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Population Death in Hawaiian Plant Communities: A causal Theory and its Successional Significance[1])

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SUMMARY

Population death or synchronized plant-group dying or dieback, as constrasted with individual plant dying or single plant death, is a common phenomenon in Hawaiian plant communities. Examples of population death are given from forest, scrub and grassland communities and from lowland, montane and higher altitude environments as well as from native and non-native plant populations.

In the better researched cases, the *Metrosideros* and *Canavalia* diebacks, it is clear that the dead standing populations are not simply relict stands left from herbivore predation of their reproduction. This explanation was given in the earlier literature for the dying *Acacia koa* and *Sophora chrysophylla* forest stands on Mauna Kea. Instead, in the *Metrosideros* and *Canavalia* diebacks and the other examples cited, reproduction from seedlings and/or vegetative reproduction are typically associated with the dieback populations. The dieback populations themselves can be considered as cohorts, i.e. groups of individuals that originated from a wave regeneration in their respective habitats.

Five characteristics, common to the described dieback populations were noted: 1) the populations belong to pioneer or seral species, 2) they occur in synusiae with low species diversity, 3) they grow in areas where disturbances gave rise to invasion of large cohorts, 4) they are associated with reproduction of the same species under or nearby the dying cohort and thus were described as "oscillating persisters" in succession, and 5) the dieback populations persist in all cases for relatively long periods for several reasons (low rates of decomposition, slow rates of successional replacement and low frequency of catastrophic perturbations).
Current hypotheses to explain population death in plant communities were reviewed as emphasizing one of four possibilities: 1) diseases or biotic stresses due to fungal pathogens or insect pests, 2) new man-imposed stresses, 3) recurring abiotic natural stresses, and 4) combinations of stresses.

A new theory is proposed which takes all the described dieback variations into consideration. It focuses on the dieback events as a chain reaction process involving: 1) senescing cohorts as the major predisposing condition, 2) dieback precipitating or triggering factors. These may operate as species-specific internal triggers (such as a heavy flowering season in the senescing stage) or as hard-to-detect environmental triggers, for example, a strong local wind that may tear off much of the foliar biomass (which then cannot be replaced because of the low carbohydrate reserves in the senescing stage), and 3) dieback-hastening factors, such as biotic agents and/or also dieback-stalling factors such as a temporary more favorable soil water or nutrient condition.

In addition, this theory is seen as providing fresh insights into the successional consequences of such diebacks. Dieback may be considered a driving force in secondary succession whenever it occurs, because of the relatively sudden opening of the canopy or death of the shoot systems. This in turn releases nutrients through death of the root systems and high litter inputs and protects the surviving undergrowth species and new seedlings (or vegetative reproduction of the dying cohort) from competition. Moreover, several indications in the Hawaiian *Metrosideros* rain forest have led to the hypothesis that the next generation of *Metrosideros* seedlings is not always genetically and physiologically identical to the dying cohort on the same site. That is, there are successional races or successional ecotypes indicating that *Metrosideros polymorpha* may have evolved into its own successional replacer. This is seen as an analogy to floristically richer areas, where the successional replacers are usually different species which form a functional sequence from pioneer, seral to climax along successional gradients. The hypothesis of successional races or ecotypes in *Metrosideros polymorpha* is currently subjected to experimental research in Hawaii using the "Hohenheimer" water table model as a transplant garden.

ZUSAMMENFASSUNG

Das mehr oder weniger plötzliche Absterben von Pflanzenpopulationen ist ein nicht ungewöhnlicher Vorgang in Pflanzengesellschaften auf den Hawaiischen Inseln. Es zeigt sich durch starken und permanenten Blattverlust im Kronendach oder Zweigsystem bestimmter bestandsbildender Baumgruppen, Strauch- und Krautarten und durch das längere Vorhandensein von abgestorbenen Beständen.

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Besser erforschte Beispiele sind das *Metrosideros polymorpha*-Baumsterben im einheimischen Regenwald und das periodische Absterben von *Canavalia kauensis*-Rankenmatten im küstennahen tropischen Grasland im Hawaii Volcanoes National Park. Andere in der Literatur beschriebene Beispiele sind das Absterben des *Sophora chrysophylla*-Waldes am oberen Mauna Kea, und das Baumsterben von *Acacia koa* über der Regenwaldgrenze desselben Vulkans.

Das Absterben von *Sophora* und *Acacia* wurde auf den Einfluß eingeführter Herbivoren, vor allem der Schafe (im *Sophora*-Wald) und Rinder (im *Acacia*-Wald) zurückgeführt. Diese fressen kontinuierlich den Nachwuchs und den Unterwuchs, sodaß nur alternde Baumgruppen in den so beeinflußten Gebieten zurückbleiben.

