

Concluding Synthesis

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THE SEVENTEEN invited papers presented here provide a cross-section of the kinds of forests affected with canopy dieback in the central and south Pacific region. Although the papers were grouped by country, they show interesting between-country similarities in research approaches and in the causes considered most plausible at the present state of knowledge. It therefore seems appropriate to recall the kinds of forests discussed and to synthesize the research highlights and findings.

KINDS OF FORESTS AND SPECIES WITH DIEBACK

The kinds of forests discussed included several montane rain forests on Pacific islands. They ranged from tropical (Hawaii and Papua New Guinea), subtropical (New Zealand's North Island), to temperate environments (New Zealand's South Island and Tasmania). Also included were temperate and subtropical mesic sclerophyll forests in Australia. Three tree genera were dominantly involved: *Metrosideros*, *Nothofagus*, and *Eucalyptus*. However, other tree genera and species, such as *Ixerba brexioides*, *Beilschmiedia tawa* (pages 385–389), and *Weinmannia racemosa* (pages 415–426, 427–431, 433–442), also were said to show synchronized dieback in New Zealand. In addition to these evergreen broad-leaved species, New Zealand conifers, such as *Podocarpus hallii*, *P. totara*, and *Libocedrus bidwillii*, were mentioned as exhibiting significant tree-group dieback (pages 415–426, 427–431).

The spectrum of species in the three main genera also was broad, including *M. polymorpha* in Hawaii; *M. umbellata* (pages 427–431, 433–442, 443–452) and *M. robusta* (pages 415–426) in New Zealand; *N. solandri* var. *cliffortioides* (pages 391–395, 397–404), *N. fusca* (pages 397–404), and *N. menziesii* (pages 385–389) in New Zealand; and *N. pullei* and *N. grandis* (pages 453–458) in Papua New Guinea. *Eucalyptus* species with synchronized canopy dieback in Australia were *E. obliqua* and *E. regnans* (pages 465–470) in Tasmania; and several *Eucalyptus* species (*E. radiata*, *E. viminalis*, *E. globulus* subsp. *bicostata*, *E. baxteri*, *E. cypellocarpa*, *E. rubida*, *E. dives*, *E. ovata*, and *E. obliqua*) were mentioned as affected by a killer disease (*Armillaria luteobubalina*) in west-central Victoria (pages 459–464). *Eucalyptus pilularis* was referred to as undergoing canopy dieback in southern Queensland (pages 471–481).

Therefore, canopy dieback can be said to occur over a wide spectrum of forest types, and it is a widely recognized phenomenon in indigenous forests of this Pacific region.

RESEARCH APPROACHES AND FINDINGS

Current research emphases represented among the symposium papers can be grouped into five areas: (1) disease and animal damage research; (2) climatic

change or perturbation analyses; (3) nutrient limitation studies; (4) stand structure and succession research; and (5) tree physiological and experimental studies.

(1) Disease and Animal Damage

This is usually the first causal implication for canopy dieback. At least four papers in this symposium emphasize this aspect (pages 415–426, 453–458, 459–464, 465–470). Kile's paper (pages 459–464) discusses the *Armillaria* root rot fungus complex in Australian eucalypt forests and considers one of four species, *A. luteobubalina*, to be a dieback-causing primary pathogen. This fungus apparently kills many eucalypt species in certain mixed-species forests of southeastern Australia, including associated subcanopy legume trees. But Kile points out that this primary pathogen is considered endemic to southeastern Australia and kept at equilibrium in native forests. It becomes aggravating only when dead woody biomass accumulates in forests. Therefore, equilibrium or balanced states are a function of both host-stand structure (or dynamics) and pathogen dynamics.

Arentz (pages 453–458) reports that the root pathogen *Phytophthora cinnamomi* was isolated from dead *Nothofagus* patches, but subsequently was found also in healthy forests and widely distributed throughout Papua New Guinea. Therefore, he considers *P. cinnamomi* to play a secondary role, while the primary dieback cause should be sought elsewhere.

