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# MORTALITY OF NATIVE FOREST VEGETATION IN THE KAIMAI RANGES

by

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Summit of Te Hunga looking northwards towards Ngatamahinerua the highest point. Study sites lies at the narrowest point of the foreground and a study ridge to the right. Foreground is healthy silver beech forest soon giving way to a scattered overwood mainly of silver beech over seral shrubland stretching to the horizon. Landslides just visible on the steep faces to the right. Pink pine stands show as dark areas near the edge of the plateau to the right and on the main skyline ridge to the right an almost intact silver beech stand is present. Photo taken in early March and yellow-green of the silver beech indicates that the foliage is still incompletely hardened.

# MORTALITY OF NATIVE FOREST VEGETATION IN THE KAIMAI RANGES.

Vegetation mortality has been evident in the Kaimai Ranges, North Island, New Zealand for at least 40 years and affects a wide range of species and forest types. The mortality occurs above 550 m altitude and on each prominence has a lower limit which corresponds closely with the predominant cloud zone in each area. The severity of the damage ranges from complete mortality of canopy species to a light mosaic of killed trees. On individual trees damage may be evident as leader dieback reduced leaf size, and other symptoms suggestive of waterlogging.

Mortality appears to be episodic and several age classes can be distinguished by vegetation height. Recent mortality can be reliably dated to droughts in 1972 and 1946 but forest age class structure suggests a number of earlier dates for similar episodes including 1656, 1804, 1861 and 1914. Many species do not survive for more than a portion of their potential life spans. Seral species do not reach their potential stature and minor droughts appear to trigger mortality releasing the more permanent species.

The distinct topographic and altitudinal bounds of the mortality and dendroclimatic analyses of mortality episodes suggested a strong direct drought effect. It was proposed that since the fog zone soil is frequently waterlogged, root systems would be restricted, and plants poorly able to respond to water stress. These proposals led to a series of investigations into plant water relations.

An empirical model of pressure-volume curves was developed. Simple manipulation of the coefficients of the the resultant function, provides estimates of osmotic potential and symplastic water content, and permits precise calculation of the bulk modulus of elasticity and turgor loss point. Osmotic potential was determined independently from freezing

point depression measurement on leaf exudates and similar values were found. The bulk modulus of elasticity and the coefficient of elasticity are closely linked and variations in the pressure potential at the turgor loss point, was closely correlated with osmotic potential.

During the summer 1981/2 water potential and stomatal aperture were monitored at a number of localities inside and outside the fog zone. Within the fog zone dawn water potentials remained high and were close to full turgor when overnight fog was present. Midday values generally compare with those published for plants of streamsides and wet habitats. Afternoon recovery was normally evident in all species except Quintinia acutifolia which was the least healthy of the species studied.

Stomatal conductances in the seral species were high and those for the canopy species near usual values found in hardwood trees. Diurnal stomatal conductance patterns changed as the season progressed and late in the season closure often began before midday. Rapid closure at moderate temperatures appeared to be related to high vapour pressure deficit and generally minimised internal water stress.

Fog lowers temperatures and light levels, for long intervals during the spring before and during budbreak slowing leaf development and maturation, and impairing stomatal development causing leaf scorch and leaf fall in fine weather. This results in part, from increased osmotic potential.

Ranking of the species using the variability of the tisssue water relations parameters indicates the presence of two distinct survival strategies; stress avoidance and stress tolerance. Similarly the effects of waterlogging could be avoided or tolerated and two canopy species (tawari and silver beech) appear to adopt opposing physiological and morphological strategies whereas the seral species maximise growth and are poorly adapted and intolerant of site induced stress.

Knowledge of the water relations of the cloud forest species provides a new perspective that allows a better understanding of the structure and function of the forests. The evidence suggests that in spite of the very wet environment, features of the cloud forest plants result from water stress. Evidence of adaptation to water stress supports the general hypothesis that drought is a significant factor in forest mortality within the Kaimai Ranges.

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# *CHAPTER 1.*

## INTRODUCTION

Many studies of forest mortality have shown a long problem history either because of number of discrete recurrences or a protracted disease. In many parts of the world there a historical record extending many hundreds of years to draw on to examine this question but in New Zealand European exploration and colonisation began in earnest scarcely 140 years ago and the historical record is even shorter.

Colonisation by the Maori began perhaps 1000 years ago and in many areas shifting cultivations and wanton fires have modified the original forests (Cumberland 1964). The Kaimai Ranges may have provided limited food resources but there is little evidence for Maori occupation within the forested areas and the vegetation may have remained in a primaeval state until European arrival. "Development" of the country has led to massive changes to the landscape and it is often difficult to distinguish man-made from natural disturbances. The Kaimai Ranges have not escaped considerable modification from mining, clearance for farms and associated communications, and browsing damage by introduced terrestrial and arborescent herbivores. Study areas were identified which minimised or recognised the extent of forest modification and investigations of distribution of the problem areas attempted to distinguish changes made by man and introduced animals.

### General history of exploration and exploitation

There is only a very poor historical record of landscape and vegetation changes within the Kaimai Ranges. This is probably a consequence of the relationship between the area and the lines of communication both in Maori and early European times. The ranges posed a formidable barrier between the Hauraki Plains and the Bay of Plenty and in the west the swamps, containing three rivers which drained northwards, further constrained pathways so that the main routes were north-south, parallel with the ranges and between the rivers (Vennell 1976, District Jubillee Committee 1930). Good routes led round the swamps through the Ohinemuri Gorge to the north or across the Whakamarama Plateau to the south. The southern route, via the Wairere Falls, was well known to the early missionaries (Brown 1838-50) but two other routes are known, the Tuahu and Thompsons Tracks. Bidwell (1841) describes a traverse of the ranges along the Maorioro Track which is now Thompsons Track. Brown (1838-50) made frequent journeys on the Tui or Wairere Track from Tauranga to Waharoa (then Matamata) and one via the Maorioro Track to Katikati.

Many early explorers including Williams (1836), Wade (1838),Dieffenback (1843), Lady Martin (1846), Hochstetter (1859), McKay (1865) and Mair (1866) traversed the region but usually passed to the south of the study areas via the Wairere falls (Matheson 1975) and leave no account of the flora or vegetation. Adams (1884) spent several days on Mt. Te Aroha and provides the first detailed account of the flora. He journeyed via the Waitawheta River from Waihi and onwards via the Waiorongomai River and Tuahu Track giving a detailed species list and a few notes on the vegetation of the Te Aroha summit and other points of interest.

Gold was discovered at Te Aroha in 1868 and near Thompsons Track at Mt. Elisa in 1895 (Bush 1975). An extensive tramway system was developed from about 1883 to mine the Buck Reef which extends the length of the the Waiorongomai valley. Tracks were established to link with the main mining areas on the north of the mountain in the Tui Stream and other mining areas in the Waitawheta valley and at Waihi to the north east. Mining records report extraction of silver beech for mine props. Clearances for camps, mining exploration and from wild fires occurred over much of Mt. Te Aroha and adjacent parts of the main range. A power line was cut across the range on the northern catchment boundary of the Pomihi Stream about 1914 to provide power for the mines at Waihi and its path was regularly burnt and cleared until about 1929. Mining activities continued sporadically until 1973, but many sites were abandoned by 1910.

Cadastral survey field notes often provide a useful record of original vegetation but, although the first survey began about 1877 and was completed by 1884, the field notes have been lost or destroyed (Clime 1969). In the central part of the ranges two attempts were made to establish a highway to Katikati. The Tuahu Track was developed between 1880 and 1885 but by 1900 had to be abandoned due to general slope instability (Matheson 1975). In 1885 work was begun on Thompsons Track and although it was completed by 1900 (Stokes 1980) disagreements between the Tauranga and Piako counties prevented full development and it was largely abandoned by 1923 (Vennell 1976). However the track was frequently used as a stock route with the result that there is a wide band of cleared forest stretching to the range crest at this point on the western side and feral cattle were common in the area until about 1965.

The main tracts were reserved as State Forest or Scenic Reserve between 1895 and 1923 (New Zealand Forest Service 1965) to control logging and mineral exploitation but there is little record of activities within the main part of the ranges. Logging of the major kauri forest resources began about 1890 in the Waitawheta Valley and later extended to the Uretara (Wharawhara) catchment of the Te Rere study area and other points to the north east of the study areas. Small lowland stands of kauri were logged only a few tens of metres from the river near the mouth of the Uretara valley (Henderson and Bartrum 1913) but extensive stands were logged at Cashmores clearing, a plateau at the northern end of the Te Rere study area at 650 m altitude. After logging much of the damaged forest was burnt in preparation for farm development, then abandoned. Logging was completed in the Te Rere study area about 1909 (Young pers. comm).

Farm development along the western flank of the ranges was rapid and resulted in extensive swamp drainage by 1900 (Vennell et al. 1951). Many fires from these developments spread deep into the forests and at Thompsons and the Tuahu Tracks clearing extended to the range crest (Drummond 1964). Early settlers used goats for weed control but they also provided milk at mining and logging camps. When the bush camps were abandoned goats were often left behind and this resulted in the establishment of feral herds. During the 1940's the herds were very large and widespread (Pracy et al 1975). Possums were released in 1914 and at several later dates (Pracy 1974, Jane and Green 1983b) to serve as a basis for a fur industry, but spread has been slow. Red Deer were liberated at the Tuapiro Stream probably in 1912 but numbers are very low (Dale and James 1977). Introduced mammals have caused considerable damage in the lowland forests but the upland forests offer a wet inhospitable environment and numbers have often remained low (Jane and Green 1983a, Green and Jane 1983).

## Recognition of the Problem and links with increased erosion

In the early days the Waihou River was a navigable waterway as far south as Matamata, and Te Aroha and Paeroa were important coastal ports. Concern over silting in the navigable parts of the Waihou system below Te Aroha, arising from drainage of the huge swamps and the waste from mining on the Ohinemuri River, became acute about 1907 (Goldfields and Mines Committee 1907, Goldfields and Mines Committee 1910, Henderson and Bartrum 1913). A Commission of enquiry led to the establishment of

Drainage Boards for swampland development and began a long period of stopbank and river control work on the Waihou River (Harris 1975, Tye 1975). Currently six main water supply catchments in the ranges supply Paeroa, Te Aroha, Katikati, Matamata, Morinsville, and many other smaller communities and concern over catchment condition led to a high national priority for animal control when hunting began in 1948. Severe storms in 1954, 1960 and in the ensuing decade scarred the landscape with numerous fresh landslides (Harris 1975, Jane and Green 1983b) and intensified interest in the vegetation health. Initial investigations concluded that browsing damage by introduced animals were responsible for the sudden increase in erosion. Dale and James (1977) clearly linked the landslides with areas of severe vegetation mortality and blamed the damage on the progressive southward colonisation of the ranges by possums. Further detailed investigations of the landslides suggested that the erosion was largely the result of natural processes (Jane and Green 1983a) and led to proposals that the increased erosion resulted from drought induced vegetation mortality.

## Scope of the investigations

Investigations into the nature of the mortality, its principal causes and the pattern of recurrence formed the basis of the current study. The study grew out of the debate surrounding the role of introduced animals in producing the marked increase in erosion and led to recognition of the role of frequent cloud in determining composition and change in the upland forests.

Investigations have proceeded along three lines:

Firstly an initial phase of delineation and mapping of the problem areas, and description of the nature of the vegetation to establish pattern in the mortality.

Secondly an investigation of the responses a few key species to water stress.

And thirdly and investigation of forest age structure and past climatic influences to establish the historical patterns of disturbance in the ranges.

The area is one of the few cloud forests studied in any detail and is of particular interest as it is an example of cloud forest in a temperate region. The gradation in rainfall along the ranges and variation in summit height provides a good environmental contrast within a short distance and the steepness of the ranges especially on the western side accentuates the environmental gradient. As a result differences between regions of the ranges can be readily seen and traversed in a short distance. These factors have been particularly valuable in determining the effects of fog since there is a a doubling in rainfall and opposed by 20 % increase in altitude.

The region has a diversity of species and a number of tropical northern elements or sub-antarctic species are at or near their distributional limits. Unique associations of these two components, such as the *Agathis australis* /*Nothofagus menziesii* stands, occur at a number of localities. In the cloud forests themselves the association of sub-tropical *Ixerba brexioides* with sub-antarctic *Nothofagus menziesii* provides a contrast in habitat adaptation between cloud and cold forest species and study of these species has shown very different responses to water stress and site waterlogging. The large contrasts in environmental conditions experienced by the plants between foggy and fine days or periods of prolonged waterlogging and followed by drought result in periods of high water stress and may lead to widespread mortality. Few species tolerate these extremes, consequently the upland cloud forests appear to be very unstable with few species surviving for more than a portion of the expected life span.

## Study Region

The Kaimai Ranges lie at approximately latitude 37° 30 'S and longitude 175° 45' E, in the North Island, New Zealand (Fig. 2.1). They are generally recognised as encompassing the hills between the Ohinemuri Gorge on State Highway 25 in the north and State Highway 29 linking Matamata and Tauranga in the south. To the west, the ranges are bounded by the Waihou River and Hauraki Plains close to sea level. To the east are the lowlands of the Bay of Plenty. The ranges, although very broken and with high points up to 950 m altitude, cannot be regarded as mountainous and the summits are well below the local tree line estimated at 1500 m. Most of the forested land forms part of the Kaimai-Mamaku State Forest Park (New Zealand Forest Service 1976). The area is relatively compact and lies within a region containing a good network of roads and tracks so that few parts of the ranges lie more distant than two or three hours walk. Within the ranges tracking and hut building since 1975 to facilitate removal of the goat population and recreational pursuits has produced easy access to most points in a very rugged area clothed in dense forest.

### Study sites

During the course of the project a number of localities were investigated and three sites (Te Aroha, Te Rere and Te Hunga, Fig. 2.1) were initially utilised. Initial selection of the study areas was governed by the distribution of areas of severe erosion but later, the need for areas free from anthropogenic influences and with good access and accomodation determined their utilisation. The road to the summit of Mt. Te Aroha provided good access but vegetation near the summit was severely affected by roading, mining and introduced animals. Two major study ridges were selected because the lower fog frequencies and higher cloud base however provide a useful contrast to the other two study

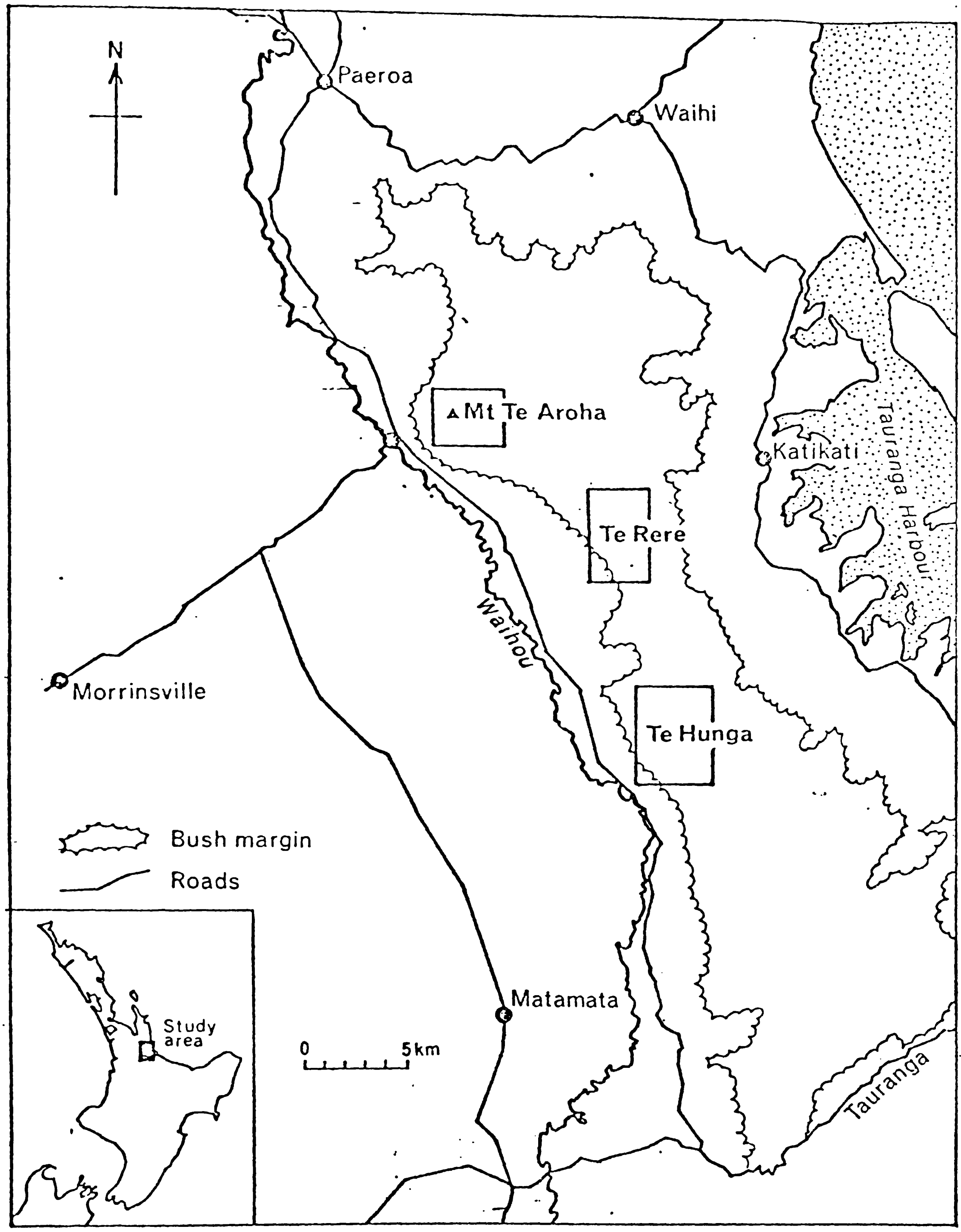


Fig. 2.1 Location of study areas.

areas. Studies in the Te Rere area were restricted because of poor access, a limited number of species and probable severe animal impact although initially the area provided good evidence for the effects of fog zonation. Only one study ridge was selected for meteorological stations and vegetation descriptions. The Te Hunga study area had a low level of anthropogenic influence although recent tracks and a good hut location near a wide range of site types proved crucial in selection of this area as the study main site. The forests remain largely unmodified by introduced animals and provide the complete altitudinal sequence within a short horizontal distance. Two main study ridges were utilised and a number of stands were studied in detail. The value of the many individual sites differed among the studies and details of important sites are described in the respective chapters.

## Geology and Soils

The ranges are composed almost entirely of Miocene andesites and dacites overlain to the south by younger ignimbrites. Three regions can be distinguished. In the south, the Waiteariki ignimbrites extend from Mamaku and Rotorua across Whakamarama Plateau to reach their northern limit just south of Te Hunga area (Healy et al. 1964). Underlying the study areas in the centre of the ranges are thick sequences of andesitic and dacitic lava and laharic breccias. To the north of the study areas, in the Waitawheta River and adjacent catchments is a complex volcanic centre (Schofield 1967) where intrusive ore bearing deposits are common and may contain sulphides of lead, zinc, copper, and arsenic as well as gold and silver (Weissberg and Wodzicki 1969). The Okauia fault system, which has a vertical displacement of over 800 m, bounds the western fall of the ranges. Lava bluffs are common on the steep western scarp but, to the east the range falls away more gradually. Both sides of the range are deeply dissected by young streams in which cascades and waterfalls are frequent because of the hardness of the underlying bedrock and shallow regolith.

Volcanic ash (Waihi or Hamilton) is a major soil parent material (Vucetich and Pullar 1969), but may also be mixed with, or dominated by, materials derived from the underlying andesitic and dacitic rock. More recent pumiceous ash from the Mangaone, Kaharoa, or Taupo eruptions (Pullar and Birrell 1973) is also present as a fine, white sand distributed throughout the A horizon. The bedrock andesites and dacites give rise to a predominance of kaolin, cristobalite, and metahalloysite (Wilson 1980) which produce massive clays. The ash-derived soils, on the other hand, commonly have a high allophane content (Birrell et al. 1977) and consequent high phosphate retention. Soils are very low in phosphates and bases (Jane and Green 1983a) but there is no visual evidence of nutrient deficiency in the plants.

On Mt Te Aroha granular brown loams form an altitudinal sequence (Wilson 1980) and to the south, in the Te Rere and Te Hunga study areas, ash derived soils predominate and form typical yellow brown loams (Jane and Green 1983a). At lower altitudes these appear similar to the Te Tuhi or Waihi soils, but at higher altitudes there is a strong intermixing of ash- and lava-derived parent materials which gives rise to soils of intermediate character. At the upland sites, gleying is common, but under Nothofagus stands a distinctive podsol is usually present.

## Climate

The climate is described in detail in a separate chapter (Ch. 5) but the salient features are described below. The Kaimai Ranges, form a prominent montane barrier between the Waikato and Bay of Plenty climatic regions. To the east, exemplified by Waihi, there are strong coastal and north-easterly influences (De Lisle 1967) whereas to the west there is a dominant westerly influence (Maunder 1973). The lowland climate is warm sub-humid with a mean temperature of about 15 °C and rainfall of 1500-2000 mm/a and is well dispersed through the year (Cox 1968).

Rainfall in upland areas ranges from 2000 mm/a at Mt. Te Aroha to 3000 mm/a at Te Rere and Te Hunga. Fog and low cloud is of frequent occurrence (Martin 1889, Clayton-Greene 1976). Cloud base is a lower and daily cloud duration is greater at Te Rere and Te Hunga than on Mt. Te Aroha (Jane and Green 1983b). Temperatures are moderate and rarely exceed 20 °C although in winter they are often close to freezing (New Zealand Meteorological Service pers. comm.). Precipitation greatly exceeds evapotranspiration in most years, and the soils are often waterlogged over considerable periods, perhaps years at a time.

## Vegetation

The vegetation of the ranges has been mapped by Nichols (1965, 1974) and described by Dale and James (1977). Detailed local studies were made by Stengs (1978), and Bergin (1979). In places forest has been cleared from the steep flanks of the ranges to altitudes of over 600 m and little forest remains on the slope foot below 300 m. Within the forests there is an altitudinal gradation in composition which is cut by two ecotones. At the lower ecotone, near 300 m altitude, lowland Kohekohe/Tawa (Dysoxylum spectabile/ Beilschmiedia tawa) forest is replaced by tawa forest, in which rimu (Dacrydium cupressinum) occurs as a scattered emergent and miro (Podocarpus ferrugineus) is common. At 600-700 m there is a broad ecotone in which tawa disappears. On Mt. Te Aroha tawa has an upper limit of 700 m and the ecotone is small but at Te Rere and Te Hunga the upper limit of tawa and a broad ecotone of tawari forest is possibly depressed by the frequent fog.

At 720 m, in all areas, silver beech (Nothofagus menziesii) appears abruptly and rapidly increases in prominence to dominate the upland forest zone. In the upland zone, seral stands dominated by quintinia (Quintinia acutifolia) and tawari (Ixerba brexioides) are common, and often cap the crest of the range. The beech forests are separated into three tracts by low points on the main range. On Mt. Te Aroha the forests contain high frequencies of red beech (Nothofagus fusca), particularly between 600 and 700 m a.s.l., but in the more southern tracts its importance diminishes, so that it is at first uncommon, and then absent, south of Wahine Rock in the the Te Rere area. Hard beech (N. truncata) is present on rocky sites at lower altitudes and is also confined to areas north of Wahine Rock.

## Principal species studied

The main dominants of the mature forest and seral stands were investigated These were: tawari, kamahi, quintinia, silver beech, kaikawaka, toro and miro. The selection varied for each study since many species were not suitable for use in particular aspects of the work:

Tawari (Ixerba brexioides A Cunn.) appears to be confined to cloud forests throughout its natural range. It is often abundant in the upland forests of the northern North Island from latitude 35°- 38° particularly in the Rotorua region. In this locality it appears to be near the centre of its ecological range. Here it shares dominance with silver beech on a wide range of sites and extends to lower altitudes as a subdominant in tawa forests. It also forms a distinct cloud zone type between 600 and 700 m altitude in the wetter parts of the ranges. The species was used in water relations studies but was unsuitable for dendrochronology.

Kamahi (Weinmannia racemosa, Lin. f.) dominates lowland seral communities throughout most of New Zealand south of latitude 37° but may appear in forests to 1100 m altitude. It is also common as a sub-dominant in older forests (Wardle 1966). In the Kaimai Ranges it is near its northernmost limit and appears to intergrade with W. silvicola, a northern species. It is uncommon in the lower altitude forests but abundant in upland seral stands. Kamahi was used in all studies but was short-lived and not suited to dendrochronology.

Quintinia (Quintinia acutifolia, Kirk) is frequently associated with kamahi but has a much narrower disjunct distribution (Wardle 1963). In the Kaimai Ranges it is confined above 600 m where it is closely associated with kamahi in seral stands. In the study areas it is abundant in disturbed forests and in older stands as a dense carpet of seedlings. Quintinia was used in all studies but was short lived.

Silver Beech (Nothofagus menziesii, (Hook.f) Oerst.) forms extensive stands in the South Island of New Zealand and descends to sea level. In the North Island it is confined to upland forests. In the Kaimai Ranges it is at the northern limit of its range but dominates the upland forests above 720 m. It has a broad ecological amplitude (Wardle 1967) but is more often found in areas of higher rainfall notably on waterlogged soils. Silver beech was of value in pressure bomb studies and dendrochronology but the leaves were unsuited to the porometer.

Kaikawaka (Libocedrus bidwillii Hook. f) is widespread in the wetter upland forests from Te Aroha southwards. It appears to establish following major forest disturbances, slowly reach dominance over hundred years or more and persists for several hundred years (Veblen and Stewart 1983b). In the Kaimai Ranges it occurs on the wettest sites. Regeneration is abundant in the seral stands above about 650 m. The distribution and density of kaikawaka was too limited for the species to be of value in water relations studies but was an important species for dendrochronology, particularly because of past studies (Clayton-Greene 1977, Dunwiddie 1978).

Toro (Myrsine salicina Hew. ex Hook. f.) is small tree of widespread distribution in seral stands but is rarely conspicuously abundant. In the Kaimai Ranges it is a common component of the quintinia seral stands and also a gap coloniser in mature stands where it may reach canopy height and persist as a minor stand component. Toro was of great interest because of prominent damage on poor sites and wide distribution however it proved unsuitable for use in the pressure chamber because of resin flows and unsuitable for dendrochronology because of complex wood structure.

Miro (Podocarpus ferrugineus, G.Benn. ex Don) is a podocarp of widespread distribution most common in more mature forests (McKelvey 1963) especially of higher rainfall areas but is rarely abundant. In the Kaimai Ranges it is a common plant of the cloud forest zone from 500 m to 800 m altitude. Leaves of miro were too small for the porometer chamber and growth rings of plants from the cloud zone were too indistinct for it to be used for dendrochronology.

Other species used in porometry included five finger (Pseudopanax colensoi, (Hook. f.) Phil ipson) and raurekau (Coprosma australis, (A. Rich. Robinson). Toatoa (Phyllocladus glaucus, Carr.), pink pine (Dacrydium biforme, Hook. f.) and yellow silver pine (Dacrydium intermedium, Kirk) are important in dendrochronology as they are gymnosperms with well defined annual rings.

All species studied are evergreen shrubs or trees endemic to New Zealand. Kamahi (Cunoniaceae), quintinia and tawari (Escalloniaceae) are all closely related and belong to tropical families whereas silver beech belongs to the antarctic element of the New Zealand flora. Many of the species including silver beech, kamahi, quintinia, kaikawaka, pink pine, yellow silver pine, five finger, and toatoa are near the northern limit of distribution and of these only kamahi is widespread below 600 m a. s. l.

CHAPTER 3.

## EPISODIC FOREST MORTALITY IN THE KAIMAI RANGES, NORTH ISLAND, NEW ZEALAND.

### INTRODUCTION

There is a growing awareness that periodic natural devastation of forests is common and may assist in the maintenance of some widespread forest types. Recently described examples include the Nothofagus forests of Chile which are maintained by periodic volcanic or seismic events (Veblen et al. 1980), wave-form regeneration in Abies forests propagated by wind (Sprugel 1976), and mosaic regeneration of New Zealand Nothofagus forest affected by periodic major snowstorms (Wardle 1970). Recent investigations of the forests of Westland (Veblen and Stewart 1982a) have similarly linked periodic disturbances in the Metrosideros/Weinmannia forests to seismic events. These disasters may affect more than forest structure and composition. For instance Grant (1965) suggested that periodic vegetation mortality over wide areas was responsible for erosion episodes in Hawke's Bay.

It is not always easy to recognise and distinguish natural from man-induced forest changes. Dead and dying trees are common in undisturbed natural forests in New Zealand. Mortality of obviously old trees is usually attributed to the natural overmaturity of the current crop. In recent years insect epidemics have frequently been observed in beech (Nothofagus) forests, particularly after dry summers (Rawlings and Gilmore 1964, Dugdale 1966, Milligan 1972). Furthermore, recent widespread mortality in lowland and seral forests has usually been attributed to severe browsing by the introduced possum (Trichosurus vulpecula). On the fringes of large forest tracts recent regeneration and scattered spars of the previous forest are commonly the result of wildfires originating in lowland areas during clearance for farming (Reed 1953, McKelvey 1973). As a result, dead and dying trees have become an accepted part of the landscape.

In the Kaimai Ranges widespread forest mortality and general ill-thrift was not reported until recent investigations into increased landslide frequency suggested a strong link between the two phenomena (Dale and James 1977). Mortality appeared to have occurred progressively since about 1950, a date determined from examination of aerial photographs and forest survey data, and was suggested to have been induced by depletion from possums. The current investigations have reinforced some of these conclusions, although they also indicate that the original explanations of the mortality are inadequate and that drought or other climatic factors are more important.

## THE STUDY REGION

The Kaimai Ranges, which rise to over 900 m, form a prominent montane barrier between the Waikato and Bay of Plenty climatic regions. To the east, exemplified by Waihi, there are strong coastal and north-easterly influences (De Lisle 1967) whereas to the west there is a dominant westerly influence (Maunder 1973). The lowland climate is warm sub-humid with a mean temperature of about 15 ° C and rainfall of 1500-2000 mm/a (Cox 1968). The upland climate is much cooler and wetter. At the summit of Mt. Te Aroha the mean temperature is 8 ° C and the rainfall is 2000 mm/a. Further south, higher rainfall and persistent fog along the crest of the range lead to a very wet environment (Martin 1889, Clayton-Greene 1976).

There is a well-marked altitudinal gradation in the forests which are cut by two ecotones. The lower ecotone, at about 500 m a.s.l.(above sea-level), separates the lowland kohekohe forests (Dysoxylum spectabile) from mid-altitude tawa forests (Beilschmiedia tawa). The upper ecotone, at about 720 m, separates the tawa from beech (Nothofagus) forests which cap the range. The beech forests are separated into three tracts by low points on the main range. On Mt. Te Aroha the forests contain high frequencies of red beech (Nothofagus fusca), particularly between 600 and 700 m a.s.l., but in the more southern tracts its importance diminishes, so that it is at first uncommon, and then absent, south of Wahine Rock in the the Te Rere area.

## METHODS

A study area was selected within each of the three beech forest tracts (Fig. 2.1), since previous work had suggested that the altitudinal distribution of the mortality and other site factors differed between them. Sampling was concentrated on the upland forests above 500 m and in the affected vegetation.

The areas of unhealthy vegetation were mapped using aerial photographs taken in 1974 (Mapping series 3731). Other photo sets, taken in 1943 (Mapping series 229) and 1960 (Mapping series 1218), were used to estimate the dates of the changes in the vegetation. The 1943 photographs were of poor quality and covered only the Te Rere and Te Aroha study areas. Field checking was required to identify many of the less affected areas, particularly in parts poorly represented on the oldest aerial photographs.

Forest descriptions were compiled on non-area "Recce" plots (Allan and McLennan 1978) and quantitative data were obtained from clusters of three or five constant-count plots at more than 25 localities in each study area. Each constant count-plot was a circular plot of area determined by the distance to the furthest plant from a randomly selected point (plot centre). In the "tree" stratum the diameters of the nearest 15 plants over 5 cm diameter breast height (DBH) were recorded by species; in the "shrub" stratum the diameters of the 15 nearest plants over 20 cm height were recorded by species; and in the "seedling" stratum the nearest 20 woody plants less than 20 cm in height were recorded but not measured.

For dendrochronological purposes samples from at least five stems of a wide range of species were taken at plot sites and many other localities. Discs were cut from the stems as close to the ground as possible to ensure a complete growth record. From each disc the radial segment containing the widest or most distinct rings was selected and a 5-mm-wide strip removed with a band saw. Each segment was polished on the radial transverse face with a series of carborundum papers to 400 grade until the growth rings were clearly visible. Where the rings were still indistinct, a finer polish was achieved by rubbing with alumina knife-grinding powder (Patel 1967).

There is considerable discussion in the New Zealand literature about the regularity of growth rings in local species. Dunwiddie (1979) examined several species to establish a dendrochronological data base and found that rings were generally annual. His species list includes some of the species studied here and by cross dating between species it was possible to establish a general chronology. This chronology also enabled the ring sequences (Table 3.1) to be cross-checked within species and sections in which compressed and missing rings were common. The chronology was compiled using key years, in which one or more of the following features occurred: distinctive latewood, abrupt changes in growth rate, or cambial mortality. Distinctive latewood was commonly formed in a wide range of species and could be dark coloured (e.g., *Phyllocladus glaucus*), composed of smaller uncoloured denser cells (e.g., *Quintinia acutifolia*), or marked by bands of resin cells (e.g., *Libocedrus bidwillii*). In all instances the feature could be attributed to dry summers recorded in the Waikato (cf Maunder 1973). Abrupt

Table 3.1

Important key years show by a combination of changes in growth rate, distinct latewood cambial mortality. Data based on examination of 220 stem sections. Species include: *Dacrydium intermedium*, *D. biforme*, *Dracophyllum latifolium*, *Libocedrus bidwillii*, *Nothofagus menziesii*, *Phyllocladus glaucus*, *P. alpinus*, *Pseudowintera axillaris*, *P. colorata*, *Quintinia acutifolia*, and *Weinmannia racemosa*.

| YEAR | FEATURE | | |
|---|---|---|---|
| | Change in growth rate | Distinct latewood | Cambial mortality |
| 1976 | *** | ** | * |
| 1972 | ** | ** | |
| 1965 | * | * | |
| 1956 | * | * | |
| 1954 | ** | ** | |
| 1950 | *** | | |
| 1946 | | ** | *** |
| 1944 | | ** | * |
| 1940 | *** | | |
| 1934 | *** | ** | |
| 1930 | *** | | |
| 1926 | ** | | |
| 1919 | | | * |
| 1914 | | | *** |
| 1907 | | * | |
| 1901 | | * | * |
| 1896 | * | * | |
| 1886 | | * | |
| 1807 | *** | | * |
| 1804 | *** | * | |

* evident ** prominent *** very prominent

changes in growth rate were present to some extent in all specimens and changes often coincided between trees and localities. The direction of the growth response was not the same for all species in any one designated key year (Fig. 3.1) but it appeared to be consistent within some species. Cambial mortality occurred in only a few years and was thus valuable as a chronological marker.

## RESULTS

### Location and extent of the decline

In the lowland forests widespread and continuing mortality of kamahi (*Weinmannia racemosa*) and kohekohe is readily attributable to intensive possum browsing (Dale and James 1977). There are areas of young seral forests close to farmlands, which are clearly the result of the spread of crown fires from the lowlands during of farm development.

In upland forests widespread mortality has no readily distinguishable cause. The intensity of the damage in the upland forests ranges from complete forest destruction, giving rise to grassland or young seral forests, to largely intact forest in which the trees show partial mortality and extensive leader die-back. The areas of complete mortality are often interconnected by zones with scattered, unthrifty surviving trees forming an overwood, or by zones of lightly affected forests almost completely stocked with largely unthrifty trees. The lightly affected forests form a discontinuous belt 100-150 m below the crest on both sides of the range and mark the lower altitudinal limit of mortality. Above this belt most of the forests in each of the three study areas are affected to some extent. The map of the Te Rere study area (Fig. 3.2) illustrates a typical example.

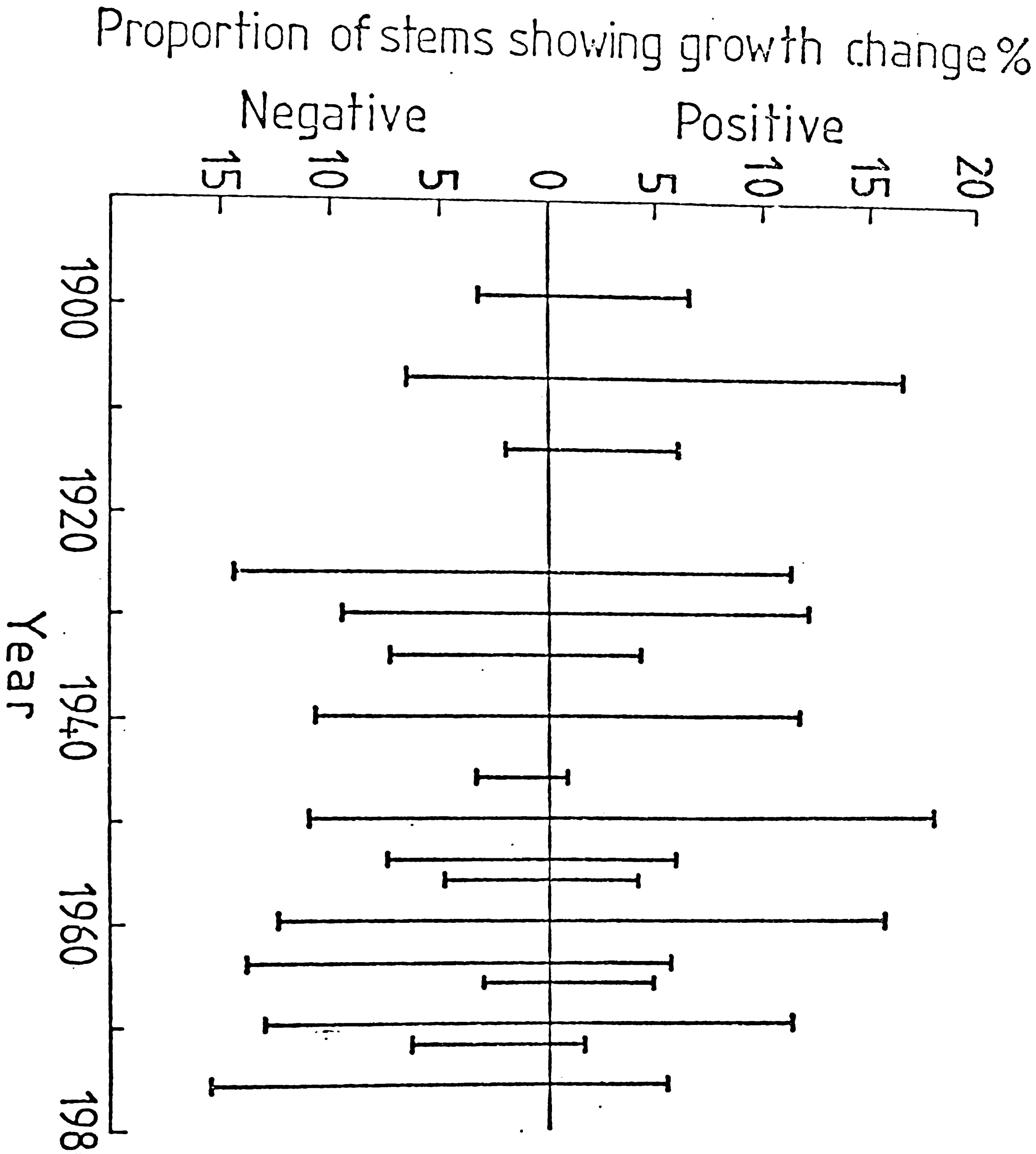


Fig. 3.1. Percentage of stem discs used for dendrochronology showing changes in growth rate, either positive or negative, in designated key years (Table 3.1).

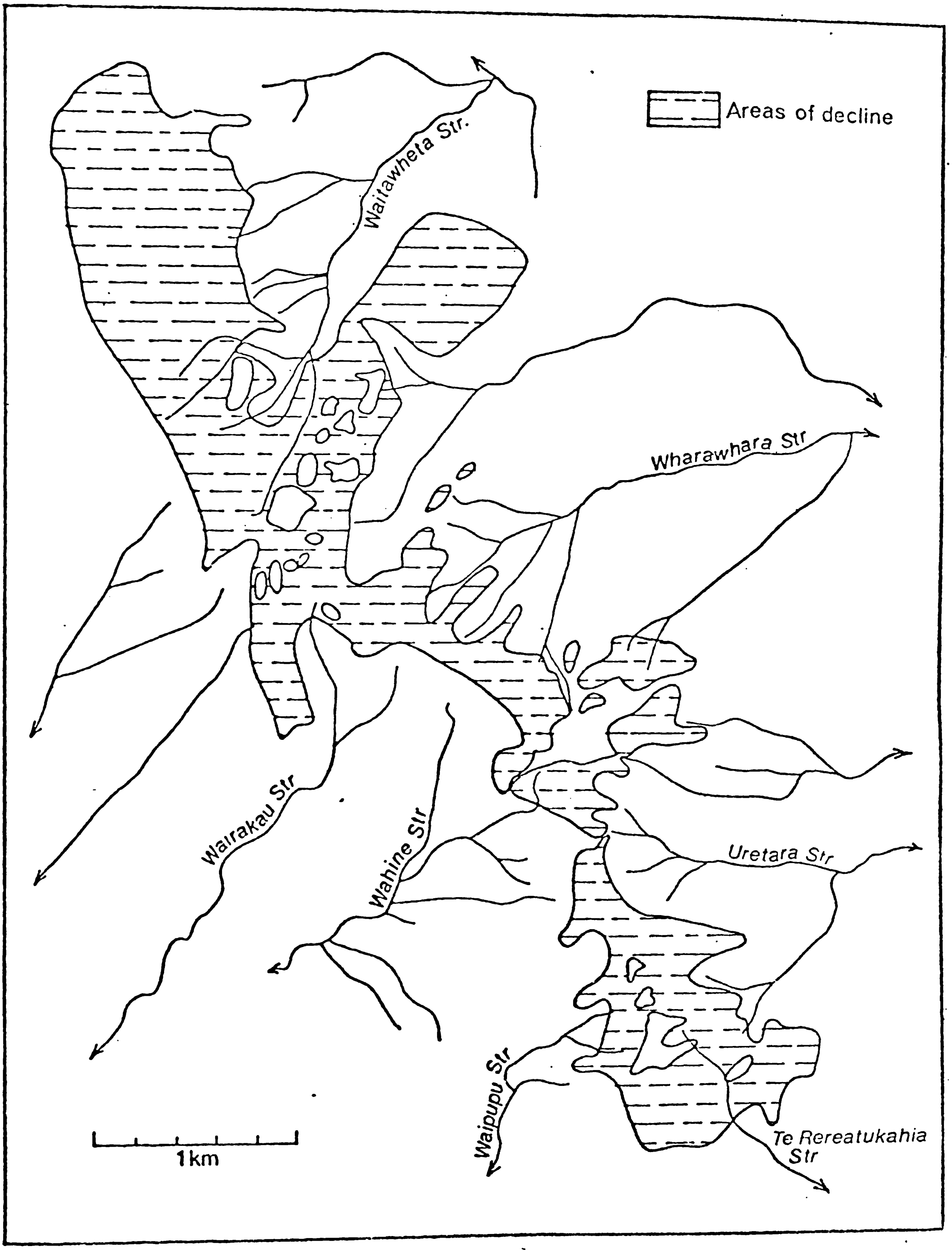


Fig. 3.2. Distribution of mortality in the Te Rere Study area.

It is difficult to rank the species in order of damage severity. In the worst affected areas all plants were killed. In the least affected stands continuing ill-thrift affects a wide range of woody plants. The undamaged plants are usually conspicuous and emergents include miro (*Podocarpus ferrugineus*), rimu (*Dacrydium cupressinum*), and often kaikawaka (*Libocedrus bidwillii*), with *Dracophyllum* spp., *Cyathodes* spp., *Pseudowintera* spp., *Coprosma australis*, pigeonwood (*Hedycarya arborea*), and broadleaf (*Griselinia littoralis*) in the shrub and tall shrub tiers. The principal canopy plants, silver beech, tawari (*Ixerba brexioides*), quintinia (*Quintinia acutifolia*), toro (*Myrsine salicina*) and kamahi, all show some leader die-back.

Evidence from residual stems in partially affected vegetation, dead stems and logs, and comparison of aerial photographs, all suggest that there was no change in vegetation type at the boundary between the affected and unaffected forest. The intensity of damage in the various forest types differed between the study areas but was largely a function both of the altitude above which damage became apparent and of the distribution of the forest types among the study areas (Fig. 3.3).

On Mt. Te Aroha damage begins above 800 m a.s.l. in the silver beech forest zone; consequently red and silver beech forests were the only vegetation types affected. Damage was most severe on an outlying knoll at 800 m (NZMS 1, Grid ref. N57, 227 778) and on a spur leading from Buck Rock (NZMS 1, Grid ref. N57, 242 753) to the summit. In these areas complete mortality has given rise to a low quintinia and toatoa (*Phyllocladus glaucus*) scrub. At other points near the summit mortality appears to have slightly reduced the density of the beech forest canopy and resulted in an invasion of quintinia/kamahi seral communities (Table 3.2).

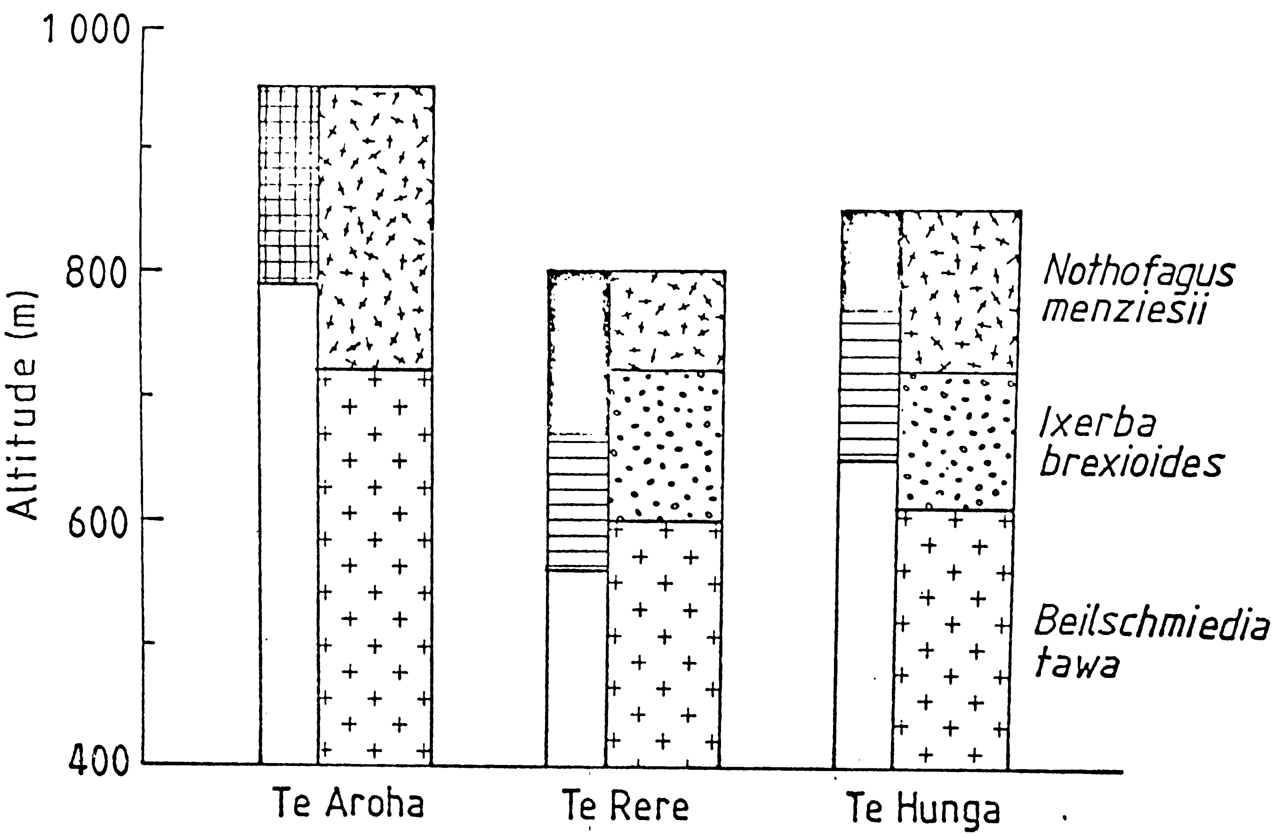


Fig. 3.3. Altitudinal distribution of the *Nothofagus menzeisii*, *Ixerba brexioides* and *Beilschiedia tawa* forest types and vegetation mortality in the Te Aroha, Te Rere and Te Hunga study areas. For each study area the left-hand portion of the histogram bar represents the severity of the vegetation mortality: [ ] very severe, severe, ==== moderate. The right-hand column indicates the vegetation types by altitude as labelled on the histogram.

Table 3.2

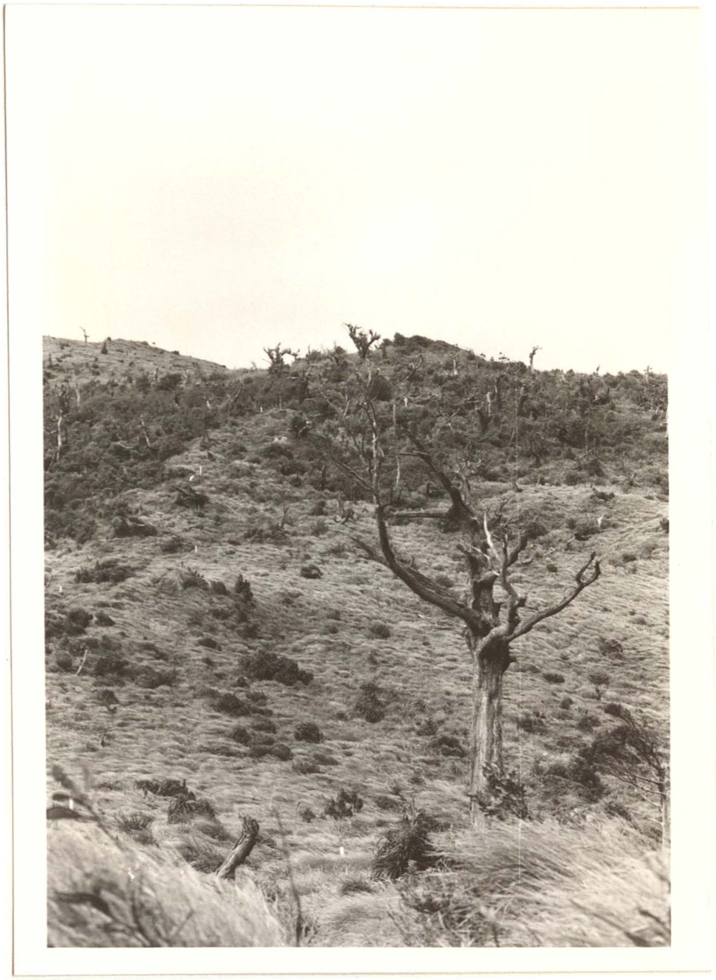
Relative densities and other parameters of intact and affected tawari (*Ixerba brexioides*) and silver beech (*Nothofagus menziesii*) forests.

| *Relative densities* | *Silver beech forest* | | | | *Tawari forest* | | | |
|---|---|---|---|---|---|---|---|---|
| *Species* | *intact* | | *affected* | | *intact* | | *affected* | |
| | *trees* | *shrubs* | *trees* | *shrubs* | *trees* | *shrubs* | *trees* | *shrubs* |
| *Nothofagus menziesii* | 31.5 | 4.1 | 14.4 | 1.3 | 5.4 | 1.8 | 5.6 | - |
| *Weinmannia racemosa* | 11.9 | 5.9 | - | 28.0 | 12.4 | 9.9 | 21.1 | 11.1 |
| *Ixerba brexioides* | 38.5 | 2.7 | 42.2 | 4.0 | 31.4 | 1.8 | 21.0 | - |
| *Quintinia acutifolia* | - | 32.3 | - | 26.7 | 3.4 | 17.9 | - | 3.3 |
| *Podocarpus ferrugineus* | 1.1 | 0.4 | 2.2 | - | 1.1 | 0.5 | - | - |
| *Griselinia littoralis* | - | 1.1 | 3.3 | 2.7 | 1.3 | 4.5 | - | 2.2 |
| *Myrsine salicina* | 4.8 | 2.2 | 2.2 | 4.0 | 6.0 | 2.8 | 15.5 | - |
| *Alseuosmia macrophylla* | - | - | - | - | - | 4.3 | - | - |
| *Dracophyllum latifolium* | 2.2 | 2.2 | - | - | 6.0 | 2.8 | - | - |
| *Coprosma foetidissima* | 3.3 | 7.8 | 7.0 | 4.0 | 5.3 | 6.1 | 11.1 | 7.8 |
| *Dicksonia squarrosa* | - | 4.4 | - | 13.0 | - | - | - | 24.4 |
| *Coprosma australis* | - | 3.7 | - | 1.3 | 5.0 | - | 15.6 | - |
| Others | 7.1 | 33.3 | 28.7 | 15.0 | 22.7 | 39.5 | 10.0 | 51.2 |
| Basal area (m3 /Ha ) | 64.9 | 0.54 | 0.15 | 0.47 | 44.5 | 0.65 | 0.67 | 2.94 |
| Density (stems 10 3/Ha ) | 1.6 | 2.4 | 7.13 | 94.6 | 1.9 | 12.8 | 0.02 | 6000 |
| Number of plots | 18 | | 8 | | 103 | | 90 | |

In the Te Rere area forest damage begins at about 550 m and includes the upper tawa/tawari, tawari, and beech forests. On some of the most severely affected sites the forest has been replaced by *Microlaena avenacea*, *Hierochloe redolens*, and *Uncinia distans* grassland (Fig. 3.4A). In partially affected forests horopito (*Pseudowintera axillaris*) or *Cyathea smithii* are often prominent (Fig. 3.4B).There are also considerable areas of pigeonwood and tall *Coprosma australis* scrub near the tawa forest ecotone and quintinia scrub of about 3 m tall at the higher altitudes.

On Te Hunga the mortality occurs above 650 m in the tawari forests. Below the plateau at 800 m the tawari forests have suffered only a partial canopy loss and, although ill-thrift in the residual trees is common, there is usually a proliferation of horopito in the understorey. At the southern end of the prominence tall pigeonwood scrub is present under sparse residual tawari. Above 800 m and extensively on the plateau, complete mortality is widespread with silver beech, kaikawaka, and pink pine (*Dacrydium biforme*) all being affected at some place. Regeneration, even on the wettest sites, has led to the development of quintinia scrub. *Juncus* spp. were rarely observed although they have begun to appear on recently constructed tracks.

Where silver beech or *Dacrydium intermedium* is present the mortality zone extends to within a few tens of metres of the ridge crest but at other places, particularly at low points or in very wet areas, it may extend across the range. Within the upland forests there are islands of unaffected vegetation in a variety of topographic localities. There are many instances where distinct boundaries separate affected and unaffected vegetation. These boundaries appear to be related to minor changes in topography or to wind shadows created by minor knolls on the west of the range (Fig. 3.5A).

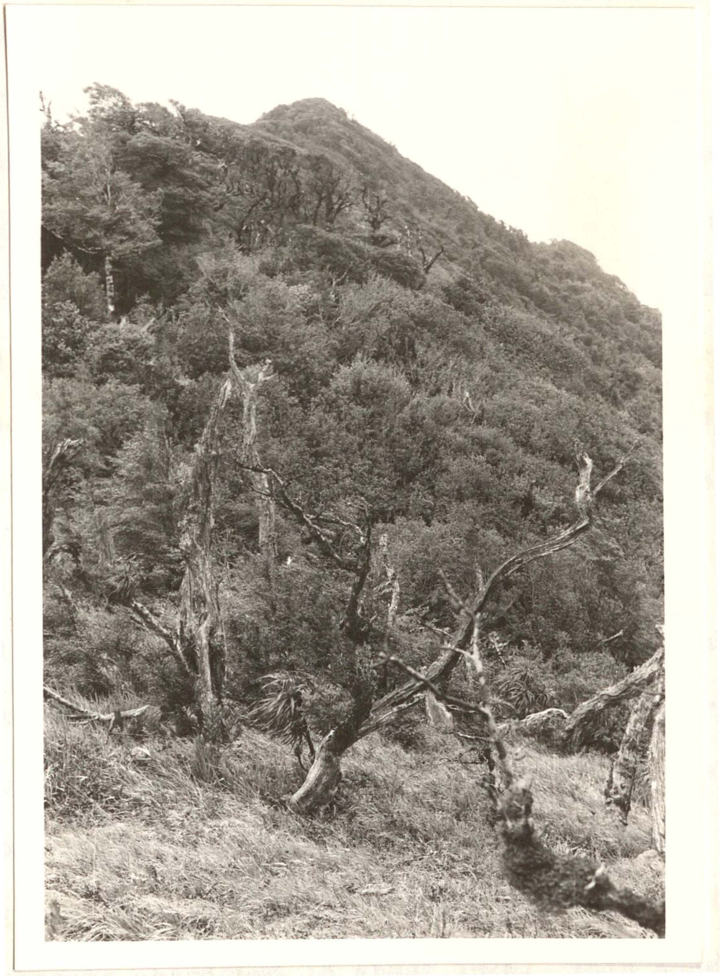


A: Replacement of forest by grassland, Te Rere.

B: Replacement of forest by understory species and tree ferns, Te Hunga.

Fig. 3.4. Variation in extent and location of the vegetation mortality.

Fig. 3.5A: Unaffected forest in a sheltered gully head Te Rere



B: Patterns in mortality, Te Rere; recent mortality, 1946 or later, shown by sedges, foreground; 1914 mortality, now seral scrub, middle ground; and old forest, upper left.

Throughout the ranges the least damaged stands were on sites which are often regarded as the most susceptible to drought damage because of their shallow soils and general exposure. On exposed spurs of the main range and on subsidiary spurs Dacrydium intermedium dominated communities appear undamaged. Similarly, silver beech stands on shallow, strongly podzolised ridge sites were apparently unaffected although on other sites silver beech was often severely affected.

### Age of the mortality

At several places along the ranges, most obviously in the Te Rere area, there appear to be two age classes in the seral vegetation (Fig. 3.5B). This same pattern can also be readily detected in the diameter frequency distributions of the more common plants such as tawari, horopito, and silver beech (Fig. 3.6). Estimation of the age of the older seral vegetation from the stem sections suggests a date near or before 1920 but not before 1914 (Fig. 3.7). This coincides with severe cambial mortality in 1914 and to a lesser extent in 1919. There was also a recruitment peak about 1934 but cambial damage was absent. In contrast, although cambial damage was present in 1946, recruitment was not abnormally high.

By careful examination of the 1943 aerial photographs it was often possible to detect the earlier mortality. In the two northern areas it was possible to use the 1943 and later photographs to compare this older seral vegetation with fire-induced vegetation datable to 1911 and clearance along the power transmission line between the Waiorongomai and Waitawheta catchments abandoned in about 1926. This suggested that the vegetation changes visible in the 1943 photographs occurred between the two dates or possibly earlier.

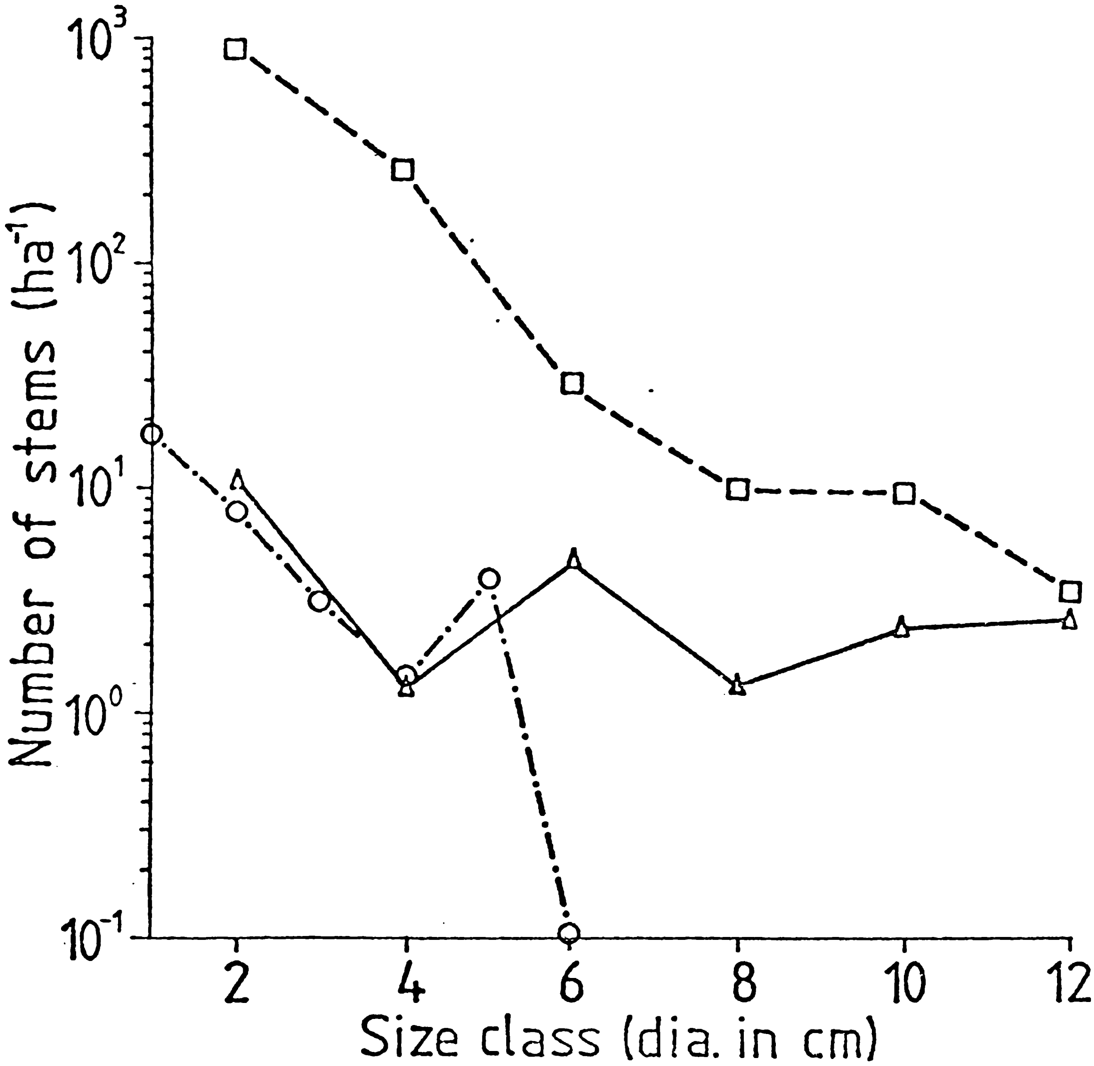


Fig. 3.6 Stem frequencies by age class; Ixerba brexioides (tawari) Δ-–. -Δ ; Pseudowintera colorata (horopito) o . . o ; and Nothofagus menzeisii (silver beech)□- -□.

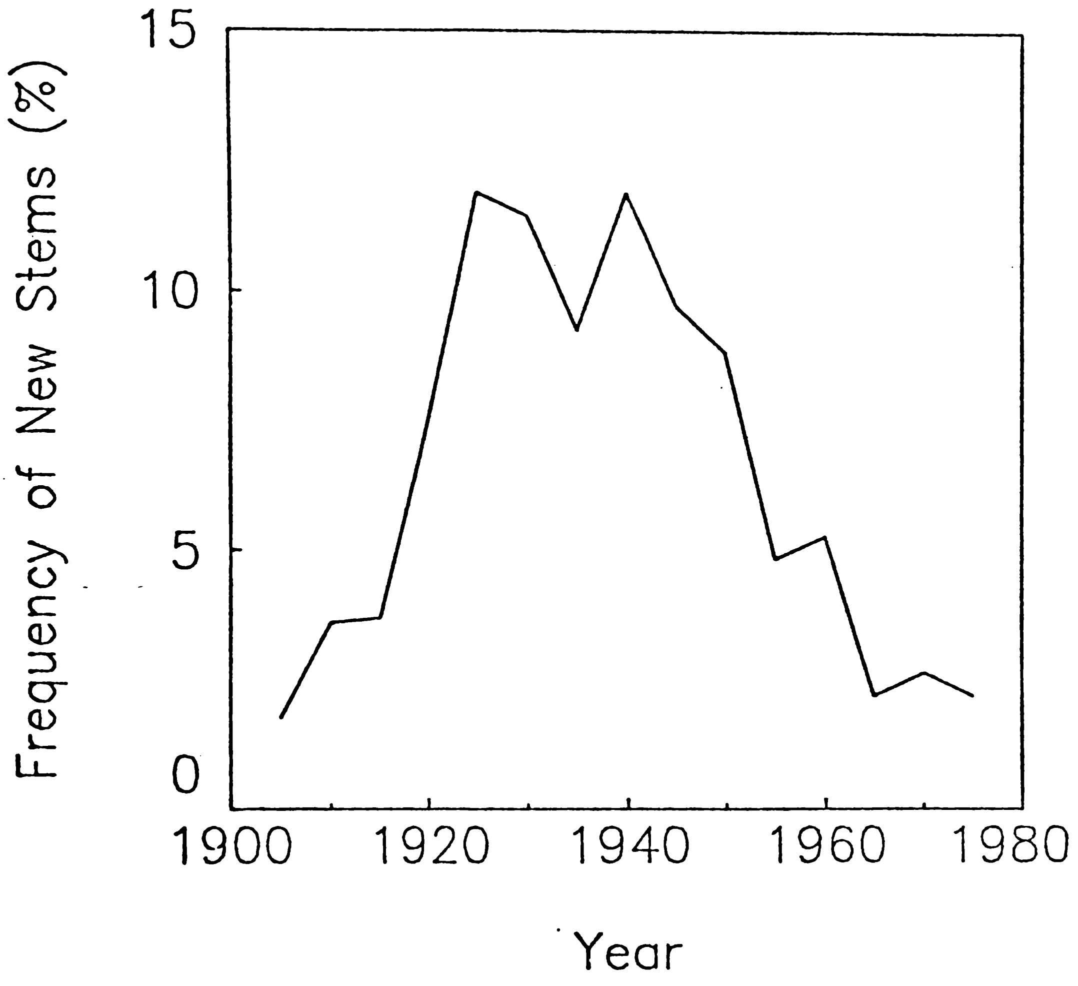


Fig. 3.7 Age class distribution of all sampled stems as indicated by the total number of growth rings present.

There is little historical information for the period before 1947. Searches of timber appraisal reports dating from 1904 to 1928 and examination of a few photographs of the Waitawheta Valley taken in 1926 suggest that the kauri (Agathis australis) forests contained many stag-headed trees which the reports described as moribund. There was no mention of widespread mortality or die-back in the upland forests but, since these forests were very inaccessible until recently, this may not be significant.

No prominent areas of mortality were shown on the aerial photographs, which could be related to the 1934 recruitment peak, and it would appear that this later recruitment peak may have been the result of some thinning of the seral vegetation by storms or other causes. Severe winds were associated with a storm in 1934.

The vegetation changes between 1943 and 1960 were dramatic and were obvious when comparing the photographs. Discussions with S. E. Fokerd (New Zealand Forest Service, Wellington) and K. Purdom (New Zealand Forest Service, Auckland) established that extensive recent mortality was apparent when operations to control goats (Capra hircus) began in 1947. Local farmers have indicated that the changes were essentially complete by 1950. Also current mortality was not reported in the records for the few forest survey plots established in 1951 and 1960 which were located within the affected forest (Plots 71/53,76/52,2999/11/E6), although long-dead trees at Te Rere and on Mt. Te Aroha were mentioned. The records describe low seral scrub dominated by Dracophyllum latifolium and quintinia which was probably similar to vegetation present today, originating from the 1914 period of mortality. Descriptions of the vegetation on the crest of the range at these times (Plots 76/52,74/46) note the apparent youth of the vegetation although estimates of 20 years for its age are contradictory.

Dendrochronological evidence is of limited value, since few stem sections could be dated to the later mortality (1946), possibly because of the impact of goat browsing and possibly because of the sampling pattern which excluded small stems. The risk of exclusion from sampling is increased by the very low seedling growth rates. Small stems less than 1 m tall and 5 mm diam, which were deliberately sampled on Te Hunga, produced dates between 1948 and 1954 and in older stems the inner core often contained rings spaced less than 0.05 mm apart. Hence, it is not unexpected that the diameter/age class distributions (Fig. 3.6) give little indication of abnormal recruitment in the smallest size classes and show little evidence of severe recent depletion from goat browsing.

Between 1900 and 1926 there were no marked changes in growth rate that might be associated with the earlier period of mortality. Similarly, it is difficult to associate the marked increase in growth rate in 1950 or 1954 (Fig. 3.1) with the later period of mortality since the cambial mortality, prominent in 1946, and observations of the mortality strongly indicate that the changes occurred rapidly about 1946 or 1947 and were completed well before 1950.

From 1960 to 1974 the photographs show only minor changes in the upland vegetation. Mortality of individual emergent trees and some extension of the bald areas are readily attributable to increased exposure and continued intensive browsing by goats. Since 1975 some improvement in stand vigour appears to have occurred, particularly in the lightly affected tawari forests (personal observation).

## Animal impact on the regenerating forests

The spread of goats and possums into the region occurred between the 2 periods of vegetation mortality and even now parts of the region have remained largely uncolonised. Goats were liberated during the mining era beginning about 1870 and have spread throughout the region. The pattern of possum dispersal appears to have followed that of the goats. Goat numbers reached a peak about 1940 in the northern study areas, just before control shooting began, but there were never high numbers on Te Hunga. Possum numbers reached a peak at different times in each area (Fig. 3.8) and a wave of severe damage spread south and northward from the liberation points.

Goats appear to have had a limited impact on the vegetation. This can be demonstrated by comparing the seral vegetation resulting from the two main periods of vegetation mortality at different areas within the ranges. On the summit of Te Hunga, where goat numbers have been low (Dale and James 1977), quintinia, toro, and tawari dominate the seral vegetation in very dense stands (Table 3.2). On very wet sites kaikawaka and pink pine become abundant among the same seral plants and *Gahnia pauciflora* is common. On the most exposed sites, to the west of the the ranges, recolonisation has been slower and *Gahnia* "grassland" with scattered woody plants up to 1 m tall is present. At lower altitudes dense horopito and *Cyathea smithii* stands are common and at the lowest altitudes pigeonwood and *Coprosma australis* form dense thickets. On Mt. Te Aroha, where goats were moderately abundant, plants similar to those on the summit of Te Hunga prevail and in the Te Rere study area, where goat numbers were reported to be high in 1974 (Dale and James 1977) the older seral vegetation is very similar to that on Te Hunga. The younger seral vegetation on Te Aroha and in the centre of the Te Rere study area is also similar to that on Te Hunga. However, to the south of the Te Rere area and below about 700 m the

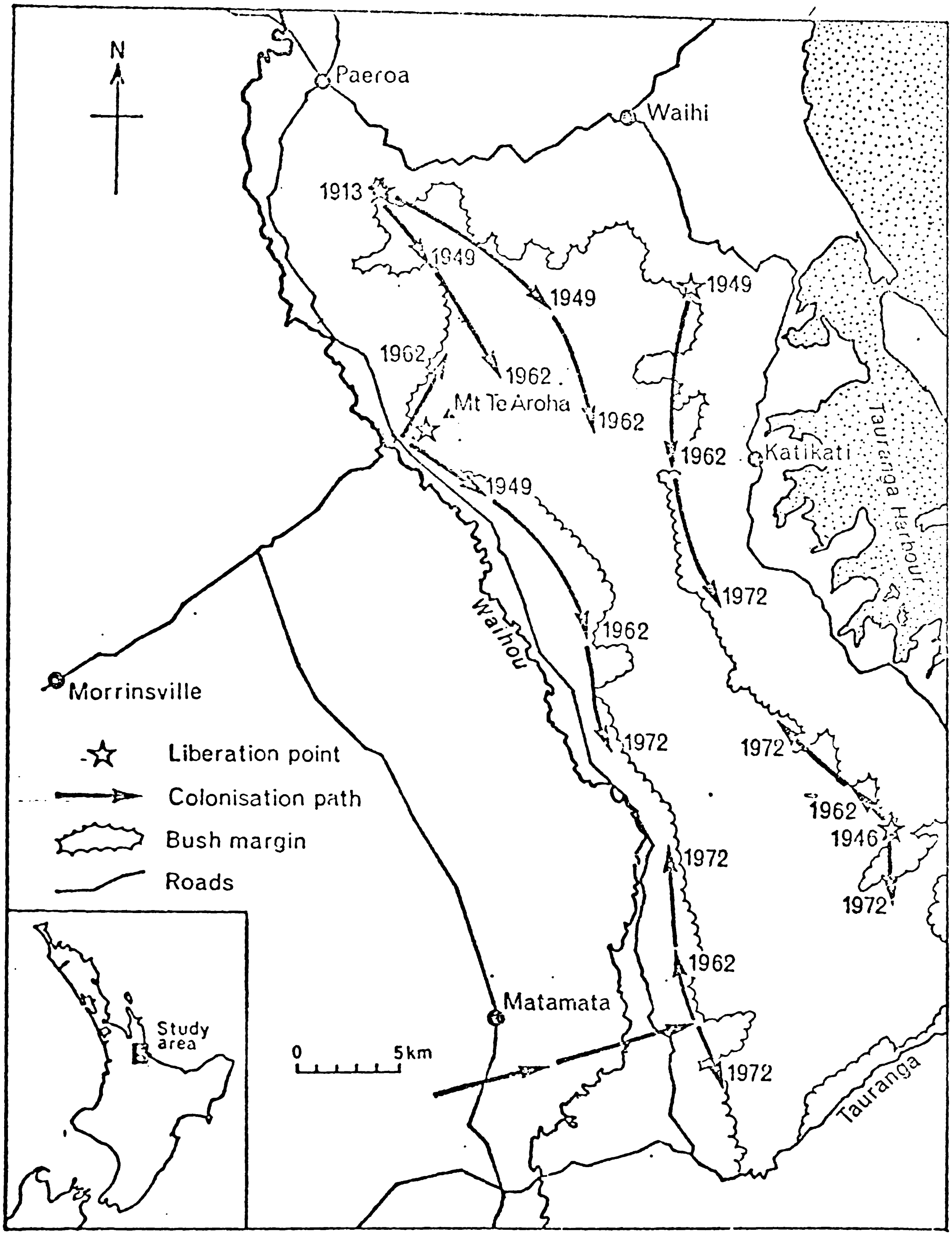


Fig. 3.8 Possum release points and subsequent colonisation routes within the Kaimai Ranges. Dates within the arrows indicate the appoximate arrival times of the possums at that locality.

recent mortality has largely resulted in the appearance of a mixed grassland which, below 600 m, is dominated by introduced pasture plants. In grassland areas the reduction in goat numbers since 1974 has resulted in an invasion by woody plants, particularly *Coprosma australis* and pate (*Schefflera digitata*). Hence, it is apparent that the impact of the introduced animals has been largely confined to areas below the affected forest zone.

## DISCUSSION

The wide range of species affected suggests that either a pathogen of broad host specificity or physical factors such as drought or windthrow caused the mortality. The problem of identifying the primary cause is complicated by the long interval since the initial mortality and the often rapid invasion by saprophytes and secondary pathogens which may be mistaken for the initial cause of the mortality. Furthermore, it is common for periods of stress, such as droughts, to trigger disease epidemics (Schoenweiss 1975) and yet not be the primary cause of mortality. *Nascioides enysii* and *Proteodes carnifex* are typical insect pathogens in these situations and the fungus *Armillaria mellea* which is present in most forest soils may become a primary pathogen under some conditions. Hence, discriminating between the primary causes of the mortality and later secondary effects may be difficult.

### Primary causes of the decline

The extent of the mortality on the most affected sites suggests that no species are wholly resistant. Many of the affected areas have strikingly distinct boundaries which can usually be related to topographic features and, even where the intensity of damage declines over a broad ecotone, there is little evidence for a mosaic boundary.

Neither of these situations would be expected if pathogens were the chief cause of the mortality.

Dendrochronological data indicate that damage occurred to the vegetation in the severe droughts of 1946 and 1914. This is at least partially supported by direct observations of mortality in 1947 (S. E. Fokerd New Zealand Forest Service, Wellington; K. Purdom New Zealand Forest Service, Auckland). Further evidence of widespread drought effects comes from a close examination of drought-prone sites at lower altitudes. There are a few rocky spurs in the Wairakau stream (NZMS 1, Grid ref. N 57,305 718) and Waipupu stream (Grid ref. NZMS 1, N 57,305 710, N 57,315 708) which were also denuded between 1943 and 1960. There are similar localities in the Waitawheta stream which may have been affected, although here damage from logging is also probable. In the Pomihi stream it is possible to identify extensive stands of young hard beech (Nothofagus truncata) on steep, stony sites which can be dated to about 1922 - corresponding about to the earlier period of mortality in the upland forests. As a result it seems probable that drought is the primary cause of the initial mortality.

### Possible cause of the continued ill-thrift

The continuing ill-thrift on many sites is typical of that induced by fungal pathogens such as Armillaria mellea or Phytopthora cinnamomi. Many of the symptoms are also suggestive of attack by Phytophthora cinnamomi, although several factors suggest that it is not involved. For instance, known susceptible species such as Coprosma australis and Cyathodes fasciculata (Newhook and Podger 1972) appear healthy, whereas miro, kaikawaka, and several other species that are not known to be susceptible are affected. Furthermore, soil temperatures remain too low for hyphal growth (10 °C) for much of the year (Weste and Ruppin 1977) and in the summer of 1980-81 reached 12 °C in only one month. Armillaria spp. can be readily detected on recently dead trees and on older logs at most sites. These fungi are saprophytic but have been known to be pathogenic where there has been extensive mortality from other causes (Peace 1960). Together these factors suggest that pathogens have not contributed significantly to the problem.

The continuing ill-thrift may reflect several physical site changes consequent on the mortality of the surrounding larger trees, including increased exposure to cold drying winds, flooding of the root systems, and changes in the mineral cycling resulting from decay of the dead trees. Changes in the degree of exposure of the residual trees are very evident on ridge sites but clearly less important at most other places. Very prominent changes in the rooting patterns of many of the trees have occurred on Te Hunga, where cores removed with a soil auger show many dead roots at all depths and a concentration at the bedrock, whereas live roots are concentrated in the upper 5 cm of mineral soil and in the overlying litter and decaying logs. Within the soil profile there is often prominent staining on the peds, which strongly suggests a widely fluctuating water table. It appears that the present water table lies nearer to the surface as a result of flooding of the soil profile after the extensive mortality of canopy plants. These changes could induce ill-thrift in the residual old trees by causing mortality of the deeper penetrating roots.

The low nutrient status of the soils is another important feature of the area. There are very low levels of available bases (typically 0.1 me%) and very low available phosphate levels, ranging from 4 ppm in the A horizon to 1 ppm in the B and C horizons (Truog available P), which results from the high allophane content of the soils (Wilson 1980). The low levels of soil nutrients reduces the ability of the plants to respond to adverse climatic conditions and disease and no doubt further compounds the problem.

## CONCLUSIONS

Some puzzling aspects to the problem of widespread forest mortality in the Kaimai Ranges remain. In particular, the most affected sites are the wettest areas and not the exposed ridge crest sites which support specialised vegetation. However plants of wetter sites can be more drought sensitive (Bannister 1976). Although the growth rings record the droughts in 1914 and 1946, many stems show wider than normal growth in these years and there is no increase in growth rate or any form of long-term growth change that can be associated with these years. This suggests that other site factors particularly climate, have strongly influenced the distribution of species, the zones of susceptible vegetation, and rates of vegetation recovery.

The pattern of the mortality shows that instability is an important component of the ecological process of the forests of the Kaimai Ranges. Introduced-animals have undoubtedly contributed to the slow recovery from the latest episode but their distribution and impact cannot explain the altitudinal localisation, pan specific nature, or episodic occurrence of the mortality. The two recent episodes are strongly linked with severe droughts, so that it now appears that drought can also initiate the rapid and extensive forest changes hitherto attributed to well recognised factors, such as windthrow, seismic activity, and volcanic events. If drought is the primary cause then this important environmental component must be considered in studies of the temperate rain forests of New Zealand.

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The widespread nature of the two recent periods of vegetation mortality suggests that either there have been recent changes in the local environment which have induced the mortality or there have been recent changes in climatic parameters which have increased the risks of drought and the consequent mortality. The recent vegetation mortality initiated a period of increased erosion within the ranges (Jane and Green 1983a) and, hence, the ability to predict the recurrence of vegetation mortality and subsequent erosion is of particular significance. The frequency of the drought-induced mortality is thus an important question which is being studied further.

## CHAPTER 1

## ETIOLOGY OF THE DIEBACK AREAS.

### INTRODUCTION

The location and extent of mortality in the Kaimai Ranges is discussed elsewhere (Jane and Green 1983b) but there is only a limited description of the nature of the affected stands. Mortality throughout the ranges is concentrated in the fog zone forests above about 550 m a.s.l. although the altitude varies with locality and may extend from the semi-lowland tawa forests through to the upland silver beech forests. It occurs on slopes up to 35° (Fig. 4.1) or on flat ground and encompasses a wide range of forest communities. Within these communities the damage is of a similar nature and affects wide range of species. In order to obtain a further understanding of the nature of the problem selected stands are described in detail together with the growth characteristics of the most significant species components.

### METHODS

Site descriptions are based on non-area (Recce) plots (Allan and McLennan 1978) and detailed measurements along line transects. Cruciform groupings of five constant count plots (Jane 1982) were placed in each major forest community (Jane and Green 1983b). Plant names are those used in the "Flora of New Zealand" (Allan 1960, Moore and Edgar 1970). Partial soil profile descriptions were made on five, or more, cores removed with a Dutch clay auger at each sample locality and from a few soil pits.

Bud break and leaf development was monitored through the summers of 1980-81 and 1982-3 and records made of leaf size, leaf number by age classes, and visible damage on leaves. Root development patterns were examined on windfalls and excavated seedlings. Surface root distribution was mapped at a few localities. Root/shoot ratios were determined on seedling material returned to the laboratory.

Fig. 4.1 A (left): Vegetation mortality in tawari forest associated with landslides. On the ridge low seral forest is present in which later mortality has produced a low sedge or grass cover. this is seen most readily on the skyline just below the ridge crest. At mid-altitude forest collapse has resulted in tree ferns (*Cyathea smithii* mainly) and associated shrubs (bottom right). B(right): Mortality on thin soils near Wahine Rock. Ground cover is *Blechnum minus* and *Gahnia pauciflora*. Scattered spars indicate the height and shape of the former canopy.

