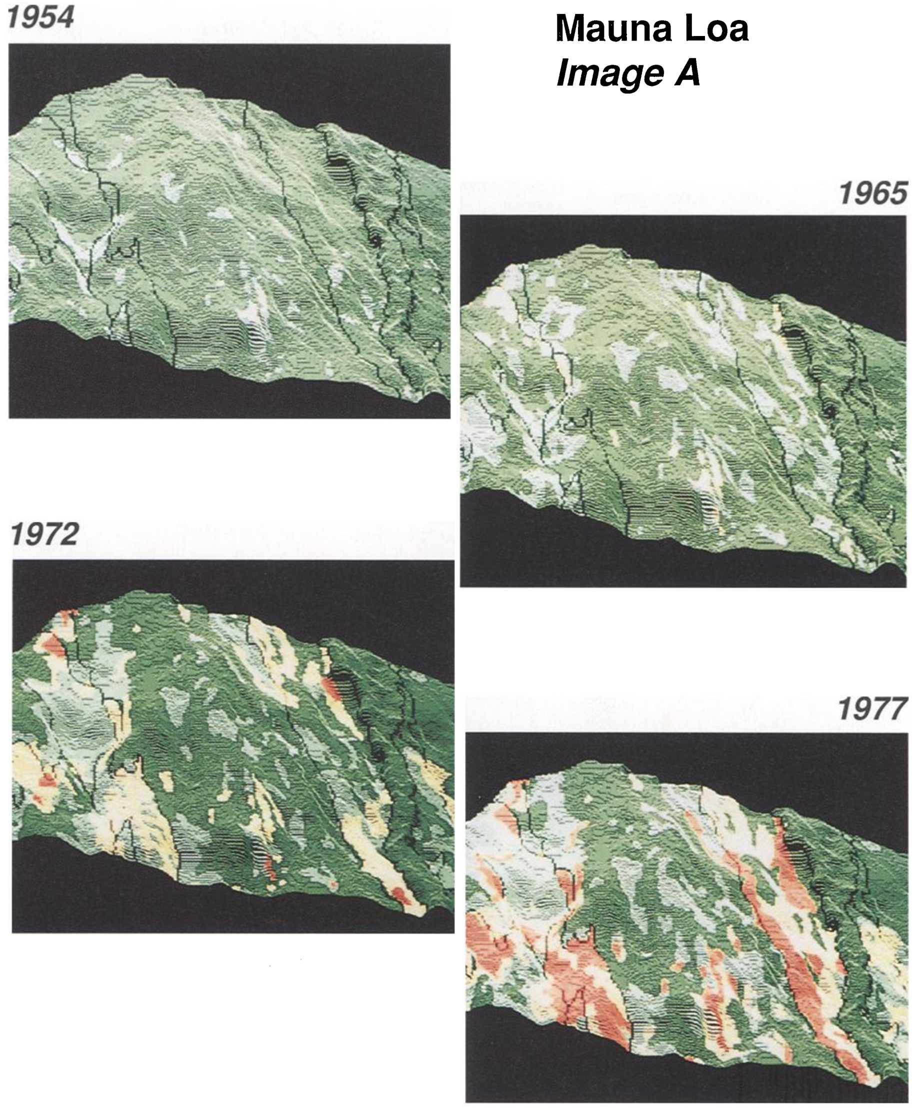

Fig. 7A. Computer-generated color prints showing development of forest canopy dieback patterns on Mauna Loa during the period 1954-1977 in relation to microtopography and underlying substrates (dark lines). Image A shows a 7 km × 5 km upper-slope section situated between the elevations 1250 m and 1600 m on Mauna Loa.

Discussion

Landscape ecology emphasizes the spatial characteristics and dynamic relationships of patches (Forman & Godron 1981, 1986). By identifying the component patches of a mosaic, the underlying processes contributing to the pattern formation may be inferred based on the characteristic scales of the component patches in time and space (Urban et al. 1987). The spatial dynamics may be described in terms of the changes in the patch boundaries (Swanson et al. 1990; Wiens et al. 1985).

