View of Mt Taranaki, taken in April 1984, from Lincoln Road, Inglewood.

KEY

A. Upper Ngatoro Valley.

B. Scree surface shown in Fig 2.1.

C. North Egmont Visitor Centre.

D. Humphries Castle.

E. Tahurangi Bluff.

F. Dieffenbach Cliffs.

1. Topographical Unit 1.

2. Topographical Unit 2.

3A. Topographical Unit 3A.

3B. Topographical Unit 3B.

SUCCESSION OF SUBALPINE VEGETATION TO LIBOCEDRUS BIDWILLII FOREST ON A LANDSLIDE-INITIATED SOIL CHRONOSEQUENCE, MOUNT TARANAKI, NEW ZEALAND

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ABSTRACT

Aspects of succession of subalpine vegetation on Mt Taranaki were examined in a vegetation chronosequence, initiated by four landslides on the same sideslope in 1333-1343 A.D., 1625 A.D., 1811-1817 A.D. and 1968-1971 A.D.. In three stands *Libocedrus bidwillii* (kaikawaka) subalpine low forest was displayed at different stages of development while the fourth stand without kaikawaka comprised mainly low herbaceous vegetation.

Core samples were collected from the three kaikawaka populations to establish the crossdating pattern, describe anomalous ring features, establish that the four stands formed a vegetation chronosequence and to examine the age-size relationships of this species.

The crossdating pattern found in the present study confirms that reported for kaikawaka at two other sites on Mt Taranaki. The absence of the 1934-1938 signature in cores from the youngest stand suggests the climatic signal is being suppressed in younger trees.

Various types of anomalous rings were described for kaikawaka and frequencies per core given. A number of features not previously reported for this species were recognised:

1) resin bands as a type of false ring
2) the presence of damaged rings, their synchronous occurrence within a tree, in different trees and with false rings
3) two types of partially absent rings
4) a highest frequency of absent rings for any single radius in datable cores of 3.4 % and
5) the phenomenon of displaced marker rings.

A linear relationship between tree age at 0 cm downslope and DBH of kaikawaka was found to be significant at the 0.1% level but as in other studies a wide variation of age within any one size class suggested that ages predicted from DBH data may be misleading.

Floristic composition of the four stands was recorded on a stratum basis and analysed by lists and through tables of species in common, species unique, total number and identity of species present and Jaccard's and Sorensen's similarity indices. These data showed that the most diverse stratum in all four stands was the ground cover and the major between-stand differences in floristic composition occurred in this stratum. The youngest stand was the most distinctive floristically with twenty-seven species of vascular plants exclusive to this stand. Few (<8) species were found exclusive to each of the 3 older stands. However, 11 species were exclusive to the two older stands and 25 species occurred in all 4 stands. These observations can be interpreted using a combination of the relay-floristic and initial-floristic-composition models. Some early-successional species persist for a period less than 170 years, others invade throughout the period of the chronosequence and another group are part of the initial flora yet persist throughout. Kaikawaka was invading and regenerating in existing vegetation at the site (three older stands) so can participate in secondary succession.

The main species in each stratum were ranked in order of decreasing cover using a semiquantitative estimate method or a point-estimate transect method. The species replacement sequence in the top layer of the four stands was described and follows a trend with time of physiognomic dominance by species with larger size at maturity.

Life-form composition of the four stands (number and percentage of species per life-form category) was compared on a stratum basis through tables and lists. This analysis showed the three older stands were similar in life-form composition except for the presence of hemi-epiphytes exclusive to the oldest stand. The youngest stand was distinctive in life-form composition with a relatively large number of composite herb species present.

Kaikawaka population structures were examined and compared using DBH size-class frequency distributions which also showed size-class mortality patterns. These distributions in the three older stands were dissimilar and indicated waves or pulses of kaikawaka regeneration have occurred rather than continous recruitment. This intermittent mode of regeneration was linked to disturbance of various kinds over a range of scales rather than to climatic change. Total basal area, mean basal area per tree and stem density were also calculated for each population and found to increase with time in the case of the former two parameters.

The cohort-senescence dieback theory and European forest life-cycle theory appear applicable to the study area and offer hypotheses to explain the widespread canopy dieback of kaikawaka found on Mt Taranaki. Whereas a full range of forest life-cycle phases were represented in the small area (<5ha) of the study site, elsewhere on a debris-fan only the dieback phase was evident over a much larger area (>200ha). This was interpreted as reflecting the dependence of disturbance regimes on topography, substrate and vegetation with different disturbance regimes operating in the two areas.

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LIST OF ABBREVIATIONS

aff.	affinities with
agg.	aggregate, comprising more than one species
incl.	including
sp.	species (singular)
s.s.	in a narrow sense, excluding species other than the original in an aggregate
subsp.	subspecies
var.	variety

CHAPTER 1: INTRODUCTION

1.1 BACKGROUND

Succession, the process of directional change in floristic composition, physiognomy and structure of vegetation over a number of years (Atkinson et al., 1968) is a central concept in plant ecology.

An understanding of succession is important to provide a basis for resolving man s present environmental crisis (Odum, 1969). This can be done through development of programmes designed to manage ecosystems and their biological resources whether for food supplies or to maintain biological diversity in conservation areas. Succession is also important because of the value of the concept in the development of ecology as a science (Finegan, 1984).

Because of the longevity of the plants involved, few direct studies of forest succession have been made. Instead most descriptions of succession are inferred from examination of spatial sequences of vegetation on adjacent sites of different known age (chronosequence studies). The necessary assumption involved in this comparative geography technique is that the consecutive members of the sequence represent different points in time in the same succession.

Few vegetation chronosequence studies have been carried out in New Zealand (e.g. Mark et al., 1964; Silvester 1969, 1976) and only one of these was concerned with forest succession following landslides (Mark et al., 1964). No such studies have occurred in Egmont National Park.

The present study examines four adjacent stands of subalpine vegetation on landslide surfaces of a sideslope, Upper Ngatoro Valley, Mt Taranaki. The three oldest stands display *Libocedrus bidwillii* (kaikawaka) forest at different stages of development while the youngest stand, without kaikawaka, consists mostly of low herbaceous vegetation.

1.2 THESIS OBJECTIVES

This research was carried out to examine aspects of succession of subalpine vegetation to kaikawaka forest on Mt Taranaki.

Specific objectives were to:

1) Establish the crossdating pattern in kaikawaka and describe anomalous ring features

2) Establish that the four stands form a vegetation chronosequence by dating the oldest kaikawaka in each using rigorous dendrochronological procedures e.g. crossdating rather than tree-ring counts.

3) Examine the age versus size relationships of kaikawaka using the crossdating procedure with a view to predict age-class structures from DBH measurements

4) Describe for the study site the successional pattern in floristic and life-form compositions on a stratum basis.

5) Assess the relative importance at the study site of the relay-floristic principle (successive appearance and disappearance of groups of species) versus the initial-floristic-composition principle (vegetation development from initial flora without additional increments by further invasion) (Egler,1954; Finegan, 1984).

6) Determine the population structures of kaikawaka in the chronosequence and consider these in relation to the regeneration-gap hypothesis, regeneration modes of New Zealand conifers, the role of disturbance and the cohort senescence theory of canopy dieback (Mueller-Dombois, 1983).

1.3 THESIS ORGANISATION

Chapter 2 describes the study area (location and topography, study-site features, recent volcanic history, soils and climate) and in Chapter 3, the methods used for collecting and analysing data are set out in two sections - field sampling and laboratory analysis.

Results and their analysis are presented in Chapter 4. Section 4.1 describes the crossdating pattern and anomalous rings (objective 1) and section 4.2 the age estimates of the four stands (objective 2). The age versus size relationships of kaikawaka are considered in section 4.3 (objective 3). In section 4.4 the vertical and horizontal structure of the vegetation, the floristic and life-form compositions and the kaikawaka population structure in the 640-year-old stand are described (objectives 4-6). This is followed by similar sequences of information for the 350-year-old stand (section 4.5) the 170-year-old stand (section 4.6) and the 10-year-old stand (section 4.7). In each of the stand descriptions after the 640-year-old stand, comparisons are made with the formerly-described stands. Chapter 4 finishes with a brief consideration of the replacement sequence apparent in nearby debris-fan vegetation (section 4.8).

In chapter 5 (Discussion and conclusions), the crossdating pattern and anomalous ring features of kaikawaka are discussed (5.1). Here, consideration is given to the implications the crossdating results have for dendroclimatology and the dating of the Burrell and Tahurangi eruptions (Druce, 1966a). In section 5.2 the age estimates of the four stands are discussed. Age versus size relationships of kaikawaka are then considered (5.3). Following this is a summary of the successional pattern in floristic and life-form composition as illustrated by the chronosequence (5.4). The relative importance at this study site of the relay-floristic principle versus the initial-floristic-composition principle (Egler, 1954; Finegan, 1984) is discussed in section 5.5. In section 5.6 the kaikawaka population structures in the chronosequence are considered in relation to the regeneration-gap hypothesis, regeneration modes of New Zealand conifers and the role of disturbance. Results are also considered in relation to the theory of cohort senescence, a recent theory put forward to explain canopy dieback phenomena observed in New Zealand and throughout Pacific forests (Mueller-Dombois, 1983).

CHAPTER 2: THE STUDY AREA

2.1 Location and Topography

Mt Taranaki, (Mt Egmont) is a magnificent 2,518 m high andesite volcano (see frontispiece) which occurs 25 km south of New Plymouth, on the west coast of New Zealand's North Island.

The north side of Mt Taranaki can be divided into three topographic units (see frontispiece) following Tonkin (1970):

1) The largely unvegetated very steep lava and scoria slopes of the volcanic cone of Taranaki.

2) The herb- and tussock-covered lava shoulder of moderate slope which terminates in the sheer Tahurangi Bluff and Dieffenbach Cliffs at about 1370 m.

3) A more gently sloping alluvial piedmont, blanketed with ash and lapilli beds and deeply dissected by a radial pattern of streams and rivers. The resulting ridges and valleys are very prominent in the upper portion of this topographical unit (3A -see frontispiece) but become less so in the lower portion where streams and rivers are less entrenched (3B).

The study area, the Upper Ngatoro Valley (Fig 2.1) is situated 1 km above North Egmont Visitor Centre, in the upper portion of the alluvial piedmont (mapped in this valley as Maero Debris Flows - Neall, 1979) immediately below the bluffs and cliffs of the lava shoulder.

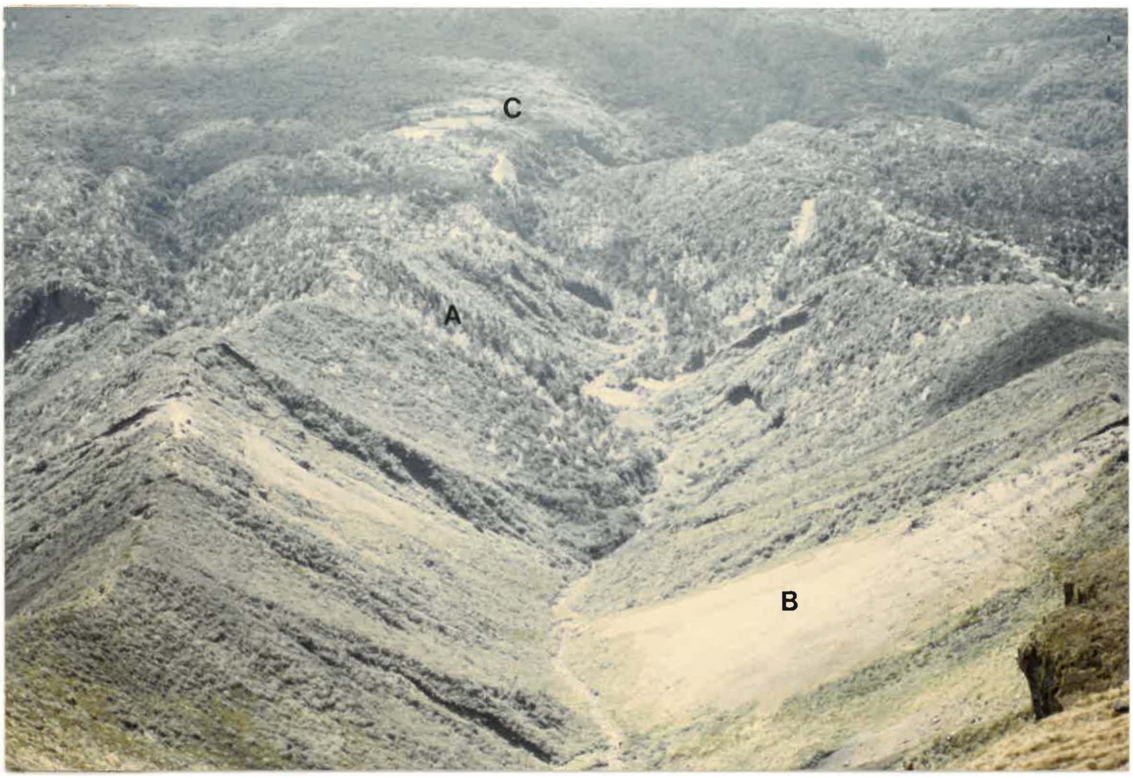


Fig 2.1 Upper Ngatoro Valley viewed from Humphries Castle at 1600 m.
A. Oldest kaikawaka stand on Razorback Ridge sideslope (c.f. Fig 2.2).
B. Scree surface marked on frontispiece.
C. North Egmont Visitor Centre.

The valley (NZMS 169 660651,7th edition) forms a catchment to a tributary of the northward-flowing Ngatoro Stream and is bounded by the Razorback Ridge to the west (left of Fig 2.1) and the Translator Road ridge to the east.

2.2 Study-site features

Within the study area, the study site comprising 4 adjacent stands of subalpine vegetation on old landslide surfaces is located on a sideslope of the Razorback Ridge (left side of Fig. 2.1). The positions of the stands relative to each other and to the treeline are shown in Fig. 2.2.

Fig. 2.2 Study site showing the 4 stands examined, oldest to youngest, left to right. The trig (circled) is at 1181 m asl. Note the Dieffenbach Cliffs of the lava shoulder in the background and the dieback of kaikawaka and Podocarpus hallii to the left of the oldest stand.

The boundaries of the 4 stands were defined artificially at the top by the Summit Track and naturally at the bottom by the bed of the Ngatoro Stream tributary. The up-valley and down-valley boundaries were largely defined in the 3 older stands by vegetation physiognomy, particularly as determined by the heights of kaikawaka, *Griselinia littoralis* and *Pseudopanax simplex*. Microtopographical features such as small gullies and associated banks coincide with these features in the case of the oldest stand and the youngest stand.

Altitudes, slopes and aspects in all 4 stands were similar. At the top of the oldest stand the altitude was measured at 1088 m asl and at the bottom, 1015 m - a drop of 73 m. The slope in this stand averaged 33 degrees but ranged from near-flat areas above some huge boulders and large-diameter kaikawaka, to near-vertical banks below these features. The aspect was east-southeast (115 degrees).

The areas of the 4 stands, from oldest to youngest were 0.6ha, 0.5ha, 0.3ha and 0.09ha. The 3 older stands had similar downslope distances but varied in average width while the youngest stand was only 1/2 the distance downslope of the other stands and was narrowest in average width.

2.3 Recent volcanic history

Recent eruptions of Mt Taranaki are of interest because of their possible direct influence through impact and burial and indirect influence through soil parent materials on the present vegetation pattern of the study area.

Following a period of quiescence lasting several hundred years, the most violent eruptions of recent times, the Newall and Waiweranui eruptions occurred between 1500 and 1550 A.D.. During that period, 4 nuées ardentes, hot gas-charged avalanches of tephra, descended the Stony River catchment on the north-western slopes, destroying much of the native forest as evidenced by carbonised logs (Neall, 1980) and depositing the Newall Formation (Druce, 1966a).

Fires started by these eruptions spread northwards for more than

3 km across the western slopes of the Pouakai Range and volcanic ash (named Newall and Waiweranui) was distributed all over the upper slopes of Mt Taranaki (Druce, 1976).

About 100 years later in 1655 A.D. further eruptions occurred depositing the Burrell Formation of ash, lapilli and nuée ardente tephra (Druce, 1966a; Topping, 1972). Again, vegetation both on the upper and lower western slopes was destroyed by fire. Elsewhere, on the east-southeast side of Mt Taranaki in the vicinity of Jacksons Lookout (end of Stratford Mountain Road) a sizeable portion of the vegetation was destroyed through impact and burial by up to 40 cm of pumiceous lapilli, but a number of small kaikawaka survived (Druce, 1976).

According to the isopach maps showing the distribution of this tephra (Druce, 1966a; Topping, 1972) the study area received less than 10 cm of this lapilli and 5-7 cm of Burrell Ash.

The most recent volcanic activity was the very small Tahurangi eruption of about 1755 A.D.. This deposited 5-12 cm of ash on the upper slopes of the mountain and 7-10 cm over the study area.

2.4 Parent materials and soils

The parent materials of soils on Mt Taranaki are generally layered systems of tephras from past eruptions and buried soils from intervening periods of soil formation. The recent tephras have been described and mapped by Druce (1966a) who grouped them into 3 formations (Table 2.1).

Table 2.1 Recent tephras on Mt Taranaki

Formation	Member	Approximate Age
Tahurangi Formation	Tahurangi Ash	1755 A.D.
Burrell Formation	Puniho Lapilli 1	1655 A.D.
	Puniho Lapilli 2	
	Burrell Lapilli	
	Burrell Ash	
Newall Formation	Waiweranui Ash	1500-1550 A.D.
	Waiweranui Lapilli	(Druce, 1976)
	Newall Lapilli	
	Newall Ash	

The Upper Ngatoro Valley is mantled in recent soils formed from these andesitic tephras. Recent soils have had insufficient time for development of those soil properties characteristic of soils on more stable sites.

Recent soils from andesitic tephras have been recognised within three environmental zones on the south-eastern slopes of Mt Taranaki and named accordingly as alpine soils (above 1680 m), subalpine soils (1680-990 m) and upland temperate soils (990-460 m), (Tonkin, 1970). The soils in the Upper Ngatoro Valley, although outside Tonkin's study area clearly fall in the subalpine category.

Within the subalpine soils category, Tonkin (1970) recognised and mapped two major types, steepland skeletal soils (1680-1370 m) and Tahurangi soils (1370-990 m). The soils in the study area occur in the latter altitudinal zone.

Of the 3 mapping units recognised within the Tahurangi soils by Tonkin (1970), the Tahurangi hill soils of moderately steep to steep slopes, including profiles modified by erosion of the Tahurangi Ash, would be the more likely to occur in the study area.

Chemical analyses of the Tahurangi hill soil type (Tonkin, 1970) show this soil is moderately acid pH (5.4-5.8) with a very high carbon to nitrogen ratio (17-26) and very low percentage base saturation (6.8-11.4) i.e. very strongly leached.

In general Tonkin (1970) found that the recent soils from andesitic tephra characteristically had very weak weathering of minerals in the upper soil layers, variable depth of melanisation, extremely leached soil profiles and marked similar soil chemical parameters over a range of slope and altitude and under appreciably different vegetation. He concluded that the extremely high rainfall so control soil processes that site and vegetation were not expressed in the measured soil parameters.

2.5 Climate

Introduction

The meteorological station nearest to the study area (1000 m asl) is located at North Egmont Visitor Centre (915 m) but records are not long enough to use in this account as the station was only established in 1980.

Summary data from the second-closest meteorological station, Stratford Mountain House (846 m), 3.4 km southeast of the study area, is shown in Table 2.2.

Table 2.2 Stratford Mountain House climatological observations (after N.Z. Met. Ser., 1980)

	Jan	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Temperatures (Deg. C)													
Mean	13	13	12	9	7	5	4	5	6	8	10	12	9
- Daily Max.	18	18	17	13	10	8	7	8	10	12	14	17	13
- Daily Min.	8	8	8	6	3	2	1	1	3	3	5	7	5
Highest Max.	26	27	23	21	17	14	13	15	20	21	23	26	27
Lowest Min.	1	-1	-1	-2	-3	-4	-5	-5	-5	-3	-2	-1	-5
Average no. of days of frost:													
-Air Frost	0.0	0.0	0.1	0.3	3.7	8.6	11.8	9.7	5.0	3.3	0.9	0.1	43.5
-Ground Frost	0.9	1.0	3.3	5.7	11.6	14.2	15.4	14.1	11.7	11.0	5.1	2.4	96.4
Rainfall(mm)	346	346	363	501	678	630	673	741	620	506	510	437	6351
-highest monthly or annual	871	898	747	921	912	1107	1573	1633	1360	933	1256	699	7294
-lowest monthly or annual	99	3	62	139	331	322	192	508	250	59	193	204	5112
-highest daily	270	408	222	286	353	300	292	427	388	189	380	248	427
Average No. of days with rainfall of 1 mm or more	12	9	13	16	17	19	20	20	19	17	16	14	192

Period:Temperatures,1965(March)-1979; Rainfall (1963-1979)

Comparisons with data from meteorological stations at New Plymouth Airport or New Plymouth City are made on occasions in the following account to give a lowland coastal perspective to the climate of the study area.

Rain

Rainfall varies seasonally at Stratford Mountain House with the months from May to October on average receiving one and a half times the rain received for the months from December to March (Table 2.2).

The mean annual rainfall (rainfall normal: 1941-70) ranges from 1565 mm near the North Taranaki coast (New Plymouth Airport - 27m asl) to 6700 mm at Stratford Mountain House (846 m) and 7390 mm at North Egmont Camphouse (975 m) (Thompson, 1981; Coulter, 1976). This rainfall pattern results from orographic uplift of prevailing moisture-laden winds blowing from the nearby Tasman Sea.

Droughts, > 14 consecutive rainless days, occurred at Stratford Mountain House starting 23 January, 1964 (23 days) and 13 February 1973 (17 days) (Coulter, 1976).

Temperatures

At Stratford Mountain House temperatures during summer (December to March) average 12-13 deg. C. and in winter (June to August) 4-5 deg. C. (Table 2.2).

The annual average temperature declines from 13 deg. C. at New Plymouth Airport (27 m asl) to 9 deg. C. at Stratford Mountain House (846 m), an effect mainly due to increasing elevation.

The mean daily range of temperature at Stratford Mountain House is 8 deg. C. (Table 2.2) and the same range occurs at New Plymouth Airport (Thompson, 1981).

New Plymouth meteorological station (49 m asl) has an average 5 days each year when maximum temperature exceeds 25 deg. C. and 2 days each year when the air temperature at 1.3 m above a grassed surface falls below 0 deg. C., an air- or screen frost. The respective figures for Stratford Mountain House are 0.8 and 44 (Thompson, 1981).

Ground frosts occur when the grass minimum temperature is -1.0 deg. C. or lower. At New Plymouth Airport the average number of ground frosts per year is 13 and the corresponding figure for Stratford Mountain House is 96.4 (Thompson, 1981).

The aforementioned data on air and ground frosts illustrate the importance of coastal influences on frost frequency and the severe frost conditions which occur at high elevations on Mt Taranaki, such as in the study area.

Snow

Mount Taranaki has a permanent snow field and during winter the snowline usually descends to about 1000 m. On average Stratford Mountain House has 18 days of snowfall per year, 97 % occurring between May to October whereas at sea level snow is very infrequent. On average snow falls at New Plymouth only on 0.1 days per year, all falls occurring between June and July (Thompson, 1981).

Wind (after Thompson, 1981)

At the 1000 m level in coastal Taranaki the most common wind direction is westerly but at the surface level winds are influenced markedly by local topography. This can be seen in the growth form of some species e.g. wind-flagging of kaikawaka and by the physiognomy of the vegetation e.g. wind-shorn canopies.

During periods of radiative cooling on clear nights, drainage of cold air occurs from mountain slopes forming katabatic winds. By contrast when slopes are heated during a summer day, air ascends up valleys.

Wind speed increases with altitude and varies seasonally. Gusts in excess of 33 knots (kt) (17 m s^{-1}) occur more frequently on Mt Taranaki than in the coastal lowlands. On average 155 days per year had such gusts at East Egmont (1037 m asl) whereas the comparable figure for New Plymouth was 80. At the stronger wind strength of over 51 kt the respective figures were 55 and 6. The maximum estimated gust for a return period of 25 years at East Egmont is 110 kt and at New Plymouth 75 kt. Highest average wind speeds usually occur in autumn and spring and are lowest during the summer.

