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Mountain beech (*Nothofagus solandri* var. *cliffortioides*) decline in the Kaweka Range, North Island, New Zealand

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Abstract Forest dieback in the Kaweka Range appears to be a stage in the natural process of replacement for mountain beech. An examination of stand structure in stable, transitional, and unstable forest showed dieback and tree mortality to be associated with mature and over mature stands. Recruitment peaks suggest periodic natural disturbance, such as severe drought, initiates tree decline. Insects and disease, although contributing to the rate of decline, were shown to be symptoms rather than causes.

Keywords *Nothofagus*; beech decline; dieback; Kaweka Range

INTRODUCTION

The *Nothofagus* forests of the Kaimai, Kaweka, and Ruahine Ranges, Tongariro National Park, and Kaimanawa Forest Park, as well as a number of South Island areas, have shown dieback and mortality for at least 20 years. Insects and disease are an inevitable accompaniment to such decline—an association which has often been interpreted, in particular by foresters, forest managers, and the general public, as cause and effect. While some researchers suggest beech is particularly vulnerable to disease (Cunningham & Stribling 1978), and that insect-caused mortality increases the probability of further outbreaks (Wardle 1984), others believe abiotic agents such as drought (Skipworth 1983; Grant 1984), snowfall (Wardle & Allen 1983), or wind (Shaw 1983) are primarily responsible for initiating stand changes. Although the importance of biotic agents in beech dieback has long been viewed with ambivalence by researchers, recent studies (Hosking & Kershaw 1985; Hosking & Hutcheson 1986) support the view that insects and diseases are more often symptoms than causes. Hosking & Hutcheson's investigation of the decline of hard beech (*Nothofagus truncata* (Col.) Ckn.) on the Mamaku Plateau led them to conclude that although insects and disease were important contributing factors to tree death, the decline process was drought induced.

The mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole) forests of the Kaweka Range provided the opportunity to further test this hypothesis in an area where insects had long been considered by foresters and ecologists to be a primary cause of canopy deterioration. For more than 30 years, thinning of the canopy, dieback of crowns, and death of trees has been evident (Elder 1959), causing concern in both the management of introduced animals and the retention of protective forest cover. Mountain beech occupies severe sites where competition from other tree species is almost non-existent. Its ability to persist in such environments is dependent upon the maintenance of a continuous protective canopy (Wardle 1970). Small canopy openings rapidly lead to much more extensive breakdown (Wardle & Allen 1983) as the stand's ability to maintain a favourable microsite is lost. It is therefore inevitable that in areas of continuous mountain beech forest, such as the Kaweka Range, collapse will be extensive and dramatic.

The primary objectives of the study were to examine the structure and growth patterns of both healthy and debilitated stands, and to investigate the roles of both biotic and abiotic factors in the process of canopy breakdown.

METHODS

The Kaweka Range is a short section of the Cook Strait–East Cape mountain axis of the North Island lying between 39°05′S and 39°30′S (Elder 1959). The study was carried out on Middle Hill and adjacent to the track between Te Puke and Middle

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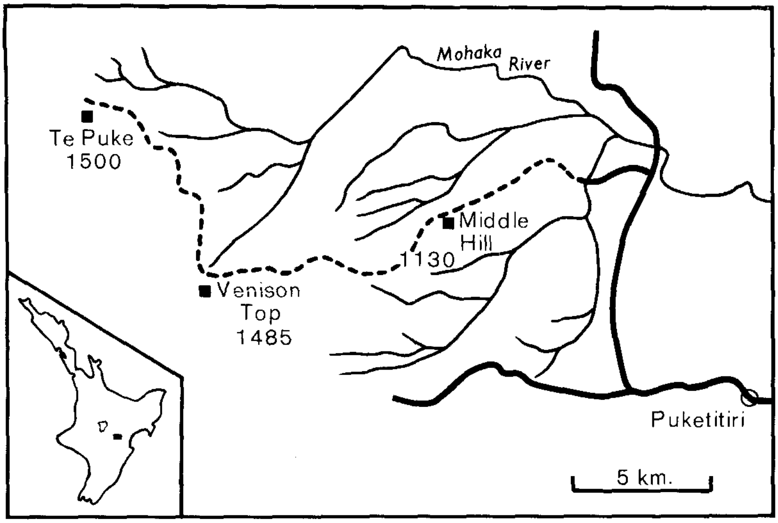