The multi-scale, landscape approach is becoming more and more popular in describing spatial distribution of vegetation characteristics (Holling 1992; Swanson et al. 1992; Mackey 1993; DeFerrari & Naiman 1994). As to the effect of disturbances, for those with well-known causes it would not be necessary to relate them to environmental patterns. For those without obvious causes, however, establishing environmental pattern relationships may be crucial. Yet, due to the patch complexity, this may not always be accomplished through investigations that depend only on the traditional stand-level approach. The change in perspective from stand to landscape and the examination at multiple scales of space and time in our analyses resulted in several new findings. Our results suggest that dieback in the Hawai'ian rain forest does not occur quite as randomly in space as seemed to be the case previously, but, indeed, has some association with the physical environment. Furthermore, the association of dieback with certain fea-

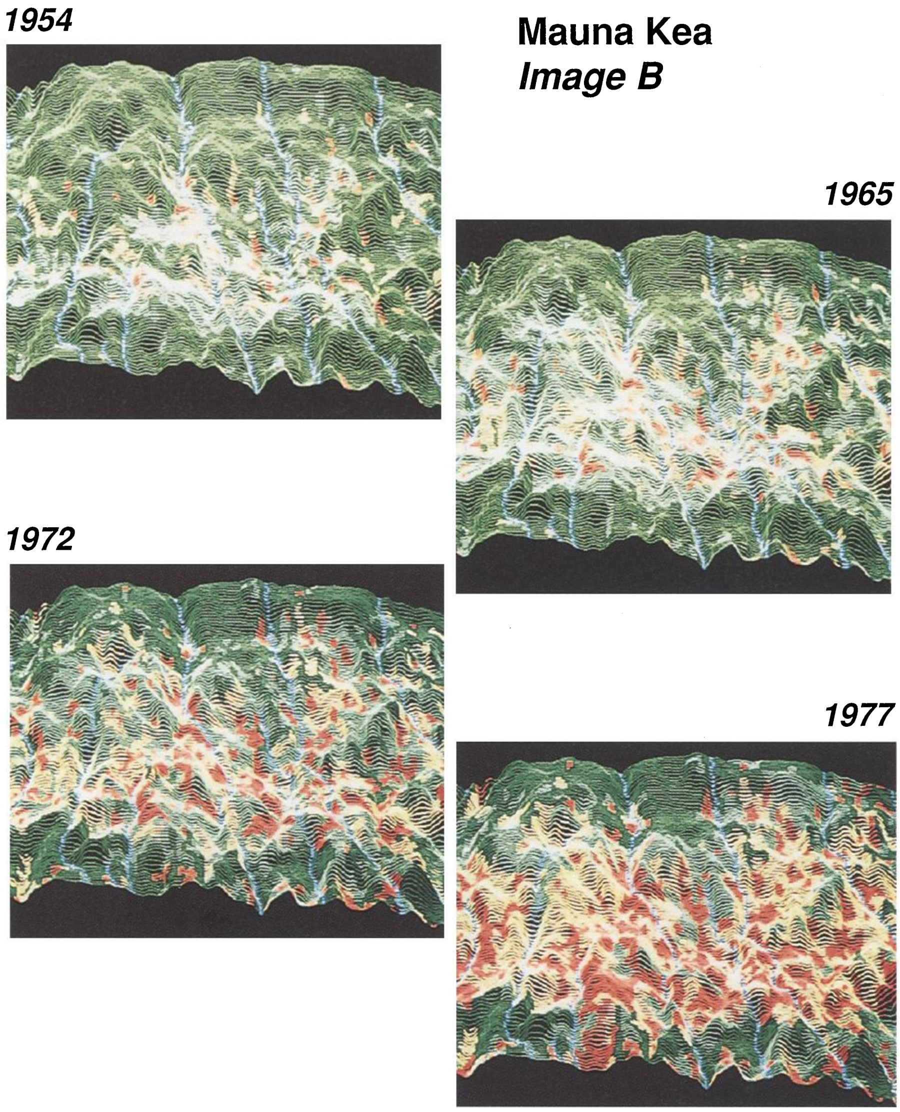

Fig. 7B. Computer-generated color prints showing development of forest canopy dieback patterns on Mauna Kea. during the period 1954-1977 in relation to microtopography and underlying substrates (dark lines). Image B shows a 5.5 km × 4.4 km middle-slope section situated between the elevations 900 m and 1200 m on Mauna Kea. The central zone of Image B corresponds to the 5000 mm rainfall zone, where the terrain forms a shelf-like structure. Colors indicate various intensities of canopy loss: green = < 20%; light green = 20-50%; yellow = 50-80%; red = > 80 %.

tures of the physical environment do not appear to be random or uniform over space and time. It appears that individual physical components had distinctive roles and scales in controlling the development of spatial dieback patterns across the rain forest landscape.

