

A COMMENTARY ON CANOPY TREE MORTALITY IN WESTLAND RATA-KAMAHI PROTECTION FORESTS

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ABSTRACT

The apparently excessive canopy tree mortality in the rata-kamahi forests of Westland has resulted in the widespread belief that persistence of the forest cover in this area may be endangered. Browsing by the Australian brush-tailed possum (Trichosurus vulpecula) is commonly believed to be the cause of the widespread mortality. Consequently, research has been directed towards studies of possum diet and vegetation condition under varying possum densities. However, browsing by possums does not appear to be the sole cause of the tree mortality. Natural stand dynamic processes appear to contribute importantly to the observed mortality patterns. The development of even-aged stands following massive disturbances such as mass movements and windthrow and, thus, the presence of groups of senescent trees appears to be an important contributory factor. Possum browsing (as well as other lethal influences) may be affecting stands already susceptible as a result of natural stand dynamic processes.

INTRODUCTION

Grey crowns of dead or apparently dying trees are often conspicuous in the highland hardwood-softwood forests of the North and South Islands of New Zealand. They are especially common in rata-kamahi forests in Westland, on the South Island, where in many areas they give a white tint to the landscape. Since the 1940s this mortality has caused concern as these rata-kamahi forests are considered vital to the protection of agricultural and forestry production in the adjacent lowlands.

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In places, the forest deterioration is believed to have led to accelerated erosion, affecting a total estimated surface (in 1955) of 0.34 to 0.45 million hectares (Chavasse, 1955c). Although there has been considerable debate over the cause or causes of this apparently excessive tree mortality (Chavasse, 1955a; Hoy, 1958), today it is generally believed to result principally from the browsing of the introduced Australian brush-tailed possum (*Trichosurus vulpecula*; Wardle, 1974; Coleman *et al.*, 1980). Possums were liberated at the turn of the century in Westland (Pracy, 1974) but are not considered to have attained populations large enough to sustain extensive forest damage until the 1940s (Gibb and Flux, 1973).

Because of the widespread belief that possums are responsible for the extensive tree mortality, a reduction in possum numbers has been considered essential to prevent further deterioration of these protection forests (McCaskill, 1973; Salmon, 1975). However, this concern has not always existed. Until 1921, possums were freely liberated and protected and no control measures were taken other than wholesale poaching (Wodzicki, 1950). From the 1920s until 1946, although not generally regarded as a serious pest, possums were trapped under a restricted licensing system which had little effect on rapidly increasing populations. By 1946, however, growing uneasiness about the increasing possum population prompted new legislation. After 1946, in some areas where depredations were considered severe, poisoning was permitted (Wodzicki, 1950). Presently, trapping and poisoning are strongly encouraged by the Forest Service, as well as some conservationists, in order to reduce possum numbers.

Despite the general consensus that browsing by possums is responsible for the apparently excessive tree mortality in central Westland forests, this explanation leaves several important questions unanswered. Several factors in addition to possum browsing may be involved in the tree mortality patterns but have received scant attention over the last 20-25 years, probably because of the overwhelming preoccupation with possum browsing as the sole causal factor. In this review these other factors are considered and future studies are suggested to assess their relative importance in the observed tree mortality patterns. Rather than exhaustively reviewing the voluminous literature on possums in New Zealand, in general only those studies pertinent to the mortality patterns in rata-kamahi forests are considered. The objective is not to deny the deleterious effects of possum browsing, but rather to stress the need for further investigation

of the complex interaction of several factors contributing to canopy mortality in rata-kamahi forests.

EARLY REPORTS OF POSSUM DAMAGE

The Australian brush-tailed possum (*Trichosurus vulpecula*), or the possum, is a member of the Phalangeridae and should not be confused with the true American opossum of the family Didelphidae. Possums were liberated in New Zealand in the middle of the nineteenth century and acclimatised to the new conditions well, spreading rapidly throughout the country. Liberations in Westland commenced in 1895 and there were at least 20 further liberations up to and including 1920 (Pracy, 1974). Although possums were liberated over large areas in the 1920s it was not until the 1940s and after that widespread and progressive canopy mortality was reported. For example, Leonard Cockayne (1926) who was familiar with indigenous forests both before and after their infestation by possums, considered that:

were the opossum doing noticeable damage, the forests would unmistakably point to this in their dead trees. But the forests, so far as damage from opossums goes, are as they were.