The absence of any clearly discernible pathogen in the "regrowth dieback" (i.e., dieback in second-growth forests) of *Eucalyptus obliqua* and *E. regnans* in Tasmania stimulated Palzer (pages 465–470) to climb into the crowns of 35-m tall trees for detailed close-up observations. He carefully describes the symptoms of reducing crown vigor, which include "witches brooming," absence of growing shoots, declining leaf sizes, chlorosis and reddening of leaves, and possible overheating of such leaves due to insufficient transpirational cooling. As an alternative for yet another biotic cause of dieback he suggests mycoplasma infection as an unexplored possibility.

Batcheler (pages 415–426) represents the view that the *Metrosideros-Weinmannia* canopy dieback in New Zealand is definitely caused by the introduced Australian possum. As primary evidence he cites repeated coincidences of high possum invasion and subsequent dieback as analyzed from aerial photographs. Stands of the same forest without significant canopy dieback contain no possum or only low numbers according to Batcheler. Or where they contain higher numbers in immature stands, he considers the greater vigor of young *Metrosideros* trees in recovering damaged foliage (as demonstrated by Payton, pages 443–452) as sufficient explanation for their apparent nondieback condition in New Zealand.

None of the other New Zealand dieback researchers disagreed with Batcheler that possums play an important role in the *Metrosideros-Weinmannia* canopy dieback, but few subscribed to the "repeated coincidence" hypothesis as a sufficient causal explanation. This view that possum is the major cause was recently challenged, particularly by Stewart and Veblen (pages 427–431).

(2) Climatic Change or Perturbation Analyses

Climatic stresses are usually considered a next alternative in the search for causes of canopy dieback where biotic agents cannot be implicated as the

primary cause. Three papers (pages 375–384, 397–404, 405–414) focused on climatic perturbations; two others (pages 385–389, 391–395) drew on climatic perturbations or periodic changes as causal hypotheses. Evenson (pages 375–384) presented evidence that the year-to-year rainfall may vary drastically over the *Metrosideros* rain forest territory in Hawaii. While the central dieback area receives an annual mean rainfall of about 3800 mm, it may be as low as 2000 mm in one year and exceed 5000 mm in another. Moreover, several wet years may be followed by several dry years and vice versa. But clearly, the spatial uniformity of year-to-year rainfall variations, as demonstrated by Evenson, does not explain the patchiness of the Hawaiian dieback, which often correlates with certain soil boundaries. Therefore, a causative relationship of rainfall fluctuations and past dieback events in Hawaii awaits further analysis. Such analysis, as pointed out by Evenson, should also include a storm event analysis for Hawaii such as done by Shaw for New Zealand.

Shaw (pages 405–414) drew attention to the observation that forests in New Zealand, particularly on the North Island, but also on the South Island, are frequently damaged by cyclonic storms. The leveling of forest stands in response to a devastating storm does not fit the definition of canopy dieback (as given in the first paper). But stand leveling may set the stage for a new wave regeneration, resulting in even-structured stands that eventually may become subject to canopy dieback rather than individual tree dieback because of their uniform life stage. Shaw drew attention not only to the stand leveling effects of cyclones but also to their more subtle effects in less impacted sites, such as foliage loss, branch loss, and stem breakage or bending. Cyclones may thereby have an effect of “ill thrift,” or decline of vigor and perhaps, delayed canopy dieback.

Snow storms, breakage, and stand leveling play an essential role in the theory of mountain beech (*Nothofagus solandri* var. *cliffortioides*) stand dynamics presented by Wardle and Allen (pages 397–404). These authors state that such events are largely responsible for the even-aged stand mosaics found in this essentially monospecific forest ecosystem on the South Island of New Zealand.

Climatic drought, on the other hand, was implicated as a cause of canopy dieback in two studies on the North Island. Jane and Green (pages 385–389) considered the indigenous montane cloud forests in the Kaimai Ranges as ill-adapted to cope with periodically recurring droughts, which they believe kill montane tree species (*Ixerba brexioides*, among others) in any life stage, young or old.

