Pacific Science (1983), vol. 37, no. 4

Regeneration of Southern Rata (*Metrosideros umbellata*) and Kamahi (*Weinmannia racemosa*) in Areas of Dieback[1]

R. B. ALLEN[2] and A. B. ROSE[2]

ABSTRACT: During the 1950s, dieback of southern rata (*Metrosideros umbellata*) and kamahi (*Weinmannia racemosa*) was documented in the conifer/hardwood forests of the Kokatahi and Fox catchments in Westland, New Zealand. Thirty years later, southern rata was usually absent as a live tree in dieback stands. Kamahi, although absent from the canopy in the Kokatahi, had partially recovered at Fox, where it was still a dominant canopy species. Regeneration studies on a range of sites indicate that in the short term, kamahi and *Quintinia acutifolia* will become the structurally dominant canopy species in many of the dieback stands, and southern rata will at best be a minor component.

DIEBACK OF INDIGENOUS FORESTS is a widespread phenomenon in New Zealand; it occurs in many of the important genera, such as *Podocarpus*, *Nothofagus*, *Metrosideros*, and *Weinmannia*. Dieback of southern rata (*M. umbellata*)[3] and kamahi (*W. racemosa*) is a feature of the steepland conifer/hardwood forests of Westland, where these species are abundant, and in many other areas where these species occur. It is generally believed that dieback of southern rata and kamahi is principally due to browsing by the introduced brush-tailed possum (*Trichosurus vulpecula* Kerr.). The importance of other factors was considered by C. G. R. Chavasse (1955, unpublished) and more recently by Veblen and Stewart (1982) who support the hypothesis that much of the apparently excessive tree mortality is related to natural stand dynamics.

The mortality and regeneration patterns in dieback stands are described for two areas: the Kokatahi catchment, at approximately 171°10′ E longitude, 42°55′ S latitude, a tributary of the Hokitika River; and the Fox catchment, at approximately 170°00′ E longitude, 43°30′ S latitude. Both areas are within the West Coast "beech gap," which extends in latitude from approximately 42°50′ S to approximately 43°40′ S. Between these latitudes, *Nothofagus* species are absent and the dominant canopy hardwood species are southern rata, kamahi, and *Quintinia acutifolia*.

Soils in this area are derived from fractured schist along the alpine fault. They are typically skeletal on steeper slopes, with increasing development on lesser slopes and podzol formation on gentle slopes. As physiography is the result of fluvial modification of formerly glaciated valleys, the forested slopes are steep, often greater than 30°, and are subject to landslides. Such landslides are usually in the form of debris slides or debris avalanches. Climate is characterized by high annual rainfall and high humidity. Extensive northerly airflows are usually accompanied by prolonged rainfall that may reach torrential intensities. Studies in adjacent areas suggest rainfall reaches a maximum just east of the alpine fault, where it exceeds 10,000 mm per annum. Much of this area receives over 6000 mm per annum (Griffiths and McSaveney 1982).

The introduction of browsing animals has caused modification to these forests. Brush-tailed possums have been present in both the Kokatahi and Fox catchments for over 40 yr.

[1] N.Z.F.S. No. 1684/ODC 182.2. Manuscript accepted 5 October 1983.

[2] Protection Forestry Division, Forest Research Institute, P.O. Box 31-011, Christchurch, New Zealand.

[3] Nomenclature follows Allan (1961) unless stated otherwise.

Chamois (*Rupicapra rupicapra* L.) occur in both areas. Red deer (*Cervus elaphus* L.) have been present in the Kokatahi for over 40 yr, but are rare at Fox. Numbers have declined markedly in the Kokatahi since the 1950s.

As a consequence of dieback, major changes occur in the structure and composition of the affected stands. This paper examines the changes that have resulted from dieback in stands dominated by southern rata and kamahi, and the resulting consequences for maintenance of the structurally dominant canopy species. The forests in each study area are first considered in altitudinal classes based on the canopy species dominant before dieback, followed by general comments on the area. These preliminary results are based on observations and some plot data.