Fog and Relative humidity

On mountains fog occurs when cloud envelops them, in day or night, frequently with strong winds. By contrast on lowland plains most fogs are produced by radiative cooling of the ground surface and the air layer near it on calm clear nights (Coulter, 1967). The incidence of fog increases with altitude. Fog occurred on average 4 days per year at New Plymouth City and 49 days per year at Stratford Mountain House.

Average monthly relative humidity at 9 a.m.at New Plymouth is 81 % which is similar to that at Stratford Mountain House at 87 %. Two features of relative humidity observed at two South Island mountain-top meteorological stations (Coulter, 1967) may be characteristic of the study area. First, very low humidities (below 20 %) were observed to occur occasionally at all hours, usually with clear skies but with varying winds. Second, average relative humidity values fell during the night, a decrease in average water content of the air more than offsetting the temperature drop. By contrast at lowland stations relative humidity usually had a maximum at night or in the early morning when temperature was at a minimum. Coulter (1967) attributes these features to vertical motions of air around mountains with night-time descending air (katabatic winds) bringing dry air from above and day-time ascending air carrying moister air up from below.

CHAPTER 3: METHODS

3.1 FIELD SAMPLING

3.1.1 Species choice

The choice of species for dendrochronological analysis is a critical decision which can govern the nature of the complete investigation, because many species in New Zealand are unsuitable. In the present study therefore, the choice of species was made before the choice of study area.

Kaikawaka was chosen partly because previous work (Wardle, 1963a; Druce, 1966a; Dunwiddie, 1978;1979) had indicated that, 1) the species could be easily cored, being a softwood (conifer), and 2) the nature of its ring morphology was suitable for dendrochronological work i.e. the species met the following criteria for determining such suitability (modified from Dunwiddie, 1979,p 252).

1. Ring boundaries must be clearly defined to permit accurate dating. This criterion is particularly important when rings are very narrow.

2. Patterns of wide and narrow rings must exist to permit crossdating i.e. the species at the site chosen must exhibit climatic sensitivity rather than be complacent to climate.

3. The species must exhibit circuit uniformity to permit crossdating i.e. ring width patterns must be consistent on all radii at any one height, with few areas of local suppression or rapid growth.

4. The species must exhibit vertical uniformity to permit crossdating i.e. exhibit the same ring width pattern at different coring heights for any one tree.

5. Site uniformity must occur i.e. wide and narrow ring patterns or

other distinctive features such as unusual latewood in certain years, false rings or frost rings must be reasonably consistent between trees at a site to permit crossdating between trees.

6. Rings must be predominantly annual.

A third reason for choosing kaikawaka was because it featured strongly in a current debate occurring in New Zealand's plant-ecology literature. This controversy involves mainly the regeneration-gap hypothesis as evidence of climatic change versus elucidation of the regeneration modes of indigenous gymnosperms. New frameworks for evaluating vegetation change have been proposed which recognise the great frequency and extent of various types of disturbance (Veblen and Stewart, 1982).

The fourth reason for choosing kaikawaka as the study species was because, on Mt Taranaki, widespread canopy dieback of kaikawaka stands is apparent from Ahukawakawa Mire to North Egmont. Although the present study does not address this phenomenon directly, it was thought the knowledge gained on stand dynamics would contribute to an understanding of kaikawaka stand-level dieback.

3.1.2 Study-area choice

The interplay of several important factors led to the choice of the Upper Ngatoro Valley, North Egmont as the study area.

The presence of the dendrochronologically-useful kaikawaka as the principal species in a successional sequence of subalpine vegetation, offered the possibility of investigating aspects of succession a central theme in plant ecology using rigorous crossdating procedures.

The close proximity of the three stands containing kaikawaka and a fourth younger stand without kaikawaka, all on the same sideslope with similar altitude, geology, slopes and aspects gave an experimental control by reducing the number of ecologically significant variables. The study area thus largely satisfied desiderata suggested for a chronosequence study (Stevens and Walker, 1970) with time probably as the most important differentiating factor in the vegetation.

The subalpine position of the stands near treeline, above a nearby site from which climatically-sensitive material had been collected by the author in January 1978 (see LaMarche et al.,1979,pp 24-25), suggested crossdating could be employed.

3.1.3 Collection of tree cores

The two principal reasons for collecting cores of kaikawaka were, 1) to determine for the three stands with kaikawaka their time-zeros - the estimated dates when the landslides occurred and new surfaces became available for colonisation; 2) to assess age versus diameter (DBH, DCH) relationships. Collection of tree cores was carried out accordingly, as detailed in the following subsections.

3.1.3.1 Tree selection

Determination of time-zeros necessitated selection of the oldest kaikawaka individuals in each stand. Assuming a linear DBH-age relationship, at least the two largest-diameter single-crowned individuals, alive or dead, were cored.

In the 640-year-old stand the two largest-diameter twin-crowned individuals, numbers 53 and 63, were also cored to gain age-estimates. These perforce were based on average radial-growth rates as the cores were incomplete due to rot.

To assess diameter versus age relationships a wider range of DBH sizes were sought, together with a large sample size, for statistical significance purposes. Fifty-one out of 79 labelled trees in the 640-year-old stand were cored, 13 out of 23 in the 350-year-old stand and 2 out of 4 in the 170-year-old stand. In total 66 out of 106 labelled kaikawaka were cored.

Trees were labelled by nailing to the upslope sides of boles, preserving-jar domes which had been numbered using hammer and punch.

For most trees more than one core was collected to facilitate crossdating, giving a potential data set involving approximately 120-130 cores, or estimating an average of 300 rings per core, 37500 rings. Given time and resource limitations, combined with methodological problems in mounting cores in the laboratory (detailed in a later subsection), this data set proved much too large to fully utilise.

Nonetheless, after the methodological problems were solved this preliminary work enabled a selected subset of unbroken cores with well-formed centre arcs to be used, when examining the diameter-age relationships.

3.1.3.2 Selection of coring height and position

Initially, coring height was held constant at 1.2 m above the ground surface on the upslope side of the tree. This height was chosen because it enabled best control of the starting of the increment borer in the tree and the subsequent coring procedure, by permitting a standing posture on the steep, often wet, slopes.

However, it soon became apparent that this coring height restriction was impractical because, even in some trees with good bole appearance, rot occurred at this level. Coring height was therefore relaxed to include any height which yielded a sound core but with a preference for lower heights so as to maximise the tree-ring information obtained. An additional requirement was that the height above the upslope ground surface at which the core was taken be measured and recorded. For those cores included in the regression analysis (Appendix 16) height above the downslope ground surface was also measured.

The position in the tree from which cores were taken was chosen to avoid bole deformities, crevices and rot - areas with distorted ring patterns. Cores were usually taken from both upslope-downslope and across-slope directions. The latter is usually preferred in studies involving conifers to avoid compression wood which forms on the downslope side of leaning stems. However, most kaikawaka in the three stands cored were remarkably vertical regardless of being wind-flagged or not. This proved fortunate because slope steepness and wetness sometimes made extraction of cores from across-slope directions too difficult. Core label, coring height and core position and direction with respect to a downslope datum were recorded in a field notebook for each tree.

3.1.3.3 Coring procedure, core extraction, labelling and storage

Notes on coring procedure are given by Stokes and Smiley (1968,pp 31-36), Ferguson (1970,pp 185-186) and Burrows and Burrows (1976,pp 28-30). In the present study the coring procedure and core removal outlined by Stokes and Smiley (1968,pp 31-34) was generally followed.

A Swedish increment borer with a 40-cm-long bit and 5-mm-diameter aperture was used. Particular care was found to be necessary when starting the borer in the tree because sideways or vertical wobbling of the borer bit caused sapwood distortion or fractures. Both make subsequent handling of the core in the field and in the laboratory much more difficult. Other studies report exclusion of data from outer core portions because of distorted sapwood rings (Wardle, 1963c, p 209) but this was not necessary in this study.

Extra care was also found necessary when inserting the extractor into the borer bit to avoid striking the core end and causing sapwood distortion.

Cores were labelled using an indelible pencil with the bark positioned to the right before removal from the extractor spoon. Plastic milk-shake straws were then slid over the cores, again before removing them from the extractor spoon and after removal, straw ends were taped with masking tape. This was labelled with tree and core designations at the bark end of the core and straws were stored in a rigid PVC container. Later, when back at the field base, small windows were cut in the straws to facilitate drying.

Core holes were sealed with anhydrous lanolin as a precautionary measure to prevent penetration of disease-causing organisms.

3.1.4 Dating of the youngest stand (10 yrs)

Because kaikawaka was not present, the youngest stand had to be dated using different methods.

The first method used involved measuring the height in June 1985 of the tallest *Hebe stricta* var. *egmontiana* specimen growing on the debris-fan at the base of the youngest stand. The height of the tallest individual of the same species growing on a similar debris-fan formed by a landslide in 1977 (B.D. Clarkson, pers. comm.) opposite the 640-year-old stand, was also measured in June 1985 and the average height-growth-rate per annum was calculated over the 8-year period. This was then used to date the *Hebe* on the debris-fan of unknown age and thus infer an age for the youngest stand on the landslide surface above.

The second method was the same except the average diameter-growth-rate of the tallest individual on the debris-fan of known age was used instead of the average height-growth-rate.

Hebe stricta var. *egmontiana* proved too hard to core so preventing a more direct non-destructive dating method. Ring clarity and the periodicity of ring formation is also unknown for this species.

3.1.5 Collection and analysis of data on vegetation structure and floristic composition

3.1.5.1 Description of strata and plant categories

For each of the three kaikawaka stands all vascular plant species, both native and adventive, were recorded in each of five strata or plant categories, where these were evident. The strata and plant categories used were:

1) Emergents trees protruding conspicuously above the shrub, small-tree canopy;

2) Canopy - shrubs and small trees with more than fifty per cent of their crowns in full sunlight forming a continuous top layer to the vegetation;

3) Subcanopy - species of shrubs and small trees beneath the shrub, small-tree canopy with less than fifty per cent of their crowns exposed to full sunlight, but taller than 300 mm;

4) Ground cover - species of herbs (dicots including composites; and monocots including orchids, grasses, sedges and rushes), ferns and seedlings of shrubs and trees below 300 mm high;

5) Epiphytes and lianes (after Mueller-Dombois and Ellenberg, 1974)

- epiphytes or perching plants: plants that germinate and root on other plants including dead standing plants.
- lianes: plants that germinate on the ground and maintain their contact with the soil.
- hemi-epiphytes or pseudo-lianes: plants that germinate on other plants and then establish their roots in the ground, or plants that

germinate on the ground, grow up the tree and disconnect their soil contact.

The main species in each stratum were ranked in order of decreasing cover (vertical crown projection) visually estimated in each of the three kaikawaka stands using the following ratings:

- principal, 20-50 % cover
- frequent, 2-20 % cover
- occasional, < 2 % cover

The general quantitative relations of the species in each stand became apparent during the numerous walks made through each to list the species on a stratum basis.

The cover ratings which apply to the entire area of each stand were assigned from locations where overviews of the vegetation could be gained, taking into account experience during the listings. Locations were: the track edge at the top of the stand, the stream banks at the bottom of the stand or from up a tree near the middle of the stand. The steep slopes and low canopy height enhanced the display of canopy species.

Although not based on measurement and therefore often referred to as semiquantitative, or quantitatively crude, this method was employed with the aim of taking into account the within-stand spatial floristic variation. Because of time constraints and the difficulty encountered in moving about in the subalpine scrub, quantitative measurements of species cover on a plot basis would not have permitted this.

This semiquantitative estimate method has similarities to the Braun-Blanquet cover-abundance-scale technique described by Mueller-Dombois and Ellenberg (1974:pp 59-62), but employs a smaller number of larger scale intervals.

Special attention was given to the presence or absence of seedlings of the principal species of each stratum in order to assess future trends.

A combination of factors easy access, low stature of the vegetation, slope steepness and small area enabled a more quantitative estimate of vegetation cover on the lower half of the 10-year-old stand to be made. Data from three 30 m transects orientated at right angles to the small-cliff face, 1 with points at 1 m intervals and 2 with points at 1/2 m intervals, were averaged to give the percentages for cover dominance (relative frequency of hits per species) used in the description. This technique is best described as a point-intercept transect method (Mueller-Dombois and Ellenberg, 1974, p88).

Floristic composition of the four stands was compared on a stand and stratum basis by lists and through tables of species in common, species unique, total number and identity of species present and Jaccard's and Sorensen's similarity indices. The comparisons used are similar to but more simple than the tabulation techniques involving raw, constancy, differential and synthesis tables described by Mueller-Dombois and Ellenberg (1974,Chapt.9). Botanical nomenclature followed Druce (1973), Eagle (1982;1986) and Clarkson (1986).

An important reason for using tabular techniques in the present study to analyse floristic composition was to assess the relative importance in succession in the study area of the relay-floristic principle (successive appearance and disappearance of groups of species) versus the initial-floristic-composition principle (vegetation development from initial flora without additional increments by further invasion) (Egler, 1954; Finegan, 1984).

3.1.5.2 Life-form composition

The rationale for describing life-form composition in the present study is to give a non-floristic perspective on the structure of each stand and on the ecological role of the species. Consideration of life-form composition also gives valuable insights into the life-history strategies of the species (Grime, 1979).

A species passes through differing life-form stages in its life cycle from seed to maturity. For the life-form composition analysis in the present study, species have been categorised by the most mature life form present in the stand. Life-form categories follow Druce (1973).

Life-form composition of the four stands (number and % of species per life-form category) was compared on a stratum basis through tables and lists.

3.1.5.3 Floristic composition

Floristic composition of each stand was further analysed to: 1) put it in a regional ecological perspective; 2) determine taxa endemic to Mt Taranaki; 3) determine species absent which are usually found in association with kaikawaka in the central North Island at a similar altitude and latitude i.e. to give a phytogeographic perspective; 4) determine the various elements of the flora according to the bioclimatic zones in which they have their ecological optima; and 5) determine number of genera and families represented and the best-represented genus and family in species number terms.

3.1.6 Collection and analysis of data on size-class distributions

For the principal species (kaikawaka) in the succession, a quantitative measure of cover was used instead of the semiquantitative estimate method described in section 3.1.5.1 Basal area, the area outline of a plant near the ground surface was measured through diameter-at-breast-height (DBH) i.e. approximately 1.4 m above the upslope ground surface, using the formula $\pi \times r^2$ where r equals 1/2

DBH. For mature kaikawaka, breast-height area is smaller than real basal area due to bole taper (c.f. DBH and DCH figs, Appendix 16). Hence this method gives an underestimate of basal area (stem cover).

Kaikawaka individuals were recorded in the following four categories which were arbitrarily defined after preliminary visits to the stands:

-labelled trees: individuals > 180 cm high and >10 cm DBH, labelled and cored.

- unlabelled trees: tree-sized individuals not labelled or cored.
- poles: individuals > 180 cm high and < 10 cm DBH.
- seedlings: individuals < 180 cm high.

The condition of kaikawaka individuals in the three stands ranged from strongly-flagged or full-crowned trees with no dead foliage and no areas of bole rot, through dying trees with small crowns, dead foliage and partial bole rot to dead individuals with no live foliage and extensive bole rot. Plant health was therefore recorded in three categories healthy, dying or dead so that mortality patterns per size class could be analysed.

The kaikawaka population structure in the three older stands is compared using DBH size-class frequency histograms which also show size-class mortality patterns. Total basal area, mean basal area per tree and stem density of the kaikawaka present in the three older stands were calculated and are compared in the text.

3.1.7 Collection of data on height classes of seedlings

The wide range of heights but small range of basal diameters (< 3 cm) of kaikawaka seedlings in the 350-year-old stand suggested seedling height would be a more meaningful measure to use when interpreting regeneration patterns. Accordingly, seedlings were recorded in three broad height-classes: 1-60 cm, 61-120 cm and

121-180 cm.

3.2 LABORATORY ANALYSIS

3.2.1 Preliminary processing

In the laboratory, label information on cores and straws was checked for each tree against fieldnotes before transferring the information to 12.5 cm by 20 cm filebox cards, ordered by tree number.

On each filebox card, tree number, tree label position, DBH, coring dates for each core, core labels, core heights, DCH's, core position with respect to the downslope datum and the direction from which the core was taken were recorded. Additional notes included stand name, tree location relative to nearest visible kaikawaka neighbours, identity of nearest non-kaikawaka species, number of crowns, condition, and direction of flagging if any, bole number and condition including location of rot, presence of epiphytes, hemi-epiphytes and lianes, and nearby atypical microtopographical features.

This procedure enabled individual trees to be relocated and sampled again to gain further tree-ring information when the need arose. Furthermore, the above data provided the opportunity to assess biotic influences e.g. crown flagging on ring patterns.

3.2.2 Core preparation

After air-drying in plastic milk-shake straws, cores were mounted in a 2.5-mm-deep (1/2 diam.) central groove 5 mm wide, in pieces of radiata pine 2.5 cm wide by 2 cm deep. Mounts were labelled with core label, coring date, species name and study area, hand-printed on the side rather than the top to avoid loss of information during sanding.

With the bark end to the right, cores were first orientated for mounting with the tracheids vertically aligned as detected by examining core ends.

Cores were then pressed into a thin stream of poly-vinyl-chloride (PVA) glue spread evenly in the central groove and wrapped tightly in masking tape to prevent warping during drying.

Cores were hand-sanded down to the shoulders of the mount using progressively finer-grit carborundum sandpaper, starting with coarse 60-grit and finishing with a very fine 1200-grit polish. Sanding the core down to the mount shoulders exposes the maximum width of ring information available in the core and permits dating marks corresponding to specific rings to be written on both shoulders.

If sanding as a method of surfacing is to be carried out, orientation of tracheids perpendicular to the sanded surface is critical to permit cell structure and thus very narrow rings to be detected in the prepared core.

Many dendrochronological studies (including this one initially) have floundered because of dating problems arising from incorrect orientation of cores in mounts and poor surfacing techniques (Fritts, 1976; Dunwiddie and LaMarche, 1980). Part of this confusion arises because of the range of methods reported in the New Zealand and overseas literature (e.g. Ferguson, 1970).

In the New Zealand literature both Druce (1966a) and Clayton-Greene (1977) used blades to cut surfaces on cores not mounted permanently. Initially, in the present study, similar techniques were tried on mounted cores including cutting the tracheids at different angles combined with a range of wetting agents (water, kerosene and sodium hypochlorite), all used to improve ring clarity. Results using these techniques on kaikawaka cores from Mt Taranaki and Mt Pirongia were at best only approximate counts. Until tracheids were orientated vertically and sanded with a series of finer-grit carborundum papers

(60 to 1200), very narrow marker rings and ring signatures (sequences of marker rings) were not detected and hence crossdating could not be achieved. Notably, neither Druce (1966a) nor Clayton-Greene (1977) reported crossdating.

3.2.3 Examination of cores and the crossdating procedure

The most important principle of dendrochronology is crossdating (Fritts, 1976), the matching of variations in ring characteristics, especially ring widths, among all samples from a given region. If there is sufficient co-variation among rings i.e. the trees are climatically sensitive and the climatic signal to biological noise ratio is large enough and provided the sample is large enough, then the crossdating procedure is used to identify the calendar year in which each ring was formed.

The procedure includes recognition of any lack of coincidences in the ring patterns being compared and determination of anomalous rings along a sampled radius. Anomalous rings are those that are false, partially absent, completely absent, damaged by frost or drought, or marker rings that are displaced. They were largely detected by the methods set out in detail by Glock (1937). Because crossdating assures the proper placement in time of each ring, it provides a type of experimental control.

In the present study, crossdating involved careful visual examination of every core and visual comparisons of ring patterns between cores, using a stereomicroscope set at 10x to 80x magnification. There is at present no fool-proof shortcut to this procedure (Fritts, 1976) even though the procedure can be facilitated by computer analysis (Baille and Pilcher, 1973).

The procedure began by using cores from live trees with known dates (sampling dates) for the outermost rings and assigning dates to distinctive features e.g. a combination of wide and narrow rings found to be common within a tree and between 2 or 3 trees. The pattern was expanded by adding new features and further samples, eventually incorporating material from dead trees with unknown outer-ring dates, and more difficult material with suppressed ring regions.

Since the growing season spans two calender years in the Southern Hemisphere, the convention used in this study, following Dunwiddie (1979), was to date a ring by the year in which growth began.

Because collection of cores occurred over several growing seasons, outermost rings were of different dates. Therefore to facilitate the direct comparison across cores of rings formed in the same growing season, rings formed in the 1978-79 growing season were arbitrarily assigned ring number 1.

Ring numbers increased positively towards the core (tree) centre and, if cored after the 1978-79 growing season, became zero then negative towards the outside of the core (tree).

Every tenth ring was marked with blue ballpoint and a line drawn down to the ring number, written on the nearest shoulder of the mount, with the bark end of the core (core-entry point for trees cored completely through) positioned to the observer's right (Fig 3.1). The number of rings from ring no. 1 to the tree centre was written in red next to the centre arcs on this shoulder.

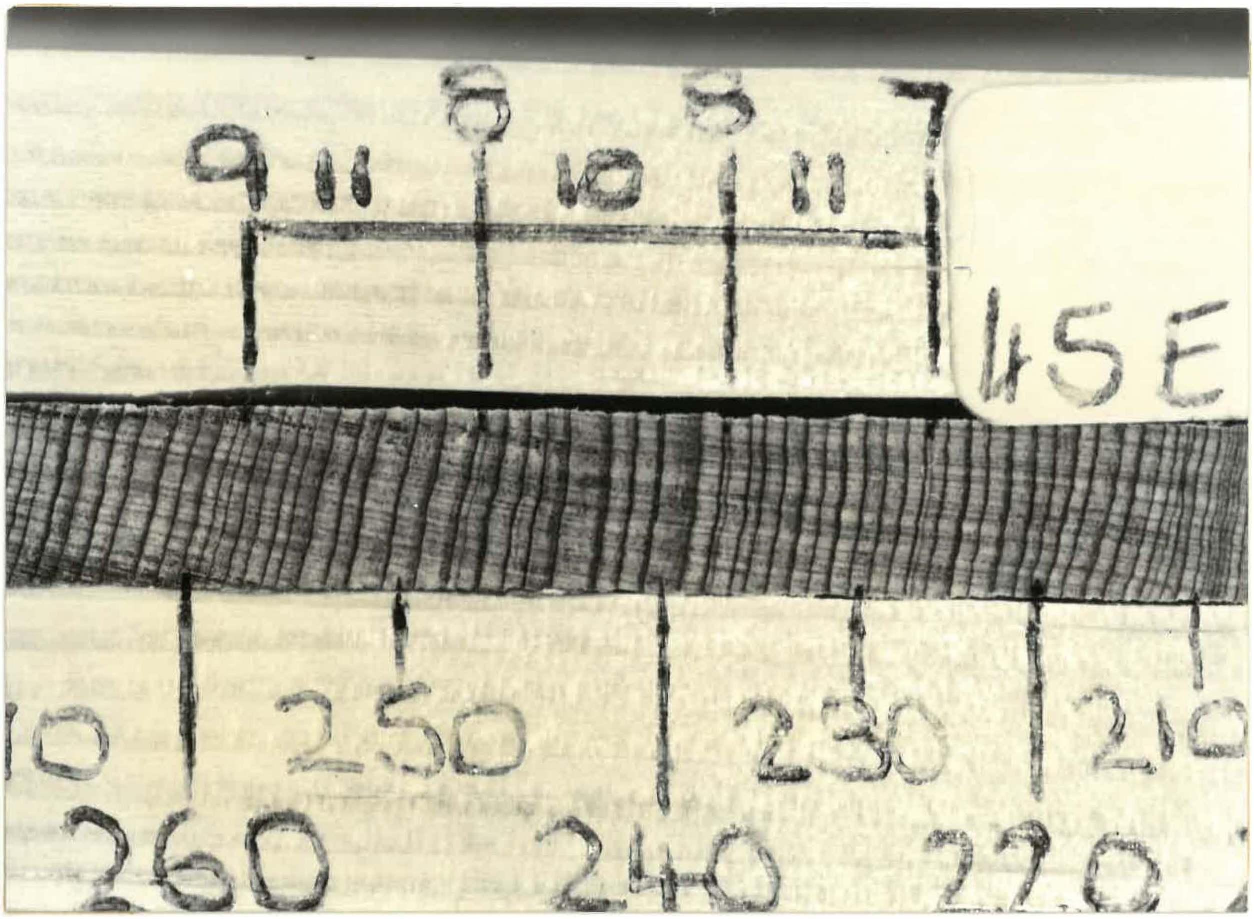


Fig. 3.1 Part of core 45E showing method used to indicate ring numbers, marker rings and ring signatures.