In dem von Baumsterben gekennzeichneten *Metrosideros*-Regenwald und im tropischen Küstengrasland mit den periodisch absterbenden *Canavalia*-Rankenmatten gibt es keine Herbivoren, die den Reproduktionszyklus unterbrechen. Hier vollzieht sich das Populationssterben unter natürlichen Bedingungen. Für das Baumsterben im *Metrosideros*-Regenwald wurden fünf unterschiedliche Typen erkannt (wetland, dryland, bog-formation, displacement and gap-formation dieback). Drei dieser Typen zeigen Korrelationen mit vorherrschenden Standortsfaktoren. Diese führten zu Kausalhypothesen, z.B. daß eine vorübergehende Austrocknung des Wurzelhorizontes der betroffenen *Metrosideros*-Bäume auf flachgründigen, schnell-dränierten Lavaböden (d r y l a n d d i e b a c k) die Ursache sein könnte. Auf schlecht dränierten, flachgründigen Lavaböden hingegen könnte man das Umgekehrte als Ursache annehmen, nämlich vorübergehende Überflutung (z.B. nach zwei oder drei Jahren überdurchschnittlichen Regenfalls hintereinander) und Absterben des Wurzelsystems durch Luftmangel (w e t l a n d d i e b a c k). Im Falle des Sumpfbodens (b o g - f o r m a t i o n d i e b a c k) waren neben Wurzelerstickung während zeitweiliger Überflutung auch toxische Einflüsse (z.B. Eisenvergiftung) als Ursache anzunehmen. Das Baumsterben mit ausbleibendem oder verdrängtem Nachwuchs (d i s p l a c e - m e n t d i e b a c k) konnte nicht auf einen kausalen Standortsfaktor oder Befraß durch Herbivoren zurückgeführt werden, denn hier waren die Böden tiefgründig, normal dräniert und nährstoffreich (eutrophisch). Als Ursache wurde deshalb eine Überalterung der betroffenen Bestände angenommen. Ähnlich war es mit dem später erkannten fünften Typ des Baumgruppen-Sterbens, dem sogenannten " g a p - f o r m a t i o n d i e b a c k ". Dieser Typ erscheint auf den Kuppen und Hängen alter, ausgelaugter Ascheböden, die zwischen den immerfeuchten, sumpfigen Böden der älteren Ascheablagerungen im Mauna Kea-Regenwaldgebiet herausragen. Hier bot sich keine direkte Standortskorrelation an. Ein vielleicht frühzeitiges Altern, verbunden mit toxischen Einflüssen von Aluminium unter stark sauren Bedingungen, konnte als Ursache angesehen werden. Diese Annahmen dienen zur weiteren Forschung.

Ähnlich verhielt es sich mit dem Absterben der *Canavalia*-Matten im küstennahen Grasland des Nationalparkes. Der einzig stark variierende Standortsfaktor, der für das periodische Absterben verantwortlich gemacht werden konnte, waren die jährlichen Niederschläge, die hin und wieder beträchtlich variierten. Jedoch bestand zwischen diesen Schwankungen und den Absterbephasen von *Canavalia* kein korrelativer Zusammenhang. Es ergab sich deshalb die Folgerung, daß die Absterbephasen hauptsächlich, wenn nicht sogar ausschließlich, auf den Lebenszyklus einiger gleichaltriger und zusammenwachsender Individuen (cohorts) zurückzuführen waren.

Das mehr oder weniger gleichzeitige Absterben von Pflanzenpopulationen wurde auch für den einheimischen Strauch *Dubautia scabra* (*Compositae*) und den eingeführten, kleinwüchsigen Unkrautbaum *Buddleja asiatica* (*Loganiaceae*) festgestellt. Beide Populationen hatten sich explosionsartig auf einem vulkanischen Aschefeld eingestellt, das ursprünglich einen Regenwald überschüttet und vernichtet hatte. Eine weitere Beobachtung betraf den Unkrautbaum *Leucaena leucocephala* (*Leguminosae*), der dazu neigt, nach Grasbränden in sommertrockenen Gebieten in Küstennähe auf allen Inseln Strauchdickichte zu bilden.

Fünf Merkmale, die allen gebrachten Beispielen gemeinsam sind, wurden erläutert:

1. Alle betroffenen Arten sind entweder Pionier- oder Sukzessionsarten.
2. Sie sind die dominanten Mitglieder sehr artenarmer Synusien.
3. Sie kommen auf Standorten vor, auf denen katastrophische Zerstörungen die Ausgangsbasis zu neuen Sukzessionen gaben (vulkanische Aschefelder, Lavaböden, Feuer usw.).
4. In keinem der Fälle waren die absterbenden Populationen mit dem Verschwinden dieser Pflanzenart aus dem näheren Wuchsbereich verbunden. Im Gegenteil, neue Individuen siedelten sich in den meisten Fällen gleich zusammen mit den absterbenden Populationen an, oder neue Individuen kamen in der Nähe hoch.
5. Die absterbenden oder abgestorbenen Populationen bleiben in allen Fällen für relativ lange Zeiträume stehen. Gründe hierfür sind: relativ langsam arbeitende Zersetzungsvorgänge an den betreffenden Standorten, geringe Wiederholungschancen für die Art der katastrophischen Standortsstörung, die den Anlaß für die ursprüngliche Sukzession bot, und sehr verzögerte oder ganz ausbleibende sukzessionelle Verdrängung der abgestorbenen Populationen mit neu heranwachsenden.

Gegenwärtig verbreitete Hypothesen zur Erklärung des Absterbens von Populationen in Pflanzengesellschaften wurden herausgestellt als:

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1) Pflanzenerkrankungen durch Pilzbefall oder Insektenfraß,
2) Pflanzensterben durch neue, von der Industrie hervorgerufene Belastungen,
3) Pflanzensterben durch periodisch wiederkehrende natürliche, abiotische Umweltstreßfaktoren, und
4) Kombinationen von Belastungsfaktoren.

Eine neue Theorie wurde aufgestellt, die jetzt weiter verfolgt wird. Sie sieht den Populations-Sterbevorgang als eine kausale Kettenreaktion. Diese beginnt 1) mit alternden Populationsgruppen (senescing cohorts) als wichtigstem Ausgangsfaktor und konzentriert sich dann 2) auf das Aufkommen von synchronischen Auslösungsfaktoren, die endogener Natur sein können, wie z.B. ein starkes Blühen im Altersstadium, oder exogener Natur, z.B. ein starker Wind, der die Hauptblattmasse abreißt, die dann aber nicht erneuert werden kann, weil den alternden Pflanzen Reserven fehlen. 3) Als dritter Faktorenkomplex kommen dann noch Intensivierungen in Betracht, wie z.B. das Auftreten von Borkenkäfern oder von Wurzelfäulnis, die den Sterbevorgang beschleunigen.
Aber auch das Umgekehrte ist möglich, wobei ein Beschleunigungsfaktor ausbleibt, und stattdessen eine Verbesserung der Umweltsbedingungen eintritt, wie z.B. besonders günstige Bodenwasserverhältnisse oder neue Nährstoffzufuhr.