Fig. 1 Location of study area. The 60 assessment plots were located along the Te Puke–Middle Hill track.

Hill huts (Fig. 1). Throughout the study, unstable stands were characterised as having <50% canopy cover, with crown dieback affecting major branches as well as terminal twigs; transitional stands were those with canopy cover between 50 and 70% with dieback affecting terminal twigs only; and stable stands possessed >70% canopy cover with healthy crowns showing little or no evidence of twig death.

Stand dynamics

Two 1 ha plots were established on Middle Hill (1130 m a.s.l.), one in a stable stand and the other in an unstable stand (Fig. 2). Although established primarily to monitor insects and diseases, these plots were used to estimate tree mortality and changes in crown condition over a three year period from February 1984 to February 1987 using colour and colour infrared aerial photography. Three flight lines covering areas between Te Puke and Middle Hill huts were photographed in February 1984, November 1985, and February 1987 at scales of 1:10 000 and 1:5000.

A series of 60 temporary plots were assessed during July 1985 in the area between Te Puke and Middle Hill huts, 24 in stable, 23 in transitional, and 13 in unstable stands. The plots were circular, of 7 m radius, and centered on one tree. The diameters of all trees >5 cm were measured at breast height (d.b.h.) and the crowns classified as healthy (full with little or no twig death), transitional (full but with extensive twig dieback), or unhealthy (reduced with dieback of twigs and major branches). Dead trees were also measured. Increment cores were taken from five canopy trees in each plot giving 197 usable cores for estimating tree age. Ground cover, as litter, grass, fern, moss, or shrubs, was estimated to the nearest 10%, and seedlings (0–40 cm), advanced growth (40–100 cm), and saplings (100 cm tall to 5 cm d.b.h.) were recorded on scale of 0 (nil) to 3 (abundant).

Rainfall data was obtained from the Ngahere Hut recording station (MOD No. 963410) 6km south of Middle Hill at an altitude of 975 m.

Insects and disease

The potentially most damaging insect *Neomycta pulicaris* (Hosking & Hutcheson 1986) was monitored using five randomly placed litter traps in each of the two 1 ha plots. Each funnel-shaped trap had a catching area of 0.283 m^2 and was serviced every four weeks during the spring and summer of 1983–84 and 1984–85.

At the same time, accessible foliage was beaten for insects and examined, along with the trunks of plot trees, for any insect or disease damage. A series of ten branches on separate trees was monitored in each plot for the incidence of fungus-induced wilt. Affected twigs were tagged and progress of the disease recorded monthly.

RESULTS

Stand structure

There was a significant decline in live basal area between stable and unstable plots (Table 1) and a corresponding increase in dead basal area (Fig. 3). More than 45% of stable plots had live basal area