H. B. Kirk (1920), commissioned by the New Zealand Government to report on the effects of possums on the vegetation, stated that "I have found no native tree that has, in my opinion, been killed by an opossum". Kirk based this statement on the inspection of many forests on the North and South Islands. Similarly, A. N. Perham (1924) in a Forest Service report also stated that he did not believe possums to be causing significant damage to the native forests. These two authors, as well as Thomson (1922), recognised that possums browse native shrub and tree species (as reflected by their lists of browsed species) but concluded that such browsing was not significantly damaging the trees. At this time, however, there was some concern that possums were damaging orchards, plantations and gardens as well as possibly detrimentally affecting native bird populations (Kirk, 1920; Skipworth, 1928).

In the 1940s apiarists in Westland noted a decline in rata honey production and attributed this to extreme rata damage by possums (Wodzicki, 1950). Also during the 1940s damage to protection forests on the North Island by possum browsing was first reported (Zotov, 1949). Increasing concern over tree mortality in Westland prompted an interdepartmental team comprising scientists and land managers from several government departments (Scientific and Industrial Research, Wildlife Division of the

Internal Affairs Department, Ministry of Works, and Forest Service) in 1955 to investigate the problem. The team's objectives were to ascertain, as far as possible, the important factors involved in the mortality and to select areas for further study. The findings of the team were presented in an unpublished report compiled and summarised by C. G. R. Chavasse (1955b, c) and containing nineteen appendixes by ten authors.

As stated in the report, opinions varied on the degree to which relevant factors were important:

The reports prepared by various specialists exemplify the difficulty of determining the relevant factors, since each specialist tended to consider that major, or at least important, causes of mortality lay in his particular sphere. (Chavasse, 1955c)

Despite the differences of opinion on the importance of various possible causal factors, the team members generally agreed on the characteristics of the mortality (Tyndale-Biscoe, 1955). Firstly, two species alone were seriously affected, rata (*Metrosideros umbellata*)* and kamahi (*Weinmannia racemosa*). Secondly, mortality was most apparent on steep slopes between 1000 and 3000 feet (300 and 900 m) in altitude and was less common on the crests of ridges or on the more gentle shingle fans at the base of spurs. Thirdly, the first signs of the mortality, and the most severe later effects, were on north-facing slopes. Fourthly, most often the trees affected were over 30 cm in diameter at breast height (dbh) but this varied with altitude and aspect. Fifthly, severely affected areas had a more open understorey and appeared to have fewer shrub species and fewer birds. Possums were present in all the forests, both affected and unaffected, and red deer in most of them; goats were also sometimes present.

An important addition to the observations of the inspection team is the presence of large numbers of dead standing stems of conifers in the rata-kamahi forests, especially at relatively high elevations. Dead or apparently dying mountain cedar (*Libocedrus bidwillii*) and Hall's totara (*Podocarpus hallii*) are common in Westland (Wardle and Hayward, 1970; James *et al.*, 1973; Burrows and Craib, 1980) and at some sites exceed rata and kamahi in dead basal area (*e.g.*, Coleman *et al.*, 1980; Veblen and Stewart, 1982). Although dead conifers were noted by the 1955 inspection team, their death was taken as evidence

*Nomenclature follows Allan (1961), Moore and Edgar (1970), and Edgar (1973) unless indicated otherwise.

of recent climate change and they were not given further consideration in their report (Chavasse, 1955c).

The 1955 team considered that the following factors were important in relation to the mortality:

- (1) *Age of trees:* Old or overmature trees are more susceptible to damage from disturbances such as attack from insects and pathogens (tree root rotting fungi), unseasonal drought, and windstorms.
- (2) *Angle of slope:* On steep slopes large trees are not common; it is possible that when the trees reach a certain size their root systems can no longer support them.
- (3) *Drought:* Short-term drought, especially on the warm northerly slopes, could cause widespread tree mortality.
- (4) *Climatic change:* It was hypothesised that rata in certain stands (especially toward higher elevations) is overmature and relict in character owing to a detrimental change in climate; climatic change might make it susceptible to damage, especially by browsing animals (Holloway, 1954, 1955).
- (5) *Insect attack:* High populations of scale (coccid) insects attacking the leaves might be responsible for the death of rata and kamahi.
- (6) *Indirect effects of browsing animals:* A reduction in understorey cover owing to deer browsing might result in a habitat less favourable to insectivorous birds. A reduction in bird populations might allow insect populations to rise to levels detrimental to tree health. Similarly, ground browsing mammals, by disturbing litter and soil layers, could make trees more susceptible to drought.
- (7) *Direct effects of browsing animals:* The direct effects of browsing of the tree canopy by possums might result in tree death.