On the far shoulder, rings distinctive for one reason or another - unusually narrow or wide relative to nearest neighbours, unusual latewood or earlywood width or colour, i.e. marker rings, and false, partially absent, absent, drought- or frost-damaged rings and displaced markers i.e. anomalous rings, were marked with ballpoint of various colours and lines were drawn upwards to the ring number.

Length of blue lines indicated relative width with conspicuously narrow rings being indicated by longer lines (Fig 3.1). Conspicuously wide rings were indicated by red lines with the ring number written above and underlined. Notations such as F for false (type 1), RB for resin band (false - type 2), PA for partially absent, D for damaged and DM for displaced marker were also drawn in red on the far shoulder above the appropriate ring number to indicate the particular type of anomalous ring.

Sequences of marker rings which were present in cores from several trees and therefore proved useful in crossdating, i.e. ring signatures, were indicated on the far shoulder by drawing lines horizontally in green connecting the member marker-ring lines. The numbers of rings between the marker-ring lines (ring intervals) in a signature were written on the horizontal signature line between marker-ring lines (Fig 3.1) when space permitted.

The above techniques for ring numbering and the marking of distinctive rings combine some features of the skeleton and number plots, which were written on paper, as reported by Glock (1937) and Stokes and Smiley (1968). By writing the information directly on the shoulders of the core mount, more detail could immediately be gained in crossdating if needed by examining the adjacent rings themselves.

The mounted cores marked as described above form a permanent record of the dates assigned (ring numbers), marker rings, anomalous rings and ring signatures discerned and used in crossdating. Because of the permanency of this tree-ring information, the material can be scrutinised by other researchers in much the same way as a herbarium sample serves as a voucher specimen for plant identification.

3.2.4 Centre estimates

Despite best attempts at aiming, only 8 out of the 120-130 cores collected in this study passed through the chronological centre or pith of the tree. In order to improve those tree-age estimates derived from pithless cores, centre arcs (curvatures of the innermost latewood bands) were used in conjunction with Pythagoras's theorem (see Fig. 3.2) to estimate the length of missing radius and the number of annual rings in it (Clayton-Greene, 1977).

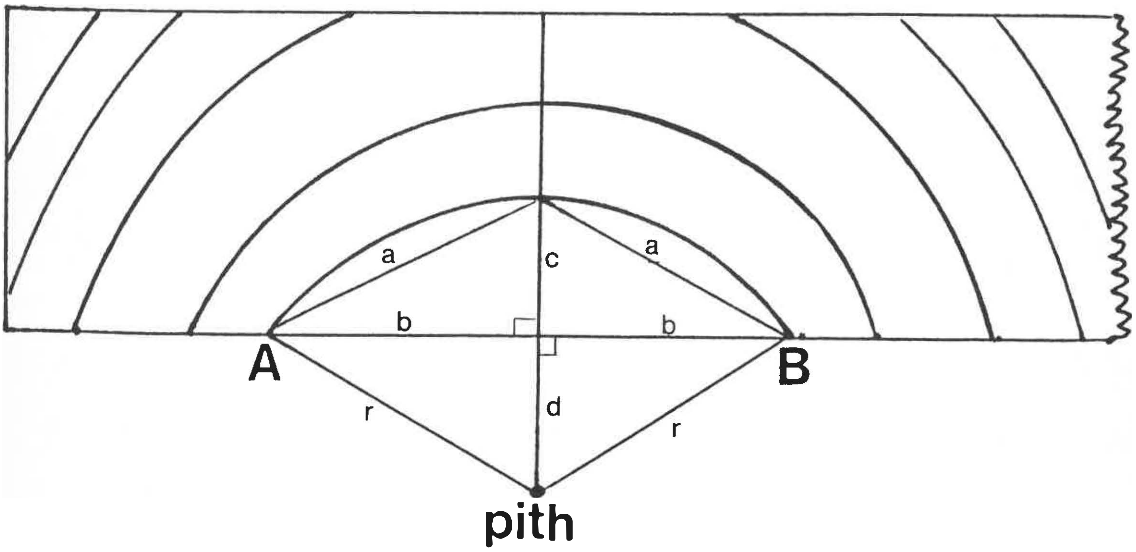


Fig. 3.2 Geometric technique for estimating length of missing radius (d) using centre arcs

The formulae used were:

$$b^2 + c^2 = a^2, \quad b^2 + d^2 = r^2$$

$$r = c + d, \qquad r^2 = c^2 + d^2 + 2cd$$

$$b^2 + d^2 = c^2 + d^2 + 2cd$$

$$b^2 = c^2 + 2cd$$

$$d = (b^2 - c^2)/2c$$

where b = chord AB/2, r = radius and d = missing radius

The chord AB was drawn in pen parallel to the edge of the core and central groove. From this chord the perpendicular line c was drawn so as to bisect AB for the smallest arc. When centre arcs were mildly irregular in shape, rays which emanate radially from the pith were used as a guide to position line c and in severe cases of irregularity, another core from the same tree was used.

Distances b and c were measured under X40 magnification using a calibrated eyepiece graticule in a stereomicroscope. Measurements of b and c were made for the maximum number of regularly-shaped arcs available on the core. This ranged from 4 to 18. The resulting values of d were averaged for use in calculating the number of annual rings.

The estimated growth rate over d, the missing radial portion was in most instances calculated by averaging the growth rate measured over the same distance for the 6 cores which had chronological centres and were from different trees. In cases judged atypical because of relatively wide rings close to the tree centre, actual widths of the rings forming centre arcs were averaged to give a growth rate to use over d.

The estimate of the number of annual rings in the missing radial portion was calculated by dividing the distance d by the calculated growth rate. A 95 % confidence interval for the additional-years estimate (centre estimate) was calculated using the method given by Bliss (1967, pp. 218-220) for the observed ratio of the two means.

3.2.5 Coring-height adjustments

In deriving tree-age estimates, adjustments to the core-age estimates need to be made to take into account the time taken for seedlings to reach coring height. Coring height in the present study ranged from 21 to 124 cm above the upslope datum. It is of interest to note that seedlings 120 cm high i.e. near maximum coring height, situated in the 350-year-old stand had basal diameters less than 3 cm. Also, the 124 cm maximum coring height is below the shrub, small-tree canopy height in the 3 kaikawaka stands.

According to Wardle (1963a) it is typical of kaikawaka along with most of the larger New Zealand conifers that seedlings, once established, grow consistently though slowly under a closed canopy but respond rather weakly to increased light.

In the present study, the height growth rate was determined to be 1 cm yr^{-1} from 2 cores taken at 43.5 and 52 cm above the upslope datum, from a tree (no. 73) situated in a midslope position in the 640-year-old stand. Both cores bisected the pith eliminating the need for centre estimate adjustments. This rate has been adopted as the average height growth rate over the coring height range.

CHAPTER 4: RESULTS AND ANALYSIS

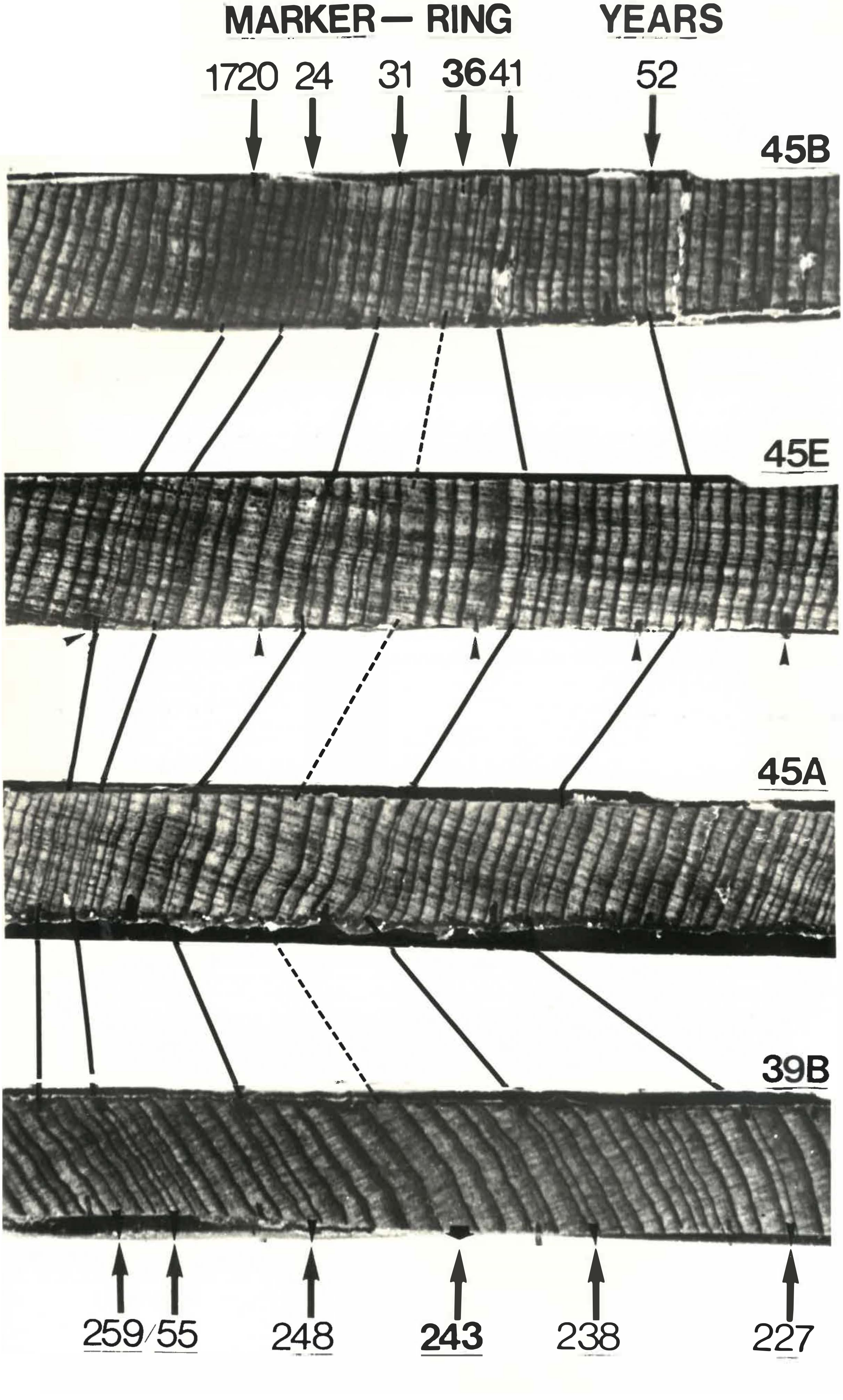
4.1 THE CROSSDATING PATTERN AND ANOMALOUS RINGS

4.1.1 Crossdating within and between trees

Crossdating is usually carried out for dendroclimatic reconstruction purposes and in such cases the usual method of recording crossdating is by measuring ring widths, computing tree-ring indices and graphing or tabulating the resulting chronology (Dunwiddie, 1979; LaMarche et al., 1979).

However, measurement of tree rings is a time-consuming and labour-intensive exercise and because dendroclimatic reconstruction was not an objective of this study - a chronology had already been developed for a nearby site (LaMarche et al., 1979, pp. 24-25) - photography was chosen as the more effective and efficient way of illustrating crossdating, climatic sensitivity, and circuit, vertical and site uniformity. Douglass (1941) and Dunwiddie and LaMarche (1980) also used photography to show crossdating.

Fig. 4.1 Crossdating within and between trees, 640-year-old stand. Tree and core labels shown on the right, cambium positioned to the right. Marker-ring years shown above and corresponding ring numbers (1=1978) shown below. Ring no. 243 is a wide marker ring relative to its neighbours, the others shown are relatively narrow. Arrows immediately below core 45E indicate every tenth ring-number.


MARKER — RING YEARS
1720
24
31
36
41
52
45B
45E
45A
39B
259/55
248
243
238
227
RING NUMBERS

In Fig. 4.1 sections of cores from trees no. 45 and 39 show the ring signature 1752-1741-1736-1731-1724-1720 comprising marker-ring numbers 227-238-243-248-255 and 259.

Cores B and E were taken at a similar coring height, 52 and 54 cm above the upslope datum respectively but on different radii, approximately 90 degrees apart. The presence of the 1752 to 1720 signature in both cores therefore illustrates circuit uniformity.

Cores E and A were taken on very similar radii but at different coring heights, 54 and 74 cm above the upslope datum respectively. This pair of photographs therefore indicates the presence of vertical uniformity.

Core 39B also displays the 1752 to 1720 signature (see photo) indicating site uniformity within the 640-year-old stand.

In addition, all 4 cores have the following 4 signatures in common with each other, and with the NET189 chronology of LaMarche et al.,1979, p.25: 1817-1826-1830; 1844-1847-1849; 1903-1904-1907-1909-1910 and 1934-1935-1938.

Crossdating was also found in the 350-year-old stand. For example cores 133A and 134A displayed the last 3 of the above-mentioned signatures. These cores were not old enough to show the other signatures listed.

The 5 cores taken from 2 trees in the 170-year-old stand are old enough to show only the 1934 to 1938 ring signature of those listed above but do not. These cores display more ring complacency (less sensitivity) than those from the 350- or 640-year-old stands. Dating was straightforward nevertheless because of the low incidence of anomalous rings and regions of growth suppression.

4.1.2 Anomalous rings

Anomalous rings as previously defined (section 3.2.3) include false, damaged (frost or drought), partially absent, completely absent and displaced marker rings. Definitions of each of these ring types, as used in the present study, follow and observations made are given.

4.1.2.1 False rings

False rings, also called intra-annual growth bands or multiple rings are additional dark bands occurring within true annual increments. When observed macroscopically i.e. with the unaided eye, such bands can be easily and incorrectly counted as true rings.

Under microscopic examination false rings were anatomically distinct and of two types. Whereas annual rings had abrupt transitions between the latewood cells of one year and the earlywood cells of the following year (Fig. 4.3) in false rings of type 1 the transitions were gradual (Fig. 4.2).

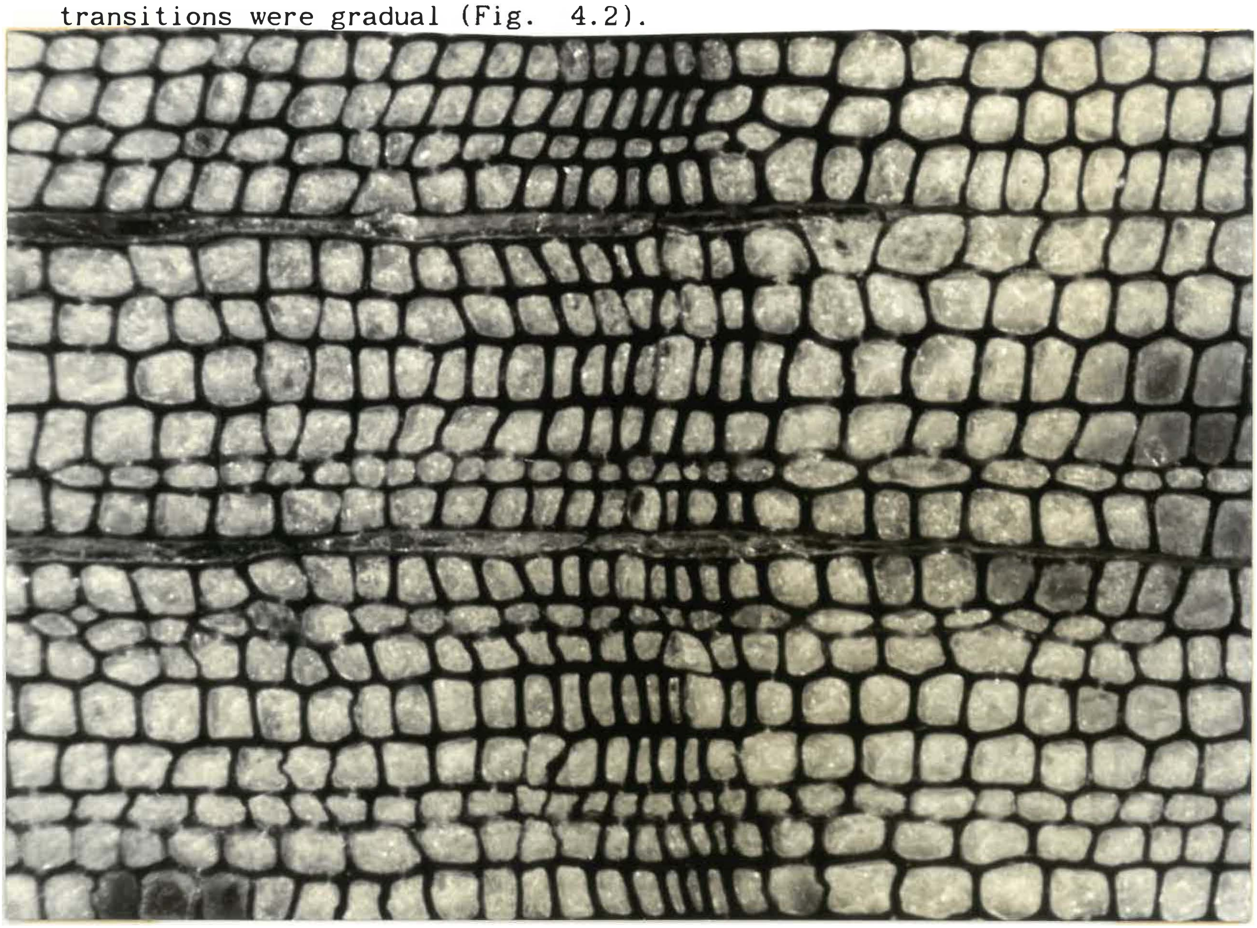


Fig. 4.2 False ring in the earlywood of ring no. 88 of core 52F. Note the gradual transitions from thick- to thin-walled cells. Cambium is positioned to the right.

Some resin bands in kaikawaka cores when observed macroscopically also look like latewood bands. Consequently such bands were classified as false rings of type 2 in this study. Microscopic examination revealed these bands were composed of thin-walled axial parenchyma cells with dark-coloured inclusions in their lumens..

Some false rings of both types merged with the latewood boundaries of annual rings and in this respect resembled partially absent or discontinuous annual rings. However, most false rings were observed to be contained completely within normal annual increments, more frequently in latewood than earlywood.

On a stand basis false rings were found most frequently in cores from the 640-year-old stand (Table 4.1).

Table 4.1 Frequency of anomalous rings in regression-data cores.

	Core label	False	Absent	Partially Absent	Annual 1=1978
640-YEAR-OLD STAND (n=15)					
	35A	0	0	0	66
	36C	2	0	0	198
	37E	0	0	0	267
	39C	1	12	2	407D
	40E	1	0	0	219
	42E	8	11	4	320
	45E	2	1	1	453
	51B	3	2	2	267
	52E	3	2	0	199
	54A	0	0	0	191
	70C	3	0	0	199
	73A	5	0	0	284
	80B	0	0	0	333
	92A	11	0	0	251
	96A	0	0	0	232
		39	28	9	3886
350-YEAR-OLD STAND (n=8)					
	56A	0	0	0	96
	133A	3	1	0	154
	134A	0	0	0	157
	138A	3	0	0	71
	141A	0	0	0	107
	58A	0	0	0	103
	137A	0	0	0	90
	139A	0	0	0	126
		6	1	0	904
170-YEAR-OLD STAND (n=2)					
	200E	0	0	2	68
	201A	0	0	0	66
		0	0	2	134
SITE TOTALS		45	29	11	4924

D=tree dead at time of coring.

Within cores, false rings were observed more frequently in regions of suppressed rings. These occurred either near the centre of trees or near the outside of those cores collected from dying or dead trees. The highest frequency of false rings observed along a single radius in the regression-data cores was 4.4 % (Core 92A, Table 4.1).

Two false rings per annual increment were observed in some instances but less frequently than one per annual increment.

4.1.2.2 Damaged rings

When viewed macroscopically the latewood band of ring no. 204 (year 1775) in core 84A appeared unusually dark and wide relative to the colour and width of the neighbouring latewood bands. A latewood false ring of type 1 was suspected and confirmed microscopically (Fig. 4.3 -2).

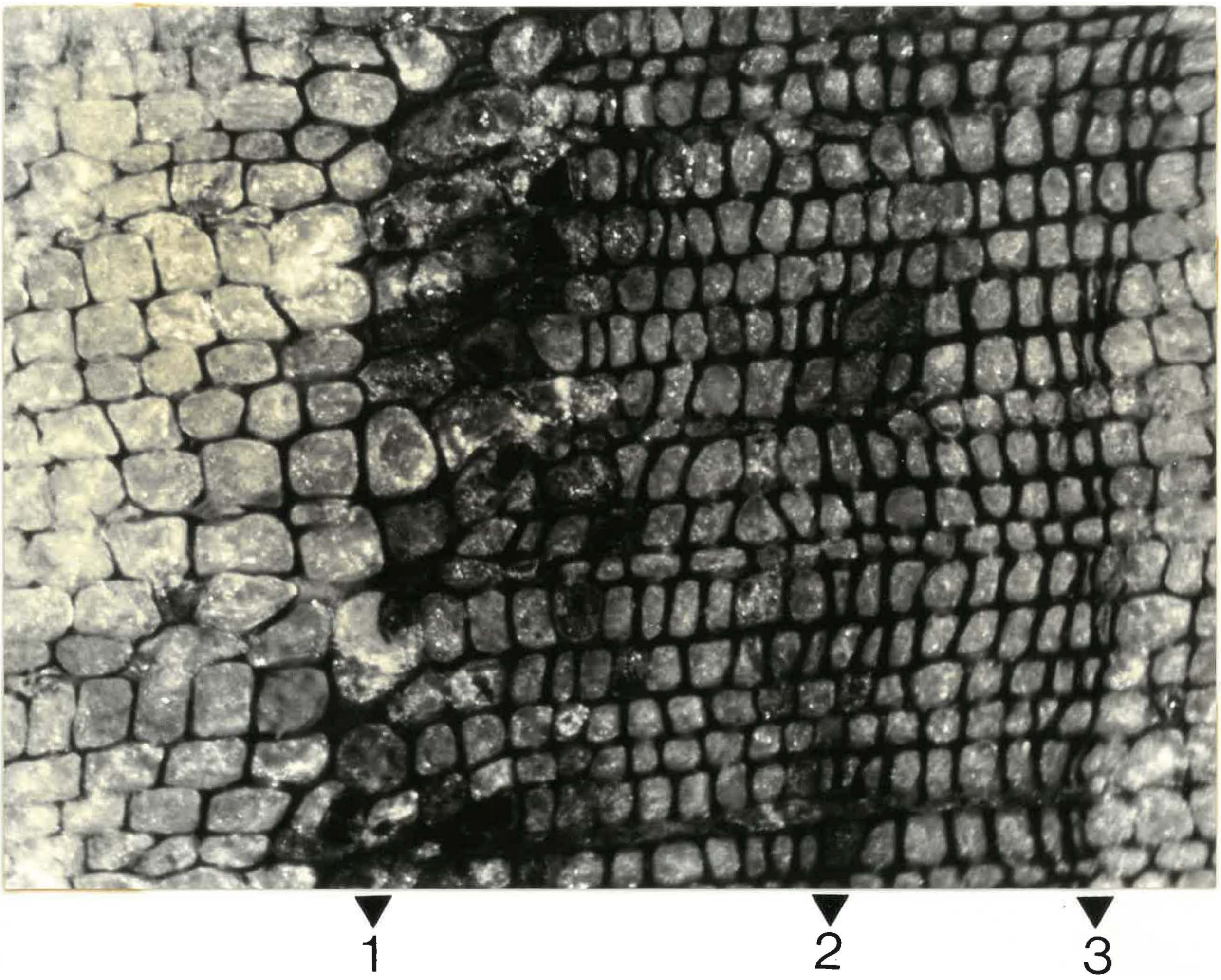


Fig. 4.3 Ring no. 204 in core 84A. Cambium positioned to the right. Zone of damaged cells (1), type 1 false ring (2) and true ring boundary (3).