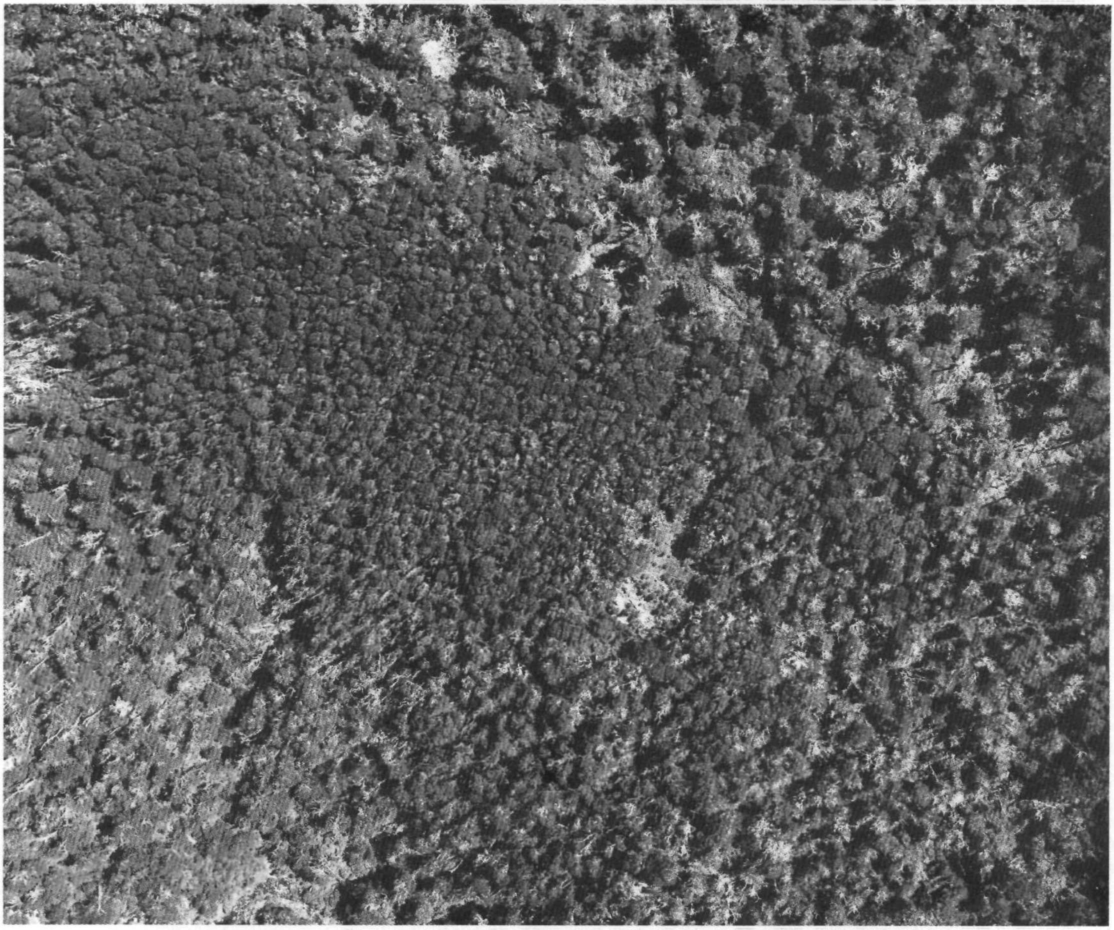

Fig. 2 Middle Hill with healthy stand centre of photograph and deteriorating stand to lower right (scale 1:5000).

Table 1 Mean live basal area, stem density, and mean d.b.h. for each plot category (only stems >5cm d.b.h. Vertical lines show no significant difference between means based on s.e. at 95% level.).

Plot category	n	Basal area ($m^2\ ha^{-1}$)			Density (stems ha^{-1})		d.b.h. (cm)	
		$\bar{x}$	±s.e.	Range	$\bar{x}$	±s.e.	$\bar{x}$	±s.e.
Stable	24	77	4.53	45–120	1478	295	24.4	0.70
Transitional	23	64	3.60	17–103	1000	87	24.7	0.77
Unstable	13	36	5.45	6–72	515	89	26.3	1.40

>80 $m^2\ ha^{-1}$, whereas only 13% of transitional plots and no unstable plots had basal areas of this order. Seventy-five percent of stable plots had dead basal area <20 $m^2\ ha^{-1}$ compared with 60% of transitional and only 23% of unstable plots (Fig. 3). Stem density declined significantly from stable to unstable plots (Table 1).