## RESULTS

### Characteristic damage on shoots and leaves

In unthrifty stands scattered emergent gymnosperms and broadleaved trees commonly have many dead twigs and branches (Fig. 4.2). Decay of some or all these branches may result in a broken appearance to the crown. In the low stature seral vegetation kaikawaka and miro seedlings normally appear healthy but varying intensities of damage are present in broadleaved species. Damage to plants on affected sites shows one of the following characteristic patterns (Table 4.1):

1. Silver beech (Nothofagus menziesii) type. Leaves are small and may have red blotches or necrotic spots. The severely affected individuals have a straggly appearance (Fig. 4.3) since old leaves are shed rapidly, often just before or soon after bud break, and rarely retained for more than one year (Table 4.1). Similar damage occurs in red and hard beech on Te Aroha.

2. Tawari (Ixerba brexioides) type. Characterised by reduced leaf size and short internodes which concentrate current foliage at the tips of the branches (Table 4.2, Fig. 4.4). Although uncommon to rare in tawari it occurs in kamahi (Weinmannia racemosa, Fig. 4.3), five finger (Pseudopanax colensoi), and neinei (Dracophyllum latifolium).

3. Quintinia (Quintinia actufolia) type. Leaf size within a crown is reduced by increased shoot exposure. Shoots from the lower stem have leaves of normal size and few red blotches. Shoots in the upper canopy undergo progressive reduction in internode length and leaf size so that finally new growth cannot be initiated and the branch dies (Fig. 4.5). During each summer leaf size gradually reduces but new leaves of the next season may be of normal size. A similar pattern occurs in toro (Myrsine salicina) (Fig. 4.6) and raurekau (Coprosma australis).

Table 4.1

Leaf size, number and foliated length of shoots from good and poor sites. Values mean are the of counts on ten shoots of each species/ site combination.

| | leaf length | | number of leaves | | | | foliated length | |
|---|---|---|---|---|---|---|---|---|
| | (mm) | | old | | current | | (mm) | |
| | 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 |

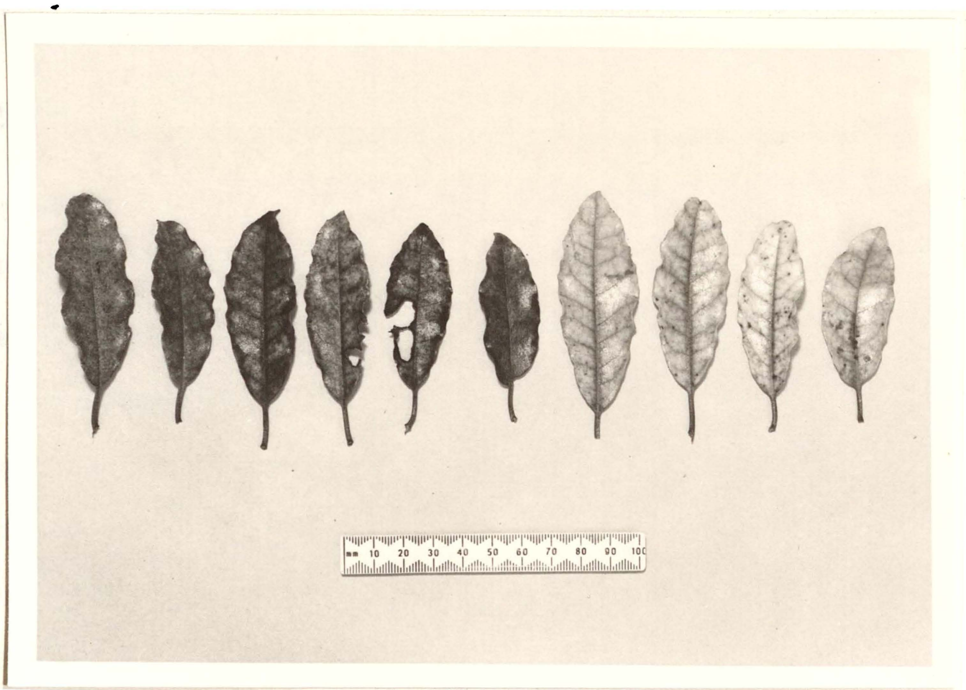
Fig. 4.2. Scattered dead and unhealthy silver beech over quintinia/tawari shrubland in which recent mortality has occurred.

Fig. 4.3. Healthy and unhealthy shoots of the main species. Upper row, healthy shoots lower row unhealthy shoots from nearby sites. Species from left to right are: kamahi, quintinia, tawari, and silver beech. Reduction in leaf size, and number and concentration of leaves at shoot tips occurs in the unhealthy plants. On the unhealthy quintina the shoot at lower right is barely foliated. Silver beech has a marked reduction in number of leaves.

Fig. 4.4. Healthy and unhealthy shoots of tawari on adjacent plants. the unhealthy shoot has reduced leaf size and leaves concentrated at branch tips.

Fig. 4.5. Straggly, unhealthy quintina typical of poor sites. Leaves are not retained for more than one year and increased exposure of shoots markedly reduces leaf size.

A



B

Fig. 4.6. (a) 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. (b) Leaf size variation on a quintinia through two seasons. The leaf on the left is oldest and the first 6 dark leaves are of the previous season and when collected in February were red in colour.

Healthy plants of kamahi, toro and quintinia at all localities appeared to retain leaves for two years and tawari or silver beech for about five years but unhealthy plants shed many old leaves not long after bud break and in extreme cases held leaves for less than one year.

Some of the damage appeared to arise during leaf development. Scorch and necrotic spots were evident in all localities on new leaves of silver beech, toro and quintinia immediately after the end of foggy weather in January 1982 and 1983 (Table 4.2). Similar damage was not evident on tawari or kamahi. In silver beech scorch resulted in considerable loss of new leaves before they had completely developed (Table 4.2) and conspicuous damage to the remaining leaves. During the same period the cuticle in many plants was glossy and in quintinia was also sticky suggesting that the cuticular waxes were incompletly hardened.

Seedling vigour

Regeneration in mature upland stands was often clustered around old stumps and logs. This may have reflected both an escape from wet soil conditions and the potential to survive above the soil surface on logs and at tree bases in the sodden moss and bryophyte cover. "Seedlings" present in wetter stands were often strongly layered but with weak root systems (Fig. 4.7). There were striking differences in the size of the fine roots. Kamahi had thin fibrous roots concentrated close to the stem. Quintinia and silver beech had well developed fine roots of moderate size but in tawari and kaikawaka primary roots were stout (Fig. 4.8). Root systems were usually well developed on silver beech seedlings; were prolific on the few plants of kaikawaka examined; but appeared to be inadequate on all specimens of tawari, on both good and poor sites.

The root/shoot ratio of seedlings at the upper altitude sites was low for all species except quintinia because of restricted root development coupled with heavily wooded stems carrying few leaves (Table 4.3). A high root/shoot ratio

Table 4.2

Comparison of leaf damage on silver beech shoots of current and last years growth between sites at Te Aroha 24/1/82

| | % leaves lost | | Scorch | Necrotic spots (number/leaf) | |
|---|---|---|---|---|---|
| | Current | last | current | current | last |
| 800 m healthy stand | nil | 6 | nil | 13 | 5 |
| Summit good stand | 4 | 70 | 5 | 92 | 25 |
| 850 m unhealthy stand | 22 | 95 | 12 | 252 | 230 |

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

Fig. 4.7. Root systems of kaikawaka (left) and kamahi (right). Seedlings of kaikawaka have deep extensive root systems whereas kamahi have shallow root systems with many dead secondary branches and few fine roots.

Fig. 4.8. 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. Kaikawaka and tawari have thick roots but the other species have thin roots. The kamahi plant has a strong coppice root to the right, which was cut when collected.

Table 4.3

Root shoot ratios and other characteristics of seedlings from Te Hunga summit good and poor sites

| | Quintinia | Tawari | Beech | Kamahi | Kaikawaka | all |
|---|---|---|---|---|---|---|
| Poor site 850 m | | | | | | |
| 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/shoot | 0.58 | 1.58 | 1.50 | 0.39 | -- | 1.49 |
| Good site 750 m | | | | | | |
| 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/shoot | 0.63 | 1.38 | 1.45 | 0.90 | 0.36 | 0.97 |

Values mean of 10 seedlings of each species, 15-30 cm in height, from each site.

and high root/leaf ratio in quintinia, was caused by roots and shoots containing few or small leaves and few fine roots in proportion to woody shoots and primary roots. These plants appeared to have died back from a more vigourous state resulting in a balanced reduction in crown and roots. The disparity in th leaf/shoot ratio of kamahi between sites resulted from differences in the foliage vigour which was readily seen in leaves of plants from the lower altitude site (Fig. 4.3) whereas the leaf/shoot ratio in quintinia remained low because of poor seedling vigour.

## Root systems and patterns in mature plants of the upland stands

Examination of windfalls and forced uprooting of stumps up to 7 cm basal diameter along a track cut on Te Hunga two years previously showed that the primary laterals of most species were confined to the top 2- 5 cm of the peaty soil. Tawari and silver beech root systems were shallow and with frequent lenticels where roots were exposed at the surface. Kamahi, toro and quintinia appeared to be deeper rooting, with few surface roots and few fine roots. Basal swelling and enlarged lenticels were quite evident on the lower stem. Conifer seedlings were difficult to uproot and seedlings of kaikawaka (*Libocedrus bidwillii*) had deep extensive root systems (Fig. 4.7).

In seral stands the stems of broadleaved species were clumped, suggesting that they originate from layered stems. In mature stands older healthy trees were clumped in groups on raised mounds on logs or perched apparently arising on logs which had subsequently rotted away (Fig. 4.9). Roots were sparse between mounds. Soil pits and Dutch auger cores show few roots below the surface layer although live roots of mature kaikawaka were found at or near bedrock adjacent to live trees even in wetter areas.

Fig. 4.9. Contorted root systems in an open stand. Many root systems such as that to the left or bottom right suggest that seedlings originated on stumps or logs.

Phenology

Typically, bud break began in early October at the lower altitude sites and in each species occurred at the highest altitude about 4 weeks later (Table 4.4). However bud break on adjacent trees could occur over a period of several months and may permit at least some trees to put on increment in adverse years. A large difference in bud break date was noted in tawari and silver beech between Te Aroha and Te Hunga in both 1981/2 and 1982/3. It was completed by early December on Te Aroha but a 6 week period of wet and cloudy weather from mid-November to early January 1981/2 and poor weather in 1982/3 caused the flush to last well into February at Te Hunga.

Leaves on shoots of miro, toatoa, tawari, and silver beech developed simultaneously in a single whorl or as a short shoot of ten or more pairs of leaflets but in kamahi, toro and quintinia single leaves or pairs of leaves appeared throughout the season. At Te Aroha development and hardening was rapid in silver beech but was much slower in tawari so that elongation and maturation in the latter was not complete until late February. Maturation on vigorous plants of silver beech was followed by progressive elongation of the leading shoots.

At the summit of Te Hunga the main leaf fall of old leaves in a wide range of species occurred in January, within two weeks of bud break, and before the new leaves were mature. At altitudes below 700 m leaf fall was not conspicuous except in tawari where falls occurred in November and March following several weeks of dry weather. The most spectacular leaf falls, however, occurred on Mt Te Aroha, where whole trees of red beech Nothofagus fusca were denuded at bud break. Red beech is common only on Mt Te Aroha where it is striking that fog occurs at a higher altitude and is less frequent than elsewhere in the ranges.

New root growth began at different times in the two study years. In 1982 it was not evident in February although it was present in the early autumn (March); in 1983 it was evident by early summer (January) following a dry winter and spring possibly because of lower soil moisture contents.

Table 4.4

Timing of bud break and leaf development summer 1981/2 and 1983/3

| | Bud break | | Fully developed | | Fully hardened | |
|---|---|---|---|---|---|---|
| 800 m Te Aroha | | | | | | |
| Silver beech | 7/11/81 | 9/10/82 | 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 | 9/12/82 | 19/12/82 | 14/1/82 | 19/1/83 | 2/82 | 3/83 |

## Soil moisture contents

Upland soils are completely waterlogged for most of the year (Fig. 5.5, Climate Chapter) but differences in soil moisture content were evident in the Te Hunga stands at the end of the dry 1981/82 summer (Table 4.5). Soil moisture content in the more open stands was lower than in the adjacent healthy stands on a similar soil type except in the very wet areas. Dense kaikawaka/silver beech stands on deep brown loams have a conspicuously wetter soil than silver beech stands on the well developed podsols. Drier soils in seral stands probably reflects differences in radiation levels and ventilation at the forest floor. This is supported by differences in soil temperature between the stands since temperatures at 20 cm depth in the most open stands are up to 1.9° C higher than in adjacent the dense kaikawaka/silver beech stands (Table 4.5).

## Stand structure

Mortality resulted in stands of Melicytus ramiflorus and Hedycarya arborea scrub in the tawa (Beilschiedia tawa) forests; dense horopito (Pseudowintera axillaris) or Cyathea smithii in tawari forests; and dense quintina /kamahi shrubland in the silver beech forests (Jane and Green 1983b). All these forest types are characterised by a range of damage intensity and similar symptoms in the residual vegetation. Hence it will suffice to describe three localities in detail. Detailed quantitative descriptions are in Appendix 1.

### 1. Tawari forest - Te Rere bald

At Te Rere bald two ages of mortality are evident on aerial photographs and until recently goats (Capra hirca) have prevented forest regeneration (Fig. 4.10, Fig. 3.5B).

Table 4.5

Soil moisture content and mid-morning temperatures of soils from adjacent closed mature and open seral stands at 850 m on Te Hunga taken on 15/2/82, at the end of 4 weeks without rain.

| | good | | poor | |
|---|---|---|---|---|
| | moisture | temperature | moisture | temperature |
| | (%) | (°C) | (%) | (°C) |
| Kaikawaka/tawari | | | | |
| 1 | 129.3 | 12.1 | 93.9 | 13.5 |
| 2 | 145.2 | 12.2 | 61.8 | 14.0 |
| Silver beech | | | | |
| 1 | 66.7 | 12.1 | 54.5 | 12.5 |
| 2 | 78.6 | 12.2 | 41.7 | 13.4 |
| 3 | 58.7 | 12.6 | | |
| 4 | 62.9 | 12.1 | 48.9 | 14.0 |
| 5 | 57.6 | 12.5 | 70.6 | 13.4 |

Differences are not statistically significant in a two by two test. Soil moisture content of specimens from 20 cm depth, oven dried at 105°C. Soil temperatures taken at 20 cm depth between 10 am and 12 noon.

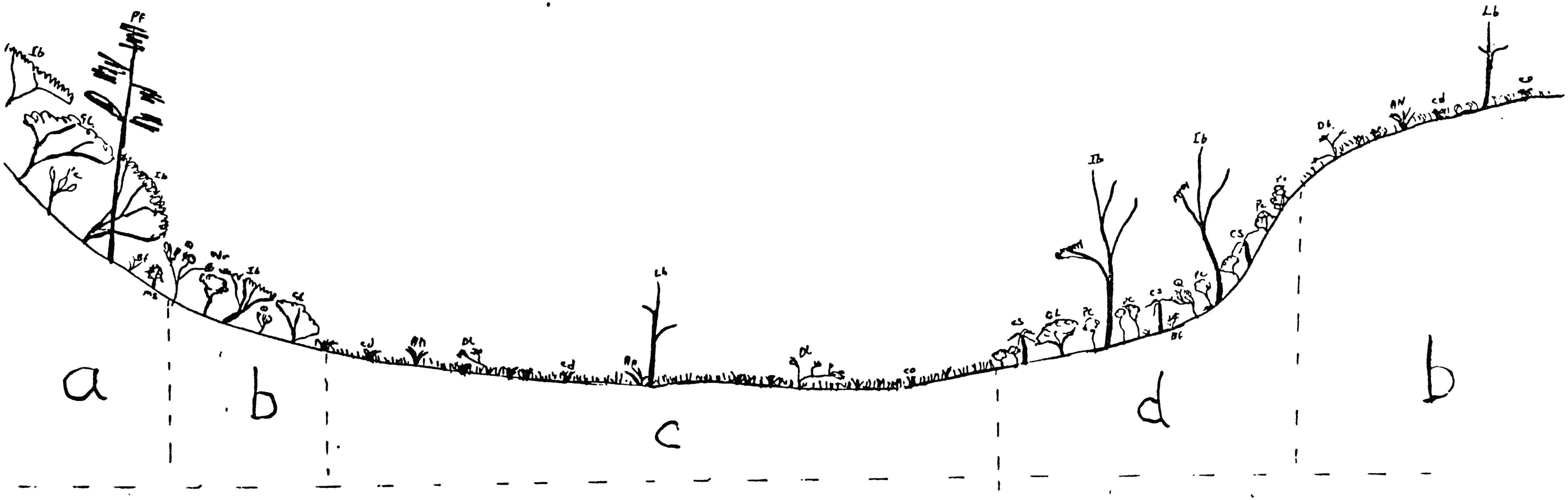


Fig. 4.10. Schematic cross section of affected stands at Te Rere Bald. (a) mature tawari forest. (b) older affected forest. (c) grassland. (d) recently effected forest. Symbols are Ib, tawari; Nm, silver beech; Pc, pepperwood.; Cs, *Cyathea smithii*; Pf, miro; Ud, *Uncinia dissita*; An, *Astelia nervosa*; Gl, broadleaf; Dl, neinei; Q, quintinia; Ms, toro; Wr, kamahi; Cf, *Cyathodes fasciculata*; Lb kaikawaka; Bf, *Blechnum fluviatile*.

### (a) Mature forest

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

### (b) Older affected forest

Dead kaikawaka and scattered miro, tawari and silver beech, usually with partially dead crowns, form an overwood to a dense shrubland. The main canopy comprises tawari, quintinia, toro, horopito, broadleaf (*Griselinia littoralis*) and *Coprosma foetidissima* and in patches quintinia or horopito may form dense stands. In more open areas a variety of ferns are present and *Astelia* spp. or *Gahnia* species may predominate.

### (c) Open grasslands

There is a well defined boundary to the grassland which is dominated by *Uncinia dissita*, *Carex secta*, *Heirachloe redolens* and *Microlaena avenacea*. Spars of kaikawaka are prominent and scattered prone, windblown neinei (*Dracophyllum latifolium* and *D. pyramidale*) stand above the grassland. *Rubus cissoides*, seedlings of kamahi, quintinia, horopito, pate (*Schefflera digitata*) and many other species are present within the 1 m high grass cover.

### (d) Affected tawari forest (Fig. 3.4B)

In the slope shadow there is a gradual transition to heavily affected tawari forest. The canopy of the old stand ranges from about 4 m to over 10 m height in the most protected area and contains dead and damaged tawari and miro. The current shrubland rises gradually out of the grassland to about 3 m high, 5 m from the margin. Horopito and *Cyathea smithii* form the main canopy but *Schefflera digitata*, *Coprosma australis*, *Hedycarya arborea* *Rubus cissoides* and

Melicytus ramiflorus are locally common. All species show some signs of ill-thrift. Some ground ferns are present particularly Blechnum fluviatile but the canopy density frequently precludes ground cover.

Soils throughout the transect are yellow brown loams about 1 m deep but much shallower on the high knoll. Gleying is common and local podsols are present under silver beech. Vegetation types before mortality were probably similar on on the two pairs of sites (a) with (d) in the slope shadows and (b) with (c) on the flatter areas.

### 2. Mature silver beech - Te Hunga. (Fig. 4.11)

#### (a) Mature Silver Beech

The mature overwood of silver beech is about 25 m tall and somewhat open. A light sub-canopy at 12 m comprises tawari, quintinia, miro and small silver beech. A sparse ill-defined shrub tier of similar composition merges with a low shrub tier that includes Cyathea smithii, Alseuosmia macrophylla, Coprosma australis, C. tenuifolia, numerous sedges and ferns and abundant bryophtes and liverworts.

#### (b) Open stand

There is a gradual transition to severely damaged forest. The canopy and overwood becomes more sparse and trees appear unthrifty with many dead branches and broken crowns. The sub-canopy tiers are also more open and the ground cover is often dominated by dense Gahnia pauciflora or Blechnum minus.

#### (c) Seral shrubland

In the most open areas a dense shrubland dominated by quintinia, kamahi, tawari and Alseuosmia macrophylla prevails. Patches of Gahnia pauciflora are common and large clumps of Astelia species fill canopy openings.

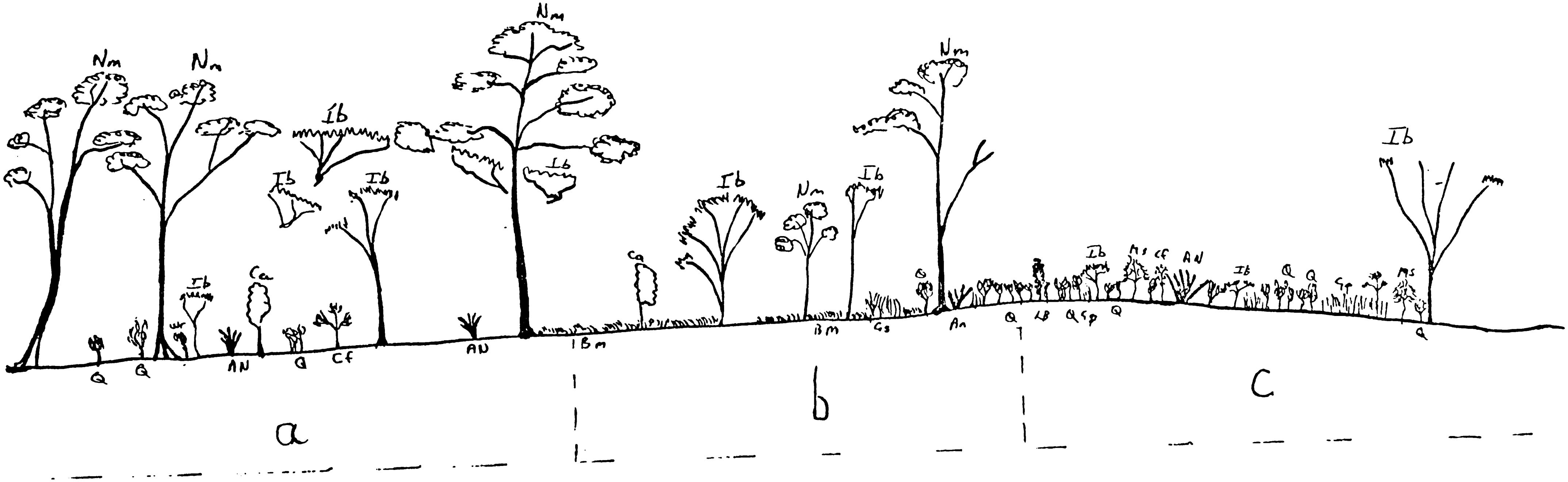


Fig. 4.11. Schematic cross-section of affected and unaffected silver beech stands. (a) Healthy, (b) partial mortality, (c) seral stand. Abbreviations are as for Fig. 4.10 but add Am, *Alseuosmia macrophylla*; Bm, *Blechnum minus*;Ca, *Coprosma australis*; Gp, *Gahnia pauciflora*;

The soils appear better drained in the mature stand but localised podsols are common in a predominant gleyed yellow brown loam up to 1.5 m deep.

3. Silver Beech/ Kaikawaka - Te Hunga (Fig. 4.12)

(a) Mature Stand (Fig. 4.13).

Emergent kaikawaka, yellow silver pine (Dacrydium intermedium) and silver beech over sub-dominant tawari form a dense canopy at about 15-20 m of elfin nature. There is no sub-canopy, but an sparse shrub tier at 2 m contains seedlings of tawari, horopito, quintinia, kamahi and toro. The ground is frequently covered by a dense carpet of Schistochila spp. with other liverworts, and mosses. In canopy gaps Pseudopanax colensoi, P. simplex, toro and tawari form prominent groups.

(b) Seral shrubland

There is a sharp transition to a dense shrubland 2-3 m high dominated by tawari, silver beech, quintinia, toro, Coprosma dodoneaifolia, and kaikawaka. Spars of kaikawaka are common but silver beech are rare. Seedlings are abundant and Astelia species and Gahnia pauciflora fill canopy gaps although Sphagnum and other mosses and liverworts fill the wetter hollows.

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

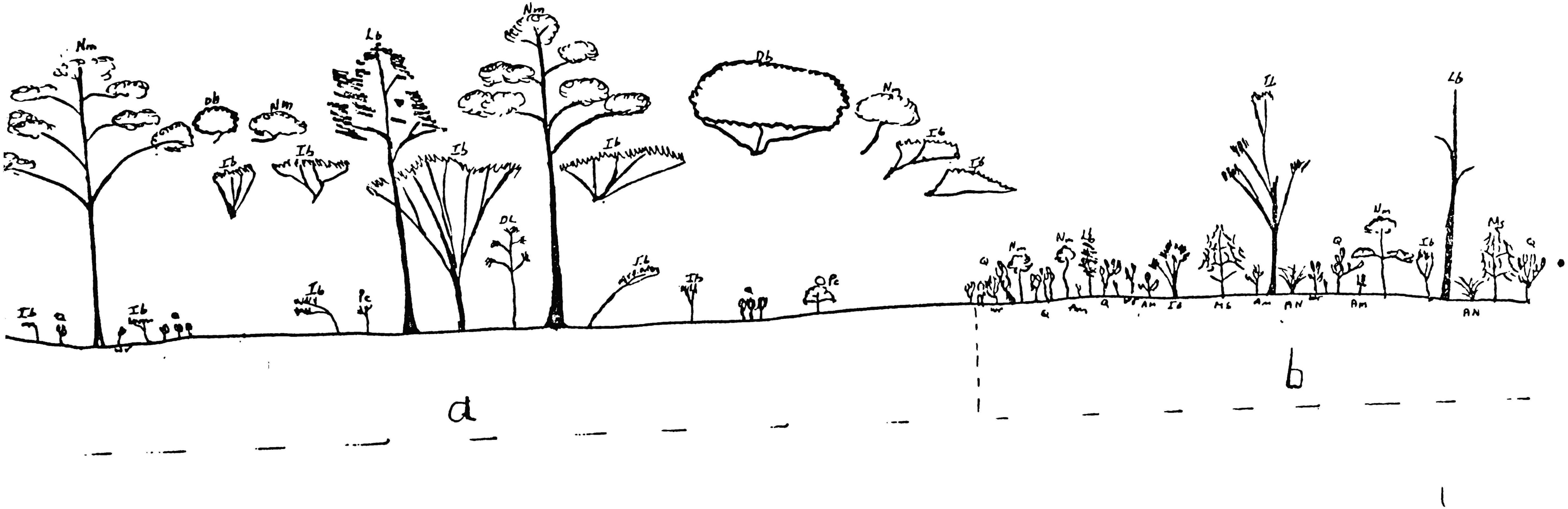


Fig. 4.12. Schematic profile of a silver beech/tawari stand. (a) Mature stand (b) seral stand. Abbreviations as for Fig. 4.10 and Fig. 4.11 but add Db, <u>Dacrydium biforme</u>

Fig. 4.13. 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. 4.11 and thus has back lighting.

## DISCUSSION

### Stand dynamics

In mature stands seedlings are often abundant but saplings and poles are rare. Even in more open stands of silver beech poles of canopy species are uncommon although seral species are present as long-lived shrubs usually less than a metre in height. The lack of understory in the dense stands is probably caused by low light intensities but in the more open beech stands the reasons for a weak shrub tier are obscure. High fog frequencies may lower total carbon fixation to marginal levels for seedlings in upland mature stands (Huber 1978, O' Rourke and Tejung 1981). Seedling turnover may also be high because of drought sensitivity in plants restricted to old stumps and logs raised above the terrain with low root shoot/ratios (Nambiar et al. 1979, Tesky and Hinckley 1981).

The surviving mature stands are perched at high points on the crest of the range in a zone of high fog occurrence. The wetness of soils suggests the closed nature of the stands, which maintains low soil temperatures and low evaporation, is in an important factor in maintaining the stands. Several factors suggest that the stands, particularly those of dense silver beech/ kaikawaka, have a high chance of complete collapse when mortality begins. Redevelopment of the stand cannot begin from shrub tier plants since they are absent and changes in the seedling environment can be expected to result in mortality in this tier (Pereira and Kozlowski 1977b) so that regeneration must begin anew. Partial stand breakdown will have a similar effect. Seedlings which survive must tolerate higher light intensities and increased water stress and surviving trees are also more exposed and may become prone to wind damage.

Neverthless, the composition of the stands is unlikely to change radically. The dominant species are present in each transect in all stands although their relative abundance and dominance varies markedly between affected and unaffected stands. Horopito, quintinia and kamahi are present as understory plants or seedlings in mature stands but become dominant in seral stands. Silver beech, kaikawaka and tawari, the dominants in unaffected stands are present in low numbers in the seral stands but in many cases their densities in the seral stands are above, or close to, values in mature stands, thus assuring a adequate representation in mature forest.

The broken nature of the canopy in affected areas and the presence of older emergent kaikawaka and silver beech suggests that the damage may be repeated with differing intensities on the same site. After each period of mortality some plants of the slower growing "climax" species of lesser susceptibility, are able to attain dominance before the seral plants become re-established. It is therefore suggested that that a gradual re-establishment of the former forest structure is achieved through the survival of the main canopy species during minor disturbances.

### Role of fog

Leaf damage and leaf fall, particularly on silver beech during the spring, appeared to be related directly to the long periods of cloudy weather. It is well known that lowered temperatures and light levels (Kozlowski 1971) slow leaf development and maturation, and may also be impair stomatal development (Brainerd and Fuchigami 1982). This may be accentuated because prolonged fog and cloud followed by fine weather produces strongly contrasting environmental conditions (Leigh 1975). This could result in water stress in the following fine weather leading to the observed scorch and leaf fall (Pereira and Kozlowski 1977b).

During the fog periods development of new leaves in the fog forests appeared to be completely halted. Fine hot days in January, exposing new leaves with unhardened cuticles to the full force of the mid-summer sun producing nearly tropical conditions will accentuate the stresses. Reduction in leaf size, such as that observed in silver beech, kamahi, toro and quintinia, could also result (Pallardy 1981, Syvertson 1982) and may trigger a major leaf fall. Shoots of plants such as kamahi and quintinia, with damaged new leaves and few leaves to sustain growth and produce further new leaves, may then show decreased leaf size through the season. Low soil temperatures in the denser stand may intensify damage (Tesky and Hinckley 1981) by delaying root growth until after bud break, as occurred in 1981/2 and produce a root/shoot imbalance (Table 4.5).

## Waterlogging

The marked reduction in leaf size, prominence of lenticels and the basal swelling in seedlings of kamahi and quintinia is characteristic of plants undergoing or adapted to prolonged flooding or waterlogging (Hook et al. 1972, Kozlowski 1976, Coutts and Armstrong 1975, Bradford and Yang 1981, Kawase 1981). The large numbers of lenticels in tawari and silver beech and thin bark in kaikawaka are also possibly important adaptations (Kozlowski 1982). Waterlogging may intensify symptoms of water stress (Kawase 1981) by reducing overall vigour, reducing root/shoot ratios, and produce marked differences between adjacent trees because of minor site differences (Levitt 1972).

There is a problem in distinguishing effects of temporary soil flooding and prolonged waterlogging. Temporary flooding of soils induces ethylene production that produces stomatal closure, leaf senescence and epinasty and a many physiological changes related to anaerobic conditions (El-Beltagy and Hall 1974, Bradford and Yang 1981, Bradford et al. 1982) but apparently has no effect on leaf water potential because of stomatal closure (Jackson et al. 1978, Tang and Kozlowski 1982, Jane and Green 1983d). Leaf shedding may occur later (Kozlowski 1976, Pereira and Kozlowski 1977a). Prolonged flooding, covering the soil surface, may produce fresh adventitious roots, enlarged lenticels in a wide range of species (Gill 1970, Clemens et al. 1978, Kozlowski 1982) and a resumption of normal stomatal activity (Pereira and Kozlowski 1977a). New leaves formed after flooding may have a reduced size (Newsome et al. 1982) and growth is generally reduced but water stress responses may be normal (Pereira and Kozlowski 1977b). Similar responses are found in all species on affected sites in the study areas.

Waterlogged soils, in contrast to flooding, tend to have the soil surface above the water level and aeration may extend to a few centimetres depth. Adaptation to the habitat might be expected in the species present but there may also be sufficient lowering of the water table in summer to permit deeper soil aeration and deeper plant roots. On the other hand severe lowering of the water table during drought might be expected to result in severe water stress followed by widespread mortality (Newsome et al. 1982). Retreat of the water table may give rise to pronounced boundaries to the affected areas as often seen the study areas (Jane and Green 1983b).

Waterlogging could explain the limited distribution of red beech in the study areas, particularly since Elder (1965) notes that it was also confined to areas with lower fog frequency in Ruahine Ranges. Similarly the general poor vigour and high susceptibility of kamahi and quintinia on the upland sites and intensification of symptoms of poor vigour in the more foggy areas suggests a low tolerance to waterlogging. The apparent vigour of the mature stands is difficult to explain. The closed mature stands may permit the interior to remain cooler and fog interception may maintain higher soil moisture contents and hence reduce water stress. On the other hand recurrent mortality in the seral stands may result from the greater fluctuations in the soil water table and from greater exposure. The close link between water stress and waterlogging is well recognised (Kozlowski 1982) and results from the reduced root systems and anaerobic soil conditions. Many of the features of poor vigour seen in the Kaimai Ranges correspond those expected of waterlogged plants. Fog may affect vegetation composition and produces conditions of soil waterlogging predisposing the vegetation to drought damage. Thus it appears possible that the widespread mortality and the current marked symptoms on seral vegetation are caused by water stress through waterlogging.

## CLIMATE PATTERNS AND TRENDS WITHIN THE KAIMAI RANGES

### INTRODUCTION

Marked variations in weather occur locally over periods as short as several minutes (Oke 1978) and over distances of a few metres (Geiger 1965). Small scale site changes moderate or intensify the effects of the weather to such an extent that data from study sites may not correlate closely with conditions at nearby permanent weather stations. As a result even the crudest of measurements, establishing local climatic characteristics, may be invaluable in ecological studies. Variation in microclimate is sufficient to produce differing vegetation types between slopes of different aspect (Daubenmire 1968, Geiger 1965) or over height changes of a few metres (Geiger 1965, Ure 1950). Temperature maxima or minima can be sufficient to determine species distributions along an altitudinal gradient and isotherms can mark out recognisable bounds to forest types and classes (Wardle 1964, Daubenmire 1968, McKelvey 1973, Wardle 1980). Gradients in precipitation are no less important but they may give rise to more gradual changes in forest composition and structure.

Events of an episodic nature may have a severe impact on vegetation. High intensity storms are often localised phenomena causing extensive windfall damage and slope erosion along a narrow path (Coulter 1967). Drought stress may cause localised mortality on sensitive sites of shallow soils (Coulter 1966a, Finkelstein 1971, Atkinson and Greenwood 1972, Ashton 1976) or may place a wide range of species at risk to disease (Peace 1960, Schoenewiss 1975, Tobiessen and Buchsbaum 1976). The resultant epidemics may lead to extended periods of mortality which can lead to major compositional changes in the vegetation (Ellis

1972, Wardle 1980). Indirect effects of climate on the ecosystem may also be important. Extremes of precipitation have a marked effect on the soils, producing structural changes such as fracturing of the solum during drought (Taylor and Pohlen 1962, Resulovich 1967) or waterlogging and gleying during periods of above normal precipitation. Effects on the root systems are then reflected in plant vigour.

The spatial distribution of vegetation mortality in the Kaimai Ranges, North Island, New Zealand, appears to be related to climatic discontinuity produced by the prevalent fog and low cloud on the ranges and the temporal incidence of mortality appears to be linked to severe drought years which may be dated and possibly predicted through dendrochronological techniques. For these reasons the climate data for the Kaimai Ranges have been examined in considerable detail.

## DATA SOURCES AND COLLECTION

The locations of the main meteorological stations around the Kaimai Ranges and periods of record are noted on Fig. 5.1. Rainfall records at Te Aroha began in 1889 and temperature records began on the same site in 1907. Between 1896 and 1907 records are fragmentary but from 1908 they can be regarded as continuous. The continuity of the record was not significantly affected when the station was shifted a few metres in 1954 (Hessell 1980). Site modification due to local clearance of forest and development of the town is regarded as insignificant compared with changes at urban meteorological stations such as at Auckland and Christchurch (Tomlinson 1976).

Devereux (Devereux 1910) began rainfall records at Waihi in 1899. Temperature records began in 1907 but many discontinuities and shifts in station location limit the value of the data. From 1960 a number of climate stations were established on the fringes of the forest, at altitudes of up to 300 m (Fig. 5.1). These provide useful detail for establishing climatic patterns but are of of limited value for determining long term trends. In 1967 a meteorological station was established within the forest, at the summit of Mt. Te Aroha. From 1967-70 the instruments were read daily but in more recent years instruments were only read when clerical staff were present, five days a week or less. As a result Monday readings are the accumulated values for the previous three days and there may be breaks in the record extending over several weeks during holidays. The Waiorongomai Hydrological Representative Basin on the south west side of Mt. Te Aroha contains three automatic rain gauges placed at 100, 300 and 800 m altitude.

River gauging stations were established within the Waihou river system at Karangahake in 1956, at the mouth of the Waiorongomai Hydrological Representative Basin in 1967, at Te Aroha in 1969, and Shaftesbury in 1969 (Fig. 5.1). The base flows from these stations provide a useful indication of the long term effects of rainfall trends on soil moisture storage levels.

### Supplementary local data

A study ridge was selected on Te Aroha, Te Rere and Te Hunga and instruments placed at a range of altitudes (Table 5.1). The Te Rere and Te Hunga ridges were traversed weekly from September 1980 to April 1981 and fortnightly for the next year. Te Aroha sites were visited monthly from October to April each year. As far as practical instruments were placed adjacent and successive measurements were made in the same place.

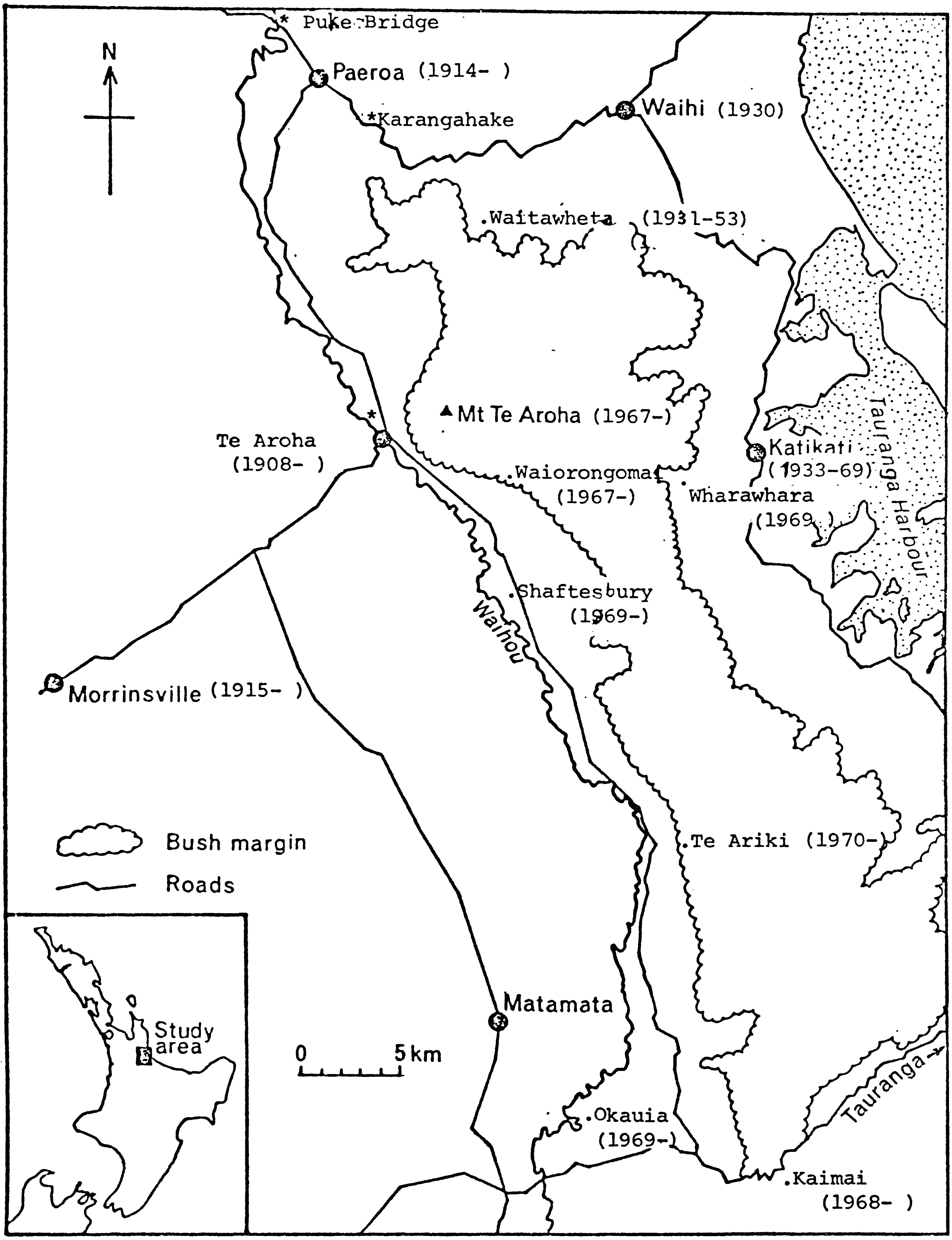


Fig. 5.1 Location of meteorological stations and river gauging stations around the Kaimai Ranges. * indicates approximate location of gauging stations. Dates by names are the establishment and closing dates for rainfall records.

Table 5.1

Location of recording stations on the three study ridges.

| | Study Area | | |
|---|---|---|---|
| Altitude | Te Hunga | Te Rere | Te Aroha |
| 300 | T S M P R | T R M S | T S M |
| 400 | T S M | T S M | |
| 500 | T S M P | T S M R | T S M |
| 550 | | T | |
| 600 | T S M P | T S M | T S M |
| 650 | T S M P | T S | |
| 700 | | T S M | T S M |
| 750 | T S M P | R | |
| 800 | T S M | | T S M |
| 850 | T S M P R | | |
| 900 | | | S M |

Instruments were : T min-max thermometers; P piche´; R rain gauges; S soil temperatures; M soil moisture samples. Summit height at Te Hunga was 850 m; Te Rere 750 m (bush line 700 m); and Te Aroha 950 m.

Simple min-max thermometers were established, without screens, under the canopy in three study areas and read at each visit. Continuous records were made at selected thermometer stations over monthly periods with a Grant thermograph. Soil samples were collected with a soil auger from 20 cm and 50 cm depth at monthly intervals from September to April for gravimetric soil moisture determination. Soil temperature at 20 cm depth was recorded at each thermometer station at each visit. Rain gauges were placed in suitable open areas and read at each visit. Piché evaporimeters were placed at a number of thermometer stations on Te Hunga from November 1981 to April 1982 and read at irregular intervals.

## SYNOPTIC SITUATIONS

New Zealand as a whole is largely influenced by the westerly movement of frontal systems (de Lisle 1967, Maunder 1973) and much of the local rain comes from a westerly quarter. The study areas are affected by two storm patterns. Summer tropical storms, originating to the north of New Zealand, characteristically sweep southwards following the east coast of the North Island to the Coromandel Peninsula, just north of the study areas, and then veer westward out through East Cape bringing intense storms to the ranges (Devereux 1909, Barnett 1938). Winter storm fronts sweep northeastwards along the central mountain chain of the North Island to Mt. Ruapehu at the centre of the Island and then swing westward to East Cape and only occassionally continue northward to give cold rains or snow to the Kaimai Ranges. The relative dominance of these patterns is determined by the location of stable blocking high pressure systems situated to the north of the Bay of Plenty and can give long dry or wet periods (Maunder 1973, Tomlinson 1980a). The general movement of these tropical high pressure systems appears to be related to sunspot activity (Tomlinson 1980b, Salinger

1979) and gives rise to long period oscillations in weather patterns.

The effect of the winter and summer storm patterns is to produce different weather patterns in Waikato basin, to the west of the ranges, and the Bay of Plenty, to the east (Coulter 1966b). For instance coastal sea breezes may moderate the climate of the Bay of Plenty at times when the barrier of the ranges leads to calm hot or frosty conditions in the Waikato. As a result the region is usually separated between two weather districts (Salinger 1979, Tomlinson 1980b) and correlations between climatic parameters for Te Aroha and Waihi are poor (Table 5.2).

## FOG AND LOW CLOUD

Low cloud or fog along the crest of the Kaimai Ranges is very frequent (Martin 1889, Clayton-Greene 1976) and, where it occurs, modifies all other weather parameters. Records kept at Mt. Te Arohoa during 1969-72 indicate an average of 200 fog days per year at 9 am. Observations made during the wet summer 1980-1981 show fog commonly persisted for much of the day (Table 5.3). Average figures indicate that the cloud base is about 150 m below the summit in each of the study areas (Jane and Green 1983a) but there is considerable variation in the cloud base with season, weather conditions, time of the day and the mechanism of fog formation.

### Mechanisms of fog formation

Fog formation on the Kaimai Ranges normally occurs through thermal or air pressure inversions with the exact mechanism depending on the weather conditions:

1. Air ponding under calm conditions can produce lowland fogs in winter (Table 5.4) which rarely extend above 300 m altitude although on

Table 5.2

Correlations between climatic parameters portrayed as a diagonal matrix.

| | T TOT | W TOT | T DEC | T JAN | T FEB | T MAR | T TMAX | T SCRF | W JAN | W DEC | W FEB | W MAR | W TMAX | W SCR | W GRN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TEA TOT | 1.00 | | | | | | | | | | | | | | |
| WAIHI TOT | -0.23 | 1.00 | | | | | | | | | | | | | |
| TEA DEC | 0.13 | 0.21 | 1.00 | | | | | | | | | | | | |
| TEA JAN | 0.30 | -0.01 | 0.01 | 1.00 | | | | | | | | | | | |
| TEA FEB | -0.05 | 0.03 | 0.13 | -0.03 | 1.00 | | | | | | | | | | |
| TEA MAR | -0.28 | 0.20 | 0.02 | 0.09 | -0.02 | 1.00 | | | | | | | | | |
| TEA TMAX | -0.16 | 0.32 | 0.15 | -0.15 | -0.31 | 0.10 | 1.00 | | | | | | | | |
| TEA SCRF | 0.07 | -0.23 | 0.07 | 0.42 | 0.08 | -0.03 | -0.08 | 1.00 | | | | | | | |
| WAIHI JAN | 0.07 | -0.22 | -0.00 | -0.02 | 0.03 | 0.23 | -0.19 | 0.16 | 1.00 | | | | | | |
| WAIHI DEC | 0.32 | -0.16 | 0.14 | 0.01 | 0.15 | -0.15 | -0.08 | -0.11 | 0.04 | 1.00 | | | | | |
| WAIHI FEB | 0.02 | 0.32 | 0.18 | 0.18 | 0.07 | 0.10 | 0.05 | -0.02 | 0.03 | -0.11 | 1.00 | | | | |
| WAIHI MAR | 0.12 | -0.04 | 0.31 | -0.06 | 0.23 | -0.05 | 0.01 | 0.08 | -0.01 | 0.12 | -0.11 | 1.00 | | | |
| WAHIT MAX | -0.27 | 0.22 | 0.03 | -0.04 | -0.08 | 0.08 | 0.23 | -0.17 | -0.21 | -0.27 | 0.11 | -0.10 | 1.00 | | |
| WAIHI SCR | 0.05 | -0.17 | -0.10 | -0.19 | -0.08 | -0.25 | 0.06 | -0.11 | -0.04 | -0.08 | -0.12 | -0.03 | 0.10 | 1.00 | |
| WAIHI GRN | 0.01 | -0.13 | -0.02 | 0.12 | -0.01 | 0.06 | -0.10 | 0.26 | 0.10 | 0.08 | 0.14 | -0.12 | -0.06 | 0.06 | 1.00 |
| | T TOT | W TOT | T DEC | T JAN | T FEB | T MAR | T TMAX | T SCRF | W JAN | W DEC | W FEB | W MAR | W TMAX | W SCR | W GRN |

Codes are in two parts: area and climate parameter
Areas are: T, TEA = Te Aroha; W, WAIHI = Waihi
Climate parameters are: TOT = total rainfall; JAN, FEB, MAR = monthly rainfalls
TMAX= maximum temperature; SCR = screen frosts; GRN=ground frosts

Table 5.3

Percentage of days clear, or with cloud cover on the summit in each of the three study areas. Based on 2 hourly observations from September 1981 to April 1982.

| Location | Full day | half day | 4 hours | 2 hours | Clear day |
|---|---|---|---|---|---|
| Te Hunga | 28.6 | 57.6 | 73.3 | 79.0 | 21.0 |
| Te Rere | 26.6 | 55.3 | 65.3 | 73.3 | 26.7 |
| Te Aroha | 25.3 | 51.0 | 58.6 | 70.0 | 30.0 |

Table 5.4.

Average number of lowland fog days recorded at Te Aroha town at 9 am by seasons, from 1926-78.

| | Spring Sept-Nov. | Summer Dec.- Feb. | Autumn March-May | Winter June-Aug. |
|---|---|---|---|---|
| Number of days per month | 2.1 | 1.6 | 7.2 | 7.7 |

several frosty occasions in winter the Waikato basin was filled to the height of the lowest points on the range (550 m). These fogs rise slowly and if strong thermal inversions are present may leave the crest of the range clear and in calm, hot conditions.

High soil moisture content, producing high local humidities, may also favour fog formation particularly in calm conditions following rain but it is usually transient. During the early part of the dry 1981/82 summer fog was often present in the lowlands in the morning, rose to arrive at the range crest in the late morning and clear about three hours later. After 6 weeks without rain the fog became restricted to only a few hours in the morning or was absent altogether as lowland soils probably dried out.

2. Trapped adiabatic air flows, resulting from normal air flows over mountains (Tricker 1970), produce a uniform cloud base particularly after rain.
3. Pressure inversions due to air waves produced in high speed upper winds (Grace 1977) produce capping fogs of variable height usually accompanied by strong winds. The barrier of the ranges is known to modify the dominant westerly surface air tides (Tremberth1977) and fog in these conditions appears to be related to incoming low pressure or frontal systems when rain is imminent. Cloud base levels are highest on Mt. Te Aroha, often capping only the summit, and lowest at Te Rere. On these days the cloud level rises rapidly to cap only the top 100 m of the range by mid-morning and may clear briefly in mid-afternoon. The high winds that frequently accompany the fog may cause down draughting easterly winds that can reach gale force in a standing wave from half to three kilometers from the western foot of the ranges.
4. Orographic cloud, directly associated with frontal rain, that

results from the normal rain cloud conditions. At times of heavy rain the cloud base is as low as 300 m altitude along the whole western side of the range but with light rain the cloud base may form a line at 800 m.

## PRECIPITATION AND WATER BALANCE

Mean annual rainfall increases eastward from 1500 mm at Te Aroha to 2000 mm at Waihi and southwards from 1500 mm at Te Aroha to 2500 mm at Shaftesbury at the base of the Te Rere study area (Coulter and Hessell 1980). It also increases with altitude from 1500 mm at Te Aroha town to 2000 mm at the summit of Mt. Te Aroha and field observations suggest an increase of 60 % at other points to give about 3000 mm per annum at Te Rere and Te Hunga summits.

During periods in which tropical influences predominate very high rainfalls occuring in one year may be followed by a year of very low summer rainfall because of changes in storm pattern. Summer rainfall for Waihi (Fig. 5.2) shows this strongly oscillating pattern. The absence of similar fluctuations at Te Aroha results from the predominant stable westerly conditions and emphasises the differences in synoptic influences between the two sides of the ranges. Rainfall records from Te Aroha show a long term trend of increasing rainfall and decreasing annual variability (Fig. 5.3), suggesting a lower occurrence of tropical storms and a predominence of less severe storms of southern origins in more recent years. Snow falls occur about every second year but melt rapidly and contribute little to total precipitation. The heaviest known falls occurred in 1918 and 1980 and extended down to Waihi and Te Aroha. These falls lay for several days at upper altitudes.

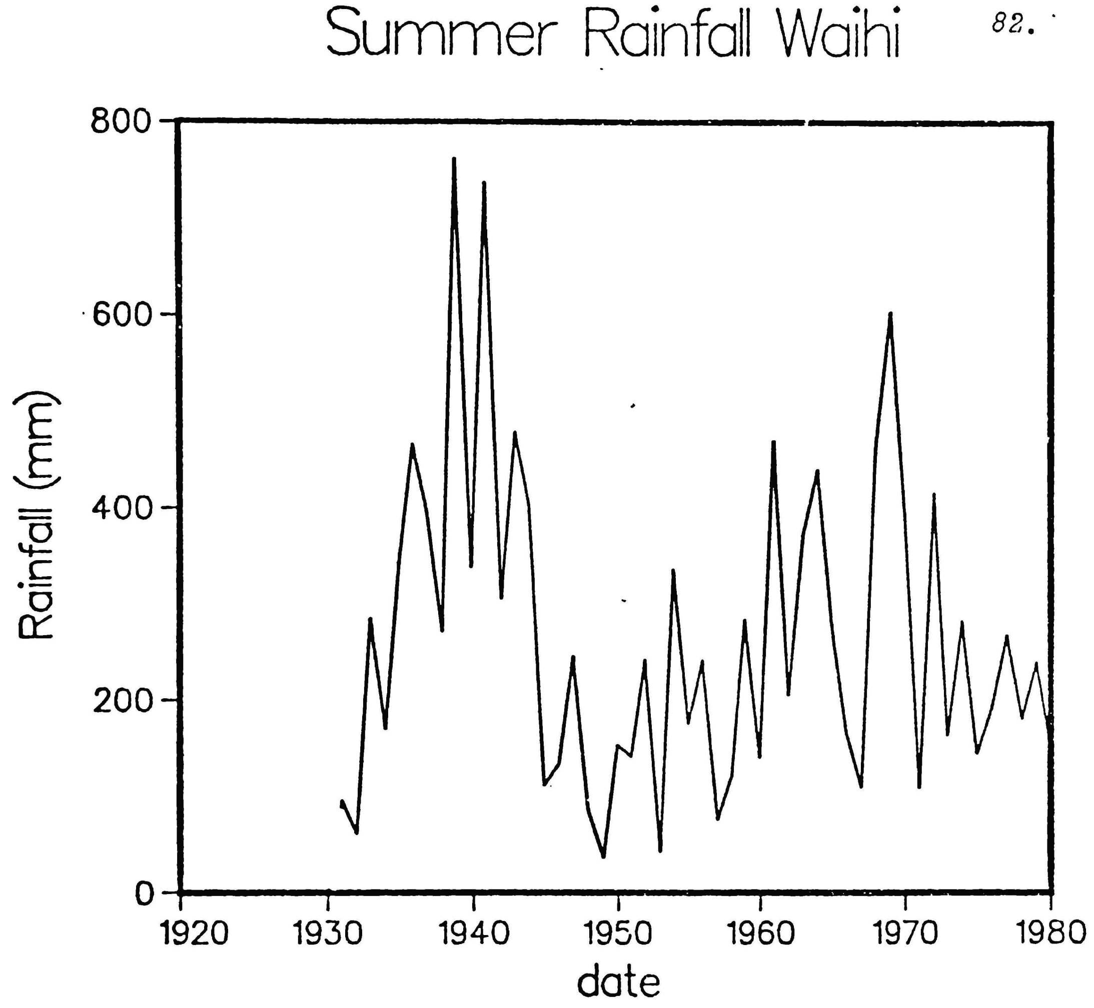


Fig. 5.2. Trends in summer (January and February) rainfall at Waihi. A strong oscillating quasi bi-annual trend suggesting influences of summer storms and a long period oscillation peaking in 1939 and 1969 suggesting

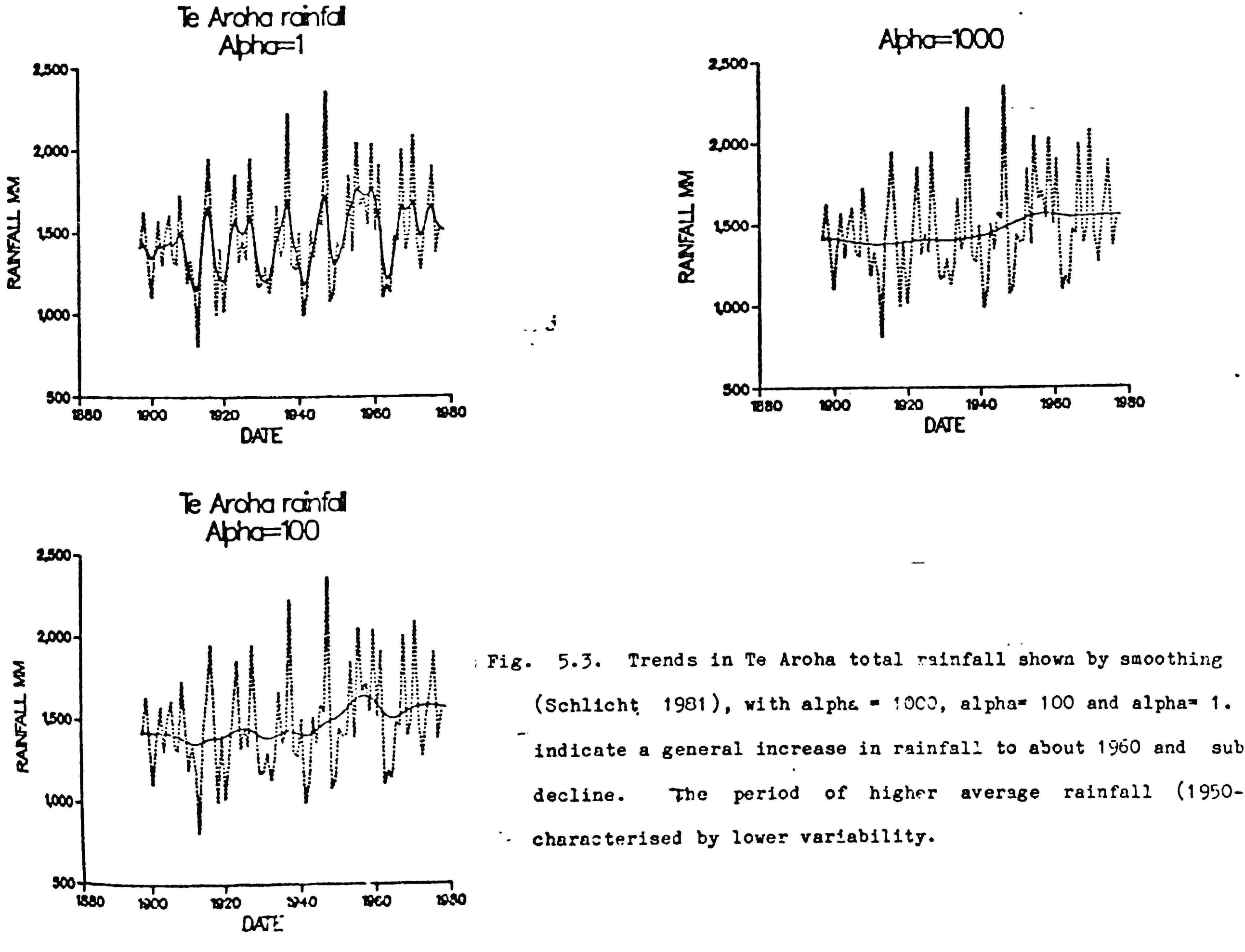


Fig. 5.3. Trends in Te Aroha total rainfall shown by smoothing splines (Schlicht 1981), with alpha = 1000, alpha = 100 and alpha = 1. Trends indicate a general increase in rainfall to about 1960 and subsequent decline. The period of higher average rainfall (1950-60) is characterised by lower variability.

Fog and accompanying light drizzle probably add considerably to annual precipitation at altitudes above 500 m. Overseas studies have indicated that fog in forested areas can contribute over 300 mm to annual precipitation (Kerfoot 1967, Chaney 1981) and examination of the rainfall records for Te Aroha summit indicate up to 2 mm per day in a normal rain gauge. Evapotranspiration is also affected by fog occurrence. Piché evaporimeters placed at Te Hunga show little difference in evaporation with altitude over periods of wet weather but a marked reduction is apparent in evaporation above 650 m during extended periods of foggy weather (Fig. 5.4). Soil moisture contents show a distinctive discontinuity above the cloud base (Fig. 5.5) reflecting the decreased evapotranspiration and increased precipitation.

### Drought

Drought intensity can be measured in a number of ways. The most commonly used measure of drought intensity is the number of days without rain or length of period with less than 5 mm precipitation. Waihi recorded 38 days without rain in 1908 and 31 days in 1928 and the longest period without rain at Te Aroha was 27 days in 1957 (Table 5.5). None of these periods were regarded as significant or severe droughts (Bondy 1950). There were a number of other periods of below normal rainfall but their effects appear localised. Finkelstein (1971) compared the severity of the 1969/70 drought with that of 1908 and noted the localised character of these and the 1928 and 1946 droughts. Other droughts reported for the Waikato or Bay of Plenty, in decreasing order of severity, occurred in 1913/14, 1918/9, 1953/4, 1927/8, 1969/70 (Bondy 1950, Kidson 1930, Finkelstein 1971).

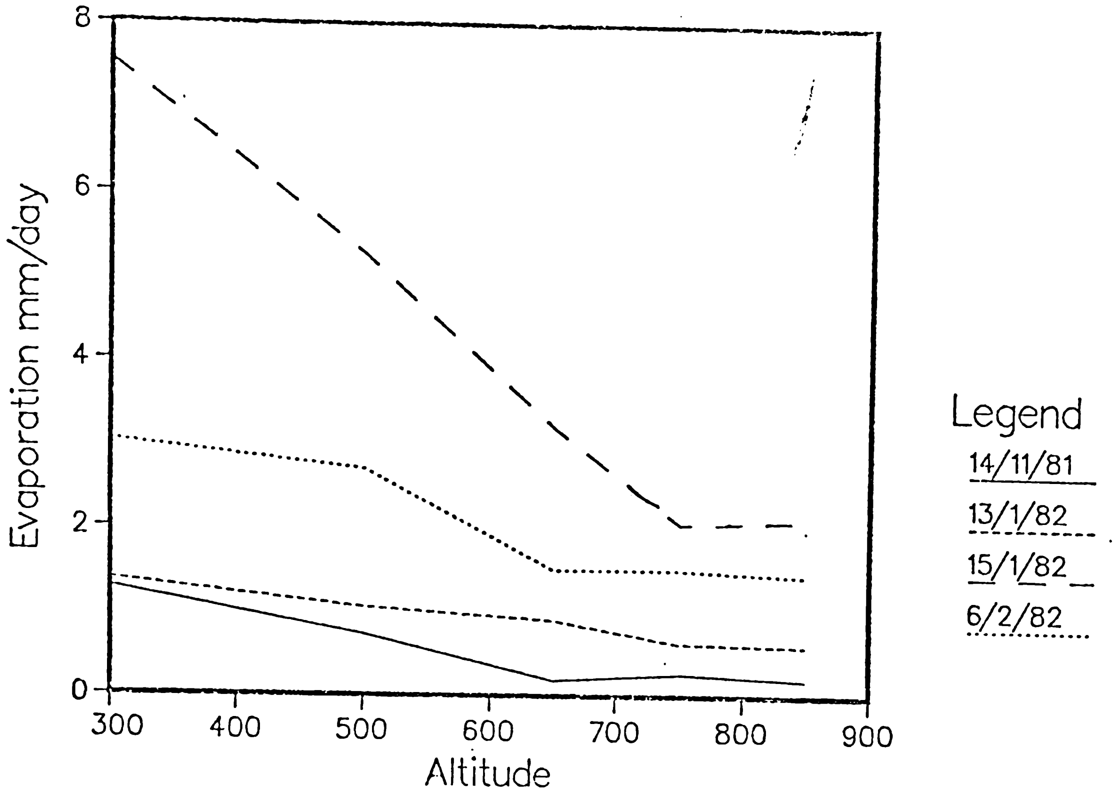


Fig. 5.4. Evaporation from Piche' evaporimeters at altitudes above and below the mean cloud base (650 m), Te Hunga.

(a) wet periods 14/11/81-13/1/82, air temperature 8-10° C.

(b) dry periods 27/12/81 -9/1/82, air temperature 12-15° C.

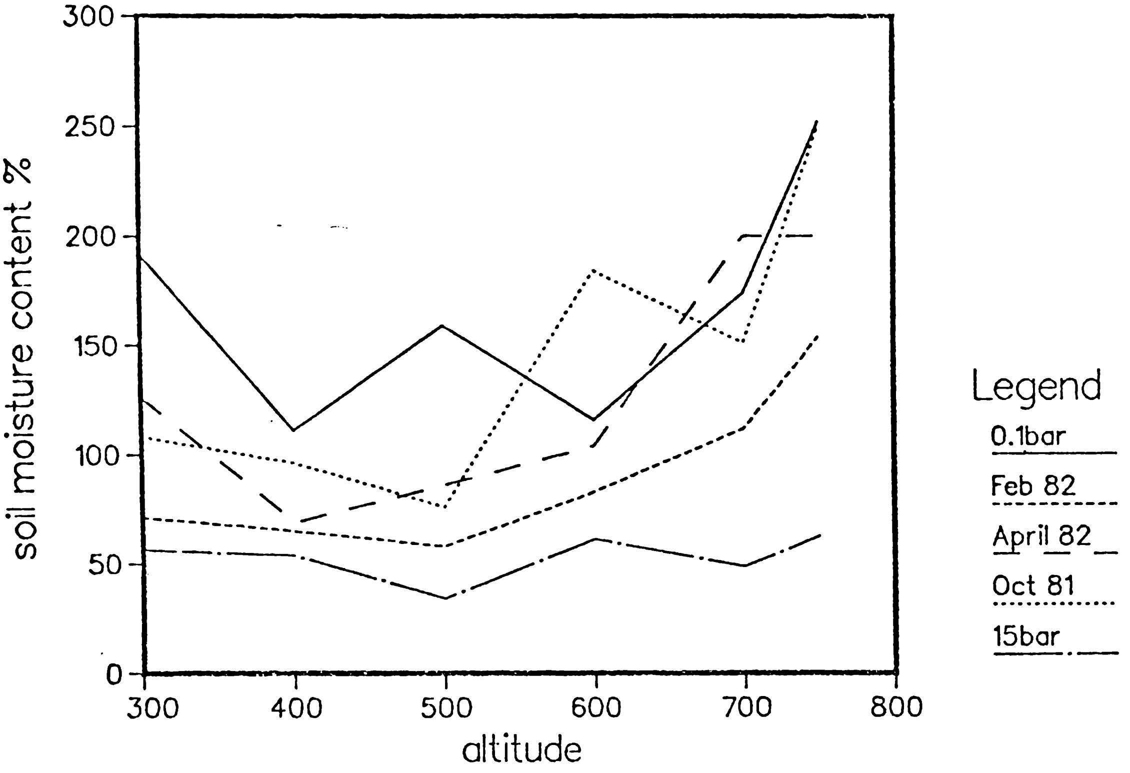


Fig. 5.5. Altitudinal profile of soil moisture content at Te Rere in spring (October 1981), late summer (February 1982) and after the first winter storms (April 1982). Field capacity (-0.1 bar) and wilting point (15 Bar) indicate important bounds of soil water content. Note rapid autumn recovery to field capacity, above the predominant cloud base (600 m).

Table 5.5.
Major droughts and dry years at Te Aroha and Waihi

| | Rainfall (millimeters) | | | |
|---|---|---|---|---|
| | Te Aroha | | Waihi | |
| Drought year | January/February | Total | January/February | Total |
| 1889 | no data | 1413 | no data | no data |
| 1890 | 81.5 | 1628 | no data | no data |
| 1900 | 64.0 | not avail | 90.7 | 2418 |
| 1908 | 2.0 | 2248 | 45.7 | 2248 |
| 1914 | 66.3 | 812 | no data | no data |
| 1915 | 92.7 | 1428 | no data | no data |
| 1919 | 69.3 | 917 | no data | no data |
| 1925 | 89.9 | 1320 | no data | no data |
| 1928* | 56.9 | 1956 | 96.3 | 3234 |
| 1939@ | 37.1 | 1300 | 126.2 | 2184 |
| 1946 | 28.96 | 1582 | 27.3 | 2358 |
| 1950 | 46.5 | 1128 | 43.2 | 1793 |
| 1954 | 39.6 | 1844 | 76.2 | 2031 |
| 1970 | 63.8 | 1432 | 95.0 | 2083 |
| 1982 | 235.7 | 1089 | | |
| Normals | 192.7 | 1498 | 246.9 | 2163 |

* December 1927 was also dry with 26.9 mm
@ Drought extended 38 days into March
March was also dry - 30.5 mm

'Days without rain' may not be a reliable indicator of drought severity because the dry periods may not occur at times of high evaporative losses or high levels of soil water depletion. Values of tank evaporation for Ruakura (in the central Waikato) are probably applicable to the local lowland area, and indicate that nett losses are about 1100 mm per annum (Maunder 1973). Rainfall fell below tank evaporation in only four years, 1914, 1919 1942 and 1982 when rainfalls were 891 mm, 994 mm, 993 mm, and 1089 mm respectively. In the period 1913-15 less than 50 % of the normal rainfall was recorded. Between 1940 and 1950 there were several years of low rainfall and in a four month period from December 1945 only 82 mm rain was recorded, resulting in severe conditions on local farms (Te Aroha News 2/3/46). Bondy (1950) and Maunder (1973) do not mention the area specifically but the Kaimai Ranges could be included in the parts of the Auckland Province affected by the 1939 and 1946 droughts. Similarly between 1928 and 1934 there were several dry years but rainfall average for the period was near normal.

Some assessment of the significance of these longterm deficits on soil water storage levels can be obtained from examining the flow data for the Waihou River system. There is a good linear relationship between summer rainfall and minimum flows in successive years but at two points 1969 and 1976 it is displaced to give a rhomboid shape (Fig. 5.6) and the displacement may be related to changes in aquifer storage. Following the 1969/70 drought the following winter rainfall was insufficient to recharge the aquifer, a situation which persisted until 1975 when two wet years may have resulted in full recharge. A marked decline in soil moisture content and decline in the extent of waterlogging has also occurred within the ranges over the last three years in the absence of any real drought (Jane and Green 1983 d).

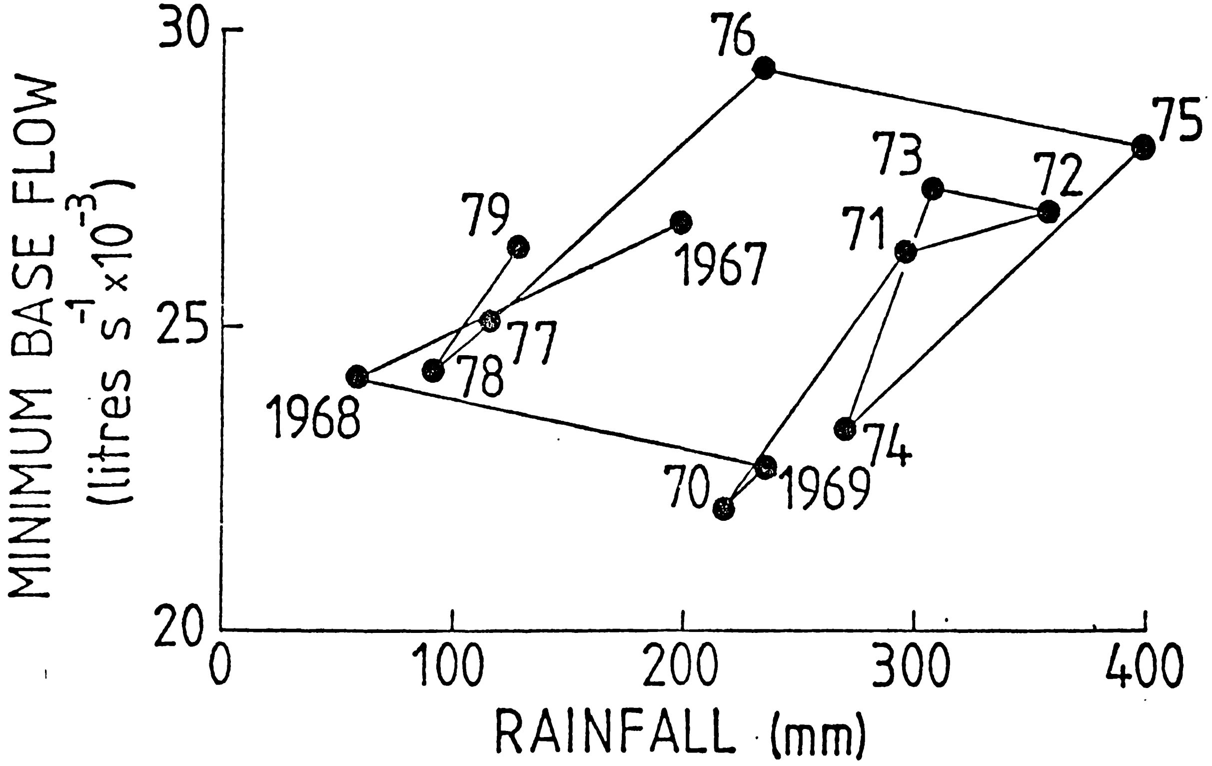


Fig. 5.6. Trends in river summer base flow at Te Aroha Bridge in relation to summer rainfall (January, February and March) at Te Aroha. A discontinuity in the relationship follows the wet 1975 and 1976 winter which was sustained

Obviously a mild drought occurring when the recharge state of the aquifers is low could have a more severe impact on river flows than a longer drought occuring when soil recharge levels were high.

No similar data are available for the earlier droughts but it is evident that those of 1914, 1919 and 1946 occurring during or at the end of a series of dry years will be more damaging than others in periods of normal rainfall such as 1928 and 1969/70. The data are difficult to apply to the upland forests because of lower temperatures, higher rainfall and greater wind runs but the same extreme years are likely to be significant.

## LOWLAND TEMPERATURES

Mean annual temperature at Te Aroha is 14.5° C but on on the coastal side of the range at Waihi it is 13.7° C. At both stations the diurnal range is about 9° C, typical of most coastal areas of New Zealand (Coulter 1973, Cox 1968). There are no general trends in the recorded mean temperatures but maximum and minimum temperatures are now less extreme (Hessell 1980). Such changes could have been brought about as a consequence of the extensive forest clearance and swamp drainage in the area, as suggested by Salinger (1976) for urban areas, however it appears more likely to be linked with changes in annual rainfall.

Ground frosts occur principally between April and September (Fig. 5.7a) although there is a large year to year variability (Fig. 5.7b). Screen frosts at Te Aroha have declined from over 30 per annum to only 10 per annum over the last 70 years (Fig. 5.7c) with a similar decline since records began at Waihi, in 1930. Unseasonal frosts are rare (Fig. 5.7a) but summer frosts were recorded in 1913 and 1914. The cold winters at Te Aroha, with monthly average temperatures below 2° C,

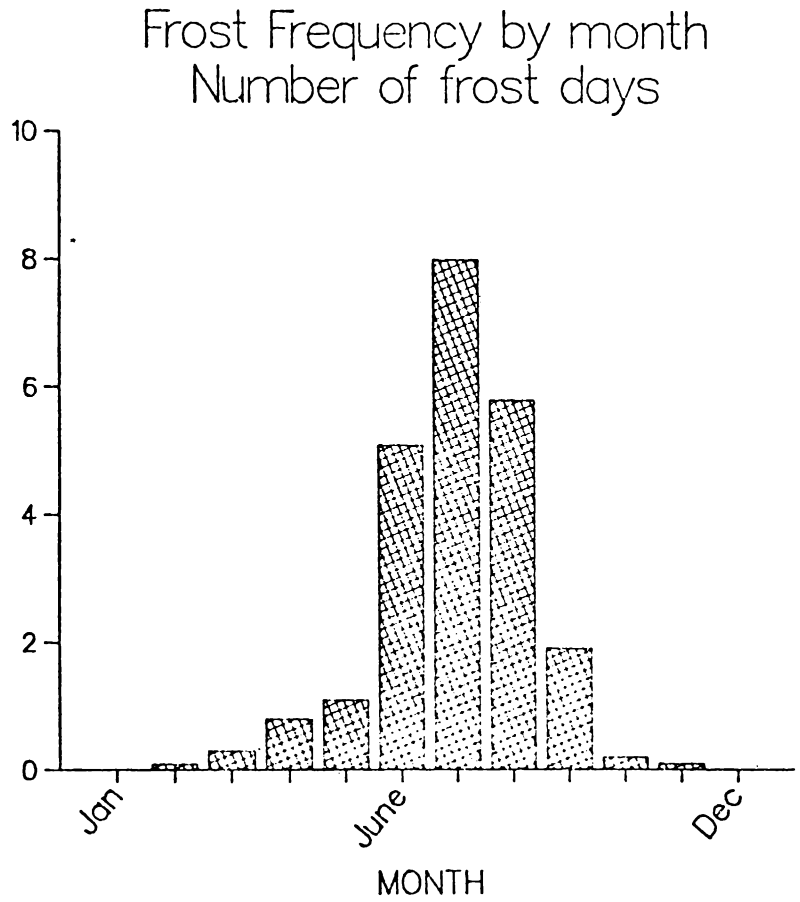
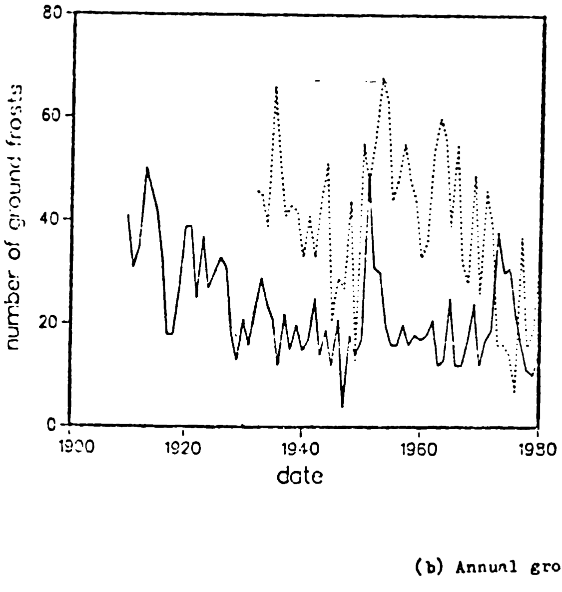
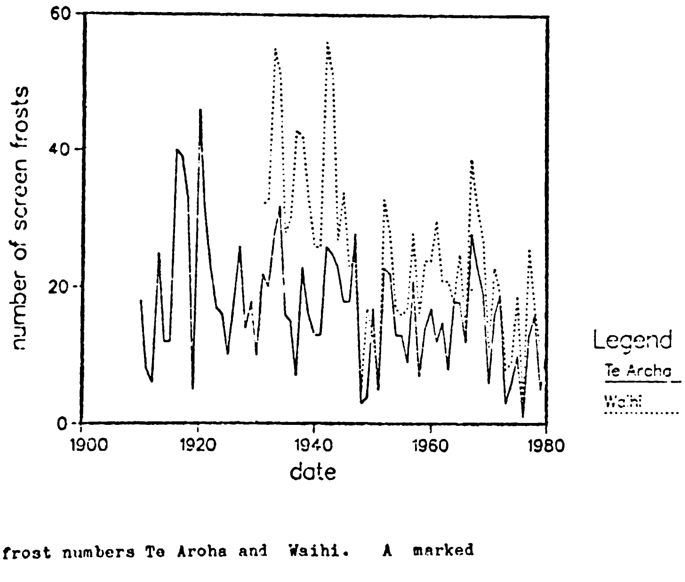


Fig. 5.7.(a) Seasonal frost frequencies at Te Aroha. Note low incidence of spring and summer frosts.





(b) Annual ground frost numbers Te Aroha and Waihi. A marked long term decline in number is evident although numbers are high at Te Aroha in the dry 1943-1946 and 1970-1972 periods.

(c) Annual screen frost numbers Te Aroha and Waihi. Note a similar decline in frost numbers and a close correspondence between numbers at Te Aroha and Waihi.

occurred in 1914, 1918, 1942 and 1945. The period 1914 to 1919 was marked by particularly low winter temperatures and the periods 1942-45 and 1969-72 contained a series of cold winters. High maximum temperatures often occurred in the same years. It is striking that these years coincide with the years of extended rainfall deficit and suggests that clear skies were particularly prevalent. On the other hand the high correlation between maximum temperatures and total rainfall reflects a more general trend for warm years at Te Aroha to to occur in years dominated by tropical influences in which one or two severe storms occurred (Table 5.2).

Maximum temperature variation and frost numbers appears to follow similar patterns to rainfall variability and this is a national trend seen in rainfall data of Tomlinson (1981) and temperature data of Goulter and Hurnard (1979).

## UPLAND TEMPERATURES

Between 1967 and 1977 Mt. Te Aroha station recorded daily temperatures of up to 17.6° C and similar values were found at the uppermost study sites (Fig. 5.8), however the lack of continuous recent data at Mt. Te Aroha does not permit direct comparison. Diurnal temperature range at the summit is lower than at Te Aroha town because of cloud influences. This was particularly well demonstrated by a thermograph record at Te Hunga during one extended fog period. A mean diurnal variation of only 2.5° C was recorded and values for individual days were as low as 1.25° C. The temperature range over 17 days was 6.0° C. In this period temperatures were governed by incoming frontal systems rather than diurnal variations in incident radiation (Fig. 5.9). Brief sunshine periods in the record on the 6th, 17th and 21st days and an arithmetic mean temperature which often lies below the

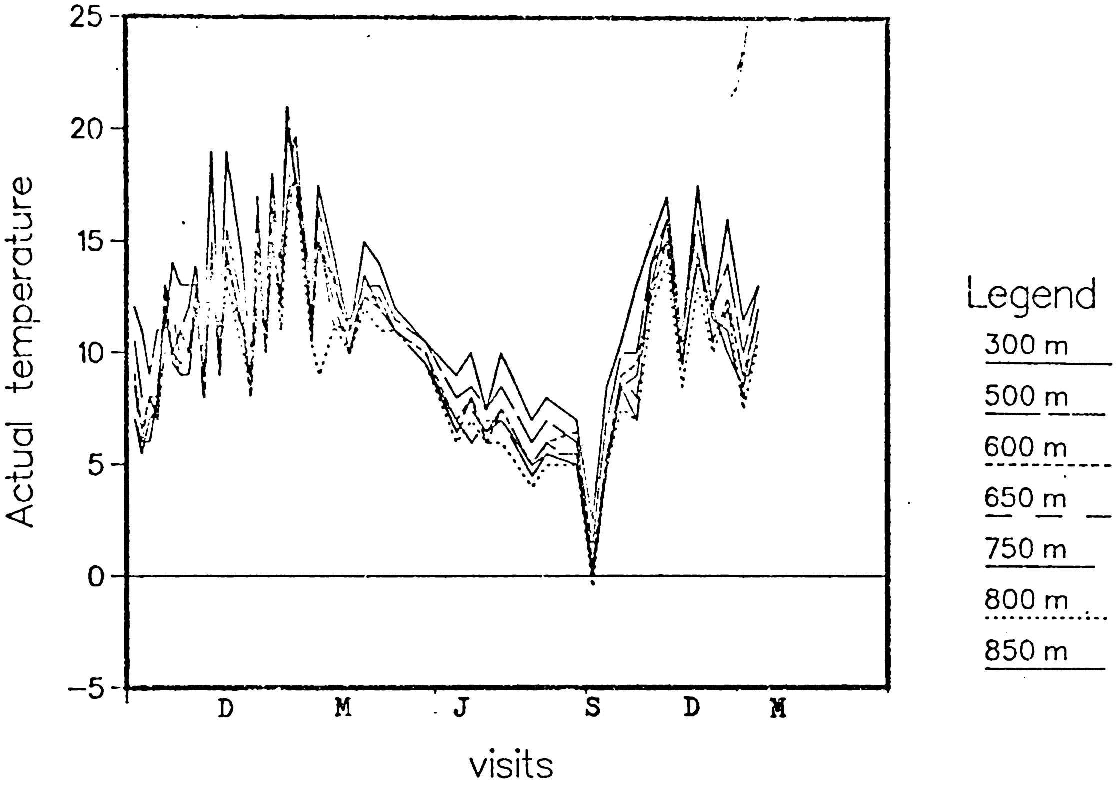


Fig. 5.8. Seasonal variation in actual air temperatures (° C) at Te Hunga measured between 8am and 10 am, ascending by altitude. Almost identical values were obtained at Te Rere. Records began in October 1980 and terminated in March 1982. Observations were made at weekly intervals from October 1980 to April 1981 and fortnightly thereafter.