KOKATAHI CATCHMENT

Dieback in the Kokatahi first became apparent in the late 1940s. The most extensive areas of dieback in Westland were considered to be those occurring on the north bank of the Kokatahi River (J. M. Hoy 1955, unpublished). On some ridges between 300 and 700 m altitude, it was estimated that 75% of the original canopy, including southern rata and kamahi, was dead (L. W. Boot 1955, unpublished). Areas of up to tens of hectares from the valley bottom to the upper altitudinal limit of southern rata were affected.

Low-Altitude Forests (300–450 m)

The hardwood canopy species dominant before dieback occurred were southern rata, kamahi, and *Quintinia acutifolia*. The conifers rimu (*Dacrydium cupressinum*) and miro (*Podocarpus ferrugineus*) were also present, rimu being limited to low-altitude stable sites.

Dieback resulted in the loss of southern rata, kamahi, and much of the *Quintinia acutifolia* from the canopy. The podocarps remained healthy. In stands affected by dieback in the canopy, the more abundant subcanopy species were *Carpodetus serratus* and *Pseudowintera colorata*. Saplings and seedlings of podocarps were present, particularly near parent trees. Seedlings and saplings of kamahi and *Q. acutifolia* were abundant, but occurred mainly on logs. Very few seedlings or saplings of southern rata were present. Intact stands of small-diameter trees occurred on the steeper slopes forming the escarpments of the Kokatahi River. These contained southern rata, kamahi, and *Q. acutifolia* in the canopy.

Mid-Altitude Forests (450–650 m)

Southern rata, kamahi, and *Quintinia acutifolia* were the dominant canopy species in stands before dieback occurred. Broadleaf (*Griselinia littoralis*) became more abundant with increasing altitude.

It is in this zone that mortality has been most extensive and complete. Figure 1 presents diameter size class distributions of the canopy species from a quadrat established in a representative stand in 1982. Within this quadrat, all southern rata stems were dead. This included small single-stemmed trees, the occasional much larger individual, and some multistemmed trees. One etiolated seedling was the sole representative of southern rata on 180 m^2 of seedling plots measured on logs, on tree fern trunks, and on the ground within the above quadrat. Most of the remaining dead stems were kamahi or *Quintinia acutifolia*. There were no live stems of kamahi, but *Q. acutifolia* was abundant in the smaller diameter size classes. The dense shrub tier was rich in species, of which *Pseudowintera colorata* and *Carpodetus serratus* were the most abundant subcanopy species, and *Q. acutifolia* was the dominant canopy species (Figure 2). Many tree ferns were present, particularly *Alsophila smithii* (Hook. f.) Tryon. Seedlings of kamahi and *Q. acutifolia* were growing terrestrially as well as epiphytically on logs and tree fern trunks.

High-Altitude Forests (650–750 m)

Southern rata and broadleaf trees formed an open-canopied forest, often on slopes of less than 10°.

After dieback, all the southern rata trees and many of the broadleaf trees died (Figure 3). The only live trees in the canopy were broadleaf, many of which had only partial