Seedlings predominated in stable plots with some advanced growth but very few saplings, while unstable plots were dominated by advanced growth and saplings (Table 2). Ground cover showed clear changes with increasing loss of canopy, from litter and moss dominance in stable, to fern and shrubs in unstable plots.

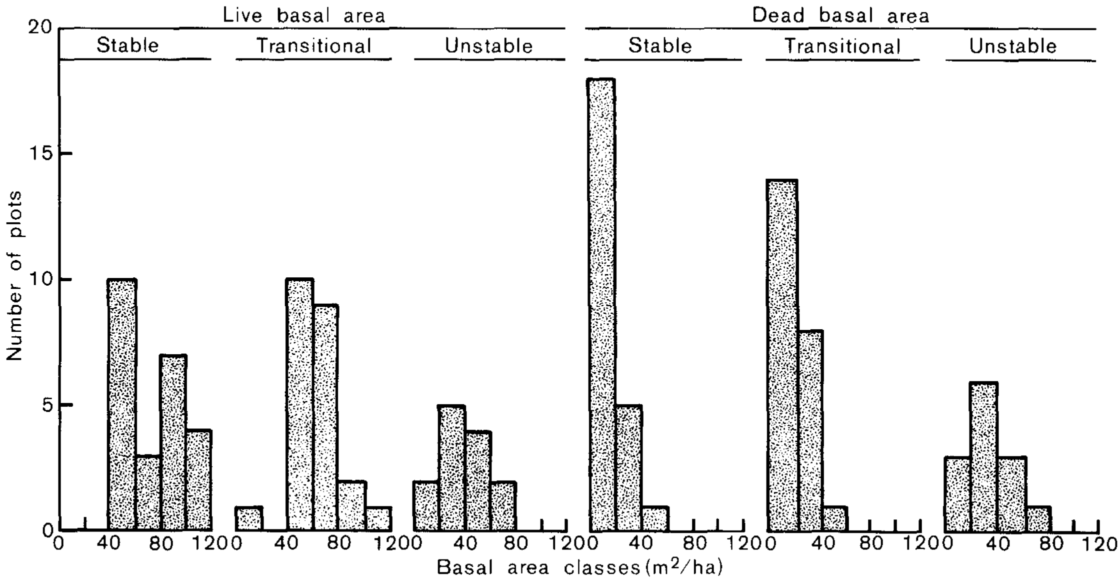

Fig. 3 Live and dead basal area distribution.

Table 2 Mean index of abundance by plot category for seedlings, advanced growth, and saplings (0 = nil, 1 = low, 2 = medium, 3 = abundant).

Plot category	Seedlings	Advanced growth	Saplings
Stable	2.2	0.8	0.20
Transitional	2.2	1.6	0.35
Unstable	0.9	2.0	1.30

Diameter distribution, age, and growth rates

There was no significant difference in mean tree diameter (d.b.h.) between the three plot categories (Table 1). However, stable plots contained a greater proportion of the trees <25 cm d.b.h. while transitional plots had a disproportionate representation of trees >50 cm d.b.h. (Fig. 4). Unstable plots showed a relatively even distribution of diameter classes up to 50 cm d.b.h., most larger trees having already died.

The age structure of stable plots was dominated by 50–70 and 100–120 year old trees, transitional by 100–130 year old trees, whereas unstable plots were characterised by having few trees younger than 70 years and a high proportion older than 170 years (Fig. 5). A regression of diameter on age for all trees gives:

