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Three types of factors influence the dieback of forest stands - factors that predispose stands, trigger factors that initiate dieback, and factors that contribute to further decline. This paper demonstrates that all known examples of dieback in New Zealand (including *Metrosideros*) can be explained using this three-factor framework.

## ECOLOGICAL CONSIDERATIONS OF DIEBACK IN NEW ZEALAND'S INDIGENOUS FORESTS

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### ABSTRACT

Three types of factors influence the dieback of forest stands — factors that predispose stands, trigger factors that initiate dieback, and factors that contribute to further decline. All known examples of dieback in New Zealand *Nothofagus* spp., *Metrosideros* spp., and beech/hardwood forests can be explained using this three-factor framework.

**Keywords:** browsing; dieback; drought; forest composition; forest structure; insect damage; predisposing factors; trigger factors; hastening factors; soil development; development; succession.

### INTRODUCTION

When trees are observed dying in groups the first causal mechanism sought is often a pest or pathogen. When their involvement is inconclusive or when it is likely that they are not the primary cause, environmental stress is the next most common explanation considered. Today in industrialised Europe, for example, air pollution is considered the likely cause of widespread forest dieback (Schutt & Cowling 1985). However, a third decline factor that has received prominence in studies of dieback recently is the influence of natural stand structure and dynamics. In Hawaii, for example, the decline of o'hia (*Metrosideros polymorpha* Gaud.) has been attributed to cohort senescence, i.e., to the synchronous dieback of similarly aged groups of trees that reach a susceptible stage at a similar time (Mueller-Dombois 1988).

### AN ECOLOGICAL BASIS FOR FOREST DIEBACK

In the dieback of forest stands, three types of factors—factors that predispose stands, trigger factors that initiate dieback, and factors that contribute to further decline—have been recognised by a number of workers in New Zealand (Rawlings 1953; Wardle & Allen 1983; Wardle 1984). A similar three-factor theory of dieback, based on disease-induced decline, has been presented overseas (Manion 1981; Houston 1984; Mueller-Dombois 1988). Workers describe a combination of deleterious causes which operate in a chain reaction as (1) predisposing, (2) inciting, precipitating, or trigger, and (3) accelerating, contributing, or hastening factors (cf. terminology of Manion 1981; Houston 1984; and Mueller-Dombois 1988). Reference to this three-factor framework has been made recently for dieback in several New Zealand forest types (Jane & Green 1986; Stewart & Rose 1988; Hosking & Hutcheson 1986, 1988).



A number of specific causes can be considered as "predisposing", such as climate change, nutrient imbalances, vegetation structure and composition, and old age. "Precipitating" causes are considered to be fluctuating or recurring environmental stresses such as flooding, drought, frost damage, salt spray, and storms, or biotic stresses such as pests and pathogens. Often there is no clear distinction between predisposing and precipitating causes, so that these categories are not mutually exclusive. For example, pests and pathogens could act as trigger factors, rather than as sole causes of tree death, or assume the third role, that of agents "hastening" dieback.

In this paper I review the main predisposing, trigger, and hastening factors (sensu Mueller-Dombois 1988) that have been implicated in the dieback of various New Zealand indigenous forests.

### Predisposing Factors

Forest composition and structure have been implicated as important predisposing factors in the dieback of rata-kamahi (*Metrosideros umbellata* Cav.-*Weinmannia racemosa* Linn.f.\*) forests. Although rata-kamahi forests are broadly characterised by the dominance of tree species such as southern rata, kamahi, mountain cedar (*Libocedrus bidwillii* Hook. f.), and Hall's totara (*Podocarpus cunninghamii* Col.), many compositionally and structurally different communities are recognised (Wardle 1977; Stewart & Veblen 1982; Reif & Allen 1988). Differences in composition and structure between the communities result in a gradient of species preferred by brush-tailed possums (*Trichosurus vulpecula* Kerr) and a parallel gradient in dieback. Possum-triggered dieback is greatest in, or adjacent to, those forests containing many old trees or those with a high proportion of possum-preferred seral shrub hardwood species (e.g., *Fuchsia*, *Aristolelia*, *Melicytus*, and *Schefflera*), or in seral communities containing these preferred species (C.G.R. Chavasse unpubl. data; Veblen & Stewart 1982; Reif & Allen 1988). Dieback is least in forests where seral shrub hardwoods are uncommon.