Control of microtopographic factors

Microtopographic factors, such as slope gradient, the shape of terrain (concave or convex) and the relative position on hill slope (hill bottom, mid-slope or hill top), affected dieback patterns at the finest spatial scales. On both mountains in our study, the dieback patches appeared first in places most frequently associated with flat slopes, concave surfaces, and/or hill bottoms. The subsequent enlargements of the patches commonly traced these features of microtopography closely. When dieback became more wide-spread across the rain forest, the heterogeneity in microtopography was reflected in the mosaic of dieback intensity. In comparing the dieback patterns of the two mountain slopes, it was easily recognized that the dieback patches on Mauna Kea were more numerous but generally more confined in area than those on Mauna Loa, and this has been quantitatively documented in a separate pattern analysis (Akashi 1994). From that analysis it is evident that the dissected slope

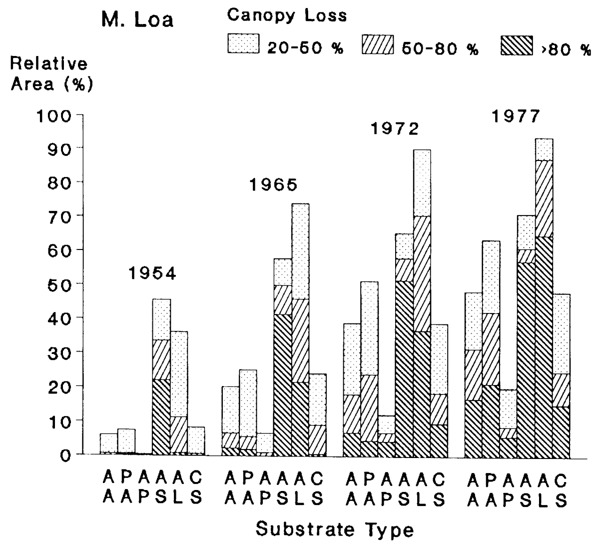

Fig. 8. Concentration of canopy dieback on Mauna Loa in relation to substrate type. Abbreviations are: CS = cinder/spatter, PA = *pāhoehoe*, AA = *'a'ā*, AP = mixed *'a'ā-pāhoehoe*, AL = ash-covered lava or mixed ash-lava, and AS = ash.