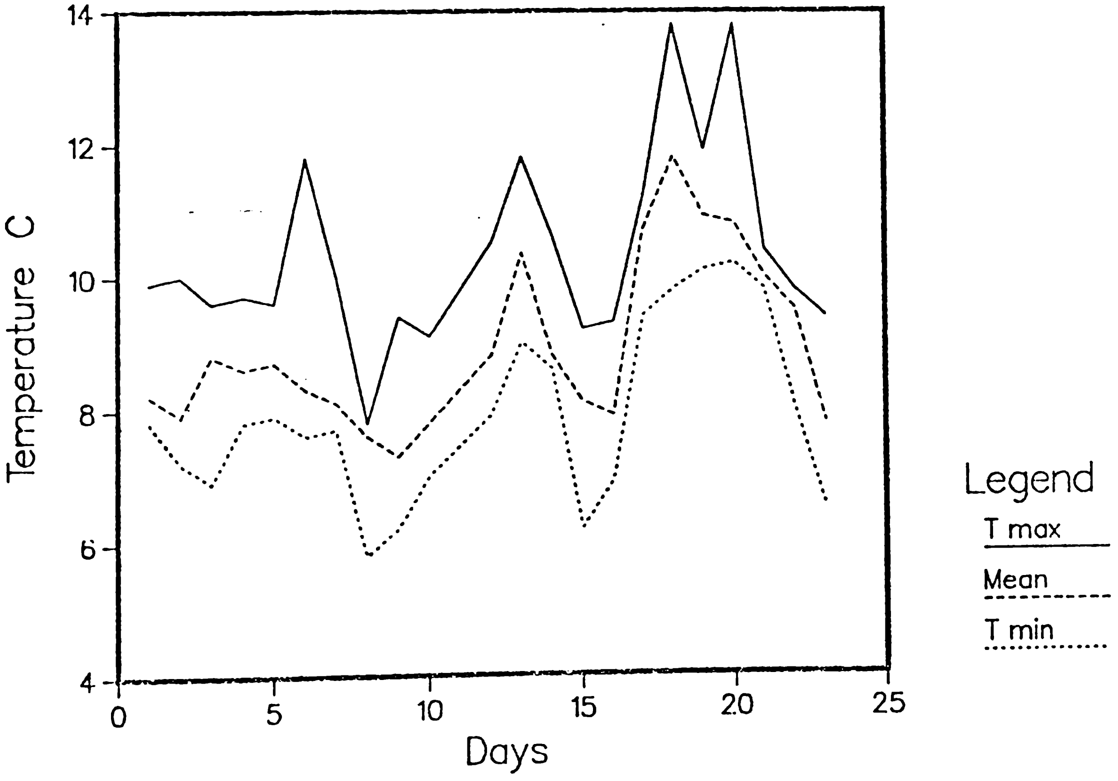


Fig. 5.9. Daily mean temperature calculated from half hourly temperature records on a Grant Thermograph made at 600 m on Te Hunga during a period of cloudy weather from 15th November to 16th December 1980.

median of daily values show the extent of deviation from potential values. Winter temperatures at Mt. Te Aroha average 4.2° C but screen frosts are not excessively frequent. In 1968 there were just over three times as many frosts as at the town (37:11) but in wet years, such as 1968, numbers were similar.

## Lapse Rates

A uniform lapse rate is often assumed for estimating temperatures at altitudes different from a recording station. In the study areas this assumption was not valid and the lapse rate varied with season and altitude. On Mt. Te Aroha lapse rate of the mean daily maximum temperature between the town and summit is uniform through the season whereas that for mean daily minimum temperatures is lowest in winter (Fig. 5.10a).

At Te Hunga lapse rates show a small depression just below the fog zone, between 500 m and 700 m altitude and there is an accompanying depression in the diurnal range (Fig. 5.10b). Temperatures below 500 m often differ considerably from those at higher altitudes where they are frequently uniform and the difference is greater from the 35th to 60th visits (June to September, Fig. 5.11). On a number of occasions a thermal inversion was present at 600 m resulting in temperatures of one to two degrees higher on the summit plateau.

Many studies of mountain areas have shown a similar thermal belt or zone of low lapse rates extending over several hundred metres altitude (Coulter 1967, Geiger 1965, Hayes 1941, Morris 1965). Examination of lapse rates for several paired stations for mountain areas (Table 5.6) suggests that thermal belts are of common occurrence in New Zealand and related to areas of high fog incidence. Sites such as Wharakite peak and Te Aroha with high fog frequencies have low lapse rates and a small

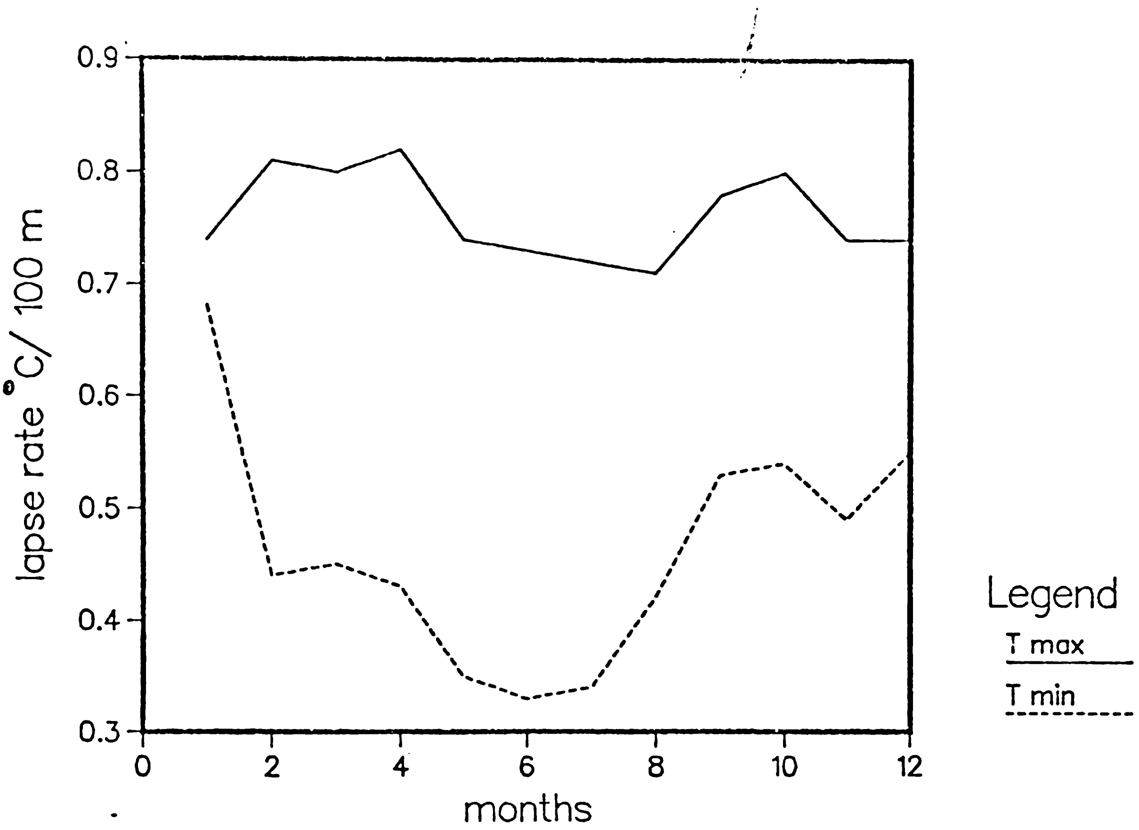
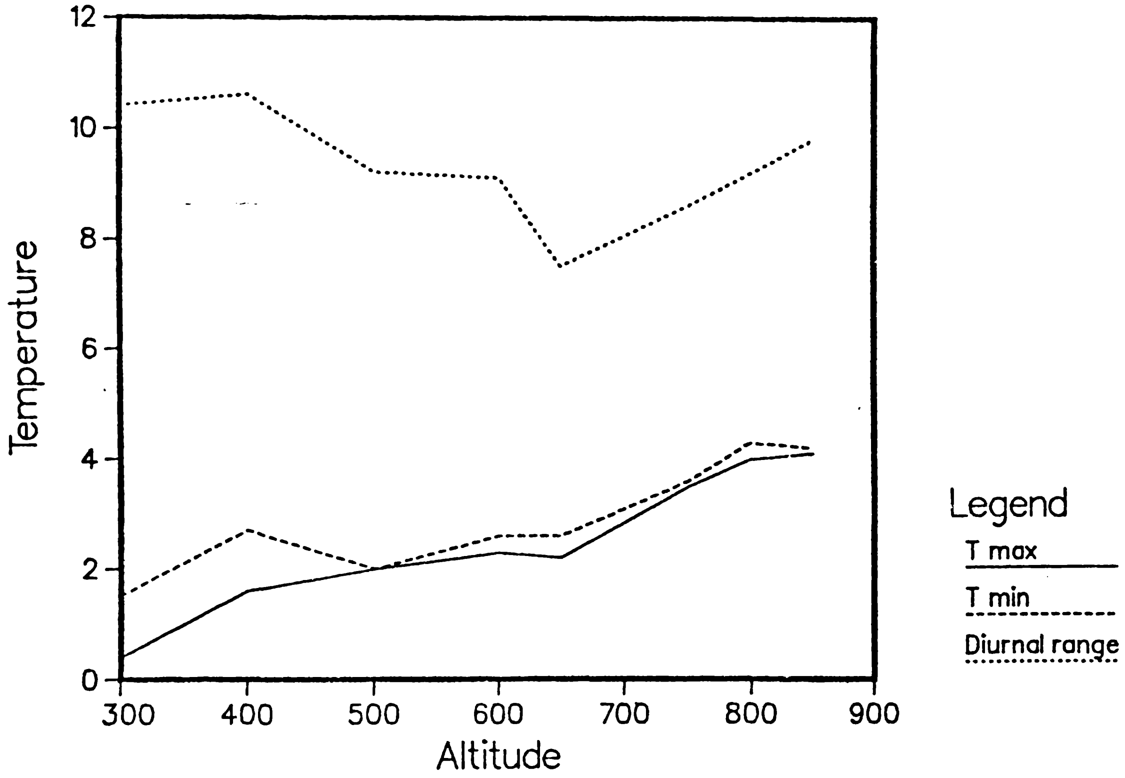


Fig. 5.10. Lapse rates. (a) Seasonal variation in lapse rates in minimum and maximum temperatures between Te Aroha Town (30 m) and the Mountain summit (950 m) for 1967- 1977.



(b) Air temperatures by altitude at Te Hunga calculated by subtracting temperatures at 500 m from the respective temperatures at other altitudes and adding 2. this shows the small differnce in temperature at middle altitudes about the cloud base and the depressed diurnal range.

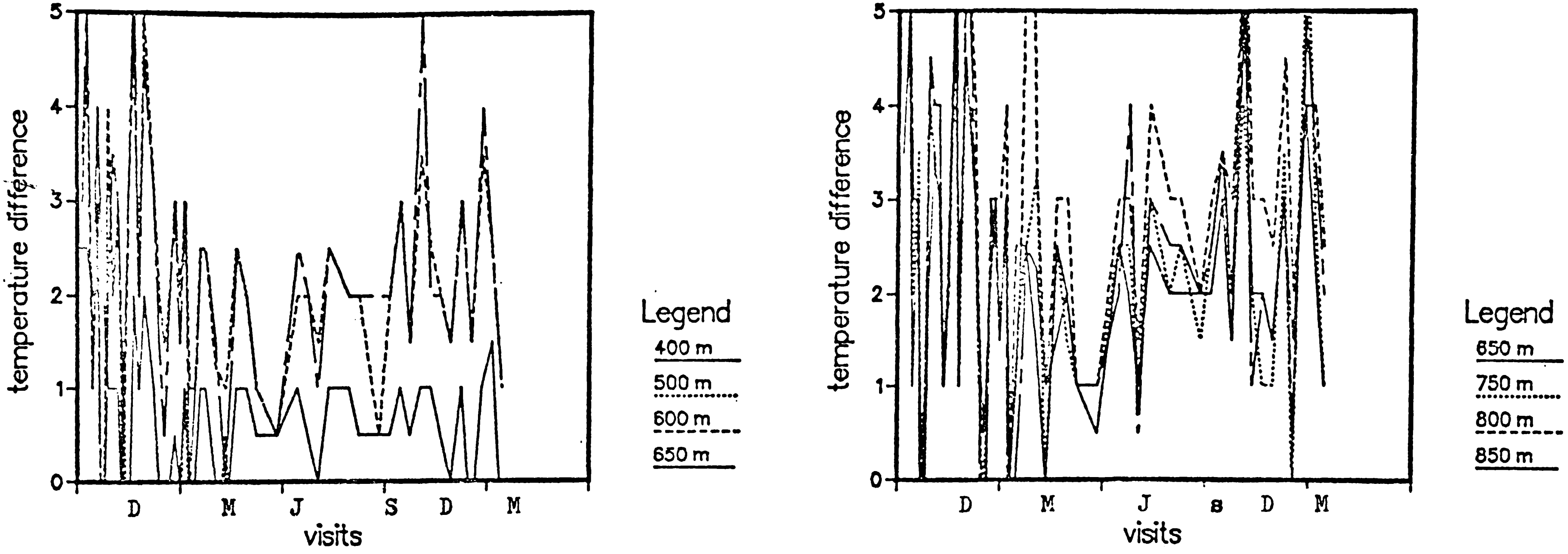


Fig. 5.11. Seasonal air temperatures diferences at Te Hunga calculated by subtracting temperatures at 300 m from the respective temperatures at higher altitudes. Left hand side: below 605 m Right hand side: above 650 m. Temperatures above 500 m were usually closely similar whilst 400 m and 300 m temperatures were one and two degrees lower respectively.

Table 5.6

Mean temperature, mean daily range, and lapse rates for selected pairs of adjacent upland and lowland meteorolgical stations in coastal situations and data for other comparable meteorological stations

| Station | altitude metres | Temperature |  |  | Number of of fog days |
|---|---|---|---|---|---|
|  |  | Mean daily ° C | Mean daily range ° C | Lapse rate °C /100 m |  |
| Te Aroha | 30 | 15.4 | 8.7 | 0.60 | 20 |
| Mt Te Aroha | 950 | 9.3 | 5.3 |  | 200 |
| Ohakea | 48 | 13.2 | 8.7 | 0.66 |  |
| Wharakite | 914 | 7.3 | 5.9 |  | 173 |
| New Plymouth | 97 | 13.6 | 9.3 | 1.0 |  |
| Mountain house | 846 | 8.9 | 8.7 |  | 51 |
|  |  | other stations |  |  |  |
| Invercargill | 20 | 9.6 | 9.4 |  |  |
| Milford | 0 | 10.3 | 8.0 |  |  |

dirunal temperature range while stations such as Egmont Mountain House, with fewer fog days, have a higher lapse rate and diurnal temperature range similar to adjacent lowland stations. Mean temperatures and diurnal range at Mt. Egmont is comparable to Invercargill and other coastal stations in the south of the South Island, but because of fog and inhomogeneity in lapse rates, similar comparisons for foggy areas can be misleading.

## Growing Season

The growing season at Te Aroha town extends from September to May and there are 1727 degree days above 10° C (New Zealand Meteorological Service 1978). No data is available for Te Aroha summit but taking Invercargill, a station with similar mean temperature and diurnal temperature range as a guide, there are only 514 degree days at the summit and the growing season extends from December to March. These figures are reduced even further by the effects of fog. O' Rourke and Terjung (1981) suggest that fog reduces net photosynthesis by 75 %, without taking into account temperature effects. This suggests that the growing season in a wet summer could be very limited.

## Soil Temperatures

Soil temperatures at 850 m altitude ranged between 4.8° C and 14.6 ° C and followed a similar annual pattern at 300 m and intermediate altitudes (Fig. 5.12). Summer temperatures rose abruptly in December during two weeks of fine weather and fell similarly in April with the onset of frosts. Apart from very dry periods temperature lapse rate at each visit was very uniform and temperatures at 850 m could usually be predicted within 0.2° C from one measurement at 300 m.

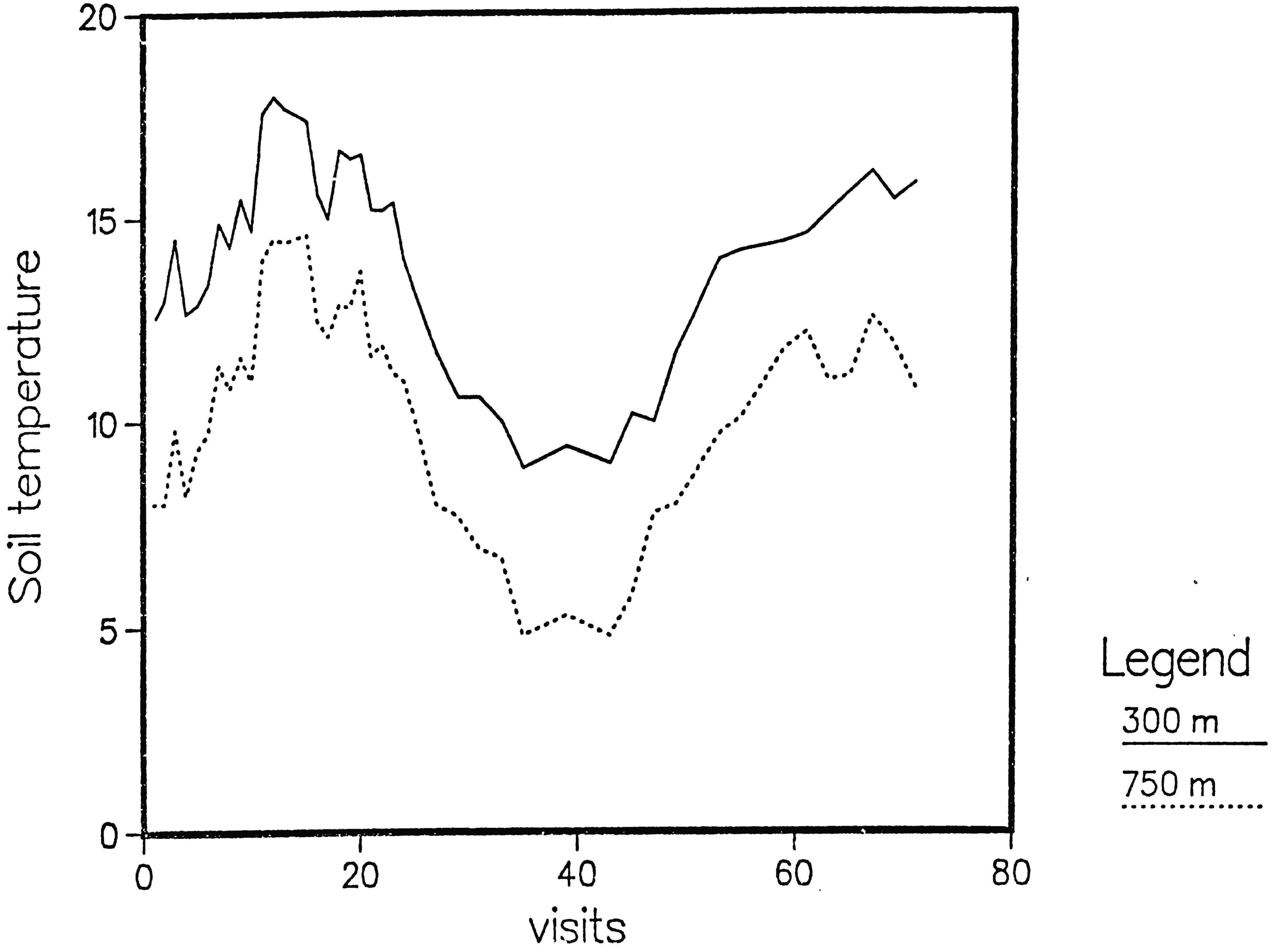


Fig. 5.12. Seasonal pattern of soil temperatures at 300 m and 850 m on Te Hunga. A very consistent lapse rate was maintained.

## DISCUSSION

### Droughts conditions

The periodic dominance of northern weather systems related to long term shifts in the weather systems and sunspot activity (Tomlinson 1980a) results in highly variable weather conditions in which droughts, severe storms and temperature extremes are likely. The most severe droughts thus appear to occur in periods of high rainfall variability when the region is most strongly influenced by tropical storms. High maximum temperatures are correlated with warm tropical conditions bringing rain to Te Aroha from intense cyclonic in January or February but the winters may be dry. This is reflected in the high positive correlation between January rainfall and frost days at Te Aroha (Table 5.2). In other years the storms may be less frequent or absent and severe droughts may occur.

Reports written at the time of the 1914-20 droughts were not readily able to assess severity since the prior climatic records were short (Bates 1915, de Lisle 1967) and population density was light especially in the Waikato and Hauraki Plains (Tye 1974, Vennel et al. 1951). In retrospect these were the most severe ever recorded in the area and Kidson (1930), states that:

"for the Auckland Province 1914 was undoubtedly the driest year hitherto recorded" and indicates that in 1919 deficits of up to 30 inches (760 mm) may have been present in the Kaimai Ranges. The 1914 drought occurred in the middle of a series of dry years a situation repeated in 1919 suggesting that the impact of these droughts must have been severe. By contrast the 1928 drought occurred in a period of above normal rainfall and the 1939 and 1946 droughts at the beginning and end, respectively, of the same series of dry years. Of the last three droughts only the one in 1946 was significant for agricultural crops.

The 1969/70 drought occurred in a period of near normal rainfall and provoked no local comment, neither was 1972 regarded as a severe drought.

Other factors also permit an assessment of the nature of the droughts. In 1908 high day temperatures over 27° C and high night temperatures, 14° C for January and 12° C for February indicate humid weather, described as sultry (Te Aroha News, Bay of Plenty Times), with frequent cloud. In contrast the summer of 1913-14 was characterised by both very hot days, over 27° C, and very cool nights. The maxima and minima for January are the most extreme on record and those for December 1913 and February 1914 are also unusually extreme. This extreme weather suggests exceptionally clear skies which appear to have continued for much of the year since the winter is the coldest on record. Further extreme conditions continued for the next five years with low rainfall and cold winters in 1915, 1916 and 1918. Similar conditions appeared in 1928 but did not persist.

From the various viewpoints expounded above it should be clear that the period 1913-1920 contained the most severe droughts recorded in the region. A similar but far less severe period occurred between 1939 and 1948 and other droughts in 1928/30, 1934/5, 1956/7, and 1969/70, although severe by various measures, were relatively unimportant.

## Climatic conditions within the ranges

The lowland climate can be very adequately described from the current meteorological data base as warm temperate, usually of adequate rainfall, but agricultural droughts may occur every 10-15 years. The upland climate in which much of the curent investigation was carried out is not well described. Extrapolation of lowland values suffer from many difficulties. Rainfall is clearly much higher and evapotranspiration can be considerably lower due to fog and lower temperatures. The climatic gradient is not even and there appears to be a sharp change at the cloud base at which there is a lowering of the temperature gradient and an increase in soil moisture to waterlogging levels. There is considerable difficulty in extrapolating lowland drought severity to the upland areas and the higher rainfall suggests that drought impact would be slight. However, there is a strong probability that plants in the cloud forests may be slow growing and unusually sensitive to small climatic perturbations. The high cloud frequencies markedly reduce light levels and consequently photosynthesis. Cooler temperatures will affect growth and frequent leaf wetting may impede stomatal gas exchange. It is also known that soil waterlogging, by restricting root systems to the upper soil horizons, places the plants at a higher risk during drought (Kozlowski 1982).

# CHAPTER 6

# FOREST HISTORY AND PAST CLIMATES IN THE UPLAND FORESTS OF THE KAIMAI RANGES

## Introduction

Dendrochronology has been widely used for establishing the ages of trees and dates in archaeology and is regarded as the most reliable and precise method available for woody material up to 1000 years old. It has also been used in the study of past climates but only to a limited extent in ecology (dendroecology). When the techniques are applied to closed stands of mesophytic forests several factors may obscure climatic information. These include competitive interactions between adjacent trees, which cause abrupt changes in growth rates sustained over many years, and sites on which no single factor has a predominant impact on tree growth (non-sensitive sites).

Much of the fundamental work in dendrochronology was carried out on conifers from dry regions of the United States (Fritts 1976). Conifers, selected perhaps because they were the predominant species of the locality, have one major advantage, prominent well defined annual rings. Recent application of the techniques to several hardwoods, most notably oak and elm in Britain (Hughes 1978, Pilcher and Gray 1982) and Europe (Eckstein 1972, Sweingruber et al. 1979) have been successful although demarcation of annual rings can be difficult. In all cases it is necessary to confirm that the rings are annual by crossdating with species in which the regularity of the rings has been established or specimens for which the absolute age is known. Annual rings in hardwoods may be delimited by a variety of features including, for instance, a concentration of large vessels in spring wood or terminal parenchyma (Jane 1956). In some species bands of parenchyma or phloem may also be included within annual rings. These difficulties have produced considerable discussion in New Zealand, on the existence and regularity of annual rings in a wide range of species and have placed doubt on the local applicability and value of dendrochronological techniques (Cameron 1960, Bell 1958). Nevertheless, recent investigations by Dunwiddie (1979) have successfully demonstrated the techniques on a range of species.

Vegetation mortality in the Kaimai Ranges can be related to at least two recent droughts (Jane and Green 1983b) and it appears probable that periods of mortality have occurred previously. The age class structure of the forests is likely to show these earlier events and to reflect variability in susceptibility between different species. Suitable chronologies from a range of long-lived species may enable an insight to be obtained into the climatic conditions prevailing at the periods of mortality since the chronologies reflect the impact of limiting environmental factors in each species (Fritts 1976).

## METHODS

### Sample collection and preparation

Samples were collected from windfallen and recently dead trees in the upland forests on Mt. Te Aroha, at Te Rere Bald and near Kauritatahi hut, Te Hunga (Fig. 6.1, Table 6.1). Samples (5-10 stems) of the dominant species were also taken from standing seral vegetation along recently cleared tracks at each locality. Discs were cut from the stems as close to the base as possible. Where the discs were large, quadrants with clearly identifiable ring sequences were removed to facilitate transport. Warping and cracking, which often ensued during drying in the laboratory, was minimised by promptly smoothing with a buzzer and recutting the samples into narrow wedges contained the clearest ring sequences. Air dried segments were sanded on a belt sander and further reduced, on a band saw, to strips 5 mm wide ("cores"). The radial transverse surface of the "core" was then

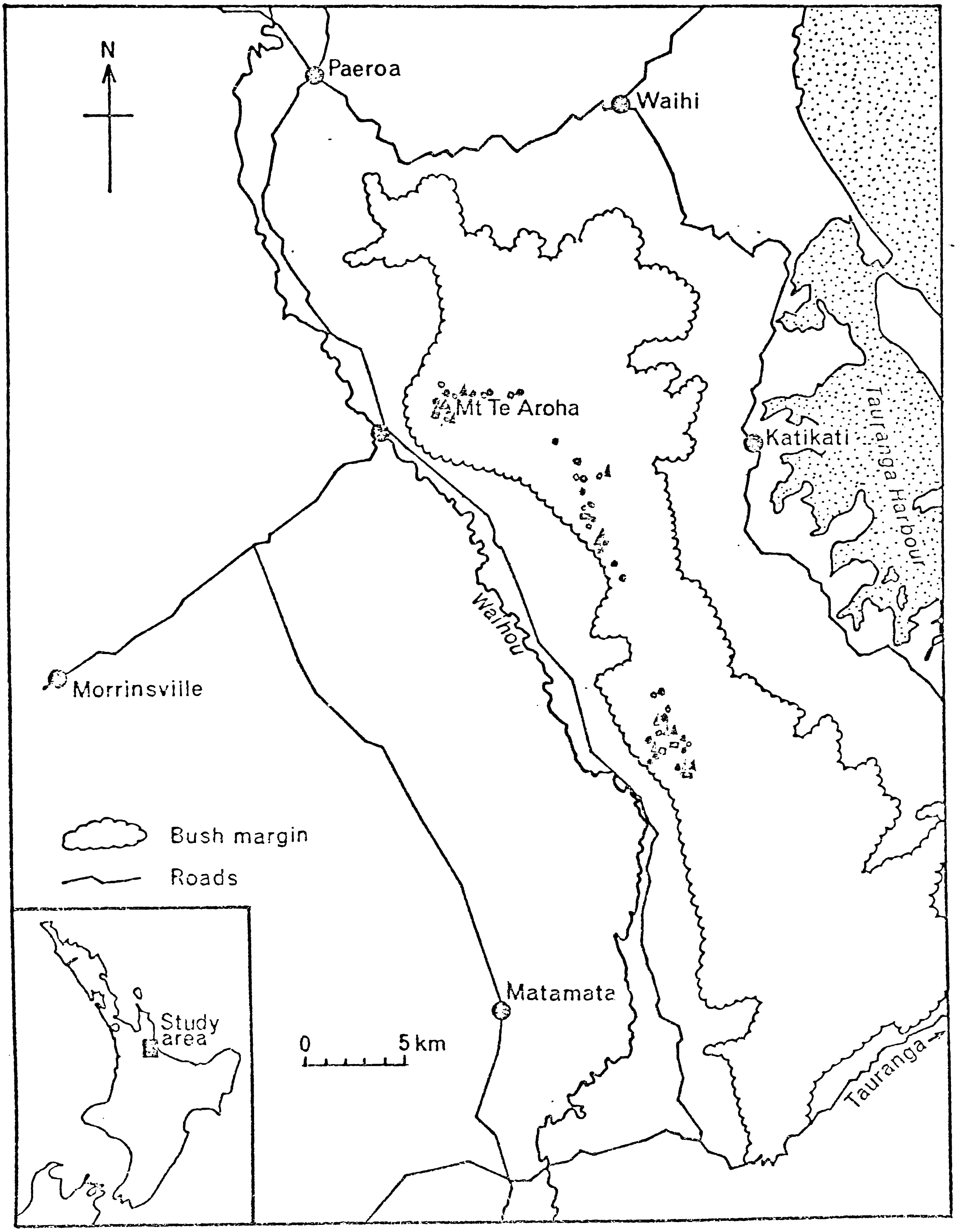


Fig. 6.1. Location of dendrochronological sample localities within the Kaimai Ranges

Λ kaikawaka, ⅄ toatoa ● seral ○ silver beech □ pink pine

Table 6.1
Age class and sample sizes of species examined.

| SPECIES | AGE CLASS<br>earlier than 1500 | <br>1501 -1600 | <br>1601 -1700 | <br>1701 -1750 | <br>1751 -1800 | <br>1801 -1850 | <br>1851 -1900 | <br>1901 -1981 | <br>TOTAL * |
|---|---|---|---|---|---|---|---|---|---|
| kaikawaka | - | 3 | 12 | 7 | 4 | 3 | 15 | 20 | 64 |
| toatoa | - | 4 | 1 | 2 | 6 | 6 | 10 | 8 | 37 |
| pink pine | 6 | - | 2 | - | - | - | - | - | 8 |
| yellow silver pine | - | - | 5 | 4 | 2 | 1 | 2 | 5 | 19 |
| *miro | - | - | - | - | 2 | - | 1 | - | 5 |
| *halls totara | - | - | - | - | - | 1 | - | 4 | 10 |
| silver beech | - | 5 | 11 | 7 | 3 | 9 | 38 | 63 | 136 |
| kamahi | - | - | - | - | - | - | 3 | 30 | 33 |
| quintinia | - | - | - | - | - | - | 19 | 63 | 82 |
| *tawari | - | - | - | - | - | - | 6 | 3 | 20 |
| neinei | - | - | 1 | - | - | 5 | 8 | 17 | 31 |
| horopito and pepperwood | - | - | - | - | - | 5 | 17 | 33 | 55 |
| *toro | - | - | - | - | - | - | - | - | 5 |
| <u>Coprosma</u> spp | - | - | - | - | - | - | 2 | 14 | 16 |
| total | 6 | 12 | 32 | 20 | 17 | 29 | 121 | 260 | 521 |

*not all stems of these species could be dated.

polished with a series of carborundum papers to 400 grade and, when required, given a final polish with a fine aluminia knife grinding powder (Patel 1967).

At the first examination the "core" was marked by decades, the distinctive features crossdated, and the master chronology progressively elaborated. The chronology was largely based on presence of distinctive latewood, cambial mortality, and changes in growth rate. In conifers distinctive latewood wood colour results from a reduction in cell size and increase in cell wall thickness as the summer proceeds. The density of the latewood is frequently an indicator of the severity of summer water stress and the width an indication of the duration of the stress (Glock and Agerter 1955) consequently rings with a wide latewood usually indicate a long dry summer. A similar feature is present in some hardwoods where the proportion and density of fibres increases in the latewood or there is a decline in size and frequency of vessels. Under severe stress part of the cambium may be killed resulting in local disruption of the radial continuity of the wood. Frost is the most frequently recognised cause of cambial damage (Glock and Agerter 1955) but it may also result from drought (Cown 1973, Glerum 1970), or pathogens (Brubaker 1978). Cambial mortality from drought damage will usually coincide with years in which latewood is especially prominent and growth rates are unusually low or high.

The initial master chronology was established for pink pine (Dacrydium biforme) a species with were very clear ring sequences, containing a few well defined markers, and showing little evidence of missing or false rings. The chronology was then extended progressively to kaikawaka (Libocedrus bidwillii), silver beech (Nothofagus menziesii) and a number of other species in which the regular nature of the rings was less certain. When the age of the innermost rings had been determined, the width of each ring was measured to the nearest 0.01 mm using the Addo-x travelling stage micrometer.

The age of the innermost ring is normally not the same as that of the original tree. For instance, the sample height from which the disc was taken may not include the growth of the first year. In small stems, up to 50 or 60 years of age in this study, the tree base is readily identified and this error is small, but in older stems the error may be considerable. Stems may arise on logs, stumps or some other position above the ground surface or the original base of the tree may be obscured by accumulation of litter. In very large stems of kaikawaka and toatoa, where initial growth rates are very slow, this error could be over 20 years. No allowance can be made for these sources of error in establishing stem age.

Data analysis

Trial graphs of a number of ring sequences established that the usual exponential and simple polynomial ring smoothing algorithms (Fritts 1976) were unable to accommodate the large fluctuations in growth present in the data. This is a common problem in ring sequences from closed or disturbed stands of mesophytic sites (Warren 1981). Several solutions were tried but the most satisfactory proved to be a simple smoothing spline normally used in economic time series analysis (Schlicht 1981). This is defined by:

$$\text{smoothed function of } y = A.\sum_{t=3}^{T} \{(y_t - y_{t-1}) - (y_{t-1} - y_{t-2})\}^2$$

for t= time; and A an arbitrary smoothing constant.

Individual coefficients are derived by inverting a simple band matrix of the form :

$$\begin{array}{cccccccc} A+1 & -2.A & 1.A & 0. & 0. & 0. & 0. & 0. \\ -2.A & 5.A+1 & -4.A & 1.A & 0. & 0. & 0. & 0. \\ 1.A & -4.A & 6.A+1 & -4.A & 1.A & 0. & 0. & 0. \\ 0. & 1.A & -4.A & 6.A+1 & -4.A & 1.A & 0. & 0. \end{array}$$

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 0. | 0. | 1.A | -4.A | 6.A+1 | -4.A | 1.A | 0. |
| 0. | 0. | 0. | 1.A | -4.A | 6.A+1 | -4.A | 1.A |
| 0. | 0. | 0. | 0. | 1.A | -4.A | 5.A+1 | -2.A |
| 0. | 0. | 0. | 0. | 0. | 1.A | -2.A | A+1 |

This was then post-multiplied by the raw data sequence to obtain a smoothed series. A similar algorithm has been recently developed by Cook and Peters (1981).

A determines the tightness of the fit of the smoothing spline to the raw data. With a value of 1 the spline follows all the main fluctuations of the series (Fig. 6.2) whereas with a value of 10,000 only the general trends are followed. A suitable smoothing spline for use in dendrochronology must remove the main growth trends but not remove climatic information. By fitting splines of successively larger A values to rainfall data, a value of A=10,000 was reached where the spline approached a straight line and this was subsequently used for the initial smoothing of the dendrochronological data. The value need not be exact since A varied exponentially and small increments at high values of A changed the spline only slightly.

The initial smoothed series containing disturbance history information was stored. Standardised residuals were obtained in the usual manner by dividing the original ring width values by the corresponding smoothed series value for each measurement of the core and stored for later pooling by species to obtain final chronologies. Further trend removal was then carried out successively on the residuals using the smoothing spline with A now set at values of 1, 10 and 1000. The splines and final residuals then were subject to regression analysis with comparably treated climatic parameters using SPSS stepwise "New Regression" procedures (Hull and Nie 1981).

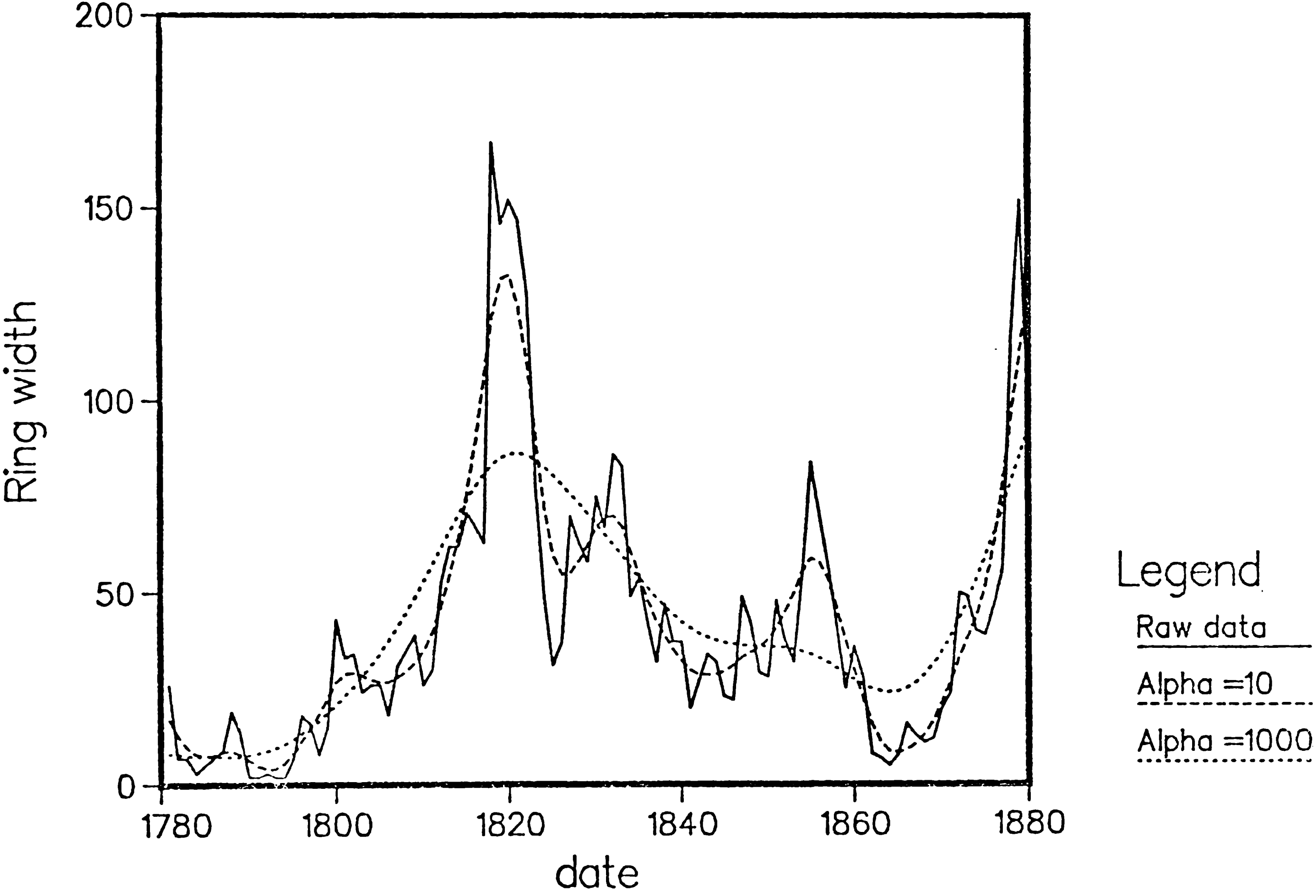


Fig. 6.2. Examples of two smoothing splines fitted to the same dendrochronological sequence demonstrating the flexibility of fit by varying one parameter (A). Unless alpa (A) is small large suden changes in growth rate may be masked.

## RESULTS

### Suitability of species

All the main canopy and sub-canopy species were examined (Table 6.1). Conifers included kaikawaka (Libocedrus bidwillii, Hook. f. ), toatoa (Phyllocladus glaucus, Carr. and P. alpinus, Hook. f.), pink pine (Dacrydium biforme, Hook.f.), yellow silver pine (Dacrydium intermedium, Kirk), rimu (Dacrydium cupressinum, Lamb.), miro (Podocarpus ferrugineus, G.Benn ex D. Don), and Halls totara (Podocarpus hallii, Kirk). Halls totara and miro were not extensively sampled as cores from the fog zone vegetation had very faint irregular rings.

Hardwoods included silver beech (Nothofagus menziesii, Hook. f.(Oerst)), kamahi (Weinmannia racemosa , Linn. f.), quintinia (Quintinia acutifolia, Kirk), tawari (Ixerba brexioides, A. Cun.), neinei (Dracophyllum latifolium, A. Cun.), horopito (Pseudowintera axillaris, J. R. et G. Forst.), pepperwood (Pseudowintera colorata, (Raoul) Dandy), and toro (Myrsine salicina, Hew. ex Hook. f.). Rings in toro and tawari were impossible to distinguish with the certainty required for dating and those in neinei and pepperwood required careful surface preparation and cross-dating.

### Master Chronology

Ring sequences obtained from pink pine extended back to 1300 AD and contained few distinct features. Cross-dating of stems established a reliable chronology to about 1700 but a scarcity of older material limits confidence in earlier dates. Examination of the rings for the last 70 years, for which climatic data available, showed that in toatoa and kaikawaka rings containing both cambial mortality and broad dark latewood were associated with drought years. Years marking the beginning or end of periods of increased or decreased growth rate which was sustained over 10 or more years in most species was similarly associated.

The most important dates, with rings containing this combination of features in a high proportion of stems, were found to be

1972, 1946, 1919, 1914,

1896, 1872, 1861, 1831, 1813, 1811, 1807, 1804,

1793, 1773, 1761, 1737, 1731, 1720,

1696, 1656, 1614.

### Growth rates and dating reliability

In general growth rates are slow. Silver beech, which had much higher growth rates than the other species, also grew much better on Mt. Te Aroha than on Te Hunga (Fig. 6.3). Limited sampling showed that growth rates in kamahi were also related to sample locality. Plants on old mining sites on Te Aroha below the fog zone at 700 m have reached 20-30 cm DBH (diameter breast height) in 100 years but plants from the summit, and upland sites elsewhere, averaged only 7 cm DBH for a similar age. It seems possible that growth rates in the upland areas are reduced by higher rainfall and fog frequencies or by soil fertility. Growth rates in toatoa are generally very slow and the biannual oscillations in growth rate noted by Dunwiddie (1979) were common. These fluctuations may occur because spring conditions retard or prevent growth initiation. An example was the summer 1981/2 which was cool and wet until mid-season. Bud-break was delayed and only small increments occurred on the observed shoots. Toatoa shows a single growth class structure at all sites possibly because of the high growth rate variability within plants (Fig. 6.4). Toatoa is found mainly in the

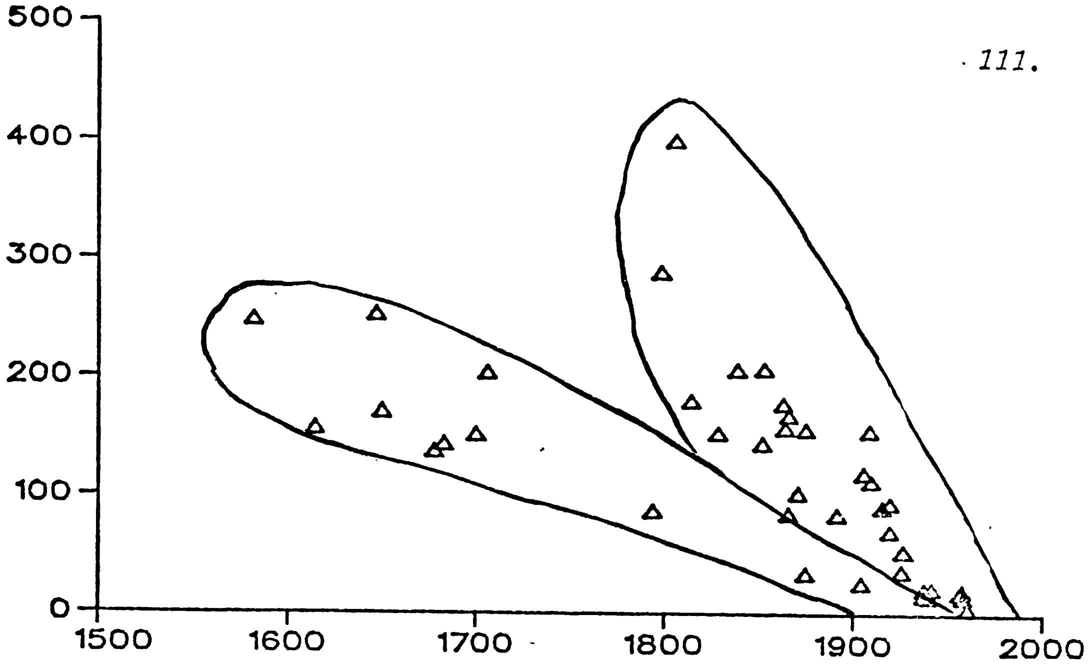


Fig. 6.3. Radius /age relationship in silver beech cores. Lines enclose data from Te Aroha (upper) and Te Hunga (lower) study areas.

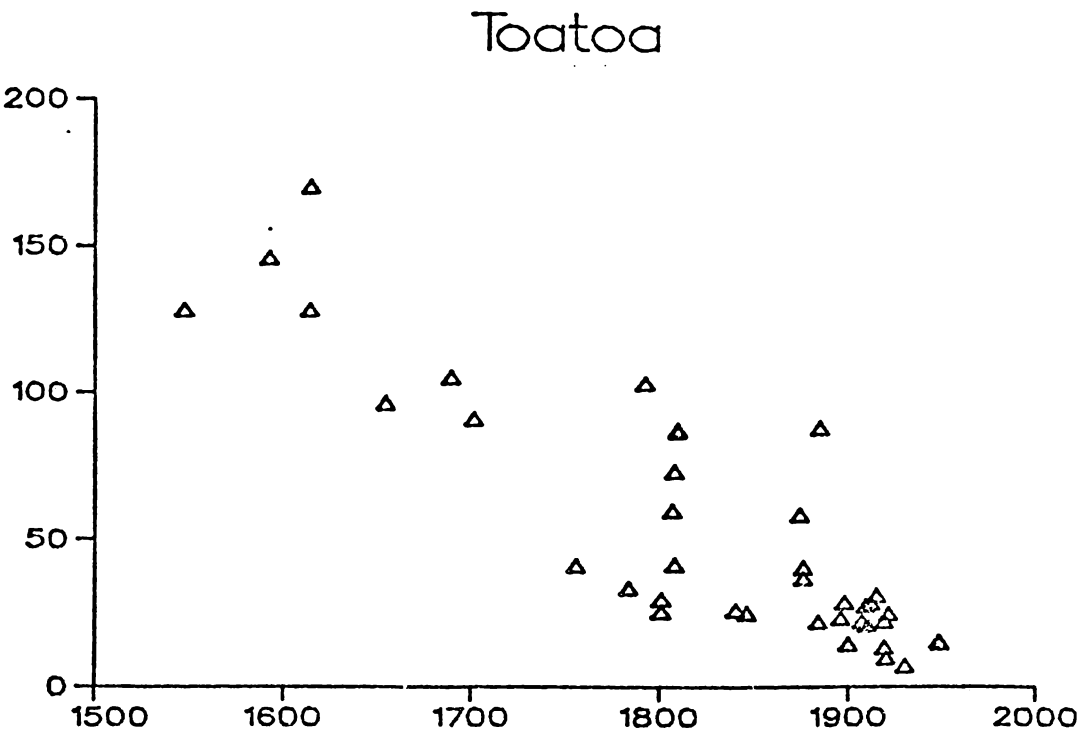


Fig. 6.4. Radius /age relationship of toatoa cores.

wet boggy habitats and initial growth rates of seedlings are erratic, possibly because of fluctuating water tables. Older stems of toatoa often showed a period of very slow growth of up to 50 years at the pole or mature stages but growth at other times was also highly variable. Seedlings and saplings of pink pine were rare and all stems examined were of great age, dating to the 13th or 14th centuries. In yellow silver pine recent seedlings were common but poles were rare and most stems dated to around 1700, suggesting that both pink and yellow silver pine have only a limited regeneration ability in the Kaimai Ranges.

A poor correlation between stem size and age is found in kaikawaka ($r^2$ =68.7 for 78 values). The relationship can be interpreted as being the result of the presence of trees which have been suppressed for various periods of time (Fig. 6.5). Once released the suppressed trees grow at approximately the same rate as non-suppressed trees but the size/age class relationship (ie. x- axis intercept) is moved to the left (Fig. 6.6a). The situation is more easily seen in size/age data from plants less than 120 years old (Fig. 6.6b). Here there appear to be three size/age relationships, one representing no suppression (upper line) and the other two representing suppression for 20-30 years (middle line) and 60-70 years (lower line).

The anomalies in the size/age relationship of many species from the upland forests mean that plant size is frequently found to be a poor guide to relative stand age between sites and between study areas. Slow initial growth or suppression is also an important source of error in determining absolute tree age since samples made a few centimetres apart at the base of a suppressed stem will yield considerably different ages. Such an error would be expected for kaikawaka, toatoa, pink pine, yellow silver pine and pepperwood which have slow initial growth rates but not for silver beech, kamahi, quintinia and neinei which generally have no

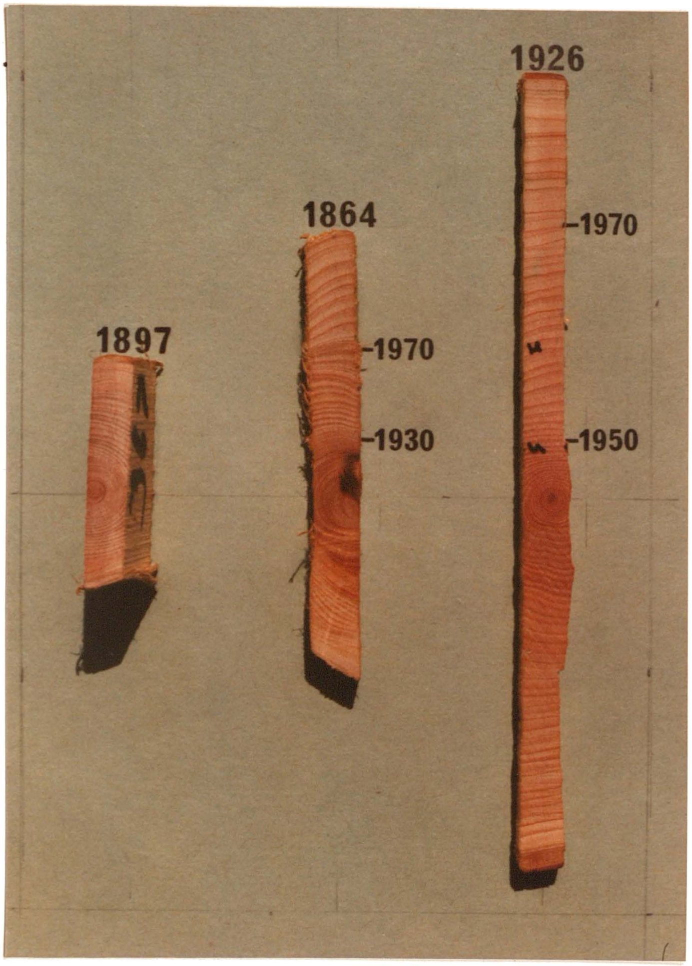


Fig. 6.5. Stem diameter and age in kaikawaka. Left hand core has a long period of slow growth without release; centre core was released in 1930 and 1970; right hand core with no significant supression.

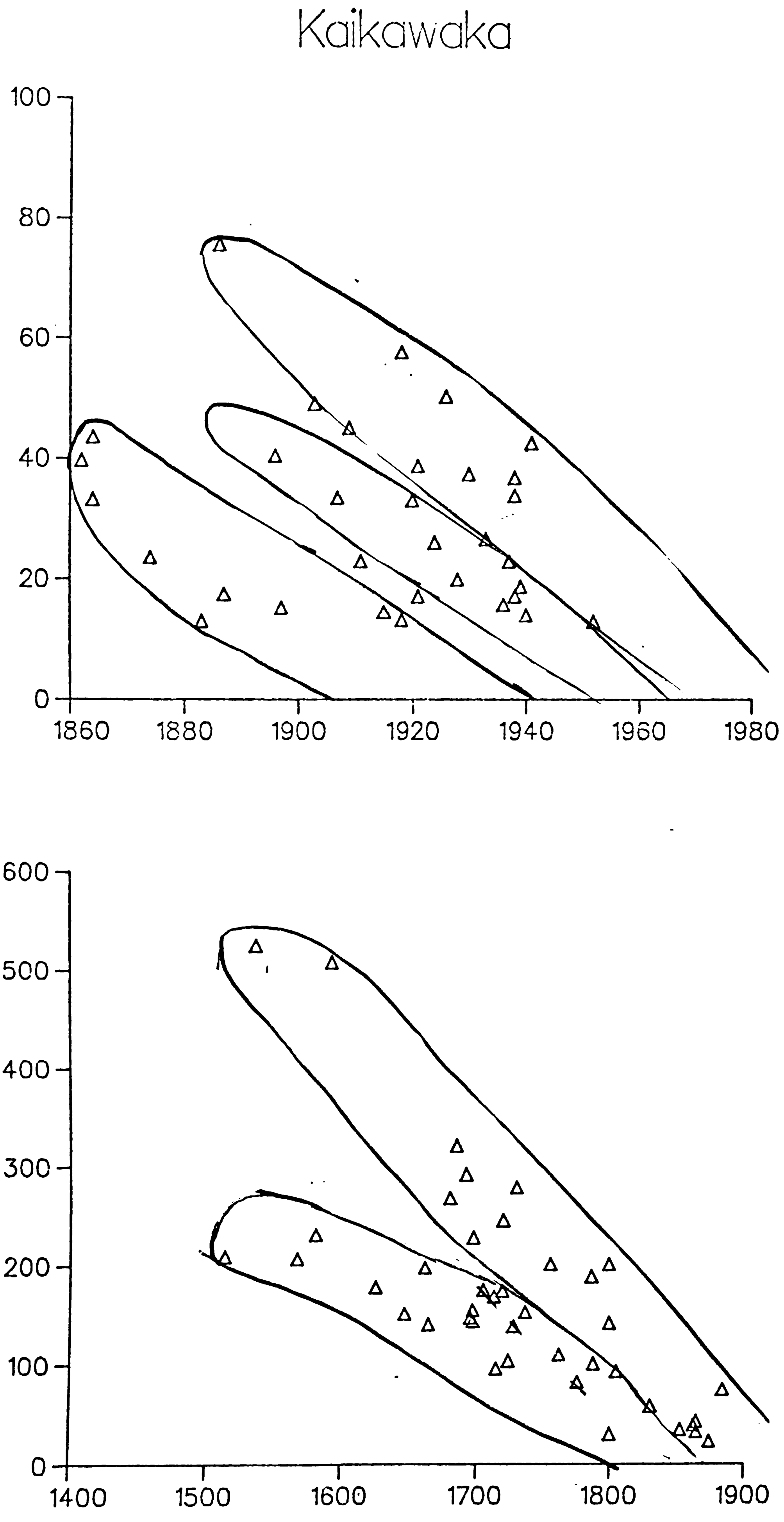


Fig. 6.6. Radius/ age relationship in kaikawaka. Lines enclose populations which apparently have the same release dates.

apparent period of suppression.

### Age Class Distributions

Age class structure of the population is only a rough guide to disturbance dates, particularly early dates. Recruitment periods may span a decade or more and repeated disturbances, by overlaying one another, may obliterate evidence of earlier events particularly on more sensitive sites. This latter effect means that evidence for older disturbances probably comes from progressively less sensitive sites and the earliest periods of recruitment will be the result of major disturbances. Regardless of habitat or ecological niche, all species show increased recruitment after the key chronology drought years 1914 and 1946. Silver beech, canopy plants of drier forest, kaikawaka of bog forest (Fig. 6.7), seral kamahi and quintinia, neinei from drier knolls and the predominantly sub-canopy pepperwood, (Fig. 6.8), all show the same general pattern. Evidence of major disturbances about 1896 and 1861 is also present showing as a prominent recruitment peak in silver beech and kaikawaka around 1860, recruitment of neinei from 1880 and the oldest seral plants from 1896. This implies that the key year 1861 was of similar significance to 1914 but for seral plants the impact is obscured by the later mortality. The major proportion of the older stems of kaikawaka, silver beech and pink pine originated around 1690-1700 and 1650. Yellow silver pine do not date before 1700 and apart from pink pine very few stems date before 1650. Two key dates 1696 and 1656 occur in the chronology near these times but dating reliability from age class structure is poor because of small sample size and the obscuring effect of later mortalities.

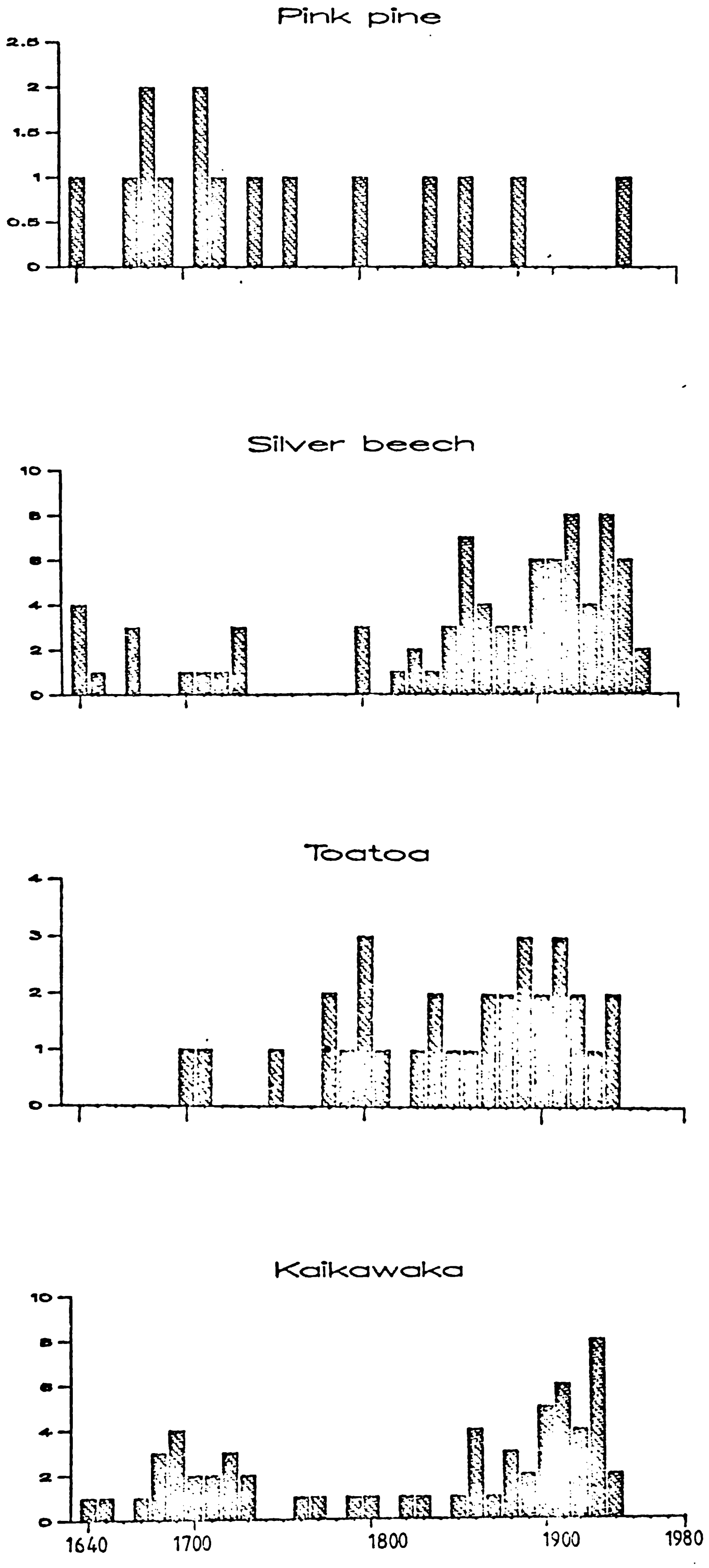


Fig. 6.7. Age class distribution of sampled stems of long-lived species from a range of sites throughout the Kaimai Ranges.

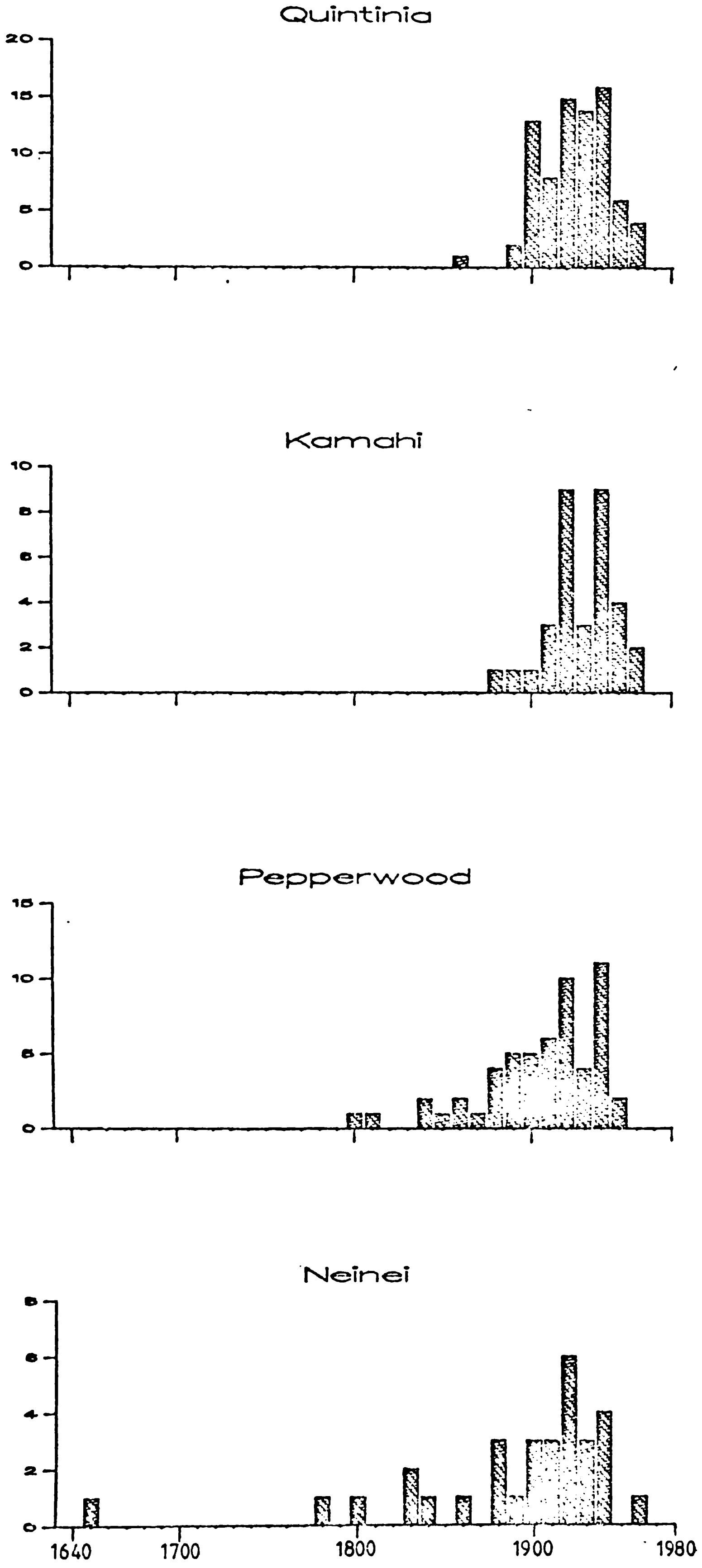


Fig. 6.8. Age class distribution of sampled stems of seral, short-lived species from a range of sites throughout the Kaimai Ranges.

Only a few plants originated around 1800 although the master chronology indicated that 1804 was a very important year. Silver beech, kaikawaka and yellow silver pine recruitment patterns all show a period between 1730 and 1860 when regeneration was very limited. This period may arise because subsequent mortality (1861 or 1914) eliminated the 1804 cohort, or possibly because a dense canopy from regeneration prior to 1700 prevented seedling establishment. Beech forests are known to show a similar long period when regeneration is limited by a dense canopy (Wardle and Guest 1977).

Kamahi and quintinia, have very similar age class distributions with a paucity of stems dating prior to 1890. The absence of older stems does not appear to be related to potential age since large kamahi and quintinia are present in lowland forests and kamahi has been reported to reach ages of over 200 years (Wardle 1966). Although kamahi has the potential to exist in the subcanopy of older upland stands, in the same way as neinei and other species, only seedlings and small shrubs are present. This suggests that the species may be sensitive to some site factor.

### Growth trend analysis

The smoothing spline fitted to each individual raw data set and subsequently averaged for each species requires careful interpretation (Fig. 6.2). Key dates from the chronology may not necessarily correspond with the growth changes since smoothing will obscure the exact point at which the sharp change occurred (Fig. 6.2). The early parts of all the data sets contain young stems showing a phase of rapidly increasing growth followed by declining growth in senescence. In the canopy species the age classes, after about 1800, are mixed and effects of youth and senescence are both present so that growth changes may be obscured. This effect is most readily seen in in silver beech

(Fig. 6.9) where growth prior to 1800 is dominated by two periods of rapid growth of poles and young trees punctuated by dramatic senescence in 1656 and 1804 but after 1804 mixed age classes produce relatively even growth. Growth rates in pink pine are influenced by a new generation from about 1656 which, after a period of dormancy or suppression found release in 1804 or 1811. Kaikawaka and toatoa sequences have lower amplitudes of growth variation and show no major peaks.

Less prominent growth changes in the smoothed series corresponding with key dates in the chronology, but inconsistent among the species, may reflect different site preferences among species as well as the intensity of disturbance events. For instance, minor disturbances could produce increased growth in seral stands with young stems through reduced competition, but may retard growth in senescent trees. Similarly climatic effects, not related to key disturbance years, may be present and may differentially effect species. The known disturbance dates, 1914 and 1946, have smaller troughs in growth rates than those for earlier dates possibly resulting from the mixed age of the sample. 1896 gave depressed growth to silver beech but release to kaikawaka and minor responses in the remaining species. 1861 was a significant date for all species. In 1831 depressed growth occurred in pink pine and toatoa but enhanced growth occurred in silver beech and kaikawaka. 1804 was the centre of a major crash in growth rates of silver beech, kaikawaka and toatoa but did not affect pink pine. 1773 marked a decline in silver beech, toatoa and pink pine but had minor effects in kaikawaka. 1731 and 1737 produced a major change in growth in toatoa and lesser effects in the remaining species. Impacts of earlier dates, although apparently large, are based on small data sets but 1696, 1681, 1656 and possibly one near 1614 are clearly important. The number of dates shown in the smoothed series is greater than the number of

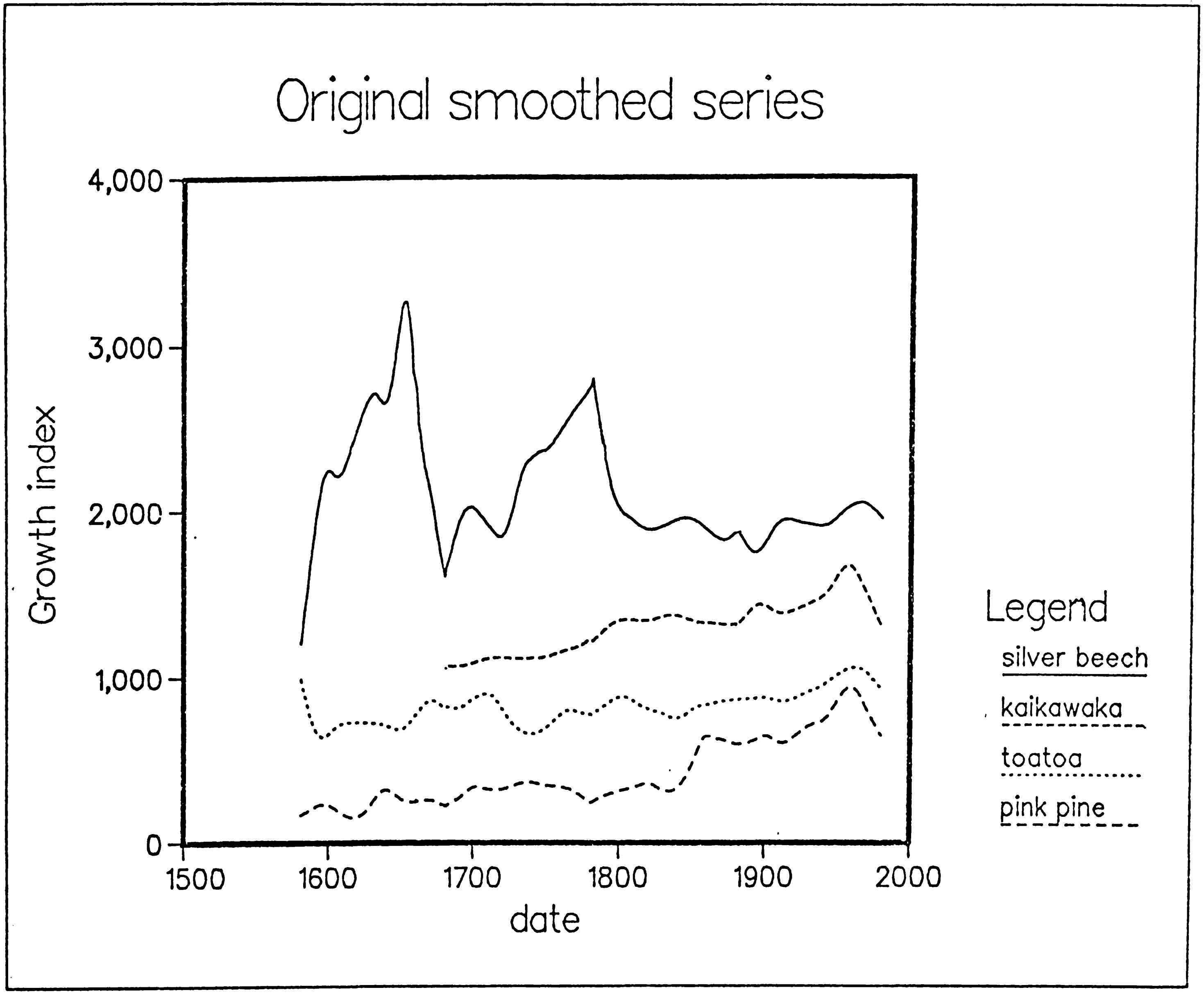


Fig. 6.9. General growth trends of the long-lived species derived from pooling of the initial smoothing splines. Each line has the same scale but are separated from one another by 250 (lower pair) or 500 units (upper pair).

recruitment peaks in the age class data and may include lesser disturbances with the resulting cohorts being killed by later events. Variations in growth between species may reflect differences in nature and severity of events, as shown in the more recent (1861, 1914, 1946) mortality in the seral species, or climatic trends with effects not related to key disturbance years.

### Residual analysis

Growth trends in the standardised residuals were examined at four levels by application of the smoothing spline to successive residuals. Smoothed splines of the long (a=1000), medium (a=10), and short term trends (a=1), were examined as well as the detrended final residuals. The long term trend (Fig. 6.10) is of much lower amplitude than the medium (Fig. 6.11) or short term (Fig. 6.12) trends and shows only small, largely climatic changes. The medium term trend shows the decade by decade fluctuations in growth whilst the short term trends show within decade variations.

The growth trends show few correspondences between species and none are consistent so that it is difficult identify years of high significance. One approach is to examine only the largest deviations from the trends, taking into account the variability for the period (Table 6.2). Both 1914 and 1804, regarded as important key dates, are of low significance but 1946, 1861, 1696, and 1656 stand out in all species. The final residuals contain quasi-random year to year growth fluctuations and have no significance beyond indicating the degree of variability in growth over longer periods (Fig. 6.13). They show periods of highly variable growth; in silver beech after about 1804 when many of the older trees sampled were senescent; in pink pine between 1800 and 1890; and in the remaining species at the beginning of the sequences, possibly related to small sample size. In all species

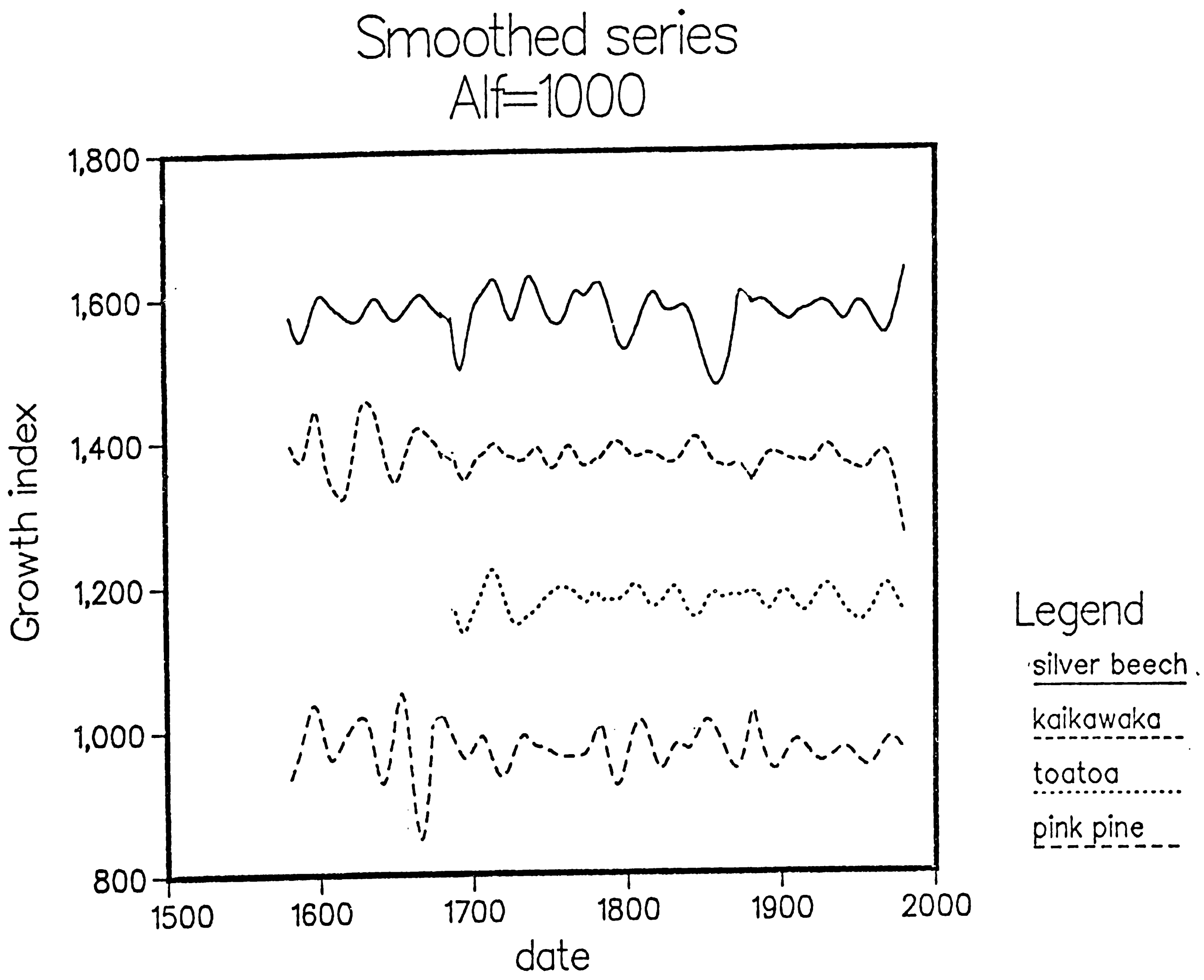


Fig. 6.10. Long term trends in chronosequences extracted from the basic pooled residuals using a spline with A=1000. Amplitude of variation is low and lines separated by 200 units.

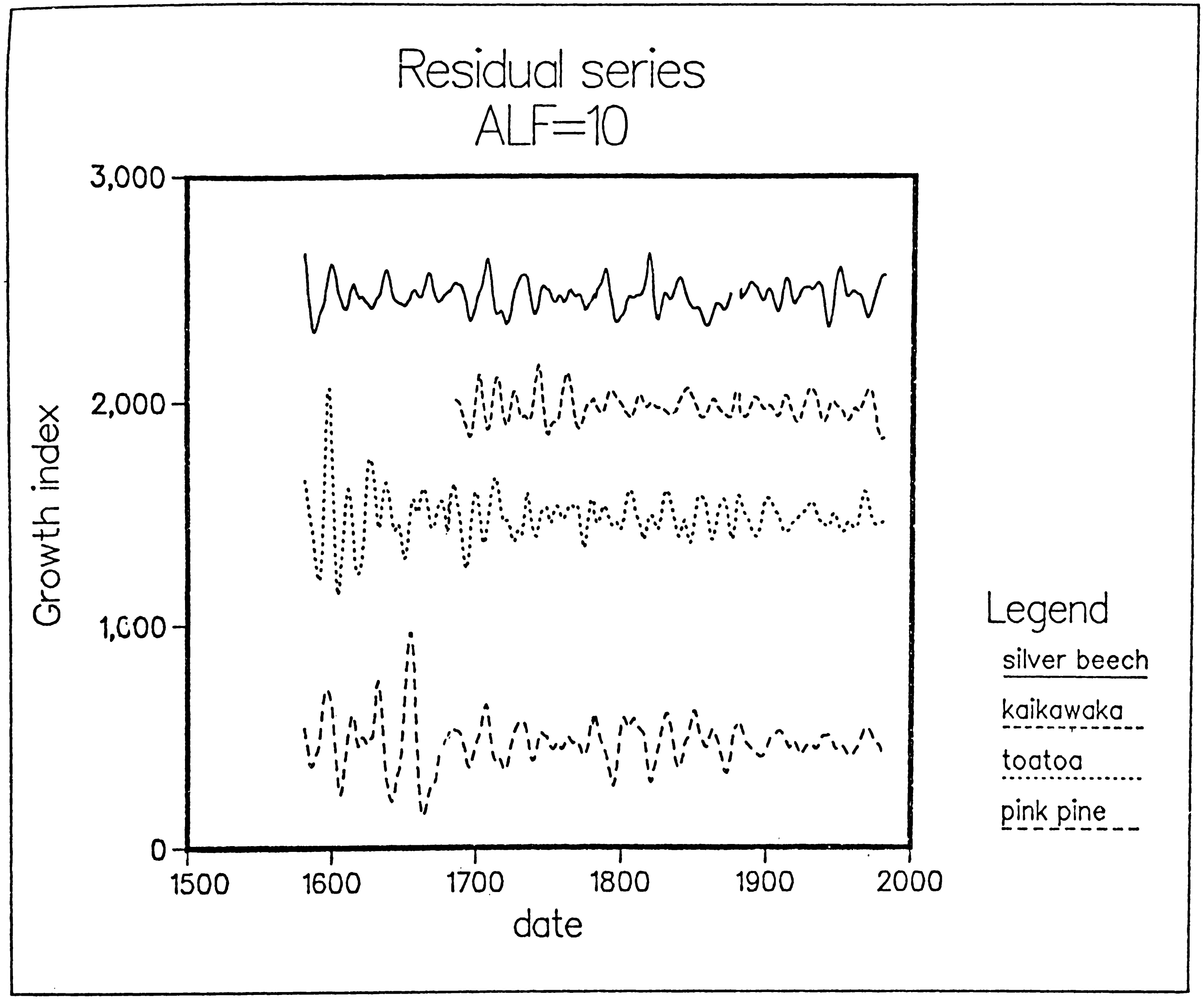


Fig. 6.11. Medium term trends in chronosequences extract with a smoothing spline with A=10 from residuals remaining after removal of long term trends. Lines centred at 500, 1500, 2000, and 2500 units.