Similarly, Skipworth (pages 391–395) suggests climatic drought as being responsible for the canopy dieback of mountain beech in Tongariro National Park. He believes that in his study area, canopy dieback is caused by a receding water table and that vegetation changes including canopy dieback respond to climatic drying and wetting cycles. However, evidence from a carefully done climatic data analysis is still lacking.

(3) *Nutrient Limitation Studies*

Two papers were presented with this approach to the problem of canopy dieback (pages 339–359, 471–481). The first paper, relating to *Metrosideros* dieback in Hawaii, established a wide range of soil nutrient regimes throughout the dieback territory. Across the site spectrum from young to older volcanic rain forest soils, it was found that nutrient relations can be suggested as stressful. This applies to exceptionally low amounts of available nitrogen found in young volcanic soils and to the very high acidity and potential metal toxicity

determined in older, more weathered, rain forest soils. However, a nonstressful nutrient regime was recorded for mid-aged (1000 yr old), fine-textured soils from volcanic ash, whose mineral soil was enriched with organic colloids. Canopy dieback occurs in *Metrosideros* stands occupying the entire nutrient regime spectrum in Hawaii, but different dieback patterns were described for these sites, notably *Metrosideros* displacement dieback on nutrient-rich sites and several forms of replacement dieback on nutrient-stressed sites.

The Australian nutrient stress study (pages 471–481) emphasized advanced soil aging, associated especially with decline of available phosphorus, as a retrogressive phase in ecosystem development (or primary succession) on Queensland sand dunes. The authors (Walker, Thompson, and Jehne) suggest that *Eucalyptus pilularis* canopy dieback, which appears to be associated mostly with the retrogressive (or aging) phase of soil development, results in a decline of biomass and a gradual dwarfing of recovering stands (after dieback) because of nutrient limitations. Biomass harvesting from human activity is said to accelerate the nutrient decline process. Moreover, complex interactions involving foliar insects as displacers of nutrients away from the dieback site are seen as major factors causing tree decline and repeating cycles of *Eucalyptus* canopy dieback. As in the two other Australian contributions (pages 459–464, 465–470), biotic agents are considered to play a major, perhaps a “trigger,” role in *Eucalyptus* canopy dieback.

(4) Stand Structure and Succession Research

Tree stand and population structure analyses formed the main data base presented in four papers (pages 327–337, 391–395, 397–404, 433–442). The eight *Nothofagus* dieback stands sampled by Skipworth in Tongariro National Park all show numerical reduction in the smaller size classes. This indicates discontinuity in reproduction. The stand structures are either unimodal or bimodal (possibly even trimodal), which suggests—as Skipworth implies—that his stands represent either one- or two-generation tree populations. A proportion of dieback or dead trees is recorded in all diameter classes. Therefore, dieback must have occurred in younger and older generations. However, it is not clear whether the smaller and presumably younger generations contain dead saplings because of self-thinning in stand development (or competitive displacement in succession) or because they died due to an outside stress, which Skipworth implies. Skipworth's data also show that the proportion of dieback trees is very different from stand to stand. This suggests either very different site conditions between stands (i.e., those with a greater proportion of dead trees occurring on the drier sites in accordance with Skipworth's climate and receding water table hypothesis) or different time phases of dieback. The data allow for the latter interpretation; that is, dieback may not have been synchronized between stands, only within stands. Of course, loss of vigor could be due to both site stress and stand age. Future research in Tongariro National Park may focus on separating the proportionate effects of each stress factor (external versus internal).

Beech canopy dieback certainly was not synchronized over the entire *Nothofagus* forest system on the South Island, according to Wardle and Allen's paper (pages 397–404). Instead, canopy dieback was localized and related to snow storms rather than drought. Again, stands appear to be unimodal or bimodal in size structure, suggesting one- or two-generation stands growing on the same sites.