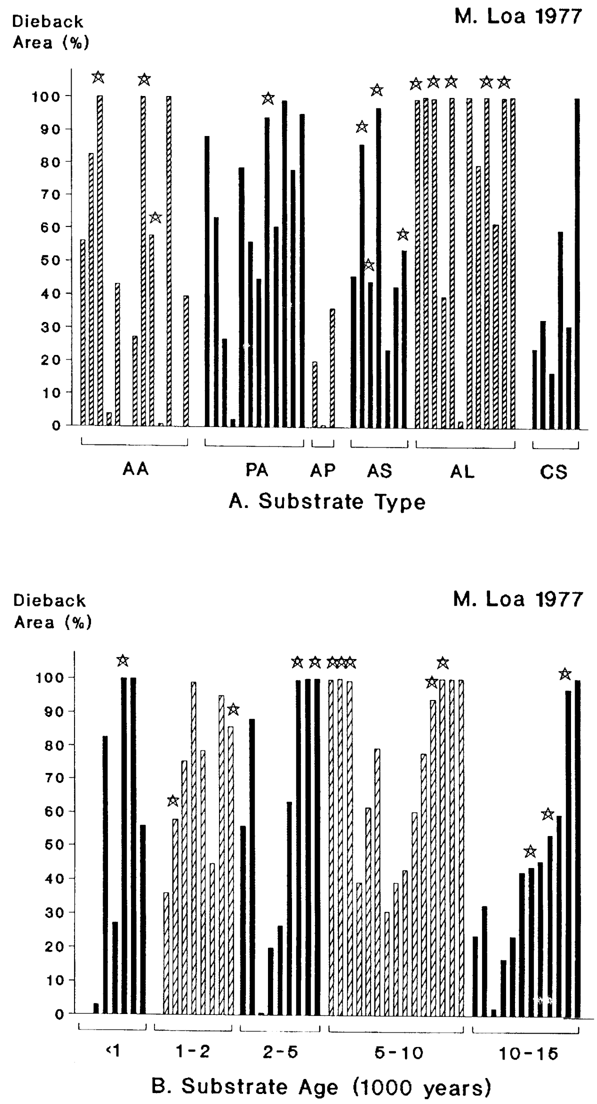

Fig. 9. Concentration of canopy dieback on individual deposits of Mauna Loa. A total of 53 deposits with > 10 ha surface areas are compared by substrate type (A) and age (B). The star symbol indicates very severe dieback, i.e. > 50 % of the dieback area suffering > 80 % canopy loss.

of Mauna Kea has provided a larger number of dieback initiation points and microtopographic pockets to control dieback concentration at finer scales. Microtopography played a primary role in determining the sites of dieback initiation and the shape, size and complexity of fine dieback patterns during the early to middle stages of the spatial pattern development.

Control of volcanic deposits or substrate patch

Substrate patch affected dieback patterns at the scales broader than those of microtopography. Substrate boundaries limit the continuity of parent material in space, and thus limits the continuity of the soils having similar general characteristics. In addition, the substantial variabilities in dieback concentration among the individual deposits even of similar types or ages on Mauna Loa imply that substrate patch also limits the spatial continuity of the canopy trees having similar life stages, physiological conditions and/or genetics.

Metrosideros polymorpha, the dominant canopy tree of the Hawai'ian rain forest, is a typical pioneer species that requires full sunlight for establishment. The regeneration of the species thus occurs typically in cohort populations of relatively similar ages on new volcanic deposits or under the newly opened canopy due to disturbances, which include dieback. On the Mauna Loa slope where the surface deposits are relatively young, small or narrow and only mildly dissected, the boundaries of cohort populations could still be closely associated with the deposit boundaries. When dieback spread across the rain forest and the dieback patches became aggregated here and there, the correlation of dieback with substrate patch increased greatly. In the final stages of the dieback pattern development, substrate patch clearly controlled the shape and spatial contagion of the patterns.

In contrast, on the old, dissected and spatially extensive surface deposits of Mauna Kea, substrate boundary had less effect on shaping dieback patterns. This could have been in part due to the low concentration of dieback in the extensive low-rainfall zones, which were included in the large central deposit of the study area, but it could also have been caused by the spatial discontinuity of cohort populations. After many cycles of dieback succession on the old substrates, the cohort populations there may no longer follow the deposit boundaries. Instead, they might have become fragmented spatially in correlation with other physical factors at scales smaller than those of the deposits, for instance, soil water as modified by topography.

Control of macro-physical factors

The macro-physical factors, such as annual rainfall, the type of substrate and the mean slope of terrain, affected dieback pattern at the broadest spatial scales. In comparison with those of microtopography and substrate patch, the effects of these factors seemed to be more indirect and statistical. The macro-physical factors had strong and relatively persistent influences on the overall trend of dieback concentration across the rain forest. At fine scales, their influence on the shape and size of individual dieback patches was minor. The complexity of the landscape pattern was less affected by the macro-physical factors.

A predisposing factor of dieback

Manion & Lachance (1992) and Huettl & Mueller-Dombois (1993) review various concepts and hypotheses concerning the causes and mechanisms of forest dieback. As far as the *Metrosideros* dieback of the Hawai'ian rain forest is concerned, it is our current understanding that the canopy trees lose vigor gradually as a result of the physiological stress accumulated during stand development. They start dying suddenly, apparently being triggered by some exogenous perturbation which brings about a physiological shock to the stress-bound, pre-senescing trees (Mueller-Dombois 1988, 1991 in press).