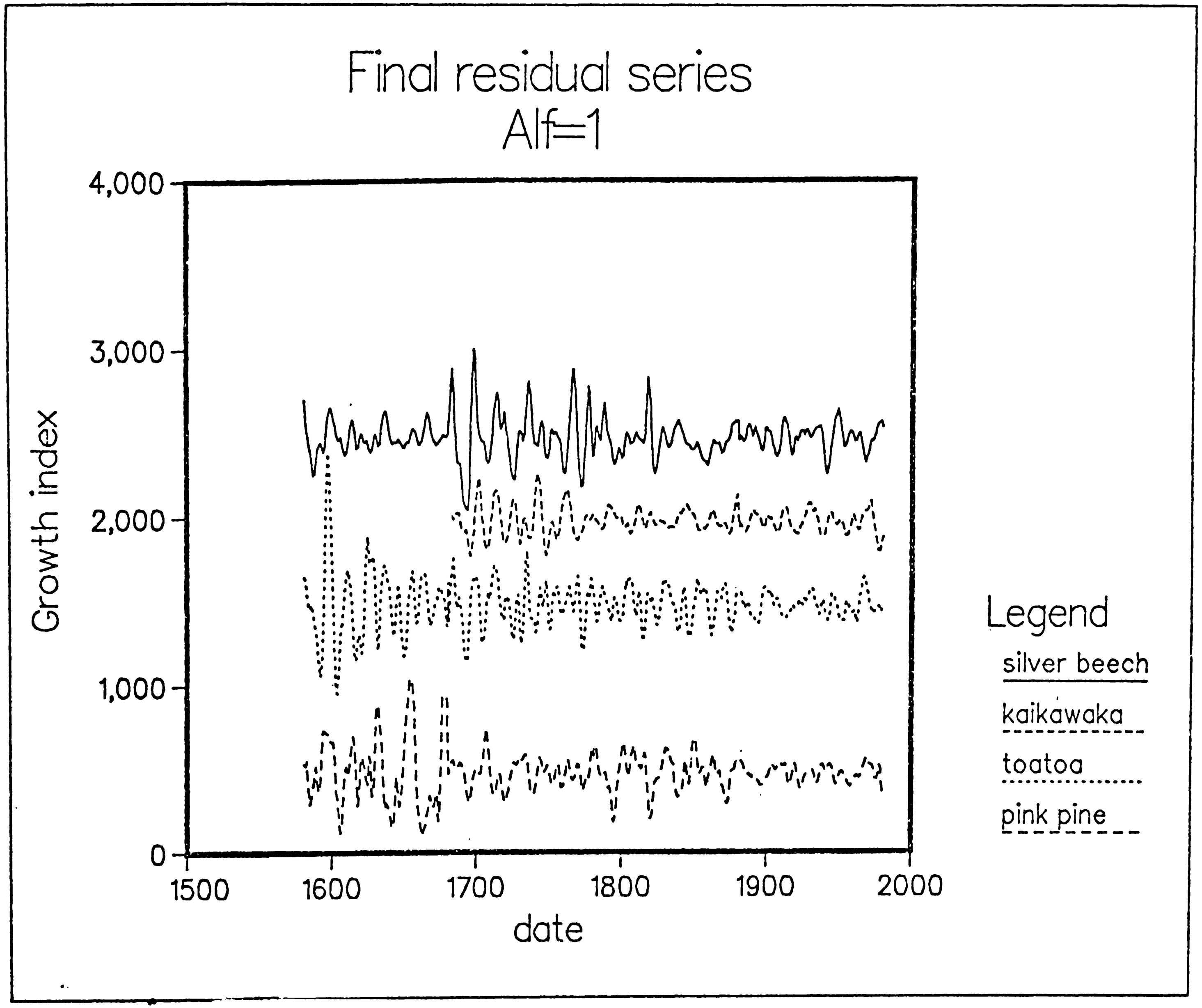


Fig. 6.12. Short term trends in the chronosequences extracted with a smoothing spline with A=1 from residuals remaining after removing long and medium term trends. Lines centred at 500, 1500, 2000, and 2500 units.

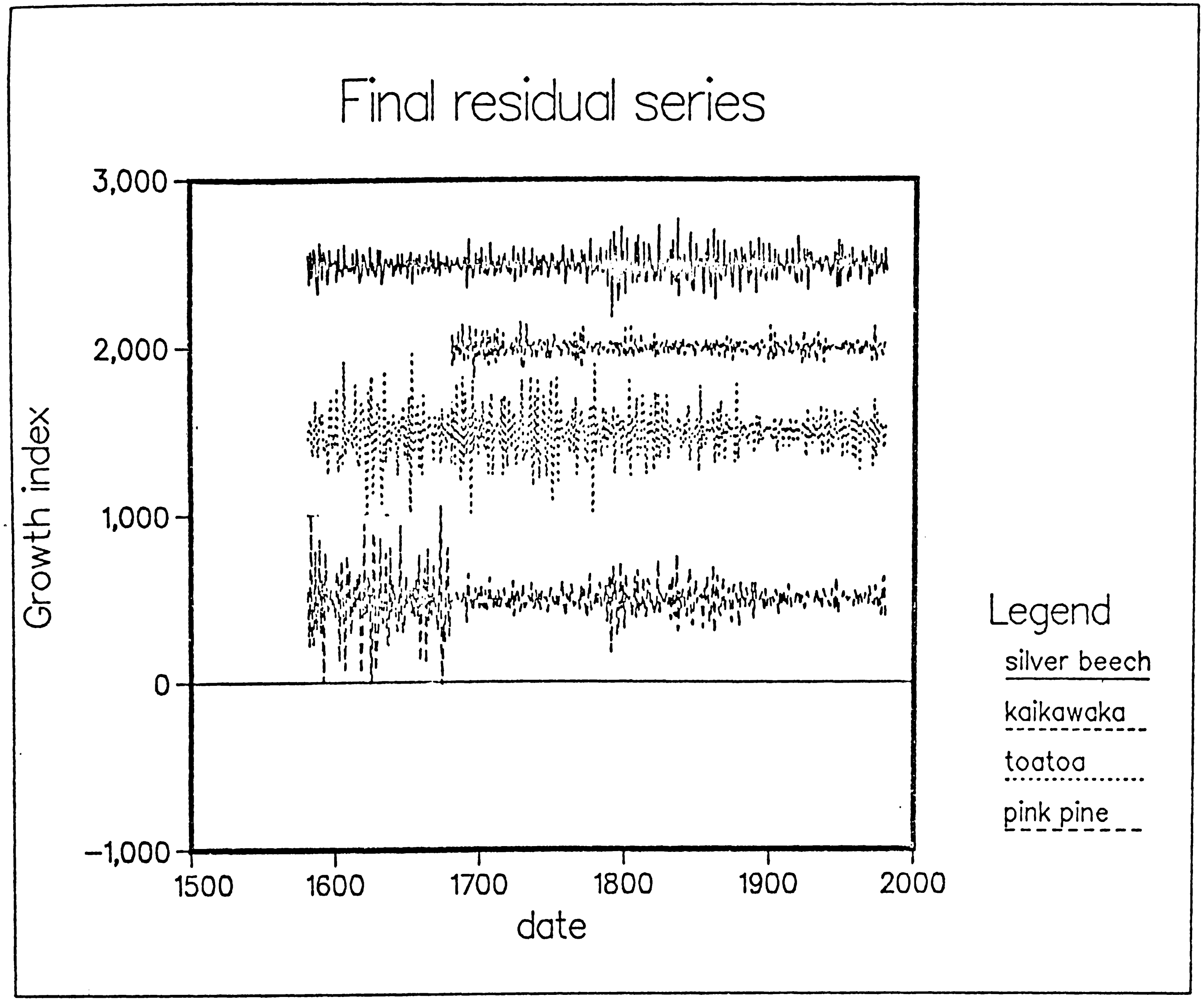


Fig. 6.13. Detrended final residuals after successive removal of long medium and short term trends. Lines centred at 500, 1500, 2000, and 2500 units.

there is a period of low variability between 1900 and 1920.

### Probable major disturbances

The master chronology provides several precise dates which indicate severe climatic perturbations but not necessarily vegetation disturbances. The age class data provide good evidence for disturbances but only low dating reliability. The poor reliability arises from factors influencing regeneration. Quintinia, silver beech, and kamahi regenerate readily in the shade of older trees, but seedling turnover rates may be high (Wardle 1967), and mortality on increased exposure when the canopy plants are removed is also likely to be high (Bazzaz 1979). Advance growth (pre-existing seedlings and shrubs) may survive the disturbance and small plants will appear to arise prior or close to the year of the disturbance. Small shrubs may predate the disturbance by many years but may show increased growth associated with release from suppression. This introduces a lack of precision possibly up to 10 or 15 years which may be difficult to identify although the release date may show as a sharp, prolonged growth increase in individual ring sequences. In seral stands mortality effects are more complex, particularly in kaikawaka and silver beech, since release from competition as well as fresh mortality may occur and result in substantial error. Seedlings regenerating after the disturbance will date to the first suitable subsequent seed year which may be delayed several years. Summit tracks on Te Hunga, cleared in 1978, have few seedlings implying that 5 or more years may occur between disturbance and fresh regeneration at this locality. In some species, such as silver beech, prolific seeding may occur only every 5-7 years following drought (Hinds and Reid 1957, Franklin 1965), and in the intervening years seed is severely limited by predation (Fitzgerald 1978, Campbell 1978). Nevertheless, similar regeneration following windfall in the

South Island (Moorhouse 1939) dates close to known dates of disturbance. Mortality is attributable to the 1914 drought but seed source or site conditions did not again become favourable for regeneration until 1920 resulting in a recruitment peak in the 1920 decade.

Changes in growth rate that can be dated precisely in individual cases may be produced by intra-stand competition or climatic factors. Release from competitive effects may be delayed until growing conditions improve at the end of a drought or until mortality reduces stand density. For instance, mortality was known to have occurred in 1946-8 and is attributable to the 1946 drought and yet the major change in growth rate, particularly in understory species such as pepperwood, did not occur until 1950 (Fig. 3.1). However the dates in Table 6.2 probably correspond with important disturbances. The most significant dates 1946, 1861, and 1656 mask the effects of many lesser disturbances. In the field it is common to see mortality patterns concentrically overlain from sensitive to resistant sites (Fig. 6.14).

### Estimation of climatic trends and related key dates

Estimation of the significant climatic parameters may enable identification of the main causes of the growth anomalies at key dates in the chronology and provide clues to the causes of the disturbances. Year to year variation in climatic parameters cannot be reliably estimated but medium and long term trends are highly predictable from the dendrochronological series (Table 6.3). Smoothed estimates of climate values excluding the year to year component (final residuals) are shown in Fig. 6.15 and Fig. 6.16 and summarised in Table 6.4. The results must be in treated with caution, particularly for early dates where variability is higher since growth responses in the younger stems may differ from the older stems. Younger plants may be more sensitive to climatic variability and extremes could be over-emphasised in the

Fig. 6.14. Gully head mortality showing concentric patterns of age classes. The grassy areas contain regeneration datable to 1946; low seral stands, vegetation datable to 1914; overwood with senescence datable to 1804 and healthy stands in the background datable to about 1650.

Table 6.2
Key years showing depression of growth rate in long (L), medium (M), and short term (S) smoothed components of the residuals (Figs. 6.10, 6.11, 6.12).

| Key date | silver beech | kaikawaka | toatoa | pink pine |
|---|---|---|---|---|
| 1972 | L S | M S | M S | |
| 1946 | L M S | M | L | |
| 1919 | L | | | |
| 1914 | | L | L | |
| 1896 | L | L | | L |
| 1872 | L | M | | M |
| 1861 | L | L M | L | M S |
| 1820 | M S | | | M S |
| 1804 | | | | L |
| 1793 | | | | L M S |
| 1773 | M S | | | |
| 1737 | M | | L | |
| 1710 | S | | | S |
| 1693 | L S | L | M S | |
| 1656 | M | L M | | L M S |
| 1614 | M | | M | M |
| 1593 | M | | M S | M |

Table 6.4

Extreme events indicated by estimated rainfall and temperatures (Figs. 6.14, 6.15) coinciding with key years.

| Key Years | Rainfall | Temperatures |
|---|---|---|
| 1972 | dry January | cool summer; mild winter |
| 1956 | low winter rainfall | ground frosts numerous |
| 1946 | dry January | warm summer; mild winter |
| 1919 | dry January; low winter and total rainfall; | ground frosts numerous |
| 1914 | dry January; low rainfall | hot summer; frosty winter |
| 1896 | low winter rainfall | hot summer; frosty winter |
| 1872 | dry January; dry February; low total rainfall | ground frosts |
| 1861 | dry January; dry February; low total rainfall | hot summer;screen frosts |
| 1820 | hot summer; | cold winter |
| 1817 | dry January; wet year-February or March storm. | |
| 1811 | low total rainfall; dry February | hot summer |
| 1804 | dry January; low rainfall | cool summer; ground frosts |
| 1790 | dry January | hot summer; frosty |
| 1773 | dry winter | hot summer; mild winter |
| 1761 | dry January; dry winter | hot summer; cold winter |
| 1745 | dry winter; low rainfall | |
| 1737 | dry January and February | hot summer; screen frosts |
| 1731 | very low rainfall; dry winter | cool summer; mild winter |
| 1696 | dry January; dry winter | cool summer and winter |

Table 6.3
Regression coefficients for predicting climatic variables.

intervals

| Yearly | Te Aroha | | | | | | | Waihi | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Final resids) | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr |
| Pink pink | | | 1.66 | | | | -.48 | | | | | | | |
| | | | .25 | .33 | .27 | .38 | .54 | | | .29 | .46 | | | |
| Silver beech | | | | -3.1 | | 1.1 | | | | | | | | |
| | | | | | 1.0 | | | | | 2.9 | 3.3 | | | |
| Toatoa | | | | | | | .22 | | | | 1.6 | | | |
| Kaikawaka | | | | 1.2 | | -1.4 | -.20 | | | | | | | |
| correlation | | | .25 | .33 | .27 | .38 | .54 | | | .29 | .46 | | | |

| Short term | Te Aroha | | | | | | | Waihi | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Alf =1 ) | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr |
| Pink pink | | -2.3 | | | | | | | | | | | | 1.1 |
| | | | | -1.6 | | | -.99 | .55 | | -1.8 | 1.9 | -1.2 | .04 | -.98 |
| Silver beech | .75 | -1.3 | -1.1 | -4.1 | | | 2.2 | -.62 | | 1.3 | | | | |
| | -.23 | | | | | | | | | | | | -.12 | -1.6 |
| Toatoa | .70 | | | | | | | | | -2.8 | | | .11 | |
| | | | | 1.9 | | | | | | | | | | 1.9 |
| Kaikawaka | | | | 1.2 | | -.16 | | | | -1.7 | | | .07 | -1.1 |
| Correlations | .42 | .50 | .31 | .58 | .50 | .41 | .56 | .43 | | .70 | .48 | .49 | .73 | .68 |

| Medium term | Te Aroha | | | | | | | Waihi | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Alf = 10 ) | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr |
| Pink pine | -.10 | 12.7 | 1.9 | 3.9 | -.03 | -.09 | | .50 | -.15 | 20.4 | .08 | | .21 | .15 |
| | | 1.0 | .20 | .07 | 1.4 | .06 | 1.1 | .51 | .25 | 2.3 | | .74 | .09 | -1.0 |
| Silver beech | -.86 | | 6.5 | -1.7 | 1.4 | .06 | .74 | | -6.5 | -19.3 | | .58 | 1.1 | |
| | | -1.6 | 8.7 | 1.6 | | | -.54 | -.45 | | 14.5 | 3.5 | | | |
| Toatoa | -1.1 | -2.4 | | | | | 5.9 | | | | -3.8 | | -.32 | 1.2 |
| | 1.5 | | | | | | 6.6 | | | | 3.4 | | .36 | |
| Kaikawaka | -.33 | | 1.2 | | .35 | | | | 3.39 | | | | | |
| Correlations | .91 | .99 | .94 | .91 | .98 | .93 | .99 | .97 | .97 | .86 | .95 | .91 | .98 | .99 |

| Long term | Te Aroha | | | | | | | Waihi | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Alf = 1000) | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr |
| Pink pine | -5.24 | 4.4 | 11.5 | -1.5 | -5.2 | -.11 | .28 | -2.4 | | 11.5 | -12.3 | | -.26 | -2.2 |
| | 8.8 | | | 8.7 | 8.7 | 1.5 | | 1.1 | -15.1 | -12.9 | -2.6 | 1.9 | | -.32 |
| Silver beech | 6.0 | 6.1 | 12.0 | -10.7 | 6.03 | | -.44 | | -1.5 | -21.2 | 23.7 | 12.8 | -.43 | |
| Toatoa | 6.6 | | 6.1 | | 6.5 | | | 3.1 | | | | .76 | | |
| | | -6.7 | 14.8 | -12.7 | 3.7 | | -.40 | 1.4 | -.43 | 13.0 | 9.4 | 9.5 | | -2.7 |
| Kaikawaka | | 5.5 | -9.7 | 9.4 | | | | | | -7.2 | -3.4 | | | |
| Correlations | .99 | .98 | .99 | .99 | .99 | .96 | .98 | .99 | .96 | .99 | .99 | .98 | .99 | .97 |

Each species may contribute a component for the current year and a lag component for growth in the previous year. In the table current year coefficients are placed on the upper line and lag coefficients on the lower line. Column headings are total annual rainfall followed by January, February March and December rainfalls, Maximum temperature and Screen frost numbers. Correlation coefficients are placed at the end of each table segment. The three sections in the table refer to smoothed trends obtained by applying a smoothing spline sequentially to both data sets.

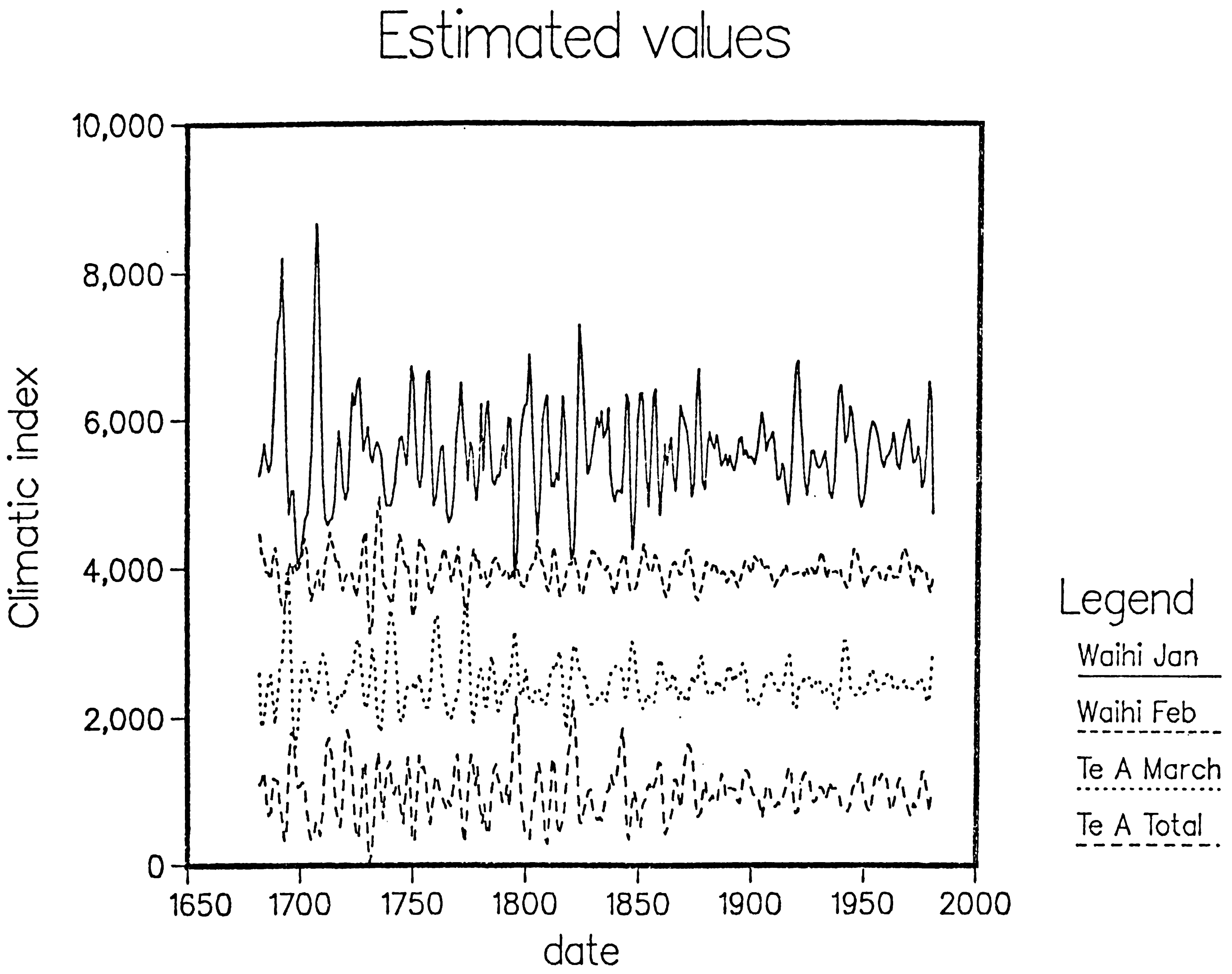


Fig. 6.15. Estimated trends in rainfall derived projection of multiple regressions of combined short and medium term dendrochronosequences of four species on climatic data. Lines arbritraily separated.

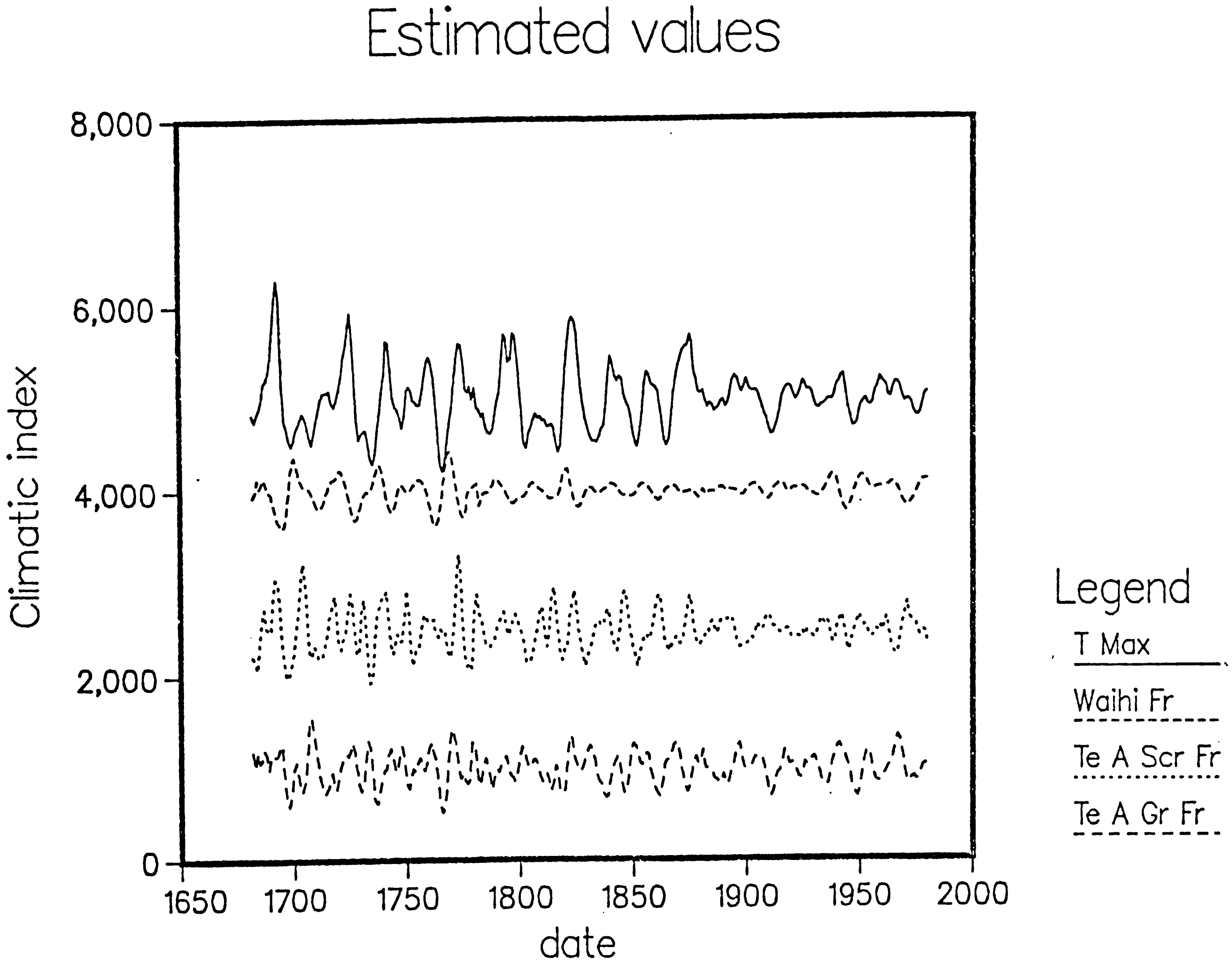


Fig. 6.16. Estimated trends in temperature trends derived projection of multiple regressions of combined short and medium term dendrochronosequences of four species on climatic data. Lines arbritraily separated.

early data.

A few parameters are good indicators of the main climatic pattern discussed in the climate chapter (Chapter 5). Waihi January and to a lesser extent February rainfall are strongly influenced by the occurrence of tropical storms which produce marked rainfall fluctuations. Te Aroha March rainfall is more stable and is an indicator of winter rainfall. Te Aroha total rainfall can be taken as an indicator of the annual rainfall within the ranges. Temperature variations are important since the occurrence of extreme high or low values may affect growth and the occurrence of both extremes together may be indicators of low fog occurrence.

Two patterns appear to be linked with key years: colder drier periods such as 1696-1710 and 1796-1810, and periods of extremely variable rainfall such as 1720-1740 and 1840-1870, Periods of extremely variable rainfall often occur at the same time as high frost numbers and are times when cloud cover was likely to be lower. These are clearly periods of very variable weather probably dominated by tropical influences during which severe droughts are probable.

The years 1914 and 1919 and 1804, 1811 suggest a series of severe droughts. 1861 and 1731 were very dry years of which 1861 appears to have been a hot summer and cold winter with low fog frequency. All the key dates suggest a strong link with exceptionally low rainfall and represent all except two (1710, 1845) of the years with low January rainfall. Other lesser dates in the chronology with a strong drought link are 1972, 1946, 1914, 1919, 1872, 1811, 1793, 1761, and 1737.

## Ecological significance of effects of climate on tree growth.

Pink pine was most strongly influenced by temperatures trends at all levels. In the final residuals and short term trends large regression components were associated with low maximum temperatures, high numbers of screen frosts and a low February Waihi rainfall (Table 6.5). Medium term trends are dominated by low total rainfall, but high maximum temperature at Te Aroha imply an influence of warm dry summers. Long term trends are dominated by high frost numbers. These conflicting influences suggest an overall preference for cooler climatic conditions but medium term warm, dry summer influences suggest conditions of reduced site waterlogging.

Silver beech growth is dominated by rainfall influences but there are no strong correlations in the final residuals. Short term growth trends, although not pronounced, are closely linked to low summer rainfall at Te Aroha and low winter rainfall and warm previous summer at Waihi. Medium term growth responses reflect the opposing trends of dry summers at Te Aroha and wet conditions at Waihi, clearly drier periods associated with tropical climatic influences at the coast. Improved long term growth trends are influenced by below average rainfall at Te Aroha in January. Depressed growth at all levels occurs in wet years or wet periods and strongly implicates the detrimental effects of prolonged site waterlogging.

Toatoa has correlations in the final residuals which suggest that years with low rainfall at Waihi give better growth. Short term trends are favoured by low maximum temperatures and more frequent frosts particularly after a mild winter. Medium term trends are strongly dominated by below average January rainfall at Te Aroha and Waihi but good winter rainfall. Long term trends are strongly favoured by lower more frequent frosts. Hence toatoa can be regarded as favouring cooler conditions but with dry summers.

Table 6.5
Multiple regression coefficients between climatic parameters
and growth in four species at yearly, short medium and long term response intervals.

| Yearly<br>(Final resids) | Te Aroha |  |  |  |  |  |  | Waihi |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr | corr | auto |
| Pink pink |  |  |  |  |  | -.49 |  |  |  |  | .05 |  | .95 |  | .74 | .28 |
|  |  |  |  |  |  |  | .61 |  |  |  |  |  | .56 | 0.8 |  |  |
| Silver beech |  |  |  |  |  |  |  |  |  | .05 |  |  |  |  | .65 | -.59 |
| Toatoa |  |  | .07 |  |  |  |  | -.12 |  |  |  |  |  |  | .67 | -.41 |
|  |  |  |  |  |  |  |  |  |  |  | .05 |  |  |  |  |  |
| Kaikawaka |  |  |  | -.11 |  |  |  |  |  |  |  |  |  |  | .81 | -.41 |
|  |  |  |  | -.06 |  |  |  |  |  |  |  |  |  |  |  |  |

| Short term<br>(A= 1) | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr | cor |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pink Pine |  |  |  |  |  | -1.72 | .28 |  | -.22 |  |  | -.13 |  |  | .73 |
| Silver beech |  | -.08 |  |  | .08 |  |  |  |  |  | -.10 |  |  |  | .76 |
|  |  | -.06 |  |  |  |  |  |  |  |  |  |  | .10 |  |  |
| Toatoa |  |  |  |  |  |  | .20 |  | -.05 |  |  |  |  |  | .86 |
|  | .11 |  |  |  |  |  | -.20 | -.22 |  |  |  |  | -2.3 |  |  |
| Kaikawaka |  |  |  | -.18 |  |  | .12 |  | -.08 |  |  |  |  |  | .83 |
|  |  |  |  |  |  |  | 1.12 |  |  |  | .17 |  |  |  |  |

| Medium term<br>(Alf =10 ) | Te Aroha |  |  |  |  |  |  | Waihi |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr | cor |
|  |  |  |  |  |  |  |  | .47 |  |  | .65 |  |  | -.06 |  |
| Pink pine | -.36 |  | .12 |  | -.53 | .58 | .27 |  |  |  |  | .22 |  |  | .99 |
|  | -.48 |  |  | .05 |  |  | -.05 |  |  | .07 |  | .07 |  |  |  |
| Silver beech |  | -.43 |  |  | .22 |  | .09 | .52 |  |  | -.04 | .07 |  |  | .99 |
|  |  | .12 |  |  | -.07 |  | .25 |  |  | .05 |  |  |  |  |  |
| Toatoa |  | -.28 |  | -.08 |  |  |  |  | -.06 |  | .26 |  |  | .04 | .99 |
|  |  |  |  |  | -.19 |  |  |  |  |  |  | -.19 |  |  |  |
| Kaikawaka |  |  |  | -.34 |  |  | .22 | -.48 |  |  | -.52 |  |  | .12 | .98 |

| Long term<br>(alf=1000) | Te Aroha |  |  |  |  |  |  | Waihi |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | total | Jan | Feb | Mar | Dec | Tmax | Scr | total | Jan | Feb | Mar | Dec | Tmax | Scr | cor |
| Pink pine |  | -.038 |  | .02 | .001 |  | .34 | .14 | -.05 |  | .16 |  |  |  | .98 |
|  |  |  |  |  | -.001 |  |  |  |  |  |  | -.03 |  |  |  |
| Silver beech |  | -.06 |  | .04 | -.03 |  |  |  | .02 |  |  |  |  |  | .98 |
| Toatoa |  |  |  | -.01 |  | -.15 | .48 |  |  |  |  | .03 |  |  | .98 |
| Kaikawaka |  |  |  |  |  |  |  |  |  |  | .02 |  |  |  |  |
|  |  |  |  | -.06 | .04 | -.48 |  | .02 | -.06 | .01 | -.01 |  |  |  | .99 |

Each species may contribute a component for the current year and a lag component for growth in the previous year. In the table current year coefficients are placed on the upper line and lag coefficients on the lower line. Column headings are total annual rainfall followed by January, February March and December rainfalls, Maximum temperature and Screen frost numbers. Correlation coefficients are placed at the end of each table row. Autocorrelations were only calculated for the final residuals. The four sections in the table refer to smoothed trends obtained by applying a smoothing spline sequentially to both data sets.

Kaikawaka has year to year growth strongly correlated with low winter rainfall. Short term growth trends are strongly favoured by a cold winter the previous year and low march rainfall at Te Aroha. Medium term growth is favoured by low March rainfall and low annual rainfall at Waihi with frosts at Te Aroha. Long term trends are dominated by lower summer temperatures at Te Aroha. Hence kaikawaka are favours generally cool dry winters.

All species show a consistent response to rainfall and temperature suggesting a link with periodic site waterlogging. There is a double relationship between summer base flows in the Waihou River and summer rainfall (Fig. 5.6) with the higher flow (right hand) possibly indicating a saturated aquifer and soil waterlogging and the left hand line a partially full aquifer and drier soils. The double relationship is also reflected in plant growth rates. For instance prior to 1969 growth was slow but in 1970 there is a marked upturn in growth related to the dry 1970-1972 period. 1976 marks the end of this period and began a new interval which continued until at least 1981 when river base flows changed and a sudden reduction occurred in tree growth and recruitment. Similarly, the first excessively wet year following the 1914-19 droughts was 1927 and this resulted in a prolonged period of below normal growth rates. Similar changes possibly occurred between 1861 and 1873, 1763 and 1773 and at less well defined periods. Enhanced growth occurs at the end of dry periods such as the 1939-1949 so that 1950 marks the beginning of mild dry summers resulting in a general increase in growth rates.

Some of the species appear better suited to cooler climates. Toatoa, yellow silver pine and pink pine have very specialised habitats and are often overtopped on sites with deeper soils or at lower altitudes and are confined to wetter sites or areas with stony soils where competition is less severe. These species may be relicts from cooler climatic periods or be present as a result of the reduced temperatures in the frequent fog. Sporadic regeneration probably occurs with shifts in temperature or rainfall means which persist for less than a decade. The presence of old specimens also suggests a high degree of tolerance to climatic perturbations and considerable persistence.

## DISCUSSION

### Dating disturbances

Precise dating of disturbance events depends on the certainty of dating a number of features apparent in the growth rings. The dates in the master chronology are based on cross-dating of many stems in several species and are probably reliable. The identification of the factors causing the growth anomalies is based on two lines of evidence; the known reasons for the recent anomalies and the actual or estimated values of climatic variables. The most distinctive feature used in the chronology, cambial mortality, can be attributed to drought. It occurs in years of low actual or estimated rainfall and in several species is unambiguously associated with wide or dense latewood which, is caused by dry summers. Both high frost numbers and high temperatures in the drier years also suggest extreme drought and a low cloud frequency at these times.

The association of low rainfall with key dates, however, does not alone provide evidence for widespread mortality, merely evidence of severe drought. Stand age class structure provides the evidence for disturbances and these correspond with the most severe droughts. In some cases, particularly minor disturbances, the evidence may be heavily modified by later events. Recruitment from some droughts, particularly the 1804, event is largely absent although growth trends suggest that a disturbance occurred. One explanation for such a lack of recruitment is that damage from droughts of progressively decreasing intensity is concentrated on the more sensitive sites. On these sites plant turnover may consequently occur at very short intervals following relatively minor droughts such as that of 1972. The seral species, particularly kamahi and quintinia, that are the main dominants on the sensitive sites, appear to be especially prone to mortality and do not survive to reach normal forest stature in upland areas.

### Causes of the mortality

Although age class evidence indicates a close link between mortality and drought it should be remembered that droughts occur in periods of disturbed weather when severe storms are also possible. Clayton-Greene (1976) found a major regeneration peak on Mt. Te Aroha at about 1820, with little earlier regeneration, and a similar recruitment peak on Mt. Pirongia as well as another about 1680. He suggested from the evidence of fallen trees that both disturbances were caused by storms. The recent Cyclone Bernie (April 1982) that devastated the Urewera region lends some credence to this proposal. Furthermore, Grant (1981) has produced strong evidence for episodic erosion throughout the North Island, New Zealand that he suggests is related to variations in storm intensity. It is difficult to verify or deny these proposals since there is a strong chance that once the stand integrity is broken by mortality, trees will be more liable to windthrow.

Severe drought damage has been reported in a wide range of forests and it is often regarded as a significant ecological factor shaping forest composition (Brunig 1969, Atkinson and Greenwood 1972, Maslov 1972, Ashton 1976, White 1979). In the North Island, New Zealand, reports of widespread forest mortality frequently follow drought years (Kershaw pers. comm) and recent occurrences followed the 1946 (Grant

1965, Coulter 1967) and 1972 droughts (Atkinson and Greenwood 1972). In the current study the striking concentration of regeneration in the 1920's following the 1914-19 droughts and other notable periods of recruitment in dry eras around 1860, 1696 and 1650 lend support to this hypothesis. The groups 1914-19, 1804-13 are also sequences of drought years clearly indicated by the presence of cambial mortality plus distinctive latewood and are also significant. Furthermore, differences in longevity between species appear to reflect differences in drought sensitivity since many do not reach more than a portion of potential age. Old kamahi and quintinia in the upland stands are less than 100 years old and barely more than saplings. Kaikawaka are only half the age of stems found on nearby Pirongia (Clayton -Greene 1977) and and few stems of the other major species are older. Only pink pine appears sufficiently resilient to survive more than 400 years. The sharp maximum age cut off that differs between species throughout the area, and the localised succession of age classes radiating from drought sensitive sites suggest that drought plays an important part in the mortality episodes.

Drought sensitivity on some sites currently appears to be related to waterlogging (Jane and Green 1983d) and climatic evidence suggests that former periods of slow growth are related to periods of above normal rainfall. 1976 appears to mark the beginning of a period of waterlogging and above normal rainfall (Fig. 5.6) with depressed growth and the pairs 1872 and 1861; 1761 and 1773 also appear to mark periods of very slow growth related to above average rainfall. Waterlogging probably adversely affects the root systems and leads to high sensitivity to water stress (Jane and Green 1983d) resulting in severe mortality during drought.

## Mortality and stand dynamics

Minor droughts appear to trigger mortality in seral species and periods of rapid growth in others. This may arise because mortality of kamahi and quintinia allows release of the more permanent species such as silver beech, kaikawaka and tawari which appear to be more able to withstand waterlogging and subsequent drought stress. Gymnosperms such as kaikawaka, toatoa, pink and yellow silver pine apparently survive through several episodes of mortality and this results in defined periods of release at disturbance dates. The growth patterns in silver beech indicate that mortality occurs when the trees mature at about 100-150 years in the Kaimai Ranges. A similar situation appears to arise in the South Island stands of this species where periodic storms and snow can lead to mortality at similar intervals (Wardle 1980). Consequently, as Wardle (1980) has suggested, it appears that instability is an inherent feature of beech forests and stands reach a phase of high sensitivity to stress as they mature.

Species composition of mature stands may change following a major disturbance because of climatic perturbations in the regeneration phase. In the most severely affected areas silver beech dominates on the gently rolling better drained slopes and gymnosperms are uncommon although heavily decayed logs of kaikawaka, possibly many hundreds of years old (Hinds and Reid 1948), are common. The former presence of kaikawaka on these sites may indicate wetter climatic conditions prior to disturbance but site conditions suited to regeneration of silver beech after disturbance. Similarly large, slow growing and very old pink pine are scattered throughout the area but only common as dense stands on the exposed rocky spurs. They are more usually found in colder areas (Wells 1971) and may be relict from a period colder climatic conditions.

## Climatic change

Much New Zealand ecological literature is coloured by consideration and proof of the climatic change hypothesis (Holloway 1948, Wardle 1963, Wardle 1978, Bathgate 1981) whereas the effects under consideration may result from successive disturbances. The "regeneration gaps" so important to the hypothesis may well arise from limited regeneration potential during the early, closed stand stage of forest development (Veblen and Stewart 1982b). The causes of the disturbances in New Zealand have been given little consideration.

Disturbances are common in forests throughout the world and arise from a wide range of factor including storms, fire volcanic activity (Veblen et al. 1980) drought and unexplained or complex causes (White 1981). Many of these events occur every 40-50 years in the particular ecosystem and major disturbances appear to occur every 150-200 years (Lorimer 1980, White 1979). In New Zealand Maori cultivations and wild fires have been responsible for considerable forest modification in the last 900 years (Cumberland 1961, Nichols 1981) and periodic seismic and volcanic disturbances have produced localised forest modification (Wardle 1967, Druce 1977, Veblen and Stewart 1980, Veblen and Stewart 1982a) but it also evident that storms (Reid 1948, Wardle 1980) and drought (Grant 1965) can result in widespread forest damage. This suggests that for some environments, perhaps even most, stability is merely an illusion (Miegroet 1978).

Recent climatic studies (Salinger 1979, Tomlinson 1980a, Tomlinson 1981) suggest that periods of below average rainfall and temperatures are frequently associated with periods of higher variability. There are a number of correspondences between these parameters and sunspot numbers (Salinger 1979, Tomlinson 1980b, Nature 1974, Clarke 1979) that appear to be related, through ionospheric disturbances on air movements, to weather patterns in the equatorial region (Newell 1979, Tomlinson 1980a). The extended Maunder minimum between 1600 and 1700 corresponds with a major climatic and forest disturbance and other dates such as 1804 and 1861 also occur at sunspot cycle minima. The dates also correspond with the postulated dates for climatic change in New Zealand (Burrows and Greenland 1979, Molloy 1979) and at least provide a guide to estimating the probability of similar severe disturbances in the future. The current long term sunspot cycle reached a peak about 1954 and appears to be leading to a minor trough in the mid 1980's. This suggests that a further period of drought and vegetation mortality is likely in the next 5-10 years.

# CHAPTER 7

## ANALYSIS OF PRESSURE-VOLUME CURVES: DEVELOPMENT OF A NEW METHOD OF ANALYSIS AND ITS IMPLICATIONS

### INTRODUCTION

The work reported here represents only a small part of an ecological investigation into the response of a number of species to water stress over a range of sites (Jane and Green 1983b). Pressure-volume techniques were used to determine the major water relations parameters for plants from a variety of sites. To facilitate the investigations A novel method of handling the pressure-volume data data was developed which utilised a composite model fitted to the raw data by non-linear least squares. The work the development, the theoretical background and implications of the model are described below.

### Theory

There have been numerous attempts to describe the components of water potential within plant cells (Slavik 1974). Upsrung and Blum (1916) proposed a simple additivity between osmotic and turgor pressures but subsequently matric pressure was added by Broyer (1947) and the system redefined in thermodynamic terms (Slatyer and Taylor 1960). Currently three components of tissue water potential ($\psi_t$)are recognised: pressure potential (turgor potential, $\psi_p$), osmotic ($\psi_s$) and matric potentials. ($\psi_m$)

$$\psi_t = \psi_p + \psi_m + \psi_s$$

Discussion on the exact definition of matric potential continues (cf Acock and Grange 1981) but Tyree and Karamanos (1981) equate it with short range dipole interactions. Matric forces are high in the cell wall but within the cell they are usually regarded as small except close to cell wall surfaces and consequently cannot be determined by the pressure volume technique.

The pressure chamber procedure assumes that by placing shoots or leaves under pressure the internal water stresses can be balanced by external gas pressure (Scholander 1965, Tyree and Hammel 1972) and, at high pressures, cell osmotic potential becomes a simple function of applied pressure. With increased pressure water is assumed to be driven only from the cell contents and this is thought to parallel the reaction of the tissue to water stresses such as drought. At low pressures both turgor and osmotic potentials are balanced, but above the turgor loss point the relationship of volume to osmotic potential obeys the law for osmotic solutions (Tyree and Hammel 1972). Determination of the osmotic potential of the extruded sap has generally confirmed these assumptions since it has been shown to contain only low levels of dissolved solutes (Tyree 1976). Furthermore above the turgor loss point calculated osmotic potential of the cell contents has frequently been shown to be close to that determined by hygrometry (Wilson et al. 1979) or by freezing point depression of extruded sap from killed stems (Henson 1982). Extrapolation of the osmotic relationship back to full turgor values also largely agrees with estimated initial osmotic potential, within the limitations of the other methods used (Tyree and Hammel 1972, Henson 1982). Consequently it is assumed that the additivity of $\psi_s$ and $\psi_p$ holds for values below the turgor loss point. No similar statement can be made for the nature of the relationship between turgor pressure and extruded volume although it is frequently assumed to be linear (Dainty 1977, Cheung et al. 1976). However, even as early as 1920, it was suggested that wall counter pressure could result in non-linear behaviour of the pressure-volume relationship near full turgor (Richter 1978).

The turgor loss point is often not sharply defined. This is assumed to result from the averaging effects of the progressive collapse of a number of different cell types each of which has their characteristic point of plasmolysis (turgor loss point). Nevertheless, even in single algal cells, the turgor- volume relationship is curvilinear at values close to the turgor loss point (Dainty 1977, Zimmerman and Steudle 1974, Zimmerman and Steudle 1975).

The turgor-volume relationship has been of used to determine the bulk modulus of elasticity at full turgor ( $\varepsilon$ ), which is equated with basic tissue strength. This is defined in mechanical terms similar to Youngs modulus (Wenkert et al. 1978), although an exact equivalence is very doubtful (Wilson 1967):

$$\varepsilon = dP/dV \ldots\ldots \quad 1$$

For small increments of pressure and volume this is approximately equal to the ratio of differences between successive values (Wenkert et al. 1978) and this numeric approximation has been the most common method for calculation of $\varepsilon$ .

## Standard procedure

The usual method for analysis of the pressure-volume data (referred to here as the standard procedure) is first to plot the reciprocal of the balance pressure ( P) against either the weight of extruded sap (which is equated with volume, $V_e$ ) or the relative water deficit, RWD= $V_e$ /[initial turgid fresh weight-dry weight of shoot] (Tyree and Hammel 1972). The osmotic potential at full turgor ( $\psi_s$) is then determined by calculating the intercept of the linear portion of the line at zero RWD, by a linear, least squares regression (Fig. 7.1). The initial portion of the graph at low RWD is strongly curvilinear and as a result there is

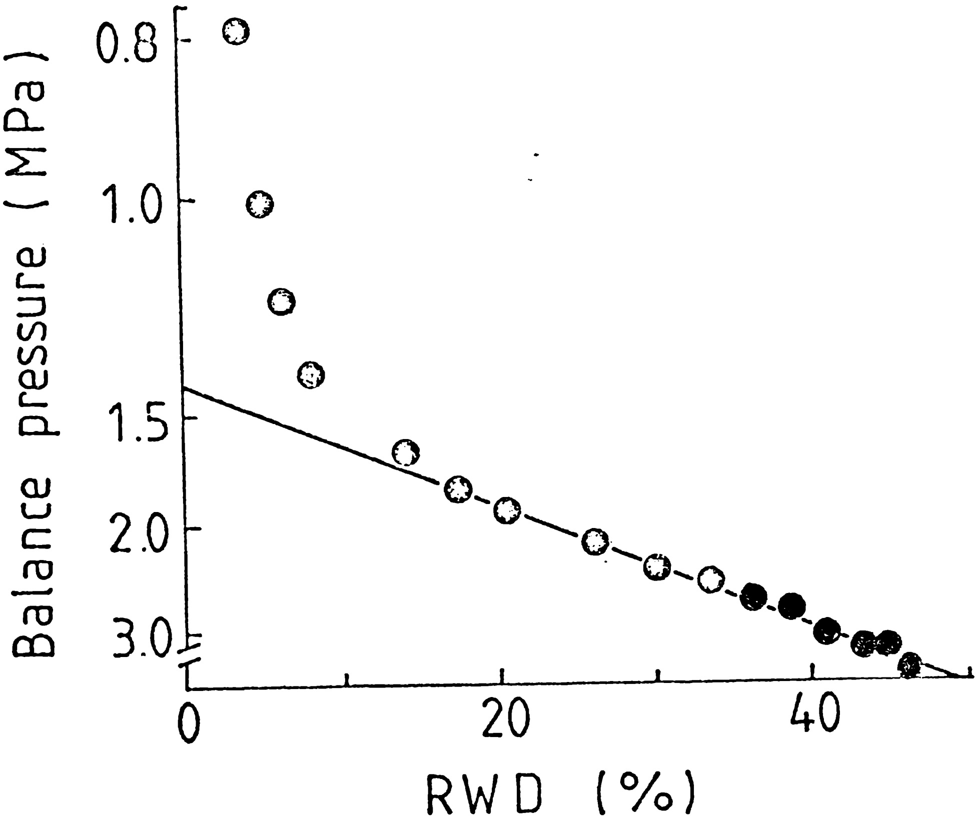


Fig. 7.1. Inverse plot of typical pressure-volume data obtained in this work. $\psi_s$ is normally obtained as the intercept on the Y axis by extrapolation of the linear portion of the graph as shown by the solid line. Turgor loss point is taken to be the junction of the linear and curvilinear portions of the graph.

often difficulty in determining data points to be included in the regression calculation. The point at which the non-linear portion of the curve disappears and the curve becomes linear has been defined as the turgor loss point,TLP, (Richter 1978, Wilson et al. 1979). Next, a second curve is derived in which turgor pressure ( $\psi_p$ ), defined as the difference between the balance pressure ($P_i$), and calculated osmotic potential

$$\psi_p = P_i - 1/(a-b.V_e)$$

is plotted against the extruded volume.

Investigations into the relationship between extruded volume ($V_e$) and $\psi_p$ (Tyree et al. 1973, Hellkvist et al. 1974, Wilson et al. 1980) have generally found a strong curvilinear relationship between the parameters. Three models have been used to fit this relationship:

(a) Linear (Wilson 1967, Cheung et al. 1976)

(b) Logarithmic (Tyree and Hammel 1972)

(c) Semi-logarithmic (Hellkvist et al. 1974)

but none has proved wholly satisfactory possibly because of the accumulated errors induced through the successive approximations made in earlier step in the procedure. There is no theoretical basis to guide a choice between these functions.

The bulk modulus of elasticity at full turgor ( $\varepsilon$ ) is then generally derived by calculating the slope of turgor function at full turgor ($V_e$ =0) but may also be determined by calculating the slope of the function at various points giving the relationship between $\varepsilon$ and $\psi_p$.

In developing a model it was evident from current practices that there was a need for objectivity and simplicity in analysis.

## METHODS

### Collection and storage of material

Three replicates were collected from tawari (*Ixerba brexioides*), quintinia (*Quintinia acutifolia*), kamahi (*Weinmannia racemosa*) and miro (*Podocarpus ferrugineus*) from several sites. Shoots of a suitable size were collected in the early morning, often after rain and before the fog lifted, then transported in sealed plastic bags containing a little water. In the laboratory, some 4-8 hours later, the shoots were recut under water, placed in beakers of water enclosed by plastic bags and stored at 5° C until needed, up to one week later. Immediately before use the surface water on the shoots was allowed to dry off completely at room temperature over 10-15 minutes. The shoots were then recut, weighed and placed in a plastic bag in the pressure chamber that was maintained at 20° C in a water bath (Fig. 7.2).

### Pressure chamber procedure

Once the shoot had been placed in the pressure chamber an initial balance pressure was obtained (usually less than 0.1 MPa). The shoots were then subjected to 10 minute cycles of over pressure followed by equilibration just below the estimated new balance point for five minutes to minimise the hysteresis problems that result from the rapid changes in pressure, as suggested by Jones and Higgs (1979). Determination of a new balance point completed the cycle. Pressures were measured with an electronic pressure sensor to within 0.01 MPa up to 1.4 MPa and 0.02 MPa at higher pressures. The extruded sap was collected by placing a pre-weighed poly-propylene tube filled with tissue paper over the cut end. This was replaced and reweighed at each

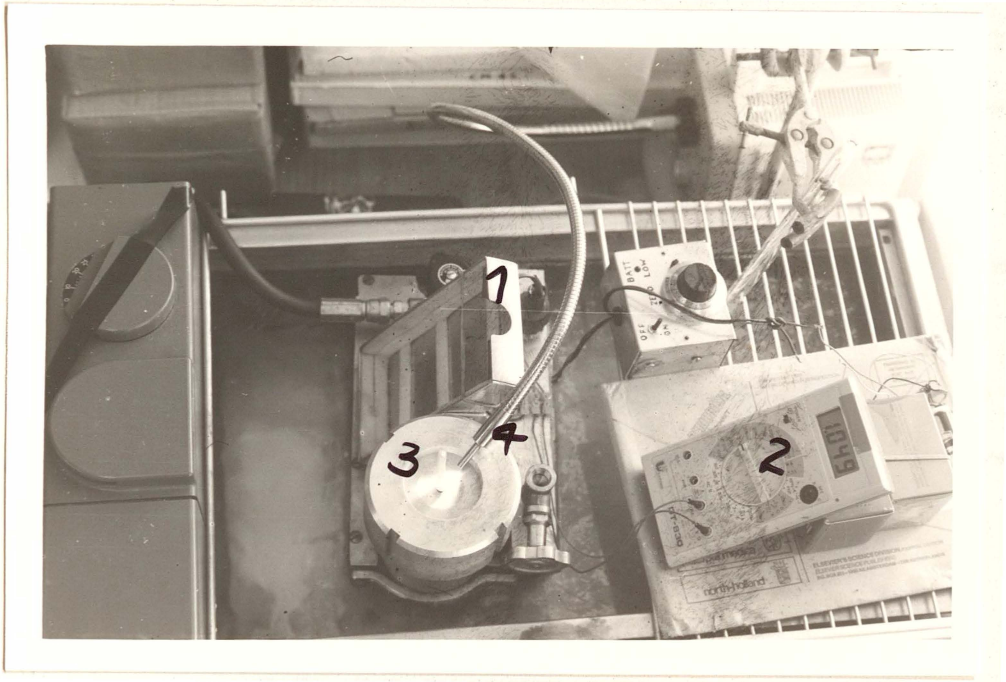


Fig. 7.2. Pressure chamber set up in water bath. 1. pressure sensor, 2. pressure meter; 3. tube of tissue over cut end; 4 light source.

successive balance point. The difference in weight between the two weighings then gave an estimate of the extruded volume. The initial over pressure was 0.3 MPa but this was increased to 0.6 MPa when successive balance pressure increments fell to less than 0.1 MPa. The procedure was terminated when the difference between successive balance pressures fell to less than 0.025 MPa.

Estimates of the uncollected water loss during the determinations were obtained by comparing the total weight of sap extruded with the difference between initial and final fresh weights of the shoots. Errors were typically: tawari, 2-5 %; kamahi, 5-7 %; silver beech, 8-15 %; quintinia, 5-7 %; and miro, 2-5 %.

## RESULTS

### Development of the P-V function

The complete function used in the analysis of the data was developed by first analysing the data in a series of steps as in the standard procedure, and then combining the best fit function into a single model. Initially the reciprocal of the balance pressure was plotted against RWD and a hyperbolic function :

$$1/P = (a - b.V_e) \;\ldots\ldots\ldots\; 2$$

was fitted to a restricted number of data points. Points were selected from the linear portion of the graph of RWD with balance pressure as in the standard procedure. The residuals (difference between actual and calculated values for a point) were then plotted (Fig. 7.3) and a suitable function sought to fit these residuals and the subsequent residuals. In more than 80 % of the cases the best fit proved to an exponential function of only the first residuals:

$$\text{Residuals} = c.e^{-d.V_e} \;\ldots.\; 3$$

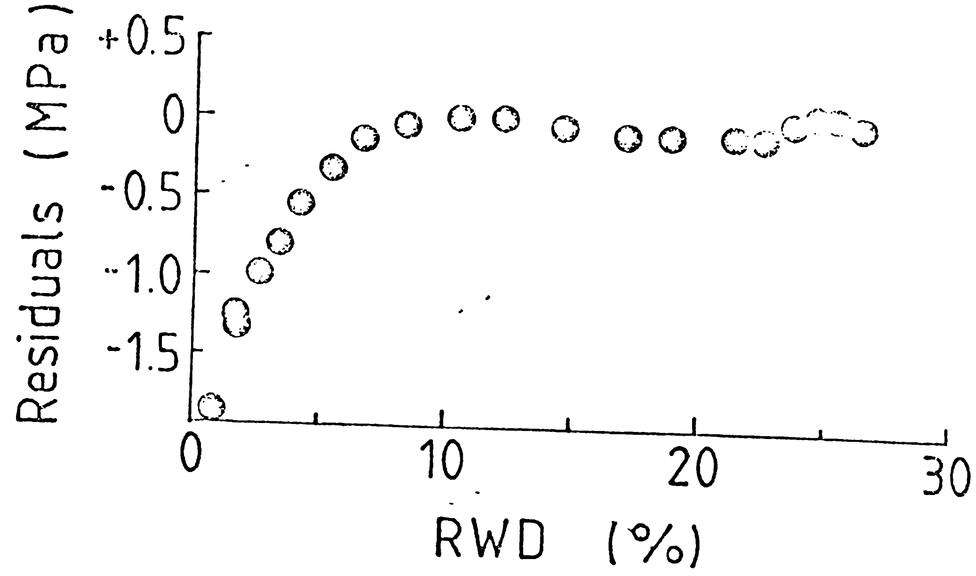


Fig. 7.3 Typical plot of the residuals after subtraction of the osmotic component.

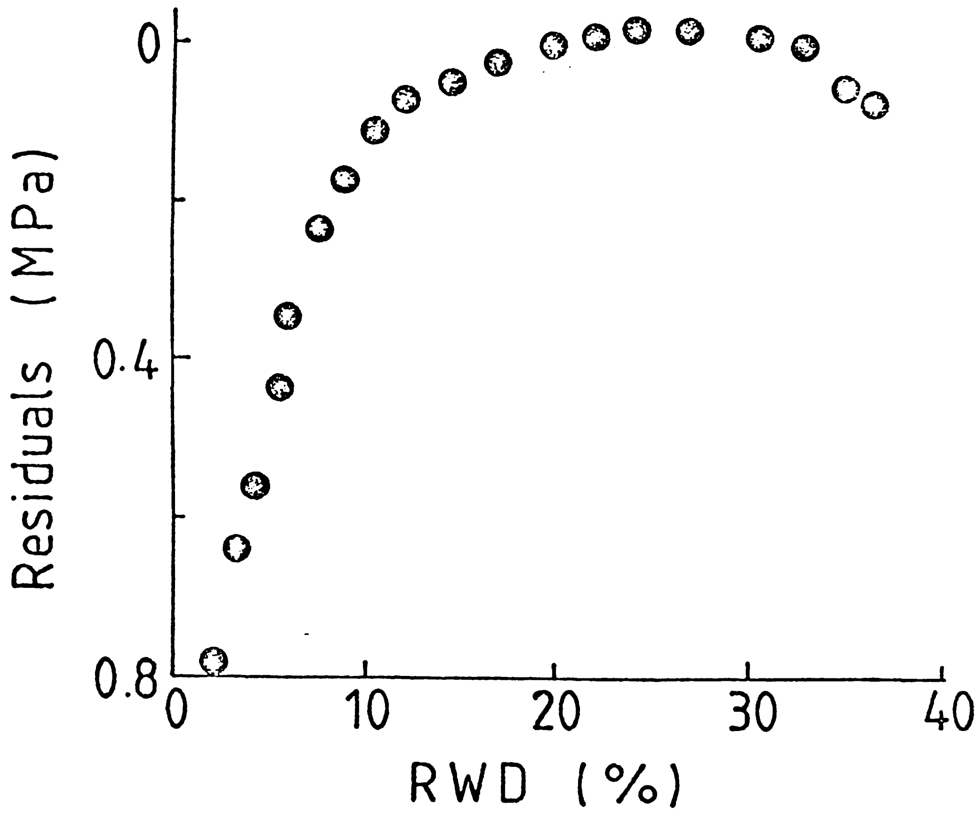


Fig. 7.4. Parabolic form of residuals after subtraction of the osmotic component resulting from incorrect selection of data points for calculation of osmotic function.

The residuals showed a marked parabolic relationship in the cases where the fit was poor (Fig. 7.4). This was apparently caused by an incorrect selection of points for calculation of function (2) since it could be corrected by deleting further data points at lower RWD.

The joint function:

$$P=1/(a-b.V_e) - c.e^{-d.V_e} \quad .... 4$$

was then obtained by combining equations 2 and 3. The first part can be regarded as determining the "osmotic line" and the second part as determining the turgor function as shown in Fig. 7.5.

Analysis of P-V data using model (function 4)

The regression model (equation 4) was fitted to the data sets by the Gauss-Newton non-linear least squares method. This technique permits the use of a large number of coefficients provided differentials of the coefficients of the equation are provided. The determinant of multiple correlation was normally more than 0.998 for 20 data points. This was larger than that obtained for the standard procedure based on fewer data points and arises because weighting of the regression is now shifted from the middle, asymptotic region of the curve to the limbs of the joint function. The residuals, which rarely exceeded 0.08 MPa, normally showed no systematic variation. However residuals up to 0.2 MPa were common at balance pressures less than 0.2 MPa (Fig. 7.6). These were usually found to be associated with the first extruded volume and exclusion of this value greatly improved the fit (Table 7.1). Examination of the more extreme cases suggested that the error resulted from the presence of surplus water within the leaf tissues and in several cases this was evident as a darkening of the mesophyll or clearly associated with minor leaf abrasion. It seems probable therefore that the poor fit in the other cases was also caused by free

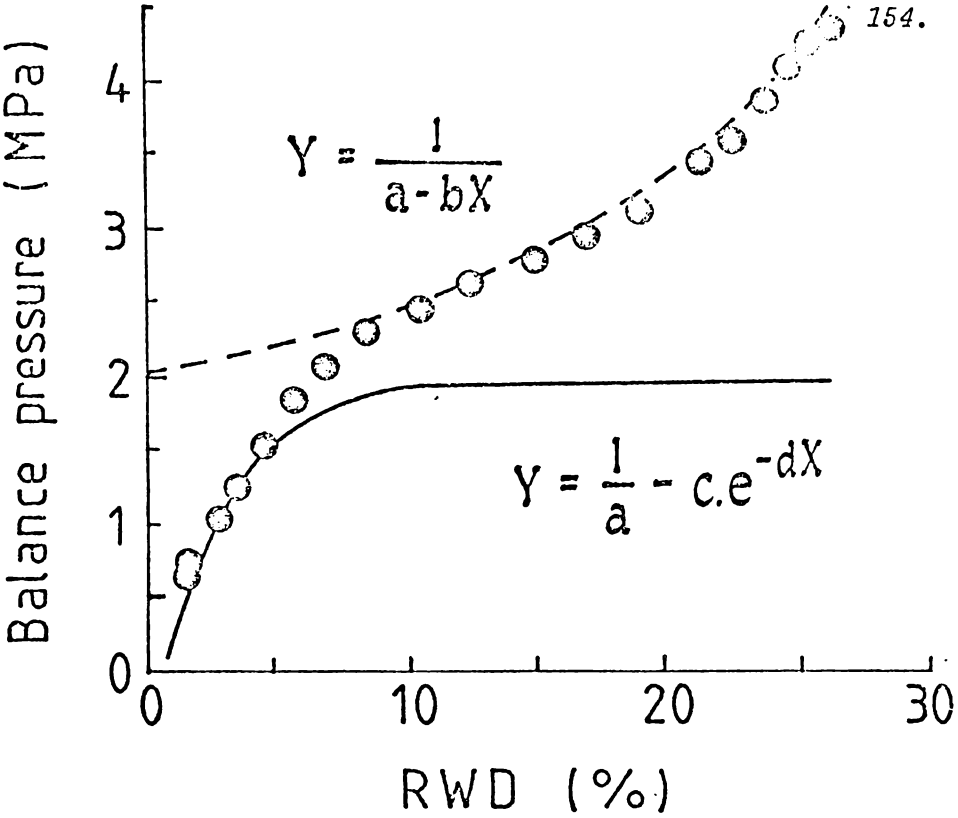


Fig. 7.5. Separate contributions of the osmotic and turgor functions to the form of a typical data set. The turgor function has been modified by addition of 1/a to place the turgor curve in correct relationship to the data points.

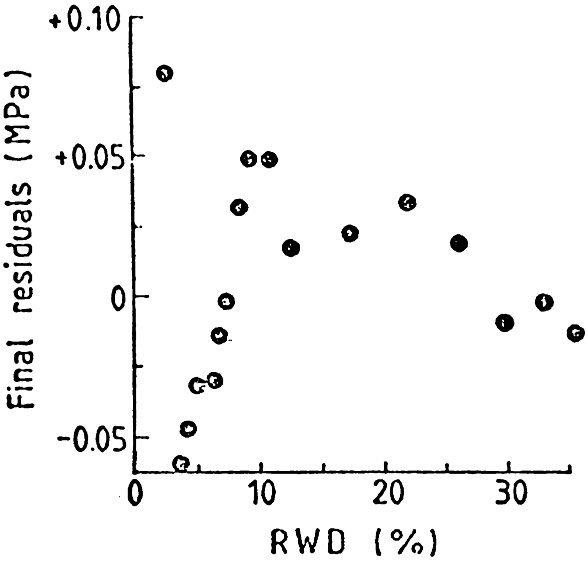


Fig. 7.6. Final residuals from both osmotic and turgor functions. Solitary point at low RWD indicates presence of free water leading to curvilinearity in the remaining residuals.

Table 7.1 Residuals from fit of model to one data set including and excluding the first data point.

| | | Residuals | |
|---|---|---|---|
| RWD(%) | P(balance pressure)* | First fit* | Second fit* |
| 5 | 0 | 157 | - |
| 2.07 | 82 | -38 | 50 |
| 3.53 | 306 | -147 | -33 |
| 5.05 | 564 | -89 | -50 |
| 6.22 | 748 | -44 | -43 |
| 7.28 | 932 | 25 | 3 |
| 8.41 | 1081 | 61 | 24 |
| 963 | 1183 | 49 | 5 |
| 10.61 | 1299 | 80 | 33 |
| 12.32 | 1455 | 99 | 56 |
| 14.78 | 1584 | 50 | 21 |
| 18.21 | 1734 | -23 | -28 |
| 20.21 | 1863 | -17 | -8 |
| 22.49 | 1986 | -31 | -12 |
| 25.03 | 2142 | -28 | -2 |
| 27.18 | 2250 | -53 | -26 |
| 29.14 | 2394 | -38 | -16 |
| 31.04 | 2564 | 1 | 13 |
| 33.43 | 2761 | 21 | 11 |
| 35.08 | 2910 | 37 | 5 |

*All values in kilopascals.

water within the tissues. A similar problem was noted by Cutler et al. (1979). Even short periods of storage caused deviations of up to 0.8 % RWD and typically this led to low initial pressure increments during experiments. An example of the magnitude of the error in an extreme case is shown in Fig. 7.7. It can be easily shown that if the error is defined as (f):

$$P=1/[a-b(V_e -f)] + c.e^{[d.(V_e -f)]} \quad \ldots . \quad 4a$$

This error is zero when the product of coefficients a and c is unity at a zero initial balance pressure as is the case if turgor and osmotic forces are balanced at full turgor. The left hand term in equation 4a can be regarded as very small for values of $V_e$ close to full turgor hence the surplus water (f) can then be estimated from:

$$f=\frac{\log_e(a.c)}{d} \quad . \; . \; \ldots . . 5$$

This correction was routinely applied to the data. A fifth coefficient (f) as in the equation 4a will permit this component to be calculated directly in the initial analysis. However it was not utilised here except on a small data set after the main analyses had been completed as it appeared to result in instability in the model.

Coefficients of the non-linear regression model (function 4)

The osmotic potential ( $\Psi_s$) is obtained as -1/a and the free (symplastic) water content (F) from a/b in the usual manner. The nature of the apoplastic (bound water) is the subject of considerable discussion. Tyree and Richter (1981) have demonstrated that it is not caused by non-ideal behaviour of the cell sap, but suggest that it may be mainly because of cell wall water bound in micellar spaces by matric forces. Tyree and Hammel (1972) suggest that this may be up to 28 % of total tissue water in leaves. Cheung et al. (1975) found lower values

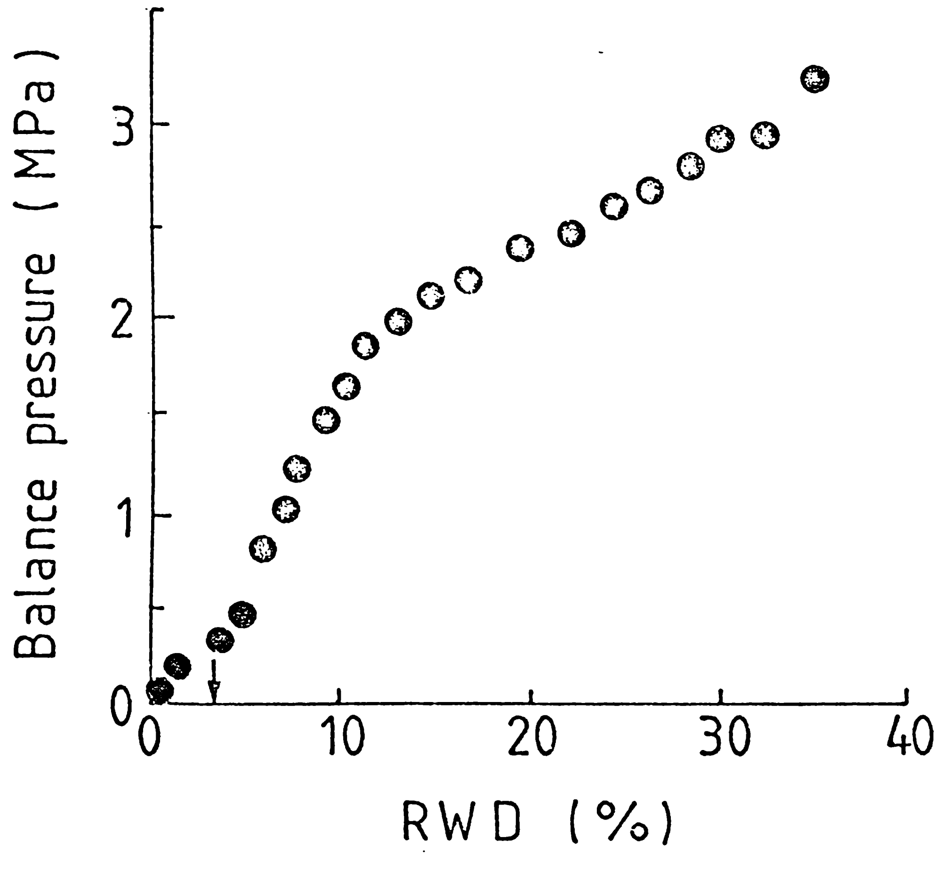


Fig. 7.7. An extreme examples of the effect of free water in the leaf tissues at low balance pressures. Free water is apparently a result of storing the samples prior to determinations.

of F in shoot samples than in leaves suggesting that estimates of apoplastic water content may be affected by the presence of water within the stem portion of the sample and this implies that F has a limited meaning where shoots rather than leaves are used, as in this investigation. This is most obvious on unhealthy specimens from the poor site where the foliage area is reduced and F is similarly affected (Table 7.2). For this reason estimates of other parameters (eg $\varepsilon$, TLP) have been adjusted so that they are expressed in terms of the symplastic water content, as recommended by Tyree and Karamanos (1981).

The coefficient c is, in effect, a second estimate of $\psi_s$ but it is strongly affected by the initial relative water content of the tissues. If surplus water is present c.a is greater than one and if the initial balance pressure is non-zero it will be less than 1.

Coefficient d governs the rate of change in turgor pressure and is an expression of cell elasticity. It is suggested that it be named the coefficient of elasticity ( $\alpha$). The bulk modulus of elasticity of a tissue, corrected for unit volume (equation 1, when $V_e$ is expressed as RWD %/100) can be determined for any value of $V_e$ from the first differential of the turgor component equation 2:

$$\varepsilon = d.c.e^{-d.Ve} \quad ..... \; 6$$

It can be seen that $\varepsilon$ is dependent on $\psi_s$ (c) and declines exponentially with increasing RWD, consequently the reference value ( $\varepsilon$ ) is normally calculated at full turgor.

One result of the model is that the estimated value of turgor pressure never reaches zero and the turgor loss point is left undefined. However, the turgor loss point can be mathematically determined. It is readily seen that the turgor loss point is the turning point of the function (2) where the slope of the turgor function equals that of the

Table 7.2
Average values of parameters obtained from pressure volume curves

| | Kamahi | Silver Beech | Tawari | Quintinia | Miro |
|---|---|---|---|---|---|
| Free water content (% RWD) | 74.2 | 51.4 | 86.7 | 86.3 | 74.4 |
| Osmotic potential | 1.67 | 1.87 | 1.56 | 1.52 | 2.06 |
| Coefficient of elasticity (-MPa) | 36.7 | 41.0 | 25.0 | 23.0 | 36.8 |
| Bulk modulus of elasticity (MPa) | 61.0 | 72.0 | 39.0 | 37.0 | 80.0 |
| Symplastic water content at turgor loss point (%) | 13.8 | 19.0 | 14.1 | 15.1 | 18.8 |
| Water potential at Turgor loss point (-MPa) | 1.78 | 2.01 | 1.70 | 1.74 | 2.25 |

osmotic line, or the differential is equal to zero:

$$b/(a-b.V)^{2} + c.d.e^{-d.V} = 0 \ldots. 7$$

Turgor loss point can be defined in terms of both balance pressure ($\Psi_{tlp}$) and relative water deficit (TLPw), which is defined in terms of symplastic water content. Plotting of the calculated values of the turgor loss point on diagrams obtained by the standard procedure showed that they lay close to the usually defined turgor loss point. Since none of the comparative estimates are precise (Hinckley et al. 1980) the differences may be trivial.

Comparison of values of $\Psi_s$ from model 3 with those obtained from the standard procedure suggest that the model provides a small, but consistently more positive estimate. Since previous studies have indicated that $\Psi_s$ obtained from the standard procedure is slightly more negative than those obtained from hygrometry and vapour equilibration methods (Wilson et al. 1979) it appears that this may originate in the mathematics of the standard procedure. As a result the composite function may give a more correct estimate of $\Psi_s$.

## GENERAL RESULTS

The absolute values for $\Psi_s$ (Table 7.2) are similar to those found in other studies with the conifer, miro, as expected, having lower values (Larcher 1975). The variation in osmotic potential between species and sites is very small compared with diurnal and seasonal variation observed in other woody plants (Cheung et al. 1975, Tyree et al. 1978, Roberts et al. 1980) and crop plants (Steponkus et al. 1981) although Tyree and Jarvis (1982) comment that variation in woody plants is often smaller than in crop plants. Even in kamahi, the most wide ranging species studied the variation between sites is small and the overall difference between the wettest site with the highest potentials and the remaining sites is only marginally significant.

Free water content appears to be closely linked to variation in leaf size within and between species and as such may reflect differences in plant stress. Variations in the $\psi_{tlp}$ were often significant and can be used to rank the drought tolerance of the species and the levels of effective precipitation at the study sites. Previous estimates of $\varepsilon$ have been determined by approximation (Wenkert et al. 1978) and hence may have underestimated the value. The values for $\varepsilon$ found in this study are usually greater than those found elsewhere where typical values range from 5-6 MPa in crop plants to 40 MPa in woody plants. This may result from differences in leaf types since much of the previous data is from agricultural crops, but it may also caused by to an under estimation of $\alpha$ (the slope of the relationship between $\psi_p$ and RWD) in the approximation methods used (cf. Hellkvist et al. 1974, Wenkert et al. 1978). Values for single algal cells obtained by direct measurement are many times larger (Dainty 1977) suggesting that the values found here are not extreme. Certainly $\varepsilon$ reflects differences in the succulence and rigidity of the leaves between species and sites in the current study and may be related to differences in cell size (Cutler et al. 1977). The coefficient of elasticity may be more useful than the modulus since the latter is closely linked with $\psi_s$ which may show short term variations, while the former probably reflects long term structural changes which in turn directly effect the turgor loss point. Both the coefficient $\alpha$ and $\varepsilon$ were found to have high variability resulting from a log-normal distribution.

# DISCUSSION

## Implications of the model

Hellkvist et al. (1974) suggested that four coefficients would be sufficient to define the pressure volume relationship. The first part of the relationship (equation 2) has a strong theoretical and empirical basis derived from fundamental considerations (Cheung et al. 1976, Tyree and Richter 1981) and numerous comparisons with other methods of determination (Wilson et al. 1979, Tyree and Richter 1981) as noted earlier, and will not be discussed further. The second part of the function describing the turgor relationship has no theoretical basis and only a limited empirical foundation, certainly not an unequivocal one. However there are features of the function that suggest that it may have a sound theoretical basis, such as the shape of curves relating various parameters, and the physical interpretations of these relationships.

There have been numerous discussions in the literature concerning negative turgor pressure, ably summarised and rejected by Tyree (1976) and contested by Acock and Grange (1981). In many cases negative turgor arises from erroneous mathematical approximations or complexities of methodological processes (Tyree 1976, Bennett et al. 1981). Further, it is suggested that apparent negative values may arise in pressure volume determinations through selection of the wrong points for commencement of the "osmotic line" as can be seen in Fig. 7.1 and was discussed in the section on the development of the model. The definition of turgor loss point used here escapes from the theoretical problem that if the turgor function is exponential turgor pressure can never be zero. Instead it implies that turgor loss occurs when elastic changes can no longer continue to control cell water content and osmotic changes predominate.

TLPw is apparently determined by all four parameters of equation (6) but the osmotic component can be eliminated by putting 1/a=c and a/b=F to give:

$$e^{d.V_e} - \frac{d.}{F}(1-V_e)^2 = 0 \ldots\ldots 8$$

Because short term changes in tissue parameters are likely to effect the slope of the osmotic line (b in equation 4) and not the free water content, the TLPw will only be affected by long term changes in cell structure which effect F or $\alpha$ . Then again if $V_e$ is expressed in terms of symplastic water ( $V_s$) it can be seen that the TLPw is solely dependent on $\alpha$ .

$$e^{\alpha .Vs} = .(1-V_s)^2 \ldots\ldots\ldots 9$$

Equation 8 implies that TLPw is wholly a structural property of the tissue since it is determined by F and $\alpha$ or in terms of symplastic water content by $\alpha$ alone. The effect of long term drought adaptation is to hold RWD as low as possible for as long as possible. If the value of $\alpha$ is high the initial part of the pressure-volume curve is steep and low RWD is more easily maintained. Changes in osmotic potential effect the scale of changes by acting as a simple multiplier to TLPw.

A strong curvilinear relationship between turgor pressure and $\varepsilon$ has often been found regardless of the method used to calculate it (cf Zimmerman and Steudle 1974, Dainty 1977, Zur et al. 1981). The dependence has been attributed to frictional forces between cells, variation in cell size or geometry and other forms of cell to cell variability. A curvilinear relationship is even found in studies of giant algal cells (Zimmerman and Steudle 1975, Buchner and Zimmerman 1982) and consequently these explanations are inadequate. Examination of equation 7 shows that both are volume dependent and $\varepsilon$ can be regard as being a product of two components, $\psi_s$ contributing to strength through plastic deformity and $\alpha$, related to elastic structural changes. $\psi_s$ then contributes to changes of scale in the relationship between turgor pressure and water content while $\alpha$ contributes to changes in slope of the relationship and perhaps can be equated with wall counter pressure (Richter 1978). These two changes are likely to be linked since increased osmotic potential will require an increased opposing cell strength and the relationship between $\varepsilon$ and $\psi_s$ will be linear, as frequently reported (Zimmerman and Steudle 1975, Cutler et al. 1979). Hysteresis in the relationship reported by Tyerman (1982) in giant algal cells can be explained by induced changes in $\psi_s$. Permanent changes in $\varepsilon$, such as those occurring during tissue development, will result from changes in $\alpha$ or F caused by changes in cell wall structure. Consequently $\alpha$ may be a more useful ecological parameter than $\varepsilon$ since it should reflect ontogenic and site determined changes in tissue structure and be free from short term changes in and most strongly expressed through changes in TLPw (Equation 8).

The link between low $\psi_s$ and high $\alpha$ between species results in maintenance of the same RWD at normal midday maximum $\psi_t$ suggesting that the strategy within the plant is twofold: to maintain an optimal water potential to draw water from the soil but at the same time to maintain minimal internal water deficit to minimise constraints on growth and other metabolic processes (Hsiao et al. 1976, Bannister 1976). These are optimised between habitats to minimise the costs of developing and maintaining high $\alpha$ and low $\psi_s$. Increased $\psi_s$ obviously transmits a greater potential deficit to the root system but changes in $\varepsilon$ are probably required to compensate.

In the short term this is achieved directly through osmotic adjustment and the effect of $\psi_s$ on $\varepsilon$ but plants that require large diurnal variations such as those from dry sandy or stony soils also require to minimise the internal water deficit and this can best be achieved by a steep slope to the turgor function, that is a large (Doley 1981). Consequently drought adapted species might be expected to have a high $\alpha$ and strong osmotic adjustment and adapted plants to have a low $\alpha$ and low variation in $\psi_s$ .

## *CHAPTER 8.*

# UTILISATION OF PRESSURE-VOLUME TECHNIQUES AND NON-LINEAR LEAST SQUARES ANALYSIS TO INVESTIGATE SITE INDUCED STRESSES IN EVERGREEN TREES

## INTRODUCTION

Episodic vegetation mortality is a widespread phenomenon at altitudes of over 600 m within the Kaimai Ranges of the North Island, New Zealand (Jane and Green 1983b). Investigations have strongly implicated drought as an important primary cause, however this has proved difficult to substantiate in an area that has a high annual rainfall and frequent fog. It is proposed that many of the species present may have a very narrow range of response to water stress and would thus be unable to tolerate relatively short droughts, particularly those that follow periods of above normal rainfall. To investigate this hypothesis five of the principal species were selected for detailed study. Four of the species are predominant in the affected forests; quintinia (*Quintinia acutifolia* Kirk) tawari (*Ixerba brexioides* A Cunn.), silver beech ( *Nothofagus menziesii* (Hook f.) Oerst.) and miro (*Podocarpus* G.Benn. ex Don.) and one of wide ecological amplitude, kamahi (*Weinmannia racemosa* Linn. f.) (Wardle 1966).

Plants have several strategies by which they tolerate or avoid water stress and are discussed by Levitt (1972). Some of these strategies are morphological, such as leaf shedding or deep rooting (Doley 1967) and some are physiological for example variation in osmotic potential or stomatal response. Tyree and Karamanos (1981), have examined the manner in which physiological factors associated with tissue water potential vary with site and plant water stress. Several different parameters are involved (Tyree and Jarvis 1982) but their exact pattern of variation with a range of site stresses is not well described. Roberts et al.

(1980), Tyree and Karamanos (1981), Ludlow (1981) and many others have placed considerable emphasis on variations in osmotic potential and turgor loss point (Hinckley et al 1980), but little is known of the significance of the other parameters. There are several methods used in their determination (Slavik 1974) but the pressure-volume technique has the potential to establish several parameters at the same time including the turgor loss point (TLP), associated with the water potential at which stomatal closure occurs, free (symplastic) water content and the bulk modulus of elasticity ( $\bar{\varepsilon}$) or resilience. For these reasons this approach was utilised in the current study.

## Site descriptions

Two study areas were selected within the Kaimai Ranges (latitude 37° 30', longitude 175° 45'), one at Te Hunga and the other at Te Aroha (Fig. 2.1). Te Aroha has an altitudinal range of 100 to 950 m and a rainfall of from 1500 to 2000 mm whilst the values at Te Hunga are 100 to 850 m and 2000 to 3000 mm respectively. Within these areas ten sites were selected along with a reference site at Rotorua (latitude 38° 10', longitude 176° 15') :

A. Te Aroha: 1. Te Aroha Summit. An isolated peak where exposure is somewhat severe. Rainfall 2000 mm, fog frequent. Soils perpetually wet but not waterlogged. All species present except miro.

2. 700 m. At lower limit of silver beech. Soils very thin such that it can be regarded as a xeric site comparable with 3 below. Only silver beech sampled.

3. 600 m. Hardies. An old mining site with very thin soils over quartz. Tawari, kamahi and quintinia present as regeneration about 60 years old.