The first three points were considered unimportant unless aggravated by the activities of animals. Thus, the inspection team in emphasising the possible interaction of edaphic and climatic factors, birds, insects and introduced animals clearly recognised the complexity of the problem. Although recognising this complexity, it was concluded:

. . . that opossums are primarily responsible for major defoliation of the canopy trees; that ground browsing animals [red deer and/or goats] are responsible for destruction of shrub and ground layers, for trampling and destroying the duff layer and for the complete

inhibition of regeneration. Both are responsible for the alteration of the microclimate possibly leading to damage by drought, and for the destruction of optimum conditions for insectivorous birds. These activities lead to insect damage to weakened trees, causing death. Insects may also have been encouraged, particularly those feeding on stems and branches, by the reduction in species of birds brought about by introduced disease, cats, rats and mustelids. (Chavasse, 1955b)

The most important evidence in support of this conclusion arose from the following observations. Where deer and/or goats were present the undergrowth was more open and in areas of high tree mortality possum signs were in evidence (bark scratching and foliage browse). Also, mortality was greatest on the warm northerly aspects which goats, deer and possums were assumed to prefer. Finally, from preliminary studies on possum diet it was found that rata and kamahi formed a large part of the ingested foliage. Possum browsing was considered the primary cause of canopy defoliation and consequently of the large number of dead standing rata and kamahi in Westland protection forests (Chavasse, 1955b). Serious forest deterioration was believed to occur only where both possums and ungulates were found in large numbers because elimination of dense undergrowth by ground-browsers, thereby creating a drier understorey, was thought to be essential to the build-up of large possum populations.

The evidence for the close interaction between ground and arboreal browsing mammals given in the 1955 report typifies the early studies which relied chiefly on observation. The general coincidence of high ungulate and possum numbers with high tree mortality led many researchers to believe that both groups of animals were responsible. For example, McKelvey (1959) considered that high possum numbers were found only where the forest floor cover had been reduced or eliminated by hoofed browsing animals; moreover, he considered that "it is no coincidence that large areas with complete mortality of rata and kamahi harbour high opossum populations". The combined influence of ungulates and possums is still believed to be the cause of tree mortality in many areas (Clayton-Greene, 1975; Dale and James, 1977; McKelvey, 1973).

Despite the importance given by the 1955 team to introduced animals in the tree mortality problem, several members stressed the relevance of other factors. Tyndale-Biscoe (1955), while accepting that introduced animals were responsible for some of the vegetation changes in Westland, questioned the degree to

which they were the sole agents of change. He noted that the consensus view did not explain why dead trees were found mainly on steep slopes nor why some stands appeared unaffected despite their infestation by possums. Kean (1955) similarly emphasised alternative factors which he considered to be important in the mortality, such as tree overmaturity, exposure to wind, plant competition, soil movement, and insect attack. Hoy (1958), a member of the 1955 inspection team who investigated the mortality problem further, questioned the importance attributed to the effects of ground-browsing animals on the loss of surface litter and the subsequent effects on tree susceptibility to drought. He thought that the loss of individual canopy trees through other causes such as competition and increased sheet erosion were important. Hoy emphasised that rata and kamahi mortality was due to a combination of factors such as overmaturity, loss of root hold on steep slopes, aspect and animal browsing. He also conducted a survey of scale (coccid) insect populations in the rata-kamahi forests of Westland. There were no significant differences in the abundance of coccids in stands with high rata mortality and stands where rata mortality was insignificant. He concluded that coccids could only be important if the rata were weakened through some other cause and in the case of kamahi they were totally discounted as a cause of death.

Thus, the complexity of the mortality problem and the probable synergistic effects of a multiplicity of factors were clearly realised as early as 1955. Ironically, most of the subsequent research on rata and kamahi mortality has centred on the single mechanism of possum browsing.

