New Zealand Journal of Botany, 1986, Vol. 24 : 513–527
0028–825X/86/2404–0513$2.50/0

Etiology of forest dieback areas within the Kaimai Range, North Island, New Zealand

G. T. JANE
N.Z. Forest Service, P.O. Box 25022
Christchurch, New Zealand

T. G. A. GREEN
Department of Biological Sciences
University of Waikato
Private Bag, Hamilton, New Zealand

Abstract Severe forest decline exists in upland areas of the Kaimai Range, North Island, New Zealand. Stand structure of major affected vegetation types is described. As stand dominants are well represented in induced seral vegetation, the overall species composition of the upland forests is not likely to change following decline. Within the decline zone a considerable range of forest damage is found. Characteristic damage types are described including effects on seedling vigour, root system development, and shoot phenology. The decline appears to result from a sequence of natural phenomena. High fog occurrence coincides with the decline zone producing soil waterlogging and generally poor growth conditions. This predisposes the forests to periodic drought damage.

Keywords forest decline; forest dieback; soil waterlogging; symptoms; roots; stand structure; phenology; fog

INTRODUCTION

Jane & Green (1983a, b) discuss location and extent of forest mortality in the Kaimai Range but provide only a limited description of the nature of affected stands. World literature on forest pathology contains references to many similar problems usually called diseases of complex or unknown causes but includes few descriptions of symptoms or investigations into site ecology. Notable exceptions are descriptions of diebacks in Australia (Weste 1981), ohia dieback in Hawaii (Mueller-Dombois et al. 1981), and oak diebacks in southern Europe (Vajda 1951). These dieback syndromes show many resemblances to the current situation in the Kaimai Range. Diebacks are often referred to as diseases or mortality events, with the inference that a pathogen is probably involved. Manion (1981) makes the point that diebacks are the result of a sequence of often abiotic events and the term disease may be inappropriate.

Mortality in the Kaimai Range is concentrated above a critical altitude, which ranges from 550 m to 700 m a.s.l., dependent on locality, and which corresponds with the fog zone (Jane & Green 1983b). Mortality, therefore, may extend from semi-lowland tawa (*Beilschmiedia tawa*) forests to upland silver beech (*Nothofagus menziesii*) forests (Jane & Green 1983a) where it may occur on slopes of up to 35°. It affects a wide range of forest communities (including induced seral communities) and species. In order to understand further the nature of the problem, selected stands are described in detail together with some growth characteristics of predominant species.

METHODS

The principal study sites within the range at "Te Hunga", "Te Rere", and Te Aroha are described in Jane & Green (1983a) and shown in Fig. 1. Height intercept and distance measurements along line transects were used to compile vegetation profiles, details of which may be found in Jane (1983). Nomenclature follows Allan (1961) and Moore & Edgar (1970). Partial soil profile descriptions were made on at least five cores removed with a Dutch clay auger along profile transects to identify the main soil types as recognised in the earlier landslide study (Jane & Green 1983c). Soil profile descriptions were also made at a few soil pits to confirm characteristics determined by soil auger.

The main species studied were silver beech (*Nothofagus menziesii*), kamahi (*Weinmannia racemosa*), kaikawaka (*Libocedrus bidwillii*), quintinia (*Quintinia acutifolia*), and tawari (*Ixerba brexioides*). These are the principal dominants in upland forests. Bud break and leaf development were monitored through summer 1981–82 and 1982–83 on tagged branches. Sample trees on three study ridges were visited weekly or fortnightly in summer, and monthly during winter between September 1980 and March 1983. Records were made of leaf size, leaf number by age classes, and visible

---

Received 27 February 1985; accepted 24 April 1986

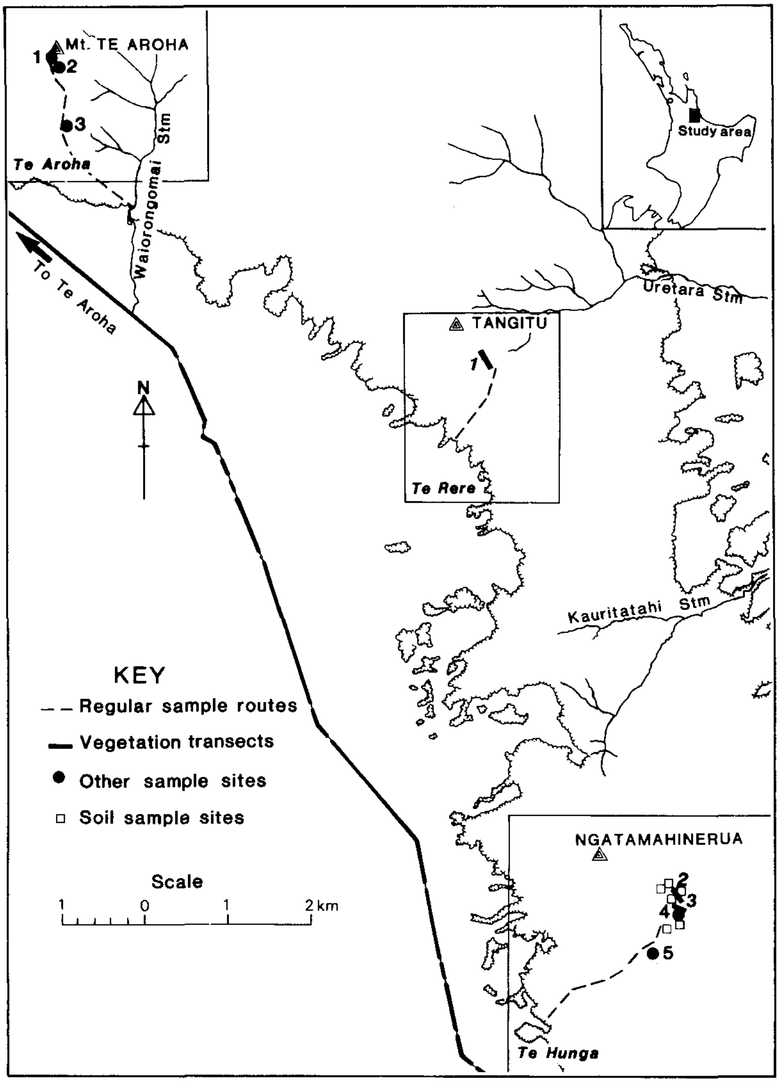

Fig. 1 Location of the study areas. Vegetation transects are numbered as in text as 1 — Te Rere; 2 — Silver beech (Te Hunga); 3 — Silver beech/kaikawaka (Te Hunga). Other sample sites are 1 — 950 m, 2 — 850 m, 3 — 850 m altitude sites at Te Aroha (Table 2); 4 — Poor site 800 m, Te Hunga, 5 — Good site, 750 m, Te Hunga (Table 4). Sites 3 and 4 are also used for Table 5. Soil sample sites (Table 1) at Te Hunga are unnumbered. Regular sample routes had soil moisture and temperature sites at 50 m or 100 m altitude intervals and were visited weekly or fortnightly.

damage on leaves. Leaf age was determined from observations on tagged branches and supplemented by estimation on other plants and older branches using leaf bud scars.