Diese Theorie erlaubt neue Einsichten über den Sukzessionsvorgang in Pflanzengesellschaften, in denen synchronisiertes Populationssterben vorkommt. Da der Pflanzenbestand sich verhältnismäßig plötzlich öffnet, verstärken sich die Lichtverhältnisse im Unterwuchs. Das Wurzelsystem stirbt ab und liefert zusammen mit dem Blattfall plötzlich freiwerdende Nährstoffe. Die absterbenden Individuen bieten Schutz gegen Wind, und es besteht keine Konkurrenz gegen den aufkommenden Jungwuchs. Die arteigene Reproduktion findet unter solchen Bedingungen oft günstige Entwicklungsmöglichkeiten. Aber auch anderer Unterwuchs wird begünstigt, und es ist eine Frage der relativen Anpassung an die neuen Verhältnisse, in welche Richtung die dann folgende Sukzession läuft.

In Hawaii haben wir im Zusammenhang mit dem *Metrosideros*-Baumsterben beobachtet, daß die neu aufkommende Generation der Absterbenden nicht gleich ist. Es scheint sich hier um ein sukzessives Ablösen verschiedener *Metrosideros*-Rassen oder Ökotypen zu handeln. Diese Hypothese der sukzessiven Rassen innerhalb des *Metrosideros polymorpha*-Artenkomplexes wird momentan experimentell untersucht, wobei das "Hohenheimer" Grundwasser-Modell als Aussaat- und Testgarten verschiedener Provenienzen dient.

For the last decade, a massive death of *Metrosideros polymorpha* trees in the Hawaiian montane rain forest has received considerable attention in terms of public concern and research (PETTEYS et al. 1975, PAPP et al. 1979, MUELLER-DOMBOIS 1980a). However, massive tree death in Hawaiian forests is not a new phenomenon (CLARKE 1875, MILLER 1900, LYON 1909, 1919, WAGNER 1961, FOSBERG 1961). In fact it can be said now that it is quite a common phenomenon, which is not restricted to forest communities, but also occurs in scrub and grass communities. Moreover, massive plant death is not restricted to indigenous Hawaiian communities, but occurs also in alien or non-native replacement communities.

A number of reasons have been suggested to explain massive tree death in Hawaiian forests. LYON (1909) suggested soil toxicity for the so-called Maui forest disease after he had searched for several years in vain for the earlier presumed killer fungus. FOSBERG (1961) suggested hardpan formation for *Metrosideros* dieback around Kauai bogs. SELLING (1948) suggested climatic change. WARNER (1961) suggested browsing by feral sheep as the cause of death of the tree line mamani (*Sophora chrysophylla*) forest on Mauna Kea. MUELLER-DOMBOIS & KRAJINA (1968) suggested cattle grazing of seedlings and/or shrubs as the reason for koa (*Acacia koa*) decline and flooding of root systems as the reason for *Metrosideros* tree death on the east slope of Mauna Kea. Disease and insect pests were considered for several years the major reasons for the massive death of *Metrosideros* trees on Mauna Kea and Mauna Loa (BURGAN & NELSON 1972, PETTEYS et al. 1975), until thorough research relegated biotic agents into a secondary role (PAPP et al. 1979).

This paper will review the dieback or plant death manifestations as found in a number of Hawaiian plant communities. It then will suggest a new dieback theory which will untangle the various hypotheses given before. It will also point out some implications to our understanding of succession, climax and ecosystem stability.

DEATH IN THE MONTANE RAIN FOREST

A rapidly spreading canopy collapse or crown foliage loss was reported by PETTEYS et al. (1975) for an 80 000 ha segment of indigenous montane rain forest

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on the windward sides of Mauna Kea and Mauna Loa. This information was obtained from a comparison of three sets of aerial photographs, the first taken in 1954, the second in 1965 and the third in 1972. The rapid rate of canopy loss spawned the disease hypothesis that determined the research efforts of the U.S. Forest Service for many years. Large areas with dead standing *Metrosideros polymorpha* trees on surface-flooded substrates in parts of the same territory (MUELLER-DOMBOIS & KRAJINA 1968) spawned the idea of a natural perturbation and successional process (MUELLER-DOMBOIS 1974) that guided the research efforts of the writer and several of his students from that time on to the present.

The subsequent discovery of *Metrosideros* stand dieback on substrates other than the surface-flooded soils required more complicated explanations for the natural (environmental) perturbation hypothesis (MUELLER-DOMBOIS et al. 1977) and it made the disease (or biotic agent) hypothesis temporarily more attractive (KLIEJUNAS et al. 1977). However, the finding that NPK fertilizer could restore full vigor in half-dead *Metrosideros* trees (KLIEJUNAS & KO 1974) and the finding that abundant *Metrosideros* regeneration was coming up in many *Metrosideros* dieback stands (MUELLER-DOMBOIS et al. 1977) was again support for the natural perturbation and succession hypothesis. This lead the U.S. Forest Service to launch a parallel but independent vegetation and soil analysis project (ADEE & WOOD 1982).

The disease hypothesis was only recently abandoned (PAPP et al. 1979), when evidence became increasingly stronger, that the two best candidates for the killer agents (the root pathogen, *Phytophthora cinnamoni* and the endemic *Metrosideros* borer, *Plagithmysus bilineatus*) could only be ascribed a secondary or subsidiary role in some cases. However, the disease hypothesis is still not totally abandoned (Pest Management Unit 1981). This again is not surprising in view of the bendable definition of what a disease is (e.g., physiological disease which is not caused by any biotic agent) and the pathological concept of the so-called "decline" diseases (MANION 1981). In spite of this semantic unclarity, it is now clear that the Hawaiian *Metrosideros* rain forest dieback or decline is not caused by any biotic agent.