4. 500 m. A low level mesophytic site near the lower limit of tawari, only tawari sampled.

5. 300 m Low level mesophytic site. Rainfall 1500 mm. Only kamahi sampled.

B Te Hunga :1. Summit of Te Hunga rainfall 3000 mm, fog frequent, soils often waterlogged. Healthy stands sampled. All species except miro sampled.

2. Close and similar to B:1 but stands showed poor vigour resulting from mortality in 1946; same species sampled as at B1.

3. 700 m Silver beech at its lowest altitude. A mesophytic site, miro and silver beech sampled.

4. 500 m Lower limit of tawari, a mesophytic site and only tawari sampled

5. 300 m Low level mesophytic site; 2500 mm rainfall and only kamahi sampled.

C Rotorua: located at the Forest Research Institute, about 60km south east of the main study areas. Rainfall 1500 mm, a mesophytic site not ideal since it lies outside the natural range of tawari and quintinia was not present.

## METHODS

Three replicates were assessed for each of the 27 species/site combinations outlined above. Particular care was taken in the transport and storage of the material as outlined in Chapter 7. Pressure-volume determinations were carried out by the standard procedure and parameters determined from Gauss-Newton least squares regression analysis. The determinant of multiple correlation was normally in excess of 0.998 for 20 data points and the residuals, which rarely exceeded 0.08 MPa, normally showed no systematic variation.

## RESULTS

### ECOLOGICAL ASPECTS

#### Water relations parameters

The site means for $\psi_s$ , F, $\alpha$ , $\varepsilon$., TLPw and $\psi_{tlp}$ are given in Table 8.1. Miro was omitted from the multiple comparison because of limited sampling but it is noteworthy that it shows the lowest mean and $\psi_{tlp}$ . Variability (measured by the coefficient of variation) was high in all species and parameters (Table 8.2) and for many of the contrasts to be statistically significant (F ratio at the 5 % point) large samples would be required. In agricultural crops it has been found that no more than two replicates were sufficient (Zur et al. 1981) and this may be attributed to a greater uniformity of genetic material and site conditions. The high variability in this study has meant that many differences between sites and areas were not statistically significant or were only evident at the 10 % significance level (Table 8.3) although differences between species were highly significant for all parameters (Table 8.4). Species-site interactions were also present and represent a diversity of responses among the species to the different site conditions.

*Free water content (F)* Quintinia and tawari have a similar high free water content, kamahi has an intermediate value whereas the small leaved silver beech has a very low free water content, just over half that of the other species. Within species there was little variation

Table 8.1. Mean values of parameters for all species and sites.

| | Te Hunga | | | Te Aroha | | | Rotorua | |
|---|---|---|---|---|---|---|---|---|
| | Summit* | | Meso | Summit | Dry | Meso | | Mean |
| | Good | Poor | | | | | | |
| Free Water Content | | | | | | | | |
| Kamahi | 82.5 | 60.7 | 81.1 | 69.5 | 73.2 | 75.4 | 77.0 | 74.2 |
| Silver Beech | 55.6 | 49.1 | 50.0 | 47.6 | 57.8 | - | 54.0 | 51.4 |
| Tawari | 85.9 | 78.8 | 93.8 | 83.7 | 89.5 | 85.8 | 89.3 | 86.7 |
| Quintinia | 82.2 | 78.7 | - | 97.6 | 86.6 | - | - | 86.3 |
| Miro | 86.2 | - | - | - | - | - | 62.5 | 74.4 |
| $\psi$s (-MPa) | | | | | | | | |
| Kamahi | 1.46 | 1.65 | 1.60 | 1.76 | 1.73 | 1.75 | 1.72 | 1.67 |
| Silver Beech | 1.89 | 1.54 | 1.79 | 1.85 | 2.35 | - | 2.07 | 1.87 |
| Tawari | 1.25 | 1.42 | 1.57 | 1.71 | 1.82 | 1.54 | 1.59 | 1.56 |
| Quintinia | 1.65 | 1.46 | - | 1.73 | 1.65 | - | - | 1.52 |
| Miro | 2.06 | - | - | - | - | - | 2.06 | 2.06 |
| $\alpha$ | | | | | | | | |
| Kamahi | 32.1 | 56.1 | 23.7 | 36.9 | 39.4 | 33.5 | 35.0 | 36.7 |
| Silver Beech | 26.8 | 35.5 | 54.6 | 47.3 | 33.1 | - | 33.6 | 41.0 |
| Tawari | 30.5 | 22.9 | 21.5 | 23.3 | 21.8 | 24.8 | 32.2 | 25.3 |
| Quintinia | 26.8 | 29.1 | - | 15.4 | 23.0 | - | - | 23.6 |
| Miro | 28.6 | - | - | - | - | - | 51.1 | 39.8 |
| $\epsilon$ (MPa) | | | | | | | | |
| Kamahi | 46.3 | 91.7 | 37.7 | 65.3 | 68.0 | 57.2 | 60.7 | 61.0 |
| Silver Beech | 49.8 | 55.3 | 89.7 | 80.9 | 75.0 | - | 69.8 | 72.3 |
| Tawari | 37.8 | 32.6 | 34.0 | 39.1 | 39.9 | 38.6 | 51.3 | 39.0 |
| Quintinia | 43.8 | 43.2 | - | 26.8 | 38.2 | - | - | 37.0 |
| Miro | 58.3 | - | - | - | - | - | 103.4 | 80.8 |
| $TLP_w$ (RWD%) | | | | | | | | |
| Kamahi | 13.3 | 14.4 | 15.8 | 14.4 | 13.1 | 13.3 | 12.1 | 13.8 |
| Silver Beech | 20.2 | 19.6 | 18.0 | 19.3 | 18.6 | - | 19.2 | 19.0 |
| Tawari | 12.7 | 16.2 | 13.9 | 15.2 | 14.6 | 14.1 | 11.7 | 14.1 |
| Quintinia | 14.4 | 15.5 | - | 16.0 | 14.8 | - | - | 15.2 |
| Miro | 13.5 | - | - | - | - | - | 14.2 | 18.8 |
| $\psi$tlp (-MPa) | | | | | | | | |
| Kamahi | 1.59 | 1.82 | 1.74 | 1.93 | 1.89 | 1.76 | 1.88 | 1.78 |
| Silver Beech | 2.02 | 1.66 | 1.99 | 2.02 | 2.57 | - | 2.25 | 2.01 |
| Tawari | 1.36 | 1.57 | 1.74 | 1.88 | 2.03 | 1.72 | 1.71 | 1.70 |
| Quintinia | 1.79 | 1.58 | - | 1.87 | 1.79 | - | - | 1.74 |
| Miro | 2.24 | - | - | - | - | - | 2.26 | 2.25 |

\- Indicates no sample.

* Adjacent sites were sampled from mature forest (good site) and forest affected by recent mortality and now being mostly seral shrubs (poor site). Each value is the mean of three replicates.

Table 8.2. Coefficients of variation (%) of parameters for silver beech, kamahi, quintinia and tawari.

| Parameter | Silver Beech | Kamahi | Quintinia | Tawari |
|---|---|---|---|---|
| F | 17.6 | 12.5 | 14.8 | 9.6 |
| $\psi s$ | 19.3 | 9.4 | 9.5 | 13.9 |
| $\alpha$ | 54.3 | 42.4 | 37.4 | 20.0 |
| $\varepsilon$ | 38.0 | 41.3 | 34.6 | 19.2 |
| $TLP_w$ | 7.0 | 13.8 | 9.5 | 12.0 |
| $\psi_{tlp}$ | 19.0 | 8.1 | 9.5 | 14.2 |

Table 8.3. Values of t for comparisons between species and sites for all parameters using analysis of variance.

| | Rotorua | Te Hunga | | | Te Aroha | | | Between Species |
|---|---|---|---|---|---|---|---|---|
| | | Summit Good | Summit Poor | Meso | Summit | Dry | Meso | (compared with tawari) |
| **$F$** | | | | | | | | |
| Tawari | - | - | -1.55 | - | - | - | - | - |
| Quintinia | A | - | - | A | -1.56 | - | A | - |
| Kamahi | - | - | -2.77 | - | -1.27 | - | - | - 4.22 |
| Silver Beech | - | - | - | - | - | - | A | -11.92 |
| **$\psi s$** | | | | | | | | |
| Tawari | - | 2.74 | 1.33 | | -1.0 | -1.9 | | - |
| Quintinia | A | - | -1.75 | A | - | - | A | - |
| Kamahi | | 2.28 | - | 1.12 | - | - | - | 1.43 |
| Silver Beech | - | - | -2.19 | -1.17 | - | -1.11 | A | -4.12 |
| **$\alpha$** | | | | | | | | |
| Tawari | - | - | -3.21 | -3.67 | -3.06 | -3.60 | -2.56 | - |
| Quintinia | A' | - | - | A | -1.71 | - | A | - |
| Kamahi | - | - | 1.74 | - | - | - | - | 2.45 |
| Silver Beech | - | - | - | 1.11 | - | - | A | 3.39 |
| **$\epsilon$** | | | | | | | | |
| Tawari | - | -2.86 | -3.98 | -3.67 | -2.58 | -2.42 | -2.70 | - |
| Quintinia | A | - | - | A | -1.61 | - | A | - |
| Kamahi | | - | 1.65 | -1.23 | - | - | - | 3.42 |
| Silver Beech | - | - | - | - | - | - | A | 5.17 |
| **$TLP_W$** | | | | | | | | |
| Tawari | - | 1.2 | 5.39 | 2.61 | 4.2 | 3.46 | 2.88 | - |
| Quintinia | A | - | - | A | 1.24 | - | A | 1.86 |
| Kamahi | - | - | 1.54 | 2.54 | 1.60 | - | - | - |
| Silver Beech | - | - | - | -1.09 | - | - | A | 9.85 |
| **$\psi tlp$** | | | | | | | | |
| Tawari | - | 2.72 | 1.05 | - | -1.32 | -2.43 | - | - |
| Quintinia | A | - | -1.77 | A | - | - | A | - |
| Kamahi | | 3.07 | - | 1.49 | - | - | 1.14 | -1.02 |
| Silver Beech | - | - | 2.27 | 1.02 | - | -1.25 | A | -3.88 |

Rotorua used as reference site for all species except Quintinia where Te Hunga summit is reference.

A - not sampled - twelve below 1.0.

Significance levels: 0.10% t=1.69; 0.05% t=2.0; 0.01% t=3.65 sign of t value indicates mean greater or less than that of comparator value.

Table 8.4. Analysis of variance of all species (excluding miro), sites, areas and parameters. Values of F-statistic given for each comparison.

| | | PARAMETERS | | | | | |
|---|---|---|---|---|---|---|---|
| Factor | Degrees of Freedom | F | $\psi_s$ | $\alpha$ | $\varepsilon$ | $TLP_W$ | $\psi_{tlp}$ |
| Species | 3/15 | 62*** | 5.13*** | 4.49*** | 8.98*** | 38.2*** | 4.31*** |
| Sites | 6/15 | 2.14* | 2.76* | - | - | 1.94 | 2.83* |
| Species x sites | 15/50 | 1.03 | 0.51 | 1.25 | 1.58* | 1.55* | 2.04* |
| Areas | 2/50 | 0.60 | 2.71* | - | 0.42 | 4.84** | 10.46*** |
| Residual mean square | - | 83.14 | 3.99 | 2.28 | 413.06 | 2.11 | 18.8 |

Significance levels; *, $0.10 > P > 0.05$; **, $0.05 > P > 0.01$; ***, $0.01 > P$.

-, F value < 0.10.

between sites although kamahi plants from Te Hunga poor site had a significantly lower value. These plants were of poor vigour and showed a large variation in leaf size, a feature noted also in quintinia. The small leaf size in silver beech, although not associated with reduced vigour, also appears to be associated with low free water content.

Osmotic potential( $\psi_s$ ) Highly significant differences between species (Table 8.3) are accounted for by the much lower mean value for silver beech (Table 8.1). Values for all species tend to be less negative in the wetter Te Hunga area than the drier Te Aroha and Rotorua sites. On the poor site at Te Hunga silver beech and quintinia had lower $\psi_s$ than the healthy site but tawari and kamahi had higher values although the differences were not significant and may merely reflect a high variability between replicates on the poor site.

Coefficient of elasticity ( $\alpha$ ) The variability of $\alpha$ was high and a logarithmic transformation was used in the analysis of variance because the values were not normally distributed. The species fall into two groups: kamahi and silver beech that tend to have high values of $\alpha$ , and are species of wide distribution; and tawari, and quintinia with consistently low values of $\alpha$ confined to the cooler wetter localities within the ranges (Table 8.1). The overall analysis (Table 8.4) shows no significant variation between sites or areas although there are a small number of individual site differences. Kamahi has the highest coefficient on the poor site and lower values on the adjacent wet site. It is also low on other mesic sites at lower altitudes. In silver beech low coefficients are found in plants from the wettest site and high values on the lower altitude Te Aroha site. In tawari differences are small except on the Te Hunga summit good site, where it shows the reverse pattern to all the other species and at Rotorua, where it was growing outside its natural range (Table 8.1).

Bulk modulus at full turgor( $\varepsilon$ ) Since $\varepsilon$ is the product of $\psi_s$ and $\alpha$ the pattern is similar to that of $\alpha$ , although for tawari there is now no significant difference between the Te Hunga summit sites, a result that appears to arise from the compensating effects of $\alpha$ and $\psi_s$ . The two groups of species proposed on the basis of $\alpha$ are retained and miro appears to have values similar to kamahi and silver beech. There is a positive correlation between F and both $\varepsilon$ and $\alpha$ , ($r^2$ =0.77, $r^2$ =0.68 respectively with 65 degrees of freedom) which suggests a relationship with cell size and, indirectly through F, with plant vigour.

Turgor Loss Point Water content at turgor loss point (TLPw) is often used to rank species in order of drought tolerance. A large difference is present between the values for silver beech and miro and those for the remaining species. Significantly lower values are found for kamahi and tawari in the Rotorua area (Table 8.4) are not consistent with differences in drought stress between the sites, suggesting that this hypothesis does not hold for these species.

Potential at the turgor loss point ( $\psi_{tlp}$) shows significant differences at the same localities as for $\psi_s$ although the significance level is often higher (Table 8.4). Silver beech has a consistently lower value than the other species; the driest site had the lowest value and the poor site the highest. Values on the Te Hunga sites as a whole were higher than those for the other sites and this may be attributable to the higher rainfall and prevalent fog. Responses of all the species on the Te Hunga sites were similar and resembled the pattern obtained for $\psi_s$ .

## Discriminant Analysis

Site differences within species were investigated using discriminant analysis, but this procedure was only successful in tawari, possibly because of low within site variability in this species (Table 8.3). Segregation within tawari (Fig. 8.1) was not wholly satisfactory but the main site trends were clearly emphasised. The first canonical variable, associated with TLPw, represents the extremes of stress from sheltered sub-canopy plants at Rotorua to extremely exposed plants at the Te Hunga summit poor site. The gradation in effective precipitation is reflected in the second canonical variable, associated with $\psi_{tlp}$ or $\psi_s$ , where the very wet Te Hunga summit site and the Te Aroha dry site represent the extremes on this axis. As shown in the diagram, the increased exposure on the Te Hunga poor site apparently reduces the effective precipitation. The placement of the Te Aroha dry and summit sites on the first axis indicates increased stress caused by exposure at the latter site. The mesophytic sites are centrally distributed on both axes and are indistinguishable, confirming their basic similarity. All data sets, except for those from the Rotorua and poor, sites contain values near those for the mesophytic sites suggesting that small microsite variations are important and may be the main reason for the failure of the analysis in the other species. In the unsuccessful discriminant analyses on the remaining species TLPw was consistently the first canonical variate.

## DISCUSSION

A number of experimental studies have linked water stress with reduced cell size and increases in $\varepsilon$ (Cutler et al. 1977, Turner and Jones 1981). In the current study $\varepsilon$ reflects differences in the succulence and rigidity of the leaves between sites within some species

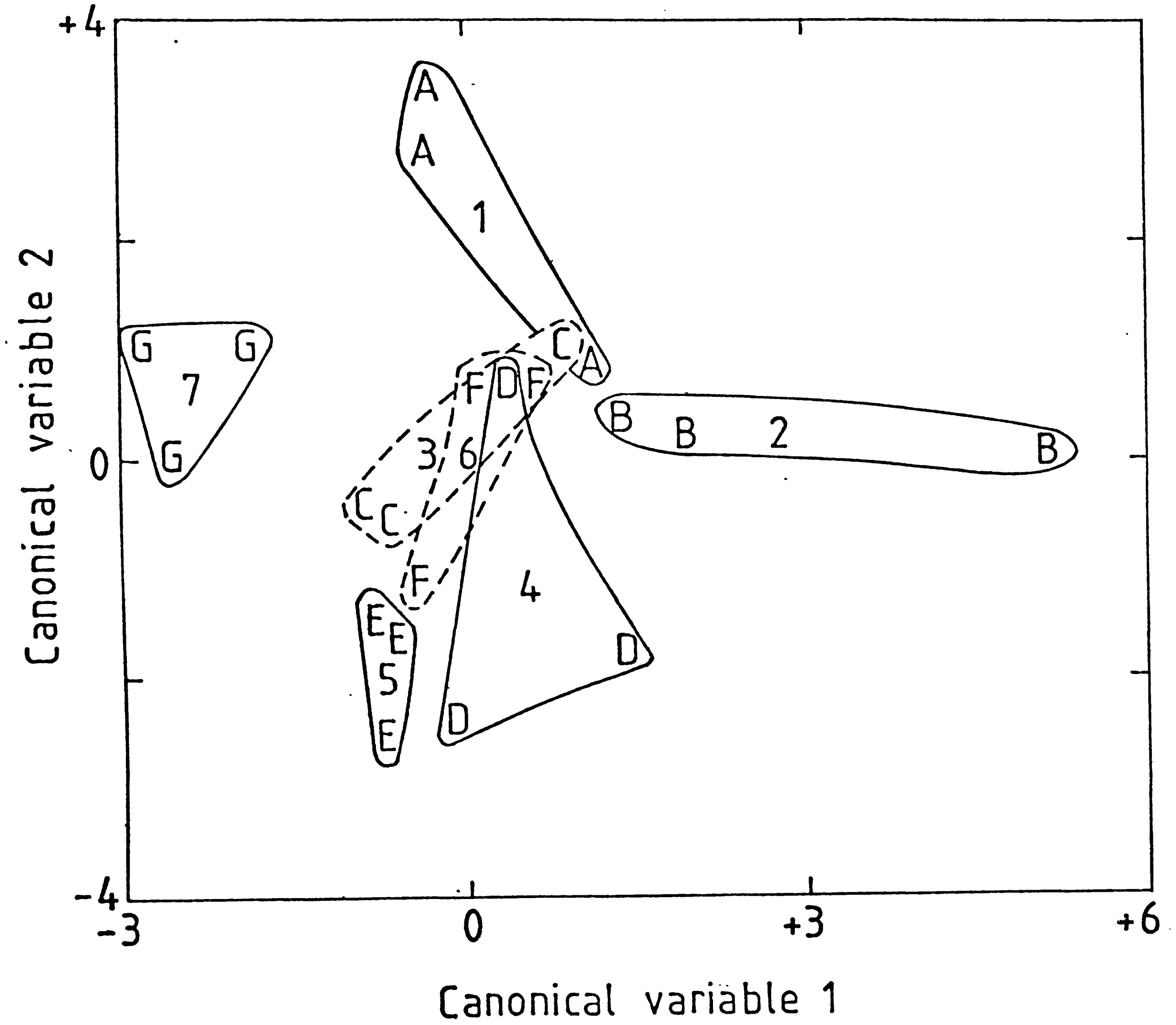


Fig. 8.1. Plot for tawari (Ixerba brexioides) of all sites on the first two canonical variates obtained by discriminant analysis. The first canonical variate represents $TLP_W$ and the second, $\psi_{tlp}$. Individual sites are coded with a letter representing the individual replicates and a number the mean value. Codes: Te Hunga summit good, A 1; Te Hunga summit poor, B 2; Te Hunga meso, C 3; Te Aroha summit, D 4; Te Aroha dry, E 5; Te Aroha meso, F 6; Rotorua, G 7. Replicates from individual sites are enclosed by solid lines with the exception of the two meso sites where a dashed line is used.

and, as such, is a useful ecological indicator. However high variability made the differences difficult to demonstrate statistically.

There are no values for $\alpha$ in the literature because of the calculation procedures and since the modulus $\varepsilon$ has been regarded as more important. The parameter may prove useful because of the close link with basic tissue elasticity noted earlier, however the high variability and log-normal distribution limited its value in this study.

Few previous studies utilise TLPw as a descriptive parameter because of the difficulties of estimation (Tyree and Karamanos 1981) and since changes in RWD in this part of the pressure-volume curve are rapid. The suggested calculation algorithm however provides a very precise method of determining TLPw. Differences in TLPw between species appear to be related to exposure, and within one species, tawari, successfully discriminates the degree of exposure of the sites. More usually however TLPw is related to dessication tolerances (Bannister 1976). Hinckley et al. (1978) and Wenkert et al. (1978) were able to relate the $\psi_{tlp}$ to stomatal closure and discriminate drought hardiness but further work would be required to establish a similar relationship with stomatal closure in the species of the current study.

The absolute values for $\varepsilon$ are similar to those found in other studies with the conifer, miro, as expected, having lower values (Larcher 1975). The variation in osmotic potential between species and sites is very small compared with diurnal and seasonal variation observed in other woody plants (Tyree et al. 1978, Cheung et al. 1975, Roberts et al. 1980) and crop plants (Steponkus et al. 1981), although Tyree and Jarvis (1982) comment that variation in woody plants is often smaller than in crop plants. Even in kamahi, the most wide ranging species studied the variation between sites is small and the overall difference between the wettest site with the highest potentials and the remaining sites is only marginally significant. Taking these points into consideration it appears that site adaptation through osmotic adjustment is slight and diurnal, ontogenic or seasonal changes are likely to be far more significant, as pointed out by Wenkert et al. (1978), Jones and Higgs (1979) Ludlow (1981) and many others. It may well be that this arises because osmotic adjustment is a short term adaptation to stress (Turner and Jones 1981). Osmotic adjustment will also proportionately effect $\varepsilon$ and $\psi'_{tlp}$ since in both cases it is a scale factor. However these changes may well be ephemeral (Turner and Jones 1981).

## Ecology

The main aim of the study was to use a variety of tissue parameters to investigate both the plant response to drought stress and drought avoidance strategies along the lines discussed by Levitt (1972) and Hinckley et al. (1978). The sample selection was therefore directed to cover the complete range of habitat stress for each species and included sites from within and outside the the areas of mortality. There are few guidelines by which to assess the performance of the species since there is no published data on the water relations parameters of New Zealand native trees and very limited data for cloud forest trees generally.

There were highly significant differences between species in all the water relations parameters. In particular silver beech always represents one extreme value and, although the exact ranking of the species differs between the parameters, tawari or quintinia are at the other extreme. As a result it is possible to rank the species in order of drought tolerance, adaptability and general health in a manner that lends support to intuitive and field observations.

The value of $\psi_s$ is often taken to reflect the ability of a species to tolerate stress (Hsiao et al. 1976) although in this study it appears that $\psi_{tlp}$ yields similar, but usually more significant results. The order shown by the species is (miro) > silver beech >> kamahi > quintinia > tawari. An identical ranking is obtained from $\psi_{tlp}$ while $\alpha$ also produces a very similar result. At one extreme tawari and quintinia have very high values of $\psi_s$ , comparable with plants from very wet habitats, in which low drought tolerance would be expected (Larcher 1975, Tyree and Karamanos 1981). These plants appear to be adapted to the wet cloud forest. At the other extreme the value of $\psi_{tlp}$ for silver beech and miro is considerably lower than that of the other three species and must indicate a far greater degree of drought tolerance. The drought tolerance of silver beech is well known in New Zealand. The species is also able to survive on waterlogged sites (Wardle 1980, Wardle 1967) and it appears that drought tolerance mechanisms also permit the species to utilise these very wet sites. This property has been found elsewhere in several other species (Bannister 1976, Aussenac and Vallette 1982) and is not as unexpected as it first appears since waterlogging is regarded as a sub-set of water stress.

If $\psi s$ and $\psi_{tlp}$ can be utilised as indicators of drought tolerance in a species then low variability of these parameters in a species over a wide range of sites would imply either that stress was not present or poor adaptability of the species to water stress. The sampling strategy should have ensured that a large amplitude of stress was present consequently the first possibility is unlikely. Compared with silver beech and tawari, kamahi and quintinia have very low variability (Table 8.2) with a range values less than 20 % of the mean and half that for the other species. This suggests a drought adaptability ranking of silver beech >> tawari >> quintinia = kamahi; effectively separating canopy from seral species and implying poor adaptability in the latter. This possibly is a reflection of the normal strategy of such species since they usually maximise growth at the expense of permanence on a site (Tobiessen and Kana 1974). Variability in tawari is expressed between sites (Table 8.3), implying uniform low sensitivity to stress within a locality. In silver beech variability is greater within sites (Table 8.3) and suggests strong microsite adaptation or sensitivity to a diversity of stresses in this species, at the northernmost extent of its natural range.

Silver beech has a markedly lower variability in TLPw than the other species. This suggests that the main mechanism for stress avoidance in this species is through osmotic adjustment. In the other species changes in both TLPw and $\psi_s$ are utilised in site adaptation as shown so well in the discriminant analysis of tawari. There is a clear mathematical link between TLPw and $\alpha$ ( Ch. 7 ) and an association of both with exposure that has been noted elsewhere (Turner and Jones 1981, Wenkert et al. 1978). The link appears to lie in the variation in leaf thickness and rigidity, and changes in cell size which is expressed as large changes in $\alpha$ and which in turn directly affects TLPw.

There are the large differences in appearance, most clearly expressed in variability of F, between tawari with little apparent stress, silver beech with necrotic spots on the leaves and the remaining species with reduced leaf size on the poor site (Table 8.2). Variability of F in silver beech is high on all sites but in all the other species similar high variability is confined to the poor site. In the former instance it represents the high within site variability noted earlier for silver beech on all sites whereas in the other species it clearly illustrates the degree of stress on the poor site. Unusually high values of $\alpha$ and $\varepsilon$ are associated with extreme stress in all species and are shown most clearly on the poor site in the seral species and on the dry exposed Te Aroha site in silver beech. Kamahi has higher values than quintinia for both these parameters and appears to be poorly adapted to the very wet site whereas quintinia appears more able to tolerate the environment. It appears that silver beech, at one extreme is able to adjust to the site stress at the very wet summit sites while at the other tawari is able to avoid it. This leaves kamahi and quintinia with intermediate properties that give them a limited ability to avoid or tolerate the stresses and in which quintinia is the better adapted. The mechanism of tolerance appears to be through possession of low $\psi_s$ and high $\alpha$ but the mechanism of avoidance is not evident in this data and may lie in morphological characteristics of the species. Under drought conditions it would appear that silver beech would be the most able to survive and tawari the least, however the poor vigour of the seral species suggests that they may have a very low resistance to such severe climatic variation.

## CHAPTER 9

## Changes in osmotic potential during bud break and leaf development of Nothofagus menziesii, Weinmannia racemosa, Quintinia acutifolia and Ixerba brexioides

### INTRODUCTION

A number of papers suggest that osmotic potential ( $\psi_s$) in evergreen plants is lowest in winter and rises rapidly at bud break (Kozlowski 1971). Tyree et al. (1978) found a strong annual cycle of $\psi_s$ in eastern hemlock (Tsuga canadensis), with minima in mid-winter and maxima at bud break, and also a marked rise in $\psi_s$ at flushing in seedlings of Norway spruce (Picea abies). Old and new leaves of Ilex opaca declined in $\psi_s$ after bud break (Roberts et al. 1980). Initial osmotic potentials of about -0.8 MPa have been frequently been reported for new leaves fallingin a few weeks to values similar to that in older leaves (Cline and Campbell 1976, Tyree et al. 1978, Meinzer 1982).

Investigations into mortality in the cloud forests of the Kaimai Ranges, New Zealand (Jane and Green 1983b) have included aspects of the water relations of the trees (Jane and Green 1983c). Differences in $\psi_s$ between a number of species were small and were suggested, without evidence, to be less than the normal seasonal variation. Leaf development in these forests was slow and, if higher potentials occur, could increase the risksof damage. A preliminary survey of $\psi_s$ was carried out to answer some of these questions since there is a lack of information on $\psi_s$ for New Zealand native trees.

### METHODS

### Development of Procedures

Sun shoots were taken from one plant within the University of Waikato campus. Leaves were killed by immersion in liquid nitrogen and the sap extract obtained either by placing the shoot or a leaf in a

Scholander type pressure chamber (Jane and Green 1983c), raising the pressure to 0.8 MPa and collecting the extruded sap (pressure bomb extract) or by placing the killed and comminuted leaves in a French press and subjecting them to very low pressure <0.05 MPa, (French press extract).

Osmotic potential was determined by freezing point depression, as described by Slavik (1974). Saline freezing mixture was maintained at minus 8-10° C and continually stirred. 0.15 ml of sap extract was placed in a 0.5 mm by 65 mm tube and immersed in the saline solution. When the temperature, monitored by a thermocouple, fell below the estimated freezing point the sap was vigorously stirred until the sap froze. The minimum temperature depression was taken as the freezing point and was proportional to osmotic potential.

The method was calibrated with sucrose solutions of known $\Psi_s$ and independent verification of tissue $\Psi_s$ was obtained by two pressure volume determinations on two species using techniques detailed elsewhere (Jane and Green 1983c).

## Field studies in Kaimai Ranges

Three collections of shoots of tawari (*Ixerba brexioides*, A Cunn.), kamahi (*Weinmannia racemosa*, Lin. f.), quintinia (*Quintinia acutifolia*, Kirk), silver beech (*Nothofagus menziesii*, (Hook.f) Oerst.) were collected at 4 weekly intervals, beginningon 5 November 1982 from the sites at 500 m, 600 m, 800 m and 900 m on Mt Te Aroha. Each collection commenced early in the mornings on cool days at the lowest altitude and were completed by 11 am to ensure that shoots were at or close to full turgor. Three sun shoots were collected from each plant and three plants of each species sampled at each site. After cutting, shoots were tightly sealed in plastic bags and transported to the laboratory in chilled containers where they were killed in liquid nitrogen. The sap was expressed with the French press and $\psi_s$ determined.

## RESULTS

### Technique comparisons

Pressure bomb extracts from single leaves had $\psi_s$ (-1.83 MPa) significantly lower (t= 2.49, 58 degrees of freedom) than from whole shoots (-1.35 MPa) probably representing dilution of the sap by xylem water in the woody parts of the shoot. Successive aliquots of sap from shoot samples and single leaves in the pressure bomb normally showed no apparent change in osmotic value but successive aliquots from damp leaves yielded increasing values of $\psi_s$ indicating movement of surface water into the tissues under pressure. French press extracts had $\psi_s$ (-1.81 MPa, n=3) that was similar to that of pressure bomb extracts from single leaves (-1.83, n=3). Since leaves of many of the species lacked a suitable petiole length for pressure bomb extraction the French press was used for all later sap extraction.

Pressure volume curves of tawari, and silver beech were used as an independent estimate of osmotic potential. Henson (1982) found a good agreement between cryoscopic and pressure-volume determinations in rice but the current results were not simple. Tawari curves yielded $\psi_s$ close to those obtained from French press extracts (tawari -1.41 MPa and -1.42 MPa, respectively). Silver beech produced pressure volume curves with two linear segments apparently related to the presence of new and old leaves of differing $\psi_s$ (Fig. 9.1). The higher $\psi_s$ of the two values obtainable ( -1.59 MPa) was close to the French press values (-1.57 MPa) but the lower value (2.06 MPa) was close to values obtained for mature foliage indicating preferential extrusion from young leaves in the French press. The opposite situation was found in tawari; only a single value was obtained from the pressure volume curves and this

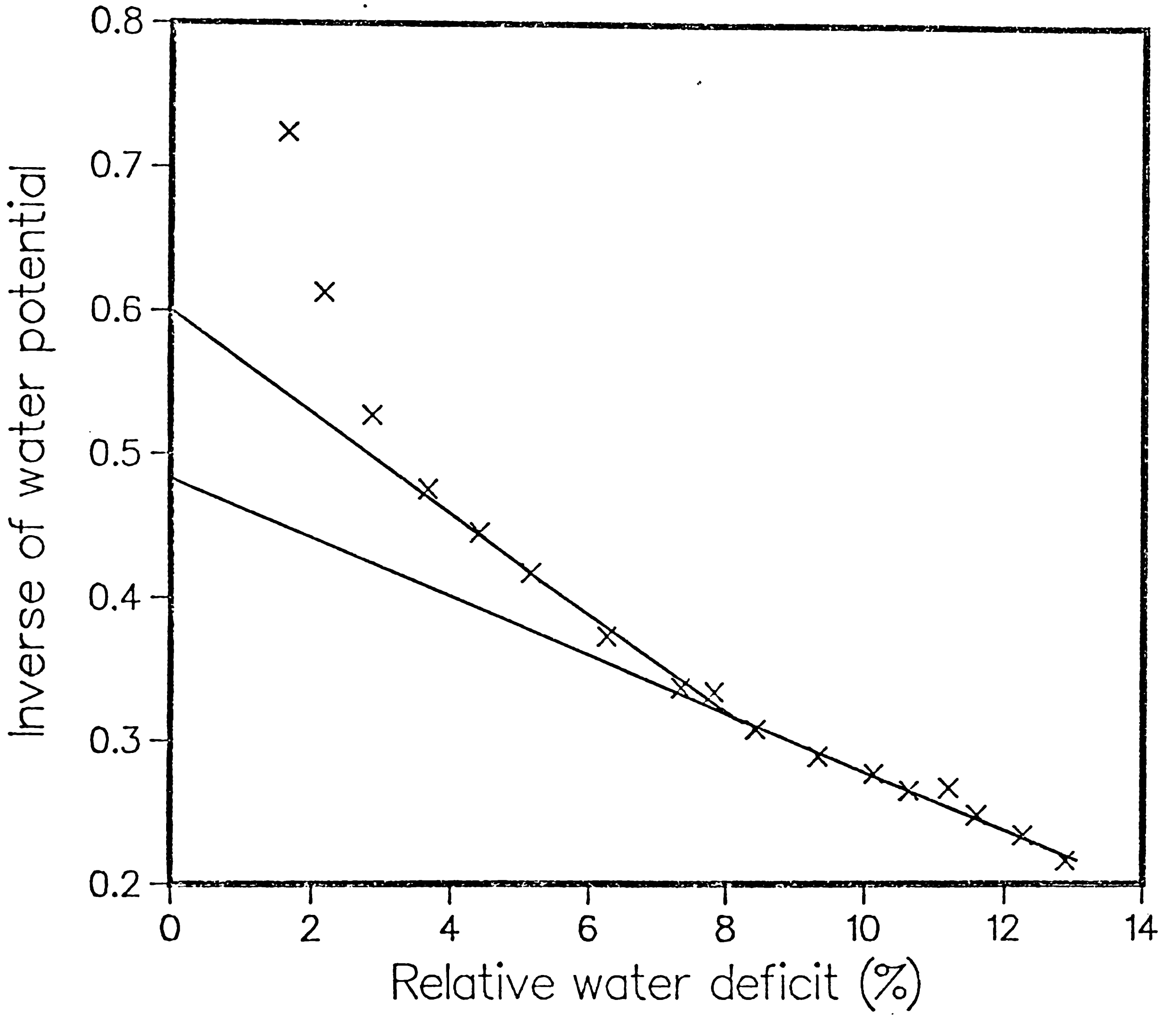


Fig. 9.1 Plotted pressure volume curve of silver beech. Two linear segments are apparent and correspond with osmotic potentials of old and new foliage determined by the cryoscopic method.

agreed with the value obtained for mature foliage.

Seasonal progression in osmotic potential

All species showed earlier bud break at the lower altitudes (Table 9.1). Tawari was the latest species and bud break had only just occurred at the highest altitude at the final sampling. Tawari also showed the slowest leaf development. Leaf maturation in tawari was slow and leaf hardening was not complete by the third visit whereas silver beech showed rapid leaf flush and development. Kamahi had an earlier bud break than quintinia but both were intermediate in leaf development to tawari and silver beech.

Osmotic potentials were higher at the highest altitude sites before bud break (Fig. 9.2), a situation identical to that found by Jane and Green (1983c). Although altitudinal differences were small, species differences were marked (Fig. 9.2). Tawari consistently had the lowest $\psi_s$ and silver beech, where present, the highest. This is almost the reverse situation to that found the previous autumn (Jane and Green 1983c) and indicates considerable seasonal variation. Variability in $\psi_s$ between sun shoots on the same plant was small but significant (Table 9.2). Variation between plants was several times higher, possibly reflecting slight differences in leaf development.

Although quantities were small, sampling of old and new foliage separately from the same shoot showed young foliage in silver beech to have a higher $\psi_s$ (-1.2 MPa) than old foliage (-1.8 MPa) the latter being close to the -1.85 Mpa obtained the previous autumn (Jane and Green 1983c). A similar situation was found for old and young foliage of tawari (-1.07 MPa, and -1.38 MPa respectively). Significant changes in $\psi_s$ occurred that could be correlated with leaf development. Osmotic potential falls before bud break, rises during bud break and then falls

Table 9.1

Timing of bud break and leaf development in the sample trees at the sample sites

| | Tawari | Quintinia | Kamahi | Silver beech |
|---|---|---|---|---|
| 5th November 1982 | | | | |
| 500 m | dormant | bud break | leaves developed | - |
| 600 m | dormant | bud break | leaves developed | - |
| 800 m | dormant | dormant | dormant | dormant |
| 900 m | dormant | dormant | dormant | dormant |
| 19th November 1982 | | | | |
| 500 m | bud break | leaves developing | leaves developed | - |
| 600 m | dormant | leaves developing | leaves developed | - |
| 800 m | dormant | dormant | bud break | bud break |
| 900 m | dormant | dormant | dormant | dormant |
| 19th December 1982 | | | | |
| 500 m | leaves developing | leaves developed | leaves developed | - |
| 600 m | leaves developing | leaves developed | leaves developed | - |
| 800 m | bud break | leaves developing | leaves developing | leaves developed |
| 900 m | bud break | leaves developing | leaves developing | leaves developing |

Table 9.2

Statistical significance of differences in $\psi_s$ and sources of variation between successive measurements made on three replicate shoots from three trees at each of the four sample sites.

| | tawari | quintinia | kamahi | silver beech |
|---|---|---|---|---|
| F-Ratio | | | | |
| time | 3442 | 4662 | 2080 | 631 |
| site within time | 217 | 465 | 219 | 425 |
| tree within site | 57 | 32 | 51 | 75 |
| replicate within trees | 12 | 15 | 13 | 24 |
| coefficient of variation (%) | | | | |
| between sites | 35.6 | 73.2 | 36.1 | 89.8 |
| between trees | 9.4 | 5.0 | 8.5 | 15.9 |
| between replicates | 2.0 | 2.3 | 2.1 | 5.1 |
| sample size | 197 | 206 | 216 | 108 |

All F-ratios are highly significant.

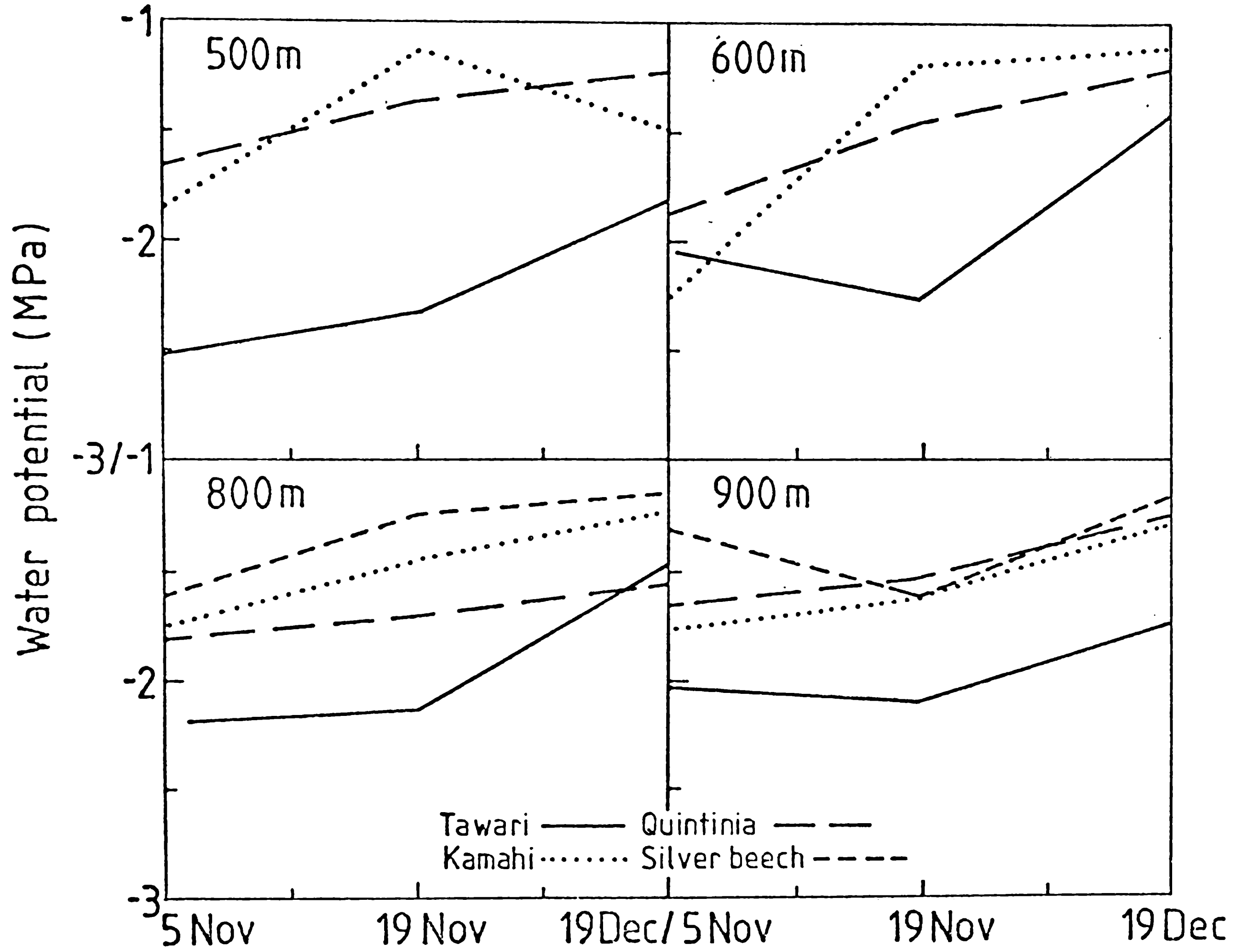


Fig. 9.2 Changes in osmotic potential in three species at the four site altitudes in early, mid and late spring.

as the leaves develop (Fig. 9.2). The situation is best shown in kamahi and tawari and least in quintinia which has constant potentials through the season. However almost all species, at all altitudes, showed $\psi_s$ at the final sampling that was higher than prior to bud break. Osmotic potentials decreased most strongly at the lowest altitude and particularly in tawari and kamahi where values approached levels present before bud break. This is probably a consequence of less frequent fog and higher temperatures at the lower altitude since it has frequently been shown that increased $\psi_s$ is associated with a period of stress exposure during hardening (Sullivan and Eastin 1974).

## DISCUSSION

The results presented here, taken with those previously published (Jane and Green 1983c), provide good evidence for large changes in $\psi_s$ during the year. Potentials appear highest at the time of, and soon after, bud break in a similar manner to that reported for Tsuga canadensis (Tyree et al. 1978). Although the sampling was not intensive, the maximum values found here (about -1.0 MPa) are close to the -0.8 MPa found for deciduous trees (Tyree et al. 1978, Roberts and Knoerr 1977). The rise in potential also reflects the different strategies of leaf development rising higher in silver beech where there is a single leaf flush and rapid leaf development, and less in tawari where the flush is followed by a period of slow leaf extension and maturation which may extend over several months. The correspondence between a slow increase in $\psi_s$ and slow maturation is particularly obvious at the higher altitudes.

One explanation for the slow leaf development and maturation in evergreen plants is that current photosynthesis is used to supplement limited quantities of stored carbohydrates mobilised before bud break

(Kramer and Kozlowski 1979). A second possibility is that since a shoot of an evergreen plant need not wholly depend on the new leaves, rapid leaf development is unneccessary. A similar contrast is seen in deciduous species such as apple (Malus) and poplar (Populus) where the first complete leaves are produced in a few days but later leaves may take many weeks to mature or in Rhododendron and pines where leaf growth can continue for several years (Kozlowski 1971).

Prior to the flush $\psi_s$ is higher at the higher altitudes in all species at fog zone sites as found in the previous study (Jane and Green 1983c). By the third sample differences between sites were generally meaningless and dependent on the stage of leaf development for each species. The rate of leaf hardening and recovery in $\psi_s$ was slow possibly because the 1982/3 summer has generally been cool and moist and other years may show a different rate of change in $\psi_s$. Kozlowski (1971) notes that changes in some species are strongly temperature dependent. The high values obtained during and around bud break would predispose the species to damage from water stress and suggest tawari, with the lowest $\psi_s$, to be drought resistant whereas silver beech would be very susceptible to damage. Field observations found leaf fall and scorch in new leaves of silver beech, moderate signs of damage in quintinia and kamahi and little damage in tawari in line with this ranking.

At any altitude the rank order of the species based on $\psi_s$ depends on the sampling date and was different at the beginning and end of this study in early summer and late autumn as in the previous study (Jane and Green 1983c). The change in $\psi_s$ through the season means any study of plant water relations parameters must be carried with caution particularly since $\psi_s$ can be shown to effect other parameters such as elastic modulus and turgor loss point (Tyree et al. 1978, Jane and Green 1983c). The likely periods of drought stress and the high susceptibilty of young leaves resulting from the high $\psi_s$ near bud break must also be taken into account.

# CHAPTER 10.

## PATTERNS OF STOMATAL CONDUCTANCE IN SIX EVERGREEN TREE SPECIES FROM A NEW ZEALAND CLOUD FOREST

### INTRODUCTION

Farquhar and Starkey (1982) and others (Wright 1970, Dina and Klikoff 1973, Bunce et al. 1977, Chabot and Bunce 1979, Hall and Schultze 1980) have suggested that the major strategy in stomatal regulation is the maximising of carbon dioxide fixation in terms of water loss in the modal part of the plant distribution. Diurnal patterns of stomatal conductance may reflect the water stress within a plant due to drought, site or altitude (Larcher 1975, Korner and Mayer 1981). Differences in patterns have been demonstrated in natural stands between different species on the same (Hinckley et al. 1978, Roberts et al. 1979, Roberts et al. 1980) or adjacent sites (Running 1976, Sinclair 1980). These variations may be related to the natural range of the species or the stage of maturity of the stand (Tobiessen and Kana 1974). Stomatal conductance can also be interpreted in terms of the ecological status of species within a site or plant community (Hinckley et al. 1978, Knapp and Smith 1981). Plants of wetter habitats often maintain higher conductances than plants from drier habitats when both are present on the same site (Dina and Klikoff 1973, Bunce et al. 1977) and seral plants usually have higher conductances than climax species. Stomatal responses may therefore be a useful indicator of both site stresses and species adaptation (Bunce et al. 1977, Fetcher 1979, Knapp and Smith 1981).

Within the cloud forests of the Kaimai Ranges, North Island, New Zealand, the vegetation shows evidence of episodic mortality that is unrelated to vegetation type but corresponds closely in location with the predominant cloud zone (Jane and Green 1983b). Dendrochronological and other evidence show a coincidence between the date of the mortality and the occurrence of drought. It was thought that high fog frequency was acting in some way to make the vegetation more susceptible to drought and that this would be reflected in the stomatal behaviour during a normal summer.

## SITE DESCRIPTION

The Kaimai Ranges, with high points up to 950 m altitude, cannot be regarded as mountainous and the summit is well below the local tree line estimated at 1500 m. The climate resembles that of the tropical cloud forests in many respects with high annual precipitation, over 2500 mm per annum, well dispersed throughout the year, and frequent fog and low cloud (Jane and Green 1983b). Temperatures are moderate and rarely exceed 20 °C although in winter they are often close to freezing (New Zealand Meteorological Service pers. comm.). Precipitation greatly exceeds evapotranspiration in most years, and the soils are often waterlogged over considerable periods, perhaps years at a time.

The principal research site was located at the summit of the Kaimai Ranges (latitude 37 ° 30' S longitude 175 ° 15' E) at 850 m altitude. Additional study sites were located on Mt. Te Aroha about 16 km further north. Details of the research area the and study sites and of the Kaimai Ranges are described in Jane and Green (1983b).

The main vegetation is evergreen, broadleaved, seral shrubland dominated by tawari, *Ixerba brexioides* A Cunn.; quintinia, *Quintinia acutifolia* Kirk; and kamahi, *Weinmannia racemosa* Lin. f. (Jane and Green 1983b). Investigations were carried out into the three dominants plus three sub-storey species toro, *Myrsine salicina* Hew. ex Hook. f.; raurekau, *Coprosma australis* (A. Rich.) Robinson; and five finger, *Pseudopanax colensoi* (Hook. f. ) Philipson.

Measurements were carried out on the same trees throughout the season. Sun leaves on the northern side of the tree were used to minimise the known variation in stomatal conductance within plants (Hinckley and Ritchie 1970, Roberts et al. 1981) and between aspects (Hinckley and Scott 1971). Three young leaves were tagged on at least two plants of each species at the beginning of the season. These leaves were then used until January (mid-summer) when, soon after bud break, many of the leaves were shed. Fresh new leaves were then selected for all species except kamahi, where selection was delayed until late in the season because of slow development. Acetate stomatal peels and scanning electron micrographs of leaf surfaces of the six species showed that stomata were confined to the lower leaf of the leaves where they were uniformly distributed.

Two instruments were used to measure stomatal aperture. A Delta T (Mark 2) unventilated transit-time porometer (Jarvis 1980), was used to measure stomatal resistances (converted to conductances for comparative purposes) during the early part of the season. This instrument had to be calibrated before each series of measurements against a standard perforated plate. A factory calibrated Licor LI-1600 steady-state ventilated porometer was used to obtain conductances later in the season. The two instruments were compared on two occasions by successive measurements on the the same leaves. The presence of either dew or fog often made measurement of stomatal conductance impossible from sunset to mid-morning. When early morning observations could be made intermittent sunlight and a slight breeze was present so that the results must be treated with due caution.

Temperature and relative humidity were recorded each site at the beginning of each series of measurements either with the Licor LI-1600 or with a portable Kahsico aspirated psychrometer placed on a branch or log about 1.5 m above the ground. Differences between the two instruments were minor and were regarded as unimportant.

Water potentials were determined on plant adjacent to those used for porometry. Each shoot was wrapped tightly in a thin plastic bag, placed in an insulated container and water potential measure within 30 minutes. Balance pressure was determined using procedures described by Ritchie and Hinckley (1975) using a pressure chamber with an electronic pressure sensor reading to 0.1 MPa. Water potential at stomatal closure was determined using shoots on the same plant and adjacent to those used for porometry on two occasions.

Rainfall was measured using a plastic rain gauge placed about 200 m from the experimental site. At monthly intervals soil samples were taken from a depth of 20 cm and soil moisture content determined gravimetrically. Soil moisture contents at field capacity (-0.1 MPa) and wilting point (-1.5 MPa) were determined on sample soil blocks by pressure plate at the Forest Research Institute, Rotorua.

## RESULTS

### Comparison of instruments

Stomatal conductances obtained by using the two instruments sequentially on identical leaves were significantly correlated (r= 0.78 for 76 observations) but the regression was not of high predictive value (Fig. 10.1). There was no apparent difference between results from the two days and no instrumental bias between species. For these reasons, and because the differences between instruments were small compared with the daily and seasonal variation, the results were not adjusted in

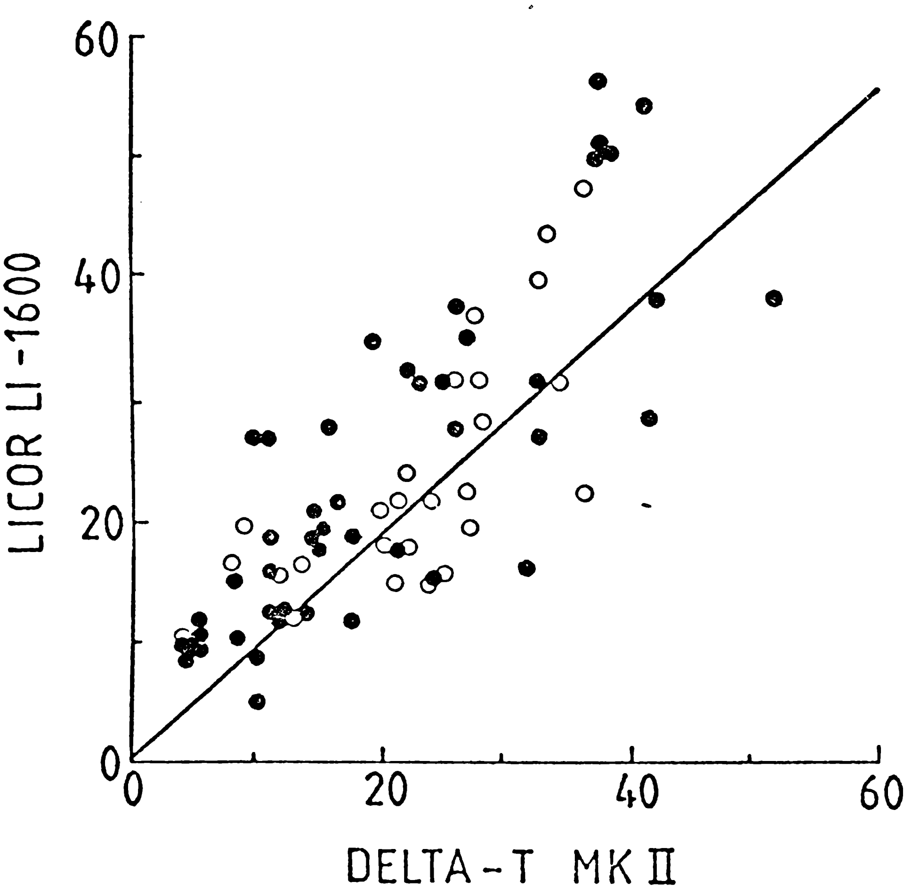


Fig. 10. 1. Comparison between conductances (cm $s^{-1}$) obtained from the LICOR LI-1600 steady state ventilated porometer and the Delta-T Mk II transit-time unventilated porometers. Instruments were used successively, LICOR LI-1600 first, on the leaves of 5 species on two days (0-9th February 1982, ●-13th February 1982). The fitted line is Y = 2.3 + 0.96X.

subsequent analysis to allow for the instrument being used.

## Stomatal conductance ranges of Species

Early in the season very similar, moderate, maximum conductances (0.21 cm.$s^{-1}$) were obtained for all species, except kamahi (Table 10.1). New leaves of all species had higher maximum conductances, with values for kamahi and quintinia approaching the highest recorded for woody plants (Korner et al. 1979). The lowest values, in tawari, are similar to those generally found in broadleaved trees. The stomata of the older leaves had lower conductances and may be partly occluded or senescent, as has been commonly found in other plants (Larcher 1975, Watts 1975, Hinckley et al. 1976, Roberts et al. 1979). Throughout the season stomatal closure was most pronounced in quintinia and least in tawari. The latter showed evidence that the stomata remained slightly open at night in the early part of the season (Fig. 10.2).

Variability in conductances within and between plants was high. The coefficient of variation (CV %) was usually between 10 and 45 % but in tawari and raurekau, was up to 120 % (Table 10.2). Variability was particularly high in the evenings when stomata were closing and this was probably a result of variations in incident radiation and leaf temperature in the rapidly shifting patches of sunlight.

## Patterns of stomatal behaviour

At the first complete diurnal sampling (27th November 1981) conductances and diurnal patterns were similar for all species except five finger (Fig. 10.2a). Maximum values were reached before 10 am, usually within an hour of the final clearance of fog. All the species began stomatal closure early in the afternoon and closure continued gradually until late afternoon. The following morning, under high

## TABLE 10.1

Variation in maximum observed conductance (cm.sec$^{-1}$) with leaf age by species.

| Species | leaves of the previous season<br>November | <br>January | new leaves<br>January |
|---|---|---|---|
| Tawari | 0.21 | 0.22 | 0.39 |
| Quintinia | 0.21 | 0.23 | 0.63 |
| Toro | 0.22 | 0.21 | 0.37 |
| Kamahi | 0.32 | not available | 0.61 |
| Five finger | 0.24 | 0.26 | 0.33 |

## Table 10.2

Coefficient of variation (%) of stomatal conductance at different times of the day (9th February 1982).

| Species | Time of day<br>8 am | <br>10 am | <br>12 noon | <br>3 pm | <br>6 pm |
|---|---|---|---|---|---|
| Tawari | 21.4 | 33.9 | 33.9 | 17.9 | 120.2 |
| Kamahi | 43.6 | 10.3 | 19.3 | 26.8 | 68.1 |
| Quintinia | 25.1 | 20.3 | 24.0 | 29.8 | 33.9 |
| Toro | 21.5 | 10.3 | 45.2 | 65.1 | 72.8 |
| Five finger | 38.1 | 20.3 | 19.0 | 41.3 | 82.1 |
| Raurekau | 17.0 | 38.3 | 42.1 | 42.2 | 117.1 |

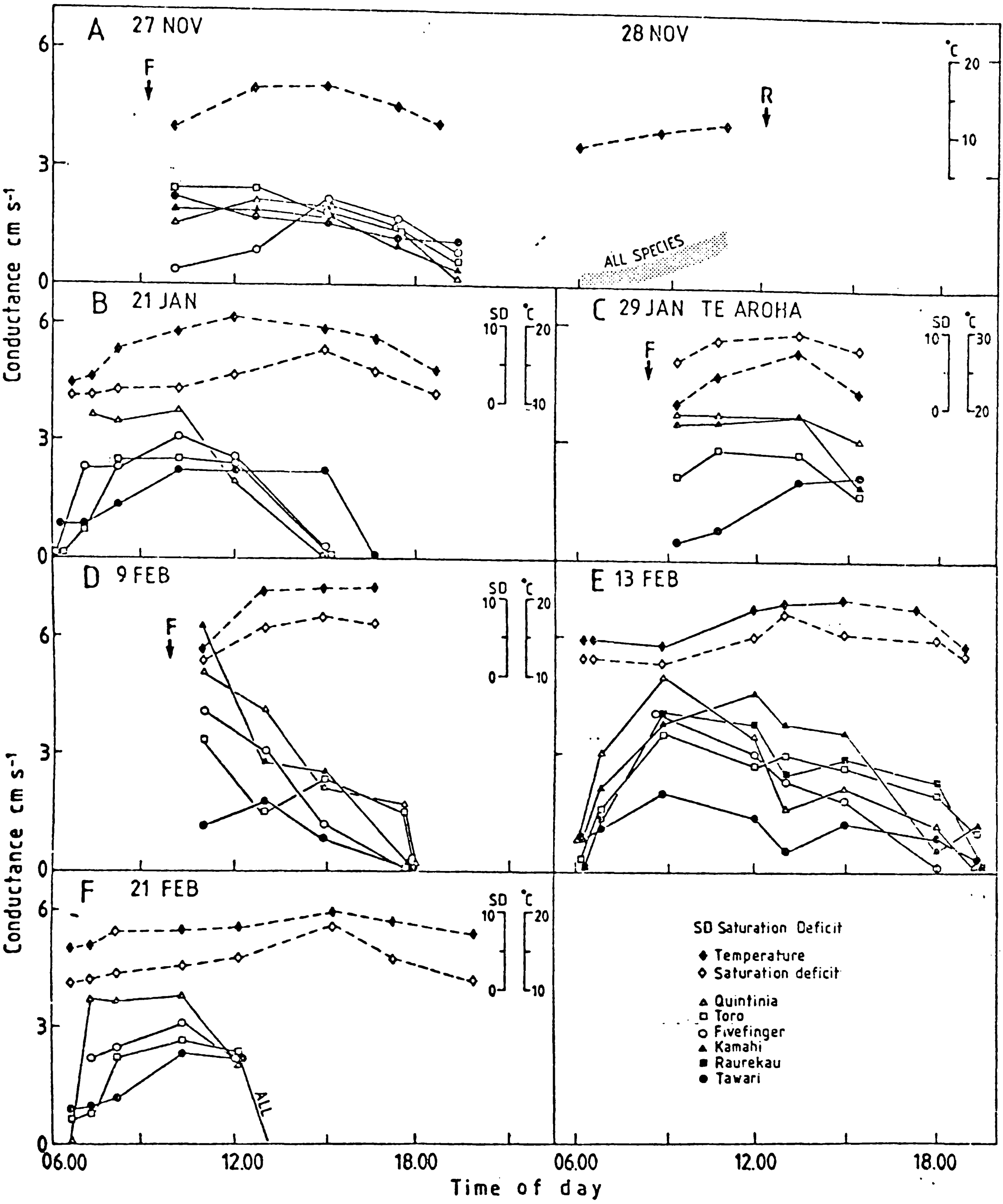


Fig. 10. 2. Diurnal patterns of stomatal conductance, temperature and SD at Te Hunga and Te Aroha (C only) through the austral summer 1981/1982. F, indicates time of fog clearance; R, indicates start of rain. Note different temperature scale for C (Te Aroha).

overcast conditions stomata opened progressively from day break (6 am) until rain terminated measurements at 1 pm. Incomplete sampling on other days confirmed this as the normal pattern for early summer.

Later in the season a similar pattern was found on mild days (Fig. 10.2e), but closure normally began much earlier in the day (Fig. 10.2b, 10.2d, 10.2f), frequently by mid-morning, and was complete by mid-afternoon (Fig. 10.2b). This pattern became more prominent as the summer progressed (Fig. 10.2b, 10.2f), although on some days closure could be delayed by morning fog (Fig. 10.2d). In an extreme case stomata of all species had closed within an hour of fog clearance at midday. By the end of summer complete midday closure occurred at an SD of 8 $g.m^{-3}$(Fig. 10.2f) and closure could occur soon after the fog lifted at a lower SD. Midday depression, was found in some species including quintinia, raurekau and tawari (Fig. 2e).

In contrast data collected at the same altitude on Mt. Te Aroha showed little evidence for rapid afternoon closure at mid-summer (Fig. 10.2c) and diurnal patterns remained similar to those earlier in the season despite higher temperatures and SD compared to Te Hunga.

### Differences between species

In quintinia stomata tend to open rapidly and reach high conductances soon after day break and closure is usually rapid and complete. Kamahi showed a similar but less striking pattern. Tawari showed progressive opening until mid-morning (Fig. 10.2b) and had slower closure that was often less complete than in species such as quintinia. Five finger appeared to show opening close to sunrise but because of persistent dew on the leaves was not be clearly demonstrated. Closure occurred earlier and more gradually than other in species.

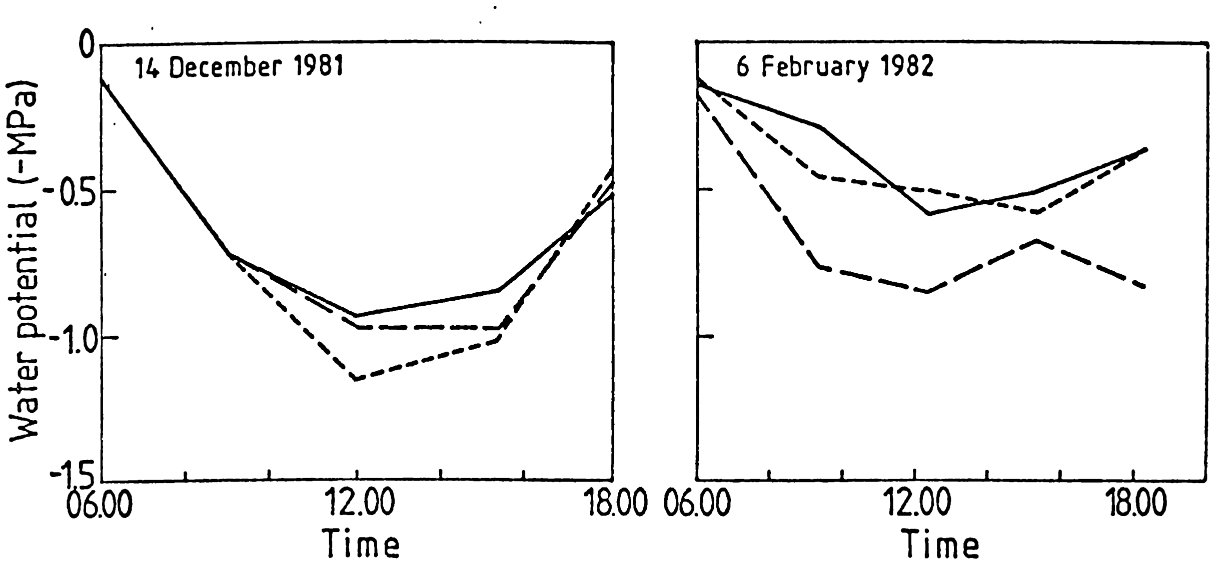


Fig. 10. 3. Diurnal pattern of plant water potential in early (14 December 1981) and late (6 February 1982) summer. Species sampled were tawari, — ; quintinia, — — — ; kamahi, - - -

### Plant water potentials

Minimum water potentials for kamahi, quintinia and tawari, and water potentials determined at early afternoon were similar and well above turgor loss point (Fig. 10.3, Table 10.3). Dawn water potentials were high indicating high soil water potentials even in mid-February following a period of unusually low rainfall (Fig. 10.3, Fig. 10.4). Soil moisture contents at Te Hunga fell below field capacity (0.01 MPa) only in February so that a degree of flooding existed for most of the season whilst at Te Aroha soils were below field capacity (Fig. 10.4). Water contents of soils at both sites were well above wilting point (-1.5 MPa) at all times.

## DISCUSSION

### Evaluation of instruments

The Licor LI-1600 porometer provided a reliable estimate of conductance but was found to be slower to operate than the Delta-T, particularly at high conductances. The Delta-T was more sensitive at low conductances but required frequent calibration, a serious limitation where conditions are changing rapidly or where there is a wide variation in conductance between species. It nevertheless provided rapid estimates of diurnal conductance patterns.

Comparisons between different types of porometers have been made on a number of occasions (Johnston 1981, Landsburg et al. 1975) but recent developments and modifications to the various instruments now make much of the early work of limited value. Comparisons by Bell and Squire (1981) and Johnstone (1981) show an underestimation of conductances by transit-time porometers such as the Delta-T similar to that found here. Instrument induced effects on the boundary layer of the leaf in the unventilated instrument chamber (Korner et al. 1979, Johnston 1981), or

Table 10.3

Comparison between leaf water potential at early afternoon stomatal closure, normal midday values and the turgor loss point.

| | Water potential (-MPa) | | |
|---|---|---|---|
| Species | at closure | normal midday value | turgor loss point* |
| Tawari | 0.63 | 0.95 | 1.34 |
| Kamahi | 0.57 | 1.02 | 1.57 |
| Quintinia | 0.87 | 1.16 | 1.77 |
| Silver beech | 0.95 | 1.22 | 2.04 |
| Raurekau | 0.74 | not measured | not measured |
| Toro | 0.86 | not measured | 1.68 |

* Values obtained by pressure-volume techniques (Jane and Green 1983 c)

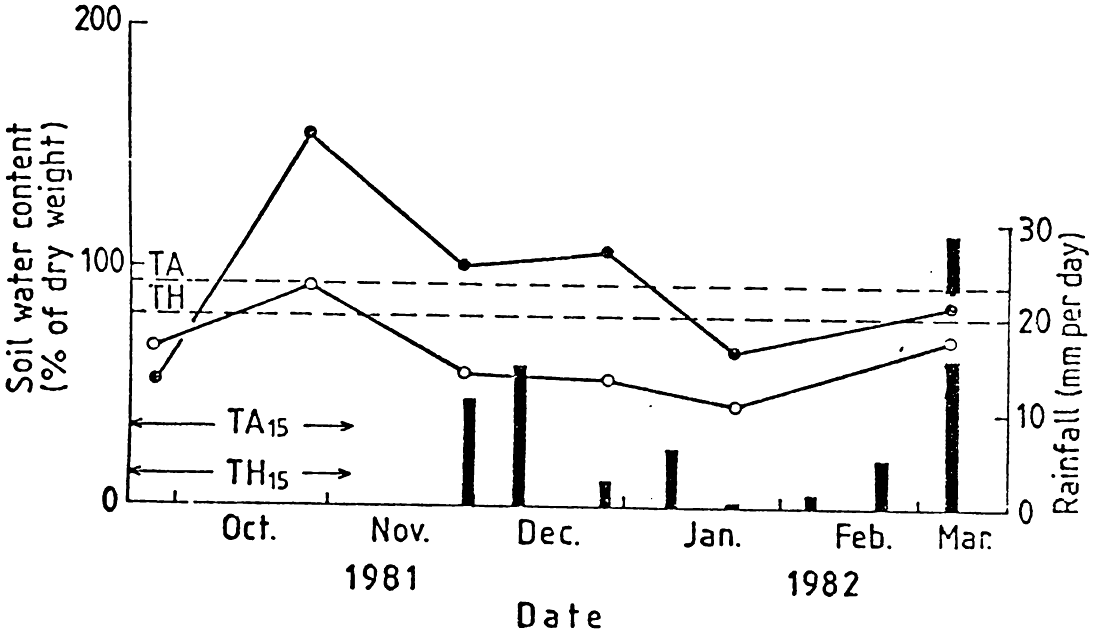


Fig. 10. 4. Soil moisture contents and rainfall through the summer, 1981/1982. Rainfall was measured at Te Hunga (850m), each bar represents the total fall since the previous measurement converted to mm day$^{-1}$. Soil moisture contents are from Te Aroha (O) and Te Hunga (●); dashed lines represent field capacity (-0.01 MPa) at Te Aroha (TA) and Te Hunga (TH) whilst $TA_{15}$ and $TH_{15}$ are the respective wilting point (-0.15 MPa).

adsorption onto the walls of the plastic chamber are suggested to be the main causes of the problems. These effects are likely to be minimal in a steady state porometer such as the Licor LI-1600 (Fanjul and Jones 1982) although they are difficult to estimate in the Delta-T, they may be small in comparison to sampling variability.

Sampling variability because of stomatal distribution and stomatal reactivity may also be important sources of error (Johnstone 1981, Fanjul and Jones 1982). Examination of cuticular peels suggested that stomatal distribution was not an important source of error in the species used in this investigation, hence stomatal reactivity, either sensitivity to vibration or stomatal cycling, appears to be the most probable explanation for the variability. Stomata may close in response to handling or to the action of instruments (Bell and Squire 1981) in a manner similar to the response to wind (Davis et al. 1974, Grace 1981). Stomatal cycling may occur in full sun over periods as short as 10 minutes (Meidner and Sherrif 1976) and vibration may trigger the closure phase of the cycle. Several observations of stomatal closure between successive measurements by different instruments on the same leaf lend support to this latter proposal. Fanjul and Jones (1982) suggest that these problems are likely to be minimal in porometers such as the Licor-1600 used in the steady state condition and this could be the main cause of bias in comparisons between these instruments and transit-time instruments such as the Delta-T.

### Comparison between species

The six species show differences in stomatal conductance that reflect their ecology.

Quintinia and kamahi are predominantly seral and have very high stomatal conductances, rapid morning opening and rapid response to increased stress later in the day. Stomatal closure at night, or under stress is more complete in quintinia. These features are characteristic of opportunistic behaviour of seral plants (Tobiessen and Kana 1974, Fetcher 1979, Roberts et al. 1979).

Tawari is the predominant canopy plant of mature stands and has a low to moderate conductance. The stomata open more slowly in the morning and remain open longer in the afternoon or under stress, behaviour common in climax species (Tobiessen and Kana 1974, Wallace and Dunn 1980).

Toro shows responses intermediate between those of canopy plants and the seral plants. The species has a moderate maximum conductance and although its stomata open gradually through the morning, they respond strongly to stress. It forms a lower tier in the seral scrub and is a gap coloniser in the older stands.

Raurekau is present on this site as young canopy plants up to 5 years of age but elsewhere is a common understory plant. It is probable that this change in status reflects the frequent fog which reduces normal light levels and water stress severity. The high conductances shown by this species would allow maximum use of sunflecks in the canopy gaps, as found in in similar situations by Smith (1981), but on this site may place it at severe risk during drought. Severely wilting of understorey plants of this species was noted at drier lowland in lowland sites during the driest part of the summer. The youth of the plants at the study site suggests that older plants were killed in a drought in 1972.

Five finger has high conductances and shows a very sharp reaction to the increasing stress during the summer. The species is most often found lining streams minor gullies where water is rarely limited and sun exposure is low. High conductances may be advantageous in these situations but may expose plants to severe stress in the more open shrubland areas of the study site.

## Stomatal conductance patterns

Patterns of stomatal water loss are probable regarded as complex and dependent on the stress level of the site for the respective species (Hall and Schultze 1980). Plants on wet sites have often been shown to exercise little stomatal control over water loss (Tobiessen and Kana 1974, Bunce et al./ 1977, Sinclair 1980). On the other hand Schlesinger and Chabot 1977) have found midday stomatal closure in evergreen swamp plants. Running (1976) found a lack of control in sitka spruce in foggy areas of the western United States but, in contrast strong evidence was found for stomatal control control in the same species on more demanding planted sites in Britain (Jarvis 1976).

Considerable control over water loss was shown by quintinia, tawari, kamahi toro and five finger with progressively earlier daily closure of stomata occurring throughout the season. Similar early closure has been shown for individual members of a species on the same site (Jarvis 1976) or within species over a several sites (Korner and Mayer 1981). The simultaneous reaction of several species on the same site as found here, is striking and suggests that some dominating physical force such as temperature, soil water deficit or SD was triggering closure.

There is little evidence that high temperature is causing early closure. Temperatures at the Te Hunga site were not abnormally high at stomatal closure, usually no more than 20° C, and are close to optima found in a wide range of other woody species (Watts 1975, Dougherty and Hinckley 1981, Jarvis 1976). Early closure was not found on Mt. Te Aroha despite higher temperatures approaching 27° C. Low soil water potential can be probable also be discounted. Although rainfall was well below average from early January to late February, only 10 % of that recorded for the same period last year, dawn water potential was high, greater than -0.2 MPa and stomatal closure occurred at relatively low plant water deficits, well above the turgor loss point (Jane and Green 1983c). SD, although never high (Fig. 10.2), could well be an important factor in determining the patterns of stomatal behaviour. Detailed studies by Running (1976) and Jarvis (1981) found stomatal sensitivity at similar values (7 $g.m^{-3}$) in scots pine and sitka spruce from temperate regions. The direct response to SD at midday on 13th February 1982 (Fig. 10.2e) lends further support to this viewpoint but closure does not appear to occur consistently at a similar SD on all days. Ludlow (1981) suggests that increased sensitivity to SD occurs as water stress increases and this could explain the remaining anomalies such as between the last two days illustrated (Fig. 10.2d, Fig. 10.2f).

Site differences are implicated by the absence of stomatal closure at higher temperatures and SD at a similar altitude on the Te Aroha site. Although the difference between the two sites could be because of acclimation (Syvertson 1982), the wetter habitat at Te Hunga with higher rainfall and greater fog frequencies (Jane and Green 1983b), may be contributing to the sensitivity to stress in some way. Poor root development induced by waterlogging (Kawase 1981) and aggravated by low soil temperatures may be responsible. Bunce (1981) has suggested that there is an inverse relationship between root relative length and stomatal sensitivity. Bradford and Yang (1981) indicate that stomatal closure can occur at high water potentials during waterlogging and that the plant hormonal balance is disturbed. Bates and Hall (1981) and Aspinall (1981) suggested that a hormonal signal originating in roots undergoing water stress may trigger closure and it appears possible that excessive hormone production because of waterlogging has increased plant sensitivity to stress. The nature of the hormones responsible have not been certainly identified. Abscissic acid is known to cause stomatal closure (Hiron and Wright 1973) but there are a number of other substances including ethylene and 1-amino propane-1- carboxylic acid (ACC) which have elevated concentrations in waterlogged plants and can be linked with stomatal closure (Bradford and Yang 1981). It appears possible that the increased sensitivity to water stress at Te Hunga is because of waterlogging and is acting through effects on the hormonal balance originating in the poorly developed root systems.

## Fog - vegetation Interactions

Jane and Green (1983b) have described the severe episodic forest mortality at, and around, the study areas in the Kaimai Ranges. The distribution of the mortality is almost identical to that of the prevalent fog whilst the time of occurrence appears to be most strongly linked with rare extreme droughts. There is an obvious contrast between the location determined by conditions likely to cause above average average water supply and the timing linked to severe water stress. The results presented here help to explain this contrast.

A feature of the research area is the prevalent fog that contributes moisture and limits transpiration and results in high soil water contents that remain above field capacity for the majority of the year. In flooded soils anaerobic conditions can lead to increased root resistances if water fluxes are sufficiently high (Jackson et al. 1978). Rapid stomatal closure is then required to prevent severe water deficits from developing even at low SD.

A severe drought, particularly following a period of sustained high soil moisture, would place the plants under water stress and limit productivity because of stomatal closure (Jarvis 1981). The reduction in radiation by the fog may reduce photosynthesis to one quarter of full sunlight levels and lower temperatures about 3° C below normal (O'Rourke and Terjung 1980), reducing productivity further. As a result several understory plants are able to survive as sub-dominant and canopy plants and the cooler temperatures have probably permitted the cool temperate silver beech (Nothofagus menziesii, Hook. f. (Oerst)) to survive at this latitude at the very north of its natural range.

The fog is suggested to act in two ways to make the plants unusually sensitive to drought. First, by maintaining waterlogged soil conditions and consequent reduction of root systems, and secondly by limiting the plant growth potential through reduced radiation and temperature. The fog is therefore an important contributing factor to the location and occurrence of the forest mortality.

## CHAPTER 11

# DIURNAL PATTERNS OF WATER POTENTIAL IN THE EVERGREEN CLOUD FORESTS OF THE KAIMAI RANGES, NORTH ISLAND, NEW ZEALAND.

## INTRODUCTION

Fog can be defined as cloud occurring close to ground level and although often thought of as being a lowland and winter phenomenon an important manifestation also includes mists and low cloud which almost perpetually envelop mountain peaks. This mountain fog gives rise to distinctive vegetation that is well recognised in tropical regions but also occurs in almost all other areas of the world including moist temperate (Zotov 1938, Siccama 1974) and arctic regions (Damman 1977).

Cloud forests pose a unique set of as yet poorly studied ecophysiological problems because of the low light intensities, reduced temperatures and the very moist hydrological regimes that are created. The impact of reduced photosynthetic activity in the periods of low light intensity have been investigated by Roth and de Bifano (1980) in the cloud forests of Venezuela but little effect on compensation point was reported. The duration of the periods of low light intensities places particular emphasis on the brief periods of clearer skies during which enhanced sensitivity to water stress may constrain growth. For instance Brunig (1969) observed drought mortality in the wet tropical forests of Borneo and in temperate forests Aussenac and Valette (1982) found that plants of wetter sites were more susceptible to water stress in dry summers than plants from dry sites.

Fog may also provide a supplementary source of water for at least some species during prolonged periods of low rainfall. In extreme situations, such as in very dry regions of the world, fog is a well known water source for plants (Kerfoot 1967). In the Namib desert and similar areas, fog may be the sole source of water for plant growth and many of the plants present are particularly adapted for fog interception (Walter 1971). In dry temperate regions such as the redwood forests of California (Azevedo and Morgan 1974, Prat 1953) and the radiata pine forests of the adjacent coastal islands fog is also a significant contributor to the water balance of the forests (Rutter 1981). Reduction in evapotranspiration and increased precipitation from interception of the fog by the foliage (Rutter 1981) are thought to be the main factors but direct uptake by the foliage is also probable (Martin and Juniper 1970, Levitt 1972, Gaertner 1964, Hellkvist et al. 1974).

In desert areas (Stone 1957, Kerfoot 1967) dew may be the sole source of water for plants and in temperate forests and grasslands it is also often regarded as a significant moisture source (Gaertner 1964, Rutter 1967). However, it is not a contributor to total precipitation and has only a minor effect on the water balance of the vegetation (Stone 1957, Kerfoot 1967). Nevertheless it may be difficult to separate the effects of fog and dew particularly where fog has only a transient presence at night.

The upland vegetation of the Kaimai Ranges has recently suffered a period of severe mortality. Mortality is most severe and extensive on the wetter more foggy Te Hunga summit than on Mt. Te Aroha. The bounds of the affected zones correspond closely with that of the cloud zone and it was suspected that the mortality was caused by severe drought (Jane and Green, 1983a). Consequently, it was thought possible that in dry periods, perhaps even during a normal summer, some of the plants in the upland forests may show severe water stress. The altitudinal variation in water stress at similar times of the day and differences between disturbed and undisturbed sites would be expected to show the main contrasts. The prevalent fog was also expected to directly influence diurnal patterns of water potential. This study set out to examine these hypotheses.

## METHODS

### Site Descriptions

In many respects the climate in the Kaimai Ranges resembles tropical cloud forests. Annual precipitation is high, over 2500 mm per annum, and is well dispersed throughout the year whilst fog is of very frequent occurrence (Jane and Green 1983b ). As a result precipitation greatly exceeds evapotranspiration in most years and the soils are often waterlogged over considerable periods, perhaps years at a time. However temperatures rarely exceed 20 ° C and winter temperatures are often close to freezing (New Zealand Meteorological Service, pers comm).

Study areas at Te Aroha and Te Hunga were described by Jane and Green (1983c). At both locations sample sites were selected over an altitudinal range that included the cloud zone. At Te Hunga the lower cloud limit was 700 m and sites were selected at 600, 700, 800 m and on the summit plateau at 850 m. At Te Aroha the lower cloud limit was 800 m and the main sites were selected at 600, 800 and 850 m with extra sites containing plants showing poor vigour (poor sites) at 800 and 850 m. In both areas the sites faced north east (sunny aspect) and slopes were steep so that the horizontal distance between topmost and lowest sites was less than 400 m. Soils were shallow clays, and declined in depth from less than 1.5 m at 600 m to less than 0.5 m above 700 m altitude.

The forests are dominated by tawari and silver beech and a number of seral species (Jane and Green 1983a ). Six species were investigated: tawari (Ixerba brexioides, A Cunn.). silver beech (Nothofagus menziesii, Hook f. Oerst.), miro (Podocarpus ferrugineus,

G. Benn. ex Don ), kamahi (*Weinmannia racemosa*, Lin. f. ), quintinia (*Quintinia acutifolia*, Kirk ), and toro ( *Myrsine salicina*, Hew. ex Hook. f.). Some of the plants may be particularly adapted to, or confined to, cloudy areas in all or part of their range. Unfortunately there is very little information available but personal observations suggest that it is true for tawari and also silver beech (Zotov 1938). Distributions of other species are less well known although several may also be similarly restricted.