Root development patterns were examined on windfalls and excavated seedlings. Stumps up to 7 cm basal diameter were also forcibly uprooted along a track cut two years previously through poor sites on "Te Hunga" with typical peaty soils. Surface root distribution was mapped at a few localities and root/shoot ratios were determined on seedling material returned to the laboratory. Root growth activity was noted in soil samples collected at the weekly or fortnightly visit to study sites (Jane & Green 1983c).

RESULTS

Stand structure

Because subcanopy species frequently survive as canopy plants in the fog zone (Jane & Green 1983a, b, e), on what can be regarded as poor sites, mortality produces seral stands of *Melicytus ramiflorus* and *Hedycarya arborea* shrubland in tawa forests; dense horopito (*Pseudowintera axillaris*) or *Cyathea smithii* in tawari forests; and dense quintinia/kamahi shrubland in silver beech forests (Jane & Green 1983a). All forest types are characterised by a range of damage intensity resulting in unthrifty plants showing similar symptoms. Hence it will suffice to describe three localities in detail.

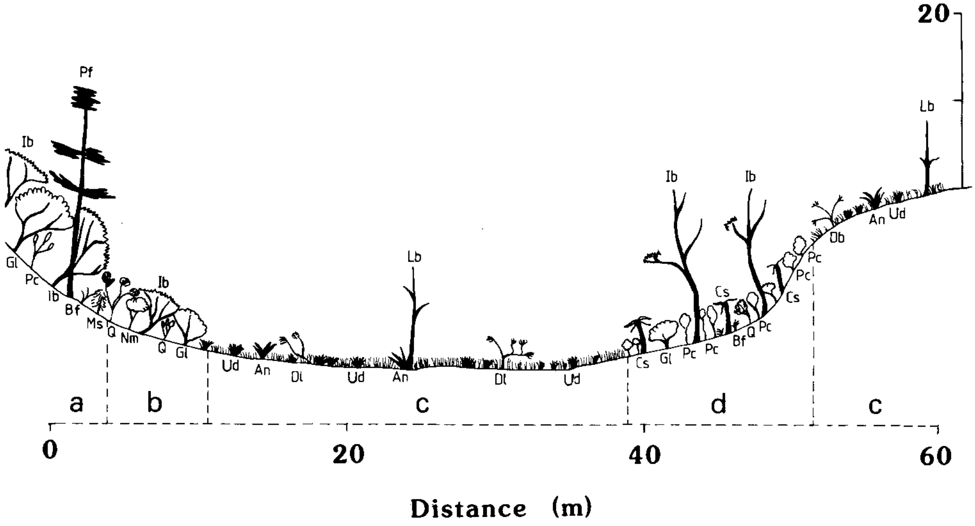

Fig. 2 Schematic cross-section of affected stands at Te Rere Bald. Bearing 160° from left to right; altitude 750 m. (a) mature tawari forest, (b) affected forest, (c) grassland, (d) recently affected forest. Symbols are Ib, tawari; Nm, silver beech; Pc, *Pseudowintera colorata*; Cs, *Cyathea smithii*; Pf, miro; Ud, *Uncinia distans*; An, *Astelia nervosa*; Gl, broadleaf; Dl, neinei; Q, quintinia; Ms, toro; Wr, kamahi; Cf, *Cyathodes fasciculata* ; Lb, kaikawaka; Bf, *Blechnum fluviatile*, Di, *Dacrydium intermedium*.

1. Tawari forest — "Te Rere" bald

At "Te Rere" bald two ages of mortality are evident on aerial photographs and, until recently, goats (*Capra hircus*) have prevented forest regeneration (Jane & Green 1983a). These age classes are shown along the first transect as scattered emergents over mature stands and low grassland and shrubland towards the end of the transect (Fig. 2). Vegetation types before dieback commenced were probably similar on the two pairs of sites (a) with (d), in slope areas protected from prevailing winds, and (b) with (c) on flatter areas.

Soils throughout the transect were yellow-brown loams about 1 m deep but were between 10 and 30 cm deep on the high knoll. Gleying was common and local podsols were present under silver beech.

(a) Mature forest

Tawari forms a dense canopy about 10 m tall with scattered emergent silver beech and miro (*Podocarpus ferrugineus*). Scattered horopito, quintinia, toro (*Myrsine salicina*), and *Cyathea smithii* form a poorly defined shrub tier at 2–3 m height which merges with a low shrub tier at 1–1.5 m containing abundant *Alseuosmia macrophylla* and scattered *Astelia solandri*. Ground cover is dense and contains a variety of ferns and sedges. *Gahnia* spp. and *Blechnum capense* are particularly abundant in more open areas.

(b) Older affected forest

Dead kaikawaka (*Libocedrus bidwillii*) and scattered miro, tawari, and silver beech of about 10 m height, with partially dead crowns, are present over a dense shrubland 2–4 m tall. The canopy comprises tawari, quintinia, toro, horopito, broadleaf (*Griselinia littoralis*), and *Coprosma foetidissima*. Quintinia or horopito from 1–2 m tall may form small dense stands in the general matrix. In more open areas a variety of ferns are present and *Astelia* spp. or *Gahnia* spp. may dominate. A well-defined boundary occurs at the grassland.

(c) Open grasslands

Grassland is dominated by *Uncinia distans*, *Heirochloe redolens*, and *Microlaena avenacea* up to 50 cm tall. Spars of kaikawaka ranging from 3–5 m tall are prominent and scattered, windblown neinei (*Dracophyllum latifolium* and *D. pyramidale*) reach 1–1.5 m. *Rubus cissoides*, seedlings of kamahi, quintinia, horopito, pate (*Schefflera digitata*) and many other species are present within grassland.

(d) Unthrifty tawari forest

A gradual transition to heavily damaged tawari forest occurs in areas protected from prevailing westerly winds. The canopy of old stands ranges from about 4 m tall in exposed areas to over 10 m in protected areas and contains dead and unthrifty tawari and miro. Shrubland emerges gradually out of grassland and reaches about 3 m high, 5 m from

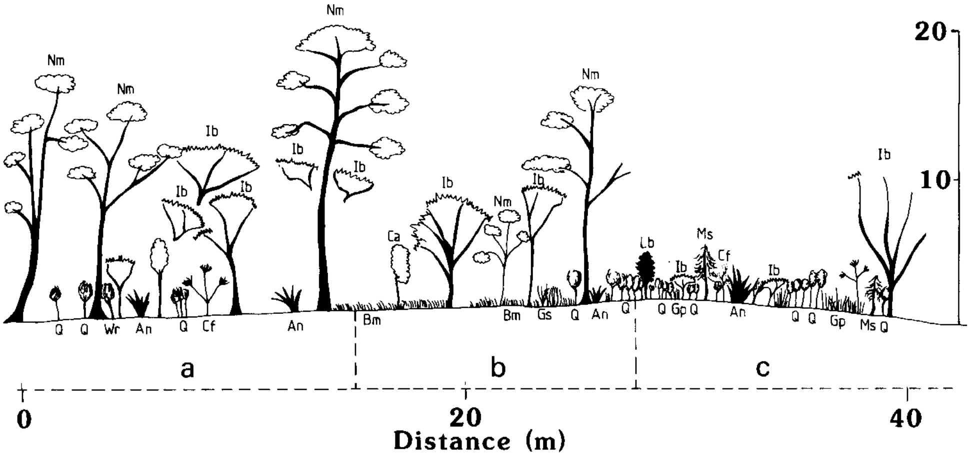

Fig. 3 Schematic cross-section of affected and unaffected silver beech stands at Te Hunga. Bearing 345° from left to right; altitude 850 m. (a) thrifty, (b) partial mortality, (c) seral stand. Abbreviations are as for Fig. 2, but add Am, *Alseuosmia macrophylla*; Bm, *Blechnum minus*; Ca, *Coprosma australis*; Gp, *Gahnia pauciflora.*

the margin. Horopito and *Cyathea smithii* form the main canopy but pate, *Coprosma australis, Hedycarya arborea, Rubus cissoides*, and *Melicytus ramiflorus* are locally common. All species show some signs of damage. Some ground ferns are present, particularly *Blechnum fluviatile.*