Further progress in the causal analysis of *Metrosideros* canopy dieback has come from detailed spatial analyses of vegetation, dieback and soil patterns, from many population structure analyses, from additional air photo analyses (BURTON 1980, JACOBI 1982), from field experiments (BURTON 1980, MUELLER-DOMBOIS 1981a) and from extending observations to other areas (GERRISH & MUELLER-DOMBOIS 1980, MUELLER-DOMBOIS 1982 a,b). One of the main advances was the discovery of several different dieback patterns in relation to site and *Metrosideros* undergrowth response. In the 1977 report (MUELLER-DOMBOIS et al. 1977) we recognized four important site-related dieback patterns, which we called dryland dieback, wetland dieback, bog-formation dieback and displacement dieback. All were canopy diebacks involving tree groups of *Metrosideros polymorpha*.
The dryland dieback was defined as usually patchy, i.e., occupying small areas of only up to one hectare on well-drained lava substrates or shallow rock outcrop soils (Fig. 1 and 2 show adjacent stands on well-drained soils).
The wetland dieback was described as usually extensive, i.e., occupying large areas, often exceeding 10 hectares, on poorly drained lava substrates or shallow rock outcrop soils.
The bog-formation dieback was described as similary broad-area in extent as the wetland dieback, but as giving more of a salt-and-pepper effect on air photos, and as occurring on deep soils from volcanic ash that are permanently watersoaked and very poor in nutrients (oligotrophic).
The displacement dieback was described also as a large-area dieback, but occurring on moderately well-drained sites with deep soils from relatively more recent volcanic ash and rich in nutrients (eutrophic).

When it became possible in the summer of 1980 to do more detailed field research in the area of the bog formation dieback, we discovered yet another form of *Metrosideros* dieback occurring on the ridges between the bog-filled depressions. This we called "gap formation" dieback (MUELLER-DOMBOIS 1981a). This was described again as a patchy canopy dieback (similar to the dryland dieback), involving only few *Metrosideros* trees at a time, which dropped their foliage without showing signs of branch or stem breakage or other wind-damage.

Such dead standing tree groups were found in several places to be associated with abundant *Metrosideros* seedlings.

Actually, all forms of *Metrosideros* tree dieback studied thus far in rain forests are associated with *Metrosideros* reproduction, but the upcoming seed-

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Fig. 1: Vigorous, mature *Metrosideros polymorpha* rain forest stand (probably a cohort) with tree fern (*Cibotium glaucum*) undergrowth on well-drained soil from volcanic ash. On Hilo Highway, just outside of Hawaii Volcanoes National Park. 10 October 1982.

Fig. 2: Dieback stand of *Metrosideros polymorpha* with vigorous *M. polymorpha* sapling undergrowth, a two-cohort stand. About 100 meters from location of Fig. 1. 10 October 1982. An example of "Dryland Dieback".

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ling crop varies from abundant to very sparse. The latter form was given the name "displacement" dieback. BURTON (1980) who studied *Metrosideros* seedling behavior in the eutrophic soil territory of the displacement dieback, found that the displacement is not complete. A few *Metrosideros* seedlings which germinate on the top or sides of tree fern (*Cibotium glaucum*) trunks may survive by penetrating upwards through the otherwise vigorous tree fern canopy to form a very scattered second stand.

If we consider only the dieback and reproduction behavior alone, we can reduce the five recognized dieback forms into two, namely into "displacement" dieback and "replacement" dieback. We now know that the factors that determine "replacement" or "displacement" under *Metrosideros* canopy dieback are merely quantitative. But they refer to a number of specific interrelated factors, such as the vigor of the undergrowth, the growth rate of *Metrosideros* seedlings, their seedbed conditions and the soil nutrient and soil-water regimes of the particular rain forest habitat in question. With further, more directed and more detailed gathering of the appropriate data, it should become possible to predict the outcome of *Metrosideros* dieback in any specific sub-area of the Hawaiian montane rain forest through a dieback recovery model. This still leaves the causal mechanism for the dieback unanswered. But I will come back to this after discussing the death phenomena observed in other Hawaiian plant communities.

DEATH IN THE COASTAL GRASSLAND

For many years the seasonal rhythm of broad-area death and recovery of the annual lovegrass *Eragrostis tenella* gave a distinctive physiognomy to the coastal grassland south of the Kau Desert in Hawaii Volcanoes National Park (MUELLER-DOMBOIS 1966). During the dry season, from June through October, the area resembled a parched, yellow desert landscape, covered sparsely with the small dead annual grass individuals and during the wet season, November through May, the area was light green from the new crop of live annuals. This was so until about 1972 when the feral goat control program of the Park Service suddenly became effective. Large parcels of land had been fenced and the goats were herded out and eliminated from most of this area. Almost immediately, perennial grasses, particularly Natal redtop, *Tricholaena* (=*Rhynchelytrum*) *repens*, became established. The grass cover soon became denser with several other non-native grass species, notably *Melinis minutiflora* and *Hyparrhenia rufa*. Almost simultaneously with the perennial grasses appeared certain chamaephytes (i.e., thin-branched shrubs) and herbaceous vines. Among the chamaephytes was an indigenous shrub, *Waltheria americana*, the other dominant ones (*Cassia leschenaultiana* and *Indigofera suffruticosa*) were non-native adventives. It was, therefore, of particular interest when one of the rapidly expanding vines, *Canavalia kauensis*, turned out to be an endemic species (St. JOHN 1972) never before described.