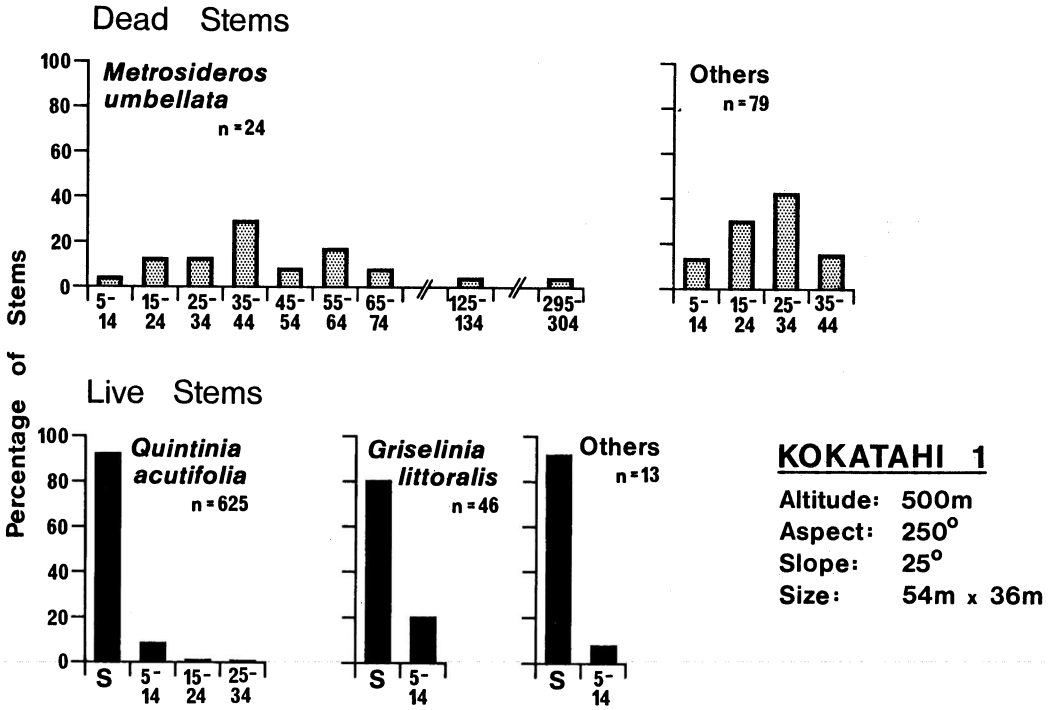

FIGURE 1. Percentage of live and relatively intact dead stems for canopy species in diameter size classes: n = number of stems >1.4 m tall; S = saplings, for stems <5 cm d.b.h.o.b. (diameter at breast height over bark) but >1.4 m tall; and then in 10 cm d.b.h.o.b. size classes.

crowns. The most abundant species forming the shrub tier were *Pseudowintera colorata*, *Coprosma ciliata*, and *Myrsine divaricata*. Broadleaf and many subcanopy species were regenerating on the bases of dead trees and fallen logs. However, seedlings of southern rata were rare.

Thirty-six 400 m^2 quadrats established in 1979 over a range of forested sites throughout the Kokatahi catchment showed little advance growth of southern rata in open- or closed-canopied stands, although seedlings and saplings of kamahi and *Quintinia acutifolia* were relatively abundant. Species highly palatable to red deer were present within the browse tier, indicating that red deer were unlikely to be limiting the regeneration of southern rata, although this may not always have been so. An earlier report considered that red deer checked the establishment of southern rata and kamahi in dieback stands in the Kokatahi catchment (Holloway 1959). Annual ring counts from disks and increment cores suggest that many of the subcanopy trees and shrubs were present before dieback. Most of the *Q. acutifolia* had been established after dieback, but individuals that predated the dieback showed more rapid growth over the last 30 yr. *Quintinia acutifolia* was flowering at ages of less than 20 yr, and because of its abundance in the developing stands was in a good position to occupy vacant sites.

The dieback stands described in this study were of the earliest described mortality. Dieback in southern rata and kamahi has occurred at other times, and extensive areas of recent dieback were present on the south side of the Kokatahi catchment. Some of these trees were not yet dead, although most of the foliage had been lost.

On recent landslides within areas of dieback, regeneration of kamahi and *Quintinia acutifolia* was usually dense. Regeneration of southern rata was more abundant on land-

FIGURE 2. Dead southern rata, kamahi, and *Quintinia acutifolia* trees in a stand at 500 m altitude. The dominant species in the shrub tier are *Q. acutifolia* and *Pseudowintera colorata*.

slides near intact forest. From field observations, few southern rata seedlings were present on recent landslide surfaces greater than 300 m from seed sources. Browse on southern rata and kamahi seedlings present on landslides was attributed to brush-tailed possums. Important colonizing species on these primary sites were *Carmichaelia* c.f. *grandiflora*, *Olearia avicenniaefolia*, and (at higher altitudes) *Dracophyllum longifolium*.