$$\text{Age} = 15.9 + 4.3 \text{ d.b.h.} \quad r^2 = 68\%.$$

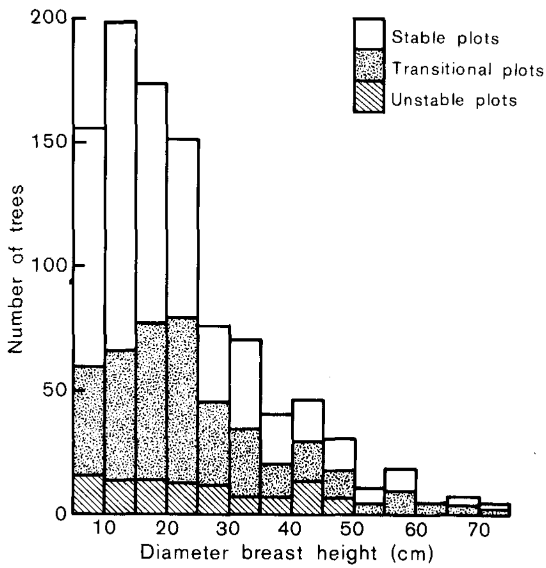

Fig. 4 Size-distribution for live stems in three plot categories.

Mean annual ring width, measured for 11 healthy canopy trees over the past 50 years, was 1.6 mm (s.e. 0.15) but ranged from 0.5 to 2.8 mm. The small sample precluded any comparison of growth rates for the three plot categories.