POSSUM FEEDING HABITS

Numerous authors have studied the dietary preferences of possums in indigenous forests, on pastoral lands and in exotic forests (Mason, 1958; Gilmore, 1965, 1967; Dunnet *et al.*, 1973; Harvie, 1973; Purchas, 1975; Jolly, 1976; Warburton, 1978). Various techniques have been implemented to determine the dietary constituents, including analysis of faeces, stomach content analysis, visual observations of browse, and feeding experiments. The first comprehensive list of foods eaten by possums was prepared by Kean and Pracy (1953) and included leaves of approximately 70 tree species, 20 ferns, a few vines and epiphytes, fruits of 38 species, and flowers of 16 species. Subsequent authors

have added to this list and now a wide range of species are regarded as palatable to possums.

Dietary studies have provided some data on the relative proportions of species eaten by possums. For example, in south Westland, 30 to 40% of the foliage eaten by possums consisted of *M. umbellata* and *W. racemosa* (Fitzgerald and Wardle, 1979). Other species forming a significant proportion of the diet of possums in Westland include the small trees *Meliclytus ramiflorus*, *Fuchsia excorticata*, *Schefflera digitata*, *Pseudopanax colensoi*, *Hoheria glabrata*, *Aristolelia serrata*, and *Carpodetus serratus*, various species of shrubs (especially *Coprosma* species), and many species of ferns (Fitzgerald and Wardle, 1979; Coleman *et al.*, 1980). The order of preference of these species varies greatly from one location to another, as well as seasonally. Some studies have attempted to relate the amount of a species eaten to its availability in the vegetation. These studies, however, have been largely unsuccessful due to the problems involved in selecting an appropriate measure to estimate the total leaf biomass available for browse. For example, point height analysis used by Fitzgerald (1978) indicated that northern rata (*Metrosideros robusta*) is only a minor component of the vegetation owing to its emergent position above the main tree canopy; however, this species clearly provided a major part of the total leaf biomass in the stands studied. Because of the lack of knowledge of how much foliage of a species is available for browse, derivation of browse pressure from the relative abundance of a species in stomach or faecal samples is difficult. For example, a high component of rata and kamahi in the diet (as measured by stomach content analysis) may not necessarily reflect heavy browsing pressure on these species because in old growth stands the total foliage available of these two main canopy tree species may be many times that of all the small tree and shrub species combined. Conversely, a small percentage of a species such as *Fuchsia excorticata* in the diet might reflect heavy pressure on this species owing to its much less abundant foliage.

Studies in the Orongorongo Valley, near Wellington, on the North Island, have revised several of the previously held beliefs about possum browsing. Elder (1965) suggested that browsing stimulated the production of new leaves which in turn are browsed selectively, thereby compounding the detrimental effects on the tree; however, for northern rata in the Orongorongo, Meads (1976) found that young shoots were not preferred. Also, Fitzgerald (1978) considered that some species in the Orongorongo

Valley were unable to produce new growth in response to browsing. In a series of experiments that involved sheathing northern rata trees to prevent access by possums Meads (1976) showed that persistent browsing by possums can result in the death of mature individuals of northern rata. He also concluded that tree size, shape or form, and the suitability of the tree as a nesting site did not correlate in any obvious way with browsing pressure and that behavioural habit may influence the possums' selection of trees. Other suggested explanations for the selectivity of possum browse investigated in the Orongorongo include chemical attractants in the leaves of some species (Fitzgerald, 1978), leaf position in the canopy (Meads, 1976), and rate of assimilation by the animal (for example, some species may take longer to digest and their intake may therefore be reduced) (Fitzgerald, 1976).

Studies of possum feeding habits show that they have a highly varied and diverse diet. It has been recently hypothesised that possums require a balanced diet and consequently must browse a range of species (Coleman *et al.*, 1980). The large amount of rata and kamahi foliage ingested provide a possible mechanism for explaining the extensive tree mortality in Westland rata-kamahi forests. However, it is not safe to assume that possum browsing is the sole mechanism responsible for the mortality, particularly when it is considered that lightly browsed tree species (*e.g.*, mountain cedar and Hall's totara) contribute importantly to the pattern of mortality.