FOX CATCHMENT

Photographs taken of the Fox glacier over the period 1920–1940 show oblique views of the forests in which dieback was not apparent. Early reports on the vegetation did not mention mortality. However, dead crowns in the canopy on the south side of the valley can be seen in photographs taken in the late 1940s and early 1950s. Death of the canopy trees,

FIGURE 3. A stand of dead southern rata trees emergent through a dense shrub tier at 700 m altitude. Live broadleaf trees remain in the canopy.

mainly kamahi and some southern rata, was described by Chavasse (1955, unpublished) as spectacular, particularly on steeper slopes. Open-canopied forest developed where dieback took place.

Low-Altitude Forests (300–600 m)

Important canopy species before dieback included southern rata, kamahi, broadleaf, *Quintinia acutifolia*, Hall's totara (*Podocarpus hallii*), and miro.

In stands affected by dieback in the 1950s, virtually all the southern rata and much of the Hall's totara had died, leaving live trees of kamahi and *Quintinia acutifolia* (Figure 4). From a quadrat established in 1982 in a representative stand, diameter size class distributions for the canopy species are presented in Figure 5. In this stand, all southern

FIGURE 4. Profile of a low-altitude dieback stand with live kamahi and *Quintinia acutifolia* trees; the dead trees are southern rata and Hall's totara. The dominant shrub tier species are *Coprosma foetidissima* and *Pseudopanax simplex*.