Allen and Rose's *Metrosideros umbellata* dieback stands (pages 433–442), at both the Kokatahi and Fox study sites, show broad and flat unimodal or bimodal (possibly trimodal) size class distributions. Again, this indicates one- or two-generation populations growing on the same sites and certainly not continuously self-recruiting stands. The same applies to *Podocarpus hallii* at the Fox study site. The live species in both study areas all show a high sapling and low mature tree component. This clearly indicates recovery by indigenous tree species in association with the canopy dieback. *Weinmannia racemosa*, a major dieback species, is among the recovering species at the Fox site. Moreover, Allen and Rose mention *M. umbellata* seedling groups as growing on new landslides in the Kokatahi catchment and in canopy gaps at the Fox site. In both areas, these appear to be *Metrosideros* displacement diebacks, i.e., where reproduction of the dieback species does not occur beneath the dieback canopy. However, there is not a total elimination of the dieback species, since its reproduction comes up on pioneer surfaces.

Jacobi, Gerrish, and Mueller-Dombois (pages 327–337) presented *Metrosideros polymorpha* sapling structures from permanent plots under Hawaiian dieback stands. It was shown that *Metrosideros* reproduction is generally numerous under dieback stands (i.e., replacement dieback). It was also shown that after 5 yr (between the first and second resurvey), small undergrowth tree structures were changing from an invasive to a modal pattern (i.e., reduction in the smallest size classes). The second trend is similar to that of all other dieback stand structures presented in this symposium. It indicates that regeneration occurs in waves rather than in the form of continuous recruitment.

Stemmermann (pages 361–373) also presented structural data of *Metrosideros polymorpha* stands. The stands were sampled on differently aged substrates, not in dieback stands. Here, the younger and drier sites showed a higher numerical representation of pubescent-leaved individuals, while the older and moister sites displayed a higher numerical representation of glabrous-leaved individuals. These and other observations in Hawaii led to the hypothesis of “successional ecotypes,” which suggests that successional functional ecotypes (races or varieties) may have evolved in the *M. polymorpha* species complex. Similar successional relationships may exist among congeneric canopy species in other forest ecosystems.

(5) Tree Physiological and Experimental Studies

Two papers incorporated a tree physiological approach (pages 361–373, 385–389) and two others (pages 361–373, 443–452) an experimental approach in relation to canopy dieback. By investigating plant water relations, Stemmermann (pages 361–373) found that pubescent-leaved varieties of *Metrosideros polymorpha* in Hawaii appear to have a more xerophytic adaptation as compared to glabrous-leaved varieties, which in turn have less negative osmotic potentials. Similarly, Jane and Green (pages 385–389) used the pressure-volume technique to determine plant water and osmotic potentials. They found low negative potentials for such fog-belt trees as *Ixerba brexioides* and *Quintinia acutifolia* and concluded that these species are rather narrowly adapted to the high-moisture environments in the Kaimai fog belt. Prolonged lifting of the fog belt is seen as causing sufficient shock or stress to affect dieback of whole stands, regardless of age or life stage.

Payton (pages 443–452) took age, or life stage, in *Metrosideros umbellata* as the prime target of his investigation by experimentally defoliating young

and old trees. He found that young trees are able to replace their foliage more easily than old trees. He thereby established that young and old trees of *M. umbellata* have different vigor states and therefore also different physiologies.

Stemmermann (pages 361–373) took seed from different *Metrosideros polymorpha* varieties and seeded them in two large water-table tanks filled with different types of volcanic soils. These tanks serve as “common transplant” gardens for testing whether morphological form (pubescent-leaved versus glabrous-leaved) is merely an environmental modification or a genetically based trait. It turned out that these forms are genetically based and that the pubescent varieties developed faster and grew more vigorously as young seedlings than the glabrous-leaved forms.

HYPOTHESES FOR COMPARATIVE RESEARCH

The research reported here was done more or less in the isolation of each country, and initially each dieback situation was considered rather unique. The symposium was a major breakthrough of this isolation. It represents a considerable advance in understanding the widespread and important dieback problem in Pacific forests. However, the present understanding is far from complete. There is a real need for more research in all cases.