POSSUMS AND VEGETATION SURVEYS

Vegetation surveys over the last 25 years, primarily by the New Zealand Forest Service, have been used to assess the condition of the vegetation in relation to animal densities and to monitor changes in forest structure and composition. Permanent datum points have been established over much of the country to allow future remeasurement of vegetation condition with the objective of assessing the long-term changes in the vegetation. Surveys prior to 1965 make mention of possum damage in areas of high tree mortality; signs of browse, bark scratching, and presence of faecal pellets are given as the evidence for possum presence (Holloway, 1959, 1966; Holloway *et al.*, 1963). Refinements in survey technique over the last decade have enabled quantitative data to be gathered on animal density for different forest associations.

The tendency in interpreting the data from surveys has been to assume that introduced browsing animals are wholly responsible for the observed variations in forest structure and composition. This has often resulted in a lack of concern for other important influences on forest structure. For example, in the Hokitika Catchment in Westland, vegetation plots established in 1957 were remeasured and updated in 1963 and in 1971 (James *et al.*, 1973). Basal area and tree stem density were used to illustrate changes in forest structure over this 14-year period. Although on a forest association basis there were no significant changes in basal area or tree densities, slight changes for some individual species occurred. From this it was concluded that a shift had occurred towards greater abundance of species more resistant to possum browsing as a result of high possum densities during the period of monitoring from 1963 to 1971. In the same survey report, a study was done comparing the vegetation of two tributaries of the Hokitika River with differing possum histories; the Kokatahi River catchment had high possum densities over the previous twenty years while the Whitcombe River catchment had a low possum population. It was assumed that factors of climate, soils, geology, and vegetation type were similar in both areas and, therefore, that the only variable was possum history. For the Kokatahi, based on the absence of stems in certain size-classes, it was concluded:

Weinmannia and *Metrosideros* mortality is simply due to opossum browsing. *Weinmannia* trees in all size-classes have been lost whereas with *Metrosideros* and *Podocarpus hallii*, the large stems have been most affected. (James *et al.*, 1973).

The assumption that the only difference between the two areas was one of possum history may not be a valid one. For example, there are important differences in the geology and topography of the two areas. The abundance of slips in the Kokatahi in fault-crush zones which could have been initiated by geological agencies has been mentioned previously (Cutler, 1955) and may account for differences in forest structure. James *et al.* (1973) also point out that in the Whitcombe the topography is easier and more stable. This difference could result in a greater frequency of mass movements in the Kokatahi which would undoubtedly affect forest structure and composition. The data presented also suggest that initial composition may have been different in the two areas. For example, relatively unpalatable tree species differ greatly in abundance in the two areas. *Quintinia acutifolia* is less abundant and *Phyllocladus alpinus* is absent in

the Kokatahi while Hall's totara is more abundant in the Whitcombe. These differences in forest composition are not attributable to possums and cast doubt on the validity of attributing differences in the abundances of palatable species (e.g., rata and kamahi) to browsing animals.

Recent Forest Service surveys have attempted to quantify the coincidence of high possum populations with extensive tree mortality. In these surveys ungulate and possum numbers are estimated from counts of faecal pellets and observations of browse (ungulates only); their densities are related to factors such as altitude, aspect, vegetation type, and vegetation condition. Data from these surveys do not always confirm previously held beliefs. For example, in contrast to the assumed preference of possums for drier northerly slopes (Chavasse, 1955c) pellet counts indicate no greater use of the north-facing slopes in the Hokitika Catchment (Pekelharing, 1973). In the Taramakau Catchment, Pekelharing (1979) monitored canopy mortality between 1960 and 1973 and found that canopy defoliation coincided with a build up and peaking of possum numbers as well as with heavy browsing of the understorey by deer. Although he documents an increase in tree mortality over the 13-year period, no information is available on the amount of mortality which would occur in the absence of browsing mammals. Thus, although a correlation between browsing mammals and tree mortality is shown, a causal relationship cannot be assumed in the absence of experimental evidence. In the Copland river catchment in south Westland, Burrows and Craib (1980) sited vegetation plots in areas of varying tree mortality and possum numbers in the rata zone to assess and predict changes in forest composition and condition in relation to possum densities. The underlying assumption in site selection was that there was a direct relationship between possum numbers and vegetation condition. For example, sites with a large dead rata component were selected where possums were abundant, and, conversely, in areas of low possum densities, plots were located under rata stands with apparently low mortality. The coincidence of high rata mortality and high possum populations, therefore, reflects nothing more than the method of site selection. Also, many of the dead trees in the areas selected were Hall's totara and mountain cedar, the death of which is rarely attributed to possums because they are only lightly browsed (Coleman *et al.*, 1980). Although these, and other studies may demonstrate a coincidence of possums with tree mortality, they are inconclusive because there are no

data presented on how many deaths to expect in the absence of possums.