Our results show large dieback concentrations on the concave and/or nearly flat volcanic surfaces, in the high annual rainfall zones, on the finer, thus comparably impermeable substrates, and on the very gently sloping positions of the terrain profile. They consistently point to habitat hydrology, in particular poor drainage, as the primary physical factor making the canopy trees very susceptible to dieback. It, however, should also be emphasized that dieback was never confined to the poorly-drained habitats of the rain forest, even though its initiations and later concentrations were definitely associated with such habitats. The gradual spread of canopy mortality from the very wet into the moderately and relatively well-drained environments would imply a gradient of moisture-related stresses among the mature trees of relatively similar ages and/or physiology, if our current understanding is correct.

There would be several ways that habitat hydrology could possibly induce stress and deterioration in the canopy trees. When continuous rainfall causes prolonged flooding in a habitat, water-logged anaerobic soils would obstruct the respiration and proper functioning of the root system. In New Zealand, Ogden et al. (1993) found substantial reductions in the annual growth rings of *Nothofagus solandri* in very wet years. These authors suspect that water-saturated habitats induced the *Nothofagus* dieback in Tongario National Park of New Zealand. Drought could be a stress factor as well in usually wet habitats. In habitats which are almost constantly supplied with moisture, trees do not need to extend their root systems to meet their water demand. As a result they often develop unusually shallow and short root systems. The physiological study by Jane & Green (1983) indicated that such trees were extremely sensitive to even minor droughts. Based on their dendrochronological analysis, these authors suggested that the

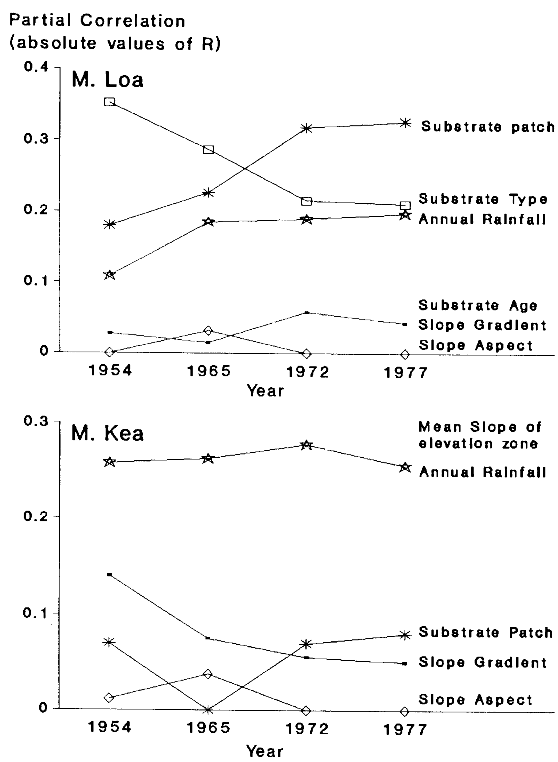

Fig. 10. Contributions of individual physical factors to logistic regression models of Mauna Loa and Mauna Kea. The *R*s for all factors except substrate patch were obtained together in a single model for each year. The *R* for substrate patch was obtained in a separate model because substrate patch is actually a combination of substrate type and age.

dieback of the cloud-zone forests on the Kaimai Ranges in New Zealand had been triggered by intense summer droughts. Recently, a similar suggestion was made for the dieback that occurred in the *Abies densa* forest of Bhutan (Donaubauer 1993). Also, large fluctuations in soil moisture may affect the vigor of trees. Auclair et al. (1992) and Auclair (1993) suggest that abrupt changes in habitat moisture, especially from prolonged water-logging to drought, can cause xylem cavitation injuries in large trees and thereby initiate canopy dieback. Accordingly, while dendrochronology may not be a very useful tool in the tropical climate characterized by year-round mild temperatures and high rainfall, future research in the Hawai'ian rain forest should certainly include studies of root morphology and physiology of *M. polymorpha* along soil moisture gradients and under conditions of greatly fluctuating rainfall.

In the meantime, our results provide a preliminary baseline for predicting spatial dieback progression across the rain forest landscape. Since spatial dynamics modeling of stand-level dieback in Hawai'i has been initiated by Jeltsch & Wissel (1993) on a mathematical basis, more sophisticated and realistic models may be developed in the future. Our results and spatial data may then become integrated into such models that simulate the life cycle dynamics of the Hawai'ian rain forest. Although the number of variables examined in our study was limited due to the limitation of time and the softwares used, the dieback predictions will improve when the spatial patterns of hill-slope position and ground shape are included in such a model, and when more information becomes available on the fluctuating site factors that produce physiological setbacks, as well as on the spatial distributions of age, physiology and genetics of the trees across the rain forest.