Thus far, the succession after goat removal had followed a more-or-less expected and predictable pattern (MUELLER-DOMBOIS & SPATZ 1975). Annuals had been displaced by perennials. Among the latter, bunchgrasses and also mat-forming grasses (*M. minutiflora* and *Cynodon dactylon*) had become prevalent in the biomass. Low-growing woody plants (the chamaephytes) had become more dense. The herbaceous vines (including in addition to *Canavalia* also *Ipomoea* species) formed a patchy overlay in some areas. At this point it was believed, according to the rainfall regime of the area (MUELLER-DOMBOIS 1979), that the grassland succession would proceed further to a woodland stage provided that a suitable seed source was available. Two weed tree species, *Leucaena leucocephala* and *Ricinus communis*, are a constant concern for Park Service management. They still form only small populations in the area, but they can spread rapidly if not controlled frequently. Since there are no other seed trees in the area, the life-form succession has become arrested in the grass-chamaephyte stage.

A less expected trend now became apparent, which was the limited expansion of the vine patches, and a general patchiness in several dominant grasses. These included particularly the stoloniferous mat-formers, *Melinis minutiflora* and *Cynodon dactylon*, but also other grass life forms, such as the bunchgrasses, *Andropogon virginicus* and *Heteropogon contortus*. These grasses have a tendency, where they are well-established, to exclude other species. In contrast to these, *Tricholaena repens* expanded its territory explosively across the available habitat and now grows diffusively, but still as the dominant grass, in mixture with the similarly widely dispersed chamaephythes, *Waltheria americana* and *Cassia leschenaultiana* (MUELLER-DOMBOIS 1980b).

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Another unexpected trend was the dieback of *Canavalia kauensis*, the progression of which was annually monitored inside and outside an experimental exclosure for a decade (MUELLER-DOMBOIS 1981b). What happened was that this vine expanded rapidly to occupy solidly almost half (46%) of the area of a 7 x 10 m exclosure in 1971. Then it died back to 11% cover in 1974. After that it increased to 25% in 1977 and then it declined again to 2% cover in 1978. It remained that low through 1980 inside the exclosure, but in the meantime had climbed over the fence and began to expand outside. Here *Canavalia* has not formed a continuously expanding mat either. Mats expand only to a certain size (usually not larger than about 200 m^2) then they break down and form a dry mass of intertwined stolons, which persist for several years. New plantlets of the same species may come up under the dead mass of shoots or other plants may penetrate them. The local succession, so far, seems unpredictable. What is predictable, however, is that mat-formation and expansion is followed by mat-decline or breakdown in short intervals of a few years. Moreover, it is now predictable also that when a *Canavalia* patch dies, the species does not disappear from the area, but instead comes up in other places. Similar trends, although not monitored, have been observed in the same grassland for *Melinis minutiflora* and *Andropogon virginicus*, except that dieback in these species is less common, probably because they are longer-lived.

Thus, the seasonally alternating pattern of death and recovery of the annual *Eragrostis tenella* grassland has now been replaced, after ten years of goat exclusion, with two new dynamic patterns. The seasonal rhythm of drying and regreening is still apparent, although it is not anymore so extreme. The drying is not synonymous with populatiion death, but simply relates to the partial dormancy of the dominant hemicrypthophytes, such as *Tricholaena repens* and *Hyparrhenia rufa*. The other pattern can be described as a dynamic patch mosaic. Patches develop for a while and then may decline or even disappear in particular places, while they expand in others. This can be explained by life-cycle behavior (MUELLER-DOMBOIS 1981b), whereby the decline phase is represented by senescing cohorts (i.e., simultaneously aging individuals growing together).

DEATH IN OTHER HAWAIIAN COMMUNITIES

Dying populations of perennial plants or dead plant-stands are not only spatially significant in the Hawaiian rain forest and coastal grassland, they have been observed in several other communities. Here, three examples will be given that were observed by the writer through repeated visits to the same locations.

One of the better documented cases is the initially rapid invasion, later followed by decline, of a small exotic tree species, *Buddleja asiatica* (*Loganiaceae*). This species became established on a new volcanic ash deposit in Hawaii Volcanoes National Park (SMATHERS & MUELLER-DOMBOIS 1974). The tree grows only 2 to 3 m tall in this area. It was one of the first invaders in the so-called "Devastation Area" near Kilauea Iki Crater, three years after it exploded in 1959. A fairly dense population of this species became established on the new pyroclastic substrate in a broad frontal belt about 1 000 m long and extending about 60 m from the surviving *Metrosideros* forest. This *Buddleja* population, together with an invading *Rubus penetrans* population, became an early concern to the Park Service. It was thought that these aggressive exotics would "swamp out" potential endemic pioneer invaders. Herbicides were used initially to counteract their advance. This was not very effective, and the program was stopped. After five to six years, the *Buddleja asiatica* tree population started to die by itself. A pair of time-sequence photos (in SMATHERS & MUELLER-DOMBOIS 1974: 80) indicate that tree death was associated with loss of moisture supply, because a *Metrosideros* tree snag had fallen where the *Buddleja* tree had grown before. Snags, in this habitat, acted as interceptors of driving rain and thus as suppliers of moisture in addition to the amount of rain received per unit ground area. This pattern of *Buddleja* seedling-establishment at the bases of snags and later death of mature trees when the snags had fallen down was repeated throughout the area. But in the following years, *Buddleja* individuals would die also where the tree snags remained standing (Fig.3).

Initially we thought that the species would die out totally in this new habitat, but that idea proved wrong. New seedlings of *Buddleja* came up here and there, but more sparingly than before. Now after 20 years, the overall population has declined substantially, but it is still there and probably will remain in the area at the lower abundance level until succession proceeds to a closed *Metrosideros* rain forest.

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Fig. 3: Dead and dying individuals of small Mexican weed tree, *Buddleja asiatica* (foreground) in same "Devastation Area". They arrived here as seedlings in 1963-1964. In background two bushy *Metrosideros polymorpha* trees that recovered soon after the 1960 ash blanquet deposit, while others died (trees in background and in center foreground). 10 October 1982.