2. Mature silver beech — "Te Hunga"

Almost pure silver beech stands are widespread at "Te Hunga". Mature healthy stands often show a gradual transition to unthrifty stands through a zone of partial mortality (Fig. 3). Soils appear better drained in mature stands but localised podsols are common in a predominantly gleyed yellow-brown loam up to 1.5 m deep.

(a) Mature silver beech

The mature canopy of silver beech is about 25 m tall and somewhat open. Tawari, quintinia, miro, and small silver beech form a sparse subcanopy 12 m tall and a sparse ill-defined shrub tier at 2–3 m. This merges with a low shrub tier at 1–2 m height that includes *Cyathea smithii, Alseuosmia macrophylla, Coprosma australis, C. tenuifolia*, numerous sedges and ferns, and abundant bryophytes and liverworts.

(b) Open stand

Mature forests show a gradual transition to severely damaged forest. The canopy cover becomes more sparse and trees appear unthrifty, many have dead branches and broken crowns. Subcanopy tiers are also more open and ground cover is often dominated by dense *Gahnia pauciflora* or *Blechnum minus.*

(c) Seral shrubland

In open areas a dense shrubland dominated by quintinia, kamahi, tawari, and *Alseuosmia macrophylla* about 1.5–2.5 m tall prevails. Patches of *Gahnia pauciflora* are common and large clumps of *Astelia* spp. occupy canopy openings whereas *Sphagnum*, other mosses and liverworts fill wetter hollows.

3. Silver beech/kaikawaka — "Te Hunga"

Stands with a high proportion of tawari are common on flatter areas of "Te Hunga". They have a sharp boundary with unthrifty seral stands (Fig. 4).

Soils throughout this transect are waterlogged yellow-brown loams 1–1.5 m deep. For most of the year surface water appears more common in seral scrub. However this impression is false since the watertable is just as high in mature stands as shown by high soil moisture contents (Table 1) but is hidden by development of perched root systems. Windfallen silver beech often display localised podsols.

(a) Mature stand

Emergent kaikawaka, pink pine (*Dacrydium biforme*), and silver beech over shorter statured, subdominant tawari form a dense canopy about 15–20 m tall of elfin nature with no subcanopy. A sparse shrub tier at 2 m height contains seedlings of tawari, horopito, quintinia, kamahi, and toro. A dense carpet of *Schistochila* spp. with other liverworts and mosses frequently covers the ground. In canopy gaps *Pseudopanax colensoi, P. simplex*, toro, and tawari form prominent groups.

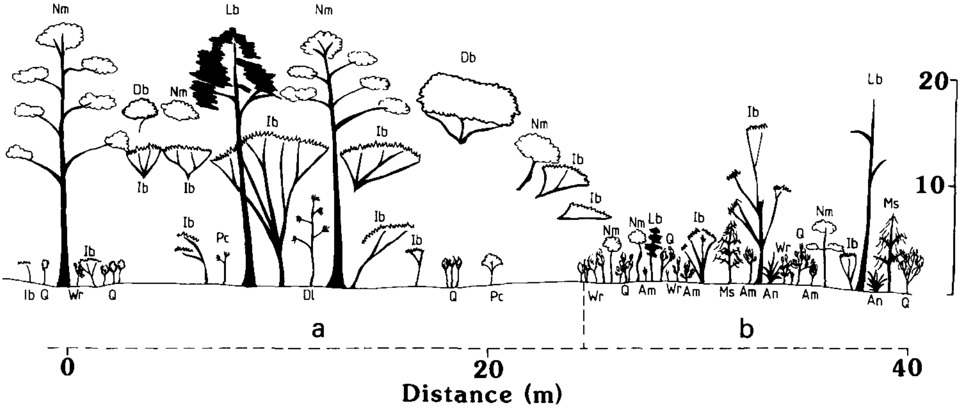

Fig. 4 Schematic profile of a silver beech/tawari stand at Te Hunga, bearing 285° from left to right, altitude 850 m. (a) thrifty mature stand, (b) unthrifty seral stand. Abbreviations as for Fig. 2 and Fig. 3 but add Db *Dacrydium biforme.*

Table 1 Soil moisture content and mid-morning temperatures of soils from pairs of thrifty closed mature stands and adjacent unthrifty seral stands at 850 m on Te Hunga taken on 15 Febuary 1982, at the end of 4 weeks without rain.

	Thifty closed mature		Unthrifty seral	
Stand type	moisture (%)	temperature (°C)	moisture (%)	temperature (°C)
Kaikawaka/tawari				
1	129.3	12.1	93.9	13.5
2	145.2	12.2	61.8	14.0
Mean	137.25	12.15	77.85	13.75
s.d.	11.24	0.07	22.70	0.35
Silver beech				
3	66.7	12.1	54.5	12.5
4	78.6	12.2	41.7	13.4
5	58.7	12.6	–	–
6	62.9	12.1	48.9	14.0
Mean	64.9	12.3	53.9	13.3
s.d.	6.5	0.4	8.5	0.3

– = no data.

Soil moisture content of specimens from 20 cm depth, oven dried at 105°C. Soil temperatures taken at 20 cm depth between 10 a.m. and 12 noon. Differences between groups are significant. For soil moisture content F = 70.3, for temperature F = 10.0. Of these groups, soil moisture contents in similar vegetation are different between thrifty and unthrifty stands at $P < 0.5$; and temperatures are similar for thrifty or unthrifty stands but differ between these groupings at $P < 0.05$.

(b) Seral shrubland

Mature forests give way with little transition to a dense shrubland 2–3 m high dominated by tawari, silver beech, quintinia, toro, *Coprosma dodonaeifolia*, and kaikawaka. Spars of kaikawaka and rare silver beech about 15 m tall may be present. A wide range of seedlings species are abundant; *Astelia* spp. and *Gahnia pauciflora* fill canopy gaps and *Sphagnum* and other mosses and liverworts fill wet hollows.

Stand dynamics

Surviving mature stands are perched at high points on the range crest in a zone of high fog occurrence. They provide some information on factors influencing stand stability and dynamics. Surviving stands have dense even canopies and soil water content is high (Fig. 5, Table 1). The closed stand structure (Fig. 5), maintains low soil temperatures (Table 1) and minimises evaporative losses, and may be important in maintaining stands. For this

Fig. 5 Structure of fully mature dense stand. Note lack of understorey and dense tawari canopy above. View is to the edge of the stand on the transect Fig. 4 and thus has back lighting.

reason, stands, particularly those of dense silver beech/kaikawaka, may have a high chance of complete collapse when mortality begins because mutually protective effects of stand structure are then lost.