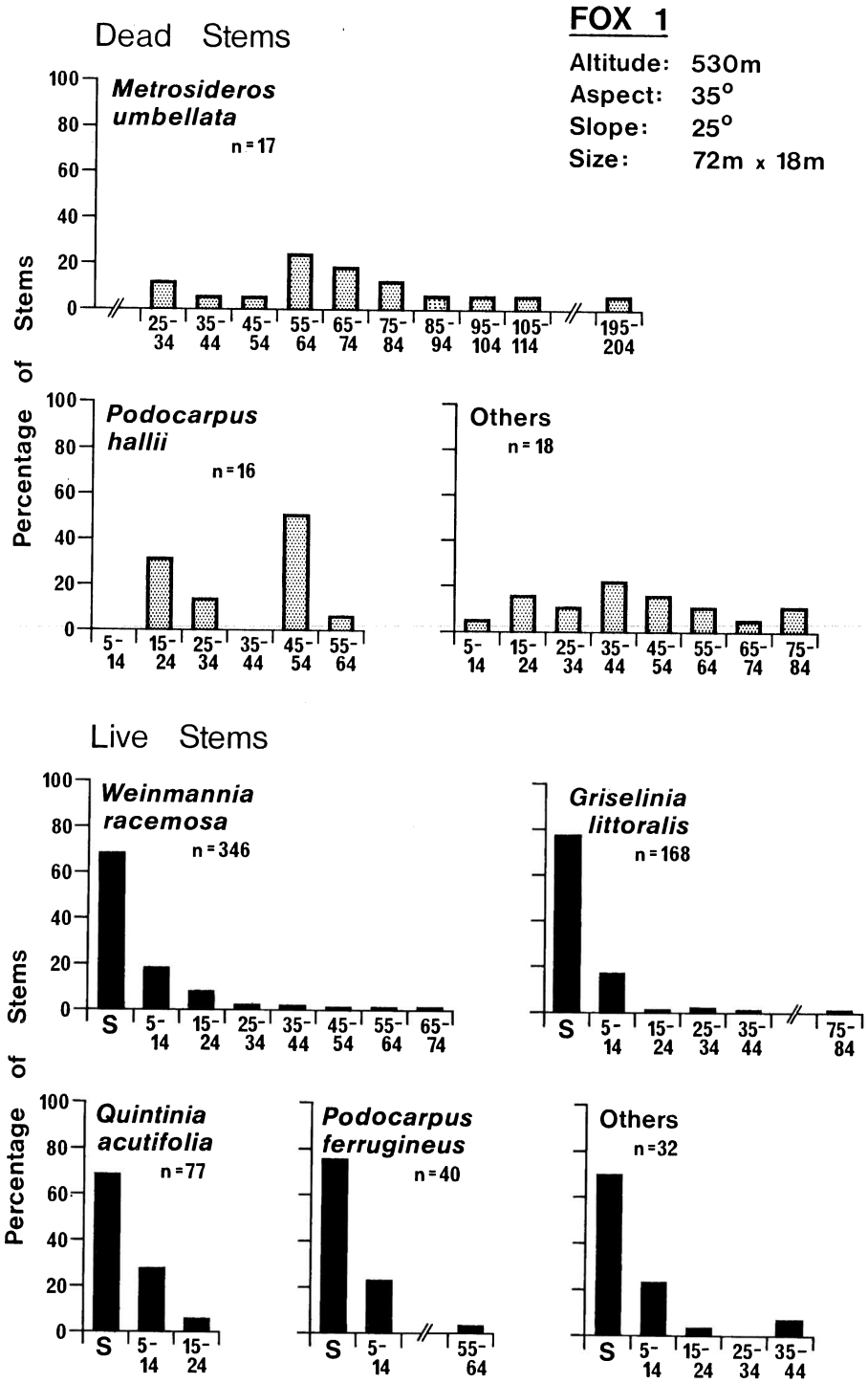

FIGURE 5. Percentage of live and relatively intact dead stems for canopy species in diameter size classes: n = number of stems >1.4 m tall; S = saplings, for stems <5 cm d.b.h.o.b. but >1.4 m tall; and then in 10 cm d.b.h.o.b. size classes

rata stems—over a wide diameter range—were dead, except for one healthy individual with a diameter of approximately 40 cm and five saplings. This stand was relatively rich in canopy species, kamahi being the most abundant. Much of the kamahi had died back, but had recovered by sprouting epicormic shoots. As a result, the intensity and extent of mortality was not as great as photographs of the dieback taken in the 1950s would indicate. The dominant subcanopy species in these stands were *Pseudopanax simplex* (Forst. f.) Philipson and *Coprosma foetidissima*. Saplings and seedlings of kamahi, *Q. acutifolia*, broadleaf, and miro were present, usually on logs. The few southern rata seedlings were restricted to raised surfaces.

Mid-Altitude Forests (600–800 m)

Southern rata, kamahi, and broadleaf were the dominant canopy species before the stands were affected by dieback. Some stands were dominated entirely by southern rata.

After dieback, mortality was most complete in stands with a high southern rata component, because nearly all southern rata trees died. Again, much of the kamahi recovered. *Carpodetus serratus* was an important subcanopy species on talus, with *Pseudowintera colorata* and *Pseudopanax simplex* important on stable areas. Broadleaf and kamahi were regenerating vigorously, with many saplings present and an abundance of seedlings on logs. Southern rata regeneration was sparse and restricted to log sites.

High-Altitude Forests (800–950 m)

Southern rata, kamahi, and broadleaf were present in stands later affected by dieback, along with the conifer *Libocedrus bidwillii*. With increasing altitude, the subalpine scrub species *Dracophyllum longifolium* and *D. traversii* were more important components of the forest canopy.

Because of greater species richness, canopy removal after dieback has not been as complete as in the mid-altitude forests. In dieback stands, dead southern rata trees were found as widely spaced individuals. Some *Libocedrus bidwillii* trees were also dead, but there were few dead individuals of the other canopy species. Regeneration of broadleaf was abundant, but there were very few seedlings of southern rata or kamahi.

Usually, live trees of southern rata were not present in dieback stands within its altitudinal range. However, there were intact stands containing southern rata within the general dieback area. In the low- and high-altitude forests, slopes were steep and the topography dissected, resulting in a mosaic of stand types, some of which were not subject to dieback. A large number of recently dead individuals of kamahi, Hall's totara, and *Libocedrus bidwillii* occurred in dieback stands. The mortality took place over a short time period (less than 10 yr) and has not spread into new areas. Much of the kamahi and *Quintinia acutifolia* were present as small trees and saplings. From annual ring counts of disks and increment cores, many of these individuals were postdieback. This contrasted with the subcanopy species, which were largely present before the dieback.