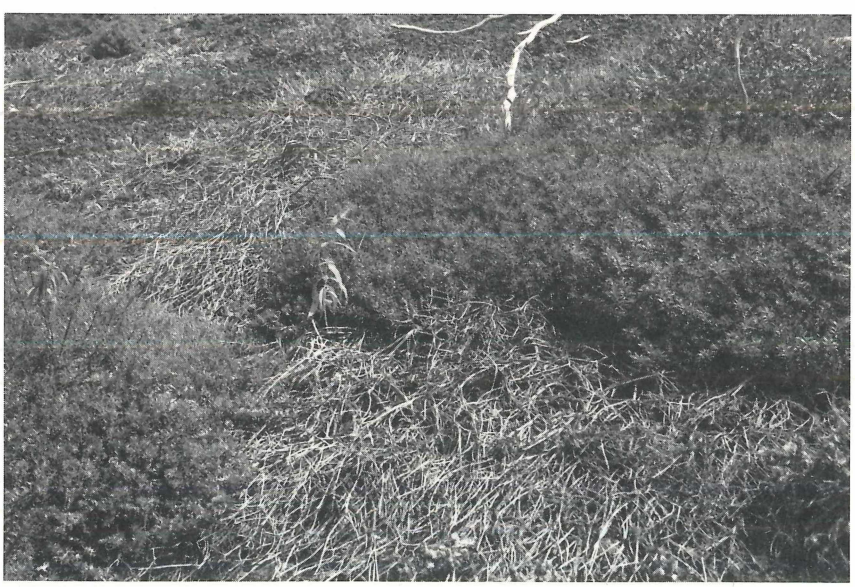

Fig. 4: Dieback stand of *Dubautia scabra* cushion shrubs in "Devastation Area" of Hawaii Volcanoes National Park. Area was covered by volcanic ash in 1960. Note: dead or dying individuals next to vigorous mature *Dubautia individuals*; a *Buddleja asiatica* seedling (center-left) at edge of dead shrub next to live individual. 10 October 1982.

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Another case in the same "Devastation Area", but in a different location, was observed more recently, involving the endemic shrub *Dubautia scabra* (*Compositae*). A fairly dense population of this shrub was established in 1974 on a loose pumice slope covering an area of about half a hectare. In 1981, most of the larger individuals were dead or dying but new *Dubautia scabra* seedlings were coming up here and there among the dead plants and the associated slower-growing, but stable, *Vaccinium reticulatum*, population.

The third case relates to the non-native haole koa, *Leucaena leucocephala*, a notorious small weed tree that forms the replacement plant community cover in much of the seasonally dry coastal lowland on all the larger Hawaiian Islands and many other Pacific islands.

During the past 12 years, I have taken students each spring semester to a number of locations near Honolulu for teaching them specific vegetation analysis techniques. One such repeat location is Waialae Iki Ridge at the southeastern outskirts of Honolulu. Here I noticed two years ago a synchronic dying of a large segment of the *Leucaena* stand on the wind-exposed side of the ridge. In the meantime, this dying, which began by foliage loss from the top of the trees down to their bases, has further intensified, but it has not spread to the remaining "healthy" stand on the ridge and side slopes. New *Leucaena* seedlings, as well as heliophytic grasses, are now coming up beneath the opened canopy of the dying stand.

THE CAUSAL CHAIN OF POPULATION DEATH: A NEW THEORY

Similarities between Communities

What do these examples of dieback populations have in common? At least five characteristics:

They, all relate to species which, in successional terminology, can be called pioneer or early seral species. They all seem to be heliophytes, i.e., species that are relatively shade-intolerant.

A second factor is the low species diversity in their respective communities. Yet, more precisely, it is not the low diversity of the total plant community but the low diversity in the respective synusia in which the dieback populations occur. For example, in the structurally most complex community given above, in the *Metrosideros* rain forest, horizontal layering or vertical stratification allows to recognize at least six divisions: an upper canopy synusia consisting of only the broad-leaved evergreen *Metrosideros* tree population, a lower growing tree synusia containing up to 20 smaller endemic tree species on areas of up to one hectare, a shrub synusia with tree ferns and a good number of endemic shrubs, and a fern species-rich herb layer. In addition one must recognize at least two more species-rich synusiae or subcommunities, the bryophyte subcommunity and the vascular epiphyte subcommunity (MUELLER-DOMBOIS et al. 1977). This is still an oversimplification but it brings out the point that the dieback population (in this case the canopy tree group) occurs in a synusia of low species diversity. This is one of the reasons why such dieback becomes spatially significant and why one cannot expect to detect it in multi-species tropical lowland forests.

A third factor in common is that these dieback examples occur in areas with well-known perturbations. These perturbations explain in part the origin of these populations, which later exhibit synchronized dying, as having resulted from a wave regeneration. This applies to *Metrosideros* forests on recent volcanic substrates, certainly also to the discussed *Buddleja* and *Dubautia* populations that died synchronously in the "Devastation Area", also to the *Canavalia* death following goat removal, and to the *Leucaena* stands which got established after grass fires.
It should be said, however, at this point that population dieback in the coastal grassland, for example, would have never been discovered if the developing succession had been interrupted by fire. Fire is very common in most other tropical grasslands (MUELLER-DOMBOIS 1981c) and this is probably one of the reasons why this form of population death appears relatively unknown elsewhere.

A similar relationship applies to the *Leucaena* and *Metrosideros* diebacks. A fire going through the *Leucaena* stand before the observed dieback, would have either killed the present stand or would have rejuvenated it through vegetative resprouting. The latter is a commonly observed reaction in this species. Similarly, a heavy ash fall-out on a vigorously growing *Metrosideros* stand tends to vegetatively rejuvenate that same stand (SMATHERS & MUELLER-DOMBOIS

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1974), if the ash blanquet deposit is not too deep relative to the height of the tree canopy.