Conclusions

The landscape perspective of the Hawai'ian rain forest dieback may again bring up the question: does this not look like an epidemic disease or insect pest? Yes, perhaps, but very thorough research in the 1970s disproved the epidemic disease hypothesis. Instead, what became apparent in this landscape study are what we may call 'wet spots' in the *Metrosideros* forest that were most strongly predisposed to canopy dieback. Analogous to fuel-loaded, ignition points or 'hot spots' in the cases of forest fires, the 'wet spots' at poorly-drained habitats in our study areas were stocked in most cases with stunted old trees that were ready to collapse upon a climatic perturbation (Mueller-Dombois 1986). On Mauna Kea these 'wet spots' were mostly boggy depressions in an undulating terrain of volcanic ash dating from the Pleistocene, while on Mauna Loa they were often large flats in the form of poorly drained, older (more weathered but post-Pleistocene) *pāhoehoe* flows with ash overlays which had sealed the formerly pervious rock fissures with fine-textured mineral and organic matter.

The progression of dieback, which looks like a spreading disease, is perhaps the most puzzling aspect. For *Metrosideros polymorpha* the dieback often moved from unfavorable, very wet habitats to favorable, well-drained habitats. Moreover, this pattern of progression was not always synchronized across the landscape, i.e. in some locations dieback already spread to well-drained habitats in 1954, while in others it started at 'wet spots' in much later years. This could have been a lag-effect following an initial very strong climatic perturbation in the early 1950s, but it can also be explained as a series of climatic perturbations (Mueller-Dombois 1986) that increasingly caused the collapse of larger forest segments.

Recent climatic perturbation analyses (Mueller-Dombois 1993; Auclair 1993) for this area, support the latter interpretation. Repeated climatic perturbations may cause stunting in trees, particularly if they are in their late-mature growing phase. Since no spectacular or catastrophic perturbations have been discovered for the 30-year dieback phase, the dieback progression over the less extreme habitats (i.e. some of the well-drained knolls on Mauna Kea and the well-drained lava flows and ash deposits on Mauna Loa) can be explained as a function of predisposition through stand-level or cohort senescence.

It should be understood that cohort senescence (Mueller-Dombois 1992a, 1993) is not simply an expression of 'old age' of an even-aged stand but rather the result of a stand's demography, which includes the perturbations and stresses that occur during its life cycle. That these factors include repeated climatic perturbations, increasing edaphic stresses such as nutrient limitations in the growing stand, and changes or fluctuations in the water table of its habitat was indicated in past studies (Mueller-Dombois 1986; Gerrish & Bridges 1984; Doty 1981).

The spatial expansion of dieback scale from smaller 'wet spot' to broader 'substrate patch', repeatedly demonstrated on the Mauna Loa substrates, shows that the dieback, which initiated in a particular microtopographic position, moved across each volcanic deposit (or patch) and then frequently came to a halt at the edge of the patch. This suggests a certain physiological uniformity in the forest stand which covered the patch. This is believed to be a reflection of the large-area cohort mosaics. The more or less even-aged character of the Hawai'ian cohort forest segments that form mosaics of forest stands in different life-stages or age-states seems to be maintained through several dieback and regeneration cycles until the spatial coherence breaks up into smaller segments. These then begin to coincide with the geomorphological aging process or the microtopographical development of the landscape if the forest is not otherwise opened up by an infrequent catastrophic hurricane or even by a rare fire. The dieback patterns on the dissected Mauna Kea slope seem to support this interpretation.

Acknowledgements. This study was funded by NSF Award DEB 89-18526 "Ecosystem Dynamics in Hawai'i" to D. Mueller-Dombois, which also paid for the dissertation research on the 'Landscape ecology of *Metrosideros* dieback' by Yoshiko Akashi, completed in April 1994. The GIS hardware and software equipments were provided by the Environment and Policy Institute of the East-West Center, Honolulu.

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Received 1 July 1994;
Revision received 30 December 1994;
Accepted 5 January 1995.