Mature stands have abundant seedlings but saplings and poles are rare. In more open stands of silver beech, poles of canopy species are uncommon although seral species are present as long-lived shrubs, less than a metre in height. Goats have had a limited impact in these stands (Jane & Green 1983c), consequently lack of understory in dense stands is probably caused by low light intensities, but in more open beech stands (such as Transect 2a) reasons for a weak shrub tier are obscure. Seedlings are restricted to better aerated sites on old stumps and logs raised above the terrain.

Surviving trees are scattered and exposed, as a result, transpiration rates are probably high and trees are prone to wind clipping and windthrow. Redevelopment of stands following major damage commences from fresh seedlings since saplings are largely absent and changes in the environment of established seedlings may cause severe mortality in that tier. Partial stand breakdown has a similar effect since established seedlings apparently do not tolerate increased light intensities and water stress following the canopy breakdown.

Table 2 Comparison of leaf damage on silver beech shoots of current and previous years growth between sites 1–3 on Te Aroha on 24 January 1982.

	% leaves lost		Scorch	Necrotic spots (number/leaf)	
	Current	Previous	Current	Current	Previous
800 m Thrifty stand	nil	6	nil	13	5
950 m Thrifty stand	4	70	5	92	25
850 m Unthrifty stand	22	95	12	252	230

Counts made on 2 shoots from each of 5 plants from each site.

Composition of stands following disturbance does not change radically unless browsing mammals are present at damaging densities (as at "Te Rere", Fig. 2), since all the major species are present in seral stands. Seral stands contain silver beech, kaikawaka and tawari, dominants in unaffected stands, at densities above, or close to those in mature stands (Jane 1983). Providing mortality is low, this assures an adequate representation in mature forest. Conversely, seral species (horopito, quintinia, and kamahi) are present as understory plants or seedlings in mature stands and provide a nucleus for rapid colonisation following stand damage.

Broken canopy in unthrifty stands and presence of older emergent kaikawaka and silver beech indicate that damage may be repeated with differing intensities on the same site. Plants of slower growing, longer lived species of lesser susceptibility appear able to attain dominance after each period of mortality and before seral plants become reestablished. Gradual re-establishment of former forest structure is therefore achieved through preferential survival of the main canopy species during minor disturbances to form a new emergent tier.

Characteristic damage on shoots and leaves

At all localities thrifty plants of kamahi, toro, and quintinia appear to retain leaves for two years, and tawari or silver beech for about five years. Unthrifty plants shed old leaves not long after bud break and, in extreme cases, retain leaves for less than one year.

Thrifty forest and shrubland stands are quite dense and contain trees with leaves of normal size and show no evidence of reduced vigour. Unthrifty forest and shrubland stands contain scattered emergent gymnosperms and broadleaved trees which have many dead twigs and branches. In low stature, seral vegetation up to 3 m tall, saplings of kaikawaka and miro normally appear thrifty but broadleaved plants exhibit varying intensities of damage.

Damage to plants on poor sites can be one of the following characteristic types:

(1) Severely affected individuals have a straggly appearance since old leaves are shed rapidly, often just before or soon after bud break, and few leaves may be retained for more than one year. Damage of this type is typically found in silver beech. Many leaves were lost from the new shoots of silver beech within a few weeks of bud break in the 1981–82 summer (Table 2, Fig. 6). Similar heavy leaf fall occurs in red and hard beech (*Nothofagus fusca* and *N. truncata*) on Te Aroha. Small leaves with red blotches or necrotic spots are also a common feature of unthrifty silver beech in the study areas.

(2) Leaves have reduced size and branches have short internodes which concentrate current foliage at branch tips. Damage of this type is typical of unthrifty kamahi (Table 3, Fig. 6) and also occurs in five-finger and sometimes in tawari or neinei where it emphasises the usual growth form.

(3) Shoots from lower stems may have leaves of normal size (similar to that on thrifty plants in the same locality) and few red blotches, whereas shoots in the upper canopy show progressive reduction in internode length and leaf size, so that finally new growth cannot be initiated and a branch dies. Each summer, the first leaf on lower branches of a plant is of normal size but succeeding leaves are smaller. This can be seen when shoots from poor and good sites are compared (Fig. 6) and, more particularly, when leaves are dissected from a shoot (Fig. 7). This type of damage occurs in unthrifty quintinia, toro, and *Coprosma australis* on poor sites.

Some damage appeared to develop during leaf maturation. Scorch and necrotic spots were evident on new leaves of silver beech (Table 2), toro, and quintinia in all localities immediately after a period of foggy weather in January 1982 and 1983. Similar damage was not evident on tawari or kamahi. Scorch resulted in considerable loss of new leaves in silver beech before development was complete (Table 2) and left conspicuous damage on remaining leaves. During the period when damage

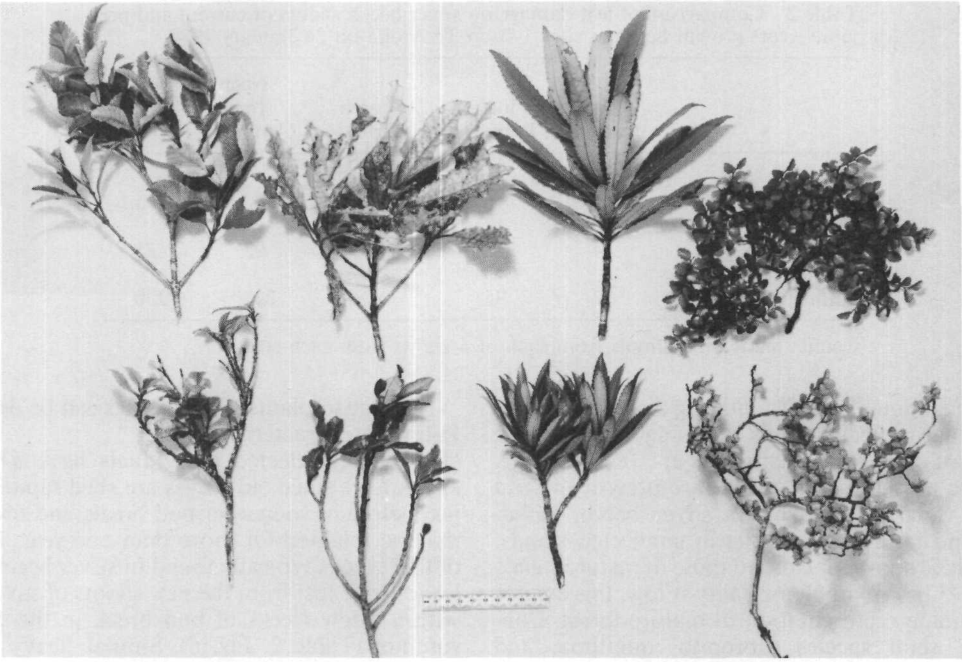

Fig. 6 Thrifty and unthrifty shoots of the main species. Upper row, thrifty shoots; lower row, unthrifty shoots from nearby sites. Species from left to right are: kamahi, quintinia, tawari, and silver beech.