### Pressure determinations

Shoots were cut from a branch and immediately wrapped tightly and sealed in a thin plastic bag to minimise early water losses, as recommended by Turner and Long (1980). The shoots were then packed by locality sets in a larger bag and kept cool and dark until pressure determinations could be made. In the diurnal studies all sites were sampled within 30 minutes and pressure determinations were completed within two hours, but in smaller studies the total time was less than five minutes. Tests by double measurement on one set of midday samples suggested that losses during storage lay within the errors of measurement of about 0.05 MPa.

Water potential ( $\psi$ ) determinations were made with a portable pressure chamber similar to that described by Scholander et al. (1965) but modified to include an electronic pressure sensor capable of reading to within 0.004 MPa from 0-1.7 MPa and 0.008 MPa at higher pressures. A pad of tissue paper was kept well moistened within the chamber to ensure humidification of the incoming gas. For each measurement pressure was at first raised rapidly (0.2 MPa/sec) to about 0.2 MPa below the estimated balance pressure and then very slowly until sap appeared. Pressure was then lowered slightly and held for at least 20 seconds before the final balance was recorded. In kamahi, quintinia, miro, and silver beech the balance point was clear cut but in tawari considerable hysteresis was often present and the balance point was not sharp. Determinations in toro were very difficult because of strong resin flows and only limited samples were made to examine within-crown stress.

Diurnal patterns of $\psi$ were established by detailed sampling on a small number of fine, clear days when stress was expected to be most pronounced. The patterns obtained were confirmed by measurements at dawn and mid-afternoon on other days. Sampling procedures were standardised since $\psi$ can vary within a tree with sample height and crown aspect (Waring and Cleary 1967, Cline and Campbell 1976, Ritchie and Hinckley 1975, Hinckley et al. 1978). Three sun shoots were normally taken from separate plants of each species at a height of about 2 m. At the lower altitudes samples came from the lower crown of tall trees and would be expected to underestimate diurnal range and maximal values (Ritchie and Hinckley 1975). Limited sampling in tawari and silver beech showed vertical gradients of 0.01 MPa/m (Table 11.1), similar to those found elsewhere (Scholander et al. 1965, Hellkvist et al. 1974, Hinckley et al. 1978). The error is small and well within the coefficient of variation between replicates from separate trees (Table 11.2). The coefficient of variation within species was quite low averaging about 16 % of the mean (Table 11.2) and was least for quintinia, possibly because the stress level for that species was uniformly very high.

Measurements of relative humidity and temperature were made with a portable Kahsico aspirated psychrometer placed about one metre above the ground and read during the sample collection cycle. Rainfall was regularly recorded at the summit of Te Aroha and Te Hunga and soil moisture determinations were made at 4 weekly intervals.

Table 11.1
Variation in water potential with sample height in tall trees of Tawari and silver beech. Water potential as ( - MPa)

| Species | Water potential<br>Ground level | <br>20 m | potential gradient (MPa /m) |
|---|---|---|---|
| Tawari | 0.461 | 0.613 | 0.0076 |
| Silver beech | 0.915 | 1.12 | 0.0100 |

6 observations on each of two trees of each species

Table 11. 2
Variability in pressure bomb measurements through a typical day
(Coefficient of variation %)

| Time of day | Species<br>Tawari | <br>Quintinia | <br>Kamahi | <br>Miro | <br>Silver Beech | Mean |
|---|---|---|---|---|---|---|
| 6 am | 22.2 | 12.2 | 11.3 | 26.9 | 22.5 | 19.0 |
| 9am | 12.9 | 10.6 | 16.7 | 10.4 | 13.2 | 12.8 |
| 12 noon | 21.4 | 18.0 | 22.6 | 20.5 | 11.8 | 18.9 |
| 3pm | 12.3 | 16.5 | 15.7 | 8.7 | 23.6 | 15.3 |
| 6pm | 13.0 | 8.2 | 12.7 | 10.2 | 18.3 | 12.5 |
| Mean | 16.3 | 13.1 | 15.8 | 15.4 | 17.9 | |

## RESULTS

### Diurnal Patterns Te Hunga

Diurnal patterns of $\psi$ were of the expected form (Fig. 11.1) although differences were found between species, altitudes and the time of the season. Dawn $\psi$ was high, particularly at the highest altitude, and minimum $\psi$ was reached around 1300 to 1400 hrs NZ summer-time (near solar midday) followed by recovery that was greater at the higher altitudes and early in the season (Fig. 11.1). The diurnal range of $\psi$ was largest at the 800 m and 850 m sites reflecting the higher dawn $\psi$ but midday minimum $\psi$ was similar to those at lower altitudes. Range was least at the 600 m site, particularly for quintinia, where $\psi$ was also low, indicating a greater level of stress.

The higher midday $\psi$ early in the season (Fig. 11.1) at the 600 m site probably reflect exploitation of the deeper soils. The absence of fog and higher depletion rates resulted in lower $\psi$ later in the season (Fig. 11.2). Dawn $\psi$ was generally taken to reflect the soil water potential at the plant roots but fog occurrence appears to modify this relationship. On fog days dawn $\psi$ is higher, particularly at the higher altitudes in the cloud zone (Fig. 11.3). The difference is most marked in the taller miro and silver beech and least in kamahi and tawari. The effect is transitory since midday minimum $\psi$ was not effected.

Rainfall was low throughout the season and there was a general decline in soil moisture contents (Fig. 10.4). However, the high dawn $\psi$ and afternoon recovery suggest that stress was mild in all species. For instance on one occasion a severe squall followed a fine morning and all plants showed full turgor recovery within two hours.

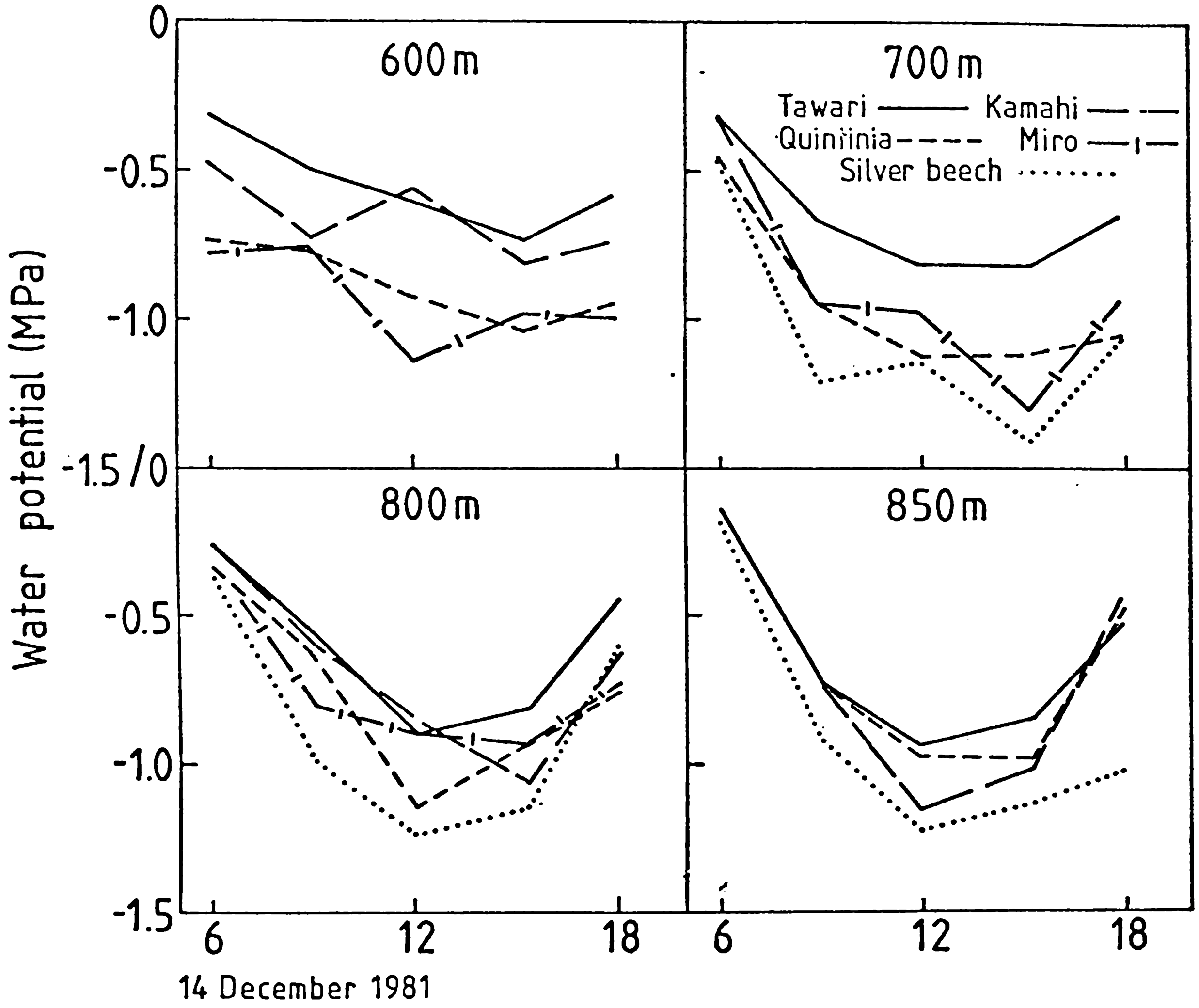


Fig. 11.1. Water potential(-MPa) in shoots of five species, at four altitudes on a single ridge at Te Hunga measured at three hourly intervals throughout the day in early summer.

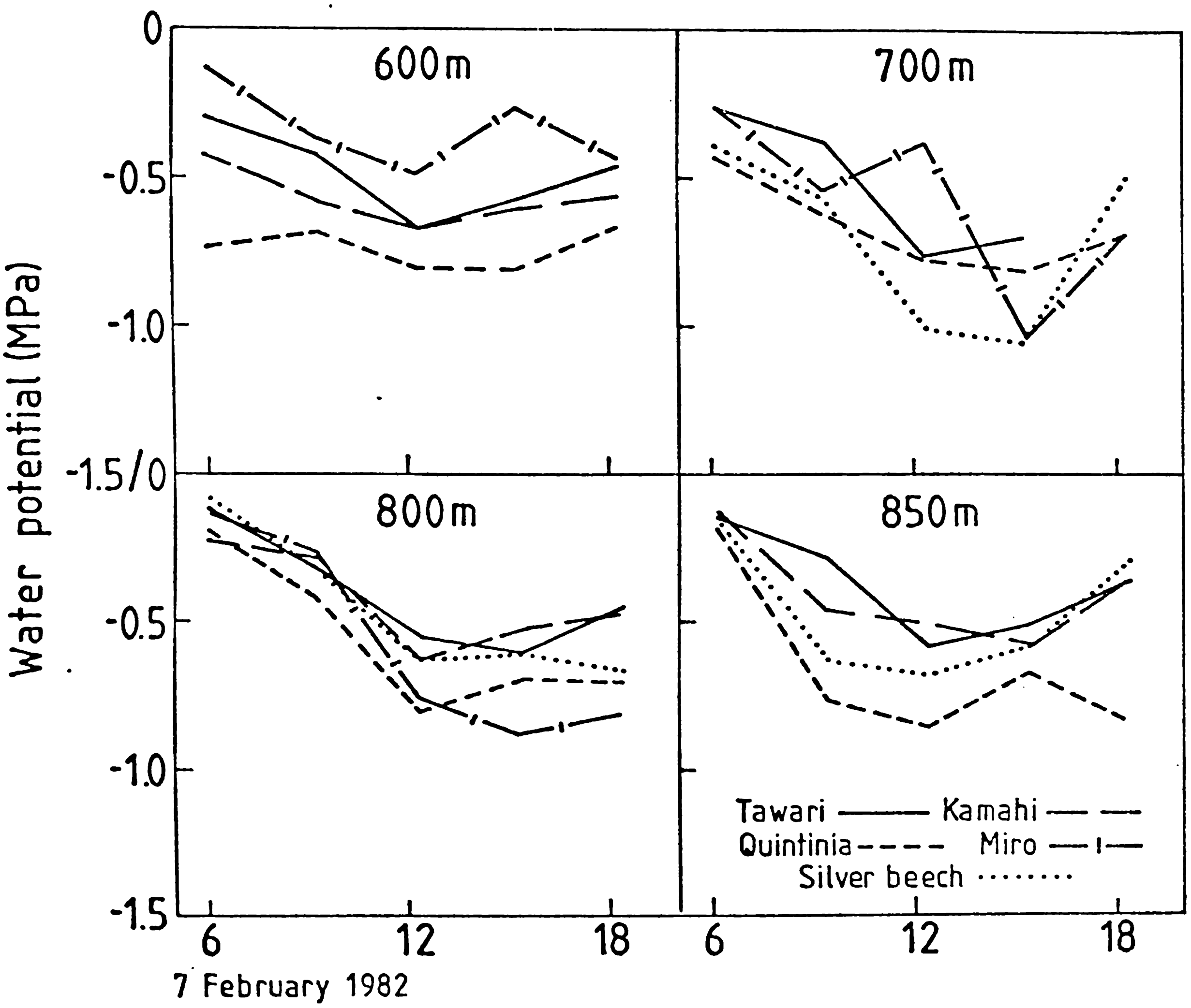


Fig. 11.2. Water potential(-MPa) in shoots of five species, at four altitudes on a single ridge at Te Hunga measured at three hourly intervals throughout the day in late summer.

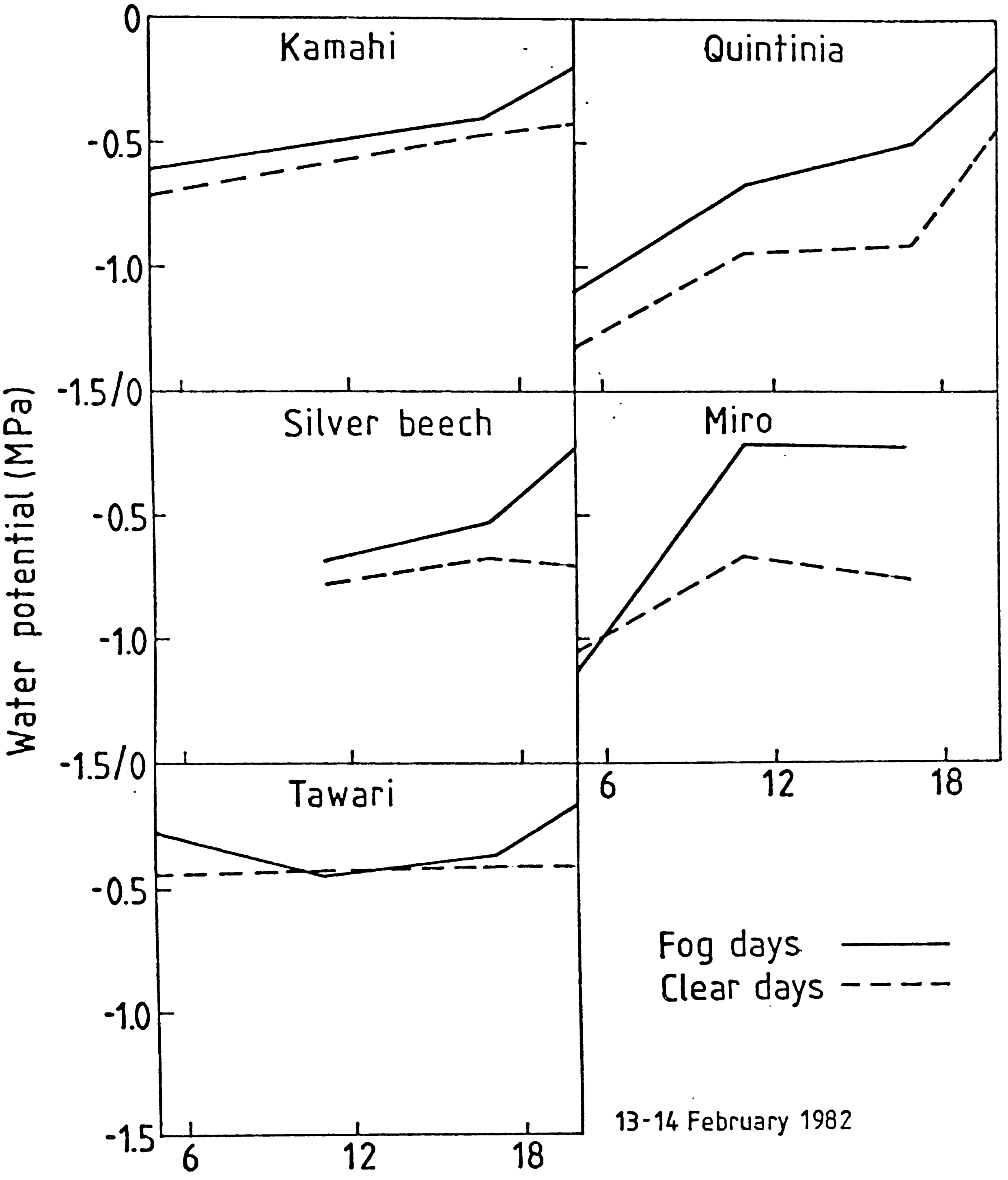


Fig. 11.3. Dawn water potential on consecutive fog and non-fog days in late summer (13th and 14th February 1982) below (600 m) and above the cloud base (700 m).

### Species Comparison

Quintinia showed the strongest evidence for stress at all sites on Te Hunga (Fig. 11.4). Dawn $\psi$ was lower than all the other species at 600 m and afternoon recovery was only slight, except at 850 m early in the season. Diurnal range at 600 m was low particularly late in the season. Kamahi and tawari had smaller ranges in diurnal $\psi$ and tawari showed slight variation between sites. Silver beech had a larger diurnal range and minimum dawn $\psi$ were consistently above those of other species. The lowest $\psi$ in beech occurred early in the season before bud break (Fig. 11.4) and it is possible that low soil temperatures (8 ° C) were a contributing factor. Miro had a low diurnal range early in the season but later in the season diurnal range was greater and particularly high dawn $\psi$ was present at the 600 m site (Fig. 11.5).

### Stress comparisons

Unhealthy, low-vigour plants of all species could be recognised by low stature and the presence of smaller leaves clustered towards branch tips. The presence of these plants was used to select poor sites adjacent to normal good sites at 800 m and 850 m on Mt. Te Aroha. Midday $\psi$ was significantly lower on the poor sites (Fig. 11.6) but there was a species-site interaction ($F= 3.5$, $p= 0.001$) indicating different species responses. Tawari had higher $\psi$ on the good sites and lower $\psi$ at the dry 600 m and poor sites (Fig. 11.6). Quintinia and kamahi had a lower $\psi$ at the 800 m poor site but no difference between good and poor sites at 850 m. Both species appear to benefit from lower temperatures and moister soils at the higher altitude. At all sites tawari had the highest midday $\psi$ and quintinia or silver beech the lowest (Fig. 11.6).

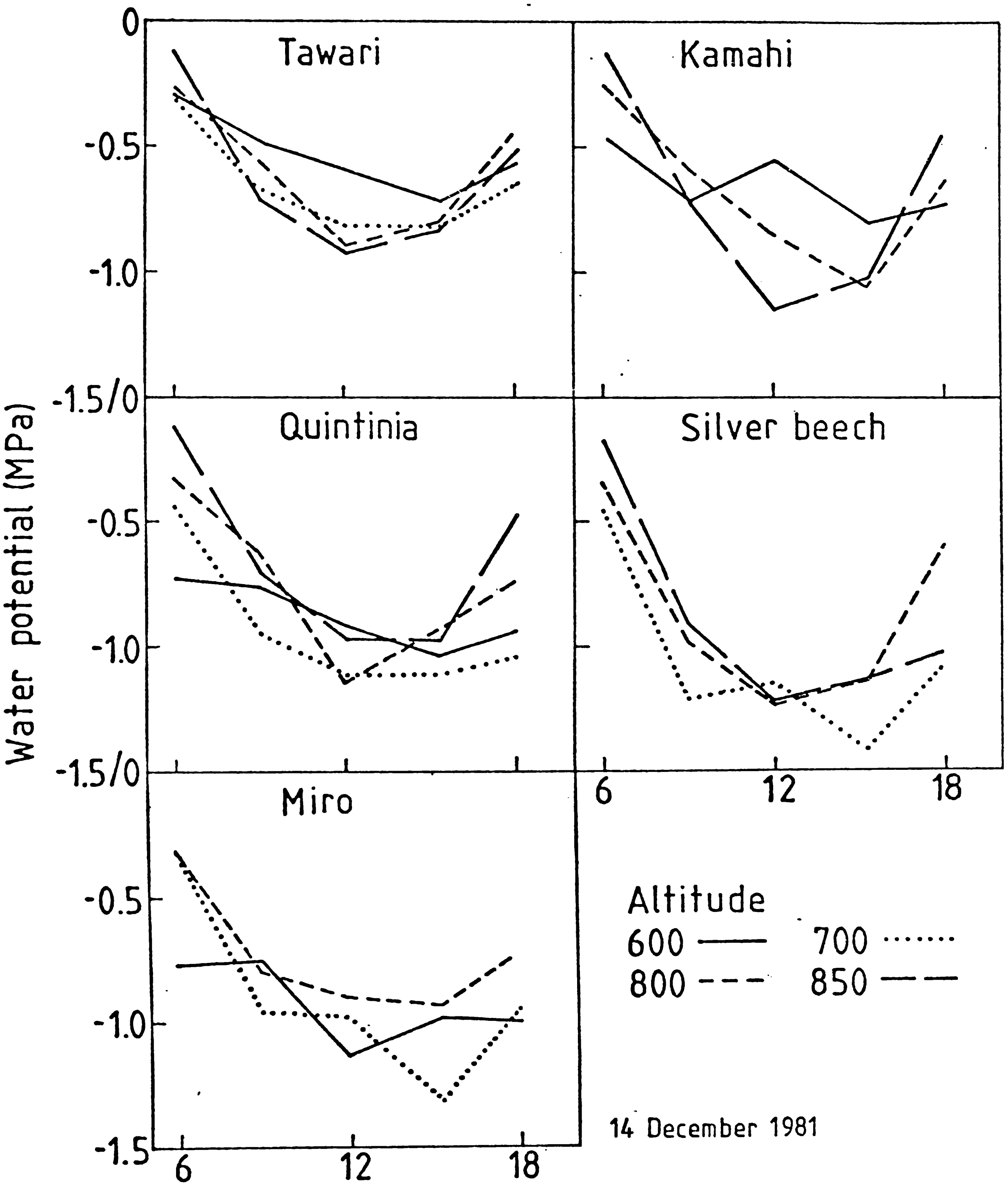


Fig. 11.4. Early in the season diurnal patterns of water potential in each species.

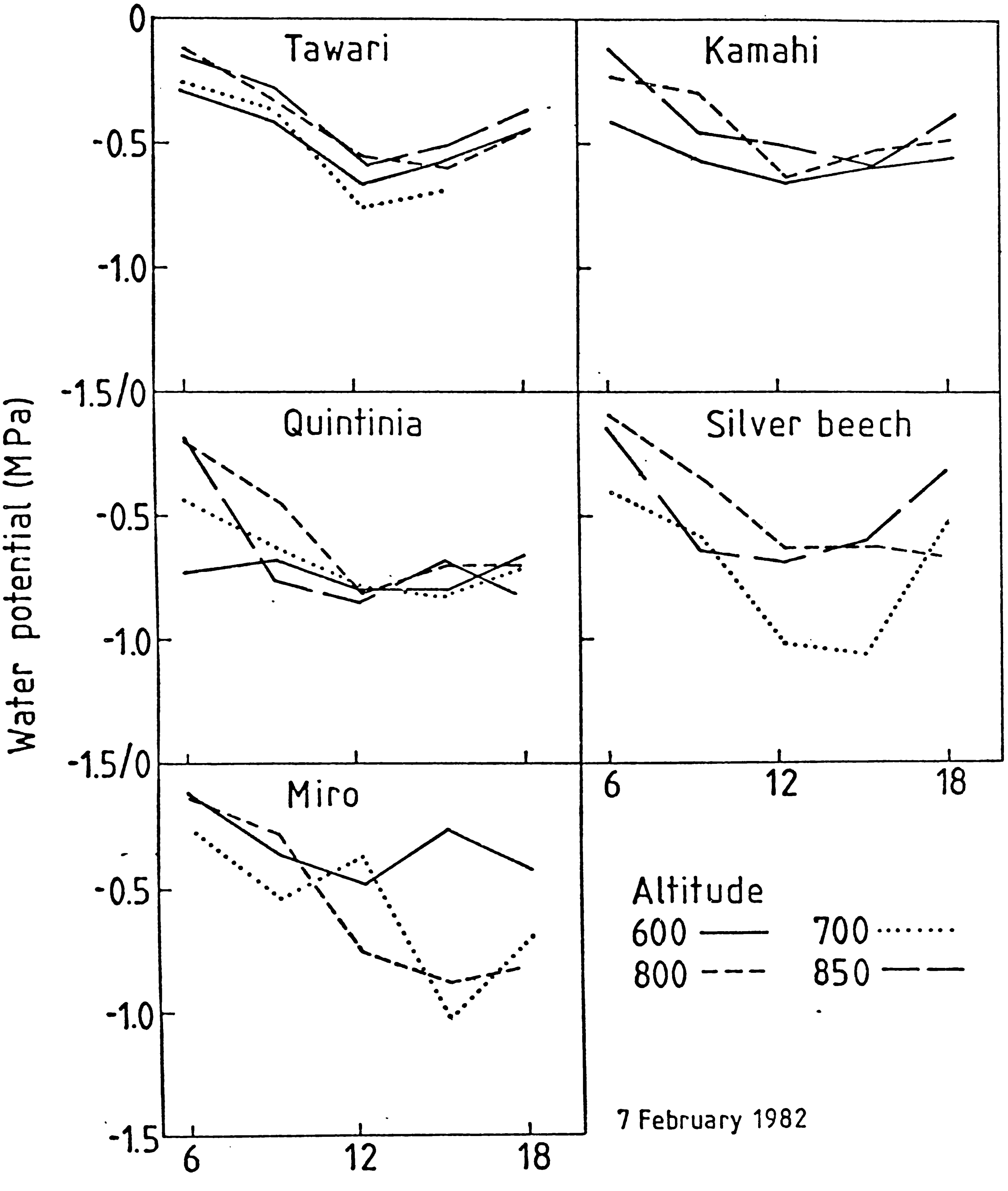


Fig. 11.5. Late season diurnal patterns of water potential in each species.

Tawari plants show only limited morphological evidence for stress. Silver beech shows differences between trees and quintinia within and between trees on the same site. Measurements of $\psi$ at dawn and midday in the healthy and unhealthy plants of quintinia and silver beech show significant differences between plants, that are most marked at dawn (Table 11.3) but none within plants. Differences within plants may be explained by variation in leaf exposure but differences between plants may indicate in water limitation at the roots.

### Comparison between areas

Limited sampling suggested that early in the season diurnal patterns of $\psi$ observed on Te Aroha were similar to Te Hunga but, in contrast, they changed little as the season progressed. Peak levels of stress were higher on Te Aroha (Fig. 11.6) than Te Hunga and did not correspond to differences in soil moisture content (Fig. 10.4). There was little variation in $\psi$ between species (Fig. 11.6) and quintinia did not show extreme patterns of stress as found on Te Hunga. Poor sites showed higher levels of stress than adjacent good sites but were similar to the 600 m site (Table 11.4). The ANOVA (Table 11.5) showed a significant difference in $\psi$ between species and there were differences in behaviour between species and sites. Kamahi and quintinia showed high levels of stress on all sites and tawari showed declining stress on the upper sites.

## DISCUSSION

The general stress levels shown by these species are very low compared with other studies (Ritchie and Hinckley 1975) and are similar to data from swamp or riverside communities (Scholander et al. 1965). Levels of soil moisture stress, indicated by dawn shoot $\psi$, were not high at any point in the season. These agree with the soil moisture

Table 11.3

Comparison od water potential at Te Hunga (-MPa) at dawn and mid-morning in healthy and unhealthy shoots on the same and separate plants of quintinia and separate plants of silver beech and toro.

| | Water potential(-MPa) healthy | unhealthy | difference in (-MPA) | significance t- value |
|---|---|---|---|---|
| Quintinia | | | | |
| Same plants | 0.65 | 0.76 | 0.12 | 1.9 |
| separate plants | 0.76 | 0.91 | 0.15 | 6.1* |
| separate plants at dawn | 0.13 | 0.22 | 0.09 | 23.0*** |
| Silver beech | | | | |
| separate plants | 0.89 | 0.94 | 0.5 | 5.7** |
| separate plants at dawn | 0.17 | 0.28 | 0.11 | 27.0*** |
| Toro | | | | |
| separate plants | 0.86 | 1.08 | 0.22 | 17.9*** |
| separate plants at dawn | 0.14 | 0.30 | 0.15 | 28.8*** |

Note 1. There were no distinguishable difference in foliage size within silver beech but in the other species foliage size and plant vigour were used as indicators of stress.

2. based on 6 observations per table entry
3. significance levels * 90 %
** 95 %
*** 99 %

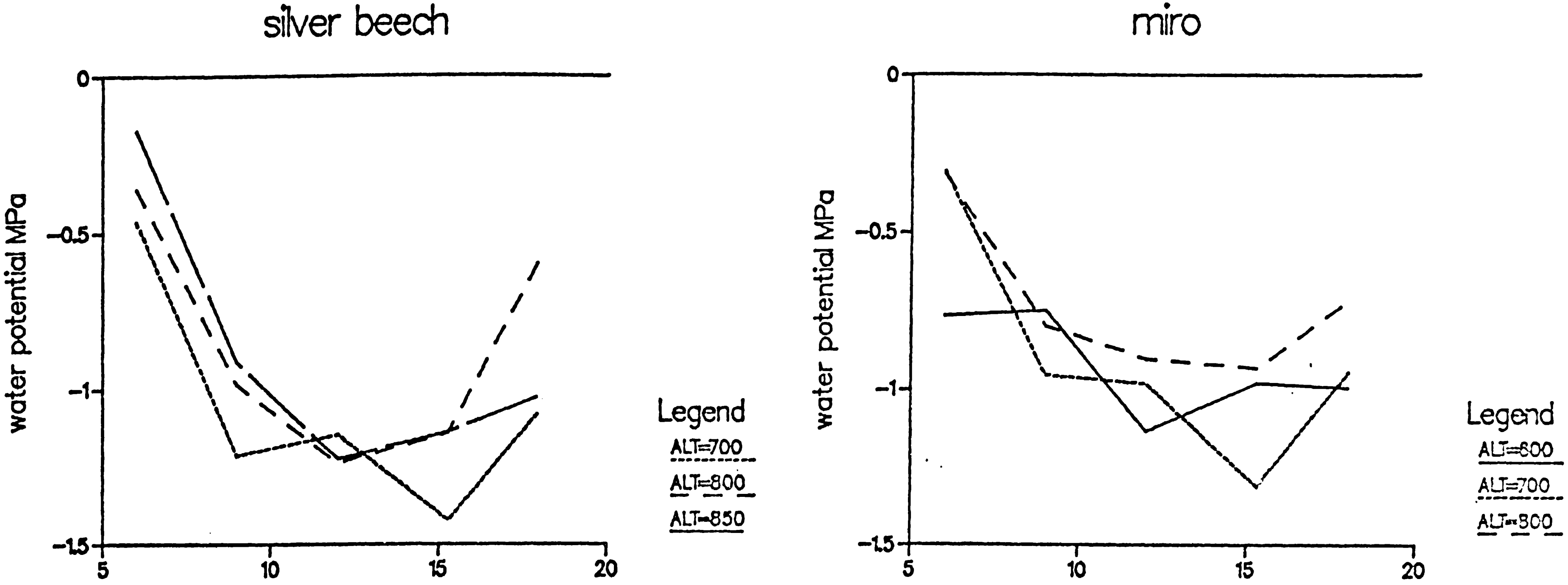


Fig. 11.6. Midday water potential on good and poor sites over an altitudinal range at Mt. Te Aroha.

Table 11.4

Comparison of water potential on adjacent poor and good sites and differing altitudes Mt. Te Aroha. Mean values for all species.

| Site | Mean value ( -MPa) | Grouping |
|---|---|---|
| 850 m poor | 1.27 | a |
| 800 m poor | 1.18 | a |
| 600 m | 1.17 | a |
| 800 m good | 0.99 | b |
| 850 m good | 0.97 | b |

Grouping based on SNK significance test at the 1% level.
Same letter denotes similar group. Based on 9 observations per site.
poor and good sites distinguished by the leaf size and general plant vigour. Measurements made at midday.

Table 11.5

Analysis of variance comparing water potential in tawari, kamahi, silver beech and quintinia at 600 m, 800 m, 850 m, 800 m poor and 850 m poor sites in two diurnal series as summarised in Fig. 11.6.

| Factor | degrees of freedom | F-ratio | Significance |
|---|---|---|---|
| Time | 3 | 280.8 | 0.000 |
| Species | 3 | 57.7 | 0.000 |
| Altitude | 4 | 52.0 | 0.000 |
| Species by altitude | 12 | 3.5 | 0.001 |
| Time by altitude | 12 | 7.4 | 0.000 |
| residual mean square | 79 | 0.617 | |

determinations which indicated values well above -1.5 MPa, the nominal wilting point (Fig. 10.4). Lower $\psi$ was recorded in miro and silver beech than in the other species and could reflect differences in the total heights of the plants or intrinsic differences determined by osmotic potential and other tissue characteristics. Miro and silver beech were usually about about 6 m tall and kamahi, tawari and quintinia 3 m tall, however tawari at 600 m were over 7 m tall and did not show decreased $\psi$ suggesting that the differences in maximum $\psi$ was determined by tissue characteristics. This is supported by pressure-volume data (Jane and Green 1983c) showing a similar rank order for the species of osmotic potential, turgor loss point and diurnal maximum deficits. Early season extreme values in silver beech appear to be related to soil factors. High spring temperatures occurring close to bud break when soil temperatures are still low may be one of the factors limiting the species here at the north of its natural range.

Fog clearly effects the dawn $\psi$ at upland sites higher than 700 m at Te Hunga and 800 m at Te Aroha. The effects of the fog appear to be quite transitory when examined in relation to diurnal patterns of stress. It appears possible that there is some foliar adsorption of moisture in tawari and miro although the same effects may be achieved by more effective root systems in these species. Water may also have been adsorbed through lenticels that are more abundant in silver beech and tawari however this may be difficult to substantiate quantitatively and the whole effect may simply be because of reductions in evapotranspiration. However there appear to be adverse effects from fog on Te Hunga that could be related to poor root development induced by lower soil temperatures or waterlogging. Soil moisture contents on Te Hunga were usually higher than those on Te Aroha and this could arise from higher average rainfall, greater persistence of fog with consequent lower evapotranspiration and increased precipitation, or lower soil temperatures or some combination of these factors.

The diurnal pattern and minimum midday $\psi$ found at the higher altitude sites are comparable with those normally found in plants of moist habitats (Larcher 1975). This strongly contrasts with the pattern found for leaf conductances at the same sites (Jane and Green 1983d). Stomatal closure occurred rapidly from early afternoon indicating the presence of considerable water stress under fine conditions with a relatively low VPD of about 10 mb (saturation deficit $= 8g.m^{-3}$). Sensitive reaction of leaf conductance at high $\psi$ is a characteristic of soil waterlogging where water uptake is limited by poorly developed root systems or high root resistance to water uptake from anaerobic conditions (Bradford and Yang 1981). Aspinall (1981) and others (Hiron and Wright 1973, Bates and Hall 1981, Davis et al. 1981) have suggested that the stomatal closure follows movement of a hormone from the roots and as a result leaf water deficit fails to reach extreme values. However experimental verification is lacking although it would be a suitable explanation for the situation reported here.

The study has failed in its basic objectives. Fog has been shown to only a minor transitory effect on diurnal water stress patterns and the minimum midday values show no evidence of the severe stress suggested by stomatal reactivity. As a result it can only be concluded that measurement of $\psi$ may be of limited value in detecting plant water stress produced by waterlogging.

## CHAPTER 12

# ECOLOGICAL SIGNIFICANCE OF VARIATIONS IN LEAF STRUCTURE AND WATER LOSS RATES IN SPECIES FROM THE CLOUD FOREST OF THE KAIMAI RANGES

## INTRODUCTION

Leigh (1975) reviews the results of ecological problems associated with tropical cloud forests but there are few equivalent physiological studies apart from those by Weaver et al. (1973), Huber (1978) and Roth and de Bifano (1980). The paucity of physiological work may arise because, although fog or cloud forests are widespread, their particular features and complexities have not been fully recognised in areas outside tropical regions. Two types of cloud forest are recognizable: the upland elfin cloud forests of Kenya (Walter 1971) and Tanganyika (Lundgren 1978), and many other tropical mountains (Leigh 1975) and the coastal fog forests of Peru and Namibia, Temperate equivalents of coastal fog forests can be found in California (Byers 1953, Martin and Juniper 1970, Spur 1975) and cool temperate equivalents in the Cape Province South Africa (Werger 1978). In these areas a forest cover can be maintained by precipitation from fog in an essentially dry climate. Cloud forests of super-humid regions are poorly recognised but examples appear to occur in Vermont, United States (Siccama 1974) and the Bay of Fundy, Canada (Damman 1977). Tropical cloud forests are characterised by stunted elfin trees and an abundance of epiphytic and terrestrial bryophytes (Leigh 1975). Angiosperm species show many xeromorphic characters including reduced leaf size, and smaller and more numerous stomata (Doley 1981). Many of these features are present in the the plants making up the upland vegetation of the Kaimai Ranges.

The upland vegetation in the Kaimai Ranges is characterised by numerous areas of dead trees and apparently young seral vegetation. Jane and Green (1983b) suggested that mortality was initiated in drought years but the timing and severity of mortality was difficult to reconcile with high precipitation, and high incidence and prolonged duration of fog. This led to suggestions that fog, through its impact on incident radiation, temperature and site hydrology, affects the ability of the plants to withstand drought stress (Jane and Green 1983d). Variations in the ability of the species to survive mortality episodes implied that some of the plants may be adapted to life in these forests and investigations sought to find physiological (Green and Jane 1983c, Jane and Green 1983d) or morphological characteristics peculiar to plants from these forests.

## METHODS AND SITE DESCRIPTION

The Kaimai Ranges, North Island, New Zealand, lie in a temperate region (latitudes 37-38° S). Temperatures are 5-10° C and rainfall is in excess of 2500 mm and well distributed throughout the year, although effective precipitation is increased by frequent fog. The vegetation is intermediate in characteristics between tropical cloud forest (Walter 1971) and higher latitude fog forests (Damman 1977) and contains both tropical and cool temperate elements (Green and Jane 1983d). The study areas at Te Hunga and Te Aroha used are described in (Jane and Green 1983d).

Study concentrated on the main tree species present, tawari (*Ixerba brexioides,* A Cunn.), kamahi (*Weinmannia racemosa,* Lin. f.), quintinia (*Quintinia acutifolia,* Kirk), silver beech (*Nothofagus menziesii*, (Hook.f) Oerst.) but toro (*Myrsine salicina,* Hew. ex Hook. f.), five finger (*Pseudopanax colensoi,* (Hook. f.) Philipson), toatoa (*Phyllocladus glaucus,* Carr.), miro (*Podocarpus ferrugineus,* G.Benn. ex Don), red beech (*Nothofagus fusca*, (Hook. f.) Oerst) and hard beech (*N. truncata*, (Col.) Ckn.) were also examined.

Surface waxes were removed by agitating whole leaves in chloroform for three minutes. Sample strips of fresh and de-waxed leaves were prepared by freeze drying, coated with gold/ palladium and examined by scanning electron microscope (Philips PSEM500). Stomatal counts and measurements were made on cellulose acetate cuticular peels using a a projection microscope.

Cuticular conductances and stomatal closure rates were determined from drying experiments where weight loss of cut shoots was measured under controlled conditions. Material was collected during rain, then transported in sealed plastic bags and used immediately or kept for 12 h in humid conditions at 5 ° C to ensure full turgor. Before the experiment shoots were exposed to sunlight for about 20 minutes, until a Delta T Mark II porometer confirmed that the stomata were largely open. The shoots were then placed on a well ventilated rack in a controlled temperature room at 20 ° C and 78 % relative humidity and weighed to the nearest 0.1 mg at 5 minute intervals for the first 30 minutes, 10 minute intervals for the following 90 minutes and then 30 minute intervals until termination of the experiment. Water potential was determined with a pressure chamber (Jane and Green 1983c) after 30 minutes, one hour and at the end of the experiment. Stomatal conductances were measured with a Delta T Mark II automatic porometer on a sample of the shoots at the beginning of the experiment, after 30 minutes and at the end of the experiment. Drying rate in the presence of free surface water was determined by first weighing the shoot, momentarily immersing the leaves in water, shaking them briskly and then reweighing immediately and at five minute intervals for up to 2 hours.

Calculations

Cuticular transpiration rates and rates of stomatal closure were derived from functions described by Hygen (1951):

$RWC= a.t +b(1-\exp(-c.t)$ . . . . . 1

a is cuticular transpiration ($\mu g.cm^{-1}.sec$).

b is equated with stomatal transpiration ($\mu g.cm^{-1}.sec^{-1}$).

c is defined by Hygen (1951) as the intrinsic rate of stomatal closure.

t = time from the start of the drying period in seconds.

RWC % is relative water content $=\frac{(\text{Fresh weight-dry weight})*100}{(\text{Weight at full turgor-dry weight})}$.

(Relative water deficit) RWD % = 100-RWC %

All functions were fitted by the Gauss-Newton least-squares method.

Intial transpiration rate may be calculated from:

$k= a + bc$ . . . . 2

and conductance $=k/VPD$.

when k is leaf specific area expressed in units of $g.g^{-1}$ RWC

VPD is vapour pressure deficit ($g.m^{-3}$)

and leaf specific area as $g.cm^{-2}$ (Idle 1977).

Time to stomatal closure was determined from:

$d(RWC)/dt =a+b(1+c.\exp(-c.t)$

and RWC at stomatal closure determine by back substitution in (1) above.

Rates of drying of free surface water from the leaves were first plotted and a common function determined. For all species it was found to be solely determined by the quantity of water retained on the surface and was analagous to evaporation from an open surface (Monteith 1975) so that:

$$\text{RWC \%} = (\text{initial wet RWC \%}) .\ \exp(-0.1\ t)$$

## RESULTS

### Leaf arrangement and Morphology

Leaves of tawari are large and linear and tend to be in whorls of 5-20. (Table 12.1, Fig 4.4). Shade leaves are set at 90° so that they are parallel to the ground, but on exposed shoots they are generally set at a low angle and held nearly erect. The main canopy of leaves is arranged as a dense umbrella. Quintinia leaves are large and elliptic with an undulate margin set at a low angle. They are alternate and normally well spaced but may be clustered on exposed shoots. Kamahi leaves are often trifoliate with small ovate leaflets; leaves are well spaced in opposite pairs on shade stems but on exposed shoots may be clustered at the tips of the branches. Toro leaves are large, entire, linear and, although alternate, are clustered towards the branch tips and set at about 60°, especially in sun shoots. Silver beech has small ovate, crenate leaves closely arranged in alternate, planar series of 30-60 on short shoots that represent a single season's growth. Branchlets are grouped to form a horizontally layered canopy. The small linear leaves of miro are similarly arranged although the layering of the canopy is less pronounced and mature trees tend to be emergent. Five finger has large closely spaced palmate leaflets which are

Table 12.1

Leaf size and shape parameters.

| Species | Length cm | Shape type | Margin | vernation | leaf spacing | Set adaxial angle ° |
|---|---|---|---|---|---|---|
| Tawari | 6- 16 | narrow linear | serrate | whorled | | 90-45 |
| Kamahi | 2- 5 | elliptic | serrate | opposite | sparse | 90-45 |
| Quintinia | 4- 10 | elliptic | entire | alternate | sparse | 60-45 |
| Toro | 7- 18 | narrow linear | entire | alternate | variable | 90 |
| Silver beech | 0.8-1.3 | ovate | crenate | alternate planar | close | 90 |
| Miro | 1.5-2.0 | linear | entire | alternate planar | close | 90 |
| Five finger | 10-15 | compound ovate | serrate | alternate planar | close | 45 |
| Red beech | 2- 4 | deltoid | serrate | alternate | sparse | 45 |
| Hard beech | 2- 4 | ovate | serrate | alternate | sparse | 45 |
| Toatoa (cladodes) | 3- 4 | compound ovate | serrate | whorled | sparse | 90 |

clustered near the branch tips to form an umbrella shaped crown. Red beech and hard beech trees are closely similar in appearance and can readily be mistaken for one another. Both species have small, ovate, serrate leaves well spaced along the branches showing little difference in size between leaves on sun and shade shoots possibly because the tall canopy intercepts lower amounts of light than in other species. Leaf colour ranges from yellow green in quintinia to dark green in tawari, five finger and silver beech.

Cuticles in toro, silver beech and tawari were deeply contoured (Fig. 12.1 to 12.3) and wax spicules, similar to those seen in Citrus mitis (Buijten et al. 1977). The spicules were removed by treatment with chloroform, but no other change was visible to the leaf surfaces. In kamahi the upper surface were composed of frills of wax and the cuticle had a porous appearance (Fig. 12.4, 12.5). In quintinia plate-like waxes covered extensive areas of both leaf surfaces (Fig. 12.6). The wax plates did not appear to be closely appressed to the leaf surface and in places loosely overlay the stomata, even in young specimens (Fig. 12.6). Large trichomes were sparsely present on both surfaces of kamahi leaves (Fig. 12.5) and hairs formed a dense row along the midrib in silver beech. Algae were a common feature of the older leaf surfaces and were abundant within one year of leaf development, an indication of the very wet habitat.

Stomata are absent from the upper leaf surfaces of all species but numbers on the lower surface are high to very high (Table 12.2). In tawari, kamahi, and the beech species densities are among the highest recorded but are comparable with densities commonly found in plants from other cloud forests (Larcher 1975, Roth and de Bifano 1980, Doley 1981). Numbers are also high in red beech and hard beech and in miro and toatoa stomata are over twice as numerous as usual in gymnosperms. Even in the

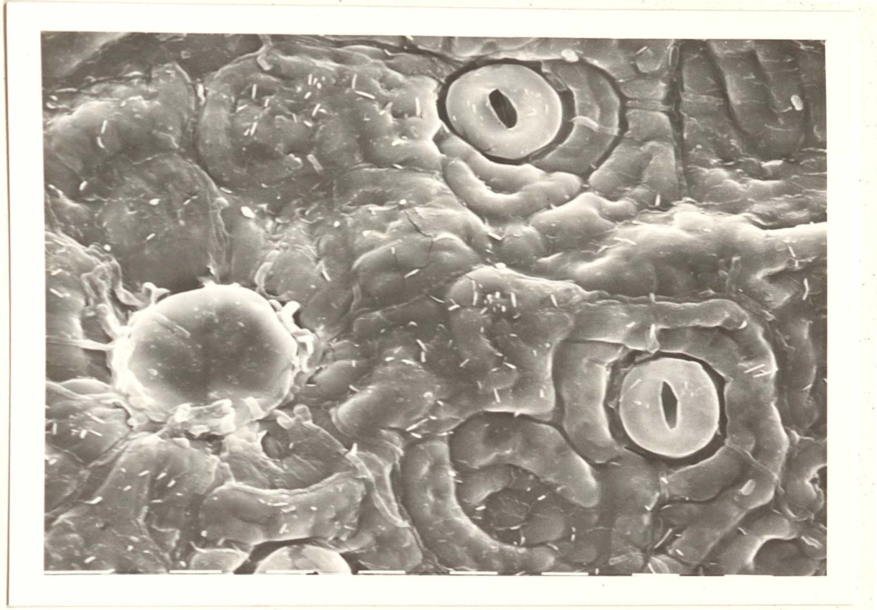


Fig. 12.1. Lower surface of toro leaf. Large dome to the left handside is an oil gland. Algae and wax spicules visible in the leaf surface. Bar along the bottom of the SCM photo has segments of 10 u length.

Fig. 12.2. Lower surface of silver beech leaf at the same scale as that of toro.

Fig. 12.3. Lower surface of a tawari leaf. Note very small perforation in most stomata and an apparently inflated, open stoma to the left. Scale bar is at the top of the photograph.

Fig. 12.4. Upper surface of a kamahi leaf. Frilled loosely appressed wax plates and abundant algae.

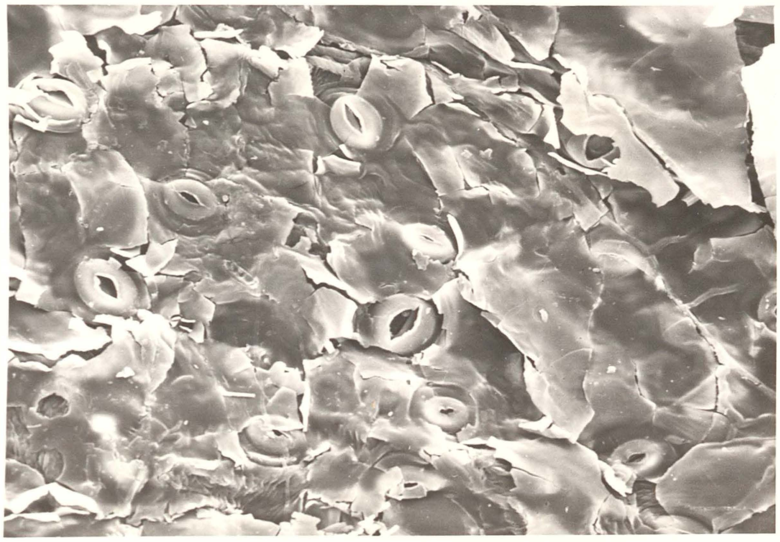


Fig. 12.6. Lower surface of a young incompletely developed quintinia leaf. In places the leaf surface can be seen below the wax plates. In older leaves several tiers of wax are often present. Scale same as earlier that of photographs.

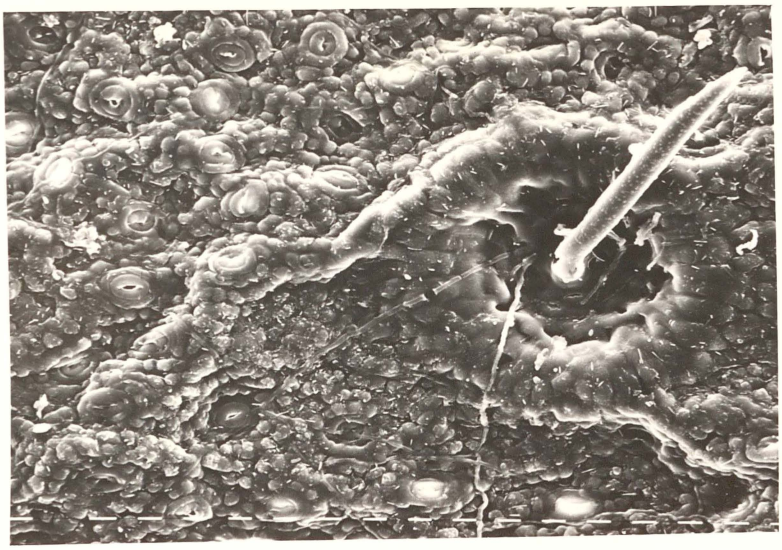


Fig. 12.5. Lower surface of a kamahi leaf near a trichome. The loosely appresed waxes are readily removed by chloroform. Scale half that of previous photographs (scale bar at the bottom).

Table 12.2

Stomatal size and density by species.

Mean of twelve counts or measurements made with a projecting microscope and optical length measurement device.

| Species | Density number, mm$^{-2}$ | Pore Length $\mu$ |
|---|---|---|
| Tawari | 1255 | 2.0 |
| Kamahi | 1088 | 20.0 |
| Quintinia | 656 | 12.0 |
| Toro | 744 | 20.0 |
| Silver beech | 1814 | 17.0 |
| Miro | 264 | 37.0 |
| Five finger | 872 | 34.7 |
| Red beech | 1588 | 15.2 |
| Hard beech | 1704 | 14.3 |
| Toatoa | 487 | 31.0 |
| Broadleaf | 820 | 34.3 |
| *Conifers | 40-120 | 15-20 |
| *Broadleaved trees | 100-500 | 7-15 |
| +Cloud forest trees | 500-1800 | 18-23 |

* from Larcher (1975); +Roth and de Bifano (1980)

remaining broadleaved species numbers are higher than normally recorded in woody plants (Larcher 1975). Stomatal sizes (Table 12.2) are within the normal range indicated by Larcher (1975) and Doley (1981). Actual stomatal structure in all species is obscured by the cuticle and there is a prominent cuticular antechamber which has a very narrow slit when closed. The cuticular perforation in tawari is very small (less than 10 μ) but in open stomata the cuticle appears to be greatly stretched and the opening is nearly circular (Fig. 12.3)

Leaf sections in most species show a thick cuticle and two or three tiers of large palisade cells and abundant mesophyll but in the thin leaved red beech and hard beech there are few intracellular spaces, small palisade cells and a dense parenchyma sheath stretching across the leaf at the veins.

### Leaf conductances and stomatal closure

Cuticular conductances for all species (Table 12.3) are relatively low but are typical of evergreen trees (Larcher 1975). The highest values are found in quintinia and red beech and lowest in tawari, five finger and the conifers. Conductances in tawari and five finger are lower than the minimum in field measurements and suggest that incomplete closure normally occurs in the field (Jane and Green 1983d). Incomplete closure may result from senescence of the leaves or faulty stomatal functioning (Tranquillini 1979) but can also occur through night opening (Tobiessen 1982, Benecke et al. 1981).

Older leaves and fresh new shoots of tawari from the same summit site have similar cuticular conductances but the lowest values are found in plants from sheltered, lower altitude localities. Wind damage to the developing cuticles is the usual cause of such differences (Levitt 1972, Sowell et al 1982, Grace 1981) however it may also reflect high fog

Table 12.3

Cuticular conductances and rates of stomatal closure

| SPECIES | Cuticular conductances cm.sec$^{-1}$ | | intrinsic rates of stomatal closure | RWD % at | |
|---|---|---|---|---|---|
| | October | November | | stomatal closure | wilting point |
| Tawari | 0.0034 | 0.0027 | 0.014 | 3.7 | 6.2 |
| Kamahi | 0.0051 | 0.0048 | 0.058 | 1.0 | 8.9 |
| Quintinia | 0.0052 | 0.0084 | 0.150 | 1.0 | 7.0 |
| Toro | 0.0044 | 0.0054 | 0.150 | 0.5 | 6.5 |
| Silver Beech | 0.0041 | 0.0032 | 0.044 | 0.6 | not evident |
| Miro | 0.0025 | 0.0027 | 0.264 | 10.9 | not evident |
| Five finger | no data | 0.0027 | 0.020 | 0.6 | 2.2 |
| Red Beech | 0.0049 | 0.0054 | 0.044 | 3.7 | 11.3 |
| Hard beech | 0.0032 | 0.0039 | 0.031 | 2.1 | 17.4 |

Cuticular conductances measured at 20°C, 78% RH. Three replicates of each species.

frequency and lower evapotranspiration demands at higher altitudes (Martin and Juniper 1970, Jane and Green 1983c). Cuticular hardening in quintinia develops slowly producing a wide range of values in any one sampling (Table 12.4, Table 12.5). Stomatal conductances and closure rates in unhealthy quintinia plants are also lower than normal (Table 12.6) and it is possible that water stress, noted in the porometry studies may be impairing leaf development. Tranquillini (1979) reports similar limitations in alpine plants.

High leaf water deficits in quintinia, red beech and hard beech were reached in less than half the time for other species (Fig. 12.7). High cuticular transpiration rates following stomatal closure compounded by the small reservoir of water within the leaf (leaf specific weight) may be responsible (Table 12.4). The high drying rates suggests that these species require a good coupling between leaf and water source to prevent water deficits and that stem sapwood storage or high soil-root-shoot conductances are essential to prevent foliar water deficit. Sapwood storage in shrubs and trees can normally be expected cope with transpiration demands for long periods (Waring and Running 1978, Whitehead 1978) but field measurements showed that severe water stress was present in quintinia for much of the season (Jane and Green 1983d) suggesting impairment of the water conduction pathway.

Initial transpiration rates, calculated from equation 2, were about half those measured with the porometer. This may be explained by the effect of averaging young and old leaf conductances or lower exposure to light over the whole the shoot sample. At the end of the experiment calculated cuticular conductances were close to measurements made with the porometer. Rates of stomatal closure were highest in quintinia, miro and toro (Table 12.3). Values one tenth as high were found in five finger and tawari. These differences are of a similar rank order to

Table 12.4

Cuticular transpiration rates and specific weight of leaves

| SPECIES | Cuticular transpiration $g.g^{-1}$ RWC | leaf specific weight $g.cm^{-2}$ |
|---|---|---|
| Tawari | 0.024 | 0.049 |
| Kamahi | 0.048 | 0.079 |
| Quintinia | 0.134 | 0.048 |
| Toro | 0.086 | 0.085 |
| Silver Beech | 0.069 | 0.035 |
| Miro | 0.029 | 0.056 |
| Five finger | 0.0096 | 0.075 |
| Red Beech | 0.130 | 0.023 |
| Hard beech | 0.118 | 0.024 |

Cuticular transpiration determined at 20° C, 78% RH.

Table 12.5

Rates of stomatal closure and cuticular conductance in healthy and unhealthy quintinia

| Relative vigour | cuticular conductance $g. cm^{-2}. sec^{-1}$ | rates of stomatal closure | RWD at stomatal closure (%) |
|---|---|---|---|
| healthy | .0084 | 0.118 | 9.82 |
| unhealthy | .0103 | 0.079 | 12.34 |
| | .0218 | 0.086 | 19.21 |
| | .0797 | 0.062 | 13.63 |

Three replicates for each group. Regressions for the healthy plants were not significantly different at r= 0.997.

Table 12.6

Comparison of cuticular conductances and rates of stomatal closure between samples of tawari from a range of sites

| Site | Cuticular conductance cm.sec$^{-1}$ | rates of stomatal closure |
|---|---|---|
| 800m young shoots | | |
| exposed | 0.0055 | 0.189 |
| sheltered | 0.0049 | 0.033 |
| 800m mature shoots | | |
| exposed | 0.0062 | 0.031 |
| sheltered | 0.0059 | 0.022 |
| 700m | 0.0037 | 0.014 |
| 500m | 0.0021 | 0.017 |

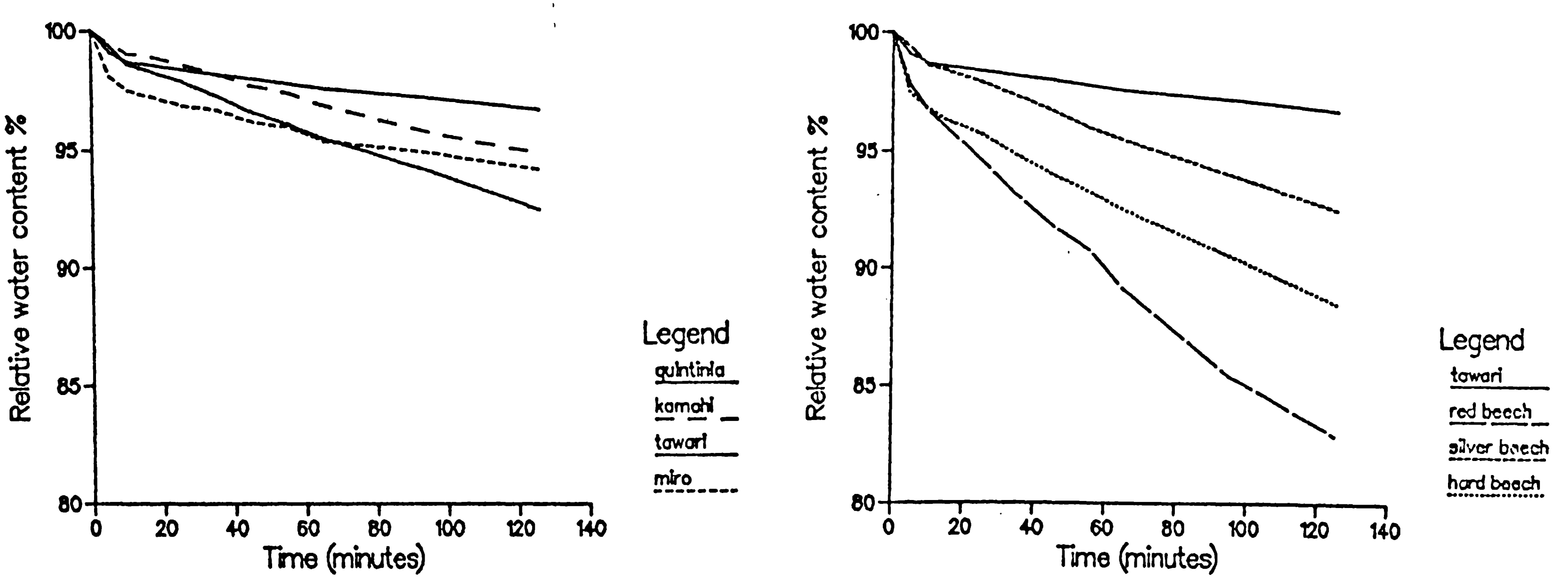


Fig. 12.7. Change in RWD with time in detached shoots in a controlled environment at 20° C and 78 % RH. Tawari and seral species to the left, tawari and the beech species to the right.

stomatal responses found in the field (Jane and Green 1983d).

The three pressure determinations obtained during drying for tawari and quintinia enabled osmotic potentials and turgor loss points to be estimated. Values for osmotic potentials of healthy plants (- 1.4 MPa) were similar to those obtained from pressure volume determinations (-1.5 MPa) but in the unhealthy quintinia shoots both osmotic potentials and turgor loss points were higher (-1.0 MPa, 7.0 % RWD, respectively). Visual wilting occurred at low relative water deficits in all species with the lowest value in five finger (Table 12.3). Values for tawari, quintinia and kamahi are close to those obtained by pressure volume techniques (Jane and Green 1983c).

### Leaf surface water

Red beech, silver beech, quintinia and miro retained the largest proportions of surface water, expressed as percentage RWC or as $mg.cm^{-2}$, and this was more than twice the amount retained by tawari, toro and kamahi (Table 12.7). Leaves of plants in the first group took more than twice as long (over 30 minutes) to dry down to 100 % RWC. Hall and Burke (1974) investigated surface characteristics of a large number of New Zealand species and found a close relationship between wettability and the presence of epicuticular waxes. Leece (1976) also found that thick waxes greatly assist shedding of water from the leaves. Nevertheless, in both the above plant groups there are leaves with highly wettable and poorly wettable surfaces according to Leece (1976). For instance quintinia has a very thick wax coating while silver beech has a very smooth leaf surface but both hold large amounts of water. Differences in the nature of the waxes may be present between species (Martin and Juniper 1977), however the presence of hairs on the stems and leaves of silver beech, that may retain water, could be responsible for the anomaly.

Table 12.7

Amounts of water held on leaf surfaces expessed as a proportion of RWC at full turgor and specific weight.

| Species | RWC | $mg.cm^{-2}$ |
|---|---|---|
| Tawari | 4.6 | 2.24 |
| Toro | 6.5 | 2.88 |
| Broadleaf | 9.4 | no data |
| Kamahi | 9.8 | 2.97 |
| Toatoa | 11.4 | no data |
| Hard beech | 14.3 | 1.86 |
| Quintinia | 17.0 | 3.92 |
| Five finger | 17.8 | 5.10 |
| Miro | 21.6 | 7.00 |
| Red beech | 28.8 | 3.33 |
| Silver beech | 35.0 | 5.22 |

## DISCUSSION

The nine species studied here show leaf morphological charateristics that reflect different responses to the cloud forest habitat. Branch patterns of trees of non-cloud forest species, such as red beech and hard beech, produce an open canopy of thin leaves that increases canopy roughness and favour high transpiration rates through close coupling to the atmosphere (Jarvis 1980, Doley 1981). The cloud forest species, tawari and silver beech, have thick leaves with low cuticular conductances, and form a tight canopy which is either tiered, (silver beech, Fig. 12.8) or dome shaped (tawari) and which acts to reduce atmospheric coupling and evapotranspiration (Doley 1981, Jarvis 1981).

Low cuticular conductance improves the degree of stomatal control over transpiration. The numerous stomata found in the cloud forest trees could allow greater regulation of transpiration or simply provide protective redundancy. Redundancy in the fog adapted species may be more important for two reasons. Firstly rapid algal growth can obliterate much of the leaf surface including many of the stomata and secondly, when leaves are partially wet, large numbers may ensure that some remain free from a water film that could limit gas exchange (Mac Donald 1975, Green and Snelgar 1981). The latter viewpoint is reinforced by the stomatal structure since the prominent sharply curved stomatal antechamber and small, but extensible, aperture of the type observed in tawari could both minimise water blockage and enhance watershedding. The presence of dark coloured leaves particularly in sun forms will raise leaf surface temperatures and aid drying of leaves as the fog clears. Leaf size may also increase boundary layer resistances and leaf temperatures under sunny conditions (Parkhurst and Loucks 1972, Givnish 1979, Geller and Smith 1982, Smith and Geller 1980) further

Fig. 12.8. Canopy structure in silver beech. Light green tall trees with prominently layered crowns are silver beech. More obscure dense dark green trees in the background are tawari. The view is towards a sharp boundary with unaffected vegetation across seral stands. The tall straight spar is kaikawaka probably killed over 100 years ago.

aiding leaf drying.

The seral species in the cloud forest, quintinia and kamahi, have moderate to low cuticular conductances and high maximum stomatal conductances (Green and Jane 1983d) with numerous stomata and abundant epicuticular waxes which will prevent water films covering the stomatal pore and may also aid in water shedding. Leaf size, colour and canopy structure are highly variable suggesting a degree of plasticity to adapt to site extremes as often reported in seral species (Chabot and Bunce 1979, Bazzaz and Carlson 1982).

Variability in cuticular conductances and stomatal closure rates between quintinia plants on stressed sites suggests that development is impaired compared with plants from adjacent good sites and tawari on the same two sites. Sowell et al. (1982) observed slowed leaf development because of a restricted growing season and Pereira and Kozlowski (1976b) found a similar effect caused by waterlogging. Rates of stomatal closure in the seral species are high and agree with observed stomatal behaviour in the field (Green and Jane 1983d). These factors suggest a high metabolic rate and a maximisation of opportunity for CO2 fixation (Bazzaz 1979, Bunce and Chabot 1979, Hall and Schultze 1980, Losch and Tenhunen 1981). In contrast low cuticular conductances in cloud forest species (tawari, miro and five finger) would provide better stomatal control of transpiration under high evaporative demands at high VPD. Furthermore slow rates of stomatal closure become unimportant because maximum stomatal conductances are low and losses from other parts of the leaf are insignificant. The low residual stomatal opening observed in the field may then represent optimisation of the rate of gas exchange with respect to the water loss.

In cloud forests soil moisture contents are high and periodic soil flooding may reduce root effectiveness by killing fine feeding roots or creating anaerobic edaphic conditions (Kozlowski 1982). Small vessel diameters in the wood also increase xylem resistance (Weaver et al. 1973) so that severe water stress may occur at only moderate temperatures or VPD. Water stress can be minimised by controlling canopy water loss, reducing soil flooding or ameliorating the physiological effects of flooding. Strong control of water loss has been found in porometry studies (Jane and Green 1983d) and this is augmented by low cuticular conductances and a canopy form that tends to reduce atmospheric coupling. Interactions between plants and soil water content are also present as well as differences in physiological responses to flooding. Silver beech and miro have morphological features that appear to ameliorate local soil water conditions.

Hairy branchlets and leaves and horizontal arrangement of branchlets in silver beech lead to retention of water in the canopy which O'Loughlin and Pearce (1978) have shown can greatly reduce precipitation particularly where falls are light such as during fog. In addition the tight canopy structure of these species would reduce the fog catching ability (Azvedo and Morgan 1974, Rutter 1981). The species also create an eggcup podsol of sandy soil beneath the tree which is more easily aerated. Low internal water potentials are often present on fine days but these might to be expected from the low osmotic potentials (Jane and Green 1983c). It is interesting to speculate that low potentials could arise from high transpiration rates leading to high rates of soil water depletion and improved soil aeration. By contrast tawari and five finger shed much of the fog condensate into the soil increasing soil flooding. Transpiration is resumed rapidly when the fog lifts but maximal transpiration rates are low (Green and Jane 1983c) and stem water potential in tawari remains high. This suggests that the species are able to tolerate the waterlogging and anaerobic conditions.

Cloud forest species normally show a number of xeromorphic features but high precipitation, high soil moisture contents and low temperatures imply that water would not be limiting. Grubb (1971) explained the characteristic features of cloud forests by effects on nutrient uptake such as enhanced soil leaching and impairment of nutrient cycling caused by poor soil aerobic conditions and other soil changes. Others have suggested that they are caused by wind influences including wind-induced water stress (Leigh 1975,. and thigmomorhogenetic responses (Lawton 1982). Leigh (1975) suggested that xeromorphy arise because the vegetation must be able to resist sunburn or occasional excess transpiration caused by alternation of sun and shade which imposes a greater variation of temperature on canopy foliage.

Increased precipitation and throughfall especially during short foggy periods will lead to frequent input of small amounts of water to superficial layers of the soil and shallow root systems and waterlogging. Consequently waterlogging is a prominent feature of upland cloud forests Waterlogging can lead to water stress during fine weather (Ch. 8) and so xeromorphic features become important adaptations. Waterlogging can be minimised by retention of water on the leaves and branches following fog clearance and tolerated through morphological adaptations in the roots. Water stress will lead to small vessel sizes in the wood (Fritts 1976) but low transpiration rates at other times will slow mineral transport restricting growth. Greatly reduced light levels in the cloud forests will also reduce growth. Compensation point does not appear to be affected (Huber 1978), possibly because the proportion of the time at high light intensities negates the advantages of adaptation (acclimation) (Mooney and Gulmon and 1979). But in order to to maximise photosynthesis following fog clearance rapid drying of leaf surfaces, to ensure early resumption of gas exchange, becomes important. Drying is assisted by thick dark leaves, large numbers of stomata and epistomatal structure. Increased radiation and water stress also reduces leaf size within trees and with altitude in many of the species studied here (Ch. 4).

Knowledge of the water relations of the cloud forest species provides a new perspective that allows a better understanding of the structure and function of the forests. The evidence suggests that in spite of the very wet environment, the xeromorphic features of the cloud forest plants result from water stress.

# CHAPTER 13

# FOG DROUGHT AND VEGETATION MORTALITY

## INTRODUCTION

Recurrent vegetation mortality is present in the Kaimai Ranges. Observations suggest at least two periods of mortality in the last 80 years and dendrochronological data suggests a further three large events in the last 300 years (Ch. 6). With few exceptions, all forest types present above 500 m and all species on a site are affected. Affected stands occur largely within 150 m of the ridge crest in spite of differences in summit height between study areas. Damage occurs on the flat summit areas and on slopes of over 35° (Ch. 3). Areas of apparently healthy, dense, old stands are often separated by sharp boundaries from unhealthy open old stands or seral stands. Older stands contain few sub-canopy or understorey shrubs consequently mortality readily leads to complete stand collapse. Isolated old trees in the partly affected stands show slow canopy breakdown and occassional windthrow which may be attributed to the increased exposure to wind.

## CAUSES OF THE MORTALITY

The interval since the last mortality episode complicates identification of causes of mortality particularly since they are obviously complex. Any theory to explain the mortality must account for:

1. Location and distribution of the mortality.

2. Recurrent nature of the problem.

3. Timing of the mortality.

4. Wide range of species and vegetation types affected.

Various aspects of the current study have suggested that fog,by producing soil waterlogging,leads to enhanced drought sensitivity in the upland zone. Reduced growth from lower light levels, slower nutrient cycling and stress in the fog zone then accentuate the primary water stress.

A chain of events may lead to mortality. Dry years,lead to reduced waterlogging and considerable root and crown extension, then a very wet year results in a raised water table and extensive root mortality, and finally another dry year places the plants with enlarged crowns and considerably reduced root systems under severe water stress and mortality or disease ensues.

The intensity of drought will influence whether improved growth or mortality will occur. A general schema might be:

| | year 1 | year 2 | year 3 |
|---|---|---|---|
| case 1 poor growth sequence | wet cold<br>poor growth | wet cold<br>poor growth | wet cold<br>poor growth |
| case 2 good growth sequence | warm dry<br>good root growth | warm dry<br>better growth | warm dry<br>very good sustained growth |
| case 3 mortality sequence | warm dry<br>good root growth | warm wet<br>limited growth<br>root mortality | warm dry<br>mortality |

Evidence for waterlogging

Rainfall at Te Aroha is 50 % greater than the regional average open pan evaporation and at Te Hunga and Te Rere rainfall is nearly double evaporation, sufficient lead to waterlogging. The very allophanic heavy, clays with poor lateral drainage and high water storage capacity (Wilson 1980) in upland soils also contribute to waterlogging. Accumulations of humic matter, peaty soils and podsols in silver beech stands indicate wet conditions and soil moisture contents at the same altitude show a lower duration of waterlogging at Te Aroha than Te Hunga, reflecting the rainfall gradients (Fig. 10.4). This would only occur where soil drainage was impaired. Also, measurements at the end of a long dry period showed high soil moisture contents remaining in the old stands.

The plants however, are probably the best guide to the presence of waterlogging. Stunted root systems of the most affected (seral) species are common within the fog zone and healthy root systems occur on the least affected species (eg. kaikawaka). Adaptations such as lenticels and basal swellings are prominent on the seral species and are a normal feature of both healthy and unhealthy tawari and silver beech (Ch. 4). High leaf size variability indicates stress in the seral species on all upland sites and appears in the more resistant species on the wettest sites. Avoidance of waterlogging is common with seedlings frequently restricted to better aerated sites on logs and stumps and shallow root systems of older trees (Ch. 4). There is a close negative correlation in several species between growth rates and high rainfall or conditions suggestive of waterlogging (Ch. 6) and the species showing the least frequent and least severe symptoms of waterlogging survive longest and form the canopy in old stands.

## Link: fog - waterlogging - mortality

Measurements in the fog zone show a large reduction in evaporation during cloudy periods (Ch. 5). Soil moisture and temperature profiles show discontinuities at the average cloud base which correspond with the lower limit of mortality in each of the study areas and are independent of summit height. The only physical parameter showing the same pattern of variation is rainfall and high rainfall apparently leads to waterlogging. Surviving stands occur on slightly better drained areas or concentrically around the most waterlogged sites and clearly link mortality with waterlogging.

## Evidence for drought sensitivity and reduced growth

Higher osmotic potential and lower turgor loss point in plants of each species (Ch. 8) suggest a low tolerance of stress, typical of plants from wet habitats. However, high stomatal sensitivity to saturation deficit increasing throughout the drier part of the summer (Ch. 10) indicated that stress could be severe if the fog was absent. Prolonged water deficit was not observed except in quintinia, the species showing many physical symptoms of stress. Measurements carried out outside the fog zone at the same altitude showed lower osmotic potentials and no evidence of water stress. Direct comparisons between healthy and unhealthy plants on adjacent sites showed higher diurnal deficits, high bulk modulus of elasticity and lower osmotic potentials in stressed plants indicating that water stress adaptation was present. The data suggest that there is a low threshold for the onset of water stress in plants from the fog zone.

Comparison of growth rates between areas shows reduced growth rates of the species in the fog zone. Longevity in the species corresponds with same broad groups based on apparent damage from waterlogging and the more susceptible, seral species survive to only a small portion of potential age. Maximum ages correspond with dates of significant droughts particularly in seral and shorter lived species. Reports of widespread mortality in silver beech in 1947-48 suggest a strong link with the 1946 drought and this is supported by dendrochronological evidence. Silver beech, kaikawaka and other species often undergo senescence or die following significant drought years such as 1804, 1861 or 1914 and the same years mark the beginning of important recruitment periods.

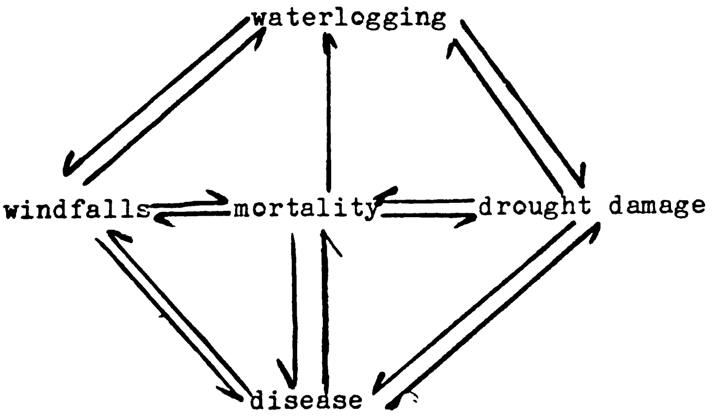
### Mechanism of mortality

The exact cause of mortality is uncertain. Water stress could cause death or may increase susceptibility to a wide range of diseases (Schoenewiess 1975). Insect epidemics are common during dry years and well known in the New Zealand beech forests (Wardle 1967, Wardle 1980). Root death following waterlogging could be caused by root pathogens such as *Armillaria* spp. or *Phytopthora cinnamomi*. Root pathogens can lead to prolonged periods of ill-thrift such as little leaf disease which has similar symptoms to waterlogging (Zak 1954). Investigations of similar problems have often revealed the presence of these two fungi but pathogenicity may be impossible to verify (Marcou and Catrina 1965, Cartledge et al. 1975, Weste 1981). Newhook (1960) studied the epidemiology of *Phytopthora cinnamomi* on coniferous shelter belts in some detail and concluded that drought played a very significant part in plant susceptibility and mortality. *Phytopthora cinnamomi* is common in New Zealand forests (Newhook and Podger 1972) but is unlikely to be important in the Kaimai problem since soil temperatures are too low (cf. Griffin 1978). *Armillaria* is widespread and frequently at first identified as the primary cause of mortality but later relegated to a secondary role as the disease syndrome is investigated but as such may be important. Each study has emphasised that there is no clear cut answer to the role of pathogens in the problem.

### Other possible causes of mortality and waterlogging

Waterlogging could reduce wind stability giving rise to extensive windthrow in rare severe storms that can occur near drought periods (Ch. 6) but several factors tend to discount this possibility. Erect healthy and dead kaikawaka are widespread in affected stands and yet the trees normally appear resistant to defoliation or secondary pathogens (Rawlings and Gilmor 1964). Mt. Te Aroha is higher, possibly colder, isolated from the main range and more prone to wind damage but mortality is of limited extent. Elsewhere wind fallen trees or hummocks attributable to the most recent mortality are largely absent. At earlier dates it is more difficult to discount the importance of wind damage however, high winds are common in the area and the vegetation usually has a low, resilient stature which is wind resistant.

Waterlogging may also be a secondary effect resulting from partial canopy breakdown or mortality from pathogens and other causes but this possibility can be largely discounted by the direct evidence of waterlogging in the old stands at the end of a dry summer. Nevertheless a complex interaction between waterlogging, wind damage, disease and mortality is probably present so that a contribution from each factor is involved on any one site:



## MORTALITY AND WATERLOGGING: OTHER SIMILAR CASE STUDIES

Strikingly similar disease syndromes have been described in the high altitude *Nothofagus* cloud forests of New Guinea (Cartledge et al. 1975), in Rumania, Bulgaria and Yugoslavia (Mihai et al 1965, Marcou and Catrina 1965) linked with Balkan cloud forests and the Ohia dieback in Hawaii (Mueller-Dombios 1981). Mortality in each case is recurrent and continual forest turnover occurs at periods shorter than the accepted life of the various components. Site factors include a range of different soils, forest types (deciduous and evergreen) and climates but in each case the key element appears to be site waterlogging associated with frequent low cloud or fog.

Mueller-Dombois et al. (1980) suggest that the problem is related to cohort senescence, site factors which set a limit to plant age and produce concurrent mortality in all stems when site potential is reached but this does not appear to explain the cause of death.

### Role of fog in mortality of other mountain areas of New Zealand

Clayton-Greene (1977), investigated kaikawaka and found similar mortality at the summit of Mt. Pirongia which he attributed to storm damage, however the windthrow could well have followed canopy opening from other causes. Moore and Cranwell (1934) examined the ecology of *Microlaena avenacea* and described and presented a number of photographs of similar mortality on Moehau but attributed damage to introduced animals. Reassessment of mortality in this locality may also implicate fog and drought as important factors. Esler (1969) in a descriptive investigation of mortality in the Tiritea Reserve in the Tararua Ranges presented many photographs of mortality and noted high cloud frequencies in the affected forests. He provided no single explanation of the causes of the mortality but dates, site descriptions and maps suggest close similarities to the Kaimai problem.

Other cases of unexplained mortality in upland forests have been reported from Tongariro National Park (Skipworth 1981) and the Ruahine Ranges (Elder 1964, James 1973) and personal observations have noted similar problems in the Urewera and Kaimanawa forests. Mortality is apparently common in the upland cloud forests of the North Island. Large scale recurrent mortality in beech forests of the South Island is commonly attributable to wind or snow damage (Wardle 1980) and specific cloud forest mortality cannot identified although some aspects of kaikawaka and rata mortality (Wardle 1978, Veblen and Stewart 1938a, 1983b) appear to be associated with wet cloud forest.

## ECOLOGICAL IMPACT OF CLOUD IN FORESTS

Kerfoot (1968) suggests that evidence for the benefits from fog precipitation is frequently conflicting. The current study suggests that although fog may be a very significant contributor to forest survival in dry areas of the world (Chaney 1981), it may have detrimental effects in other areas. Lowered soil temperatures in the mature Eucalypt cloud forests in Tasmania result their in replacement by Nothofagus forests (Ellis 1972). Coastal fog in the taiga forests of Canada results in high precipitation which prevents the development of forest and confines trees to raised bog mounds where drainage is improved (Damman 1977). Hoar frost formation from fog can apparently cause wave form dieback (Iwaki and Totsuka 1959, Sprugel 1976) in cold upland climates. Here frost accumulation on the mature trees to the windward results mortality and in the slow retreat of the forest margin followed by the formation of a new wave of regeneration. Finally the effects on ecological processes may not be immediately evident, for instance Siccama (1976) suggests that frequent cloud may be responsible for a scrubby ecotonal forest in the Green Mountains, Vermont but does not mention dieback in the shrubland.

Zotov (1938) has suggested that fog may determine the upper forest boundary by limiting light. High fog frequencies strongly influence carbon fixation ability by restricting light intensities so that many species, particularly understory plants, may remain close to compensation point for long periods (Huber 1978). At other times rapid changes in light intensity and relative humidity as the fog clears can produce water stress and rapid stomatal closure which may result in reduced photosynthesis and low carbohydrate reserves (Jane pers. comm.). Prolonged fog may impair leaf development by depleting reserves, or cause leaf damage by slowing leaf hardening and raising osmotic potentials (Ch. 9).