A fourth factor common to these population death examples is that the species is not dying out in any of these areas. In fact there are other stands in the same general areas that are perfectly vigorous. Moreover, among most of the dieback populations, young individuals of the same species are coming up. In certain *Metrosideros* and *Leucaena* stands, reproduction from seed is abundant, in others less so. In certain cases where reproduction from seed is sparse (*Metrosideros* displacement dieback) or not apparent (*Canavalia* dieback) new populations are coming up nearby in other locations.

A fifth factor common to the Hawaiian dieback examples is that the dead or dying populations persist for a relatively long time. This is in part a function of the slow rates of decomposition. For example, the *Metrosideros* tree dieback is spatially so significant, because the snags remain standing for so long. Hawaii is not in the Pacific hurricane belt so that very strong storms that would result in flattening the dead standing trees are extremely rare. There are also as yet no termites in the Hawaiian montane rain forest. Moreover, fire, which in other forest types may substitute for the role of decomposers or consumers (MUELLER-DOMBOIS 1981c), does not occur in our rain forests (except under very unusual circumstances), because the climate is too wet. On new volcanic substrates, where *Buddleja* and *Dubautia* dieback was observed, there is no sizable decomposer fauna or flora because of the low amounts of organic matter present. In the seasonal lowlands with *Canavalia* and *Leucaena* dieback, decomposer activity is considerably slowed down during the dry season.

Hypotheses to Explain Population Death

The hypotheses advanced to explain massive dying of indigenous trees in Hawaii can be grouped into four categories:

1. Disease. For the *Metrosideros* dieback on Hawaii, it was originally assumed (BURGAN & NELSON 1972, BEGA 1974, PETTEYS et al. 1975) that a new, exotic disease had entered the Hawaiian Islands. This seemed logical since island ecosystems were popularly considered more fragile than continental ecosystems (CARLQUIST 1965)[1]. LYON (1909) also believed strongly that the so-called "Maui forest disease" was caused by pathogens until he proved this to be wrong. In the current *Metrosideros* dieback syndrome on the island of Hawaii, the disease hypothesis has only recently been discarded in its simple host-pathogen relationship (PAPP et al. 1979), although it has been resurrected by the U.S. Forest Service Pest Management Unit (1981) in a more complex form. This will be referred to under the "combination of stresses" hypothesis below.

2. New man-imposed stresses. This explanation applies without any doubt to the decline of the *Sophora chrysophylla* tree-line ecosystem (WARNER 1961) and the upper-elevation *Acacia koa* forests (MUELLER-DOMBOIS & KRAJINA 1968) on Mauna Kea. But the decline there is a function of the introduced herbivores feeding on the reproduction (i.e., seedlings and suckers) while the dead standing trees have outgrown their life cycle. Therefore, disruption of the reproduction cycle is the cause of forest decline in these cases. This aspect had never been investigated in the disease research of Lyon or the U.S. Forest Service until our research (MUELLER-DOMBOIS et al. 1977) showed that *Metrosideros* seedlings and saplings are commonly abundant under the more severe forms of canopy dieback. However, earlier guesses made to explain the *Metrosideros* dieback included also the idea of new stresses such as introduced herbivores (feral cattle and pigs), and/or air pollution or acid rain. These factors certainly cannot explain the phenomenon.

3. Recurring abiotic natural stresses. Climatic change was first suggested by SELLING (1948) as an alternative to LYONs (1909) soil toxicity hypothesis. However, climatic change does not explain the site-related patchiness of the *Metrosideros* rain forest dieback. Other climatic factors, such as lightning discharges have been considered (MUELLER-DOMBOIS 1980a) to explain the small-area patchiness in the so-called "hotspot dieback" (JACOBI 1982), a form of what we have recognized more generally as the "dryland dieback" (MUELLER-DOMBOIS et al. 1977).

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[1] A different viewpoint has now evolved from more detailed community studies of island biology (MUELLER-DOMBOIS et al. 1981).

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4. Combination of stresses. Certainly, lightning discharges cannot explain the larger-area dieback manifestations as recognized in the so-called "wetland-dieback", the "bog-formation dieback" or the "displacement dieback" (MUELLER-DOMBOIS et al. 1977, MUELLER-DOMBOIS 1980a). Therefore, we proposed a site-adapted "combination-of-factors" hypothesis. This involves at least three factors: a perturbation-sensitive stand condition, a climatic fluctuation and locally special habitat properties (MUELLER-DOMBOIS 1981a). For example, we assumed that a period of years with wetter than normal rainfall may result in prolonged inundation and drowning out of *Metrosideros* tree roots on poorly drained lava substrates. Conversely, we assumed that an unusually dry month, expected in some years during the warmer season, may precipitate a "dryland dieback" in stands on well-drained lava substrates, particularly, if these stands were suffering under nutrient deficiencies (KLIEJUNAS & KO 1974).

The current U.S. Forest Service view (Pest Management Unit 1981) considers abiotic site factors to be the primary causes followed closely by involvement of pest organism, i.e., the root fungus *Phytophthora cinnamoni* and/or the endemic host-specific *Metrosideros* tree borer, *Plagithmysus bilineatus*.

The stress-combination hypothesis in its first-mentioned form comes close to our present understanding of the Hawaiian dieback phenomenon, but it still does not explain all of its variations.