Table 3 Leaf size, leaf number, and foliated length of shoots from a good and a poor site selected from the upper crowns of all plants. Values are the mean of counts on ten shoots of each species/site combination. Samples collected February 1982.

	Leaf length (cm)		Number of leaves old		Number of leaves current		Foliated length (cm)	
	poor	good	poor	good	poor	good	poor	good
Tawari	7.4	12.1	12.4	24.1	21.5	58.8	11.5	26.3
Kamahi	3.8	8.4	11.8	14.8	7.2	19.5	10.3	19.0
Quintinia	4.8	10.7	3.5	14.1	1.2	22.8	1.5	21.3
Silver beech	1.0	1.2	27.1	93.4	3.2	106.7	4.5	15.7
Toro	7.6	12.2	7.4	9.9	1.5	7.4	2.0	8.8

occurred leaf cuticle in many plants was glossy and in quintinia was also sticky to touch, compared with the scaly cuticle of mature leaves, suggesting that cuticular waxes were incompletely hardened.

Seedling vigour

In mature upland stands seedlings are often clustered around old stumps and on logs (Fig. 8). This probably indicates a better potential for survival above the wet soil surface in an aerated, but sodden, bryophyte cover. Seedlings present in poorly drained thrifty and unthrifty stands are often toppled by moss and liverwort epiphytes and become layered, producing a number of vertical shoots. These plants have reduced root systems (Fig. 9).

Fine roots are of strikingly different sizes in species studied (Fig. 9). Kamahi has thin fibrous roots concentrated close to the stem. Quintinia and silver beech have well developed fine roots of moderate size and tawari and kaikawaka have stout primary roots. Root systems on silver beech seedlings are well developed and roots are prolific on kaikawaka seedlings (Fig. 9). Root systems on all seedling specimens of tawari in both thrifty and unthrifty stands were much smaller than in the other species (Fig. 9) and when compared with the

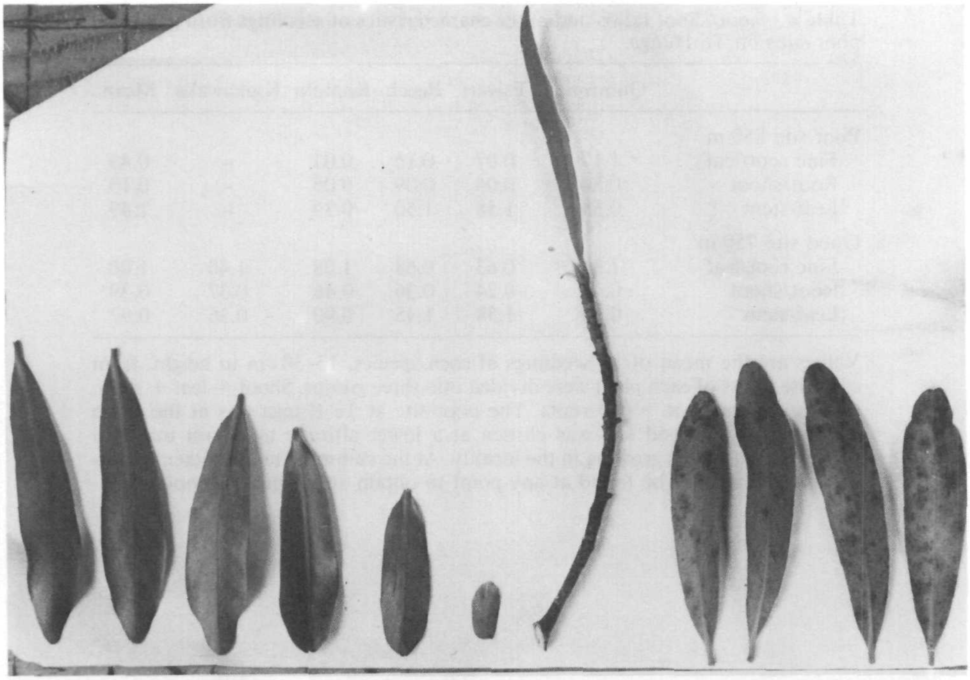

Fig. 7 Leaf size variation on a toro plant from a poor site through two growing seasons. The leaf on the left is the oldest and the smallest 'leaf' to the left of the shoot is a stipule which marks the beginning of the second year growth.

Fig. 8 Contorted root systems in an open stand. Root systems such as that to the left or bottom right suggest that seedlings originated on stumps or logs.

Table 4 Root/shoot ratios and other characteristics of seedlings from good and poor sites on Te Hunga.

	Quintinia	Tawari	Beech	Kamahi	Kaikawaka	Mean
Poor site 850 m						
Fine root/leaf	1.17	0.07	0.16	0.07	-	0.43
Root/shoot	0.36	0.04	0.09	0.05	-	0.15
Leaf/stem	0.58	1.58	1.50	0.39	-	1.49
Good site 750 m						
Fine root/leaf	1.34	0.63	0.68	1.08	1.40	1.00
Root/shoot	0.47	0.24	0.36	0.48	0.37	0.39
Leaf/stem	0.63	1.38	1.45	0.90	0.36	0.97

Values are the mean of 10 seedlings of each species, 15–30 cm in height, from each site. Parts of each plant were divided into three groups. Shoot = leaf + stem; and root = tap root + fine roots. The poor site at Te Hunga was at the range summit and the good site was chosen at a lower altitude to obtain maximal values for all species growing in the locality. At the summit site insufficient plants of kaikawaka could be found at any point to obtain an adequate sample.

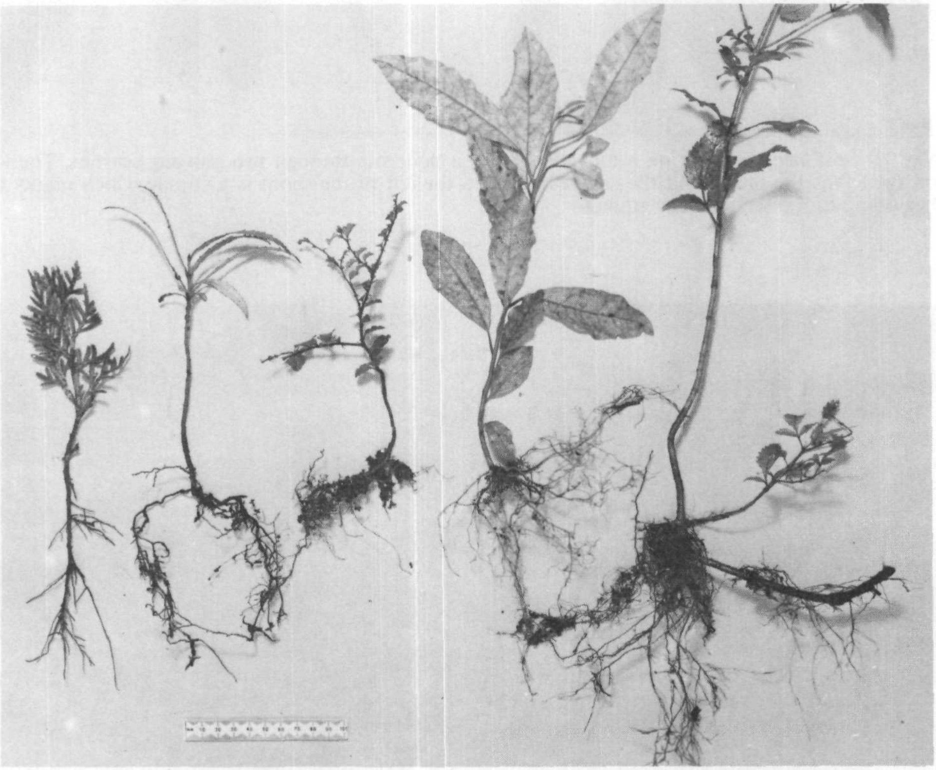

Fig. 9 Root systems of seedlings of the main study species. From left to right are: kaikawaka, tawari, silver beech, quintinia, and kamahi. Only a small part of the kaikawaka root system is shown. The kamahi plant has a strong coppice root to the right, which was cut when collected.