A promising approach to the closing of knowledge gaps, particularly in ecological problems, is to make careful ecosystem comparisons. This symposium can be seen as a start in this direction. For continuing work in this direction, it may be of value at this point to suggest new research goals for comparative analyses of the dieback phenomenon and associated processes in different ecosystems. New research goals are best defined through hypotheses which in themselves are tentative conclusions requesting verification. As tentative conclusions of this sort with respect to our present symposium, it may thus be appropriate to consider the following hypotheses.

HYPOTHESIS NO. 1: The patterns of canopy dieback and the associated population, community, and ecosystem structures are strongly indicative of the dieback causes and processes—in other words, a group of dead standing trees may have died for any number of reasons. However, when the dead trees are analyzed quantitatively and symptomatically in the context of their population, community, and broader ecosystem structure, the dieback causes may be narrowed down considerably.

For example, Kile (pages 459–464) reported that the undergrowth legume tree species were also dying in his fungi-infested dieback forests. This is certainly very different from the Hawaiian situation, where the main canopy species is dying and then also reproducing as seedlings and saplings in the understory or on nearby disturbed sites. Such was reported for the *Nothofagus* forest in Papua New Guinea by Arentz (pages 453–458); for the *Nothofagus* forest on New Zealand's South Island by Wardle and Allen (pages 397–404); and also, with some modification, for the *Metrosideros-Weinmannia* forest dieback by Stewart and Veblen (pages 427–431) and by Allen and Rose (pages 433–442).

Along the same line, the receding water-table hypothesis as proposed by Skipworth (pages 391–395) for the *Nothofagus* dieback in Tongariro National Park, can be further verified by an analysis of the associated undergrowth species in the dieback stands. If undergrowth species are also dying and me-

sophytic species are being replaced by xerophytes, the receding water-table hypothesis may become a plausible theory.

HYPOTHESIS NO. 2: A species is not a physiologically uniform or rigid entity but instead exhibits different vigor states in its successive life stages. The focus here is on the possibly greater vitality of tree species in their adolescent or early mature life phases as opposed to a lower vigor state in their late mature, or senescing, life phases. Wardle and Allen (pages 397–404) observed that in *Nothofagus solandri* var. *cliffortioides* stands there may be two weak life stages: late maturity, or senescence, and the sapling stage. This is an important concept, and may be related to overcrowding of sapling cohorts with insufficient self-thinning. Insufficient self-thinning during stand development leads to early growth stagnation and therefore loss of stand vigor. It can result in the formation of so-called “toothpick” stands. This phenomenon may be considered a form of premature senescence. It is not uncommon in certain tree species, particularly when these grow in dense cohorts on rather poor or marginal sites. I have observed such toothpick stands developed by *Thuja plicata* and *Tsuga heterophylla* on Vancouver Island and by *Pinus banksiana* and *Picea mariana* in central Canada.

This second hypothesis calls for comparative perturbation research on different life stages in stands of the same species, similar to the approach taken by Payton (pages 443–452). An extension of this research with regard to the possum damage would be to find out whether late mature trees of *Metrosideros umbellata* may have lost their capacity to synthesize unpalatable phenolics. The same may apply to juvenile stands in overcrowded condition.

HYPOTHESIS NO. 3: Stresses developing from inside the population are just as important as external stresses in the general etiology of canopy dieback. This implies that a satisfactory ecosystem model for canopy dieback should consider at least three general stress complexes equally at first: (1) biotic impacts, such as disease-causing pathogens or animal damage; (2) abiotic impacts, such as climatic perturbations and/or nutrient stresses; and (3) internal population stresses such as are associated with the tree population's life stage or premature low-vigor states in overcrowded stands. After careful analysis in any specific case, a causal chain reaction among all three factor complexes may be found (such as proposed for the Hawaiian *Metrosideros* dieback, pages 317–325) or, alternatively, one or the other factor complex may prove its dominant role over that of the others (or even to the exclusion of the others).

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