Microscopic examination of ring 204 also revealed a zone of damaged cells (zone damage) at the earlywood to latewood transition (Fig. 4.3 -1). In this zone the shape and size of cells are highly distorted and enlarged compared to those in the radial files of tracheids previously developed (to the left - Fig. 4.3). Most cells in the damaged zone are thin-walled, resin deposits are common and some cells have collapsed. The continuity of radial files of tracheids has been disrupted with some files stopping and others being laterally displaced. Rays were also laterally displaced and expanded in the damaged zone on occasion (not shown).

Examination of ring no. 204 in the nearby trees (determined from map, Fig. 4.13) which had been cored and were old enough revealed the presence of damaged cells with similar features in cores 51B, 53A (zone damage) and to a lesser extent laterally with normal seriation either side (pocket damage) in core 80B. In the same ring and at the same time of year in other nearby trees, false rings of both type 1 and 2 were observed: 75A, 75A2 - type 1; 73A, 73A2 type 2. The latter 2 cores also displayed a relatively dark and wide latewood band in this year.

Examination of the above-mentioned cores for damaged zones in other rings revealed instances in 3 samples - cores 51B, 53A and 84A. Core 51B showed disruption of radial files and enlarged distorted cells in 6 rings: nos 202-205, 210 and 212. In 3 instances this occurred at the earlywood to latewood (EW-LW) transition but in ring numbers 202, 210 and 212 pocket damage occurred in the earlywood (EW) and in the latter case together with a false ring. Damage was most extensive in rings 204 and 205 where zone damage was evident. In the other rings only pocket damage occurred. In core 53A damage was apparent in both rings 203 (pocket) and 204 (zone and pocket) and in core 84A, 5 pockets of damage at the EW-LW transition occurred in ring 217.

A further set of 9 cores from 4 pre-Burrell trees present in the 640-year-old stand were examined microscopically (X20-50) for damage throughtout with special attention being given to eruption-date rings, nos 204 (1775) and 324 (1665). While no damage was evident in either of these 2 rings several instances were found elsewhere as detailed below.

Core 39A (111 cm coring height, upslope datum) displayed 6 rings with pocket damage, 4 instances in the EW (ring nos 202, 207, 228, 246) and 2 instances at the EW-LW transition (ring nos 203, 205). Core 39B (105 cm CHus) showed no damage while core 39C (76 cm CHus) displayed EW pocket damage in ring 158 and EW zone damage in ring 159.

Core 45A (74 cm CHus) showed another type of damage (hole damage) in which radial files of small-sized latewood cells curve around a hole (rings 166 and 185). Ring 180 in core 45B (52 cm CHus) showed the same type of damage. Pocket damage in rings 163 (EW) and 165 (EW-LW transition) was also evident in this core. Core 45E (54 cm CHus) displayed earlywood pocket damage in rings 243, 267 and 346 and pocket damage at the EW-LW transition of ring 267. Earlywood zonal damage occurred in ring 345.

Cores from 2 trees (38F, 49A,C) showed no damaged rings.

4.1.2.3 Partially absent rings

Partially absent rings (also called "locally present" or "discontinuous" rings) are present only in part of the sample under study. In the core samples used in the present study, 2 types of partially absent rings were identified.

In type 1, an annual ring wedged out part-way across a core and the latewood band merged with an adjacent latewood band (Figs 4.4, 4.5).

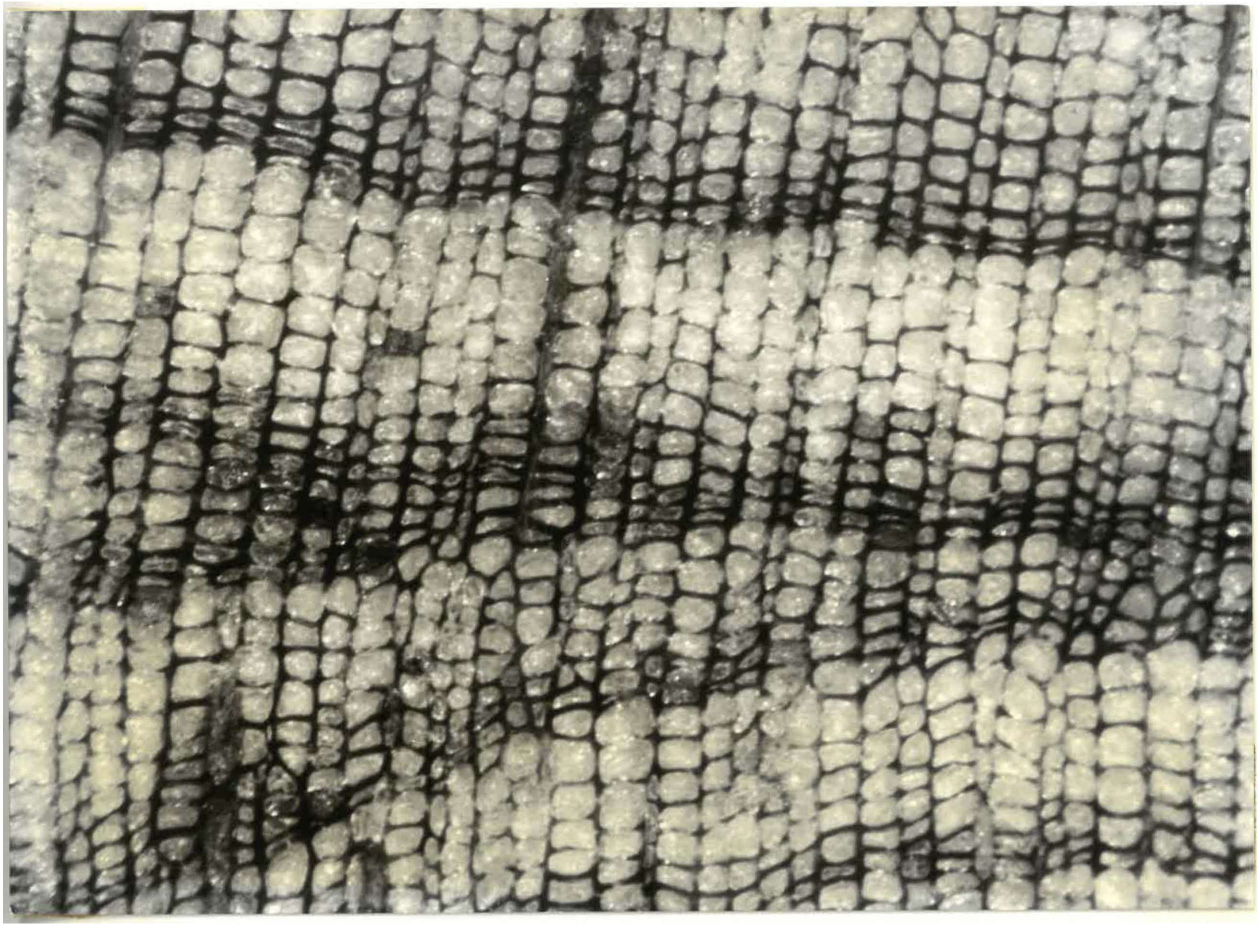


Fig. 4.4 Type 1 partially absent ring within suppressed-ring region near tree centre, core 80C. Cambium positioned to the bottom.

Partially absent rings of type 2 were more difficult to detect but often occurred where a very narrow marker was expected and within suppressed regions among other narrow rings. In this type a latewood band 1 or 2 cells wide occurred adjacent to another latewood band of similar width with a discontinuous band of earlywood cells in between (Fig. 4.5).

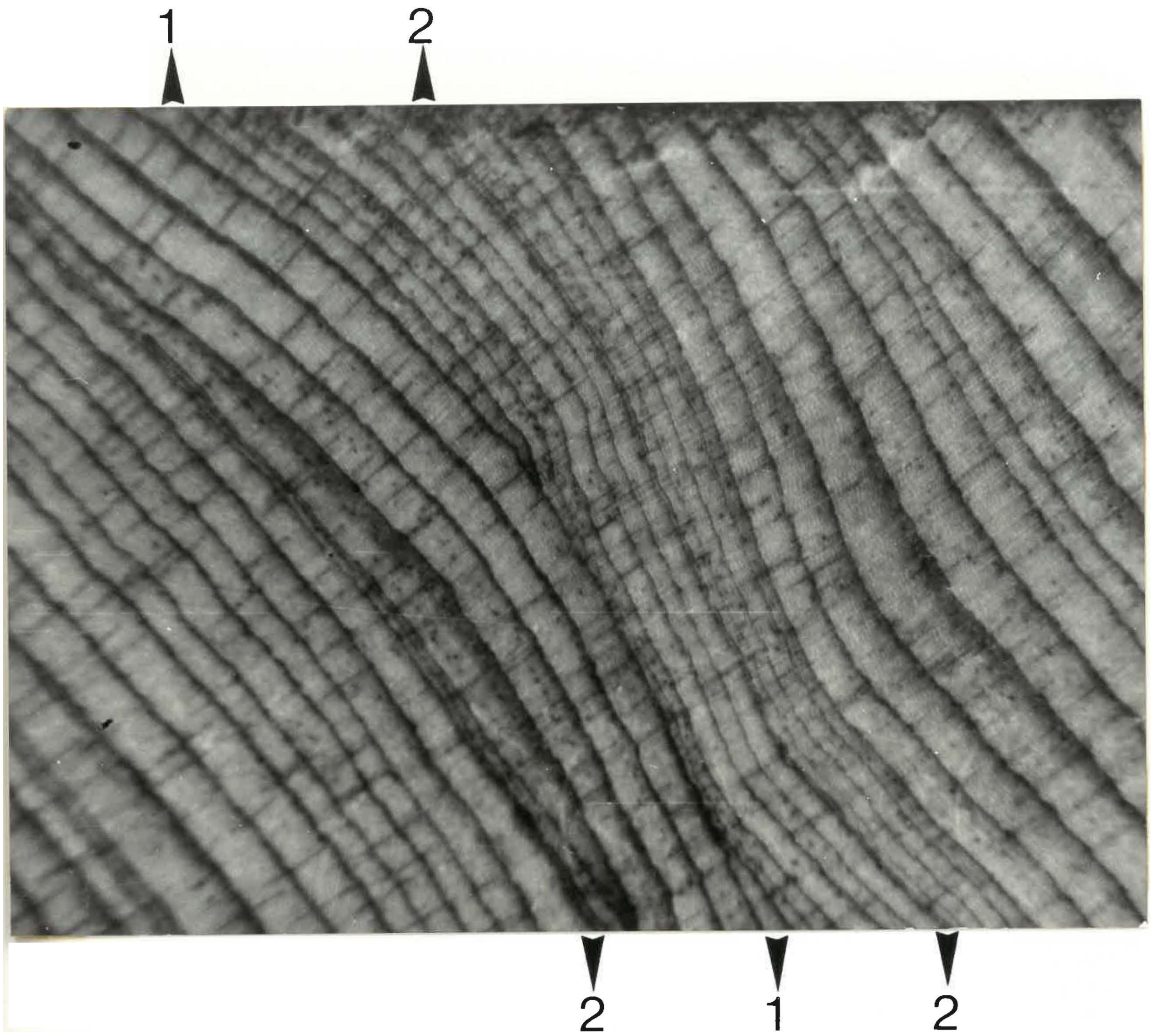


Fig. 4.5 Partially absent rings of type 1 (1) and type 2 (2) in core 80A. Cambium positioned to the right.

In the regression data cores, partially absent rings were found most frequently in the 640-year-old stand (Table 4.1). The highest frequency observed along a single radius was 1.25 % (core 42E, Table 4.1).

4.1.2.4 Absent rings

Absent rings can lead to underestimates of core and tree age. The frequency of absent rings in the regression-data cores is shown in Table 4.1. The highest frequency observed along a single radius in these cores was 3.4 %, core 42E.

At the time of coring, tree no. 42 had a sparse crown with some live foliage and several broken and dead branches. Also some rot was evident on the outside of the bole. For purposes of assessing mortality patterns per size class the tree was classified as dying.

The 11 absent rings in core 42E occurred near the bark and can be interpreted as representing cambial death at this point, 11 years prior to 1979 i.e. in 1968.

Another core (42A) taken in a similar radial position but at 114 cm above the upslope datum, 71 cm higher up the bole (Table 4.1) revealed 8 absent rings on the outside of the core. On the other side of the tree at the same height (the tree was cored right through) 9 absent rings were detected (core 42B).

A fourth core was taken from 105 cm above the upslope datum at a height between the coring heights of 42E and 42A, but on a different radius (Table 4.2). This core revealed 18 absent rings near the entry point of the corer (42C) and 7 absent rings on the other side of the tree (42D).

These data suggest cambial activity over the distance cored is not directly related to radial or vertical position in the bole.

Table 4.2 Number of absent rings within kaikawaka according to coring height, radial position and tree health.

Tree No. and Core Label	Core Ht. upslope (cm)	Radial position of core relative to downslope (top of table)	No. of Absent Rings	Plant Health Category
42A	114	↑	8	dying
B	114	↓	9	
C	105	↗	18	
D	105	↙	7	
E	43	↗	11	
39A	111	↗	19	dead
B	105	↘	20	
C	76	↘	12	
45D	86	↑	1	healthy
C	76	↘	2	
A	74	↓	11	
E	54	↓	1	
B	52	↓	6	

The second highest frequency of absent rings along a single radius in the regression-data cores was 2.9 % in core 39C, from a dead tree. The number of absent rings in other cores from this tree and associated data are shown in Table 4.2. All absent rings were found adjacent to the cambium. Given the variation in the number of absent rings, it is difficult to determine exactly what year the tree as an entity died.

A third tree (no. 45) possessed a healthy crown at the time of coring but still showed variations in the number of absent rings (Table 4.2). Again all absent rings occurred near the outside of the tree.

Only on one occasion in the regression-data cores (core 133A) was an absent ring detected in a core position other than in suppressed regions near the outside of the tree or near the tree centre. Where suppressed regions were absent, dating was straightforward.

4.1.2.5 Displaced marker rings

A phenomenon I have termed marker-ring displacement which has not been previously reported for kaikawaka (to the best of the author's knowledge) was observed when crossdating cores and in disc material. It consists in its simplest form of narrow rings being apparently displaced by one ring from the position/calendar year/ring number in which they were expected.

The core pair 53A and 53B illustrate this phenomenon. They were taken 52 cm and 50 cm above the upslope datum respectively on radii 110 degrees apart. Expected marker-ring numbers were those either commonly present in other cores from nearby trees and/or shown by a small index relative to those either side in the NET189 chronology (LaMarche et al., 1979). In core 53A ring 224 was an expected NET189 marker, present in core 53B, yet ring 223 was distinctively narrow. The other core regions of 53A fitted the crossdating pattern expected. For example the distinctively narrow and light coloured rings numbers 227 and 238 (Fig. 4.1) are present in 53A and 53B. Invoking an absent ring before ring number 223 in core 53A therefore does not solve the problem.

Similarly in core 53B ring 135 (1844) was an expected marker (53A, NET189, Fig. 4.1) yet ring 134 was narrow with a false ring in the earlywood and ring 135 was relatively wide. Again in other core regions the expected crossdating pattern is displayed so reclassification of the false ring as true (if anatomical grounds were ignored) would not resolve the issue.

The same phenomenon was evident in many other cores (displaced marker-rings in brackets): 36B (73, 76); 40A (103, 104), 73A (62); 80C (117); and in discs 50, 101D and 102D.

A special case of marker-ring displacement occurred in cores 40C, 42A, 42B, 42C, and 42D where ring 129 (1850) was narrowest compared to ring 130 (1849) in NET189.

4.2 AGE ESTIMATES OF THE FOUR STANDS

4.2.1 The Oldest Stand (640 yrs)

Fifty-one out of 79 labelled trees in this stand (65 %) were cored including the largest and second largest twin-crowned and single-crowned trees.

The largest twin-crowned, twin-boled individual was no. 63 (67.9 cm DBH, 23/3/80) which was rotten in the centre in 4 core locations over the coring height range 64 to 120 cm upslope. The age estimate was therefore based on the average radial growth rate (0.72 ± .09 mm yr $^{-1}$) determined from the maximum datable region in common between the 2 longest cores (1-330 ring no. region). Adjustment was made from breast-height age to ground-level age (+140) and a tree age estimate of 621 years was calculated.

The largest single-crowned tree (no. 84, 54.3 cm DBH, 1/9/79) was dead and rotten in the centre at coring height 55 cm and so was not aged. The second largest (no. 98, 53.8 cm DBH, 2/9/79) was estimated to be 345 years old at the upslope ground level.

The oldest single-crowned kaikawaka cored in this stand was no. 49 (38.9 cm DBH, 31/1/79) at 611 ± 13 years. Of the 5 cores taken from the tree the 3 of lowest coring height (16 cm, 57 cm and 127 cm above the downslope datum) taken from the downslope side of the tree were incomplete because of rot near the tree centre. Two cores taken higher up (164 cm, 173 cm) from the upslope side of the tree were both sound, crossdated well but although showing centre arcs did not intersect the pith.

The uncertainty given with the age estimate is only that derived from the two components of a centre estimate (distance and growth-rate estimates) using the core from 173 cm coring height. Further uncertainty which is undetermined is associated with the height-growth-rate, assumed to average 1 cm yr^{-1}. This rate was used with the coring height to adjust the tree-age estimate from coring height to that at the downslope datum (ground level). In this instance the size of the height-growth-rate uncertainty could not be reduced by choosing lower coring heights because of rot at these levels.

Because of its great age the condition of tree no. 49 was of interest. It still had a full healthy crown, strongly flagged in a downvalley-downslope direction. The bole leaned slightly in this direction too, probably because of crown weight distribution combined with rotting of the tree interior at its base. This leaning was unusual. Most wind-flagged kaikawaka in this stand were remarkably vertical.

Kaikawaka no. 49 was a pre-Burrell tree being about 287 years old in 1655, the time of the Burrell eruption (Druce, 1966a). Druce (1966a) describes two features of pre-Burrell kaikawaka that he observed in the Dawson Falls - Jacksons Lookout area on the east side of Mt Taranaki. First, the trees were characteristically very short boled, generally shorter than those of post-Burrell trees, and usually less than 3 m (10 ft.) and as short as 1.2 m (4 ft.). Second, these trees had boles without root flanges at the ground surface, indicating a base buried by tephra deposits. Tree no. 49 did not have a short bole but was without root flanges at ground level. Considering its relatively small DBH as well, its pre-Burrell status would have been most difficult to predict before coring. The steep slope complicates prediction of Burrell status at this site because tree bases can be buried by soil accumulating on upslope sides ie. soil creep. Another factor to take into account is much less Burrell tephra fell at North Egmont than in the Dawson Falls - Jacksons lookout area (Druce, 1966a, Figs 15, 18).

Examination of the youngest stand suggested kaikawaka was not an initial species on slip-faces at this location. Hence the date-estimate of the landslide initiating the oldest stand is the tree-age estimate at 0 cm downslope plus the number of years kaikawaka took to colonise the site and successfully establish ie. the invasion-lag period. From observations of both the successional sequence which kaikawaka is involved in (described later) and the general lack of colonisation of the youngest stand, this invasion-lag period is estimated to be 20-30 years.

Using data from kaikawaka no. 49, the oldest stand is therefore estimated to have been initiated by a landslide which occurred 611 + 25 = 636 years before 1979 ie. around 1343 A.D. Data from kaikawaka no. 63 gives a landslide date estimate of 621 + 25 = 646 years. Hence in this study the oldest stand is referred to as the 640-year-old stand.

4.2.2 The Second Oldest Stand (350 yrs)

Of the 23 labelled kaikawaka trees in this stand, 13 were cored including all those of larger DBH. The largest tree (no. 129, 32.5 cm DBH, 14/7/85) was estimated to be 171 years old at the downslope datum and the second largest (no. 128, 30.3 cm DBH, 14/7/85) was estimated to be 154 years old at this level.

However, the oldest kaikawaka cored in this stand was no. 134 (DBH 28.9, 2/3/80) at 329 ± 5 years (excluding height-growth-rate uncertainty). This age estimate is based on a core taken 163 cm above the downslope datum. Adding the 25-year estimate for the invasion-lag period of kaikawaka, a landslide-age estimate of 354 years before 1979 is arrived at, i.e. around 1625 A.D. Therefore the age estimate used in this study for the second oldest stand is 350 years.

4.2.3 The Third Oldest Stand (170 yrs)

Of the 4 emergent kaikawaka in this stand the 2 of larger diameter were labelled and cored. The largest tree (no. 200, 12.5 cm DBH, 2/6/85) was estimated to be 143 years old at the downslope datum. This age estimate is based on a core taken 75 cm above the downslope datum and because the core intersected the pith there was no centre-estimate component or uncertainty. A second core which also intersected the pith was taken 70 cm above the downslope datum and gave an age estimate of 137 years. Adding the 25-year estimate for the invasion-lag period of kaikawaka gives landslide-age estimates of 168 and 162 years before 1979, respectively. Hence, for this stand the age estimate of 170 years old has been used.

The second largest tree (no. 201, 11.7 cm DBH, 14/9/85) was aged at 114 years at the downslope datum based on a coring height 48 cm above this point.

4.2.4 The Youngest Stand (10 yrs)

The tallest *Hebe stricta* var. *egmontiana* growing on the debris-fan at the base of the 1977 landslide, situated opposite the 640-year-old stand, was 1.6 m high in June 1985. The average height-growth-rate therefore calculates as 20 cm yr^{-1}.

The tallest *Hebe stricta* var. *egmontiana* present in June 1985 on the debris-fan at the base of the youngest stand was 2.8 m high. Using the 20 cm yr^{-1} height-growth-rate determined for the similar stand nearby, the age of this specimen is estimated to be 14 years old at June 1985. Because *H. stricta* var. *egmontiana* is an initial species i.e. establishes early-on after destruction of previous vegetation, no invasion-lag-period adjustment is required to arrive at a landslide-age estimate. Therefore the youngest stand is estimated to be 14 years old as at June 1985 or 8 years old as at 1979 and the landslide date estimate is 1971.

To gain a second age estimate the basal diameters of the tallest *Hebe stricta* var. *egmontiana* specimens in the two debris-fan stands were measured. In the 1977 debris-fan stand the tallest specimen which was multistemmed (5) had a diameter aggregate of 16.6 cm in June 1985 i.e. an average diameter-growth-rate of 2.08 cm yr^{-1}. The tallest specimen (5-stemmed) on the youngest stand's debris-fan had an aggregate diameter of 34.8 cm giving an age estimate of 17 years before June 1985 or 11 years before 1979 i.e. 1968 landslide date-estimate.

The age estimate used in this study for the youngest stand is therefore the average of these two estimates rounded to the nearest ten i.e. 10 years in 1979.

4.3 AGE VERSUS SIZE RELATIONSHIPS

4.3.1 Tree age at 0 cm downslope versus DBH

Fig. 4.6 shows a scatterplot of tree age at 0 cm downslope versus DBH. Tree age data used in this plot were chosen from all 3 stands containing kaikawaka so as to include the DBH size range 6.1 to 47.2 cm and the most reliable age data.

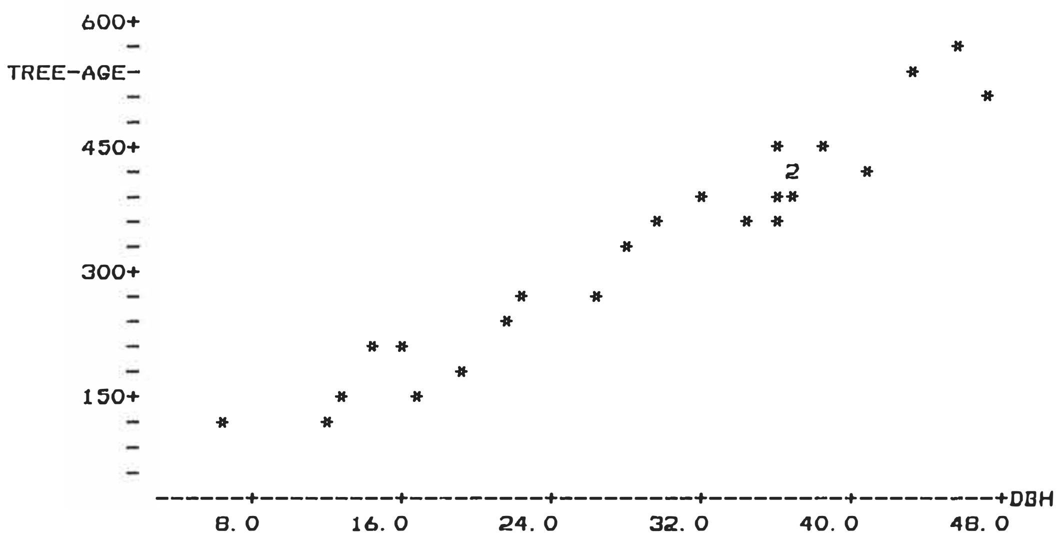


Fig. 4.6 Scatterplot of tree age versus DBH for kaikawaka

Appendix 16 shows the various components of the tree age estimates. In those cases where the coring date differed from the DBH measurement date, tree age was adjusted to the year the DBH measurement was made.