Table 5 Timing of the main bud break and leaf development during the summers of 1981–82 and 1982–83.

	Bud break		Fully developed		Fully hardened	
Summer	1981–82	1982–83	1981–82	1982–83	1981–82	1982–83
800 m Te Aroha						
Silver Beech	7/11/81	9/11/82	14/12/81	19/12/82	2/82	2/83
Tawari	20/11/81	19/11/82	14/2/81	2/83	3/82	3/83
Kamahi	20/11/81	29/9/82	7/11/81	19/12/82	progressive for season	
Quintinia	14/10/81	2/9/82	7/11/81	19/12/82	progressive for season	
Miro	12/12/81	19/12/82	19/1/82	19/1/83	3/82	3/83
800 m Te Hunga						
Silver beech	7/11/81	20/10/82	21/11/81	19/11/82	3/82	3/83
Tawari	29/11/81	19/11/82	14/2/82	10/1/83	2/82	3/83
Kamahi	14/10/81	29/9/82	7/1/81	19/12/82	progressive for season	
Quintinia	14/10/81	29/9/82	14/10/81	29/9/82	progressive for season	
Miro	9/12/81	19/12/82	14/1/82	19/1/83	2/82	3/83

other species appear to be inadequate to provide nutrients to the attached shoot.

Root/shoot ratios of seedlings at upper altitude sites were found to be low for all species except quintinia (Table 4), apparently a result of restricted root development coupled with heavily wooded stems carrying few leaves. However, in quintinia, high root/shoot and fine-root/leaf ratios were produced by woody shoots with few or small leaves and few fine roots in proportion to primary roots. These quintinia plants appeared to have died back from a more vigorous state and a balanced reduction in crown size and fine roots had occurred but not in the woody material of taproot and main stems. Disparity in leaf/shoot ratio of kamahi between good and poor sites resulted from differences in foliage vigour and consequent leaf size. This was readily seen when leaves of plants from the lower altitude site were compared with those from a good or poor plateau site (Fig. 6).

Root systems and patterns in mature plants of upland stands

Primary laterals of most species examined are confined to the top 2–5 cm of peaty soil. Root systems of tawari and silver beech trees are often at the soil surface and lenticels are frequent where roots are exposed. Trees and shrubs of kamahi, toro, and quintinia are more deeply rooted so that few surface or fine roots are present. However, basal swelling and enlarged lenticels are quite evident on lower stems. Conifer saplings are difficult to uproot and those of kaikawaka have deep, extensive root systems.

Stems of broadleaved species within seral stands are clumped, and excavation of saplings frequently shows that they have originated from prostrate stems which have produced fresh shoots in the deep bryophyte ground cover and upper peaty soil horizons. Older thrifty trees of mature stands are also clumped on raised mounds and logs which in some cases have rotted away to leave roots perched above the ground (Fig. 8). Between mounds, roots are sparse and soil pits or Dutch auger cores reveal few roots below the superficial layer. However, even in wetter areas, live roots of kaikawaka can be found near bedrock at depths of about 80 cm.

Phenology

Bud break typically begins in kamahi and quintinia in early October and a month later in tawari and silver beech at 500 m altitude sites (Green & Jane 1983b). In each species, bud break begins at the highest altitude about 4 weeks later. Bud break on adjacent trees of the same species at higher altitudes occurs over a period of several months and at least some trees may take advantage of delayed onset to put on increment in adverse years.

A large difference in bud break date at the same sites was noted between tawari and silver beech in both 1981–82 and 1982–83 (Table 5). On Te Aroha the flush on all trees occurred more or less uniformly and was completed by early December but at "Te Hunga", it was less well defined and for a few trees it occurred well into February. Delayed and irregular flush at "Te Hunga" appeared to be related to lower temperatures recorded during a 6 week period of wet and cloudy weather from mid-November 1981 to early January 1982 and cloudy weather in the summer 1982–83 (Jane & Green 1984) whereas Mt Te Aroha remained clear for much of this period.

The sequence of leaf production in the species studied partly explains the damage patterns characteristic of the species. Miro, toatoa (*Phyllocladus glaucus*), tawari, and silver beech produce a single whorl, or a short shoot of ten or more pairs of leaflets which develop within a short period and so there is no variation in leaf size within a shoot. Kamahi, toro, and quintinia produce single leaves or pairs of leaves throughout the season, and growth may be affected by varying environmental factors through the season and modified by the contrast between good and poor sites.

At Te Aroha leaf development and hardening in silver beech is rapid, but on Te Hunga it is slower particularly on poor sites. This makes the thin leaves particularly susceptible to adverse climatic conditions. Leaf maturation on vigorous plants of silver beech is followed by progressive elongation of leading shoots. Leaf development in tawari is much slower, so that elongation and maturation may not be complete until late February (Table 5). The slow leaf maturation in these thick leaves may moderate the adverse effects of climatic variations.

The main leaf fall of old leaves on poor sites at "Te Hunga" summit was observed in a wide range of species in January 1982 within two weeks of bud break, and before new leaves were mature. Spectacular leaf falls were observed on red beech at Te Aroha in both years. Here whole trees were denuded at bud break. Leaf fall in most species was not conspicuous at altitudes below 700 m in the study area. Tawari was the exception. Leaf fall in this species occurred in November 1982 and March 1983 following several weeks of dry weather.

New root growth began at different times in the two study years on both sites. New root growth began between February and March 1982 (early autumn), but was evident in all species and on all sites by January 1983 (early summer). The difference could have arisen from lower soil moisture contents following a dry winter and spring in 1982 as shown in soil moisture content change in associated projects (Jane & Green 1983d, Jane & Green 1984).

DISCUSSION

Distribution of vegetation damage

Manion (1981) has produced a general outline of decline syndromes in forests. Both biotic and abiotic factors may be involved but an important feature of the development of the syndrome is the sequence in which factors affect the forests. In particular, droughts are regarded as important inciting factors which precipitate a mortality event in forests that have already been predisposed by other site factors.

Examination of particular stands in the Kaimai Range showed that no consistent link is present between dieback areas and stand composition or structure. Dieback occurred on flat ground (Transect 3) or on slopes (Transect 1) and without any evidence of a change in species composition (Transect 2). Similarly, soils types vary between and within affected areas both in depth and type. Thus, on Transect 1, mortality occurs on soils both 1–1.5 m deep at the slope foot and soils 0.1–0.3 m deep on the knoll with a transition from more affected areas to areas now in grassland both on the slope and at the slope foot. It occurs on deep soils (Transect 3) and shallow soils (Transect 2). The main difference between transects lies in damage intensity. In tawari forests boundaries of affected areas are sharp whereas a buffer of partially affected vegetation is present in silver beech forest (Transect 2). Distinctness of damage boundaries is often a characteristic of drought-damaged areas.