The stage of forest development or stand age influences composition, and so predisposes stands to dieback. Rata-kamahi stands with large (>35 cm dbh), even-sized, diameter distributions are apparently some of the stands most affected by dieback in Westland (Allen & Rose 1983; Stewart & Rose 1988). Many of these mature stands are probably even-aged, reflecting their establishment soon after mass movements or windthrow (Wardle 1980; Stewart & Veblen 1982), or of mixed age, reflecting intermittent establishment in treefall gaps (Allen & Rose 1983). Rata-kamahi stands dominated by small (<35 cm dbh) even-sized trees, however, are apparently young and even-aged, and seem less susceptible to dieback than more mature stands. Their lower susceptibility could be due to the lack of possum-preferred seral shrub hardwoods in these stands, in addition to high tree vigour, and high resistance of the closed canopy to damage by wind (Payton 1988).

Stage of forest development has also been associated with dieback in beech (*Nothofagus* spp.) forests. Because many beech forests go through a cycle of destruction and regrowth, stands often tend to be even-aged (Wardle 1984). They become vulnerable when in the dense pole-stage (cf. resilience of young rata-kamahi

\* Nomenclature follows Allan (1961) unless indicated otherwise.



stands) and again when most trees enter the larger size-classes and are "over-mature" (Wardle 1984; Jane 1986). The cycle of destruction or dieback and regrowth therefore spans c. 120–150 years (Wardle 1984; Jane 1986; Ogden 1988). Such dieback, related to stands reaching a vulnerable stage of development, has been recorded in many mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole) forests, including some stands in the Rakaia catchment (Wardle & Allen 1983), on Mt Ruapehu (Skipworth 1981) and the Kaweka Range (Hosking & Hutcheson 1988), and in forests dominated by other beech species (Hosking & Kershaw 1985).

Regional differences in the patterns of dieback can be related to the influence of soil development on forest composition and structure. Soil development in rata-kamahahi forests in Westland follows a sequence from young recent (c. 50–200 years), to yellow-brown earth, to well-developed gley podsol soils often over 2000 years old (Stewart & Harrison 1987). Little dieback occurs in the rata-kamahahi forests characterised by species such as mountain toatoa (*Phyllocladus alpinus* Hook.f.) and pink pine (*Halocarpus biformis* (Hook.) Quinn) that occur on well-developed soils. In contrast, dieback is common on younger soils that support either seral communities or forest with a seral component (Reif & Allen 1988). These patterns of soil development and forest composition may explain why rata-kamahahi dieback is less common in forests on the stable granitic mountains west of the Alpine Fault in the Southern Alps than on adjacent unstable schist ranges to the east. According to Reif & Allen (1988), the high frequency of landslides and therefore younger soils in the schist ranges has resulted in high proportions of seral communities or forest with a seral component, which seem to suffer the most severe dieback. In some areas on schist, such as the Kokatahi Valley in Westland, large patches of rata canopy dieback (tens of hectares) cover most of the catchment (Allen *et al.* 1988).

Various other site characteristics which may predispose stands to dieback have been suggested. Lee slopes provide shelter for and promote better growth of mountain beech forests under normal weather conditions but are the slopes most susceptible to damage from storms and subsequent dieback (Jane 1986). The increased precipitation and reduced evapotranspiration due to fog at certain altitudes may make trees particularly sensitive to drought and subsequent dieback, especially on waterlogged soils where trees have reduced root systems (Jane & Green 1986).

### Precipitating or Trigger Factors

Drought as a trigger factor of dieback has been implicated for dieback in mountain beech (Elder 1962; Grant 1984; Hosking & Hutcheson 1988), black beech (*Nothofagus solandri* (Hook.f.) Oerst. var. *solandri*) (Hocking 1946), hard beech (*Nothofagus truncata* (Col.) Ckn.) (Hosking & Hutcheson 1986), and red/silver beech (*Nothofagus fusca*/*Nothofagus menziesii* (Hook.f.) Oerst.) (Grant 1963; Hosking & Kershaw 1985) forests. It has also been used as an explanation for dieback of isolated podocarp-hardwood forest remnants in the North Island (e.g., Atkinson & Greenwood 1972; Ogden 1976) and suggested for rata-kamahahi dieback in Westland (C.G.R. Chavasse unpubl. data). Stewart & Rose (1988) suggested that extended periods of below-average rainfall in the Westland forests could have stressed canopy rata trees making them particularly susceptible to the effects of defoliation (e.g., by possums). Jane & Green



(1986) considered drought as the principal trigger factor of beech/hardwood forest decline in the Kaimai Ranges in the North Island.