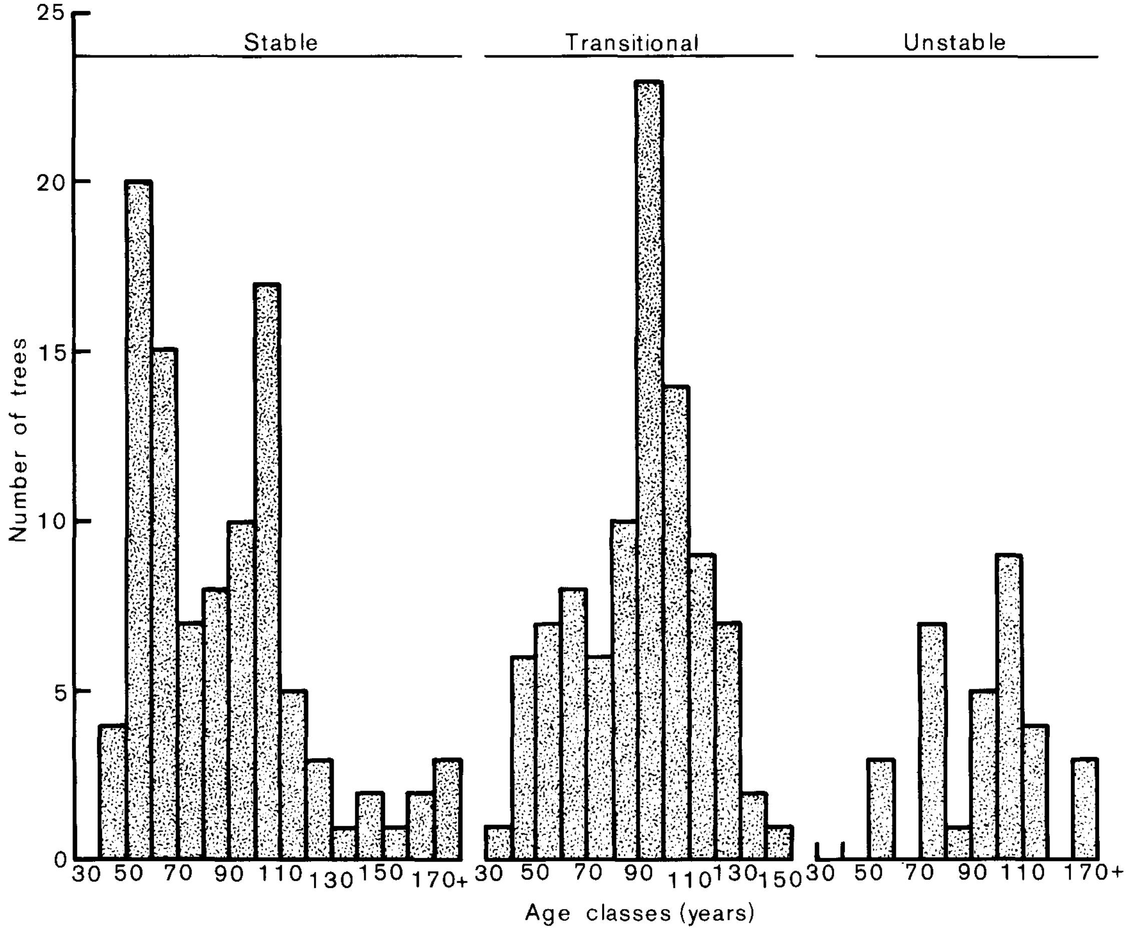

Fig. 5 Tree age structure for three plot categories.

The growth pattern of one dominant healthy tree was examined in detail because of its unusually even growth throughout its 179-year life. No periods of sustained high or low growth were evident with the exception of an abrupt decline in the mid 1860s and an equally abrupt return to normal growth in the early 1870s (Fig. 6).

Insects and diseases

The only insect found to be causing measurable damage to the Kaweka stands was the small leafmining weevil *Neomycta pulicaris*. Defoliation in the unstable Middle Hill plot was more than twice that of the stable plot. Infestation levels peaked in early January 1984 with the loss of 165 newly flushed leaves m^{-2} wk^{-1} in the unstable plot and 75 leaves m^{-2} wk^{-1} in the stable plot.

Extensive foliage wilt, affecting the terminal 10–20 cm of shoots, scattered throughout the canopy was recorded on Middle Hill in late 1983. While scattered twigs were affected in the stable plot, up to 30% of all twigs showed wilt symptoms in the unstable plot. The fungus *Nodulisporium* sp. was consistently isolated from wilting tissue (M. Dick pers. comm.). In January 1984, the ten branches being monitored in the stable plot showed a total of six separate wilted twigs while the ten in the unstable plot supported 28. By March 1984 the incidence had increased to nine in the stable plot and 42 in the unstable plot. No further wilt had occurred at the final assessment in March 1985. Wilted twigs have been rare in both plots since 1984.