The scatterplot indicated a linear model was appropriate so a regression analysis was computed. The regression equation is:

TA = 10.5 + 11.0 DBH (DBH = 0.95 + 0.0850 TA)

r2 = 93.6 %, r = 0.97 ± .01, which is significant at the 0.1 % level.

i.e. 93.6 % of the variation in tree age at 0 cm downslope of kaikawaka at this study site (3 stands) is accounted for by variation in DBH.

A scatterplot of residuals (differences between observed and fitted values) versus tree age at 0 cm downslope (Fig. 4.7) shows no strong pattern, confirming the suitability of the linear model.

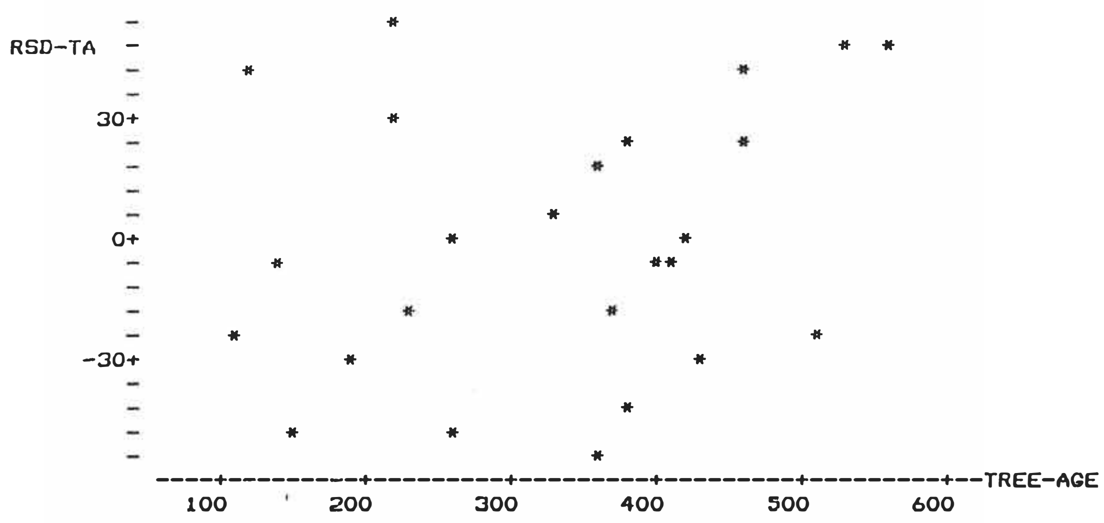


Fig. 4.7 Scatterplot of age-residuals versus tree age at 0 cm downslope.

In preliminary regression analyses, several outliers were identified and checked for possible errors or special causes. As a result the data from tree number 49 was excluded being atypical in having radial growth rates well below average (< 0.425 ± .009 mm yr^{-1}) at 0.30 ± .06 mm yr^{-1} over the ring no. region 1-300. This tree was therefore categorised as being unusually small-diametered for its age. Data from trees nos. 53, 63 and 85 were also excluded because they were double-leadered and had above-average radial growth rates (>

0.425 ± .009 mm yr^{-1}) over the 1-240 ring no. region of 1.07 ± .09, 0.70 ± .08 and 0.95 mm yr^{-1} respectively. These exclusions improved the regression coefficient to 0.97 ± .01 ($r2$ = 93.6 %).

The highly significant ($P<0.001$) linear relationship between tree age at 0 cm downslope and DBH at this study site, suggests size class distributions can be generally interpreted in an age sense. This has been done in sections 4.4.2, 4.5.2 and 4.6.2.

4.3.2 Core age versus DCH

Because tree-age-at-0cm data include an assumption involving the use of the height growth rate average for all individuals, it is of interest to exclude the coring-height adjustment and examine the relationship between core age and diameter at core height (DCH). Fig. 4.8 shows a scatterplot of these two variables.

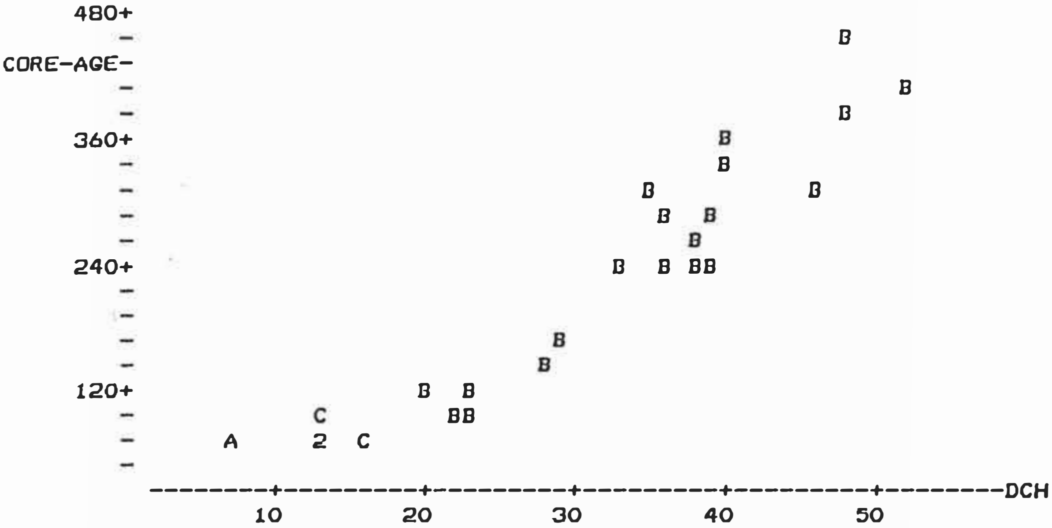


Fig. 4.8 Scatterplot of core age versus DCH for kaikawaka

The scatterplot (r2= 89.6 %) reveals a departure from linearity by cores of small-diametered young trees. Although data from all 5 cores labelled C and A did not include centre estimates these would accentuate the departure by increasing age estimates slightly. Fig. 4.9, a plot of core-age residuals from the straight line fit shows more clearly by the strong pattern displayed, the inadequacy of the linear model. Residuals are generally positive for low values of core age, negative for middle values, and positive again for the high values of core age.

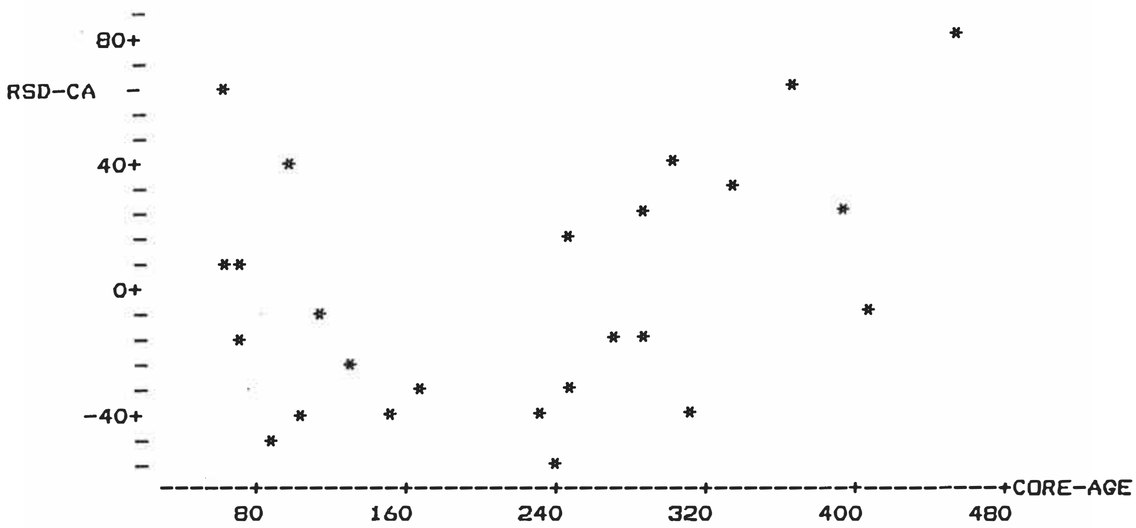


Fig. 4.9 Scatterplot of core-age residuals versus core age

To make the data more symmetrical and hence easier to analyse, various transformations of core age were tried including square root, logarithm (base 10) and negative reciprocal. The plot resulting from transforming core age to LOG core age (LCA) resulted in a straight line fit (Fig. 4.10).

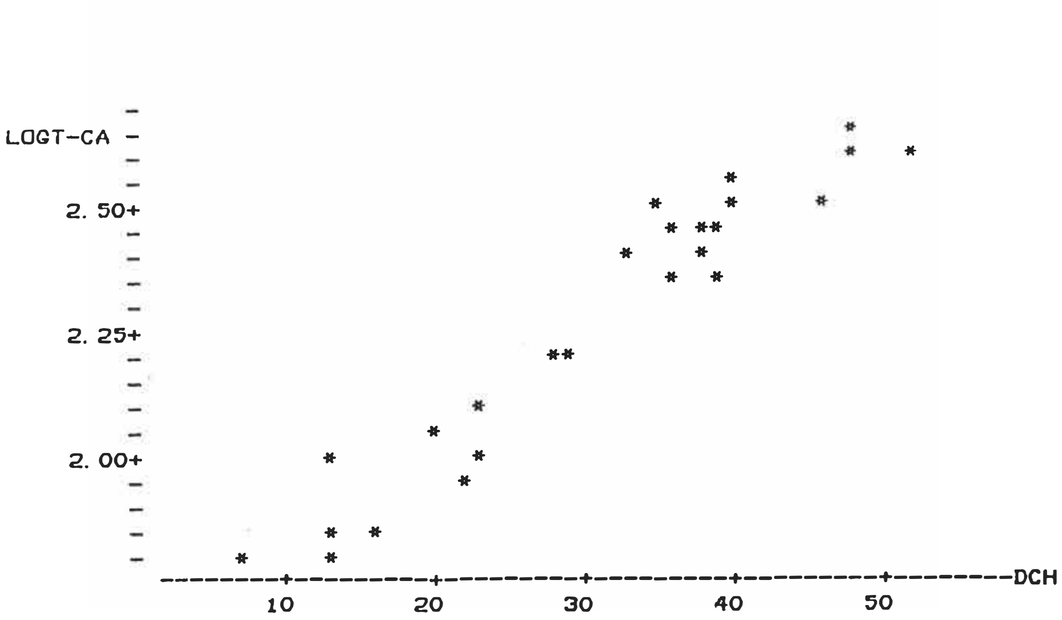


Fig. 4.10 Scatterplot of LOG core age versus DCH.

The regression equation is:

$$\text{Log CA} = 1.60 + 0.0214\ \text{DCH}$$

r2 = 93.3 %, r = 0.97 ± .01 which is significant at the 0.1 % level i.e. 93.3 % of the variation in the log of core age of kaikawaka at this study site (3 stands) is accounted for by variation in DCH.

To check the conditions necessary for inference in regression were still met, a scatterplot of LCA residuals for the linear fit was plotted (Fig. 4.11) and reveals no strong pattern. Hence this linear model is more appropriate.

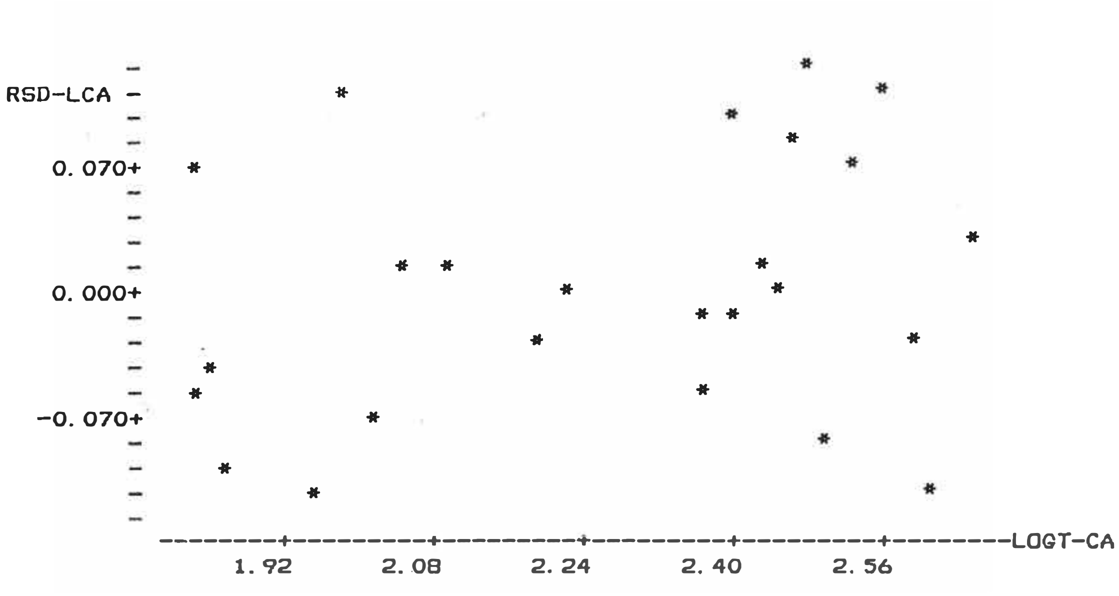


Fig. 4.11 Scatterplot of LCA residuals versus log core age.

4.4 THE 640-YEAR-OLD STAND

4.4.1 Vegetation structure and floristic composition

4.4.1.1 Description of strata and plant categories

Emergents

Kaikawaka is the dominant emergent species in this stand, occurring mostly in clumps throughout and reaching 9-12 m. *Podocarpus hallii* the other emergent is smaller (6-8 m), occurs singly except on the upper slopes and is physiognomically less important.

Canopy

Between the emergent trees and at a much lower height (2-5 m), there is an uneven shrub, small-tree canopy composed principally of *Griselinia littoralis* followed by *Pseudopanax simplex*. Both species commonly have diameters at 1.4 m above ground, of 15-25 cm. Often they can be found rooting at the bases of the tall straight vertical boles of kaikawaka (see Fig. 4.12) and less frequently of *P. hallii*. In strong contrast to kaikawaka and *P. hallii*, *G. littoralis* and *P. simplex* have bent short trunks which lean downslope and their crowns fill the nearest canopy opening. Although both species can be found with the same leaning growth habit independent of kaikawaka and *P. hallii*, it appears that the latter two species provide favoured sites on these steep slopes. This is partly because of their strong stabilising influence on downslope soil movement as evidenced by microtopographical features around them.

Fig. 4.12 Pseudopanax simplex with basal diameter of 18.8 cm rooting at the base of kaikawaka No. 48 (40.1 cm basal diameter) and leaning downslope (December, 1984).

Other species occurring in the shrub, small-tree canopy stratum are generally of smaller basal diameter and total height than most *Griselinia littoralis* and *Pseudopanax simplex* adults. Among those rated as frequent are *Hebe stricta* var. *egmontiana*, *Pseudowintera colorata* and two large leaved *Coprosma* shrubs - *C. grandifolia* and *C. tenuifolia*. *Brachyglottis rotundifolia* var., the divaricating *Coprosma pseudocuneata*, and *P. hallii* were also assigned this rating. Occurring occasionally are: *Coprosma lucida*, *C. "taylorae"*, *Carpodetus serratus*, *Myrsine divaricata* var. *divaricata*, *Melicytus lanceolatus*, *Myrsine salicina*, *Gaultheria antipoda*, *Olearia arborescens*, *Carmichaelia arborea* var., *Cordyline indivisa*, *Schefflera digitata* and *Pseudopanax colensoi*. Poles of the emergents - kaikawaka and *Podocarpus hallii* and of the canopy dominants - *G. littoralis* and *P. simplex* can also be found occasionally.

Subcanopy

Beneath the shrub, small-tree canopy, species with less than 50 % of their crowns exposed to full sunlight, but taller than 300 mm, comprise the shrub - dominated subcanopy stratum. *P. colorata* is the most prominent species in percentage cover and density terms followed by *C. grandifolia* and *C. tenuifolia*. Most species present in this stratum occur in the shrub, small-tree stratum somewhere on site so the floristic composition can be taken to be the same as previously described for the canopy.

Ground cover

In the ground cover the overall cover dominant is *Astelia fragrans*. The common form of *Blechnum capense* is locally dominant on the upper slopes near the summit track, appearing to be favoured by disturbance resulting from track outwash.

A distinctive feature of this stratum not noticed in the

350-year-old stand is that frequent hummocks of the pine- tree-like moss *Dendroligotrichum dendroides* occur throughout. Another feature, found also in the 350-year-old stand is that the ground cover is noticeably denser in canopy gaps where illumination is higher.

Seedlings of the shrub, small-tree canopy and subcanopy strata and of the emergent trees are also present in the ground cover, those of *Pseudowintera colorata* which dominates the subcanopy being particularly abundant. Seedlings of the dominant emergent kaikawaka have a marked localised distribution as shown on the distribution map, Fig. 4.13. They are found mostly in the top quarter of the stand beneath relatively open upper strata.

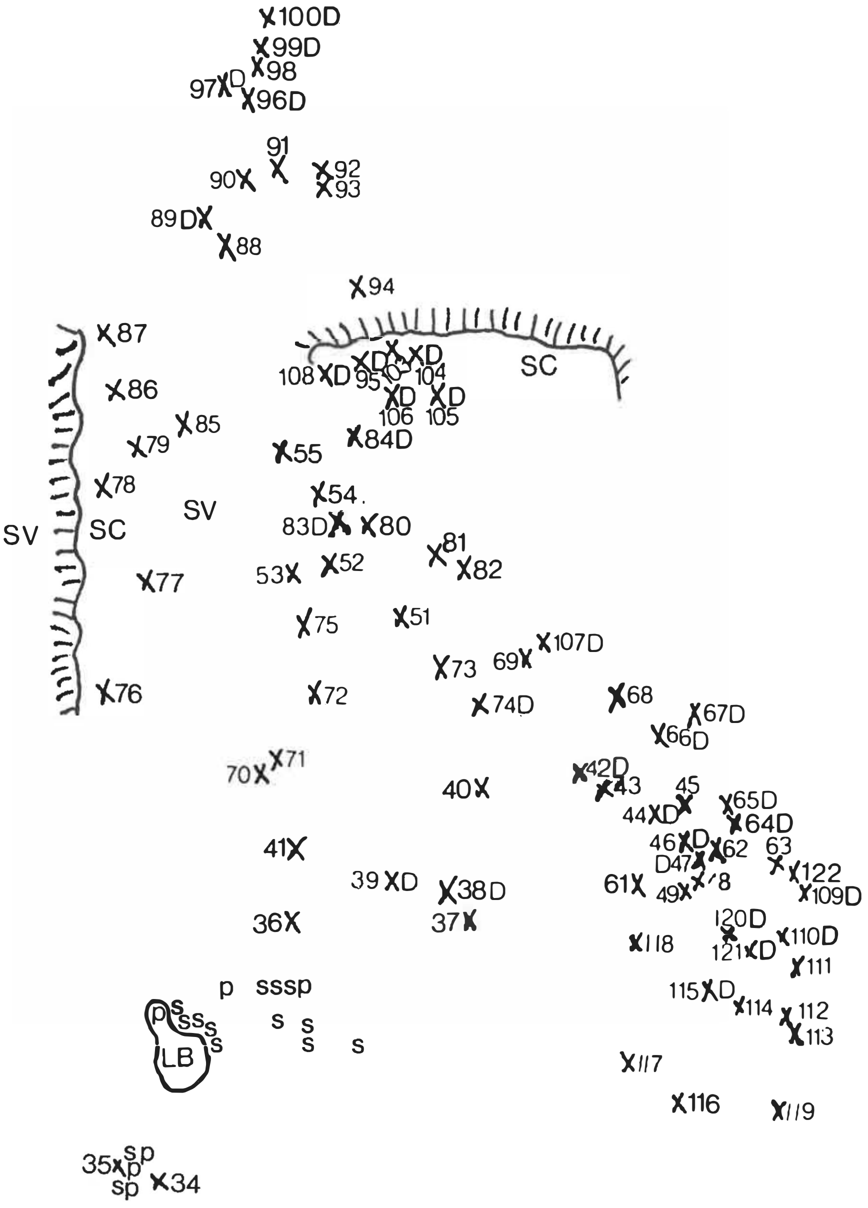


Fig. 4.13 Map showing relative positions of kaikawaka in the 640-year-old stand. Top of stand is at bottom of page. LB = large boulder, SC = small cliff, SV =small valley, D = dead or dying, s = seedling, p = pole.

Epiphytes and lianes

In addition to the vegetation structure of the 640-year-old stand already described i.e. emergent tree over shrub, small-tree canopy, over shrub subcanopy over ground cover, there is an epiphytic and lianoid flora present. Scientific names of taxa in this plant category, arranged according to life-form group are shown in Appendix 2.

Among the lower plants in this plant category there are several epiphytic lichens e.g. *Sticta* spp., *Pseudocyphellaria* spp., mosses and liverworts present. The moss *Weymouthia mollis* is noticeable, being abundant on *P. hallii*.

The epiphytic and lianoid flora on kaikawaka includes two filmy ferns *Hymenophyllum multifidum* and *Hymenophyllum sanguinolentum*. However *Hymenophyllum malingii*, a common associate of dead kaikawaka trunks (Crookes and Dobbie, 1963, p.87), although present elsewhere on Mt Taranaki (Druce, 1973) was not found in this stand. Other species found on kaikawaka in this stand (life form and tree no. in brackets) were: *Grammitis billardieri* (fern,no.63); *Brachyglottis rotundifolia* var. (dicot shrub,nos 41,68), *Pseudopanax simplex* (dicot tree,nos 34,41,63), *Griselinia littoralis* (dicot tree,nos 41, 91,94),*Coprosma* "taylorae", *C. tenuifolia* and *Myrsine divaricata* var. *divaricata* (dicot shrubs,no.41), *Rubus cissoides* var. *cissoides* and *Clematis paniculata* (dicot lianes,no 41).

The broad surfaces and tree architecture e.g. branch-stem angles, of the lower branches of kaikawaka in this stand allow bryophytes to grow in the accumulated humus under the moist conditions which prevail (Fig. 4.14). Such a bryophyte cushion with the humus beneath provides a favourable site for the germination of the seeds of some angiosperms and supplies water and nutrients required by the seedlings. However survival beyond the seedling stages is a challenge that can only be met by a few species.

Fig. 4.14 Kaikawaka No. 37 with its lower branches supporting bryophyte-lichen cushions.

Hemi-epiphytes (pseudo-lianes); a notable feature

Two species are able to accomplish the transition from epiphytic seedlings to saplings and beyond and both make the transition by becoming terrestrial. To accomplish this both species *Griselinia littoralis* and *Pseudopanax simplex*, send long liane-like adventitious roots from their perching sites, on the lower branches (Fig. 4.15) or in the fork of a twin-boled tree, down to the ground.

On four kaikawaka trees, *Griselinia littoralis* displayed this hemi-epiphytic growth habit and on three other kaikawaka trees, *Pseudopanax simplex* accomplished the same. On one other kaikawaka tree (no. 114) both *G. littoralis* and *P. simplex* exhibit this remarkable root development side by side (Fig. 4.15). Characteristically the adventitious roots of *P. simplex* divide into several smaller-diameter strands part-way-down, whereas those of *G. littoralis* remain single (Fig. 4.16).

Fig. 4.15 Adventitious roots of Pseudopanax simplex (left) and Griselinia littoralis emanating from a perching site on a branch stump of kaikawaka No. 114.

Fig. 4.16 Hemi-epiphytic Pseudopanax simplex and Griselinia littoralis roots side by side on kaikawaka No. 114.