Exposure to salt-laden winds has been implicated as a trigger factor for the dieback observed on Stewart and Bench Islands (Veblen & Stewart 1980), the Auckland Islands (Campbell & Rudge 1984), and on Secretary Island (L.E. Burrows pers. comm.).

Physical damage by wind, snow storms, and heavy snow-packs has been considered a trigger factor in New Zealand, especially in mountain beech forests (Wardle & Allen 1983; Jane 1986). Even a mild disturbance that results in a small opening of the forest canopy (e.g., 2.3% loss of basal area—Wardle & Allen 1983) may be followed by widespread dieback because the stands are rendered more vulnerable to accelerating factors such as stem-boring insects (see also Payton 1988 for a similar view in rata-kamahi forests). Various other natural disturbances such as earthquakes (Rawlings 1953), flooding (Mark *et al.* 1972), frost (MacKenzie & Gadgil 1973), and hailstorms (Shaw 1987) can also trigger dieback episodes.

Browsing by brush-tailed possums has been the predominant trigger of dieback from the 1940s to the present day in forests containing species of *Metrosideros* in many areas of New Zealand. The onset of dieback often coincides with possum invasion, and dieback progresses as possum populations peak in southern rata (Pekelharing 1979; Pekelharing & Reynolds 1983; Batcheler 1983; Leutert 1988), northern rata (*Metrosideros robusta* A. Cunn.) (Batcheler 1983), and pohutakawa (*Metrosideros excelsa* Gaertn.) (L. Pracy unpubl. data) forests. Species that are preferred foods of the possum are often common in *Metrosideros* forests, including southern rata, northern rata, pohutakawa, kamahi, and seral shrub hardwood species such as *Fuchsia*, *Aristolelia*, *Melicytus*, and *Schefflera* (Kean & Pracy 1953; Mason 1958; Fitzgerald 1976; Fitzgerald & Wardle 1979; Coleman *et al.* 1980, 1985; C.L. Batcheler & P. Cowan unpubl. data).

### Accelerating or Hastening Factors

In mountain beech forests, any disturbance that causes physical injury to trees (e.g. snow breakage or windthrow) attracts *Platypus* spp. pinhole borer beetles which act as vectors for the fungal pathogen *Sporothrix* spp. (summarised by Wardle 1984). After being attracted to damaged trees the beetles then attack nearby living trees, especially large old trees and those under stress (Milligan 1974). Therefore, once some mortality has occurred, further tree death is likely to spread rapidly, resulting in the dieback phenomenon. For example, in mountain beech forests, after an initial 2.3% loss of basal area due to snowbreak, an 11% net loss had occurred after c. 10 years, and basal area was continuing to decline (Wardle & Allen 1983). *Platypus* spp. play a similar role in the decline of other beech forests (Milligan 1974; Wardle 1984), and defoliating insects such as *Neomyctra pulicaris* Pascoe, *Proteodes carnifex* Butler, and *Inglisia fagi* Maskell, and pathogens (e.g., *Armillaria* spp.—Rawlings 1953), are also associated with crown deterioration in beech trees after periods of extreme climatic stress such as drought (Conway 1952; Hosking & Kershaw 1985; Hosking & Hutcheson 1986).

Insects and pathogens have also been associated with the decline of other tree species. For example, decline and death of kauri (*Agathis australis* (D. Don) Lindl.) associated with *Phytophthora cinnamomi* Rands has been observed after heavy



rainfall on soils with impeded drainage (Newhook & Podger 1972), and in rata-kamahahi forests stem-boring and cockid insects appear to hasten the decline of stands already weakened by some other cause (Hoy 1958; Payton 1989).

### CONCLUSIONS

All the known examples of dieback in New Zealand *Nothofagus* spp., *Metrosideros* spp., and beech/hardwood forests can be explained using a three-factor framework. Any investigation of dieback should therefore include the roles of predisposing, trigger, and hastening factors. Predisposing factors are of special interest since they influence tree vigour before the onset of dieback. Future research should concentrate on analysing each factor individually as much as possible, with special attention given to the response of stands to climatic and physical disturbances.

Factors that promote synchronous mortality (dieback) are beneficial for the survival of some tree species because in the absence of synchronisation a given site is more likely to be lost to competitors (Wardle 1984; Ogden 1988). In mountain beech, for example, synchronisation in annual growth, seedling release, and mast seeding could contribute to synchronous dieback and regeneration, and the continued maintenance of mountain beech forests. This example emphasises the importance of the life-cycle characteristics of the species under study and the fact that they deserve special consideration.

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