Soil water content

Forests in the dieback zone appear to be sensitive to even slight water stress (Jane & Green 1985), a sensitivity which is almost certainly a consequence of reduced root systems in waterlogged soils. It is also in this zone that fog both increases precipitation and reduces evapotranspiration, making vegetation particularly sensitive to droughts.

Study of soil moisture content in waterlogged soils when drought was absent but during a relatively prolonged dry spell yielded limited information on soil moisture differences between thrifty and unthrifty stands (Table 1), probably because important differences are only evident at times of extreme water stress, during drought. However, longer-term data over two study years showed that upland soils in the fog zone are almost perpetually waterlogged but were below field capacity at lower altitudes (Jane & Green 1983c). The impact of soil waterlogging can be seen in growth characteristics of the species.

Marked reduction in leaf size, prominent lenticels, and basal swelling in seedlings of kamahi and quintinia are characteristic of plants undergoing, or adapted to, prolonged flooding or waterlogging and have been reported from many species (Hook et al. 1972, Kozlowski 1976, Coutts & Armstrong 1975, Bradford & Yang 1981, Kawase 1981). Large numbers of lenticels in tawari and silver beech and thin bark in kaikawaka are also important adaptations seen in other species growing under waterlogged conditions (Kozlowski 1982). In many species waterlogging may intensify symptoms of water stress (Kawase 1981), reduce overall vigour, reduce root/shoot ratios, and produce marked differences between adjacent trees because of minor site differences (Levitt 1972). All these features are noted in seral species such as quintinia, kamahi, and toro studied here.

General poor vigour and high susceptibility to water stress in kamahi and quintinia on upland sites

(Green & Jane 1983b) and intensification of symptoms in more foggy areas, as noted here, suggest a low tolerance to flooding or waterlogging. Kozlowski (1982) recognised a close link between waterlogging and water stress resulting from low rates of water transport from reduced root systems and poor root growth limited by anaerobic soil conditions. In physiological studies it was shown that there is a strong sensitivity to water stress in seral species at the height of a normal summer, as might be expected from plants undergoing waterlogging (Green & Jane 1983a, b; Jane & Green 1983e).

Two strategies to minimise the effects of waterlogging appear to be present. First, plants such as kaikawaka, show deep vigorous root growth because of tolerance to anaerobic conditions; and second, shallow rooted plants, such as silver beech and tawari, avoid anaerobic conditions. Seral species are deep rooted but intolerant of anaerobic conditions. This leads to poor root development in waterlogged soils and higher drought sensitivity. Dendrochronological data suggest that growth of these plants improves rapidly as watertables fall, in drier conditions, but is halted when watertables rise again (Jane 1983).

Although trees of mature stands are small (Transect 3) and appear to be young and vigorous, in fact, they are several hundred years old and slow growing. They are probably protected from severe water stress both by closed stand structure, with consequent cooler stand interior and reduced wind turbulences, and by location in areas of higher fog frequencies.

Role of fog

The altitudinal zone in which forest damage is found has been shown to coincide with the fog zone (Jane & Green 1983b). Fog would lead to lower light intensities and may reduce total carbon fixation to marginal levels and limited seedling survival in mature upland stands (Huber 1978, O'Rourke & Tejung 1981). It may also affect leaf development. Leaf damage and leaf fall, particularly on silver beech during spring, appeared to be related directly to long periods of foggy weather. Development of new leaves in fog forests also appeared to be completely halted particularly as noted in January 1982 and 1983 at "Te Hunga". Lowered temperatures and light levels slow leaf development and maturation (Kozlowski 1971), and may impair stomatal development (Brainerd & Fuchigami 1982). Prolonged fog and cloud followed by fine weather produces strongly contrasting environmental conditions (Leigh 1975). Fine hot days in January, exposing new leaves with unhardened cuticles to the full force of almost overhead midsummer sun, accentuates water stress (Green & Jane 1983b) and may cause scorch and leaf fall in thin leaves. Water stress has frequently been noted to cause leaf scorch and leaf fall in waterlogged plants (Pereira & Kozlowski 1977). Reduction in leaf size, observed in silver beech, kamahi, toro, and quintinia, is also similar to that resulting from water stress in plants growing on waterlogged soils (Pallardy 1981, Syvertsen 1982). Water stress similar to that noted in stomatal conductance (Jane & Green 1985) and water potential measurements in the study area (Green & Jane 1983b) may also trigger a major leaf fall as in other species under waterlogged conditions (Kozlowski 1971). Shoots of plants such as kamahi and quintinia, with damaged new leaves, have reduced photosynthate reserves (Green & Jane 1983a). There are also few leaves to sustain growth and produce further new leaves (Fig. 7). As a result, the shoot may show the observed decreasing leaf size through the season. Low soil temperatures in denser stands, as observed in 1981–82, may intensify damage by delaying root growth until after bud break (Tesky & Hinckley 1981) and could produce the reported root/shoot imbalance (Table 4).

Red beech, which is common only on Mt Te Aroha, serves as an example of severe fog impact in the study area. It occurs at 600–750 m a.s.l., below the fog zone, on Mt Te Aroha, the study area with lower fog frequencies (Jane & Green 1983d), and it was noted to suffer severe spring leaf fall. Red beech was not noted elsewhere in the Kaimai Range. It appears possible that high fog frequencies at the same altitude in other study areas at "Te Rere" and "Te Hunga" prevent its presence by affecting leaf growth and survival and reduces its competitive ability. Similarly, Elder (1965) notes that red beech is confined to areas with lower fog frequency in Ruahine Ranges.

CONCLUSIONS

The common factor linking dieback areas appears to be water stress. Forests in the mortality zone are sensitive to even slight water stress (Jane & Green 1985), almost certainly a consequence of reduced root systems in waterlogged soils. Increased precipitation and reduced evapotranspiration, consequences of high fog frequency, also make plants particularly sensitive to drought.

The role of soil moisture stress in mortality is well recognised but the association of dieback syndromes with soil/water problems is less commonly recognised. More often the dieback syndrome is first recognised as a pathological problem associated with root saprophytes and weak pathogens such as *Armillaria mellea* or *Phytophthora cinnamomi.*

Work by Newhook (1959), Podger et al. (1980), Weste (1981), and Helliwell (1983) and many others has gone far towards recognising the more complex ecological links in forest dieback syndromes.

A firm general framework for these syndromes, involving previous forest history, intricate ecological links between climate, soil moisture and disease, has been succinctly enunciated by Manion (1981). Both biotic and abiotic factors may be involved but the time sequence of their occurrence is very important. In particular, droughts are regarded as common inciting factors precipitating mortality events in forests already predisposed by other site factors.

The data, taken together, suggest that for forest mortality to occur in the Kaimai Range several conditions must coincide:

(1) There must be a high watertable producing waterlogging.

(2) There must be a slow fall in watertable, perhaps over several years (in widespread mortality episodes). During the early phase of a dry period plant growth may be vigorous, particularly in sensitive seral species.