Although hemi-epiphytic *G. littoralis* and *P.simplex* plants are better lit than their terrestrial counterparts, they are still unable to overtop and shade their host tree at this subalpine site. Instead their crowns occupy the canopy spaces below and to either side of the kaikawaka crowns. By comparison, in the lower montane forest around 500 m altitude at North Egmont, the ecologically- equivalent species are *Metrosideros robusta*, another dicot tree, as the hemi-epiphyte, and *Dacrydium cupressinum*, another gymnosperm, as the emergent. However in this lower situation the hemi-epiphyte in most instances overtops and shades out the initially supporting emergent. (See Figs. 4.17 and 4.18).

Fig. 4.17 Metrosideros robusta in the process of overtopping and shading-out an emergent Dacrydium cupressinum in the lower montane forest, North Egmont.

Fig. 4.18 Adventitious roots of a hemi-epiphytic Metrosideros robusta enclasping the bole of a Dacrydium cupressinum, lower montane forest, North Egmont.

The free-standing individuals of *P. simplex* and *G. littoralis* previously mentioned as being found rooting at the bases of kaikawaka and *P. hallii*, mostly have cylindrical trunks (Fig. 4.12) showing none of the distortions expected when adventitious roots coalesce to form a self-supporting trunk. Nor is there any evidence of decayed host trunks embraced in adventitious roots of the hemi-epiphytes (c.f. *M. robusta* and *D. cupressinum* situation, Fig. 4.18). Hosts in most instances are still healthy. Hence it would appear these free-standing individuals germinated and grew in situ rather than began life epiphytically, then became hemi-epiphytic and finally free standing.

Other angiosperms observed to occur as epiphytes on the adult kaikawaka trees of this stand, for example, *Brachyglottis repanda* var. and *Myrsine divaricata* var. *divaricata*, cannot establish terrestrially after an epiphytic beginning and hence they rarely survive the seedling stages when epiphytic. Such species are sometimes called ephemeral epiphytes e.g. Oliver, (1930).

4.4.1.2 The life-form composition of various strata

Table 4.3 summarises the life-form composition of the various strata (excluding the subcanopy) and of the epiphytic and lianoid plant category of the 640-year-old stand. (See Appendix 1 for species names). This summary is presented as a supplement to the detailed vegetation descriptions already provided to enable a simple and rapid comparison to be made of the life-form composition of each stratum.

Table 4.3 Comparison of the life-form composition of various strata in the 640-year-old stand.

LIFE-FORM CATEGORY.	STRATUM OR PLANT CATEGORY.							
	Emergent		Canopy		Ground cover		Epiphytes, and lianes	
	Spp.	%	Spp.	%	Spp.	%	Spp.	%
Ferns					13	46	5	36
Gymnosperm trees and shrubs	2	100						
Dicot trees			8	38			3*	21
Dicot shrubs			12	57	1	4	3*	21
Dicot lianes							2	14
Composite herbs								
Dicot herbs (other than composites)					6	21		
Monocot trees and shrubs			1	5				
Monocot lianes								
Orchids					1	4		
Grasses					2	7		
Sedges					3	11		
Rushes								
Other monocot herbs					2	7	1	7
Total	2		21		28		14	
% of Spp. in each stratum relative to total Spp. No. in 640-yr stand (59)		3		36		47		14

*Also found in the canopy and subcanopy layers.

Table 4.3 shows that the emergent stratum is composed entirely of gymnosperm trees, a feature characteristic of the subalpine forest elsewhere on Mt Taranaki.

In contrast, in both the canopy and subcanopy strata the principal life form group in terms of number of species represented (Table 4.3) and relative cover is dicot shrubs. Dicot tree species are also well represented in these strata. Both features are characteristic of this altitudinal zone of Mt Taranaki in which there is a transition from upper montane forest dominated by kamahi to a subalpine scrub (> 81 % shrub cover, Atkinson, 1962) dominated by *Brachyglottis repanda* var.

Within the ground-cover stratum the most prominent life form group in species number terms is ferns and these are also the most numerous epiphytes.

4.4.1.3 The floristic composition

The floristic composition of this stand is shown in the alphabetically ordered checklist of native vascular plants, Appendix 3. The combination of species present characterises the site sufficiently for its location to be recognised by anyone familiar with the North Island flora. Species combinations at other altitudes on Mt Taranaki, (pers. observations; Clarkson, 1986) outside the National Park on the remainder of the volcanic ringplains (Clarkson and Boase, 1982; Bayfield and Benson, 1986), on the uplifted sedimentary hill country of inland Taranaki (Bayfield et. al. 1986), and on the North Taranaki uplifted marine terraces to the north-west (Neall, 1982, p210; Clarkson and Boase, 1982) are quite different.

Several taxa are present, which, according to current knowledge, are endemic to Mt Taranaki. These are: *Carmichaelia arborea* var.

(*C. egmontiana*), *Hebe stricta* var. *egmontiana*, *Ourisia macrophylla* var. *macrophylla* and *Poa laevis* var. (*P. caespitosa* var. *leioclada*) (Druce, 1973).

The flora is also distinctive because of the absence from Mt Taranaki of particular species found in association with kaikawaka at similar altitude and latitude in the central North Island. Such absent species include *Nothofagus solandri* var. *cliffortioides*, *Dacrydium colensoi*, *Dacrydium biforme*, *Phyllocladus aspleniifolius* var. *alpinus* and *Leucopogon juniperina* (personal observations; LaMarche et. al. 1979, p18 and 64).

An element of the flora is characteristically distributed in the upper montane lower subalpine zone (800-1200 m) at this latitude (pers. observations). The species forming this element are: *Alseuosmia pusilla*, *Brachyglottis repanda* var., *Coprosma pseudocuneata*, *C. "taylorae"*, *C. tenuifolia*, *Cordyline indivisa*, *Gahnia procera*, *Griselinia littoralis*, *Hebe stricta* var. *egmontiana*, kaikawaka, *Luzuriaga parviflora*, *Myrsine divaricata* var. *divaricata*, *Olearia arborescens*, *Ourisia macrophylla* var. *macrophylla*, *Pseudopanax simplex*, and *Viola filicaulis*.

Another element of the flora in this stand consists of species which have their ecological optima at lower altitudes in the upper lowland - lower montane zone (460-800 m asl) but this stand is within their ecological range. These species include: *Cyathea smithii*, *Leptoperis superba*, *Melicytus lanceolatus*, *Myrsine salicina* and *Pseudopanax colensoi* (pers. observations).

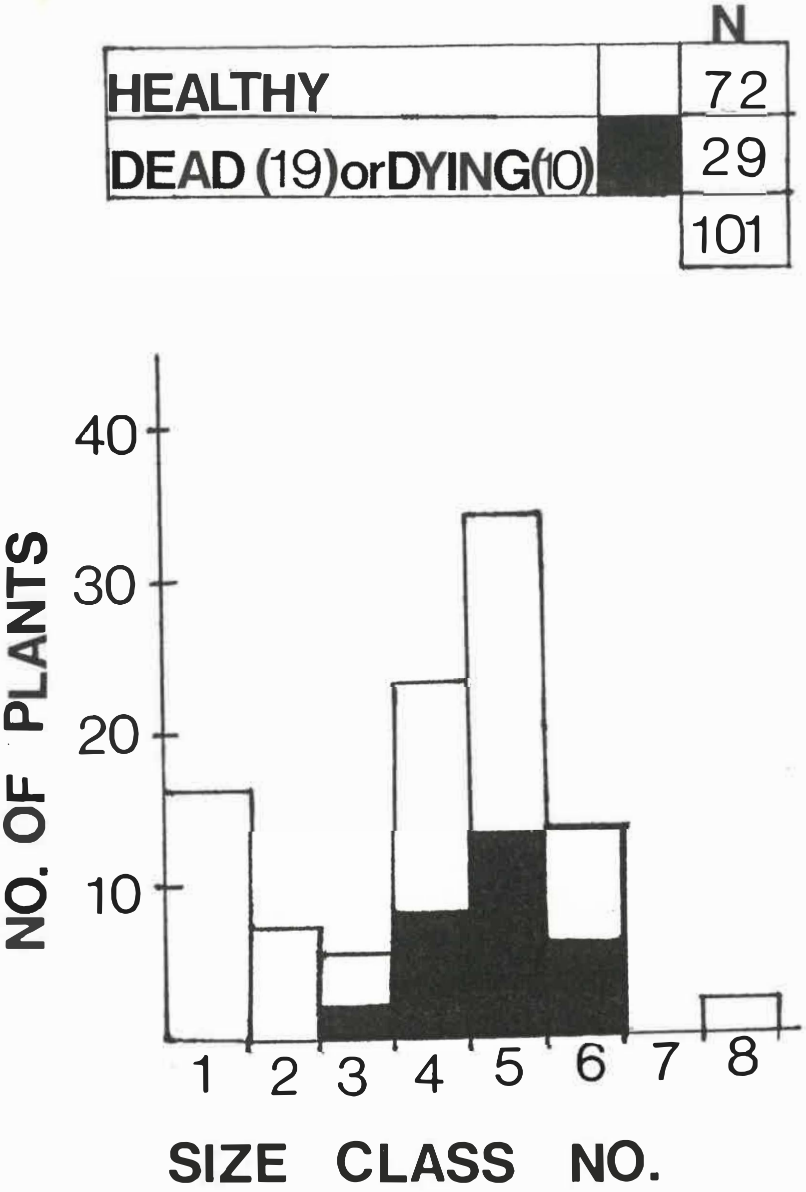
Other species have ecological optima in the lowlands (0-460 m) e.g. *Asplenium bulbiferum*, or at higher altitudes than this stand, within the subalpine scrub vegetation belt e.g. *Brachyglottis repanda* var. (pers. observations).

4.4.2 Size-class distribution, basal-area measures and density of the kaikawaka population

Fig. 4.19 shows the size-class distribution of kaikawaka in the 640-year-old stand, using 10 cm size-class intervals after 5 cm. Ten centimetre size-class intervals permit direct comparison with data in some of the published literature e.g. Veblen and Stewart (1982).

The size-class distribution shown in Fig. 4.19 suggests three main establishment periods/events. Trees in size class 8 (66-75 cm) appear to be survivors of a former population which existed on a previous surface. However both trees in this size class, numbers 53 and 63, are double-leadered with twin crowns. Hence their capacity for photosynthate production is greater than the surrounding trees which are single boled - single crowned. Examination of cores taken from tree no. 53 and tree no. 63 indicate that both trees exhibit an above-average radial growth rate (> 0.425 ± .009 mm yr^{-1}) of 1.07 ± .09 and 0.70 ± .08 mm yr^{-1} respectively, over the 240-year period before the 1978-79 growing season. Their larger sizes therefore do not necessarily indicate greater ages. Tree no. 63 was determined to be 621 years old (sect. 4.2.1) which is comparable to the oldest single-crowned tree (no. 49) at 611 years old. Yet this tree had a DBH of only 38.9 cm.

Trees in size classes four to six (26-55 cm) appear to represent another main establishment period/event. Seventy per cent of the population occurs within these size classes. Because D.B.H. is linearly related to age (P=0.001,section 4.3.1), Fig. 4.19 suggests three colonising groups with those trees in size class 5 (36-45 cm)



DBH size class	
no	interv.
	cm
1	1 – 5
2	6 – 15
3	16 – 25
4	26-35
5	36-45
6	46-55
7	56-65
8	66-75

Fig. 4.19 Size-class frequency distribution of kaikawaka in the 640-year-old stand.

having the highest relative abundance at the 34 per cent population level. This indicates a period during which the establishment rate was considerably greater than during the current one.

Plants in size classes one to three (1-25 cm) appear to comprise the third establishment phase, in which a decreasing number of plants occur in successively larger-size classes, suggesting continuous recent regeneration with a reduced level of recruitment into the higher size classes.

Fig. 4.19 also shows the portion of every size class which is made up of dying or dead trees. Interestingly the pattern of mortality spans a range of size classes from 16 cm DBH to 55 cm DBH suggesting trees are not merely dying from old age.

The number of dead trees is greater than, or, less often, equal to the number of dying trees in every size class (see Table 4.4).

Table 4.4 Numbers and percentages of dead or dying kaikawaka trees per size class in the 640-year-old stand.

Dbh Size Class (cm)	Total no.	Nos dead	Nos dying	% dead and dying per size class
1-5	16	0	0	0
6-15	7	0	0	0
16-25	6	2	0	33
26-35	23	5	3	35
36-45	34	8	5	38
46-55	13	4	2	46
56-65	0	0	0	0
65-75	2	0	0	0
Total	101	19	10	

Such a trend is supported by more widespread observations made personally, from Ahukawakawa Mire to North Egmont where most of the kaikawaka trees have died already (see Figs. 4.20, 4.21,). However dead trees stay standing for a considerable period until their roots have decayed and therefore dead trees accumulate. Without dendrochronological data from crossdated cores on the period dead trees have remained standing and on the time taken for trees to die, the ratio of dead to dying trees cannot tell us whether the death effect is diminishing.

Table 4.4 also shows the percentage of trees per size class that are dying and dead. This increases from 33 per cent to 46 per cent in successively larger-size classes suggesting, for this population, that larger and generally older trees are more liable to die. However this trend is not statistically significant. Notably the seedling and pole size classes (1 and 2) displayed no mortality, neither did the largest size class, (8), 66-75 cm DBH. As mentioned previously, both trees in this size class were double-leadered with twin crowns and exhibited above- average growth rates.

Fig. 4.20 Canopy dieback in kaikawaka stands situated below the Pouakai Range at 1000 m elevation (March, 1984).

Fig. 4.21 Closer view of kaikawaka dieback seen in Fig. 4.20 (March, 1984).

The geographic distribution of dead and dying trees in the 640-year-old stand is shown in Fig. 4.13. Dead and dying trees occur throughout the stand but with clusters present in certain areas. The occasional live tree occurs within these clusters. Mortality does not appear to be density dependent as clusters of live trees also occur.

Total basal area (stem cover) of live and dead kaikawaka in the 640-year-old stand calculated from DBH measurements and estimates was 9.73 m^2 (1.73×10^1 m^2 ha^{-1}) in the 1978-79 growing season. Seventy nine tree measurements were used in this calculation together with 22 estimates for 16 seedlings (2.5 cm av. DBH) and 6 poles (5.0 cm av. DBH).

The mean basal area per tree for the 79 trees (excluding seedlings and poles) was 1.2×10^{-1} m^2. The density of kaikawaka plants was 183 stems ha^{-1}.

These values of basal area and density will be used in a later section to quantitatively show the relative dominance and abundance of kaikawaka in the 3 older stands.

4.5 THE 350-YEAR-OLD STAND

4.5.1 Vegetation structure and floristic composition

4.5.1.1 Description of strata and plant categories

Emergents

In this stand, as for the 640-year-old stand, two emergent species kaikawaka and *Podocarpus hallii* (6-8 m high), are present. Very few emergents occur on the upper slopes (see Fig. 2.2) and on the lower slopes kaikawaka is the dominant emergent scattered throughout while *P. hallii* occurs occasionally.

Canopy

The canopy layer is comprised of shrubs and small trees with top height varying generally between 2-4 m. On the upper slopes the canopy is composed almost entirely (>80 %) of a dead dicot shrub species. These dead shrubs have lost their bark and their fine branches and the remaining larger diameter branches are full of small insect holes. Taken together such features suggest they have been dead for a considerable period. A comparison of branch pattern was made with other subalpine shrubs nearby and this suggested the identity of the dead species as being either *Pseudopanax simplex* or *Pseudopanax colensoi*. The former is most probably correct as it is much more abundant in the surrounding shrubland than the latter.

On the midslopes and lower slopes the canopy appears healthy and is comprised principally of *Pseudopanax simplex*, *Brachyglottis rotundifolia* var., *Hebe stricta* var. *egmontiana* and *Griselinia littoralis*. While *P. simplex* and *B. repanda* var. are more important on midslopes *H. stricta* var. *egmontiana* and *G. littoralis* are particularly prominent on the lower slopes.

Other members of the shrub small-tree canopy mosaic rated as frequent are: *Coprosma "taylorae"*, *C. tenuifolia*, *C. grandifolia*, *Pseudowintera colorata*, *Myrsine divaricata* var. *divaricata* and *Carmichaelia arborea* var.. *Coprosma pseudocuneata*, *C. lucida*, *Dracophyllum longifolium* var., *Melicytus lanceolatus*, *Carpodetus serratus* and *Pittosporum tenuifolium* var. *tenuifolium* were rated as occasional. *Pseudopanax colensoi* s.s. and poles of *Podocarpus hallii* and of kaikawaka also occur occasionally.

Scientific names of the members of the shrub small-tree canopy layer, categorised according to life form, are included in the species checklist of Appendix 4.

Table 4.5 Comparison of the life-form composition of the shrub-small tree canopy strata of the 350- and 640-year-old stands.

Life-form category	350-year-stand		640-year-stand	
	Spp.	%	Spp.	%
Dicot trees	9	39	8	38
Dicot shrubs	13	57	12	57
Monocot trees	1	4	1	5
Total	23		21	

Table 4.5 shows the life-form composition of the canopy, excluding poles of the two gymnosperm emergents, and permits comparison with the 640-year-old stand. The life-form composition of this stratum is very similar in both stands with the dicot shrubs life form category containing the highest species number followed by the dicot trees category.

The canopy species composition is the same in both stands except for two species found only in the 350-year-old stand. These were the dicot tree, *Pittosporum tenuifolium* var. *tenuifolium* and the dicot shrub, *Dracophyllum longifolium* var. (*D. urvilleanum*) (incl. *D. filifolium*). Scientific names of the canopy species common to both stands are shown in Appendix 9.

Subcanopy

The subcanopy stratum is similar in composition to the canopy stratum and includes seedlings of the two emergent species.There is no clear dominant species but *Pseudowintera colorata*, *Coprosma tenuifolia* and *Coprosma grandifolia* are most common, with seedlings of *Weinmannia racemosa* present but not occurring in the canopy.

Comparison of the subcanopy strata of the 350- and the 640-year-old stands indicates this stratum is taller, more separate from the canopy and more easily seen in the latter stand.

Ground cover

The ground cover is comprised of 9 fern species, 1 species of dicot tree - *Aristotelia serrata*, found only in the ground cover, 8 species of dicot herbs, 2 species of orchids, 2 species of sedge and 3 species of other monocot herbs (see Appendix 4 for names). Furthermore, several members of the emergent and canopy strata are represented by seedlings in the ground cover. Numerous seedlings of the dominant emergent, kaikawaka, were noted, these having a markedly clustered distribution around parent trees. Seedlings of *Hebe stricta* var. egmontiana, *Carmichaelia arborea* var. and *Coprosma tenuifolia* were also observed, those of the latter species being particularly abundant. As was the case in the 640-year-old stand, the overall cover dominant is *Astelia fragrans*.

Table 4.6 Comparison of the life-form composition of the ground cover of the 350- and 640-year-old stands.

Life-form category	350-year stand		640-year stand	
	Spp.	%	Spp.	%
Ferns	9	36	13	46
Dicot trees	1	4		
Dicot shrubs			1	4
Dicot herbs	8	32	6	21
Orchids	2	8	1	4
Grasses			2	7
Sedges	2	8	3	11
Other monocot herbs	3	12	2	7
Total	25		28	
No. of life form categories represented	6		7	

In both relative and absolute terms the distribution of life forms in the ground cover of two older stands is similar (Table 4.6) with ferns being predominant and a similar number of categories being represented in each case. Species totals are also similar. However a non-quantitative comparison indicates there is greater total cover (less bare ground) in the 350-year-old stand.

Table 4.7 Differences in the floristic composition of the ground covers of the 350- and 640-year-old stands.

Life form category	Taxa unique to 350-year stand.	Taxa unique to 640-year stand.
Dicot tree	Aristotelia serrata	
Dicot shrub		Alseuosmia pusilla
Dicot herb	Epilobium pedunculare E. sp.	
Orchid	Pterostylis banksii	
Fern		Asplenium terrestre ssp. terrestre Blechnum chambersii B. colensoi Gahnia procera
Sedge		Hymenophyllum pulcherrimum
Grass		Microlaena avenacea Poa laevis var.
Spp. total	4	8

The two older stands possess unique species in their ground covers (Table 4.7). Without detailed autecological information on the species involved and without further searching, it is difficult to determine whether these differences are significant successionally. Some of the species shown in Table 4.7 occur in low numbers only at a few scattered sites in the stand e.g. *Aristotelia serrata.* Obviously then the relatively small probability of such species being found during a survey may account for some differences. Furthermore, not all the species recorded as present are successful at establishing themselves in the stands. Where the only record of presence is a seedling specimen e.g. *Aristotelia serrata* the species is likely to be impermanent.

The situation is further complicated by the presence of canopy gaps in each stand which tend to be in earlier successional states than the surrounding vegetation. For example, two taxa unique to the 350-year-old stand, *Pterostylis banksii* and *Aristotelia serrata* were found in canopy gaps. Field observations throughout the Taranaki Land District suggest that these taxa have relatively high light requirements as they usually occur in recently disturbed areas. Such areas include roadside banks (Mt. Messenger *P. banksii*) and colluvium at the bottom of sedimentary cliffs (Awa-te-take Pa Historic Reserve -*A. serrata*).

Like *Pterostylis banksii* and *Aristotelia serrata*, *Gahnia procera* and *Poa laevis* var., unique to the 640-year-old stand, were also found in canopy gaps and have relatively high light requirements. However in contrast to *P. banksii* and *A. serrata*, *G. procera* and *P. laevis var.* have their ecological optima at higher altitudes in the subalpine zone. Here their requirements for relatively high light can be more easily met as vegetation stature is generally much lower. *G. procera* and *P. laevis* var. are also probably more tolerant of colder temperatures than *P. banksii* and *A. serrata*, even though *P. banksii* is a summer-flowering tuberous annual.

Epiphytes and lianes

The 350-year-old and the 640-year-old stands support a similar range of life forms in this plant category and Table 4.8 shows ferns are dominant in both stands

Table 4.8 Comparison of the life-form composition of the epiphytic and lianoid plant category of the 350- and 640-year-old stands (see Appendix 5 for species names).

Life-form category	350-yr stand		640-yr stand	
	spp. no.	%	spp. no.	%
Ferns	5	50	5	36
Dicot trees	1	10	3	21
Dicot shrubs	1	10	3	21
Dicot lianes	2	20	2	14
Monocot herbs	1	10	1	7
Spp. totals	10	100	14	99

Although not shown in Table 4.8 because of the way the life form categories have been defined, one important difference between the two stands is that the 640-year-old stand supports both hemi-epiphytic and free-standing dicot trees, *Griselinia littoralis* and *Pseudopanax simplex* whereas in the 350-year-old stand these species occur free-standing but not as hemi-epiphytes. A second difference (Table 4.8) is that the 640-year-old stand supports a wider range of epiphytic dicot tree and shrub species (6) than the 350-year-old stand (2). Thirdly, these epiphytes were much more numerous and taller in the 640-year-old stand. Fourthly, comparison of the species totals (Tables 4.8, 4.9) indicates that the 640-year-old stand supports four more species in this plant category than the 350-year-old stand (See Table 4.9 for names).

Table 4.9 Differences in the floristic composition of the epiphytic and lianoid plant category of the 350- and 640-year-old stands.

Life-form category	Taxa unique to 350-year stand.	Taxa unique to 640-year stand.
Ferns	Polystichum silvaticum	Hymenophyllum multifidum
Dicot trees		Melicytus lanceolatus Pseudopanax simplex
Dicot shrub		Brachyglottis rotundifolia var. Myrsine divaricata var. divaricata
Spp. total	1	5

4.5.1.2 The life-form composition and comparison with the 640-year-old stand

Table 4.10 summarises the life-form composition of the various strata (excluding the subcanopy) and of the epiphytic and lianoid plant category of the 350-year-old stand. It also permits a summary comparison with the corresponding strata in the 640-year-old stand.

Table 4.10 Comparison of the life-form composition of various strata of the 350- and 640-year-old stands.

LIFE FORM CATEGORY					STRATUM								PLANT CATEGORY			
	Emergent				Canopy				Ground cover				Epiphytes, and lianes			
	Stand				Stand				Stand				Stand			
	350		640		350		640		350		640		350		640	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Ferns									9	36	13	46	5	50	5	36
Gymnosperm trees	2	100	2	100												
Dicot trees					9	39	8	38	1	4			1	10	3	21
Dicot shrubs					13	57	12	57			1	4	1	10	3	21
Dicot lianes													2	20	2	14
Composite herbs																
Other dicot herbs									8	32	6	21				
Monocot trees					1	4	1	5								
Orchids									2	8	1	4				
Grasses											2	7				
Sedges									2	8	3	11				
Other monocot herbs									3	12	2	7	1	10	1	7
Totals	2		2		23		21		25		28		10		14	99
*		3		3		40		36		43		47		12		14

1. Excludes Weinmannia racemosa found only in the subcanopy.
2. Includes Polystichum silvaticum also found in the ground cover.
3. Also found in the canopy and subcanopy strata.