Surfaces exposed by landslides over the last 20 yr within areas of dieback, often with logs of the former forest present, had abundant regeneration of southern rata, kamahi, and *Quintinia acutifolia*. For southern rata, this contrasted with the successions described on stable sites. On landslide surfaces, height growth of southern rata was often at least equal to other woody species. As the upper altitudinal limit of a species was reached, it became less abundant on recent landslides. However, subalpine scrub species (for example, *Dracophyllum traversii* and *D. longifolium*) colonized landslides well below their lower altitudinal limit in mature communities to compete with seedlings of canopy species. The shrubs *Olearia avicenniaefolia* and *Coprosma rugosa* were also early colonizers of landslides. The tussock *Chionochloa conspicua* Zotov preferred moist areas and gullies where it limited the establishment of canopy species.

DISCUSSION

In the two study areas, the extent and intensity of canopy removal after dieback

was largely dependent on the spatial pattern of stands susceptible to dieback and the species richness of the canopy. Apparently even-aged stands, usually with diameters of less than 30 cm and often originating on landslide surfaces, remained intact. These stands, which contained southern rata, kamahi, and *Quintinia acutifolia*, were more frequent at Fox, although they were still only a small part of the total area. Trees within these stands were possibly vigorous because they occurred on recent mineral surfaces and were relatively young. Before dieback occurred, the forests in the Kokatahi were less rich in canopy species than those in the Fox catchment. Additional factors led to a more complete dieback in the Kokatahi; the kamahi trees did not recover as they did at Fox and the mortality of southern rata and kamahi spread into other parts of the catchment. This pattern parallels the spread of brush-tailed possums (I. L. James et al. 1973, unpublished).

There were other floristic differences between the two areas studied. In the Kokatahi, the upper altitudinal limit of many species was lower than at Fox; for example, southern rata was found to an altitude of 750 m in the Kokatahi, but up to 950 m at Fox. Regeneration of *Quintinia acutifolia* was less abundant at Fox, which probably reflects its lesser importance in the canopy. Understories were dense in both areas, although tree ferns and *Pseudowintera colorata* were more abundant in the Kokatahi. *Pseudopanax simplex* and *Carpodetus serratus*, species palatable to deer, were more abundant at Fox. This can be related to the absence of deer at Fox, but it is also likely that some of these species were more abundant because they are early successional species that prefer mineral soils.

The change in physiognomy of the forests caused by dieback has important consequences. The density of the understory increases, even though the understory of forest in the schist zone is already naturally diverse. The seed source of species that die back is locally removed. Mineral surfaces can be formed by landslides in areas of dieback, sometimes as the result of the death of canopy trees.

Individual species react differently to such changes. Kamahi and *Quintinia acutifolia* seedlings are shade-tolerant compared with southern rata and can develop under relatively intact canopies, as well as in canopy gaps. In old stands on stable sites, southern rata can maintain a presence by regenerating in canopy gaps, often on raised surfaces (Stewart and Veblen 1982, Wardle 1971). This intermittent regeneration results in the development of mixed-age stands. Southern rata and kamahi are opportunistic species that can establish themselves on landslide scars (Stewart and Veblen 1982, Wardle 1980), as does *Q. acutifolia*. On these sites, even-aged stands develop, particularly where slopes are steep (Stewart and Veblen 1982, Wardle 1980). Southern rata (Wardle 1971), kamahi (Wardle 1966), and *Q. acutifolia* all produce small, light wind-dispersed seeds, an advantage in colonizing areas without a seed source. Seeding is unlikely to be limiting for southern rata, because some flowers are produced each year, with good flowering every 3–4 yr (Wardle 1971), which can probably be related to frequency of good seed years. It is not likely that the small seeds of any of these species remain viable for long under natural conditions. Vegetative propagation of canopy species was not important in these dieback stands, except for the epicormic recovery of kamahi noted at Fox.