5. Chain-reaction of factors and the theory of cohort senescing. The *Metrosideros* "displacement dieback" and the *Canavalia* dieback cannot be explained by abiotic stresses. *Metrosideros* "displacement dieback" occurs on well-to moderately well-drained and nutritionally-rich (eutrophic) deep soils from volcanic ash. Here trees are dying and have died in groups (BURTON 1980) without any apparent environmental stress. Their group-dying can only be explained as a response to uniform senescing in cohorts. Absence of any conceivable environmental stress has also been suggested for the *Canavalia* dieback (MUELLER-DOMBOIS 1981b) in the coastal grassland. Moreover, following observations in several other Pacific islands forests with similar dieback phenomena (MUELLER-DOMBOIS 1982a, b) and in view of the various, seemingly disassociated facts brought together through research in these other islands and the Hawaiian rain forest dieback, it is now possible to suggest that cohort senescing is the principal predisposing factor for population death or synchronized dieback in these plant communities. The combination-of-factors idea, particularly as concluded by the U.S. Forest Service Pest Management Unit (1981), is still quite unsatisfactory. Instead, a sorting out of factors into a) predisposing, b) precipitating and c) hastening, will come much closer to the truth. That is what is meant here by a causal "chain-reaction of factors" concept or model.

Cohort senescing is suggested as the predisposing factor. Cohort senescing is here defined as a uniform loss of vigor in a population of plants of similar stature. This loss of vigor is considered to be the result of both aging and environmental stress (such as nutrient deficiency or nutrient imbalance or a constant stress from wind). Precipitating factors may be more-or-less nonobvious perturbations, such as a gale or tropical storm that may be strong anough to shake off a critical amount of the foliar biomass of a stand. If the leaves are not regenerated, the stand probably represents a senescing cohort. Biotic agents have so far not been found to be among the precipitating factors in Hawaiian plant communities. They may however come in at the third level, as hastening factors in some areas.

This "chain-reaction-of-factors" concept is similar to the model proposed for the so-called "decline diseases" in a recent forest pathology textbook by MANION (1981). Except that the new theory of cohort senescing proposed here has nothing to do with disease. When biotic agents come in as hastening factors in population death, they can only be considered as weak parasites or precursors of the decomposers.

SUCCESSIONAL IMPLICATIONS

The role of the dieback hasteners, i.e., particularly that of indigenous pathogens or insects, may be critical for the success or failure in the rejuvenation process of the dieback species. A strongly shade-intolerant species may fail to rejuvenate successfully if the canopy collapse of the senescing cohort is not fast enough.

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The successional outcome of the dieback process depends also on several other factors, such as the germination chance and seedbed conditions under the dying stand, the early growth rate of the juvenile cohort that follows the senescing cohort, on the competition by undergrowth species and the habitat itself. For example, in the Hawaiian *Metrosideros* "displacement dieback", the germination chance for *Metrosideros* seeds is good, the seedbed conditions are excellent, the eutrophic soil would support faster early growth rates of *Metrosideros* seedlings than expected on lava-rock substrates, but the competition from the here particularly vigorous tree-fern growth is too strong for a successful re-establishment of a replacement cohort (BURTON 1980).

The new dieback theory provides a fresh view for studying successional processes in ecosystems with such population death phenomena. On a small-area basis such dieback species may have pioneering or seral importance. On a somewhat larger-area basis they may be regarded as "oscillating persisters", a concept coined earlier (MUELLER-DOMBOIS 1981b) with regard to the behaviour of *Canavalia*. The concept applies equally well to *Metrosideros*, and it will help to define how large an ecosystem should be for conserving an indigenous vegetation type in perpetuity. Certainly, such size criterion will be more adequate than to base ecological reserve sizes on the "minimal area" outlined by the "constant persisters", i.e., a representative species combination of climax species populations.

There is still another dimension to the successional significance of *Metrosideros* dieback in Hawaii. We have several indications that the new *Metrosideros* seedlings coming up under or nearby a dying canopy population are not always genetically similar to the dying *Metrosideros* population (MUELLER-DOMBOIS 1981a). We believe that there is a genetic shift or racial turn-over from pioneer to seral to near-climax ecotypes in the species complex of *Metrosideros polymorpha* during the course of primary succession from new lava flow to forest bog. This hypothesis of successional ecotypes is studied now through initially verifying the hypothesis that edaphic ecotypes or races exist within the montane *Metrosideros* rain forest ecosystem of Hawaii. For this we use the model of the "Hohenheimer" water table experiment (ELLENBERG 1954, WALTER 1971, MUELLER-DOMBOIS 1964), i.e., large tanks containing soil wedges with sloping surfaces on which different provenances of *Metrosideros* populations are tested in relation to two gradients of depth-to-water table.

A final consideration may be given to the question of whether such population dieback phenomena are unique to island communities. The answer is certainly no. However, such dieback phenomena are probably more clearly represented in some island or otherwise isolated (e.g., young mountain) communities than in floristically rich continental communities. As pointed out earlier, dieback populations are prevalent in species-poor synusiae. This also means they are prevalent, where there are no immediate successional competitors to replace the dying cohorts. Therefore, they can be expected in areas where the floristic history is either young or has not evolved into a series of ecophysiologically differentiated plant types that overlap with each other along a successional gradient. The presence of a large senescing cohort may represent a weak link in the successional development of a community, but it does not necessarly indicate a lower level of ecosystem stability. This question depends on the degree of vegetation recovery associated with the dieback.

CONCLUSIONS

It is of some interest to note here that these new insights into the Hawaiian dieback phenomena have come largely from applying the aims and methods developed in vegetation ecology. Vegetation science or vegetation ecology is often considered a mere descriptive science. There is no argument that plant community description is its fundamental basis. But description is only its necessary starting point. This has been well expressed in Professor ELLENBERGs own philosophy which became manifested in his first textbook classic (1956). The main aims of vegetation science were restated in our joint text (MUELLER-DOMBOIS & ELLENBERG 1974) as four, namely:

1. Description of plant communities,
2. Their ordination and/or classification,
3. Their correlation with environment and history, and
4. Their causal analysis (etiology) of community development.

It is reasonable to proceed to aim number four with some confidence only after having plodded through aims 1 to 3. The latter provide for the necessary fami-

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liarity with the regional community- and species-distribution patterns for developing appropriate research hypotheses which then lead to the most challenging aspect of vegetation science as outlined by aim number four.

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