* Percentage of species in each stratum relative to species total of appropriate stand.

As is the case for the 640-year-old stand, the emergent stratum of the 350-year-old stand is composed entirely of gymnosperm trees although these are relatively shorter in the 350-year-old stand (see Fig. 4.22). In the canopy and subcanopy the principal life form group in both stands in terms of species number and relative cover is dicot shrubs followed by small dicot trees. The ground cover and the epiphytic and lianoid plant category of both stands are dominated by the fern life form group. A similar range of life form categories in each stratum or plant category occurs in both stands.

Comparison of the species totals per stratum (Table 4.10) indicates that 43 per cent of the species diversity of the 350-year-old stand is found in the ground cover stratum (47 per cent in the case of the 640-year-old stand) followed by 40 per cent in the canopy stratum (36 per cent in the case of the 640-year-old stand) i.e. both stands are very similar in this respect.

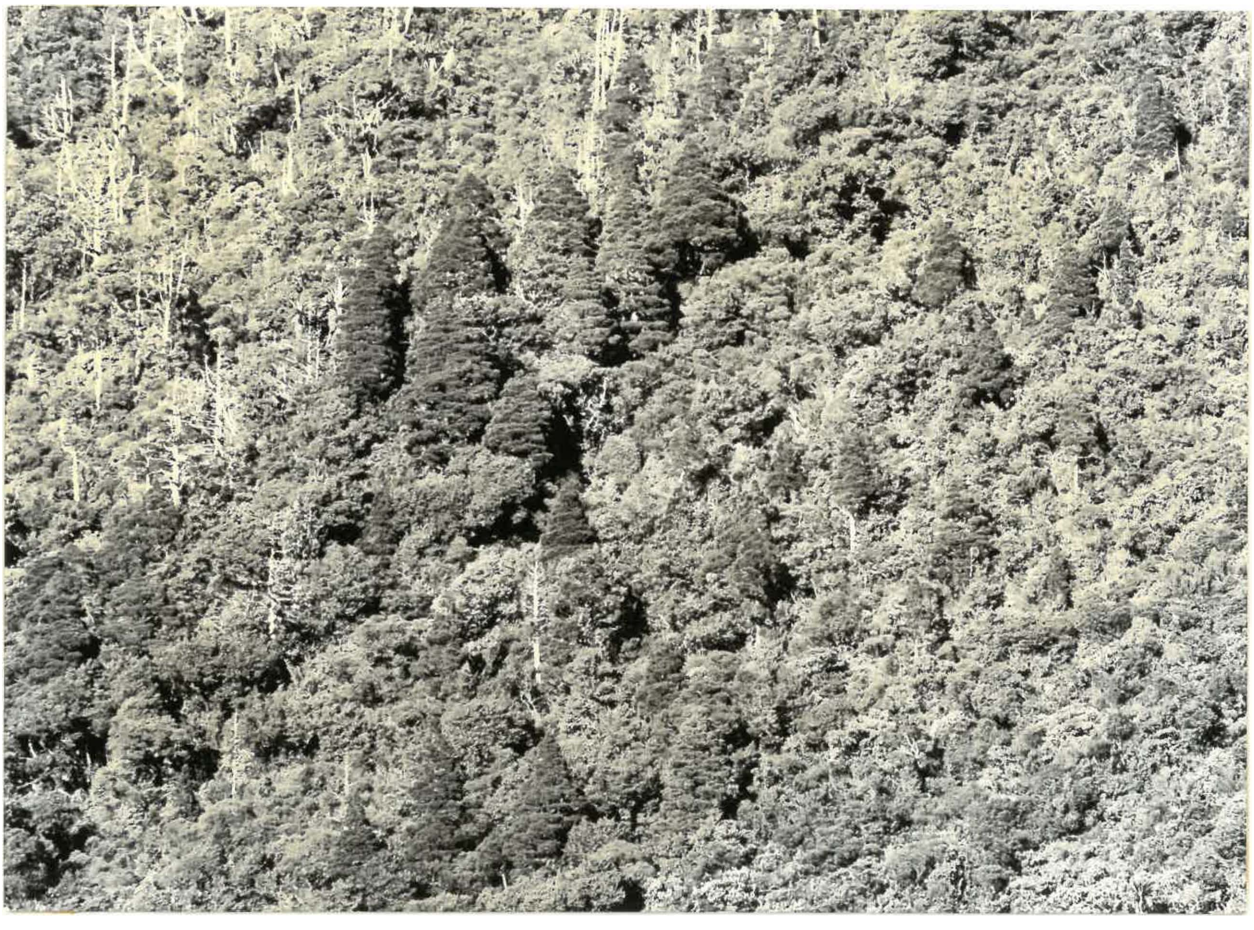


Fig. 4.22 Emergent kaikawaka in the 350- and 640-year-old stands, December 1984.

4.5.1.3 The floristic composition and comparison with the 640-year-old stand

The floristic composition of the 350-year-old stand is shown in Appendix 6. As is the case for the 640-year-old stand, the combination of species present characterises the site as a subalpine location on Mt Taranaki. The reasons for this floristic distinctiveness are the same as those given for the 640-year-old stand and so will not be repeated here. Rather, what follows is a comparison of the species diversity of the two stands and a consideration of whether the differences reflect successional status or can be explained in other ways.

Those native vascular plants unique to the 350- and 640-year-old stands are listed in appendices 7 and 8 respectively. Appendix 9 shows those species common to both stands while Table 4.11 summarises some statistics of the species complements of the two stands.

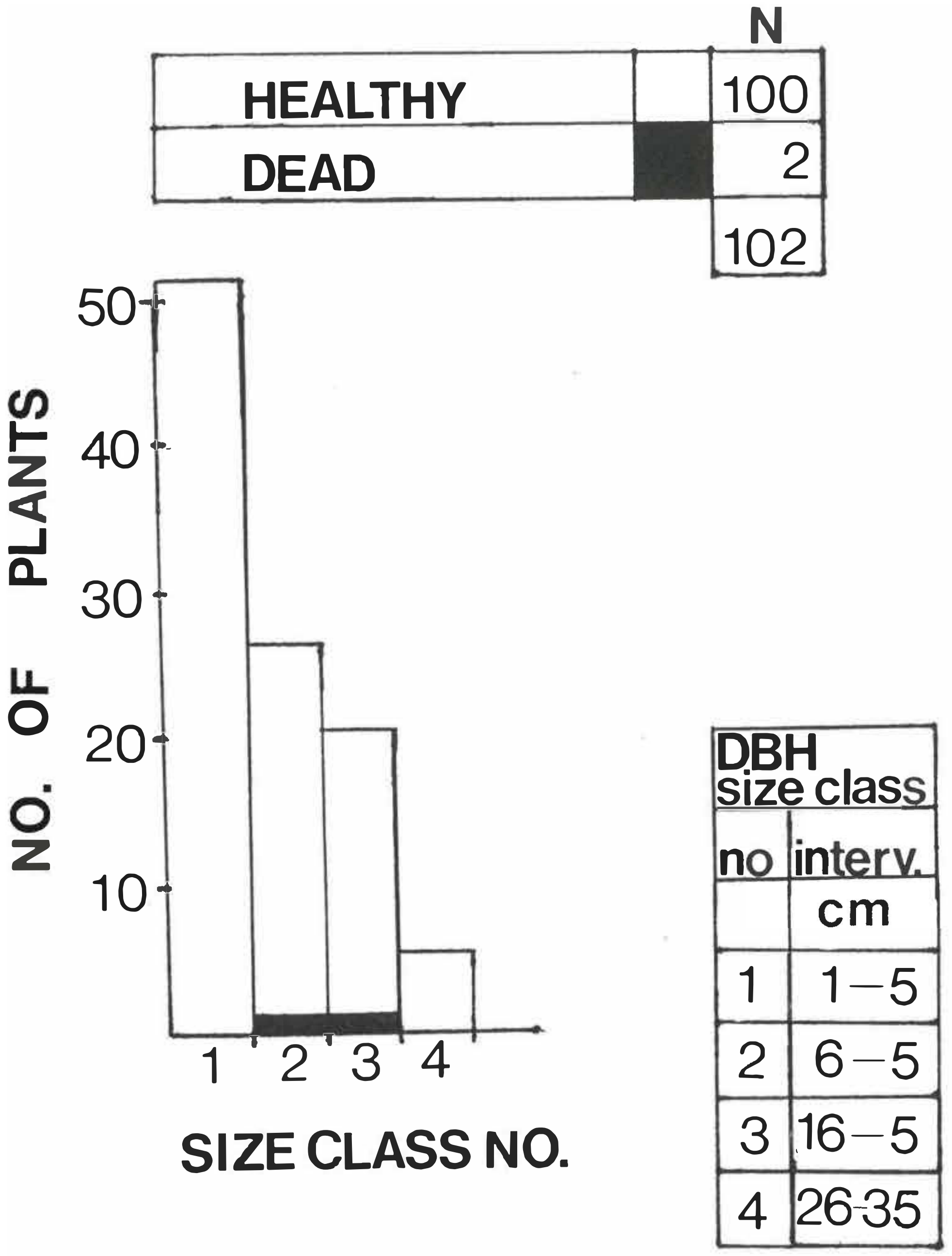
Table 4.11 Comparison of floristic composition of 350- and 640-year-old stands.

Description	Species No.	%
Unique to 350-yr stand	8	12
Unique to 640-yr stand	9	13
Common to both stands	50	75
350 yr stand total	58	87
640 yr stand total	59	88
350- & 640-yr stands combined total	67	100

Table 4.11 shows that the combined species complement of the two stands numbers 67, 87 per cent of these occurring in the 350-year-old stand and a similar percentage (88) in the 640-year-old stand. Interestingly the number of species recorded for each stand is nearly the same which is surprising considering the age differences. Of the 8 species unique to the 350-year-old stand (see Appendix 7) 50 per

cent are ground cover members. Similarly, of the 9 species unique to the 640-year-old stand (see Appendix 8), 89 per cent are ground cover members. The majority of differences in species composition of the two stands can therefore be accounted for by differences in ground cover members.

4.5.2 Size-class distribution, basal-area measures and density of kaikawaka population and comparison with the 640-year-old stand



DBH size class	
no	interv. cm
1	1–5
2	6–5
3	16–5
4	26-35

Fig 4.23 Size-class frequency distribution of kaikawaka in the 350-year -old stand.

The largest kaikawaka in the 350-year-old stand (Fig. 4.23) was that of tree no. 129 at 32.5 cm DBH while in the 640-year-old stand (Fig. 4.19) the largest tree (no. 63) had a DBH of 69.3 cm.

In the 350-year-old stand all size classes up to 35 cm DBH were represented. The majority of the population (50 per cent) had DBH sizes between 1-5 cm (size class 1). Thirty four of the 51 specimens in this size class were seedlings (< 180 cm high) and the other 17 were poles (> 180 cm high and < 5 cm DBH). In comparison the same size class for the 640-year-old stand was represented at the 16 per cent level of the population. Other classes for the 350-year-old stand i.e. nos. 2-4 had an average representation at 16.7 per cent of the total population.

Fig. 4.23 shows diminishing numbers of plants in successively larger-DBH size classes suggesting continuous regeneration with reduced levels of recruitment into the higher classes. The comparatively small size-class range suggests a young population relative to the life span of the species.

In contrast the majority of the kaikawaka population of the 640-year-old stand (70 per cent) were of much larger DBH sizes, between 26 and 55 cm and the size-class distribution (Fig. 4.19) suggests discontinuous regeneration occurred in three main phases. Most of the population established during a period much earlier in time than those individuals in the 350-year-old stand.

Figure 4.23 also indicates the portion of each size class made up of dead or dying trees. Only two individuals out of 102 (2 %) were observed to be dead, one in size class two (6-15 cm DBH) and another in size class three (16-25 cm DBH). No individuals were observed to be dying. This is in marked contrast to the 640-year-old stand where 29 per cent of the kaikawaka population was found to be dead or dying (Fig. 4.19 and Table 4.4).

Total basal area of kaikawaka in the 350-year-old stand calculated from DBH measurements of all trees (44) and from DBH estimates of seedlings (34 at 2.5 cm DBH) and poles (24 at 5 cm DBH) was 1.26 m^2, (3.9 m^2 ha^{-1}) while the total basal area of all kaikawaka in the 640-year-old stand was 1.73×10^1 m^2 ha^{-1}, 4.4 times larger.

The mean basal area per tree for the 44 kaikawaka trees in the 350-year-old stand (excluding seedlings and poles) was 3.0×10^{-2} m^2. The comparable figure for the 640-year-old stand is 4.0 times greater at 1.2×10^{-1} m^2.

Finally, the density of kaikawaka plants in the 350-year-old stand was 204 stems ha^{-1} compared to 183 stems ha^{-1} for the 640-year-old stand.

As expected total basal area and mean basal area per tree both increase with stand age while density decreases.

4.5.3 Height-class distribution of kaikawaka seedlings and comparison of kaikawaka regeneration in the 350- and the 640-year-old stands

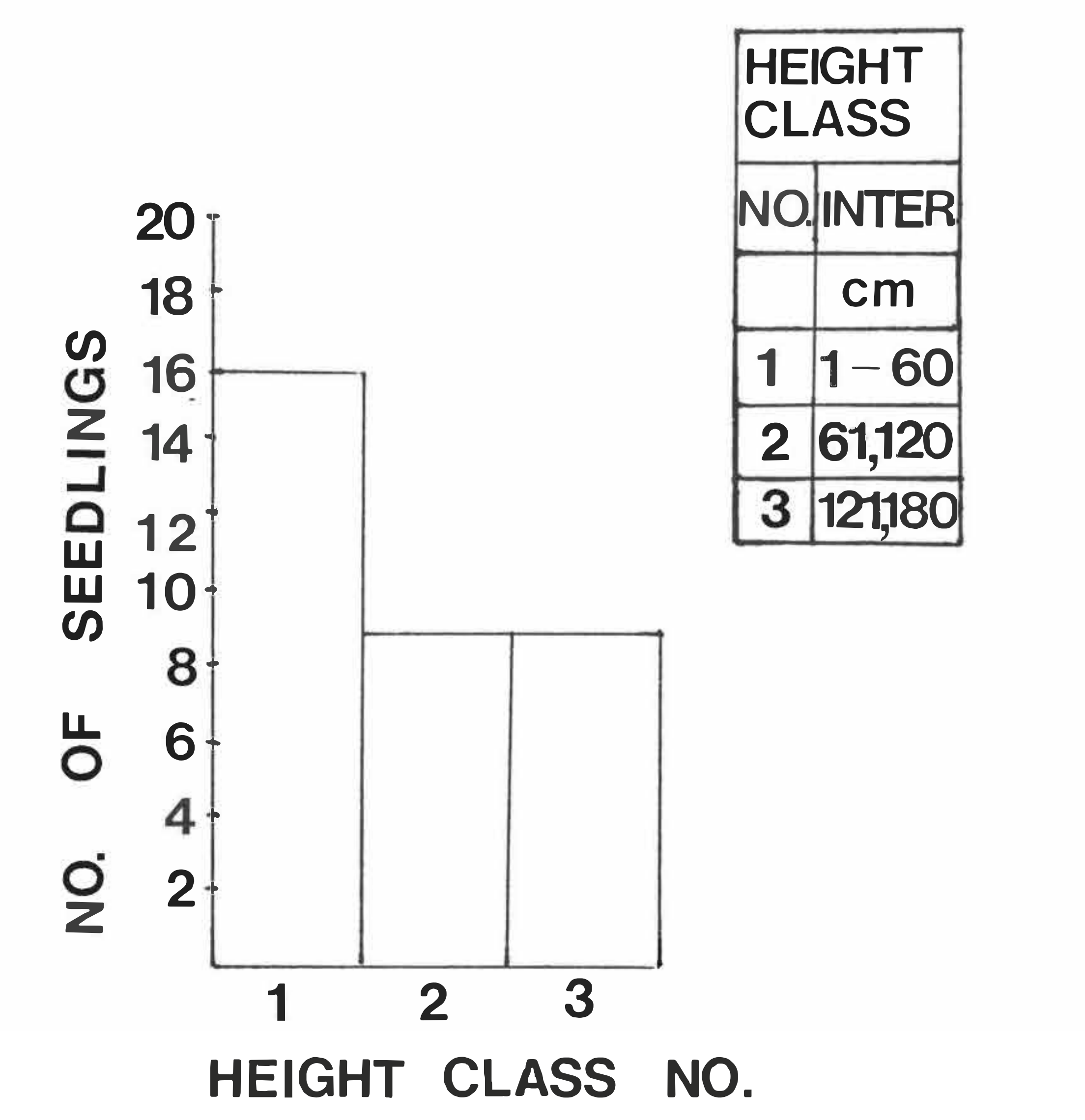


Fig. 4.24 Height-class distribution of kaikawaka seedlings in the 350-year-old stand.

Fig. 4.24 shows the height-class distribution of kaikawaka seedlings (< 180 cm high) in the 350-year-old stand. Forty seven per cent of the 34 seedlings were in height class one (1-60 cm) while height classes two and three were both represented at the 26.5 per cent level. Such a height-class distribution suggests recent continuous regeneration with reduced recruitment into the height classes of taller plants because of seedling mortality. An alternative but less probable explanation is that continuous regeneration has occurred recently with the larger number of shorter recruits having resulted from particularly favourable events e.g. heavier seed fall combined with favourable germination conditions at a later date.

A notable feature of the 350-year-old stand is that seedlings and poles of kaikawaka can be found throughout the stand where there are emergent kaikawaka trees i.e. mid and lower slopes and that these seedlings and poles have a markedly clustered distribution around the emergents. Such a regeneration pattern suggests the emergents, which established early, reached reproductive maturity and were then the parents (seed source) of the current crop of seedlings and poles. This pattern also suggests that the majority of seed is dispersed near to the parent tree.

However, in the 640-year-old stand only 16 seedlings and 7 poles were recorded and these were almost exclusively found in the top quarter of the stand where above strata were relatively open and where few emergent kaikawaka occurred. Most seedlings occurred clustered near to each other suggesting a common parent source probably tree numbers 116, 117, and 119 which occur upslope and upwind.

4.6 THE 170-YEAR-OLD STAND

4.6.1 Vegetation structure and floristic composition

4.6.1.1 Description of strata and plant categories

Emergents

The 170-year-old stand has very few emergent gymnosperms, unlike the 640- and 350-year-old stands. Only occasionally on the lower slopes do kaikawaka individuals protrude conspicuously above the average canopy height, and there are no emergent *Podocarpus hallii*.

Canopy

The canopy is composed of a number of small trees and shrubs as shown in Figs. 4.25 and 4.26. *Brachyglottis repanda* var. is the overall cover dominant with *Pseudopanax simplex*, *Hebe stricta* var. *egmontiana* and *Dracophyllum longifolium* var. ranked as second, third and fourth cover dominants respectively.

Fig. 4.25 Canopy of the 170-year-old stand viewed from the Summit Track. White flower buds belong to Brachyglottis repanda var.. Emergent kaikawaka of the 350-year-old stand occur in the background (January, 1985).

A number of other species occur less frequently in the canopy. These include *Griselinia littoralis*, *Coprosma pseudocuneata*, *C. lucida*, *C. robusta*, *Pseudopanax colensoi* and *Carmichaelia arborea* var., kaikawaka and *Podocarpus hallii*.

Fig. 4.26 Close-up of the canopy of the 170-year-old stand showing kaikawaka , a potential emergent (January 1985).

The canopy surface of the 170-year-old stand appears more even and close-knit than that of the 350- or 640-year-old stands (see Figs. 4.25 and 4.27). This is partly due to the paucity of emergent gymnosperms and partly because the small tree members - *Pseudopanax simplex* and *Griselinia littoralis*, have had insufficient time to reach their full height.

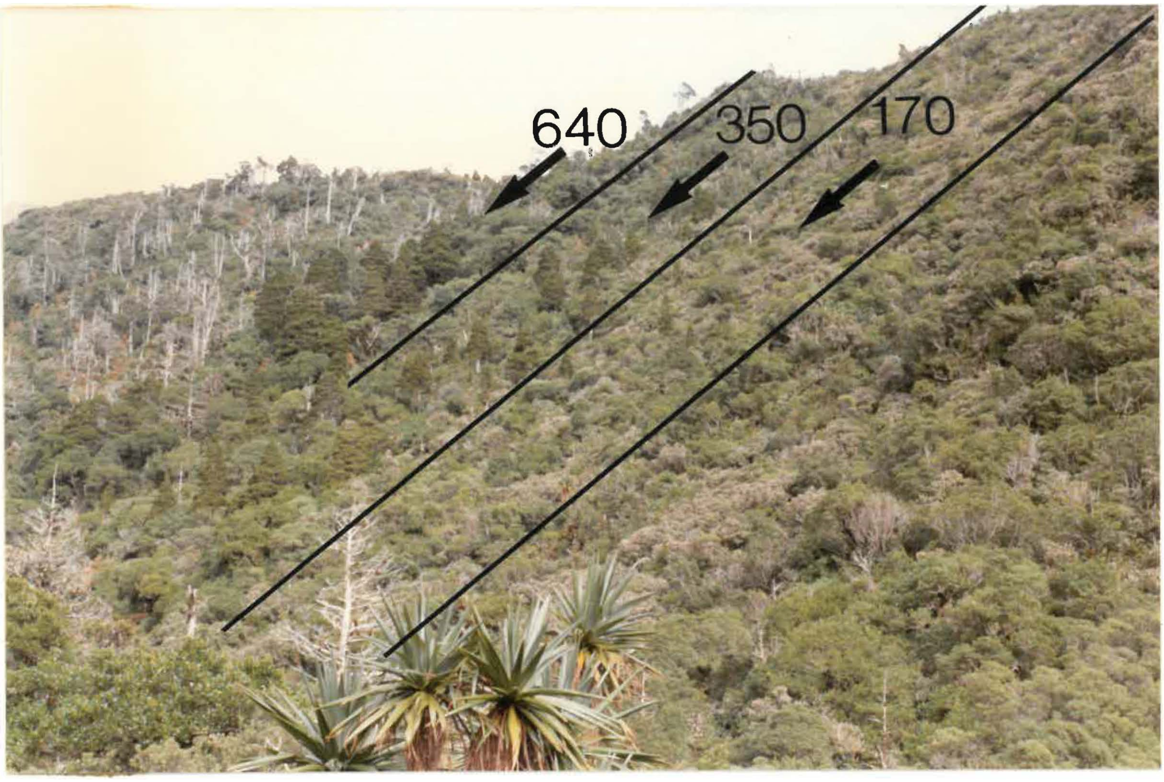


Fig. 4.27 The 170-, 350-, and 640-year-old stands (arrowed) viewed from the Translator Road. Note relative evenness of canopy surfaces.

Numbers of species per life-form category for the shrub small tree canopy are listed in Table 4.12 (see Appendix 12 for names). To enable comparison, the same characteristics of the 350-year-old stand are also included.

Table 4.12 Comparison of the life-form composition of the shrub - small tree canopies of the 170- and 350-year-old stands.

Life-form category	170-yr stand Spp.	170-yr stand %	350-yr stand Spp.	350-yr stand %
Gymnosperm trees	2	11	2	8
Dicot trees	3	17	9	36
Dicot shrubs	13	72	13	52
Monocot trees	-	-	1	4
Total	18	100	25	100

Table 4.12 shows that the predominant life-form category in both stands is dicot shrubs followed by dicot trees. However, the 170-year-old stand has a higher proportion of dicot shrubs and lower proportion and number of dicot trees in comparison with the 350-year-old stand.

Table 4.12 also highlights the comparative floristic paucity of the 170-year-old stand's canopy. Seven species, 6 being dicot trees, were found exclusively in the canopy of the 350-year-old stand. These species are: *Carpodetus serratus*, *Cordyline indivisa*, *Fuchsia excorticata*, *Melicytus lanceolatus*, *Myrsine salicina*, *Pittosporum tenuifolium* var. *tenuifolium* and *Schefflera digitata*.