The condition of the hardwood-softwood forests of eastern Southland raises serious doubts about the role of possum browsing in the canopy mortality of rata-kamahi forests. In the Catlins area possums have been so abundant that more than 60 000 skins were taken in the area in 1912 (Thomson, 1922) but rata is reported as not showing any significant damage (Wardle, 1973; N.Z. Forest Service, 1979). The relative lack of dead standing trees in hardwood-softwood forests of this area contrasts markedly with the mortality observed in Westland. Clearly there are important exceptions to many of the general beliefs regarding possum and ungulate browsing and the condition of the rata-kamahi forests.

THE IMPORTANCE OF STAND DYNAMICS

If possums are accepted as the *sole* cause of the conspicuous tree mortality, several unanswered questions remain.

- (1) Why are many young (*i.e.*, 5-10 cm dbh) rata and kamahi apparently healthy, even though some are browsed by possums, in the midst of older dead and dying individuals of the same species?
- (2) Why, as observed by the 1955 inspection team (Chavasse, 1955c), are many dead rata found on steep slopes whereas ridge summit stands and gentle slopes generally show much less excessive mortality?
- (3) Why are some rata-kamahi forests, such as those of the Catlins area in eastern Southland, unaffected by excessive canopy mortality despite a long history of high possum numbers?
- (4) Why are many of the dead trees in Westland forests the conifers Hall's totara and mountain cedar which are only lightly browsed?

We propose that the above questions may be answered by considering the natural stand dynamics of the Westland rata-kamahi forests. Forest Service surveys and other published works provide accounts of the composition and descriptions of the rata-kamahi forests of Westland (Holloway, 1966; Wardle and Hayward, 1970; Wardle *et al.*, 1973; James *et al.*, 1973; Wardle, 1974, 1977, 1978). However, the information provided by these

surveys is relevant mainly to the assessment of ungulate effects and is of relatively little use in evaluating the effects of possums. Although some information is available on the reproductive biology of the major tree species (Wardle, 1966, 1969, 1971) and on seed and litterfall (FRI, unpublished data), there is no comprehensive understanding of forest regeneration processes in the rata-kamahi forests. This is a serious deficiency, because an understanding of the effects of animals on these forests depends on a knowledge of how the major tree species regenerate. One reason for this may be that very few situations remain where it is possible to study the vegetation free from introduced animals. However, there are numerous situations where the forests are regenerating (even in the presence of introduced animals) and these are useful for studying the regeneration processes. Comparative studies of similar forests lacking introduced animals indicate how easily some forest structures can be incorrectly attributed to introduced animals. For example, in the lowland rata-kamahi forests on Bench Island, off the coast of Stewart Island, saplings and small stems of rata and kamahi are rare and a similar underrepresentation occurs in the coastal forests of Stewart Island. However, Bench Island is free of introduced animals whereas Stewart Island is heavily infested with white-tailed deer and possums. On Stewart and Bench Islands the underrepresentation of small individuals of rata and kamahi is attributable to the discontinuous mode of regeneration of these species rather than to browsing animals (Veblen and Stewart, 1980). Nevertheless, deer have drastically reduced the abundance of saplings of subcanopy tree species on Stewart Island.

In Westland, we suggest that much of the mortality of species such as rata and kamahi is partially related to synchronous establishment in even-aged stands where the previous vegetation has been devastated by some form of natural disturbance. These even-aged stands eventually may give rise to many senescent trees at approximately the same time in a given area. Because these trees are senescent they are more likely to be killed by insects, pathogens, drought, severe frosts, possum browsing or other deleterious influences. In this explanation of mortality the synchronous senescence of the trees is an essential contributory factor to the mortality; the possum browsing therefore cannot be considered the sole cause. It is likely, however, that possum browse may make the mortality more coincident than it would be otherwise, because browsing appears to often be the immediate factor which hastens the death of the trees.