(3) A subsequent rise in watertable produces soil flooding and waterlogging resulting in considerable root death in sensitive species, a consequent decline in vigour, and formation of maladjusted root systems.

(4) A further dry period will then produce severe water stress and widespread mortality.

Such a sequence would give rise to the widespread mortality which occurred in 1914–20 and 1940–48 and possibly 1807–1814 (Jane 1983). A shorter sequence of dry years would cause mortality in sensitive seral species and produce the symptoms already outlined for unthrifty plants.

ACKNOWLEDGMENTS

The authors particularly wish to thank the referees for constructive comment. Thanks are also due to R. Julian the photographer and Mrs D. Whitehead the draughtswomen. Dr T. G. A. Green received support from the University Grants Committee for equipment purchase.

REFERENCES

Allan, H. 1961: Flora of New Zealand Volume I. Wellington, Government Printer.

Allen, R. B.; McLennan, M. C. 1983: Vegetation assessment. Part I. Forest vegetation. *New Zealand Forest Service, Forest Research Institute, bulletin 83.*

Bradford, K. J.; Yang, S. M. 1981: Physiological responses to waterlogging. *Horticultural science 16*: 3–8.

Brainerd, K. E.; Fuchigami, L. H. 1982: Stomatal functioning of *in vitro* and greenhouse apple leaves in darkness, mannitol, ABA and CO_2. *Journal of experimental botany 33*: 389–392.

Coutts, M. P.; Armstrong, W. 1975: Role of oxygen transport in the tolerance of trees to waterlogging. *In*: Tree physiology and yield improvement. Cannell, M. G. R.; Last, F. T. *ed.*, Academic Press. Pp. 361–386.

Elder, N. L. 1965: Vegetation of the Ruahine Range. An introduction. *Transactions of the Royal Society of New Zealand 2*: 1–37.

Green, T. G. A.; Jane, G. T. 1983a: Changes in osmotic potential during bud break and leaf development of *Nothofagus menziesii, Weinmannia racemosa, Quintinia acutifolia* and *Ixerba brexioides. New Zealand journal of botany 21*: 391–395.

——— 1983b: Diurnal patterns of water potential in the evergreen cloud forests of the Kaimai ranges, North Island, New Zealand. *New Zealand journal of botany 21*: 379–389.

Grace, J. 1981: Plant response to wind. *In*: Plants and their atmospheric environment. Grace, J.; Ford, E. D. *ed.*; Jarvis.

Helliwell, D. R. 1983: Tree growth and changes in soil moisture — 1. Effects of changing water levels in the soil. *Arboricultural journal 7*: 93–100.

Hook, D. D. C.; Brown, C. L.; Wetmore, R. H. 1972: Aeration in trees. *Botanical grazette 133*: 443–454.

Huber, O. 1978: Light compensation point of vascular plants of a tropical cloud forest and an ecological interpretation. *Photosynthetica 12*: 382–390.

Jane, G. T. 1982: Constant count — a solution to problems of quadrat size. *New Zealand journal of ecology 5*: 151–152.

——— 1983: Vegetation mortality in the Kaimai Ranges, North Island, New Zealand. D. Phil. thesis, University of Waikato.

Jane, G. T.; Green, T. G. A. 1983a: Episodic forest mortality in the Kaimai Ranges, North Island New Zealand. *New Zealand journal of botany 21*: 21–31.

——— 1983b: Vegetation mortality in the Kaimai Ranges, North Island, New Zealand. *Pacific science 37*: 385–389.

——— 1983c: Biotic influences on landslide occurrence in the Kaimai Range. *New Zealand journal of geology and geophysics 26*: 381–393.

——— 1983d: Morphology and incidence of landslides in the Kaimai Range. *New Zealand journal of geology and geophysics 26*: 71–84.

——— 1983e: Utilisation of pressure-volume techniques and non-linear least squares analysis to investigate site induced stresses in evergreen trees. *Oecologia 57*: 380–390.

——— 1984: Ecological aspects of climate patterns within the Kaimai ranges, North Island, New Zealand. *New Zealand journal of ecology 7*: 183–196.

——— 1985: Patterns of stomatal conductance in six evergreen tree species from a New Zealand cloud forest. *Botanical gazette 146* : 413–420.

Kawase, M. 1981: Anatomical and morphological adaptation of plants to waterlogging. *Horticultural science 16*: 30–34.

Kozlowski, T. T. 1971: Growth and development of trees. I. Seed germination, ontogeny, and shoot growth. Academic Press. Pp. 260–263.

——— 1976: Water supply and leaf shedding. *In*: Water deficits and plant growth. Kozlowski, T. T. *ed.*, Academic Press. Pp. 191–231.

——— 1982: Water supply and tree growth. Part II. Flooding. *Forest abstracts 43*: 145–161.

Leigh, E. G. 1975: Structure and climate in tropical rain forest. *Annual review of ecology and systematics 6*: 67–86.

Levitt, J. 1972: Responses of plants to environmental stresses. Academic Press.

Manion, P. D. 1981: Tree disease concepts. Prentice Hall.

Moore, L.; Edgar, E. 1970: Flora of New Zealand. Volume II. Wellington, Government Printer.

Mueller-Dombois, D.; Jacobi, J. D.; Cooray, R. G.; Balakrishnan N. 1981: Ohia rain forest study: Ecological investigations of the dieback problem in Hawaii. College of Tropical Agriculture and Human Resources, Hawaii Agricultural Experiment Station, Botany Department University of Hawaii, miscellaneous publication 183.

Newhook, F. J. 1959: The association of *Phytophthora* spp. with mortality of *Pinus radiata* and other conifers. I. Symptoms and epidemiology in shelter belts. *New Zealand journal of agricultural research 2*: 808–843.

O'Rourke, P. A.; Terjung, W. H. 1981: Total stand leaf net photosynthetic rates affected by cloud types and amounts. *Photosynthetica 15*: 504–510.

Pallardy, S. G. 1981: Closely related woody plants. *In*: Water deficits and plant growth. Kozlowski, T. T., *ed.*, Academic Press. Pp. 511–543.

Pereira, J. S.; Kozlowski, T. T. 1977: Influence of light intensity, temperature, and leaf temperature on stomatal aperture and water potential of woody plants. *Canadian journal of forest research 7*: 145–153.

Podger, F. D.; Kile, G. A.; Bird, T.; Turnbull, C. R. A.; McLeod, D. E. 1980: An unexplained decline in some forests of *Eucalyptus obliqua* and *E. regnans* in southern Tasmania. *Australian forest research 10*: 53–70.

Syvertsen, J. P. 1982: Minimum leaf water potential and stomatal closure in citrus leaves of different ages. *Annals of botany 49*: 827–834.

Teskey, R. O.; Hinckley, T. H. 1981: Influence of temperature and water potential on root growth of white oak. *Physiologia plantarum 52*: 363–369.

Vajda, Z. 1952: Uzroci epidemijskog ugibanja brijetova. *Glasnik za sumske pokuse 10*: 105–197.

Weste, G. 1981: Changes in the vegetation of sclerophyll shrubby woodland associated with the invasion by *Phytophthora cinnimomi*. *Australian journal of botany 29*: 261–276.