The wide diameter range of dead southern rata stems found on the quadrats indicates that these were mixed-age stands (cf. Coleman, Gillman, and Green 1980). This probably also applies to kamahi. In general, the regenerative process that established these stands would have been individual tree or group replacement requiring relatively stable landforms, such as ridges. This conclusion conflicts with previous studies in that it does not support the idea that dieback occurs in synchronously senescent stands established after large-scale disturbances (Chavasse 1955, unpublished; Veblen and Stewart 1982). Hoy's (1955, unpublished) contention that mortality of southern rata and kamahi is heaviest on steep slopes is merely a reflection of where most southern rata and kamahi occur. Dieback is present on a range of sites, including gentle slopes.

The effect of dieback is to create large

canopy gaps over short time periods. The gradual opening up of the canopy and the presence of a dense shrub tier favors the more shade-tolerant canopy species. Where the extent of dieback increases, as in the Kokatahi, a point is reached where the seed available for regeneration is limiting. This is particularly important for southern rata, which has limited sites for establishment. Standing dead trees are not as suited for the establishment of seedlings as fallen logs. Although southern rata seedlings are comparatively abundant on landslide surfaces, at present these are only a small part of the total surface area, even at Fox. In larger areas of dieback, availability of seed appears to become limiting as there are few southern rata seedlings, even on the most suitable sites. It is concluded that this species will be neither as abundant nor as extensive in the post-dieback stands as it was before dieback. In some areas like the Kokatahi, where dieback is extensive, it will remain virtually absent as a canopy tree for at least one generation of the replacement canopy. Southern rata is a relatively long-lived species in these forests, with slow recruitment rates. Provided seed sources are near, southern rata will be established as sites become available, but it will take a number of generations before it can possibly establish its former abundance. At Kelly's Creek, central Westland, Stewart and Veblen (1982) described vigorous regeneration of the main canopy species, including southern rata, after "massive" mortality. By comparison, the mortality of southern rata in dieback stands in the Kokatahi and Fox catchments has been more complete and extensive, and the density of regeneration is much lower.

Kamahi and *Quintinia acutifolia* were found to regenerate successfully under a greater range of conditions than southern rata. Although removal of these species from the canopy has not been as complete as southern rata, it is considered that this success is due to their greater competitive ability. The successions after dieback in the areas studied favor kamahi and *Q. acutifolia* as the structurally dominant canopy species. Extensive even-aged stands of these species can be expected to develop in most dieback stands. On many sites, these stands will include other canopy species such as broadleaf, rimu, miro, or Hall's totara.

LITERATURE CITED

ALLAN, H. H. 1961. Flora of New Zealand. Vol. 1. Govt. Printer, Wellington, New Zealand.

COLEMAN, J. D., A. GILLMAN, and W. Q. GREEN. 1980. Forest patterns and possum densities within podocarp-/mixed hardwood forests on Mt. Bryan O'Lynn, Westland. New Zealand J. Ecol. 3:69–84.

GRIFFITHS, G. A., and M. J. MCSAVENEY. 1982. Distribution of mean annual precipitation across some steepland regions of New Zealand. Christchurch Water and Soil Science Centre Rept. WS 648. Ministry of Works and Development, Christchurch.

HOLLOWAY, J. T. 1959. Noxious animal problems of the South Island alpine watersheds. New Zealand Sci. Rev. 17(2):4–10.

STEWART, G. H., and T. T. VEBLEN. 1982. Regeneration patterns in southern rata (*Metrosideros umbellata*)—kamahi (*Weinmannia racemosa*) forest in central Westland, New Zealand. New Zealand J. Bot. 20:55–72.

VEBLEN, T. T., and G. H. STEWART. 1982. The effects of introduced wild animals on New Zealand forests. Ann. Assoc. Amer. Geogr. 72(3):372–397.

WARDLE, P. 1966. Biological flora of New Zealand. 1. *Weinmannia racemosa* Linn. F. (Cunoniaceae) kamahi. New Zealand J. Bot. 4:114–31.

———. 1971. Biological flora of New Zealand. 6. *Metrosideros umbellata* Cav. [Syn. *M. lucida* (Forst. f.) A. Rich.] (Myrtaceae) southern rata. New Zealand J. Bot. 9:645–671.

———. 1980. Primary succession in Westland National Park and its vicinity, New Zealand. New Zealand J. Bot. 18:221–232.