The apparently even-aged structure of many Westland forest stands has been documented previously (Wardle, 1966, 1971, 1980; Stewart and Veblen, 1982) and very likely reflects past periods of massive synchronous establishment. Chavasse (1955c) describes and interprets this phenomenon as follows:

As can be observed throughout Westland, at some time in the past regeneration of strips and patches has taken place in the rata/kamahahi forest. These patches appear to be even-aged, whether rata, kamahahi or a mixture of the two species. Throughout the areas inspected these young stands appeared to be the same age, whether forming thin strips down ridges or in broader patches on country of relatively smooth contour. These stands are judged to be 100 to 200 years old . . . The origin of these stands cannot of course be determined. They form a similar pattern, in some places, to the present mortality pattern; but if they originated after an insect epidemic, mortality was restricted compared to that of the present day . . . The most probable explanation is that they originated after a major earthquake.

The pattern described by Chavasse of stands characterised by high mortality in strips down steep ridges and at the end of spurs and of other young vigorous rata-kamahahi stands on similar sites is common throughout Westland (Hoy, 1958). Chavasse (1955c) observed that this mortality pattern "suggests that there might be periodic or cyclic disturbance of some sort leading to excessive mortality in the older, and probably relatively even-aged stands".

In the late 19th century Charles Douglas also observed widespread groups of similar sized trees resulting from massive disturbances:

At one time the Westland Rivers must have been subject to slips larger and more numerous than in the present day. A slip coming down into a riverbed is a rarity nowadays, but up every river there is evidence of whole hillsides having come down, sweeping all before them, at what date this took place is hard to say. They are now covered with full grown trees but all appear about the same age. As if some exceptional commotion had taken place along the [West] coast, perhaps a very wet season combined with an earthquake shock at the right moment did the business. (Holloway, 1957)

This interpretation has also been offered by Wardle (1980) who suggests that numerous, apparently even-aged rata-kamahahi stands on steep slopes along the Alpine Fault may have arisen following a major earthquake which triggered massive slides about 1730-40 A.D. Mass movements are extremely frequent in Westland on steep slopes and when viable seed is available, rata and kamahahi establish directly on the devastated sites (Wardle, 1966,

1971, 1980; Stewart and Veblen, 1982). Frequent heavy rainfall and the abundance of fault-crushed zones of rock also contribute to the frequency of mass movements (Morgan, 1908). Mass movements are a visually significant feature of Westland, especially where large numbers of slip faces are associated with fault-crush zones (in particular those of the Alpine Fault).

Windthrow is another disturbance affecting the forests of Westland; massive windthrow is well known in the lowland podocarp forests (Hutchinson, 1928, 1932; Roche, 1929) and rata-kamahi forests are also significantly affected. For example, regeneration of *Quintinia acutifolia* and kamahi as pole stands has been observed in recently windthrown forest in central Westland (Coleman *et al.*, 1980; Veblen and Stewart, 1982).

Although numerous apparently even-aged rata-kamahi stands in Westland may be attributable to widespread mass movements and other disturbances, and synchronous senescence of trees that established at a similar time probably contributes importantly to the conspicuous tree mortality, the general coincidence of high possum densities with tree mortality must still be explained. We propose that the same circumstantial evidence for possum browsing as the sole cause for the mortality could be used in support of an alternative explanation. Young, apparently even-aged rata-kamahi stands are dominated mainly by these two species and the dense, homogeneous canopy prevents the development of small understorey trees and shrubs. Natural mortality of the canopy dominants as the stands age creates canopy gaps and in open areas proliferation of understorey species (including ferns) and tall shrub and small tree species occurs (James *et al.*, 1973; Chavasse, 1955d). Stands with a discontinuous main canopy (such as those resulting from massive mortality of the dominants) are characterised by a greater abundance of small trees and shrubs such as *Pseudopanax* species, *Griselinia littoralis*, *Aristotelia serrata*, *Carpodetus serratus*, *Fuchsia excorticata*, *Schefflera digitata* and *Melicactus ramiflorus*. The greater diversity of diet available in these areas may permit the attainment of greater possum densities which may account for the incidence of high tree mortality with high densities of these animals. The association of dense possum populations with areas of greater species diversity has been documented previously (Coleman *et al.*, 1980). In this explanation, then, the possums may or may not be responsible for the tree canopy mortality but are attracted to these areas because of the increased diversity of diet.