In the Kaimai ranges several species appear have modifications which enable rapid leaf drying and resumption of stomatal gas exchange and other adaptations may aid survival. Strategies of tolerance and avoidance appear to be best exemplified in comparing quintinia, tawari and silver beech:

| Parameter | quintinia | tawari | silver beech |
|---|---|---|---|
| waterlogging | susceptible | tolerator? | avoider |
| drought | susceptible | tolerator? | avoider |
| stress symptoms | severe | rare | moderate |
| survival ability | very low | ?high | high |
| morphological variability | high | low | high |
| leaf development | progressive | single slow | single fast |
| roots | few deep | shallow extensive | shallow restricted (podsol) |

| | | | |
|---|---|---|---|
| osmotic potential | high | high | low |
| bulk modulus of elasticity | low | low | high |
| turgor loss point | low | low | high |
| seasonal change in osmotic potential | low | mod | high |
| foliar carbohydrates | low | high | very low |
| water held on leaves | high | low | high |
| foliar waxes | abundant | low | low |
| cuticular conductance | high | low | medium |
| stomatal closure rate | fast | slow | fast |
| stomatal conductance | high | low | ? |
| stomatal number | med | med | high |

Tawari and silver beech are both prominent components of the cloud forests and although they may have similar life spans it can be seen that they often exhibit opposite kinds of adaptations and responses. One explanation may be that tawari is a tropical species adapted to the cloud forests and tolerates waterlogging with deep or extensive root systems whereas silver beech is a southern species which avoids waterlogging and water stress and although evergreen has a many deciduous -type responses (eg. short period of bud break and leaf development). The seral species, quintinia is a typical opportunist and maximises growth at the expense of survival.

The cloud forests are apparently a specialised environment in which carbon fixation and nutrient supply are limited by cloud (Grubb 1977). Cloud forests must also tolerate waterlogging in high rainfall areas. Water stress imposed during prolonged fine periods then becomes highly significant and mortality may ensue. The return of the normal cloudy conditions may slow the repair processes by restricting regeneration and allowing only slow growth before reimposing the same stresses. Few species appear able to tolerate the extreme radiation fluctuation or sudden imposition of water stress, consequently many wet cloud forests appear to undergo periodic dieback. The study of plant water relations then becomes important for a full understanding of the structure and function of cloud forests.

## FUTURE WORK

In the current project and perhaps others (Mueller-Dombois 1981) the most important aspect neglected to date has been study of the development, seasonality of growth and limitations in the roots of many of the affected species and the ability of the roots of less affected species such as kaikawaka to survive at depth. A second important aspect appears to be detailed investigation of a number of similar problems in New Zealand and elsewhere to confirm the apparent link of mortality with cloud zonation evident in the current studv.

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## APPENDIX I.

Description orf forest structure in Figs. 4.10, 4.11, 4.12.

Abundances : A abundant
C common
o occassional
R rare

Site 1 plot 1 (26)
Mature tawari forest Te Rere. Terrain gently sloping.

| | Canopy | | | Sub-canopy | ground | Frequency | |
|---|---|---|---|---|---|---|---|
| Density (n/ha) | 1850 | | | 26,000 | | Trees | shrub. |
| Basal Area (m2/ha) | 45 | | | 0.33 | | | |
| | emergent | dominant | subdominant | | | | |
| Height (m) | 15 | 10 | 3-5 | 2-5 | | | |
| Species | | | | | | | |
| Ixerba brexioides | | a | o | | o | 55 | 0 |
| Podocarpus ferrugineus | o | | | | | 5 | 0 |
| Coprosma foetidissima | | | o | o | | 9 | 7 |
| Pseudowintera axillaris | | | a | a | c | 4 | 4 |
| Myrsine salicina | | | o | o | o | 5 | 2 |
| Coprosma colensoi | | | | o | | 0 | 1 |
| Alseuosmia macrophylla | | | | a | a | 0 | 22 |
| Coprosma australis | | | | o | a | 2 | 16 |
| Cyathea smithii | | | | o | | 0 | 2 |
| Weinmannia racemosa | | | | o | o | 2 | 1 |
| Quintinia acutifolia | | | | c | c | 13 | 16 |
| Griselinia littoralis | | | | o | o | 2 | 9 |
| Hedycarya arborea | | | | o | r | 0 | 2 |
| Melicytus ramiflorus | | | | r | | | |
| Schefflera digitata | | | | o | o | | |
| Pseudopanax edglerii | | | | r | | | |
| Senecio kirkii | | | | c | c | 0 | 13 |
| Astelia solandri | | | | | o | | |
| Astelia nervosa | | | | | o | | |
| Blechnum discolor | | | | | o | | |
| Uncinia rupestris | | | | | o | | |
| Uncinia zotovii | | | | | r | | |
| Uncinia filiformis | | | | | r | | |
| Microlaena avenacea | | | | | o | | |
| Blechnum nigrum | | | | | r | | |
| Blechnum fluviatile | | | | | c | | |
| Luzuriaga parviflora | | | | | o | | |
| Todea hymenophylloides | | | | | o | | |
| Grammitis billardieri | | | | | o | | |
| Hymenophyllum multifidium | | | | | o | | |
| Asplenium falcatum | | | | | o | | |
| Trichomanes reniforme | | | | | o | | |
| Rumorha aristata | | | | | o | | |
| Tmesipteris tannensis | | | | | o | | |
| Earina autumnalis | | | | | c | | |
| Earina mucronata | | | | | c | | |

Soil: 0-1cm litter. 1-15 cm dark brown loam very wet some Taupo pumice. 16-43 cm chestnut brown sandy loam very friable becoming strong yellow brown with and often somewhat mottled. 43-80 cm Yellow brown stony clay loam. Merging with bedrock at about 85 cm.
Abundance ratings used in the body of the table are: r =rare; o=occasional;

c=common; a=abundant; va= very abundant

Site 1 plot 2
Low seral scrub Te Rere. Terrain gently sloping.

| | Canopy | | | Sub-canopy | ground | Frequency | |
|---|---|---|---|---|---|---|---|
| Density (n/ha) | 2300 | | | 60,000 | | Trees | shrubs |
| Basal Area (m2/ha) | 16.7 | | | 2.94 | | | |
| | emergent | dominant | subdominant | | | | |
| Height (m) | 15 | 4 | 2-3 | | | | |
| Species | | | | | | | |
| Ixerba brexioides | o | o | c | | o | 24 | 2 |
| Podocarpus ferrugineus | r | | | | | 1 | |
| Coprosma foetidissima | | | o | o | | 4 | 2 |
| Pseudowintera axillaris | | | a | a | c | 14 | 26 |
| Myrsine salicina | | | o | o | o | 7 | 2 |
| Coprosma colensoi | | | | o | | 0 | 2 |
| Alseuosmia macrophylla | | | | o | o | 0 | 11 |
| Coprosma australis | | | o | c | a | 2 | 11 |
| Cyathea smithii | | | | c | c | 17 | 6 |
| Weinmannia racemosa | | | | o | o | 6 | 8 |
| Quintinia acutifolia | | | o | c | o | 16 | 13 |
| Griselinia littoralis | | | o | c | o | 13 | 7 |
| Olearia rani | | | | o | | 3 | 2 |
| Hedycarya arborea | | | | o | r | | |
| Melicytus ramiflorus | | | | | r | | |
| Schefflera digitata | | | | o | o | | |
| Pseudopax edglerii | | | | r | | | |
| Blechnum discolor | | | | | o | | |
| Uncinia uncinata | | | | | o | | |
| Uncinia rupestris | | | | | r | | |
| Uncinia filiformis | | | | | r | | |
| Microlaena avenacea | | | | | o | | |
| Blechnum nigrum | | | | | r | | |
| Blechnum fluviatile | | | | | c | | |
| Todea hymenophylloides | | | | | o | | |
| Histiopteris incisa | | | | | o | | |
| Astelia solandri | | | | | r | | |
| Grammitis billardieri | | | | | o | | |
| Hymenophyllum multifidium | | | | | o | | |
| Asplenium falcatum | | | | | o | | |
| Trichomanes reniforme | | | | | o | | |
| Tmesipteris tannensis | | | | | o | | |
| Earina autumnalis | | | | | c | | |
| Earina mucronata | | | | | c | | |
| Asplenium falcatum | | | | | o | | |
| Asplenium flaccidum | | | | | o | | |

Soil: 0-1cm litter. 1-15 cm dark brown loam very wet some Taupo pumice. 16-43 cm grey brown sandy loam very friable becoming strong yellow brown with and often somewhat mottled. 43-80 cm grey brown stony clay loam. Merging with bedrock at about 85 cm.

Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant

Site 1 plot 3
Grasslands Te Rere bald. Terrain gently sloping.

| | Canopy | | | Sub-canopy | ground | Frequency Trees shrubs |
|---|---|---|---|---|---|---|
| Density (n/ha) | | | | 1,000 | | |
| Basal Area (m2/ha) | | | | 0.57 | | |
| | emergent | dominant | subdominant | | | |
| Height (m) | | | | | | |
| Species | | | | | | |
| Pseudowintera axillaris | | | | o | | |
| Alseuosmia macrophylla | | | | | | r |
| Coprosma australis | | | | | | o |
| Cyathea smithii | | | | | | r |
| Weinmannia racemosa | | | | | | o |
| Quintinia acutifolia | | | | | | o |
| Griselinia littoralis | | | | | | r |
| Melicytus ramiflorus | | | | | | r |
| Schefflera digitata | | | | o | | o |
| Dracophyllum latifolium | | | | o | | |
| Metrosideros perforata | | | | | | r |
| Rubus cissioides | | | | | | c |
| Microlaena avenacea | | | | | | va |
| Heirachloe redolens | | | | | | a |
| Uncinia distans | | | | | | va |
| Astelia solandri | | | | | | r |
| Astelia nervosa | | | | | | r |
| Gahnia pauciflora | | | | | | o |
| Blechnum discolor | | | | | | r |
| Uncinia rupestris | | | | | | r |
| Uncinia zotovii | | | | | | r |
| Uncinia filiformis | | | | | | r |
| Blechnum fluviatile | | | | | | o |

Soil: 0-1cm litter. 1-15 cm dark brown loam very wet some Taupo pumice. 16-43 cm chestnut brown sandy loam. 43-60 cm dark brown stony clay loam. Merging with bedrock at about 85 cm.
Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant.page

Site 1 plot 4 (30)
Severely damaged tawari forest Te Rere. Sloping terrain.

| | Canopy | | | Sub-canopy | ground | Frequency | |
|---|---|---|---|---|---|---|---|
| Density (n/ha) | 2,400 | | | 36,000 | | trees | shrubs |
| Basal Area (m2/ha) | 17.0 | | | 4.31 | | | |
| | emergent | dominant | subdominant | | | | |
| Height (m) | 15 | 3 | 1-2 | | | | |
| Species | | | | | | | |
| Ixerba brexioides | c | o | o | | o | 8 | 0 |
| Podocarpus ferrugineus | o | | | | | 2 | 0 |
| Coprosma foetidissima | | | o | o | | 4 | 2 |
| Pseudowintera axillaris | | a | a | a | c | 16 | 28 |
| Coprosma colensoi | | | | o | | 0 | 2 |
| Alseuosmia macrophylla | | | | c | o | 0 | 3 |
| Coprosma australis | | | | o | a | 0 | 2 |
| Cyathea smithii | | o | a | | | 44 | 24 |
| Weinmannia racemosa | | | | o | o | 2 | 2 |
| Quintinia acutifolia | | | | r | r | | |
| Griselinia littoralis | | | | c | o | 0 | 2 |
| Olearia rani | | | | o | o | 0 | 4 |
| Hedycarya arborea | | | | o | r | 0 | 7 |
| Melicytus ramiflorus | | | | o | | 0 | 4 |
| Schefflera digitata | | | | a | a | 0 | 4 |
| Geniostoma ligustrifolium | | | | c | c | 0 | 16 |
| Astelia solandri | | | | | o | | |
| Astelia nervosa | | | | | o | | |
| Blechnum discolor | | | | | o | | |
| Uncinia rupestris | | | | | o | | |
| Uncinia filiformis | | | | | o | | |
| Microlaena avenacea | | | | | c | | |
| Blechnum fluviatile | | | | | c | | |
| Todea hymenophylloides | | | | | o | | |
| Grammitis billardieri | | | | | o | | |
| Hymenophyllum multifidium | | | | | r | | |
| Tmesipteris tannensis | | | | | r | | |
| Earina autumnalis | | | | | r | | |
| Earina mucronata | | | | | r | | |

Soil: 0-1cm litter. 1-15 cm dark brown loam wet some Taupo pumice. 16-32 cm grey brown sandy loam very friable becoming yellow brown with depth and often somewhat mottled. 33-60 cm Yellow brown stony clay loam. Merging with bedrock at about 65 cm.
Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant

Site 2 plot 1 (6)
Good stand 850 m Te Hunga. Silver beech/ tawari
Terrain flat to slightly rolling

|  | Canopy |  |  | Sub-canopy | ground | Frequency |  |
|---|---|---|---|---|---|---|---|
| Density (n/ha) | 1621 |  |  | 25,000 |  |  |  |
| Basal Area (m2/ha) | 67.5 |  |  | 1.65 |  |  |  |
|  | emergent | dominant | subdominant |  |  | trees | shrubs |
| Height (m) | 15-20 | 15 | 5-15 | 2-5 |  |  |  |
| Species |  |  |  |  |  |  |  |
| Nothofagus menziesii | a | a | a | a | a | 31 | 14 |
| Ixerba brexioides |  | a | o | o | o | 39 | 4 |
| Libocedrus bidwillii | r |  |  |  |  |  |  |
| Dracophyllum latifolium |  |  | o | o |  | 3 | 3 |
| Pseudopanax colensoi |  |  | o | o | c | 0 | 8 |
| Coprosma foetidissima |  |  |  | c | c | 3 | 8 |
| Pseudowintera axillaris |  |  |  | o | o | 2 | 1 |
| Myrsine salicina |  |  | o | o | o | 4 | 2 |
| Pseudopanax simplex |  |  |  | r |  |  |  |
| Coprosma colensoi |  |  |  | o |  | 0 | 1 |
| Cyathodes fasciculata |  |  |  | r |  |  |  |
| Alseuosmia macrophylla |  |  |  | a | a | 0 | 13 |
| Weinmannia racemosa |  |  |  | c | c | 11 | 11 |
| Quintinia acutifolia |  |  |  | o | a | 1 | 32 |
| Griselinia littoralis |  |  |  | o | o | 4 | 1 |
| Podocarpus hallii |  |  |  | r |  | 0 | 1 |
| Astelia solandri |  |  |  |  | o |  |  |
| Astelia nervosa |  |  |  |  | o |  |  |
| Gahnia pauciflora |  |  |  |  | o |  |  |
| Gahnia setifolia |  |  |  |  | o |  |  |
| Libertia pulchella |  |  |  |  | o |  |  |
| Uncinia gracilis |  |  |  |  | o |  |  |
| Luzuriaga parviflora |  |  |  |  | o |  |  |
| Grammitis billardieri |  |  |  |  | o |  |  |
| Hymenophyllum multifidium |  |  |  |  | o |  |  |
| Hymenophyllum revolutum |  |  |  |  | o |  |  |
| Asplenium falcatum |  |  |  |  | o |  |  |
| Trichomanes reniforme |  |  |  |  | r |  |  |
| Rumorha aristata |  |  |  |  | o |  |  |
| Hymenophyllum flabellatum |  |  |  |  | r |  |  |
| Tmesipteris tannensis |  |  |  |  | o |  |  |
| Hymenophyllum malingii |  |  |  |  | r |  |  |

Soil: 0-2cm litter. 3- 35 cm grey white sand. 35-40 cm dark brown sandy loam mottled with dead roots and black on peds, merging with light brown sandy loam of varible depth, about 75 cm. Rapid transition to grey white sandy loam of 10 cm depth at bedrock.

Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant

Site 2 plot 2
Broken canopy of scattered silver beech 850 m Te Hunga.
Terrain flat to slightly rolling

| | Canopy | | | Sub-canopy | ground | Frequency | |
|---|---|---|---|---|---|---|---|
| Density (n/ha) | 7.15 | | | 95,000 | | Trees | shrubs |
| Basal Area (m2/ha) | 0.15 | | | 3.08 | | | |
| | emergent | dominant | subdominant | | | | |
| Height (m) | 3-20 | 3 | 1.5-3 | | | | |
| Species | | | | | | | |
| Nothofagus menziesii | o | c | c | | | 14 | 6 |
| Ixerba brexioides | o | a | o | o | | 42 | 11 |
| Libocedrus bidwillii | r | | | | | | |
| Dracophyllum latifolium | | | o | o | | 5 | 3 |
| Pseudopanax colensoi | | | o | o | | 0 | 17 |
| Coprosma foetidissima | | | | c | c | 7 | 9 |
| Pseudowintera axillaris | | | o | | | 10 | 5 |
| Myrsine salicina | | | o | o | o | 12 | 4 |
| Pseudopanax simplex | | | | r | | 1 | 0 |
| Coprosma colensoi | | | | r | | | |
| Cyathodes fasciculata | | | | o | | 0 | 3 |
| Alseuosmia macrophylla | | | | a | a | | |
| Weinmannia racemosa | | | a | c | c | 3 | 12 |
| Quintinia acutifolia | | | a | a | o | 0 | 21 |
| Griselinia littoralis | | | | o | o | 3 | 1 |
| Coprosma dodonaeifolia | | | | c | c | 1 | 6 |
| Phyllocladus alpinus | | | | r | | | |
| Coprosma australis | | | | r | | | |
| Senecio kirkii | | | | r | | 0 | 1 |
| Astelia solandri | | | | | o | | |
| Astelia nervosa | | | | | o | | |
| Gahnia pauciflora | | | | | o | | |
| Gahnia setifolia | | | | | o | | |
| Libertia pulchella | | | | | o | | |
| Uncinia gracilis | | | | | o | | |
| Luzuriaga parviflora | | | | | o | | |
| Grammitis billardieri | | | | | o | | |
| Hymenophyllum multifidium | | | | | o | | |
| Hymenophyllum revolutum | | | | | o | | |
| Asplenium falcatum | | | | | o | | |
| Trichomanes reniforme | | | | | o | | |
| Rumorha aristata | | | | | o | | |
| Hymenophyllum flabellatum | | | | | r | | |
| Tmesipteris tannensis | | | | | o | | |
| Hymenophyllum malingii | | | | | r | | |
| Earina autumnalis | | | | | c | | |
| Earina mucronata | | | | | c | | |
| Lycopodium billardieri | | | | | c | | |

Soil: 0-2cm litter. 3-8 cm dark brown loam very wet 9- 35 cm grey white sand. 36-43 cm dark brown sandy loam mottled with dead roots and black on peds, very wet and variable in colour merging with light brown sandy loam of varible depth, about 75 cm. Rapid transition to grey white sandy loam of 10 cm depth at bedrock.

Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant.

Site 2 plot 3 (14)
Scattered silver beech over dense quintinia 850 m Te Hunga.
Terrain flat to slightly rolling

| | Canopy | | | Sub-canopy | ground | Frequency Trees shrubs |
|---|---|---|---|---|---|---|
| Density (n/ha) | | | | 73,000 | | |
| Basal Area (m2/ha) | | | | 4.99 | | |
| | emergent | dominant | subdominant | | | |
| Height (m) | 3-20 | 3 | 1-2 | | | |
| Species | | | | | | |
| Nothofagus menziesii | r | c | c | c | | 2 |
| Ixerba brexioides | | c | o | o | | 4 |
| Libocedrus bidwillii | | | r | c | | |
| Dracophyllum latifolium | | | o | o | | 3 |
| Pseudopanax colensoi | | | o | o | | 8 |
| Coprosma foetidissima | | | | o | o | 2 |
| Pseudowintera axillaris | | | o | | | 1 |
| Myrsine salicina | | | c | o | o | 5 |
| Pseudopanax simplex | | | | r | | 1 |
| Coprosma colensoi | | | | o | | 1 |
| Cyathodes fasciculata | | | | o | | 1 |
| Alseuosmia macrophylla | | | | a | a | 13 |
| Weinmannia racemosa | | | | c | c | 28 |
| Quintinia acutifolia | | | a | a | o | 27 |
| Griselinia littoralis | | | | o | o | 3 |
| Coprosma dodonaeifolia | | | | o | o | 1 |
| Phyllocladus alpinus | | | | r | | |
| Coprosma australis | | | | r | | |
| Senecio kirkii | | | | c | | |
| Dicksonia squarrosa | | | | o | | |
| Astelia solandri | | | | | c | |
| Astelia nervosa | | | | | o | |
| Gahnia pauciflora | | | | | o | |
| Libertia pulchella | | | | | r | |
| Uncinia gracilis | | | | | r | |
| Luzuriaga parviflora | | | | | o | |
| Nertera dichondraefolia | | | | | o | |
| Blechnum minor | | | | | o | |
| Histiopteris incisa | | | | | o | |
| Grammitis billardieri | | | | | o | |
| Hymenophyllum multifidium | | | | | o | |
| Hymenophyllum revolutum | | | | | o | |
| Tmesipteris tannensis | | | | | o | |
| Hymenophyllum malingii | | | | | r | |
| Earina autumnalis | | | | | o | |
| Earina mucronata | | | | | o | |
| Lycopodium billardieri | | | | | r | |

Soil: 0-2cm litter. 2-7 cm dark brown loam very wet 8- 25 cm grey white sand. 26-53 cm dark brown sandy loam very wet with dead roots and variable in colour merging with light brown sandy loamof varible depth, about 75 cm. Rapid transition to grey white sandy loamof 10 cm depth at bedrock.
Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant.

Site 3 plot 1 (10)
Good stand 850 m Te Hunga. Kaikawaka/silver beech/ tawari
Terrain flat to slightly rolling

| | Canopy | | | Sub-canopy | ground | Frequency | |
|---|---|---|---|---|---|---|---|
| | | | | | | Trees | shrubs |
| Density (n/ha) | 1,800 | | | 17,500 | | | |
| Basal Area (m2/ha) | 49.0 | | | 0.40 | | | |
| | emergent | dominant | subdominant | | | | |
| Height (m) | 20 | 15 | 5 | 2 | | | |
| Species | | | | | | | |
| Nothofagus menziesii | a | | | | c | 27 | 2 |
| Ixerba brexioides | | a | | | c | 44 | 4 |
| Libocedrus bidwillii | o | | | | o | 4 | 0 |
| Dacrydium biforme | o | | | | | 4 | 0 |
| Dacrydium intermedium | r | | | | | | |
| Dracophyllum latifolium | | | r | | | | |
| Pseudopanax colensoi | | | o | c | o | 13 | 24 |
| Coprosma foetidissima | | | | o | r | | 8 |
| Pseudowintera axillaris | | | | o | c | 0 | 11 |
| Myrsine salicina | | | r | o | c | 0 | 2 |
| Pseudopanax simplex | | | | r | o | 0 | 7 |
| Pseudopanax edgerleyi | | | | | r | | |
| Weinmannia racemosa | | | | | o | 0 | 7 |
| Quintinia acutifolia | | | | | c | 0 | 22 |
| Alseuosmia macrophylla | | | | | o | 0 | 4 |
| Myrsine salicina | | | | | o | 8 | 7 |
| Astelia colensoi | | | | | o | | |
| Gahnia pauciflora | | | | | o | | |
| Gahnia setifolia | | | | | r | | |
| Dicksonia squarrosa | | | | | r | | |
| Libertia pulchella | | | | | o | | |
| Uncinia gracilis | | | | | o | | |
| Luzuriaga parviflora | | | | | o | | |
| Microsorium diversifolium | | | | | o | | |
| Grammitis billardieri | | | | | o | | |
| Hymenophyllum multifidium | | | | | o | | |
| Hymenophyllum revolutum | | | | | o | | |
| Asplenium falcatum | | | | | o | | |
| Trichomanes reniforme | | | | | r | | |
| Rumorha aristata | | | | | r | | |
| Hymenophyllum flabellatum | | | | | r | | |
| Tmesipteris tannensis | | | | | r | | |
| Hymenophyllum malingii | | | | | o | | |

Soil: 0-30 cm dark chocate saturated brown loam. 30-35 cm sandy yellow brown ash compacated. 35-70cm saturated dark brown loam. 70-80 cm grey-white stony clay becoming drier with depth. 80 cm bedrock.
Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant.

Site 3 plot 2 (212003)
Poor stand 850 m Te Hunga. Kaikawaka/silver beech/ tawari
Terrain flat to slightly rolling

| | | Canopy | | Sub-canopy | ground | Frequency | |
|---|---|---|---|---|---|---|---|
| Density (n/ha) | | 100 | | 82,000 | | Trees | shrubs |
| Basal Area (m2/ha) | | 5.2 | | 5.70 | | | |
| | emergent | dominant | subdominant | | | | |
| Height (m) | 3-20 | 2-3 | 1.5 | | | | |
| Species | | | | | | | |
| Nothofagus menziesii | r | c | c | | c | 6 | 5 |
| Ixerba brexioides | r | c | c | | c | 43 | 6 |
| Libocedrus bidwillii | o | | o | | r | 4 | 3 |
| Dacrydium biforme | | | r | | | 0 | 1 |
| Dracophyllum latifolium | | | c | c | | 4 | 3 |
| Pseudopanax colensoi | | | o | o | o | 5 | 6 |
| Coprosma foetidissima | | | | c | c | 6 | 3 |
| Pseudowintera axillaris | | | | o | c | 5 | 1 |
| Myrsine salicina | | | o | o | o | 5 | 2 |
| Pseudopanax simplex | | | | o | o | 5 | 4 |
| Pseudopanax edgerleyi | | | | | r | 0 | 0 |
| Coprosma colensoi | | | | o | | 0 | 1 |
| Coprosma dodonaeifolia | | | c | c | | 0 | 14 |
| Senecio kirkii | | | | o | o | 0 | 1 |
| Cyathodes fasciculata | | | | o | | 0 | 1 |
| Alseuosmia macrophylla | | | | a | va | 0 | 10 |
| Weinmannia racemosa | | | a | a | a | 9 | 21 |
| Quintinia acutifolia | | | va | a | a | 5 | 17 |
| Phylocladus glaucus | | | r | | | 1 | 0 |
| Astelia solandri | | | | | o | | |
| Astelia nervosa | | | | | o | | |
| Gahnia pauciflora | | | | | o | | |
| Gahnia setifolia | | | | | o | | |
| Dicksonia squarrosa | | | | | o | | |
| Libertia pulchella | | | | | o | | |
| Uncinia gracilis | | | | | o | | |
| Luzuriaga parviflora | | | | | o | | |
| Grammitis billardieri | | | | | o | | |
| Hymenophyllum multifidium | | | | | o | | |
| Hymenophyllum revolutum | | | | | o | | |
| Asplenium falcatum | | | | | o | | |
| Trichomanes reniforme | | | | | r | | |
| Rumorha aristata | | | | | r | | |
| Hymenophyllum flabellatum | | | | | r | | |
| Tmesipteris tannensis | | | | | r | | |
| Hymenophyllum malingii | | | | | r | | |

Soil: 0-30 cm dark chocate saturated brown loam. 30-35 cm sandy yellow brown ash compacted. 35-80cm saturated dark brown loam. 80-90 cm grey-white stony clay becoming drier with depth. 80 cm bedrock.
Abundance ratings used in the body of the table are: r =rare; o=occasional; c=common; a=abundant; va= very abundant.

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APPENDIX II

# MORPHOLOGY AND INCIDENCE OF LANDSLIDES IN THE KAIMAI RANGES NORTH ISLAND, NEW ZEALAND.

G. T. Jane; T. G. A. Green,

ABSTRACT Studies of aerial photographs show clear evidence of increased erosion, since 1943, concentrated at differing altitudes in different parts of the Kaimai Ranges North Island, New Zealand. In the Te Rere area, the increase was greatest between 1943 and 1960, but in the other 2 areas (Mt Te Aroha and Te Hunga) the increase was greatest between 1960 and 1974. There is also a high normal erosion frequency at Te Hunga due to steep terrain. Landslides do not appear to be concentrated on slopes of any particular aspect, slope, soil type, or basement geology, but may be linked with areas of poor vegetation.

A sample of landslides in each area was visited and mapped in detail. Measurements demonstrated a marked difference between upland and lowland landslides. At the upland sites, landslides occurred on slopes as low as 15° and on slopes of over 35° bedrock was usually exposed, even in the track. Presence of allophane at the failure plane, and unhealthy vegetation at the landslide sites, markedly reduces slope stability and causes a lower natural angle of repose. At lowland sites, most landslides occurred on slopes steeper than 40° and bedrock was less frequently exposed. Examination of scars suggests that the landslides occurred under saturated soil conditions during a storm.

In the scar, bedrock is usually exposed, minimising the risk of further erosion; but in the track, deep soils and slow revegetation may increase the risk of further erosion, particularly if browsing mammals are present.

Keywords erosion; soils; geology; climate; distribution; altitude;

vegetation; landslides; frequency.

## INTRODUCTION

There have been a number of recent studies of erosion on pastoral lands (Eyles 1971; Selby 1972; Leslie 1974; Selby 1979; Crozier et al. 1980) and studies have been facilitated by good access and ease of identification of landslides. The landslides are readily attributed to particular storms, and the recent increase in landslide occurrence is frequently attributed to the clearance of forest cover for agriculture (Selby 1972, O'Loughlin 1974).

By contrast, studies of landslides in forested areas are uncommon due to lesser economic significance and the difficulties of inspection, access, and dating. Yet, in many areas, there has been an increase in erosion which has paralleled the changes in agricultural areas. The increased erosion has usually been ascribed, at least in part, to the high population of introduced mammals particularly deer and goats, and to a lesser extent possums (Holloway 1959; James 1973). The most recent studies of landslide occurrence in forested areas have been directed towards evaluating the risks of erosion when forests are cleared for conversion to introduced conifers (cf. O'Loughlin & Pearce 1976; Laffan 1979) and their later management (Gage & Black 1979). These studies have attempted to relate the risk of failure to geology and soil types, although other studies in the Wairarapa (Crozier et al. 1980) and Hunua Ranges (Pain 1969) suggest that landslide locations do not always conform to expectations and that recent changes in land use, climate, or other factors may confound the issue.

### Location of study areas

The Kaimai Ranges, approximately latitude 37 ° 30 °S and longitude 175 ° 30° W, and the location of the research sites are shown on Fig. 1. The Kaimai Ranges are generally recognised as encompassing the hills between the Ohinemuri Gorge on State Highway 25 in the north and State Highway 29 linking Matamata and Tauranga in the south. To the west, the ranges are bounded by the Waihou River and Hauraki Plains. To the east are the lowlands of the Bay of Plenty. Most of the forested land forms part of the Kaimai-Mamaku State Forest Park (N.Z.F.S. 1976).

Earlier studies of erosion in Kaimai Ranges (Pracy et al. 1975; Dale & James 1977) recognised that the main areas of intensified erosion occurred above 600 m altitude. These areas of higher terrain were found principally between Mt. Te Aroha in the north and Mt. Ariariparitapu in the south in 3 more or less discrete tracts. The tracts had different histories of colonisation by introduced animals, and different climates and patterns of landslide distribution were suspected. Within these tracts the 3 study areas were defined (Fig. 1).

## METHODS and SITE DESCRIPTION

### Methods

Over 150 landslide sites were visited in the 3 study areas and details of the failure, geology, soils, and vegetation at each site were recorded. At each landslide 3 zones were recognised and sketched (Fig. 2): the scar, track and deposit (Crozier 1973). The width of each zone was measured at the widest part, to the nearest metre, and the total length was subdivided between the 3 regions. The beginning of the track was defined as the point where soil removal was minimum, usually corresponding to the lowest point on the ellipse of the scar. The end of the track was defined as the beginning of the continuous deposit.

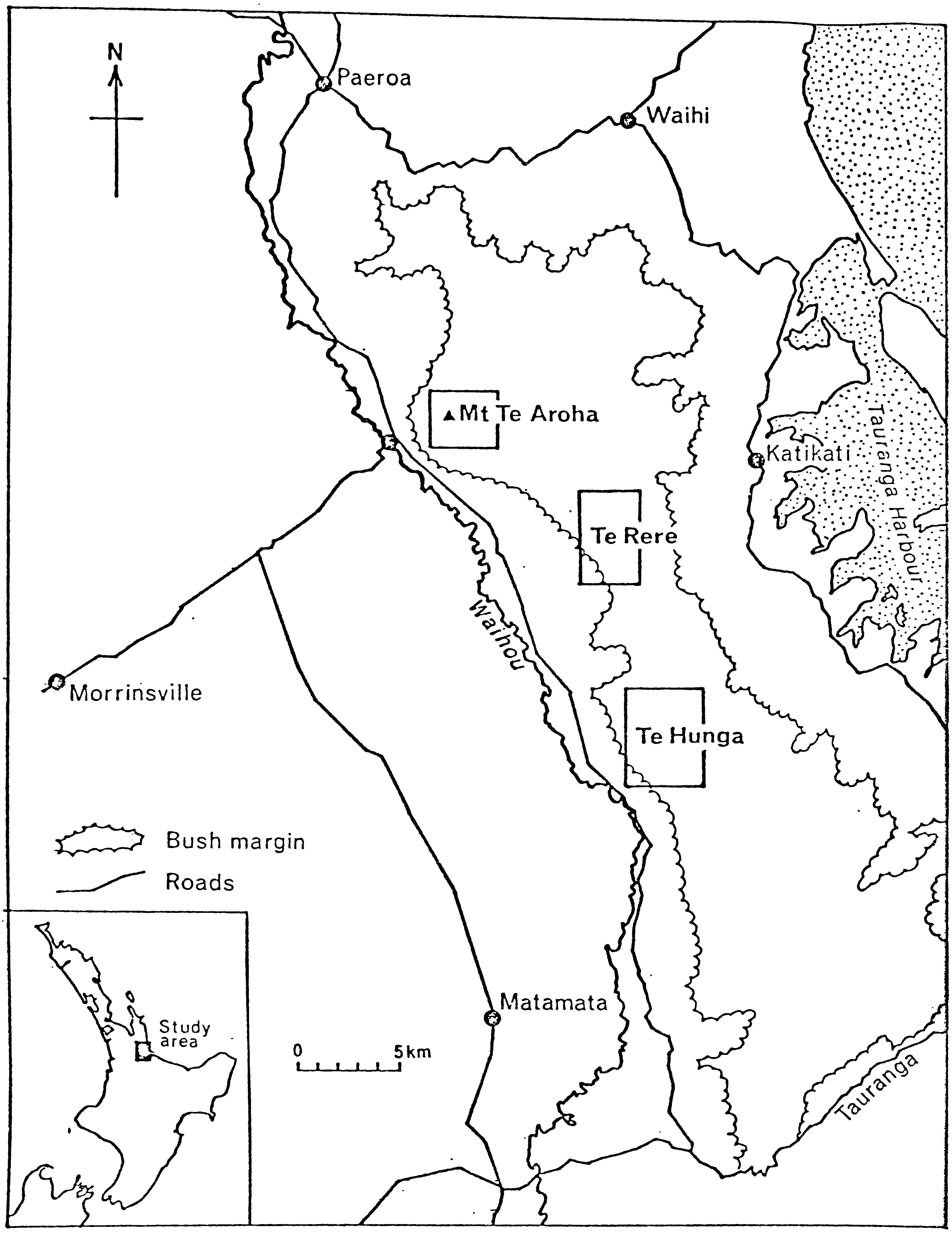

Fig. 1. Location of the three study areas, Te Aroha, Te Rere and Te Hunga in the Kaimai Ranges.

Distances of over 100 m were estimated, particularly where the track extended into a stream channel. The depth of regolith removed in each zone was estimated to the nearest centimetre. A soil profile was described at the head of each landslide and soil samples were collected from a limited number of profiles for detailed chemical and physical analysis.

The locations of the landslides were mapped from aerial photographs. The coverage of the 1959-60 ( Survey 1218) and 1974 (Survey 3731) photographs is complete, but coverage of the 1943 photographs (Survey 229) is restricted to the northern study areas and is of poor quality as much of the area is obscured by cloud. Photographs are also available for 1964, but these cover only a limited part of the Te Rere area. Dot-grid determinations of the area, mapped from the photographs, were also used to determine the proportion of the area affected by landslides.

For the purposes of comparison the landslides were divided into two groups based on altitude: upland landslides occurring above 600m and lowland landslides below 600m.

## Vegetation

The vegetation of the ranges has been mapped by Nichols (1965, 1974) and described by Dale & James (1977). Forest has been cleared from the steep flanks of the ranges, in places to altitudes of over 600 m and little forest remains on the slope foot below 300 m. Within the forests there is an altitudinal gradation in composition which is marked by 2 ecotones. At the lower ecotone, near 300 m altitude, lowland *Dysoxylum/Laurelia/Beilschmiedia* forest is replaced abruptly by *Beilschmiedia* forest, in which *Dacrydium cupressinum* occurs as a scattered emergent and *Podocarpus ferrugineus* is common. At 600-700 m there is a broad ecotone in which Beilshmiedia tawa disappears. At 720 m, Nothofagus menziesii appears abruptly and rapidly increases in prominence to dominate the upland forest zone. In the upland zone, seral stands dominated by Quintinia acutifolia and Ixerba brexioides are common, and often cap the crest of the range.

## Climate

The Kaimai Ranges lie in the northern climatic region (Garnier 1958) and separate 2 weather districts. To the west, the Waikato Region is largely influenced by the predominant easterly movement of frontal systems onto New Zealand (Maunder 1973). In the Bay of Plenty Region, to the east, much of summer rainfall arises from tropical storms which originate north of New Zealand (De Lisle & Kerr 1963). Within the Kaimai Ranges, as in many mountain areas, there are few meterological stations, and climatic conditions must be inferred from surrounding recording points.

Rainfall There is a marked gradient in rainfall southward along the ranges between Waihi (2160 mm) and Wharawhara (2500 mm) which is paralleled to the west by a rise from Te Aroha (1500 mm) to Shaftesbury (2000 mm). There is also a steep altitudinal gradient in rainfall on the western face of the ranges. For example, at the summit of Mt Te Aroha, the annual total is 2000 mm, yet 2 km away, the town at the base of the mountain has an annual rainfall of only 1500 mm. This decreases further to 1100 mm at Morrinsville on the Hauraki Plains 20 km to the west. The same gradient in rainfall appears to be maintained at Te Rere and Te Hunga where a 60% increase in rainfall was recorded between base and summit of the range at temporary rain gauges established during 1980-81. Assuming an annual fall of 2000 mm at the base of these series (the same as that at Shaftesbury) it is suggested that falls in excess of 3000 mm occur at the crest of the range.

Very high intensity rainfalls arise from tropical storms which strike the area from the north (De Lisle 1967). 24-h falls in excess of 200 mm can be expected every 10 years at Waihi, Katikati, and eastern points along the ranges, and about every 50 years at Te Aroha and points along the western face (Coulter & Hessell 1980). Falls of over twice this intensity have been recorded at Waihi and Wharawhara and can be expected within the ranges. These storms can give rise to exceptionally intensive precipitation which may be of a very localised nature (Devereux 1909; De Lisle & Kerr 1963). For instance, the storm of 28 February 1966 was described as the most severe storm in 60 years at Katikati (Bay of Plenty Times 29/2/66) but did little damage elsewhere. Similarly, the storm of 15 September 1960 produced the second-largest flows on record in the Waihou river system which drains the west of the ranges, but showed only a small storm peak on the flow records for Ohinemuri River draining northern catchments.

Temperature Temperatures are mild in the lowland areas at Te Aroha (14.5 ° C) and Waihi (13.7 °C). The diurnal range is approximately 9 ° C, typical of most coastal areas in New Zealand (Garnier 1958). Frosts are uncommon - only about 10 screen frosts occur each year. Summer temperatures rarely exceed 30 ° C (De Lisle 1967). There are few data available for the upland climate. Records kept at Mt Te Aroha for the last 10 years suggest an annual mean temperature of 8.4 ° C. Summer temperatures may exceed 20 ° C, but winter temperatures, particularly for June and July, may remain close to freezing. Along the higher parts of the range, frequent fog or low cloud can be regarded as important modifiers of the environment (Clayton-Greene 1976).

## Geology and Soils

Lava bluffs are common on the steep western scarp of the range, but, to the east, the range falls away less steeply. Both sides of the range are deeply dissected by young streams in which cascades and waterfalls are frequent, due to the hardness of the underlying bedrock.

The ranges are composed almost entirely of Miocene andesites and dacites overlain to the south by younger ignimbrites. Three regions can be distinguished. In the south, the Waiteariki ignimbrites extend across Whakamarama Plateau to Mamaku and Rotorua (Healy et al. 1964), bounding the Te Hunga area at its southern end. Underlying the study areas in the centre of the ranges are thick sequences of andesitic and dacitic lava and laharic breccias. The flows are 20-100 m thick, usually with a slope of 10-20° to the southeast. The flows are occasionally interspersed with lacustrine deposits or thick, reddish, lateritic breccias, which formed in the tropical climates of the Miocene, between eruptive events. To the north of the study areas, in the Waitawheta River and adjacent catchments, is a complex volcanic centre (Schofield 1967). Intrusive ore bearing deposits are common and may contain sulphides of lead, zinc, copper, and arsenic as well as gold and silver (Weissberg & Wodzicki 1969). The Okauia fault system, which has a vertical displacement of over 800 m, bounds the western fall of the ranges. There is no indication of the location of this fault trace and it is assumed to lie beneath the alluvial deposits of Hauraki Plains. Although several faults within the ranges were postulated by Henderson & Bartrum (1913), there is no clear evidence for their existence (Houghton pers. comm.).

Soils Volcanic ash (Waihi or Hamilton) is a major soil parent material (Vucetich & Pullar 1969), but also it may be mixed with, or dominated by, materials derived from the underlying andesitic and dacitic rock. More recent pumiceous ash from the Mangaone, Kaharoa, or

Taupo eruptions (Pullar & Birrell 1973) is also present as a fine, white sand distributed throughout the A horizon. The difference in the parent materials gives rise to marked differences in the type of clay and to soil properties. The andesites and dacites give rise to a predominance of kaolin, cristobalite, and metahalloysite (Wilson 1980). These minerals produce massive clays which respond to changes in moisture content by swelling and cracking. The ash-derived soils, on the other hand, commonly have a high allophane content (Birrell et al. 1977) which reduces fertility due to its high phosphate retention, and gives the soils low cohesion (Wilson 1980).

At altitudes above 700 m, stones are an important component of the soils and frequently comprise 30% of the profile surface. Even in samples from which the larger stoness have been removed up to 30% of the material is over 2 mm mesh size. The stones sampled were usually well rounded and ranged in size from a few centimetres across to over 1 m in length. The stoniness is possibly due to soil creep or solifluxion causing mixing of the ash with fragments from the underlying bedrock (Wilson 1980). On Mt. Te Aroha, an altitudinal gradient in soils, similar to the described by Wilson (1980), comprising the Te Aroha and Komata soils is present. These soils are predominantly derived from the underlying andesites and dacites and form characteristic granular brown loams. To the south, in the Te Rere and Te Hunga study areas, ash derived soils predominate and form typical yellow brown loams. At lower altitudes these appear similar to the Te Tuhi or Waihi soils, but at higher altitudes there is a strong intermixing of ash- and lava-derived parent materials which gives rise to soils of intermediate character. At the upland sites, gleying is common, but under Nothofagus stands a distinctive podsol is often present.

## RESULTS AND DISCUSSION

### Landslide morphology

*The scar* Debris avalanches are the most common form of mass movement and the point of failure was in the upper 10m of the landslide. The scar was frequently somewhat elliptical (Fig. 3) and averaged 28 m in width and 43 m in length. The crown scarp was nearly vertical, and the soil loss usually extended to the full depth of the regolith exposing the underlying bedrock or compacted breccia. The depth of regolith removed varied with soil type and ranged from 20 cm in soils composed largely of organic matter, to over 2 m in ash-derived soils. The most common depth was about 0.8 m. From the crown scarp to the widest point of the scar, the surface of rupture remained at the same slope and depth but from this point down to the beginning of the track the depth varied with the slope of the failure. At slopes of more than 35 °, no track could be distinguished, and the region of total soil loss extended to the waterway. At slopes of approximately 30 ° soil loss was almost complete to a point two-thirds of the distance to the lower limit of the scar. At slopes of 20 °, there was a rapid decrease in soil loss on the lower part of the scar. A few landslides with slopes as low as 15 ° occurred but at 10 ' slope, deposition was present. Bedrock was exposed on the surface of rupture at 97% of the upland sites and at 57% of lowland scars where the rupture usually occurred at the B/C horizon junction, coinciding with an increase in soil stone content. Deep fissures more or less perpendicular to the slope and linking adjacent scars at the level of the crown scarp, were present in the soils at 4 of the upland landslide sites. Similar tension cracks were also found between widely separated landslides in the headwaters of the Uretara Stream.

Fig. 2. Landslide morphology and distribution; A, two landslides showing typical morphology: elliptical scar at bedrock and long track;

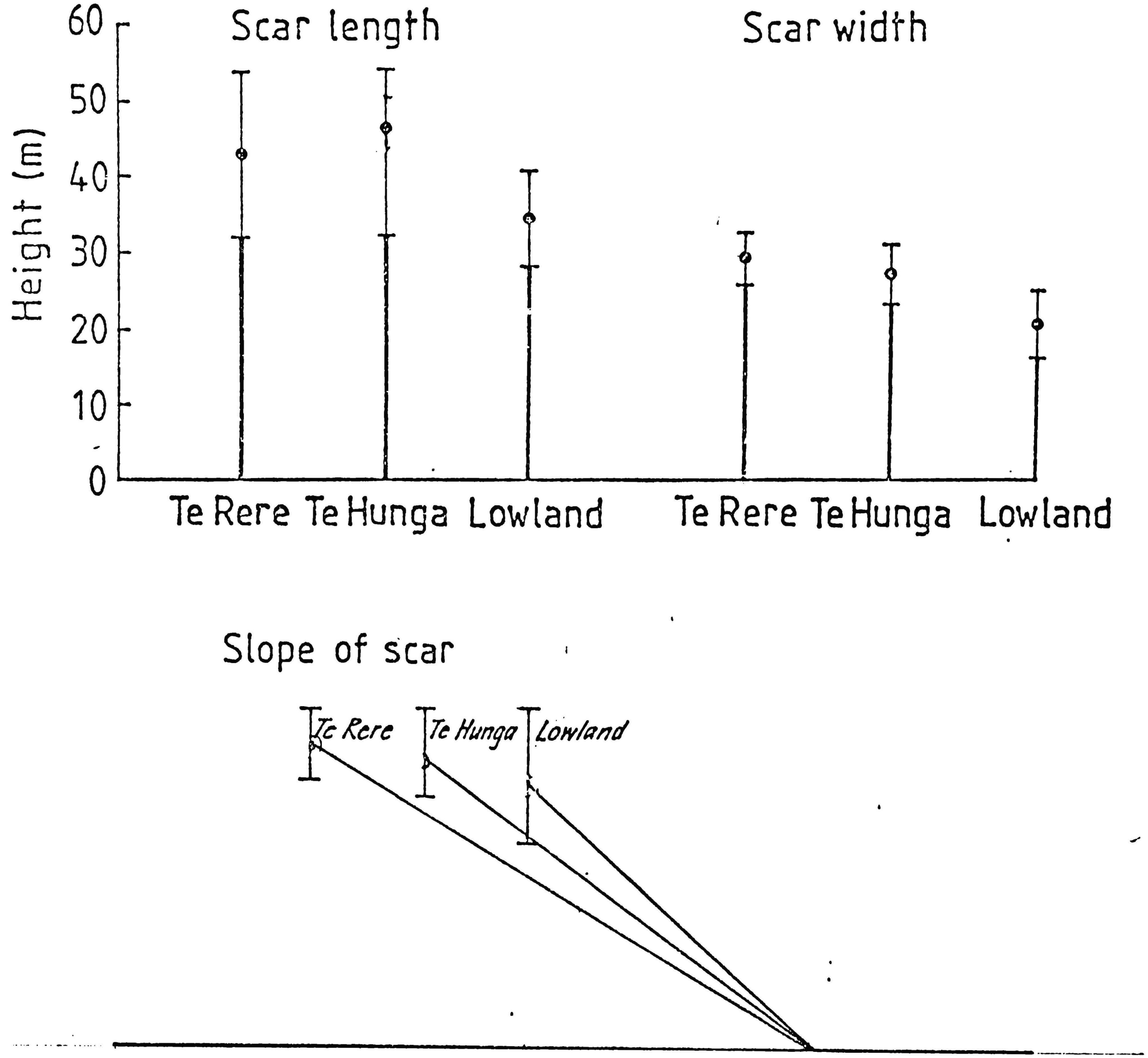

Fig. 4. Comparison of landslide scar length, width and slope between the three study areas.

*The landslide track* The profile, shape, and nature of the track was closely controlled by topography. Near the scar, for most of the width only a few centimetres of soil was removed containing only superficial tree roots and the upper A horizon. One or 2 secondary watercourses were usually present. Further downslope, where the slope exceeded 35°, corrasion from debris flow frequently caused deep secondary erosion, occasionally extending to bedrock. Conversely, at slopes less than 10°, deposition occurred. On some tracks there were several areas of scouring to bedrock and patches of deposition at changes in slope angle (Fig. 2). At 30-60 m from the scar, the zone usually ended in a larger watercourse which led into a creek at the foot of the principal slope. In the creek there was often evidence of a temporary debris dam, which had been removed by later floods.

*Differences between localities* Sample size of the field data resulted in successful comparisons only being possible between upland Te Hunga, upland Te Rere and the combined data for all lowland sites. The differences in dimensions of landslide scars between localities was statistically significant (Fig. 4). The slope of the plane of failure which was the same as the predominant slope in the scar region, differed between data groups (Fig. 4). The difference between Te Rere and Te Hunga reflected a true difference in the average slope of the terrain ($t = 4.96$, $P < 0.01$) but the difference between lowland sites and Te Rere upland ($t = 6.22$, $P < 0.01$), and Te Hunga upland areas ($t = 3.08$, $P < 0.01$) reflected the difference in the location of the landslides within the landscape in lowland areas. Lowland landslides were confined to the steepest parts of the terrain (Fig. 5), suggesting a basic difference in the natural angle of repose of the regolith between upland and lowland areas. Explanation of differences in scar length is also complicated by differences in slope (Fig. 6). For instance the bimodal distribution of scar length on Te Hunga upland results from the

Fig. 5. Western face of Te Hunga region of Kaimai Range showing concentration of landslides at higher altitudes.

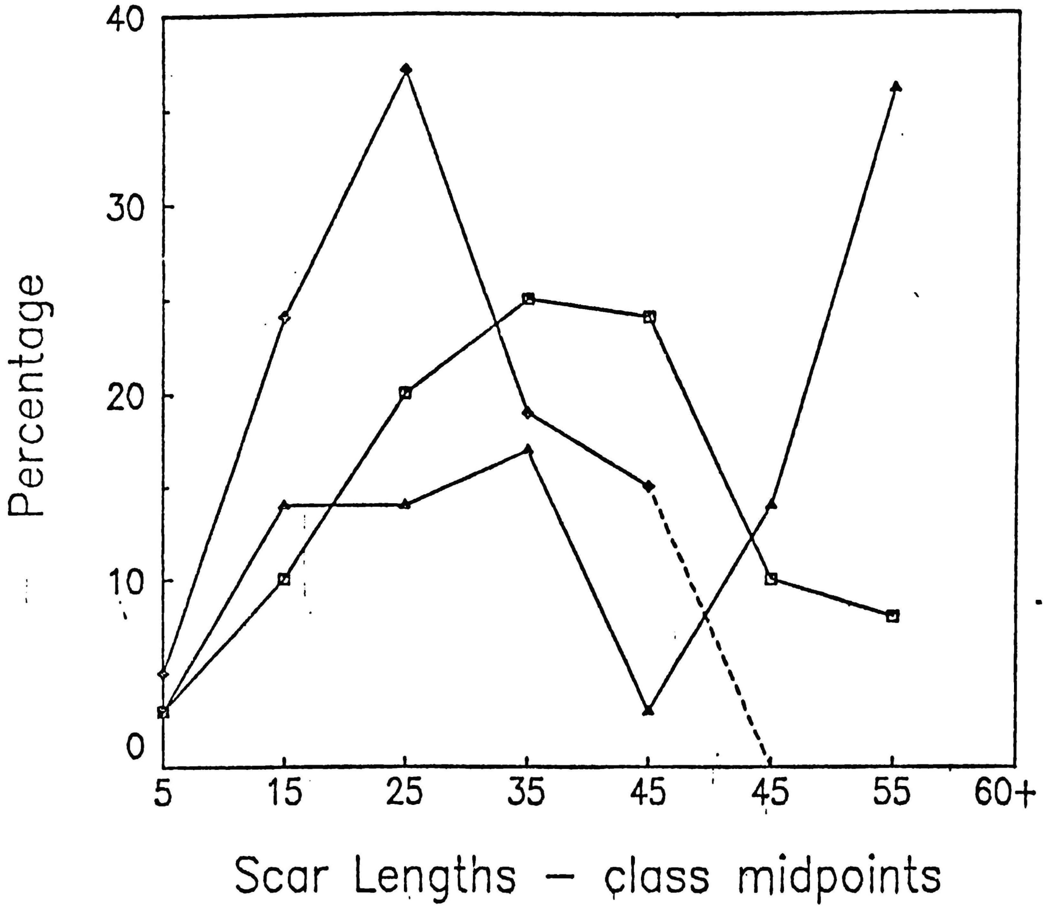

Fig. 6. Distribution of scar lengths in lowland, Te Rere and Te Hunga landslides; ◇—◇ lowland landslides (dashed line indicates no observations for next higher size class; □—□ Te Rere; △—△ Te Hunga.

predominance of slopes of over 35° where no track could be defined and scar lengths which exceed 60 m.

Nature of the landslide At slopes of less than 35°, where the scar could be defined, it was clear that rupture began in the upper half of the scar, possibly as a rotational movement that carried the regolith over the soil surface of the downslope region. The saturated moving soil segment then broke up as it gained downslope momentum and proceeded as a debris avalanche, or flow, that carried downslope vegetation with it to the foot of the slope or into the stream channel. Indications of the velocity of movement of the debris avalanche were often evident, particularly where the avalanche became entrenched in a watercourse. The path of destruction was in places centrifugally displaced outwards at sharp bends in a minor watercourse or, at other points, the avalanche track crossed a watershed into an adjacent channel, or split around more resistant ground to form islands. Most landslides occurred as a single failure at a site, but some secondary ruptures also occurred at the top of the track of a previous landslide. In these cases, it appeared that wash from the old scar surface, and soil changes related to root decay or greater extremes of wetting and drying, had been important factors contributing to their ocurrence. It is possible that the likelihood of secondary rupture was increased by slow rates of revegetation of the older track which may have been aggravated by goat browsing.

### Altitudinal distribution

There are a few landslides in the 3 study areas below 600m (Fig. 7), but above this altitude numbers rise sharply, particularly in the Te Rere and Te Hunga study areas.

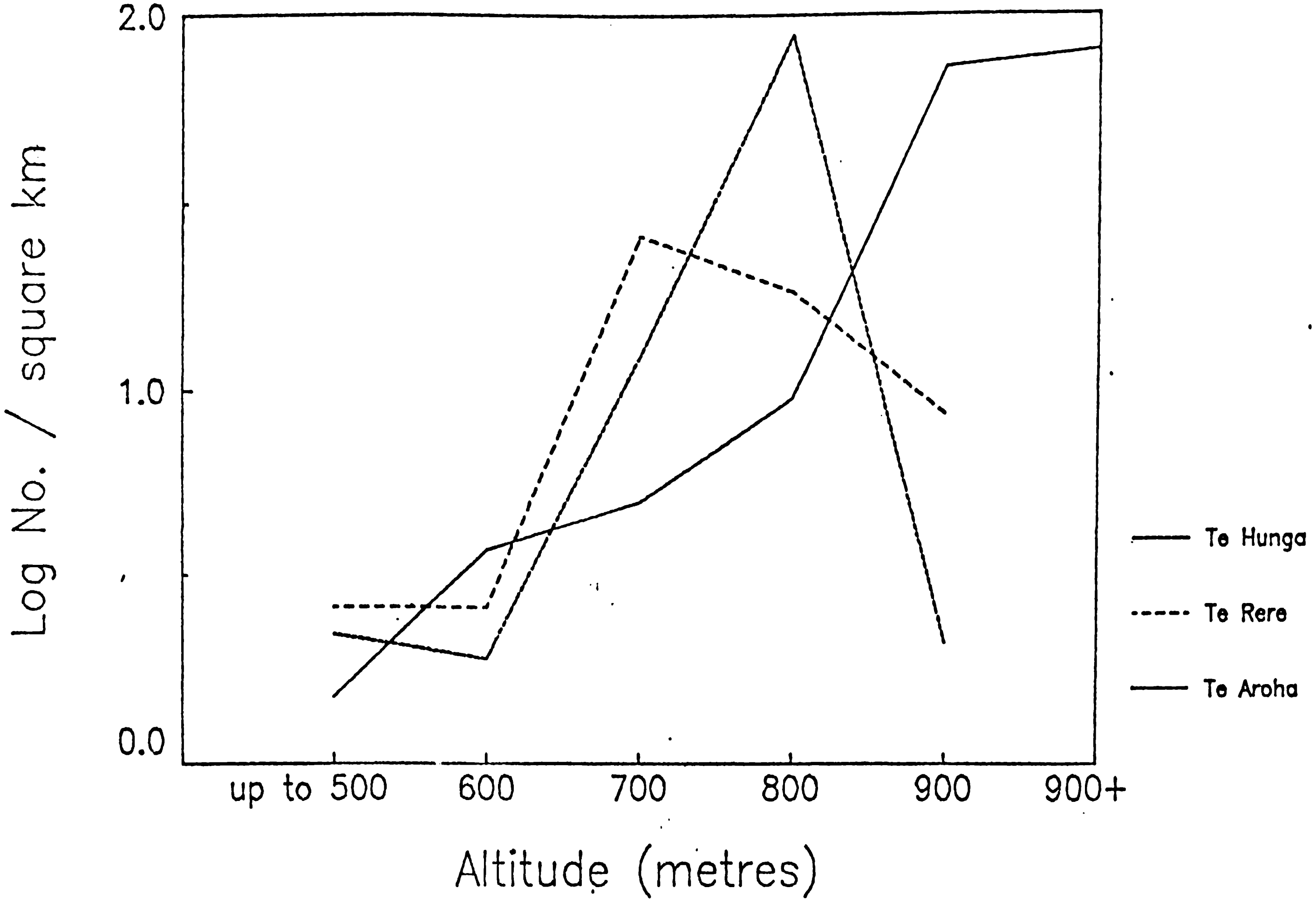

Fig. 7. Increase in landslide occurrence with altitude at the three study areas. The Y-axis has a logarithmic scale. Te Rere, ------; Te Hunga, ---------- ; Te Aroha, ————————.

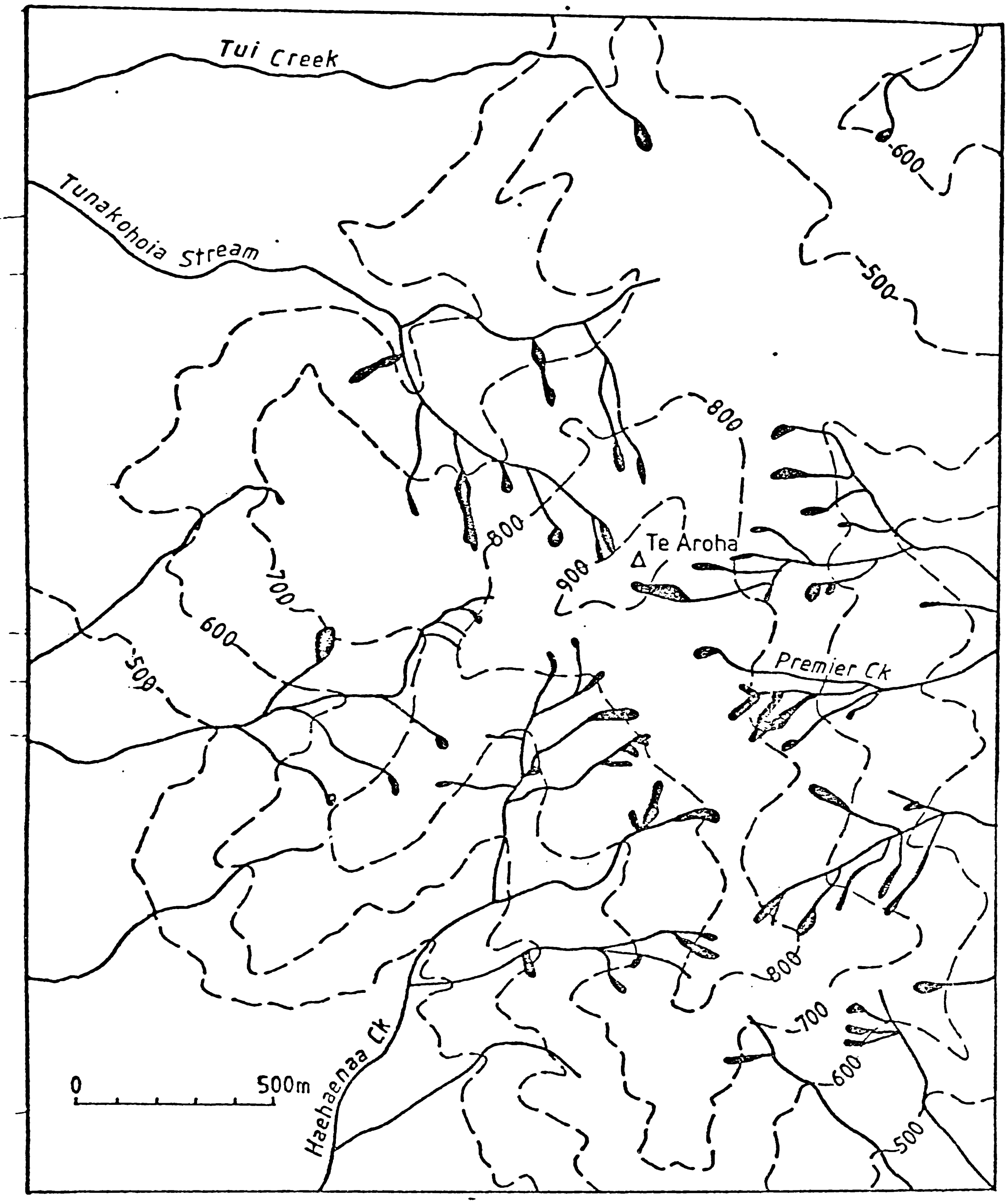

Fig. 8. Distribution of landslides in the Te Aroha study area.

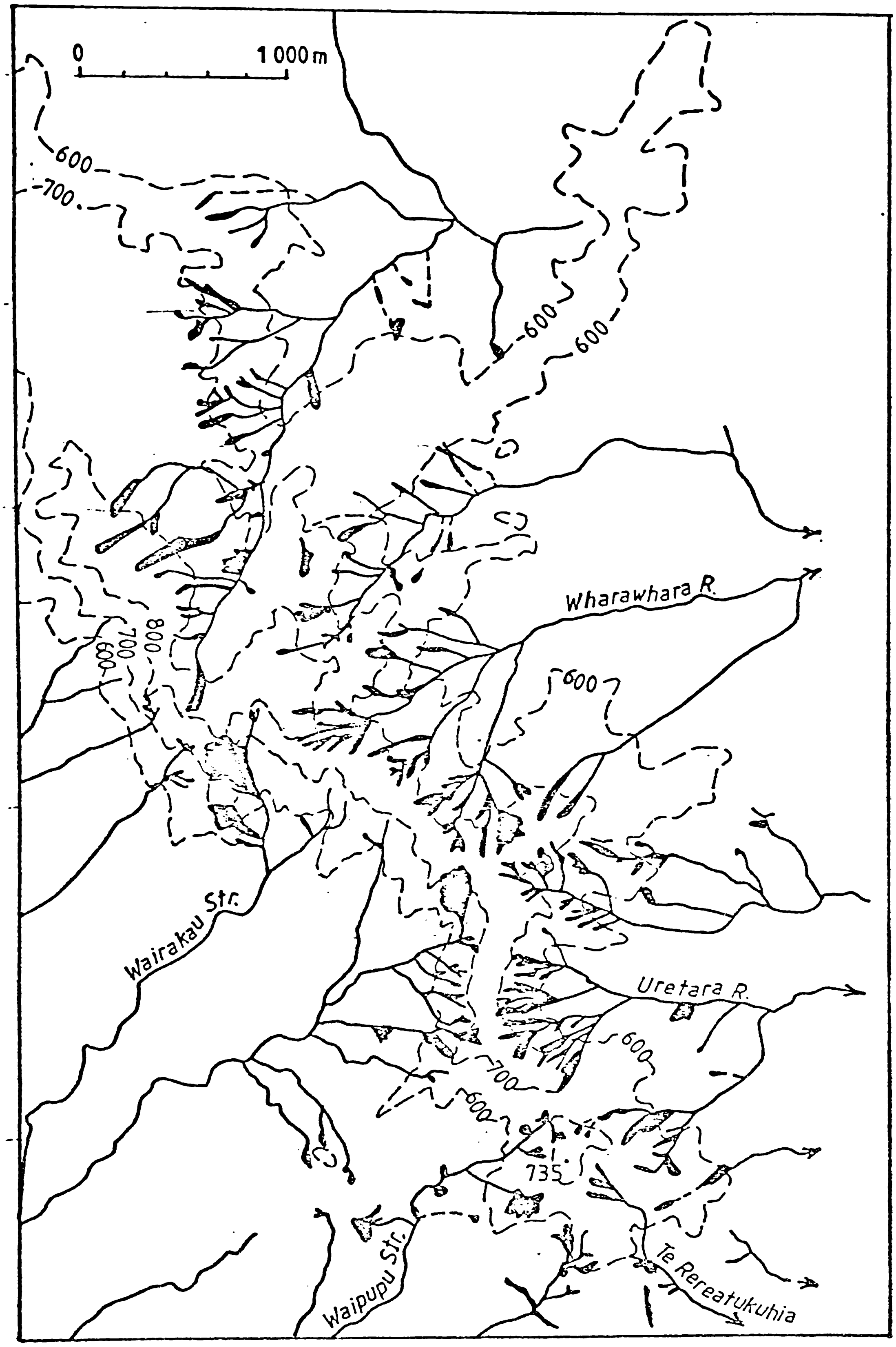

Fig. 9. Distribution of landslides in the Te Rere study area.

The lowland landslides are irregularly distributed in the terrain, although many are related to undercutting along stream banks. Away from the stream channels, most are found on steep terrain with slopes of over 40 ° at the failure point. Even in steep areas, such as the western side of Te Hunga, densities are low compared with those at higher altitudes (see Fig. 5). The low number of lowland landslides and their irregular distribution suggest that they can be regarded as constituting part of the normal continuing erosion processes.

The density of upland landslides increases to a peak at different altitudes in each of the 3 study areas (Fig. 7). On Te Aroha, the density increases steadily with altitude, but there is an abrupt change between 800 and 900 m. The small area and sharp prominence of the peak however, may exaggerate the significance of the 2 landslides found above 900 m (Fig. 8). At Te Rere, an abrupt change in density occurs between 600 m and 700 m altitude, and numbers decline above 800 m. (Fig 9). The maximum density is lower than in the other 2 areas and appears to be related to a lower predominant slope as suggested by the lower average slope of the surface of rupture and contour intervals (Fig. 9). On Te Hunga, the increase in landslide density occurs between 700 and 800 m altitude (Fig. 10). Few are found above 800 m due to the large central plateau at about 820 m. There are unusual instances of many landslides occurring in linear series across a face, particularly where a secondary failure has occurred in the track of an earlier landslide (Fig 11). In the Te Hunga area, secondary failures form a significant proportion of the recent landslides and constitute 54% of the fresh landslides on the most recent photographs. In the other study areas, although a few secondary failures were noted, they form only a small portion of the total number of landslides (Table 1).

TABLE 1

Proportion of secondary failures occurring in each study area.

| Area | 1943-60 | 1960-74 | initial number 1943 | new total | percentage |
|---|---|---|---|---|---|
| Te Aroha | 0 | 3 | 10 | 71 | 4.2 |
| Te Rere | 10 | 19 | 34 | 265 | 7.1 |
| Te Hunga | unknown | 72 | 155 | 387 | 54.5 |

TABLE 2

Estimated erosion rates by altitudes in the three study areas.( m3.Km-2)

| Altitude | Te Aroha | | Te Rere | | Te Hunga | |
|---|---|---|---|---|---|---|
| (m) | 1943-60 | 1960-74 | 1943-60 | 1960-74 | 1943-60 | 1960-74 |
| 8-900 | 2180 | 6280 | 490 | 1080 | 150 | 240 |
| 7-800 | 290 | 830 | 1050 | 2300 | 6200 | 9930 |
| 6-700 | 150 | 430 | 1490 | 3260 | 870 | 1390 |
| 5-600 | 110 | 320 | 150 | 320 | 130 | 210 |
| up to 600 | 70 | 208 | 150 | 320 | 180 | 280 |

Selby (1979) notes that 1000 m3/km2 = sufrace degradation of 1mm/year

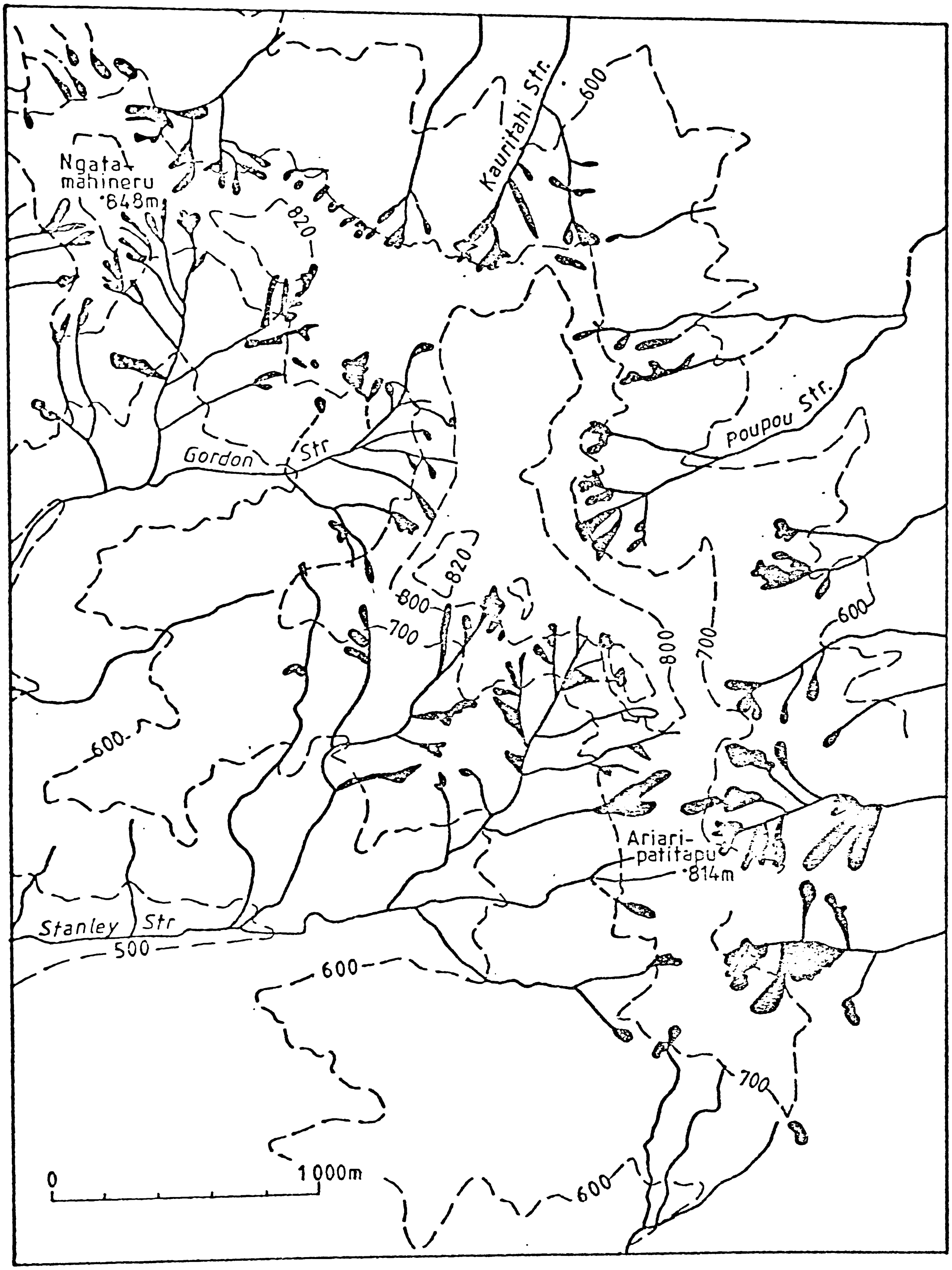

Fig. 10. Distribution of landslides in the Te Hunga study area.

Fig. 11. Landslides on Te Hunga forming linear series running from a face to ridge

The proportion of the total area affected by landslides is difficult to determine, because the scar and track have different rates of revegetation and cannot be readily separated on the photographs. Estimates based on the mean scar size in each area and on dot-grid counts of map areas, suggest that up to 5% of the area is bared to bedrock (scar) and up to 10% of the area, in both scar and track, is affected at the critical altitudes on Te Hunga (Fig. 12).

Crude estimates of the rates of erosion can be obtained by assuming an average depth of soil loss of 0.8m in the scar over half the area of the average scar in each locality class. This suggests rates of erosion of over 9000m3/km2 (Table 2) and average rates of surface lowering of over 4.5mm/annum in the most severely affected Te Hunga area although erosion rates in lowland parts of all areas average only 0.02mm/annum. The upland rates are somewhat extreme perhaps because the presence of tephra predisposes the sites to removal of all soil mantle to bedrock and hence exaggerates the soil loss.

## Physiographic distribution

In other studies it has been found that there is a strong tendency for landslides to be concentrated on slopes of a particular aspect. (Pain 1969; Selby 1976; Crozier et al. 1980). However, maps of the Te Hunga and Te Aroha study areas do not show strong asymmetry in landslide distribution about the main ridges or on opposite sides of the main range. In the Te Rere area (Fig. 9) a bias in densities between opposite sides of the range is due to photo interpretation difficulties created by shadows produced by the presence of bluffs, and asymmetry in the distribution about the ridges due to differences in slope. For example, in the headwaters of Waitawheta River, there are few landslides to the south, due to a gentle slope into Wharawhara River, while in the symmetric Uretara River basin, the landslides show a uniform

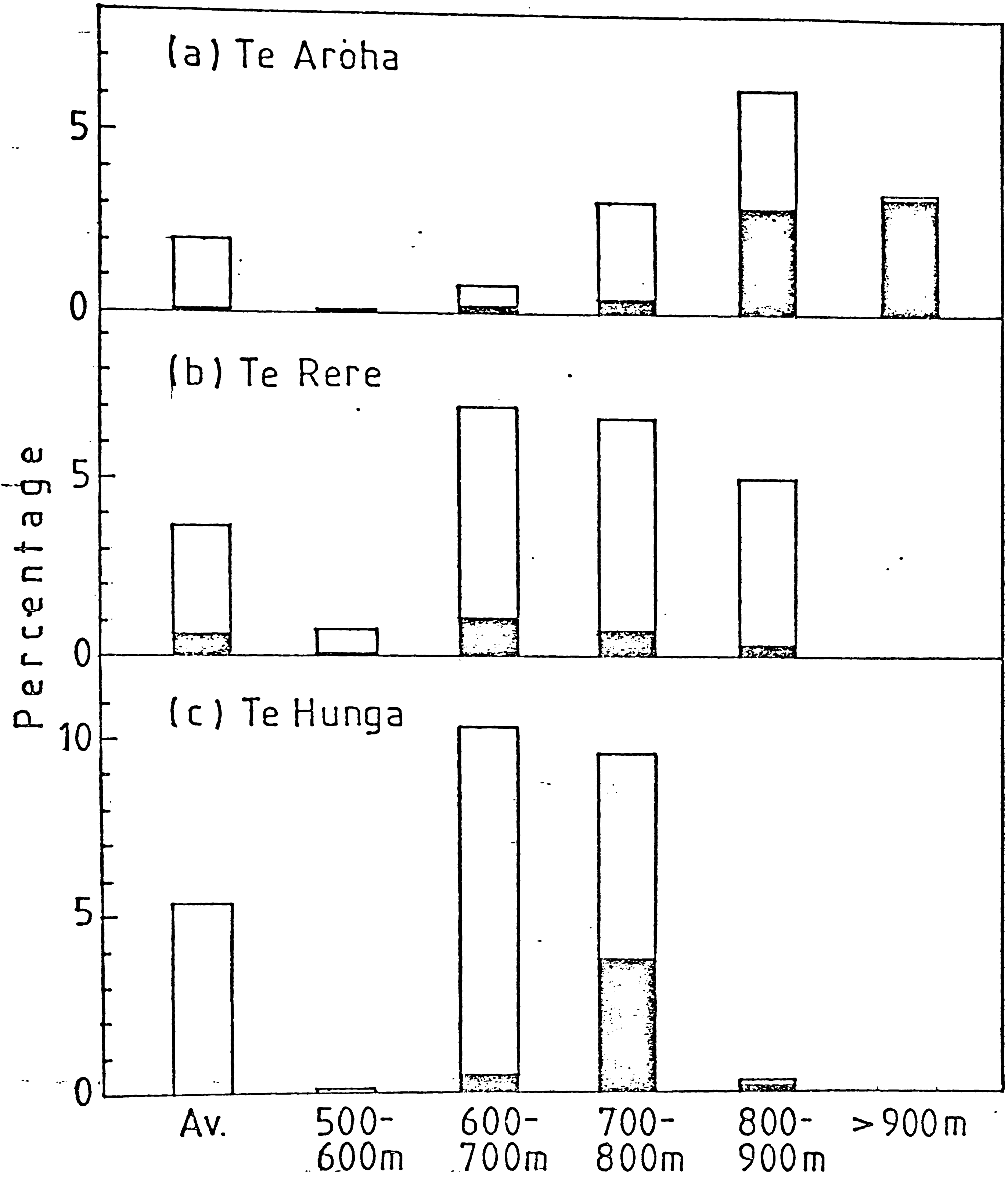

Fig. 12. Percentage of the land area affected by landslides in the three study areas. The unshaded portion of each bar is the area deforested and the shaded portion is area in which bedrock is largely exposed. The data is grouped by 100m altitudinal intervals.

distribution (Fig. 9). These basic differences invalidate a statistical comparison and suggest that there are no fundamental differences in landslide occurrence between slopes of differing aspect.

Although mass movements commonly originate close to the ridge crest in minor slope depressions and gully heads (Selby 1976, Crozier et al. 1980) this is not always so in Kaimai Ranges. Most landslides occur in gully heads or are marked by 2 or more slope depressions, but many apparently occur at midslope, a feature that is most conspicuous where the landslides occur as a linear series (Fig. 11). At these sites, the head of the scar of several landslides can be linked by an almost straight line, even where the height of the slope increases across the sequence.

## Relation of landslides sites to soil types

Classification of the soil in a landslide was determined by the predominent soil in the crown scarp but frequently mosaics of gleyed and ungleyed soils occurred which were related to minor topographic variations. At the upland sites landslides were associated with all soil types except the *Nothofagus menziesii* podsols (Table 3). The absence of landslides in the *Nothofagus menziesii* podsol may be due to the low clay content and the absence of a zone of clay or iron deposition in the soils. This could arise because *Nothofagus menziesii* sites have been subject to landslides in the past, resulting in new soils which, because the highly allophanic soil was largely removed by erosion, contain little clay. The frequent occurrence of *Nothofagus menziesii* colonising fresh scars supports this possibility. Twenty-one landslide were examined in lowland areas and found to be confined to silty soils similar to those in the surrounding forests, with the exception of 3 sites associated with gleyed soils in seepages.

## TABLE 3

Distribution of soil types at landslide sites. Values are given as a percentage of total sample in each study area.

| | Upland | | Lowland |
|---|---|---|---|
| Reference Name | Te Rere | Te Hunga | all areas |
| Yellow-brown loam | | | |
| Te Tuhi | 39.5 | 15 | 85 |
| Intermediate | 8.6 | 20 | 0 |
| Granular brown loam | | | |
| Te Aroha | 28.4 | 16 | 0 |
| Komata | 11.1 | 24 | 0 |
| Shaftesbury | 6.2 | 15 | 15 |
| Skeletal organic | 6.2 | 12 | 0 |
| Beech podsol | 0 | 0 | 0 |
| Sample size | 81 | 42 | 21 |

The soil at upland landslide sites had several unusual features. At the base of the soil profile, an iron pan frequently capped the bedrock. There was often a zone of dark humic clay, or occasionally only a clay pan (Table 4) associated with it, linked to humic-stained cracks in the regolith. Investigations using a soil auger revealed similar features in the surrounding soils except when there was a change in the vegetation type. The basal humic horizon was up to 5 cm thick, but sometimes was only a thin fracture line. The presence of an iron pan and iron concretions at the bedrock surface suggest active movement of water at this depth, and high proportions of allophane and carbon in the horizon (Table 5) also support this hypothesis. The concentration of allophane at the bedrock surface, however, will produce a zone of soil weakness which Wilson (1980) states could lead to progressive soil creep and may act as a major cause of slope failure during storms and earthquakes.

## Distribution of landslides in relation to vegetation

At lowland landslide sites, adjacent plants were healthy, but at all the upland sites the vegetation in the scar region was usually poor (showing many dead branches and dead branch tips throughout the crown) or even dead (Fig. 13). In areas where the canopy plants were dead, the vegetation was dominated by *Cyathea smithii*, *Pseudowintera axillaris*, or *Quintinia acutifolia*, but at most sites unthrifty plants of the predominant forest communities of the area were also present.

The affected vegetation included representatives of the *Ixerba brexioides* and *Nothofagus menziesii* forests, but types varied between the study areas according to the altitude of the greatest frequency of landslides. Thus, the affected forests were: on Te Aroha, only the *Nothofagus menziesii* forests; at Te Rere, some of the *Beilschmiedia tawa* forest as well as *Nothofagus menziesii* and *Ixerba brexioides*

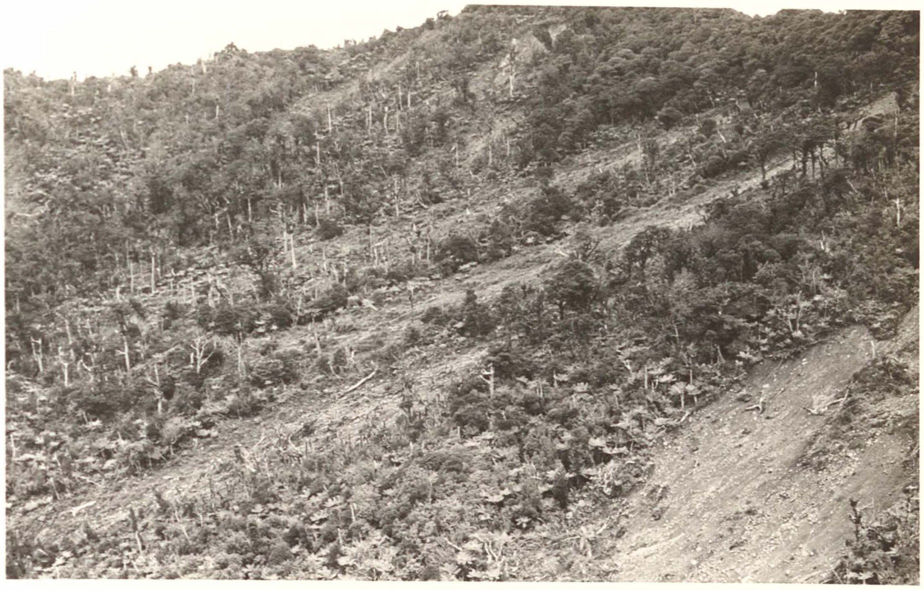

Fig. 13. Typical widespread unthrifty vegetation in the landslide zone. The unthrifty vegetation reaches the ridge crest at the upper left of the photograph but at the upper right there is an area of healthy forest capping the ridge.