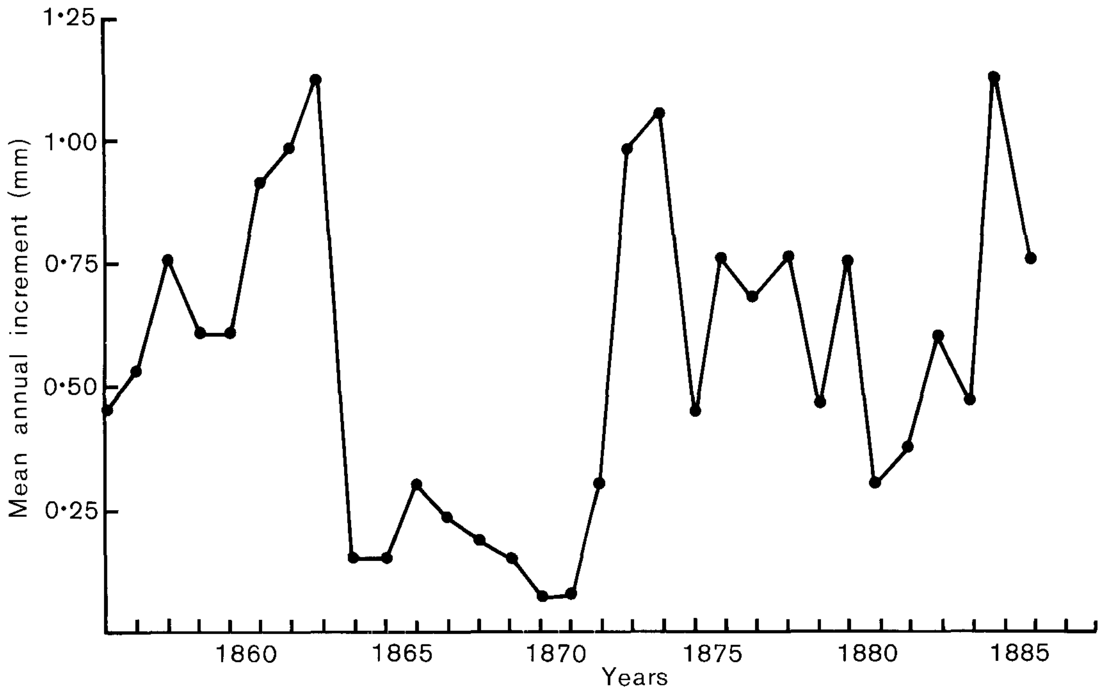

Fig. 6 Thirty year growth pattern of tree 2, plot 20, showing growth reduction between 1863 and 1870 (tree age 58–65 years).

Rainfall and tree growth

Monthly rainfall data was only available from the Ngahere Hut site from 1973, allowing a 12 year comparison with tree growth. Using departure from the long-term mean rainfall for the November to January active crown growth period, a strong agreement was found with mean annual ring width for a sample of 11 trees (Fig. 7).

Tree mortality

The average annual mortality for the stable Middle Hill plot was 1.4% while for the unstable plot it was 6.4% (Table 3). There was also a basic difference in the class of trees affected and the resulting impact on the forest canopy. Mortality in the unstable plot predominantly affected large mature trees and resulted in increasing opening of the canopy whereas in the stable plot small suppressed trees were mainly affected with little canopy impact.

DISCUSSION

Low live basal area, low stem density, and greater tree age suggest unstable stands are in a more advanced stage in the forest cycle than stable stands. Unstable stands also appear to occupy drier and more stony sites than stable stands which contain younger trees of similar diameter. Tree decline therefore predominates in more mature stands on less favourable sites.

There was no evidence to suggest insects or disease occupied other than a minor contributing role in tree death. The only insect causing damage worthy of note was *Neomycta pulicaris*, which, although responsible for twice as much foliage loss in unstable compared with stable stands, still only reached a quarter of infestation levels found by Hosking & Hutcheson (1986) in declining hard beech stands. Foliage wilt, while periodically spectacular, did not persist in either stable or unstable stands. Manion's (1981) definition of "contributing" factor fits well the impact of insects and disease in the Kaweka stands, as opposed to an "inciting" or causative role.

It is from the age structure and growth patterns of the three classes of Kaweka stands that strongest evidence for the nature and causes of stand decline can be drawn. Two periods of increased recruitment

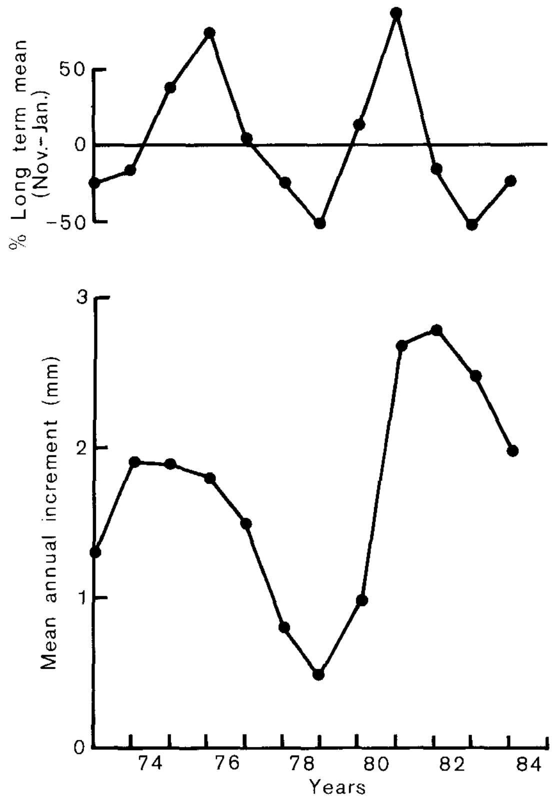

Fig. 7 A comparison of mean annual increment for 11 trees with % departure from long-term mean rainfall from November to January (Ngahere Hut rainfall station).