As mentioned earlier, the widespread concern for the protection function of the rata-kamahahi forests originated in the 1940s when both deer and possum populations were high in many areas. However, extensive tree mortality was characteristic of these forests much earlier. Kirk (1920) and Perham (1924) observed dead rata, kamahahi and *Fuchsia excorticata* at Lake Kaniere in 1920, when animal numbers were still low; neither author could find evidence to suggest that tree death was related to possums. Charles Douglas in the late 19th century described dead mountain cedar in the Whitcombe Valley as so numerous that they gave a white tint to the landscape (Holloway, 1957). Photographs taken by Morgan (1908) between 1905 and 1907 in the Whitcombe, Mungo and Toaroha tributaries of the Hokitika River show extensive areas of dead trees. Some of these trees have a conical form characteristic of conifers such as mountain cedar and Hall's totara; some, however, appear to have rounded crowns suggestive of broadleaved tree species such as rata (Morgan, 1908). Furthermore, the extensive areas of dead stems in these photographs suggest that more than just conifers must be involved. This extensive tree mortality would be difficult to attribute to possums as they are not believed to have occupied these valleys in large numbers until at least the 1920s (James *et al.*, 1973). Further searching for old photographs and nineteenth-century descriptions of these forests could yield useful information on natural mortality patterns.

A highly similar canopy mortality to that described for Westland rata-kamahahi forests also occurs in Ohia (*Metrosideros polymorpha* Gaud.) forests in Hawaii. Extensive dieback of *Metrosideros* has occurred in Hawaii in the absence of possums or any other mammalian canopy folivore. It has not been possible to relate the dieback of Ohia to either insect infestation or fungal pathogens (Papp *et al.*, 1979), and it has been suggested that the dieback is a totally natural phenomenon (Mueller-Dombois, 1980). Adee and Wood (unpublished manuscript) have recently related the Ohia dieback to the senescence of even-aged stands which establish following volcanic disturbance. Thus, explanations (arrived at independently) for the remarkably similar patterns of *Metrosideros* dieback in Hawaii and in New Zealand both stress the importance of natural stand dynamic processes.

CONCLUSIONS

It is apparent that defining the underlying causes for the extensive mortality in the rata-kamahahi forests of Westland is

a complex problem. A pattern (dead trees) has been described in many studies, and processes to account for this patchy mortality and regeneration have been suggested. The many mechanisms which probably contribute to this pattern include disturbance and natural stand dynamics, attack by insects and pathogens, and browsing by possums. Most previous interpretations, however, have relied chiefly on a single mechanism — browsing animals (especially possums). Although it is not disputed that on many occasions (if not, most) possum browsing is the immediate cause of death of many trees in Westland, we propose that the other mechanisms require further investigation. Special attention should be given to the probable role of natural stand dynamic processes in rata-kamahi forests in making the dominants of many stands more susceptible to lethal influences from various factors.

We therefore propose that priority should be given to studies in the following fields:

- (1) *Studies of natural disturbance regimes.* Information on the types, scales and frequencies of disturbances such as mass movements, windthrow, extreme frosts and severe drought should be gathered in the affected areas. Also the suitability of disturbed sites for regeneration of the major species should be evaluated.
- (2) *Further studies on the regeneration ecology of the major species.* Detailed studies of forest structure and regeneration are required to further elucidate the conditions under which the main canopy tree species regenerate (see Stewart and Veblen, 1982).
- (3) *Autecological studies of the major tree species.* Information is required on the periodicity and quantity of seed production and its viability and germination requirements for the major tree species. Particular emphasis must also be placed on individual tree health in relation to peaks of flowering and seeding. For example, massive crown die-back of yellow birch following a heavy seed year has been documented in Ontario, Canada (Gross, 1972).
- (4) *Experimental possum/vegetation studies.* Several areas should be selected where the vegetation can be intensively monitored in relation to possum populations, the sizes of which can be manipulated by intensive control activities. Priority should be given to finding areas with no possums or at least a

very low population. The primary objective of such a study would be to attempt to compare natural tree mortality patterns and mortality induced by possums.

- (5) *Studies of rata and kamahi pathogens.* Heart rot appears to be typical of kamahi and could contribute to its mortality. The role of pathogens in these forests requires further investigation.

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