### TABLE 4

Percentage of unusual features in soil profiles at landslides sites

| | Upland | | Lowland |
|---|---|---|---|
| Feature | Te Rere | Te Hunga | all areas |
| Humic zone of secondary deposition | 31 | 25 | 15 |
| Iron Pan | 70 | 81 | 15 |
| Clay pan | 3 | 0 | 0 |
| Sample size | 81 | 42 | 21 |

TABLE 5

Distribution of clay and allophane in three upland profiles in the Wharawhara catchment, Te Rere Study Area.

| Horizon | depth (cm) | clay % | % allophane in clay fraction | % carbon |
|---|---|---|---|---|
| A | 10 | 10 | 60 | 7 |
| B | 30 | 4.5 | 26.5 | 4 |
| Redeposition zone | 140 | 13.3 | 75.6 | 10 |

Determinations

Clay: by standard mechanical analysis (Nicholson 1978).

Allophane:by differential thermal analysis.

Carbon content: by titration with potassium chromate. (Nicholson 1978).

TABLE 6

Rates of increase in landslide numbers on the three study areas

| Study Area | Rates of increase per annum | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | (a) Simple percentage | | | (b) Exponential | | | (c) Exponential | | |
| | 1943-60 | 1960-74 | 1943-74 | 1943-60 | 1960-74 | 1943-74 | 1943-60 | 1960-74 | 1943-74 |
| Te Aroha | 12.9 | 18.2 | 23.8 | 0.063 | 0.087 | 0.065 | 0.088 | 0.087 | 0.088 |
| Te Rere | 19.5 | 15.2 | 22.2 | 0.067 | 0.054 | 0.061 | 0.143 | 0.069 | 0.107 |
| Te Hunga | 9.6 | 10.8 | 8.1 | 0.029 | 0.037 | 0.029 | no data | 0.065 | no data |
| Total Numbers | | | | | | | | | |

Landslide numbers obtained from the compound interest formula:

rate=(t2-t1 ) log (n2/n1)

where t1 and t2 are two dates and n1 and n2 are the respective numbers of landslides as either: column (b) total numbers of landslides at each date or column (c) numbers of fresh landslides only.

forests; and on Te Hunga only the Ixerba brexioides and Nothofagus menziesii forests. The unthrifty vegetation extended between landslides of an altitudinal series and often for a distance either side of the erosion sites. Unthrifty vegetation also continued below the landslide scar for many metres, but it could cease abruptly above the scar or below it. This often coincided with a change in vegetation, such as to Nothofagus menziesii, Dacrydium intermedium or Beilschmiedia tawa stands.

## Evidence for increased erosion

Landslide occurrence is frequently determined by the incidence of storms of either severe intensity (Selby 1967) or long duration (Eyles 1979). Such events may occur at irregular intervals. Often there are intervals of 20 years or more between erosion-inducing storms. With these relatively short intervals, the erosion can be regarded as essentially continuous, but where there is an interval of several hundred years between events, the pattern is usually regarded as episodic and triggered by major site or climatic changes (Schumm 1975).

The best evidence for recent increased erosion in the Kaimai Ranges arises from comparison of aerial photographs taken in 1943, 1959-60 and 1974 which clearly show an increase in the number of new erosion scars (Dale & James 1977). Within the 2 northern study areas the number increased 6-fold between 1943 and 1974 but on Te Hunga the proportionate increase has been less apparently because of the high initial number present (Table 6a). Landslide occurrence shows an exponential increase between 1943 and 1974 and, within each area, similar rates of increase based on total landslide numbers are found for the periods 1943-60 and 1960-74 (Table 6b). Recalculation, of the exponential rates based on fresh landslides visible on the 1943 and 1960 photographs, eliminates the effect of the different initial numbers. A continuing high rate of increase is found for Te Aroha whereas Te Rere and Te Hunga have similar, but lower, rates for the period 1960-74 (Table 6c). Unfortunately no suitable data are available for 1943 on Te Hunga. A more detailed analysis of part of the Te Rere area covered by the covered by the 1960 and 1964 photographs (Table 7), shows a large change in landslide numbers over this period which can be related to the major storm of 15 September 1960.

Later, increases between 1964 and 1973 occurred when there were only two major storms in March and November which followed the 1972 earthquake. Since 1974, there appear to have been few new landslides, in spite of a severe storms in 1976 and 1981. During the course of the field-work, no new landslides were encountered on Te Aroha or at Te Rere, but four were encountered on Te Hunga, principally on steep slopes. This suggests that the current period of severe erosion has moderated or ended and confirms the high natural and continuing rates of erosion on Te Hunga.

### Character of the increased erosion

Landslides visible on the 1943 aerial photographs are still very evident nearly 40 years later, suggesting that the rate of revegetation is very slow at the upland sites. The main woody plants appearing are *Weinmania racemosa, Pseudopanax simplex, P. colensoi, P. laetum, Griselinia littoralis* and *Quintinia acutifolia* all of which grow slowly on these sites. Landslide scars should then be visible for many decades because of their distinctive vegetation, yet examination of aerial photographs show few discontinuities in the vegetation which can be attributed to old landslide scars. Furthermore, in the areas in which numerous recent landslides have occurred, the vegetation surrounding the scar is fully mature, and probably many hundreds of years old (Fig 14). In many cases, the vegetation removed by the landslide can be seen to be

TABLE 7

Increase in landslide numbers between 1960 and 1974 in part of the Te Rere study area

| | 1960-64 | 1964-74 | 1960-74 |
|---|---|---|---|
| Numbers ($Km^{-2}$) | 8.5 | 17.2 | 39.9 |
| Increase (%) | 103 | 131 | 370 |
| Increase (compound rate) | 0.177 | 0.075 | 0.119 |
| Actual numbers | 33 | 67 | 155 |

similarly mature. This suggests that, in a large proportion of the affected upland area, it is several hundred years since a similar episode of intensive erosion occurred.

## GENERAL CONCLUSIONS

Erosion in the northern study areas appears to be episodic with an interval of at least 100 years. However, in the southern area, Te Hunga, erosion is at least partly continuous. The recent increase in landslide incidence which has occurred throughout the ranges, even on Te Hunga, began with a major storm in 1954. It was concentrated at differing altitudes and times in the 3 study areas. On Te Aroha the increase was greatest above 800 m altitude and occurred between 1960 and 1974; on Te Rere the increase was greatest between 600 and 700 m altitude and occurred between 1943 and 1960, and on Te Hunga the increase was greatest between 700 and 800 m altitude. On Te hunga there is a high "normal" erosion frequency due to steep terrain on which is superimposed an increase between 1960 and 1974. The intensity of the erosion now appears to be declining.

There is a strong zonation of landslides in which the critical altitude varies between different parts of the ranges. This zonation is not related to differences in slope, aspect, soils, or vegetation type.

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# BIOTIC INFLUENCES ON LANDSLIDE OCCURRENCE IN THE KAIMAI RANGES

## ABSTRACT

Recent changes in landslide frequency within the Kaimai Ranges, North Island, New Zealand appear to be related to storms and the 1972 earthquake. Two other factors have predisposed the area to the erosion: high soil moisture and widespread vegetation mortality. The rainfall increase occurs gradually from 1940 to about 1960, the year of maximum storm damage and would act through effects on ambient soil moistures. Vegetation mortality, linked with the fog zone, appears to have begun about 1946 just before the main erosion events. It occurs at the critical altitude, at the right time and is apparently episodic in nature. Thus it appears to be the most significant cause of erosion. Animal impact has not contributed to the erosion increase. Reports from many forested areas of New Zealand suggest that episodic vegetation mortality is a significant contributor to the recent increase in landslide incidence.

Explanations are sought for the recent increased erosion in the Kaimai Ranges. Vegetation mortality is present adjacent to the landslide scars and is thought to be the most important factor predisposing the area to erosion. No evidence was found to suggest that the mortality was due to browsing mammals but it was linked with a severe drought in 1946. Furthermore, prevalent fog by maintaining high soil moisture contents enhances vegetation drought susceptibility the and increases the landslide risk in the fog zone. Severe storms in 1954, 1960, 1966, and 1972 followed a period of below average storm intensity and triggered th current erosion episode. An earthquake in 1972 post-dated the main erosion increase but intensified the erosion episode. The same factors have produced increased erosion elsewhere in New Zealand consequently greater attention must be given to natural forest devastation of long return period which acts indirectly on the regolith.

Keywords: erosion, storms, vegetation mortality, cloud forest,earthquake, fog, goats, possums.

## INTRODUCTION

Erosion is generally recognised to occur in discrete episodes linked with random changes in climatic or other physical factors (Schumm 1975). Although some investigations within New Zealand have studied fundamental causes of landslides (Selby 1976a; O'Loughlin 1974; Rogers & Selby 1980) with the exception of Grant (1981), and James (1973) few studies in New Zealand have attempted to establish the reasons for increased incidence. There are, however, two well established preconceptions. On pasture land developed by forest clearance increased erosion has naturally been attributed to removal of forest cover (Selby 1972; Selby 1976b; Crozier et al. 1980). In forested areas the erosion has been readily ascribed to the impact of introduced animals and little weight given to the impact of other site and climatic changes (James 1973). Nevertheless evidence exists for erosion episodes in forested areas prior to the presence of introduced animals (Cunningham 1978, Mosley 1978, Hubbard & Neale 1980, Grant 1981)

### Erosion in the Kaimai Ranges

Jane & Green (1983a) have described the recent landsliding in the ranges. Evidence from aerial photographs showed a large increase in mass movements between 1943 and 1974 with few landslides since that time. Storms in 1954, 1960, 1966 and, following an earthquake, in 1972 were the trigger events for the landslides. The increased erosion was almost entirely confined to the higher parts of the ranges and occurred above a distinctive critical altitude which differed between areas. No link was found between the erosion and basement geology, soil type, aspect, slope, or vegetation type although extensive mortality and unthrifty vegetation was noted about the scar of the landslides.

## Vegetation condition

Mortality in the upland forests, first reported by Dale & James (1977), has been described by Jane & Green (1983b). Aerial photographs and dendrochronology dated the onset of the most recent mortality to 1946 and an earlier episode to 1914 coinciding in each case with severe droughts in the region. At any particular locality the mortality occurs above a critical altitude similar to that noted for increased landslide intensity. Above that altitude it is not confined to any particular forest type and all vegetation shows some damage. It was suggested that introduced browsing animals were not important in causing mortality.

## Causes of increased erosion

Slopes evolve towards equilibrium with the environment but seismic disturbances, climatic, or vegetation changes may initiate episodes of intensified erosion (Schumm 1975). Debris slides and avalanches are the most common forms of mass movement within the Kaimai Ranges. The threshold for debris slide failure is determined by soil strength and may be reduced by soil saturation, by extensive root death (Ziemer 1981) or structural modification of the soil. Changes may occur rapidly by a single trigger event such as earthquakes, treefall or intense rainfall; or gradually so that the threshold for failure is greatly reduced, for instance by soil saturation or root decay. Loss of root strength occurs directly in treefalls and eathquakes or from vegetation mortality, due to pathological causes, forest clearance, windthrow or perhaps animal browsing.

In the Kaimai Ranges the close link between landslides and vegetation mortality has been well recognised (Dale & James 1977, Jane & Green 1983a) but the nature of the link remains contentious. Whilst it is tempting to suggest that a direct link exists between the two phenomena other factors such as changes in rainfall, storm incidence, or seismic activity must be excluded.

Futhermore any explanation must encompass two important factors:

- the concentration of the landslides at or above a critical altitude which differs between different parts of the ranges
- the timing of the increased erosion.

In this paper we attempt to demonstrate that vegetation mortality was the major factor predisposing the area to landslides in a series of storms. It is also suggested that the fog that commonly covers covers the range summits is a central feature that affects the water balance and predisposes the regolith to landlides and the vegetation to severe droughts.

## The Area

The Kaimai Ranges are bounded on the west by the Waihou River and Hauraki Plains and to the east by the lowlands of the Bay of Plenty. The higher terrain can be divided into three discrete tracts with differing histories of colonisation by introduced animals, climates and landslide distribution. A study area was established within each of these areas and details are described in Jane & Green (1983a).

The vegetation has been described by Dale & James (1977) and mapped by Nichols (1965, 1974). Below 300 m the forest is dominated by *Dysoxylum/Laurelia /Beilschmiedia* forest; between 300 m and 6-700 m *Beilschmiedia* forest containing scattered emergents of *Dacrydium cupressinum* and *Podocarpus ferrugineus* predominates; above this a broad ecotone of *Ixerba brexioides* usually marks a change to *Nothofagus menziesii* forest. In the upland forests *Quintinia acutifolia*, *Weinmannia racemosa* and *I. brexioides* form dense seral stands which often cap the crest of the range.

## METHODS

Animal impact and vegetation condition within the ranges was assessed using constant count plots established at the landslide sites and in the adjacent vegetation. Details of these methods are described elswhere (Jane and Green 1983b). In the three study areas soil moisture content at 20 and 50 cm depth was determined by gravimetric methods at monthly intervals from September 1980 to April 1981 and October 1981 to March 1982. Soil water potential- moisture content characteristics were determined by pressure plate techniques at the Forest Research Institute Rotorua. Piché evaporimeters were installed from November 1981 to March 1983 at the Te Hunga site and read at fortnightly or lesser intervals. Cloud base was recorded at 3 hourly intervals through the day from an observation point near Matamata from September 1980 to April 1981. Meteorological, seismic, Catchment Board and Forest Survey reports together with other historical information were searched for evidence of major changes in erosion and vegetation condition within the ranges. Relevant dates in the Bay of Plenty Times (Tauranga), Waikato Times (Hamilton) and the Te Aroha News were also searched where appropriate. Information on the liberation and spread of introduced animals was obtained from New Zealand Forest Service, Agricultural Pest Destruction Council, Department of Internal Affairs (Wildlife Branch) reports and personal observations of L. T. Pracy.

## RESULTS and DISCUSSION

### Introduced animals

Goats (*Capra hircus L.*) Goats escaped from mining and logging camps in the extreme north of the ranges about 1870 and gradually spread southward. During the 1920's liberation on many farms for weed control spread goats around the forest. Numbers peaked about 1940 but declined rapidly in following decades from intensive hunting campaigns. Between 1943 and 1974 goat numbers were highest in the Te Rere study area and to the north but low on Te Hunga where they apparently remained absent from the summit (Table 1). The wet upland habitat restricts goat invasion particularly in areas such as Te Hunga. Comments from hunters and others, including notes on National Forest Survey Reports of 1951, indicate that goats were largely confined to open drier-habitat areas such as landslide sites.

Vegetation structure shows little evidence of goat impact (Fig. 1). Regeneration of the smaller size classes is not repressed and large plants of palatable species remain. Older stems of Coprosma australis are common although it is a very palatable plant normally killed out completely in the early stages of forest damage by browsing and ring barking (Fig. 1). The same diameter distribution pattern is present in all study areas in spite of differences in animal colonisation history. The main variations between areas most probably reflect changes in rainfall. Typical examples are the greater abundance of unpalatable plants on Te Aroha, such as Nothofagus fusca which prefers drier sites (Fig. 2) and their southward replacement by Ixerba brexioides, which prefers wetter sites. Browsing of the key seral plants has modified the composition of seral communities producing grass and sedge communities on recent landslide scars and areas of vegetation mortality, especially in the northern areas, but these points are not easily demonstrated without a photographic record.

TABLE 1 Summary of pattern of animal dispersal and impact with indications of the years of peak animal numbers in each area.

| | Lowland areas | | | Upland areas | | |
|---|---|---|---|---|---|---|
| | Te Aroha | Te Rere | Te Hunga | Te Aroha | Te Rere | Te Hunga |
| POSSUMS | | | | | | |
| Numbers | Peak 1962 | Peak 1962 | still low | Peak 1962-72 | Peak 1962-72 | largely absent |
| Vegetation depletion | moderate | severe, recovery by 1972 | low - increasing | light | light to moderate | very light |
| GOATS | | | | | | |
| Numbers | moderate to 1963 | high to 1963 | moderate to 1963 | moderate to 1963 | high to 1975 | low to absent |
| Vegetation depletion | severe to 1975 | severe to 1975 | severe to 1975 | moderate | moderate to severe | light |

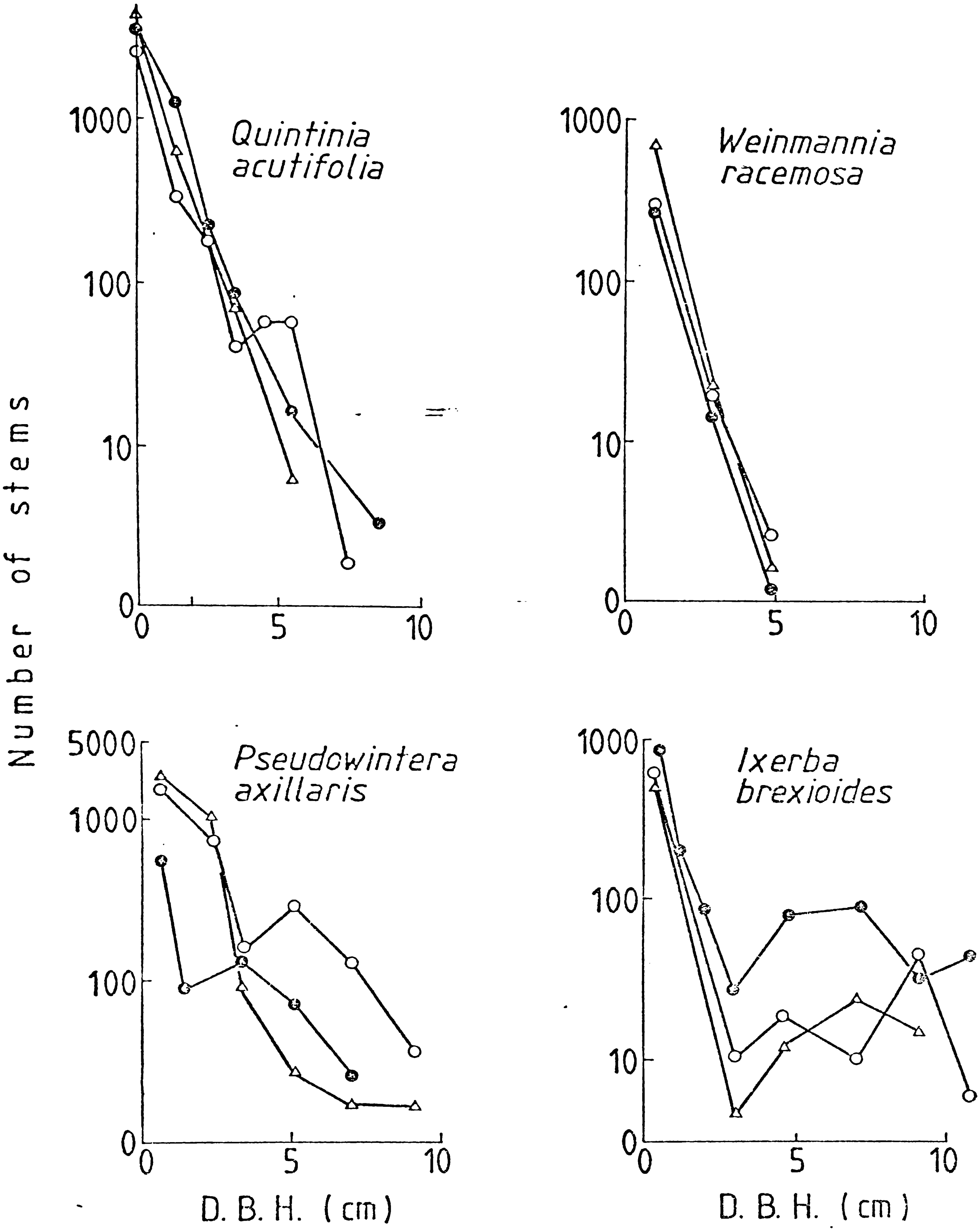

Fig. 1 Diameter size class distributions, plotted on a log scale, for four common species at Te Aroha - ; Te Rere o - o; Te Hunga @ - @.

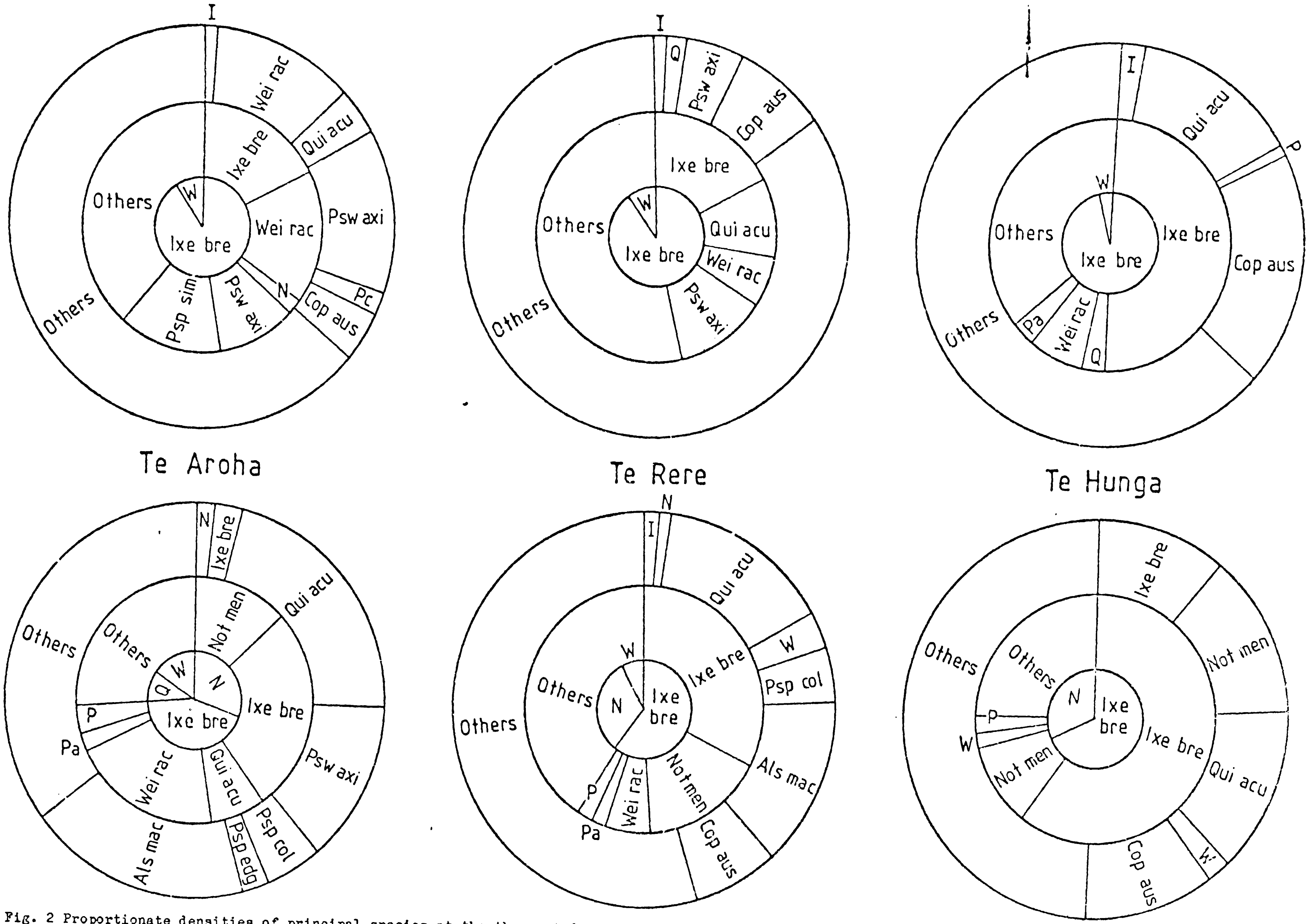

Fig. 2 Proportionate densities of principal species at the three study areas in the tree class (inner circle) shrub class (middle circle) and seedling class( outer circle). The upper row is *Ixerba* forests, the lower *Nothofagus menziesii* forests. Abbreviations are *Weinmannia racemosa* (Wei rac or W); *Pseudowintera axillaris* (Psw axi or Pa); *Pseudopanax simplex* (Psp sim or P); *Quintinia acutifolia* (Qui acu or Q); *Pseudopanax colensoi* (Psp col or Pc); *Coprosma australis* (Cop aus); *Alseuosmia macrophylla* (Als mac or A); *Pseudopanax edglerii* (Psp edg or Pe).

## Possums (*Trichosurus vulpecula*)

Possums were liberated at several points around the Kaimai Ranges from about 1914 but the main spread has been southward from the Karangahake Gorge (Fig. 3). Prior to 1948 they were generally in low numbers and confined to areas north of Mt. Te Aroha. By 1963 possums were numerous in lowland forests as far south as the end of Te Rere area but were absent from Te Hunga. To the south invasion occurred from two points, but numbers remained low. Since 1963 the spread has continued but numbers are still low in the central part of the ranges and, as indicated by pellet frequencies from the 1975 and 1980 surveys, decline markedly in the upland forests (Fig. 4).

The upland environment is cold and wet with persistent fog and this, plus the presence of a dense understory of *Astelia* species, *Gahnia pauciflora*, and other sedges, makes the forest an unfavourable possum habitat (Fig. 5). Few highly palatable plants such as *A. serrata*, *F. excorticata* and *Pseudopanax* species are present. Staple plants of the possum diet are also uncommon. *Metrosideros robusta* is absent and *Weinmannia racemosa* is not a common canopy constituent although it is abundant in the sub-canopy and shrub tier (Fig. 2). The relative abundance of *Weinmannia racemosa* in different parts of the ranges (Fig. 6) suggests that selective mortality of this species has not occurred and slight differences in the abundance of the uncommon but highly palatable *Pseudopanax* species, especially in the shrub tier, probably reflects local differences in climate.

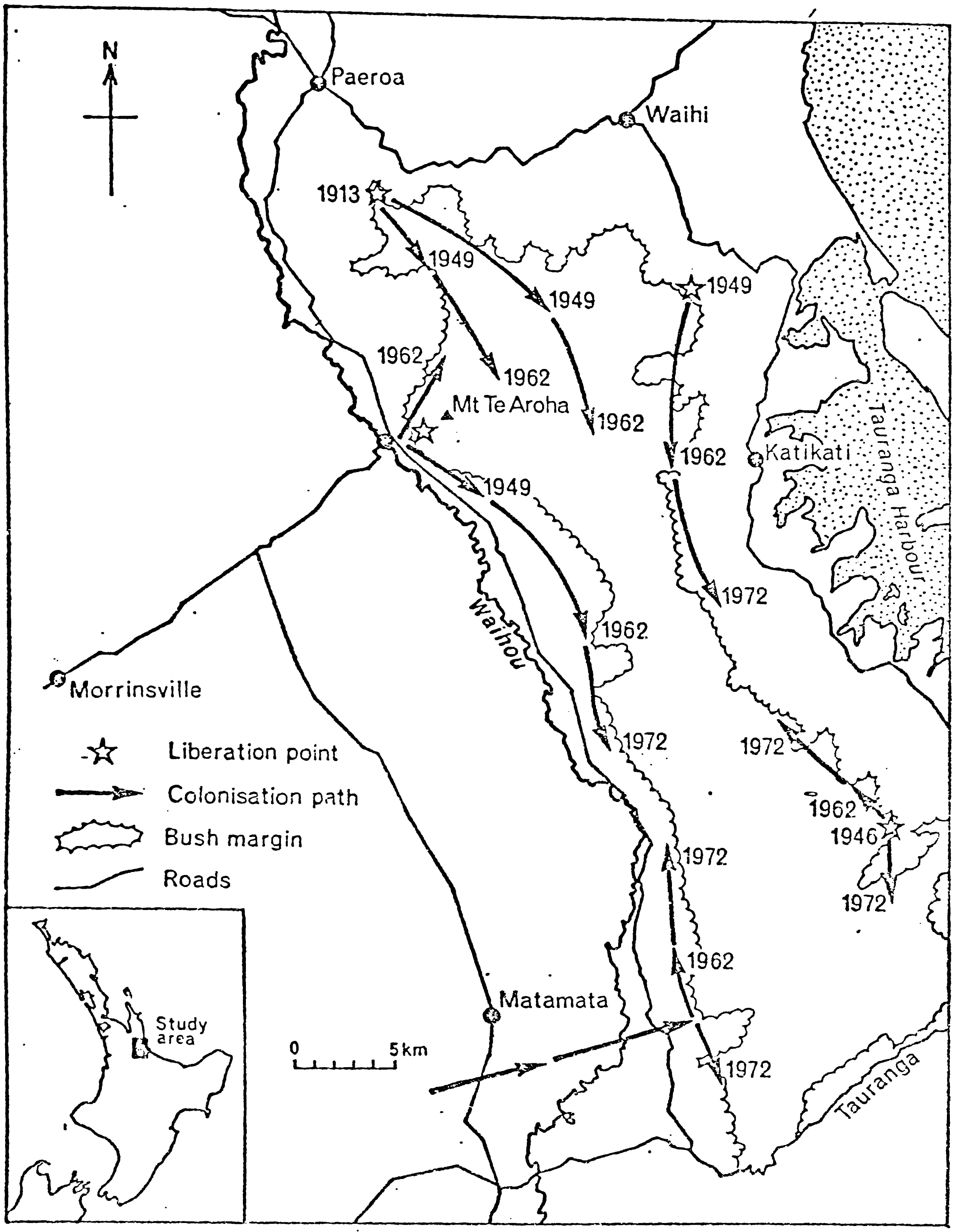

Fig. 3. Possum liberation points and subsequent disperal patterns in Kaimai Ranges. Dates indicate location of peak possum numbers at a survey date.

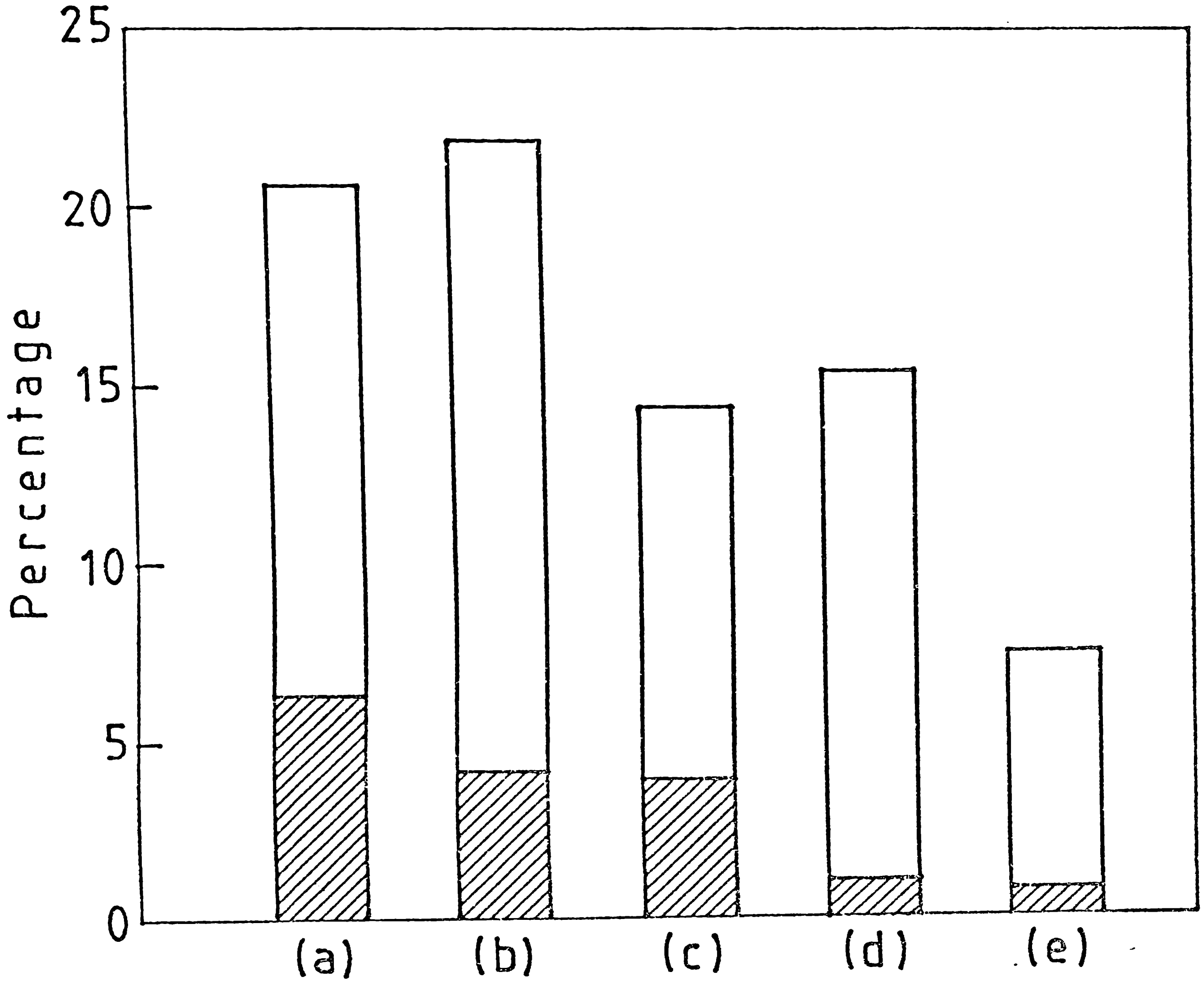

Fig. 4. Possum pellet frequencies (%) by forest types: (a) lowland (b) Beilschmiedia /Weinmannia, (c) Beilschmiedia /Ixerba, (d) Agathus /Nothofagus (e) upland. Data from 6000 presence/absence plots. Total bar heights are 1975 frequencies; shaded heights are 1980 frequencies.

Fig. 5. Dense understory of *Astelia* spp., *Gahnia pauciflora* and other sedges in upland forests resulting in an unfavourable habitat for possums.

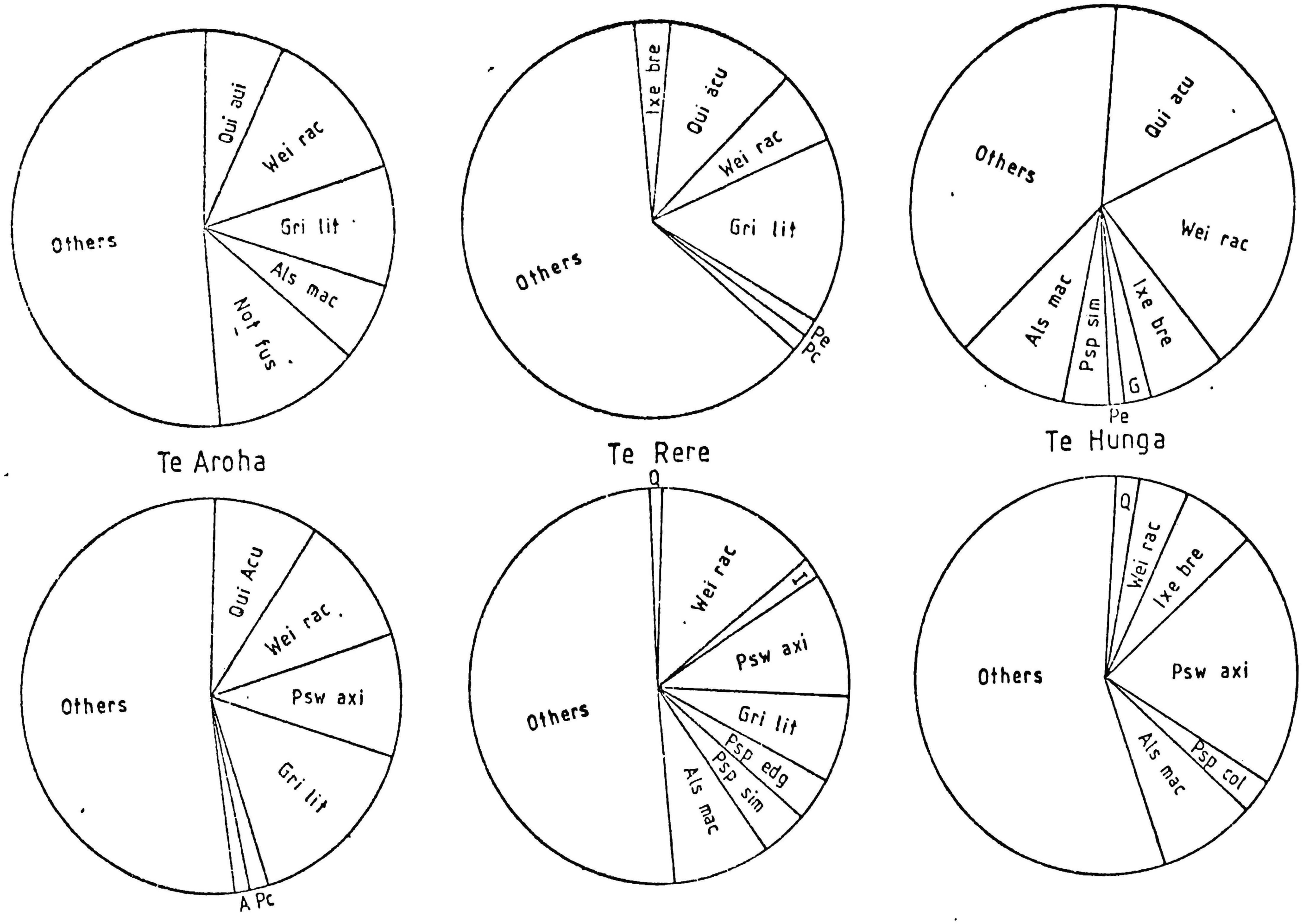

Fig. 6 Proportionate densities of principal shrub species at the three study areas. Upper row is *Quintinia* dominated shrubland and lower row is *Pseudowintera* dominated shrubland. Abreviations as for Fig. 2. with the addittion of *Griselinia littoralis* (Gri lit or G) and *Nothofagus fusca* (Not fus)

## Browsing and Landslides

Experiences on Mt. Egmont, New Zealand, where goats have been known to cause extensive canopy mortality in low seral forest (Atkinson 1964), and in many other highly eroded mountain areas (Holloway 1959; Howard 1965), initially suggested that they were the cause of increased erosion in the Kaimai Ranges (Revington, Bay of Plenty Catchment Board, pers. comm.). Dale & James (1977) suggested that the landslide increase has: "extended down beyond Ngatamahinerua, following approximately 5 years behind the expansion of the possum colonisation down the ranges". They suggested that mortality of *Metrosideros robusta* and *Weinmannia racemosa* from the *Beilschmiedia tawa-Metrosideros* forest was due to possums leading to canopy breakdown and later was a primary cause of landslides. Careful re-examination of the data lends little support for these hypotheses. Jane & Green (1983b) indicate that landslide numbers increased uniformly throughout the ranges particularily in the period 1960-74. The peaks in population densities of goats and possums fail to correspond with the increased landslide frequency on Te Hunga, and to a lesser extent Te Aroha and Te Rere. Furthermore, possum densities decline steadily with altitude, and zones of preferential animal usage fail to coincide with the pronounced zonation of the landslides.

Dale & James (1977) were unable to demonstrate any browsing impact in 1974 and examination of the diameter frequency distributions of a few key species shows no evidence for recent depletion within or between the study areas despite past differences in animal numbers (Fig. 4). The inaccessibility of the upland areas until recently, when a track system was developed, also suggests that depletion was insignificant. Damage on low seral forests on the range crest may have resulted in a few small clearings (Fig. 7) but browsing was most severe on landslide scars where the open drier habitat and abundance of palatable seral plants were attractive. This has given a false impression of their impact.

Dale & James (1977) also suggested that possum induced mortality of riparian plants has increased channel erosion and caused undercutting of slopes leading to landslides. The nature of the debris avalanche described by Jane & Green (1983a) precludes this form of mass movement and the characteristic riparian vegetation of other regions such as the Urewera or Pohangina (James 1973, Wallis & James 1973) composed of <u>Aristotelia serrata</u> and <u>Fuchsia excorticata</u> is totally absent. We believe that vegetation differences are not due to introduced animals but to soil or climatic limitations. The presence of these species on the Whakamarama plateau, a few kilometres to the south of the Kaimai Ranges, in logged forest, on well drained pumice soils and at moderate possum densities, supports this proposal.

Fig. 7. View southwards along the range showing Te Rere bald, an area of mainly sedges possibly maintained by animal browsing. Dead spars in the foreground and on the right are caused by vegetation mortality of complex causes. Te Hunga is in the distant background.

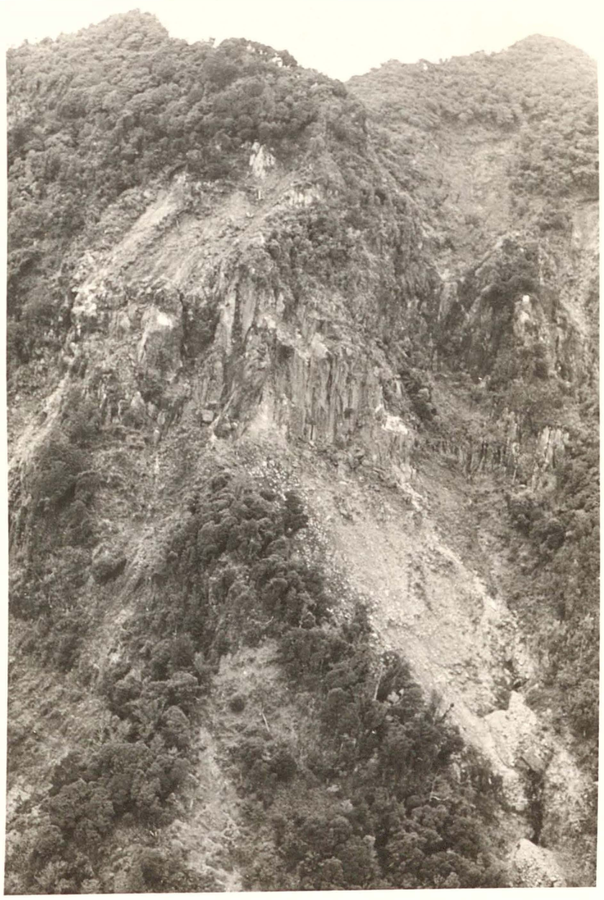

Fig. 8. Landslides above and rockfalls on bluffs in the Wairakau stream triggered by the 1972 earthquake.

There is therefore little evidence that introduced browsing mammals have had a significant effect on the vegetation, certainly not sufficient to produce widespread vegetation mortality in the areas of the Kaimai Ranges where increased erosion has occurred. The widespread vegetation mortality in the upland forests predates significant possum numbers and the intensity of the mortality does not reflect the variations in goat numbers. Browsing animals therefore may be discounted as a factor predisposing the terrain of the ranges to landslides.

## Seismic activity

Earthquakes greater than Mercalli magnitude (MM) VII may cause landslides (Eiby 1966). The Kaimai ranges are west of the main seismic belt of the North Island where many deep earthquakes occur each year (Smith 1978). Isoseismals of the deep earthquakes are displaced hundreds of kilometers to the east of the epicentre so few shocks are felt in the Kaimai area (Hatherton 1970). Few of the many small, shallow earthquakes associated with this belt generate intensities greater than MM VI.

The most severe earthquakes felt in the region have been associated with the Hauraki Rift bounding the Kaimai Ranges to the west (Hochstein & Nixon 1979). The earthquake of December 1920 of MM V at Te Aroha was of unknown epicentre hence the impact cannot be assessed. The Morrinsville earthquake of 1926 had very strong local effects (Eiby 1968) and, although no damage was reported from Te Aroha, it is possible that landslides in the headwaters of the Waiorongomai stream and on Te Hunga originated at this time.

An earthquake in 1972, centred just south of Te Aroha (Adams et al. 1972), caused damage at Te Aroha and landslides as far away as Lake Karapiro (23 km). Local people attribute many of the recent scars in the Wairakau (Fig. 8) and adjacent catchments to this earthquake, a view supported by aerial photographs (Jane & Green 1983a). Isoseismals (Adams et al. 1972) suggest an intensity of MM VII for a distance of less than a kilometre from the epicentre, smaller than might be expected from the area over which landslides occurred.

Trifunac (1971) and Boore (1972) reported intensification of an earthquake at a seismic recording station and proposed that it was due to topographic focussing of the seismic wave. The nature of the focussing is poorly understood, particularly in complex terrain, but the shape of the hills in the Kaimai Ranges is such that topographic focussing of the shock waves could follow the model of Trifunac (1971) (Smith pers. comm.). The broad plateaus and steepness of the terrain could focus the energy of the seismic shock waves resulting in linear series of landslides along a steep face near the crest, and at right angles to the path of energy transmission. In this respect the secondary landslides on Ngatamahinerua, a flat topped peak, are particularly striking. Here scars of secondary landslides are aligned across different points in the track of earlier landslides on slopes facing towards and directly away from Te Aroha. Topographic focussing is a reasonable explanation for these linear series of landslides which otherwise appear unrelated to the topography. In other localities the earthquake may have produced failure by disturbance of the allophanic clays in the basal humic horizon of the soils leading to tension cracks joining adjacent scars and increased erosion risk in the storms of late 1972. Similar circumstances have been reported elsewhere (Pain & Bowler 1973, Cotechia & Melidoro 1974).

The earthquake cannot explain the increase in landslide occurrence between 1943 and 1972, but it produced renewed landslide activity in already unstable terrain both immediately and in later storms.

### Rainfall and storm occurrence

Rainfall increases markedly southward along the ranges. At Waihi annual rainfall is 2160 mm, at Wharawhara it is 2500 mm; to the west at Te Aroha it is 1500 mm and at Shaftesbury 2000 mm. A steep altitudinal gradient in rainfall occurs on the western side of the ranges from Mt. Te Aroha summit (2000 mm) to Te Aroha town (1500 mm) and Morrinsville (1100 mm). Fitting a spline curve to the Te Aroha town rainfall data for the past 73 years shows that there has been an increase in rainfall between 1940 and 1960 with the higher level maintained until the present time (Fig. 9). Early records (1880-1890) indicate a similar rainfall to that before 1940. Prolonged periods of above normal rainfall lead to increased base flows in the rivers particularly in the summer (Fig. 10).

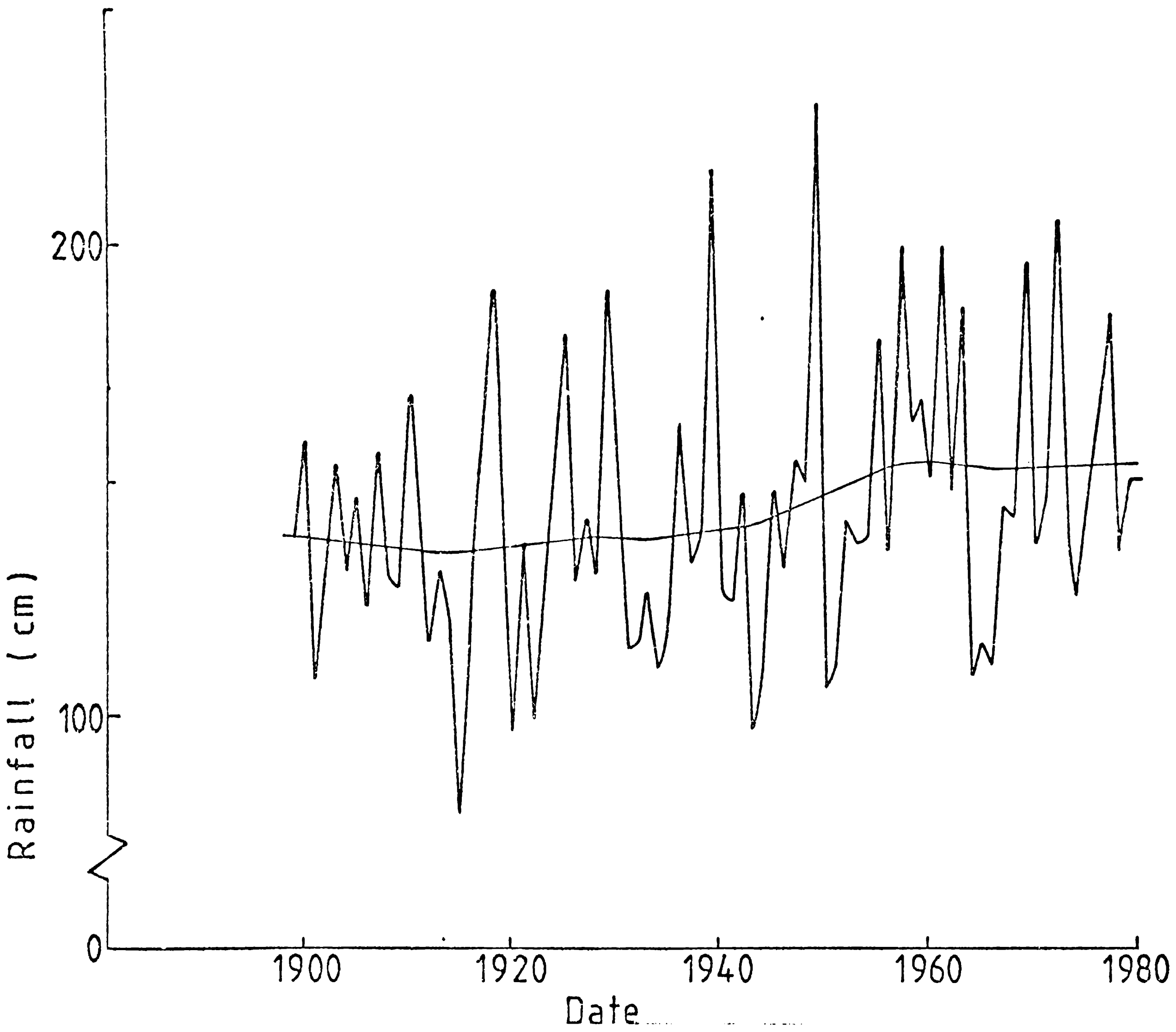

Fig. 9. Annual rainfall at Te Aroha from 1900 to 1980 with an approximately 30 year running mean superimposed.

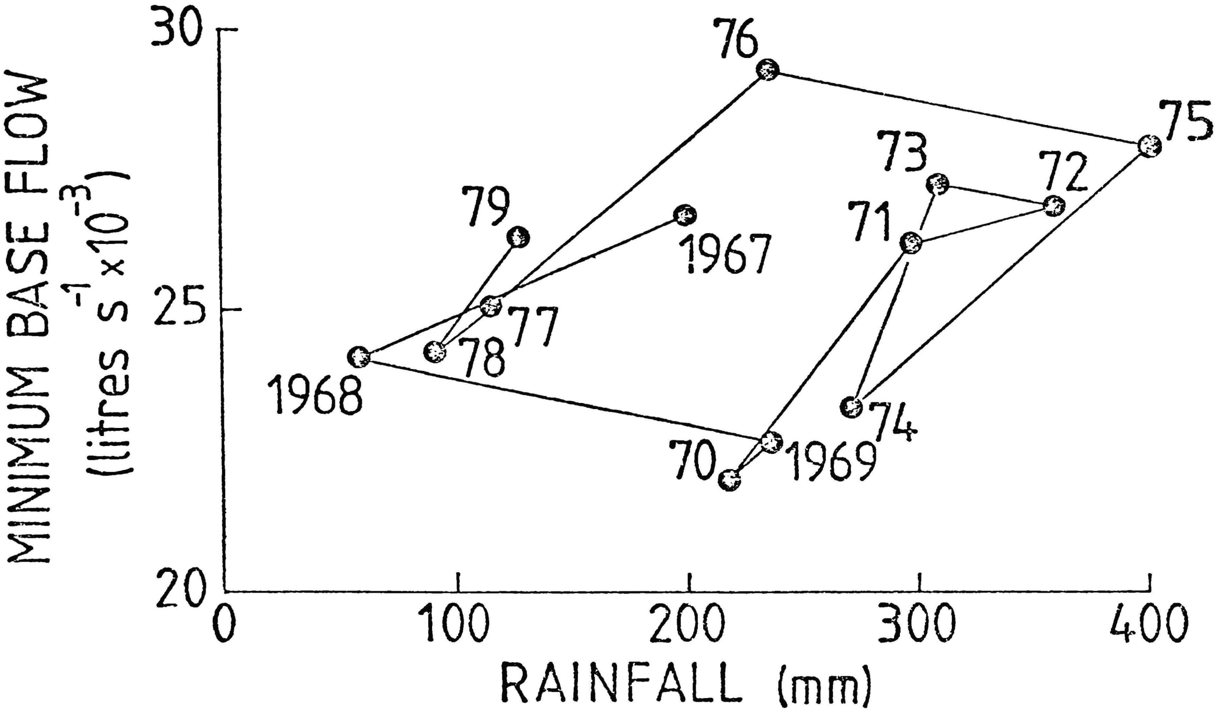

Fig. 10. Minimum summer base flows in the Waihou River at Te Aroha plotted against summer rainfall from 1967 to 1981. Successive values are dated and joined. Changes in base flow /rainfall relationship occur in the dry year 1969 and the very wet year 1976.

Very high intensity falls result from tropical storms which approach the area from the north (De Lisle 1967). These storms occur irregularly and may not reflect any general change in annual rainfall. In 1948 and 1976 large storms occurred in otherwise dry years. 24-hr falls in excess of 200 mm have a 10 year return period at Waihi, Katikati and eastern points along the Ranges, and about a 50 year return period at Te Aroha and points along the western face (Coulter & Hessell 1980). Falls well in excess of this figure have been recorded at Waihi and Wharawhara and may be expected within the ranges. The exceptionally intense precipitation of these storms is of a very localised nature (Devereux 1909, De Lisle & Kerr 1963). A simple listing for points around the region shows that largest and second largest falls at any one station are rarely of importance at adjacent stations (Table 2). Similarly, a comparison of dates shows that maximum single-station falls are rarely the same as those of major floods, indicating that they do not represent widespread storms (Table 2 and Fig. 11). For instance, the storm of the 28th of February 1966 (Table 2) was described as the most severe storm in 60 years at Katikati (Bay of Plenty Times 29/2/66) but did little damage elsewhere.

Data for peak flow discharges in the Ohinemuri River at Karangahake (which drains the north of the ranges and parts of the Coromandel Peninsula), the Waihou River at Te Aroha (which drains the west of the ranges), and their combined flows at Puke Bridge provide a further indication of the local nature of storms. The ten largest storm flows for each station (Fig. 11) show

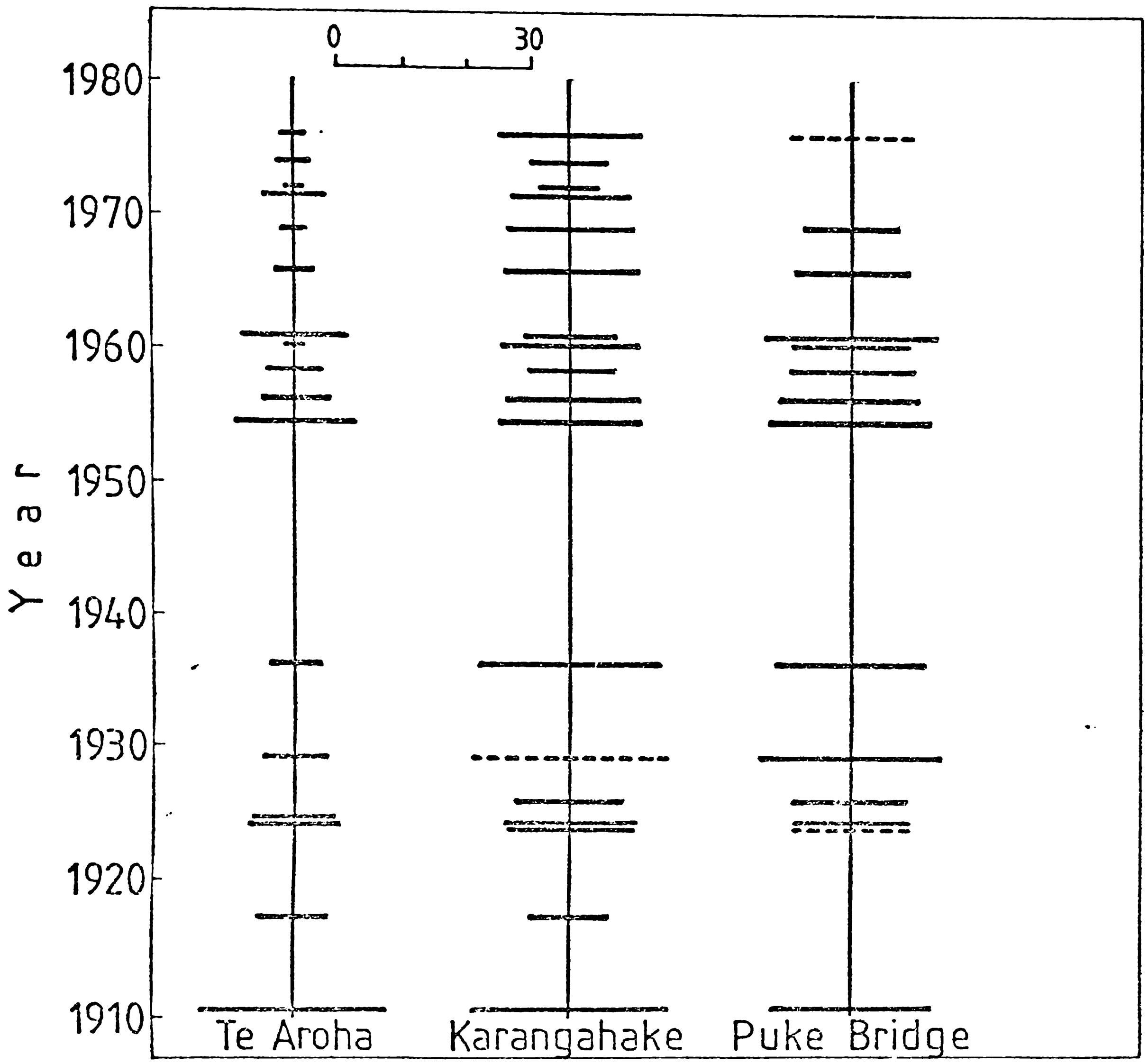

Fig. 11. Comparative flood sizes on the Ohinemuri River at Karangahake; the Waihou River, at Te Aroha; and below their confluence, at Puke bridge. Horiontal scale is thousands of cusecs. Data by courtesy of the Hauraki Catchment Board. Broken lines indicate that no value is available but relative size is known.

TABLE 2 Largest and second largest 24 hour rainfalls at points around the Kaimai Ranges (to 1975) and size of one large fall on 28/2/66. Stations listed clockwise from northwest corner of the Ranges. Data by courtesy of Hauraki Catchment Board.

| LOCALITY | largest fall |  | second largest fall |  | Fall of |
|---|---|---|---|---|---|
|  | Size (mm) | Date | Size (mm) | Date | 28/2/66 |
| Paeroa | 183 | 31 July 1938 | 174 | 19 November 1950 | 118 |
| Karangahake | 176 | 15 April 1971 | 133 | 2 July 1971 | NA |
| Waitawheta | 160 | 23 February 1974 | 120 | 29 November 1972 | NA |
| Waihi | 416 | 4 February 1938 | 308 | 29 March 1910 | 229 |
| Te Aroha | 237 | 18 May 1954 | 200 | 28 February 1966 | 200 |
| Shaftesbury | 309 | 6 March 1954 | 206 | 28 February 1966 | 206 |
| Matamata | 145 | 2 February 1967 | 119 | 8 April 1959 | 100 |
| Okauia | 164 | 2 February 1967 | 162 | 6 March 1954 | 134 |
| Waitcariki | 159 | 29 October 1970 | 153 | 3 July 1971 | NA |
| Wharawhara | 269 | 28 February 1966 | 184 | 8 May 1974 | 269 |

NA Not available

striking differences in rank order. For example the storm flow of 28th June 1960 was third largest on the Ohinemuri but a very small storm flow on the Waihou River, whereas that of 15th September 1960 was second largest on the Waihou but only twelth largest on the Ohinemuri River.

Discharge records show that the largest flood in both the Waihou and Ohinemuri catchments occurred in 1910. There was a gap of 22 years in the occurrence of major storms from 1936 to 1954 but the rank order of all these later storms differs between catchments. The two largest storms on the Waihou River at Te Aroha occurred in 1954 and 1960. The next largest storm was two-thirds as large and occurred 30 years earlier in 1924. In the Waihou there is an 18 year gap in the occurrence of important storms from 1936-1954.

Interpretation of the Karangahake data is not straight forward as over half the catchment of the Ohinemuri River lies to the north of the Kaimai Ranges. Once more there is a gap between 1936 and 1960. Moreover, newspaper reports, supported by storm reports of the Catchment Authorities and by the lack of landslides attributable to these storms, indicate that the 1936 storm was most severe outside the study areas.

The very localised nature of the storms makes interpretation of their possible effects very difficult. Apart from the 1936 storm, which was mainly significant outside the region, the storm of 1954, which was concentrated in both the Waihou and Ohinemuri catchments marked the end of a period of below normal storm intensity stretching back to the 1920's. This storm was followed in 1960 by an exceptionally severe and damaging storm concentrated in the Te Rere study area.

Both sustained and high intensity rainfall leading to soil saturation can trigger landslide initiation (Swanston 1970, Eyles 1979, Caine 1980, Crozier & Eyles 1980). The increased mean rainfall between 1940 and 1960 might be expected to produce a rise in the average level of soil moisture and enhance the risks of landslides during the storms of 1954 and 1960's. In this way both rainfall and storm occurrence together could explain the recent increase in landslide occurrence between 1943 and 1972. However neither of these factors are able to easily explain the location or altitudinal zonation of the landslides.

### Fog and related parameters

Observations from September 1980 to April 1981 show that fog (low cloud) obscured the summits of the ranges at some time on 60% of days. Records from Mt. Te Aroha summit show a similar pattern with an annual average of 200 fog days for the five years that full records have been kept. The fog forms during the evening or night and may last well into the following day (Table 3). The cloud base is lowest in the early morning and tends to rise about 100 m by early afternoon (Fig. 12). The altitude of the cloud base at Mt. Te Aroha, Te Rere and Te Hunga is about 150 m below the respective summits during the middle of

Table 3

Occurrence and duration of capping fogs at three points in the Kaimai Ranges and relationship to the lower limit of vegetation mortality.

Based on observation made between September 1980 and April 1981.

| | Duration (days/month) | | | | | |
|---|---|---|---|---|---|---|
| Location | Full Day | ½ day | ¼ day | ⅛ day | Mean Altitude | Mortality Altitude |
| Te Aroha | 8.6 | 17.3 | 22.0 | 23.7 | 740 | 800 |
| Te Rere | 8.0 | 16.6 | 19.6 | 22.0 | 600 | 550 |
| Te Hunga | 7.6 | 15.3 | 17.6 | 21.0 | 680 | 650 |

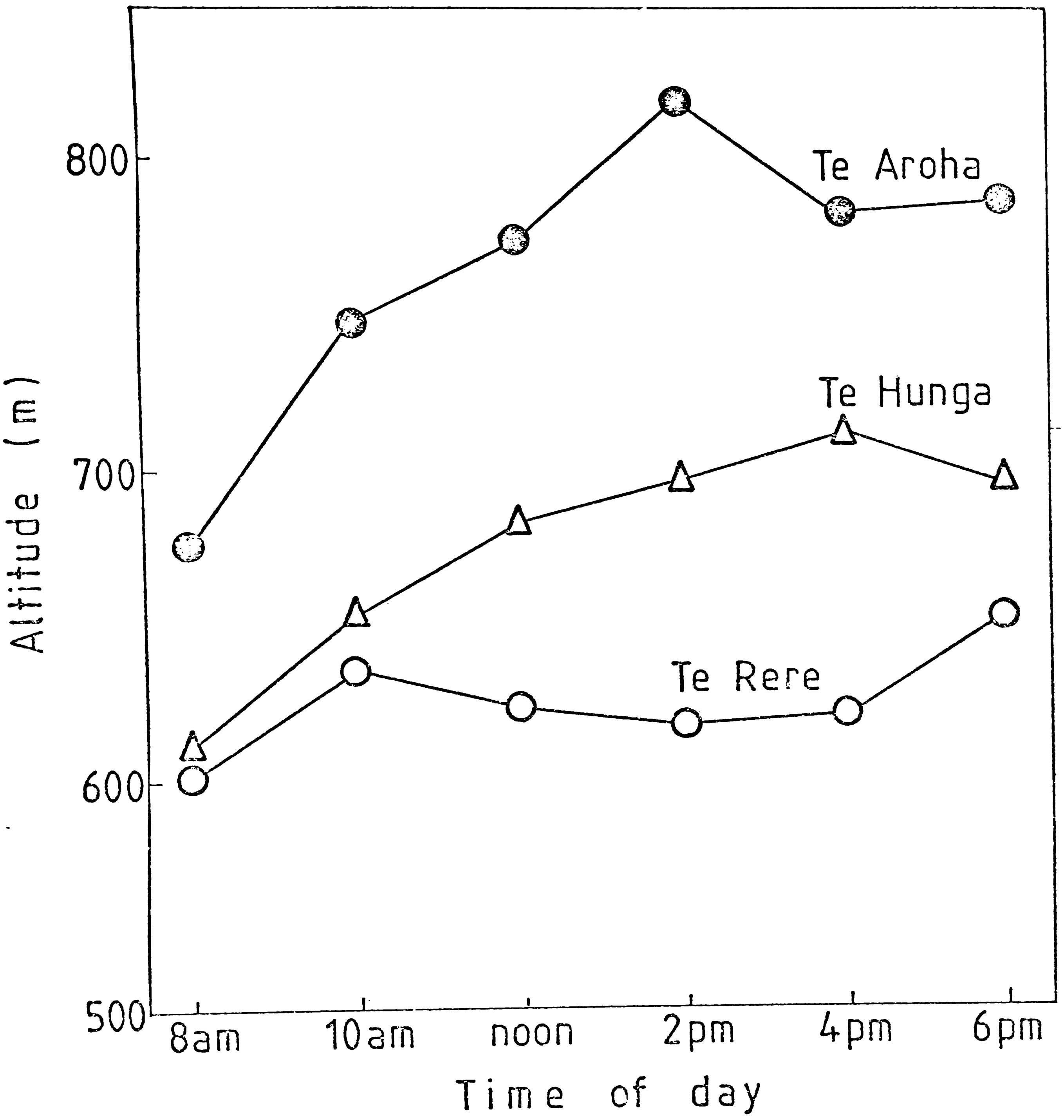

Fig. 12. Variation in cloud base altitude during the day at three study sit based on observations between September 1980 and April 1981.

the day, despite the differences in summit elevation.

Evaporation, measured by Piche evaporimeters, is reduced at altitudes greater than 650 m on Te Hunga (Fig. 13). During foggy or wet periods in summer evaporation at 850 m may be only 10 % of that at 300 or 500 m (Fig. 13). Transpiration rates would be similarly affected although the relationship is not exact (Slavik 1974). The lowered evapotranspiration is reflected in soil moisture contents. For the whole period, from October 1980 to March 1982 soils were close to or greater than field capacity (-0.1 bar) above 750 m altitude but remained well below field capacity at lower altitudes from November 1980 onwards. Soil moisture contents fluctuate more at altitudes above 650 m and recharge at the higher altitude occurs rapidly often by April (Fig. 14).

The fog zones correspond closely with those of high landslide incidence and vegetation mortality in all three study areas (Fig. 15). The high incidence of fog tends to maintain high soil moisture contents in 2 ways. First, on foggy days up to 2 mm of precipitation is normally recorded at Mt. Te Aroha and studies elswhere (Kerfoot 1967, Chaney 1981) have recorded over 300 mm precipitation per annum from fog drip in similar forest situations. Second, reduced radiation levels in the fog zone, possibly to less than 10 % of full sunlight (O' Rourke and Terjung 1981), lead to reduced evaporation, about 40 % of that below the fog zone (Fig. 13), and reduced transpiration. The high ambient soil moisture contents in the fog zone permit soils to saturate more rapidly during storms. Soil strength would be reduced due to hydrostatic

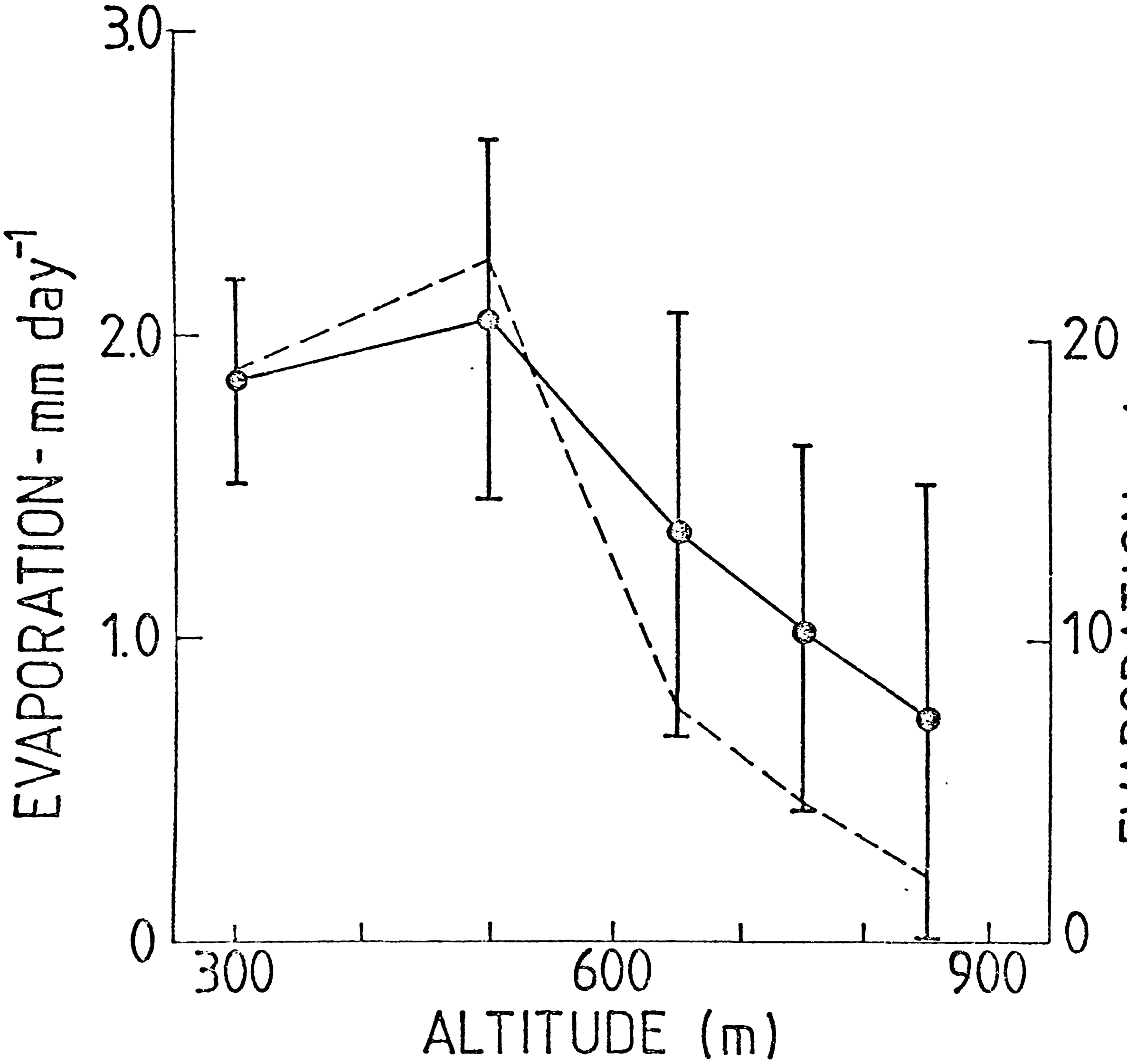

Fig. 13. Evaporation from Piche' evaporimeters placed at points on the Pukepenga ridge, Te Hunga. Total evaporation over varying intervals averaged to mm/day.

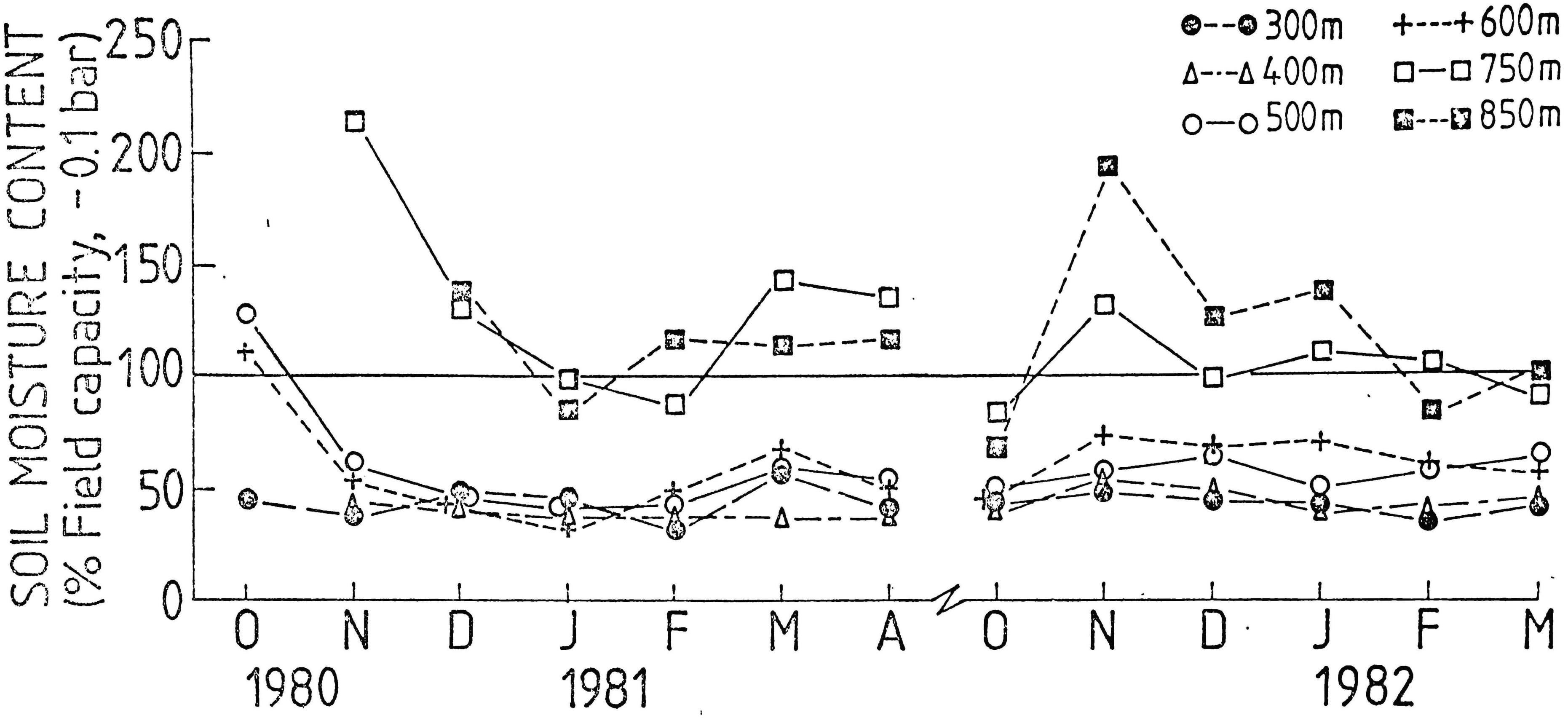

Fig. 14. Altitudinal variation in soil moisture contents (20 cm depth) at Te Rere at the end of winter (October 1981), end of summer (February 1982) following 4 weeks without rain and one month later following two severe storms. Field capacity (0.1 bar) and wilting points (-15 bar) included as reference points.

mechanisms (O' Loughlin 1974; Rogers & Selby 1980) and landslides would initiate more readily. This provides a possible explanation for the increase in landslide occurrence at a critical altitude in each locality. Fog may also moderate or remove the gradients in soil moisture created by the rainfall patterns across the range and minimise the difference in landslide risk related to aspect as found in many other studies (Pain 1969; Eyles 1971; Selby 1976b; Crozier et al. 1980).

## Summary and Synthesis

Any explanation of the recent increased erosion in the Kaimai Ranges must encompass two important features.

1. Location. The increase is confined to areas above a different critical altitude in each of the three study areas.

2. Timing. The increase occurred between about 1950 and 1974, there is no evidence of an equivalent level of erosion over the last 100 years and most of the landslides have occurred in mature forest (Jane and Green 1983a).

The landslides were shown to be unrelated to soil type, basement geology, aspect and vegetation type (Jane and Green 1983a). Introduced browsing mammals, although previously implicated (Dale & James 1977), are not responsible since population densities in the affected areas have been low and there is no evidence for browsing damage. The earthquake of 1972 triggered a number of mass movements and possibly lead to enhanced erosion in later storms but it cannot account for the main erosion increase which began before 1972.

The severe storms of 1954, 1960 and 1966 produced most of the landslides. However the storms do not readily explain the altitudinal zonation of the landslides. However, at each study area there is an excellent coincidence between the altitude of the cloud base and the critical altitude for landslide occurrence (Fig. 15). The prevalent cloud, which limits evapotranspiration and contributes to precipitation so that high soil moisture contents, would predispose the slopes to debris slides at the fog altitudes. However this does not explain the episodic nature of the erosion since large storms and earthquakes have occurred previously this century without precipitating severe erosion.

The vegetation mortality, which occurs at the critical altitude in each study area and is closely linked with the sites of landslide initiation, appears to be to be episodic with the most recent vegetation mortality coinciding with a severe drought in 1946 (Jane & Green 1983b). The critical altitude for vegetation mortality coincides with the cloud base and therefore the mortality occurs in a zone where some degree of long-term soil flooding would be expected. A feature of trees growing in intermittantly flooded soils is reduced root development and root death resulting in shallow root systems leading to increased susceptibility to drought (Kozlowski 1982). The decay of the roots following the mortality would gradually lower the soil strength and predispose

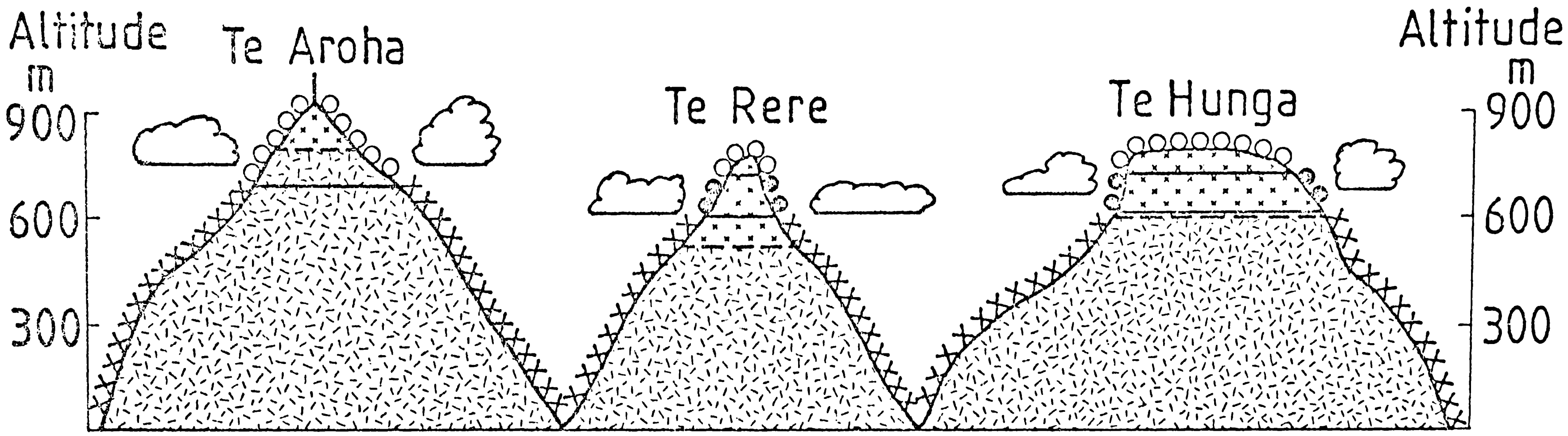

Fig. 15. Schematic profile of three points on the Kaimai Ranges showing vegetation distribution, vegetation vigour and relative fog levels. Beilschmiedia tawa forests xxxxx ; Ixerba brexioides forests @@@ Nothofagus menziesii forests oooo. Forest type boundaries marked by solid line, lower altitude boundary of vegetation mortality by dashed line. Healthy forest """""" unhealthy forest ++++ . Base of clouds indicates average cloud level.

the area to landsliding (Ziemer 1981). The rate of decline in soil strength is difficult to estimate and in the cold wet environment it may be several years before soil strength is severly affected. The lack of landslides attributable the 1910 storm can then be explained by the absence of a vegetation mortality to reduce soil strength to a critical level. Similarly, although the vegetation mortality of 1914 was followed by storms, none was apparently of sufficient intensity to produce widespread erosion.

Thus a complex process exists in which severe storms increased rainfall, earthquakes and vegetation mortality all contribute, with prevalent cloud as the single strong link between the location of vegetation mortality and the zone of increased landsliding. This coincidence of events not only adequately explains the timing of the erosion episode but also the correspondence between cloud base, landslide densities and vegetation mortality. For an episode of widespread severe erosion to occur, a period of vegetation decline and recovery must be followed by important trigger events such as severe storms or a major earthquake.

Grant (1963) linked periods of vegetation mortality in the Huiarau Ranges, caused by climatic peturbations, with episodes of erosion. Later investigations in the Hawkes Bay (Grant 1965; Grant 1981) showed a comparable pattern of episodic erosion. More recently Hubbard & Neale (1980) dated erosional events in the southern Ruahine Ranges to 770, 68 and 5 years before the present. They suggested that these events were triggered by changes in climate, or earthquake frequency along the marginal faults of the ranges. Studies of vegetation age in the North Island (Clayton-Greene 1976; Clayton-Greene 1977) and elsewhere (Wardle 1978, Veblen & Stewart 1980, Veblen & Stewart 1982) have suggested that the upland forests are periodically affected by major disturbances. These may have serious short term effects on slope stability and, as we are seeing in many areas, these may be major trigger events for erosion episodes.

Recognition of the episodic nature of vegetation mortality and erosion in forested highland areas of New Zealand means that introduced animals can no longer be regarded as a primary cause of vegetation disturbance or landslides and even their role as a secondary factor must be carefully examined. Full cognisance must now be given the primary role of natural events of long return periods which act through their effects on the forests rather than directly on the regolith.

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