Table 3 Number of trees for the two 1 ha Middle Hill plots showing tree mortality and decline for the three year period from February 1984 to February 1987.

	Stable		Unstable	
Tree crown	1984 (%)	1987 (%)	1984 (%)	1987 (%)
Healthy	188 (64)	164 (58)	29 (25)	5 (4)
Unhealthy	83 (28)	95 (34)	55 (48)	57 (50)
Dead	24 (8)	24 (8)	30 (27)	52 (46)
Total	295	283*	114	114

*12 dead spars visible in 1984, not visible in 1987.

are evident in the age structure of all three stand classes, one from 50 to 70 years ago and the other from 90 to 110 years. Since recruitment peaks follow closely upon periods of high mortality (Wardle & Allen 1983) it is reasonable to assume extensive dieback occurred in the Kaweka Range around 1910–20 and 1870–80. In view of the well documented relationship between natural disturbance and stand mortality in mountain beech (Wardle 1970; Skipworth 1983; Grant 1984; Allen & Wardle 1985) the growth pattern of the single tree presented in Fig. 6 is of particular interest. The abrupt decline in growth around 1862 and equally dramatic recovery around 1870 is quite atypical of intraspecific competition, especially as it affects a young vigorous tree. It is not, however, atypical of a sustained period of environmental stress such as drought. The coincidence of this unusual growth period and the recruitment peak of 1870–80 is difficult to ignore. We suggest the event responsible for the growth decline in this particular tree was also responsible for extensive tree mortality leading to the 1870–80 recruitment peak.

The relationship between rainfall and tree growth supports Hosking & Hutcheson's (1986) finding of a strong association between low spring and summer rainfall, and depressed radial stem growth in hard beech. Circumstantial evidence has also been advanced to link periods of severe spring and summer drought with dieback of mature red beech (*Nothofagus fusca* (Hook. f.) Oerst.) (Hosking & Kershaw 1985). Evidence from studies of other hardwood species linking drought with reduced growth and dieback is extensive (Tobiessen & Buchbaum 1976; Hinckley et al. 1979; Tainter et al. 1983). Although the link between the 1870–80 recruitment peak and drought-induced dieback rests with the growth pattern of a single tree, a more direct link can be established for the 1910–20 recruitment peak. Grant (1984) examined drought and forest dieback in the Ruahine Range, south of the Kawekas, and documented abnormally high mortality shortly before 1917. He attributed the damage to an intense drought during 1914–15 which followed three already dry years. There is no doubt this widespread drought affected the Kaweka Range and is almost certainly linked to the 1910–20 recruitment peak.

It is our contention that forest decline in the Kaweka Range is a natural process primarily affecting mature and over-mature stands. Stands of mountain beech become predisposed to collapse after about 100 years. However, they may remain healthy for in excess of 150 years in the absence of a period of severe environmental stress, commonly drought, which appears necessary to initiate the process of stand decline and replacement.

Predisposed but healthy stands, characterised by high basal area (80 m^2 ha^{-1}), high stem density (1500 stems ha^{-1}), and with low mortality (<2% yr^{-1}) confined to small subcanopy trees, eventually enter the decline phase. A transition period of 10–20 years leads to the final stages of collapse, with a decline in both basal area (40 m^2 ha^{-1}) and stem density (500 stems ha^{-1}) and increased mortality (>6% yr^{-1}) affecting dominant canopy trees. During this period increased light at the forest floor encourages seedling advance to saplings and invasion by ferns and shrubs where litter and moss dominated in the past. Dense regrowth of saplings surrounding dead spars characterises the early growth stage of the new stand.

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