Subcanopy

Several species form an indistinct subcanopy stratum beneath the canopy, with less than 50 % of their crowns exposed to full sunlight but taller than 300 mm. These include: *Coprosma pseudocuneata*, *C.*

tenuifolia C. "taylorae", *Gaultheria antipoda* and *Coprosma lucida*.

Ground cover and comparison with the 350-year-old stand

The ground cover is comprised of scattered ferns (6 species), dicot herbs (8), orchids (1), grasses (1), sedges (2) and other monocot herbs (3). Three dicot trees are also included here because they were not found in other strata (see Appendix 12 for names).

Seedling representatives of several members of the higher strata also occur in the ground cover. These include: *Hebe stricta* var. *egmontiana*, *Gaultheria antipoda*, *Dracophyllum longifolium* var., *Carmichaelia arborea* var., *Brachyglottis rotundifolia* var., *Pseudopanax colensoi*, *Pseudowintera colorata*, *Myrsine divaricata* var. *divaricata* and *Coprosma "taylorae"*.

Table 4.13 Comparison of the life-form composition of the ground cover of the 170- and 350-year-old stands.

Life form Category	170-yr stand Spp. No.	%	350-yr stand Spp. No.	%
Ferns	6	25	9	36
Dicot trees	3	13	1	4
Dicot shrubs	-		-	
Dicot herbs	8	33	8	32
Orchids	1	4	2	8
Grasses	1	4	-	
Sedges	2	8	2	8
Other monocot herbs	3	13	3	12
Totals	24	100	25	100
No. of life form categories represented	7		6	

Dicot herbs and ferns are the predominant life forms in the ground covers of both stands (Table 4.13). Only dicot trees and dicot shrubs exclusive to the ground cover have been included in this analysis. The floristic differences in the ground covers of the 170- and 350-year-old stands largely occur in the fern life-form category

(Table 4.14).

Table 4.14 Fern species exclusive to the ground covers of the 350- and 170-year-old stands.

	Exclusive to the 350-yr stand.	Exclusive to the 170-yr stand.
1	Blechnum fluviatile	Blechnum penna-marina
2	Cyathea smithii	
3	Histiopteris incisa	
4	Hypolepis rufobarbata	
5	Leptopteris superba	
6	Polystichum silvaticum	

The overall cover dominant in the ground cover of the 170-year-old stand is *Blechnum* sp. (a) which locally dominates canopy gaps, followed by *Astelia* sp. (unnamed; aff. *A. nervosa*). There is a much greater cover of *Astelia* sp. relative to *A. fragrans* in this stand compared to the 350-year-old stand. *Astelia fragrans* can grow much taller than *Astelia* sp. and dominated the ground cover in both the 350- and 640-year-old stands. Therefore, relative to *Astelia fragrans*, *Astelia* sp. (unnamed; aff. *A. nervosa*) is an early-successional light-demanding species at this site. This explanation is confirmed by field observations in the 10-year-old stand where *Astelia* sp. occurs frequently but *A. fragrans* is absent (see Fig. 4.31).

Epiphytes and comparison with the other stands

The vascular epiphytic flora of the 170-year-old stand consists of 4 fern species and 1 monocot herb (see Appendix 12 for names). In contrast to the situation in the 350-year-old stand, no epiphytic dicot trees, shrubs, or dicot lianes were found. Furthermore, the dicot trees - *Griselinia littoralis* and *Pseudopanax simplex*, which in some instances are hemi-epiphytic in the 640-year-old stand, occur only as free-standing individuals in the 170-year-old stand. These features can be attributed to the fact that potentially suitable hosts eg. kaikawaka and *Podocarpus hallii* are of insufficient size in the 170-year-old stand to provide the habitats required. There are also numerous non-vascular epiphytes - lichens, liverworts and mosses in the 170-year-old stand in addition to the vascular epiphytes described.

4.6.1.2 The floristic composition

The floristic composition of the 170-year-old stand is shown in Appendix 11. The combination of species present characterises the site as being a subalpine location on Mt Taranaki, for the same reasons previously given in the case of the 640-year-old stand. To examine floristic differences which may reflect differing successional status, the floristic composition of the 170-year-old stand is compared in Table 4.15 with that of the 350-year-old stand. Species common to both the stands are listed in Appendix 13. Examination of Table 4.15, together with field observations made in the oldest (640-yr) and youngest (10-yr) stands reveals 4 out of the 6 species listed in section A are most abundant, both numerically and in terms of cover, in the 10-year-old stand. None of these 4 species were recorded for the 640-year old stand (Appendix 3) ie. these 4 species become less important in the vegetation as one progresses from the 10-

through to the 170-year-old stand and all were absent in the 350- and 640-year-old stands.

Table 4.15 Species unique# to 170- and 350-year-old stands.

	A Unique to 170-yr stand	Life-form group	Stratum or Plant category
1	Blechnum penna-marina*	Fern	Ground cover
2	Coprosma robusta	Dicot shrub	Canopy
3	Cotula squalida subsp. squalida	Composite herb	Ground cover
4	Lycopodium australianum*	Lycopod	Ground cover
5	Poa anceps var. anceps	Grass	Ground cover
6	Pratia angulata	Other dicot herb	Ground cover
	B Unique to 350-yr stand		
1	Blechnum fluviatile	Fern	Ground cover
2	Carpodetus serratus*	Dicot tree	Canopy
3	Clematis paniculata*	Dicot liane	Liane
4	Cordyline indivisa*	Monocot tree	Canopy
5	Cyathea smithii*	Fern	Ground cover
6	Epilobium pedunculare*	Other dicot herb	Ground cover
7	Histiopteris incisa	Fern	Ground cover
8	Hypolepis rufobarbata*	Fern	Ground cover
9	Leptopteris superba*	Fern	Ground cover
10	Melicytus lanceolatus*	Dicot tree	Canopy
11	Myrsine salicina*	Dicot tree	Canopy
12	Olearia arborescens	Dicot shrub	Canopy
13	Parsonsia capsularis*	Dicot liane	Liane
14	Pittosporum tenuifolium var. tenuifolium*	Dicot tree	Canopy
15	Polystichum silvaticum*	Fern	Ground cover
16	Pterostylis banksii*	Orchid	Ground cover
17	Rubus cissoides var. cissoides*	Dicot liane	Liane
18	Schefflera digitata*	Dicot tree	Canopy

* Not found in 10-yr stand.
\# Unique only in the sense of this comparison.

Comparison of the species listed in section B of Table 4.15 with the checklist of vascular plants for the 10-year-old stand (Appendix 10) reveals 15 out of the 18 (83 %) were not found in the 10-year-old stand either ie. these 15 species have not established and persisted in the two younger-aged (170- and 10-year-old) stands. An indication of the persistence of these species in the age sequence can be gained by checking for their presence in the 640-year-old stand. Appendix 3 reveals 14 out of the 18 species in question (78 %) were recorded for the 640-year-old stand ie. they are persistent. The four exceptions are: *Epilobium pedunculare*, *Parsonsia capsularis*, *Pittosporum tenuifolium* var. *tenuifolium* and *Pterostylis banksii*.

Some summary statistics of the species complements of the 170- and 350-year-old stands are shown in Table 4.16. Ninety-one per cent of the combined species complement of the two stands was found in the 350-year-old stand and 72 % in the 170-year-old stand. Of the 6 species found only in the 170-year-old stand, 5 (83 %) are ground cover members (Table 4.15). Of the 18 species found only in the 350-year-old stand, 44 % are ground cover members and 33 % are canopy members. Therefore, as was the case in the comparison of the two older stands (640- and 350-years) the majority of the floristic differences between the 170- and 350-year-old stands (54 %) can be accounted for by differences in the ground cover.

Table 4.16 shows Jaccard's similarity index and permits calculation of Sorenson's similarity index (77 %). These indices of similarity, when compared with figures for the comparison of the 640- and 350-year-old stands (IsJ= 75 %, IsS= 85 %) show that the 350- and 170-year-old stands are less similar floristically than the two older stands (640- and 350-years).

Table 4.16 Summary statistics of species complements for 170- and 350-year-old stands.

	Species	No.	%
1	Unique to 170-yr stand	6	9
2	Unique to 350-yr stand	18	28
3	Common to both stands	40	63*
4	170-yr stand total	46	72
5	350-yr stand total	58	91
6	170- and 350-yr stands combined total	64	100

* This is Jaccard's presence-community coefficient (index of similarity).

Comparison of species totals per stratum or plant category (Table 4.17) indicates 54 per cent of the species diversity of the 170-year-old stand is found in the ground cover stratum (43 % in the case of the 350-year-old stand) followed by 37 per cent in the canopy stratum (40 % in the case of the 350-year-old stand). Clearly both stands are similar in this respect.

Table 4.17 Comparison of species numbers per stratum for the 170- and 350-year-old stands.

STAND	STRATUM						PLANT CATEGORY	
	Emergent		Canopy		Ground cover		Epiphytes and lianes	
	No.	%*	No.	%	No.	%	No.	%
170-yr	1	2	17	37	25	54	5	7
350-yr	2	3	23	40	25	43	10	12

* Percentages are species no. per stratum divided by species total of stand x 100.

4.6.2 Size-class distribution, basal-area measures and density of the kaikawaka population

Figure 4.28 shows the size-class frequency distribution of the kaikawaka population of the 170-year-old stand.

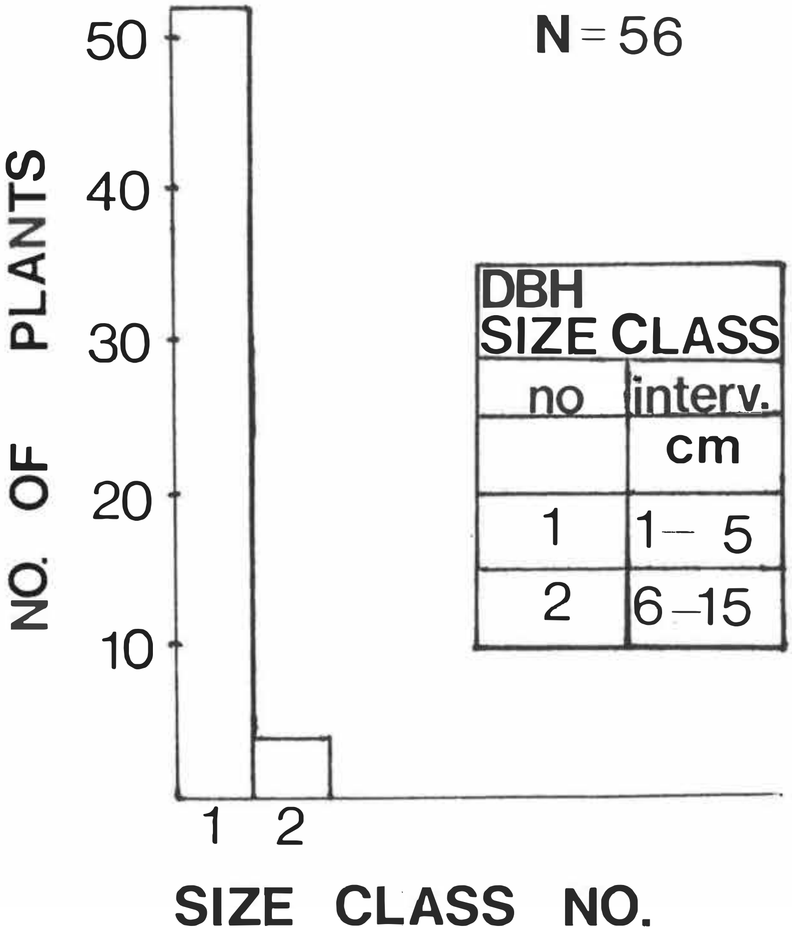


Fig. 4.28 Size-class frequency distribution of kaikawaka in the 170-year-old stand.

The largest DBH recorded was 12.5 cm for tree no. 200. Consequently size classes range up to 15 cm DBH. Comparable figures for the 350- and the 640-year-old stands are 35 cm (largest tree, 32.5 cm DBH) and 75 cm (largest tree 69.3 cm DBH) respectively. Obviously the kaikawaka population of the 170-year-old stand is young relative to the life span of the species.

The majority of the population (52 %) have DBH sizes between 1-5 cm. Twenty nine of the 52 individuals in this size class were seedlings (<180 cm high) and the other 23 were canopy members. In the 350-year-old stand 50 % of the kaikawaka population occurred in the 1-5 cm size class compared to only 16 % for the 640-year-old stand.

Total basal area of kaikawaka in the 170-year-old stand, calculated from DBH estimates of emergent trees (4 at 11 cm), canopy poles (23 at 5 cm) and understorey specimens (29 at 2.5 cm) was 0.3 m^2 ha^{-1}, 13 times less than the value for the 350-year-old stand (3.9 m^2 ha^{-1}), and 58 times less than the value for the 640-year-old stand (1.73×10^1 m^2 ha^{-1}).

The mean basal area per tree for the 4 emergent kaikawaka in the 170-year-old stand was 9.5×10^{-3} m^2, compared to 3×10^{-2} m^2 for the 350-year-old stand (3.2 times greater) and 1.2×10^{-1} for the 640-year-old stand (12.6 times greater).

Finally, the density of kaikawaka in the 170-year-old stand was 187 stems ha^{-1} compared to 204 stems ha^{-1} in the 350-year-old stand and 183 stems ha^{-1} in the 640-year-old stand.

4.7 THE 10-YEAR-OLD STAND

4.7.1 Vegetation structure and floristic composition

4.7.1.1 Description of the vegetation

As shown in Fig. 4.29, the 10-year-old stand is divided approximately in half by a topographic discontinuity in the form of a small cliff. Vegetation on the lower half of the open slip-face is less advanced successionally than most of that on the upper half. Hence the two halves are described separately.

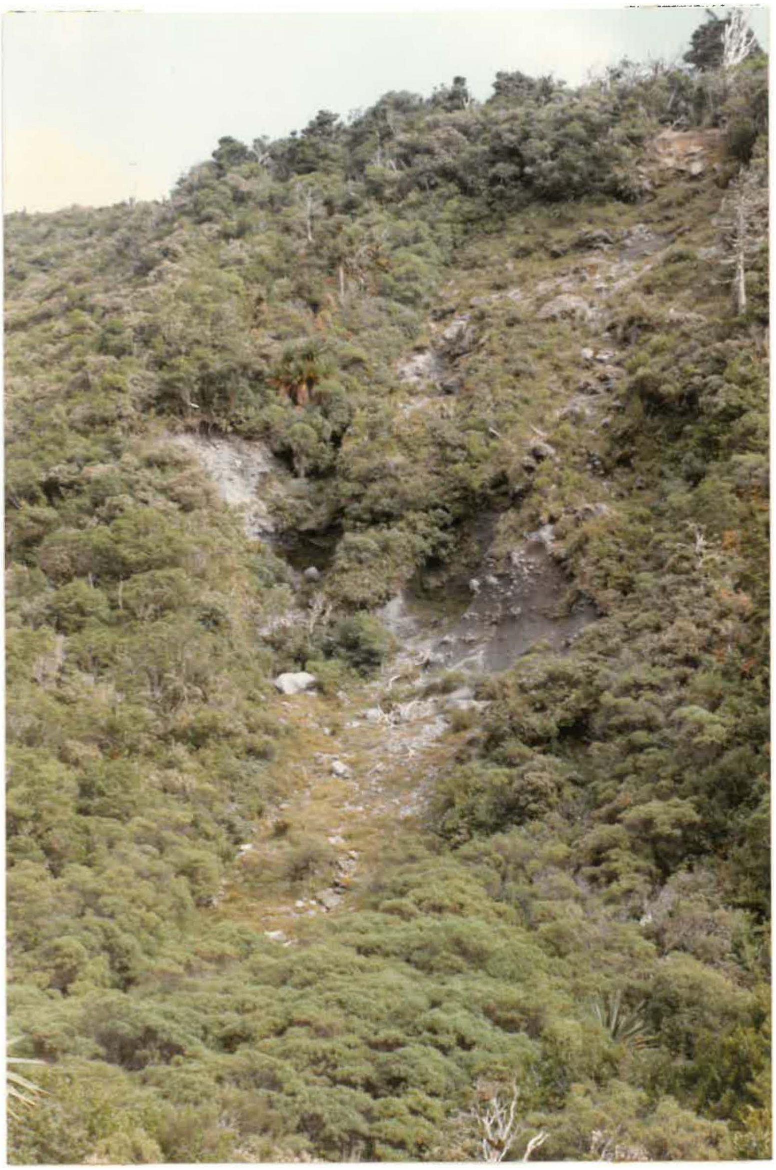


Fig. 4.29 View of the vegetation on the open slip-face, the 10-year-old stand. Note the small cliff, midslope (December, 1984).

The lower half of this stand is predominately made up of an array of herbaceous mat-forming species (Fig. 4.30).

Fig. 4.30 Herbaceous vegetation, lower slopes, 10-year-old stand. Helichrysum sp. (unnamed; aff. H. bellidioides) occupies the foreground. Diameter of camera cap = 6 cm.(January, 1985)

Principal amongst these mat-forming species in cover terms is *Raoulia glabra* (31 %). Other species present forming mats are *Helichrysum* sp. (unnamed; aff. *H. bellidioides*) (7 %) (see Fig. 4.30), *Cotula squalida* subsp. *squalida* (4 %), *Gunnera monoica* var. *monoica* (11 %), *Hydrocotyle moschata*, *Euphrasia cuneata* (3 %) and *Raoulia tenuicaulis*. Occurring occasionally are *Nertera depressa* (1 %), *Luzula* sp., *Epilobium rotundifolium*, *E. brunnescens*, *Celmisia gracilenta* var., *Ourisia macrophylla* var. *macrophylla*, *Lagenifera pumila*, *Pratia angulata* and several species of grass *Poa laevis* var., *Poa anceps* var. *anceps* (1 %) and *Lachnagrostis* sp.(b). *Astelia* sp. (unnamed; aff. *A. nervosa*) (2 %), *Dracophyllum longifolium* var. (1 %), *Cassinia vauvilliersii* (2 %), *Coprosma "taylorae"*, and *Hebe stricta* var. *egmontiana* (13 %) form a taller shrubby stratum but with a discontinuous cover. Only scattered individuals (see Fig. 4.30) or small clumps of these species occur infrequently. Bare substrate (rocks, stones, gravel, sand including non-vascular cover) was estimated at 25 %. As one approaches the small cliff situated midslope, the proportion of bare substrate generally increases.

The upper half of this 10-year-old stand consists of a range of cover (Fig. 4.31).

Fig. 4.31 Vegetation on upper half of the 10-year-old stand (January, 1985). Note the prominence of Astelia sp. (unnamed; aff. A. nervosa).

In the upper portion of this upper half, scattered *Poa anceps* var. *anceps* and *Hebe stricta* var. *egmontiana* occur amongst bare substrate (including moss-covered rocks) and mats of *Helichrysum* sp. (unnamed; aff. *H. bellidioides*). Mats of *Raoulia tenuicaulis*, *R. glabra* and *Gunnera monoica* var. *monoica* are also present here. Shrubby cover (see Fig. 4.31) is present in the central part of the lower portion. On either side of this central part, water channels dominated by gravel and supporting very little cover occur.

Faecal pellets and tracks testify to the recent presence of goats and hares above and below the small cliff. These probably retard the rate of succession through browsing and trampling influences, which selectively affect the vegetation composition. Selective feeding would favour the persistence of less palatable species at the expense of more palatable ones.

The small cliff dividing the two halves of this stand may provide a refuge or favourable microhabitat for some species as these were not found elsewhere. They include *Asplenium flaccidum* subsp. *flaccidum*, *A. terrestre* subsp. *terrestre*, *Blechnum fluviatile*, *Epilobium rotundifolium*, *Hymenophyllum multifidum*, *H. sanguinolentum*, *Senecio rufiglandulosus* var. *rufiglandulosus*, *Stellaria parviflora*, *Trichomanes reniforme* and *Viola filicaulis*.

4.7.1.2 The life-form composition and comparison with the other stands

Appendix 14 lists all species of the 10-year-old stand according to life-form. In Table 4.18 the life-form composition is summarised and a comparison is made with the life-form compositions of the 3 other stands.

Table 4.18 Comparison of the life-form composition of the 10-year-old stand with that of the 170-, 350- and 640-year-old stands.

Life-form category	10-yr		170-yr		350-yr		640-yr	
	Spp. No.	%	Spp. No.	%	Spp. No.	%	Spp. No.	%
Lycopods	3	5	1	2	0	0	0	0
Ferns	9	14	8	17	13	22	18	31
Gymnosperm trees and shrubs	2	3	2	4	2	3	2	3
Dicot trees	3	5	6	13	11	19	8	14
Dicot shrubs	15	23	13	28	13	22	13	22
Dicot lianes	0	0	0	0	3	5	2	3
Composite herbs	10	16	1	2	0	0	0	0
Dicot herbs (other than composites	13	20	8	17	8	14	6	10
Monocot trees	0	0	0	0	1	2	1	2
Orchids	0	0	1	2	2	3	1	2
Grasses	5	8	1	2	0	0	2	3
Sedges	2	3	2	4	2	3	3	5
Monocot herbs (other than orchids, grasses, sedges, rushes)	2	3	3	7	3	5	3	5
Species total	64		46		58		59	

Table 4.18 shows that 4 life-form categories are predominantly represented in the 10-year-old stand. In order of decreasing species number per life-form category these are: dicot shrubs (15), dicot herbs other than composites (13), composite herbs (10) and ferns (9). Comparison of the life-form composition with that of the other stands (Table 4.18) reveals that the 2 most distinctive life-form features of the 10-year-old stand are the prominence of the composite herbs (10 spp.) and the poor representation of the dicot trees (3 spp.). Both features reflect the previously illustrated and described structural differences in the four stands.

Two other features of note that show as trends in Table 4.18 are the number of fern species as a percentage of the stand's species complement increases from the 10- to the 640-year-old stand and the proportion of dicot herbs other than composites decreases in the same direction.

Table 4.18 also reveals that only the 10- and 170-year-old stands support representatives of the lycopod life-form category. Lycopod cover, visually assessed, is much greater in the 10-year-old stand. Notably lianes and monocot trees are absent only in the two youngest stands (Table 4.18).

4.7.1.3 The floristic composition and comparison with the other stands

Forty-seven genera are represented in this stand and these belong to 29 families (see Appendix 10 for complete list of species). The best-represented genus is Coprosma with 6 species and the best-represented family providing 13 species is the Asteraceae (characteristically wind-dispersed). The latter fact distinguishes this stand from the other three in which the Rubiaceae (bird-dispersed) was the best-represented family.

Appendix 15 enables comparison of the floristic composition of the 10-year-old stand with that of the other 3 stands. Table 4.19, extracted from Appendix 15, lists the vascular plants found in the 10-year-old stand but not in the other 3 stands.

Table 4.19 Checklist of the vascular plants found in the 10-year-old stand but not in the 3 other stands.

Species	Family
Acaena anserinifolia	Rosaceae
Anthoxanthum odoratum (Adv.)	Poaceae
Cassinia vauvilliersii	Asteraceae
Celmisia glandulosa var. latifolia	Asteraceae
C. gracilenta var. (C. major var. brevis)	Asteraceae
Coriaria pteridoides	Coriariaceae
Epilobium brunnescens	Onagraceae
E. rotundifolium	Onagraceae
Euphrasia cuneata	Scrophulariaceae
Gunnera monoica var. monoica (incl. G. albocarpa and G. strigosa)	Haloragaceae
Helichrysum filicaule	Asteraceae
H. sp. (unnamed; aff. H. bellidioides)	Asteraceae
Hydrocotyle moschata	Apiaceae
Hypochoeris radicata (Adv.)	Asteraceae
Lachnagrostis sp. (b) (unnamed)	Poaceae
Lagenifera pumila	Asteraceae
Luzula sp.	Cyperaceae
Lycopodium fastigiatum	Lycopodiaceae
L. scariosum	Lycopodiaceae
L. volubile	Lycopodiaceae
Nertera ciliata	Rubiaceae
Raoulia glabra	Asteraceae
R. tenuicaulis	Asteraceae
Rytidosperma sp.	Poaceae
Sagina procumbens (Adv.)	Caryophyllaceae
Senecio rufiglandulosus var. rufiglandulosus	Asteraceae
Trichomanes reniforme	Hymenophyllaceae
Spp. Total = 27	

Many of the species listed in Table 4.19 produce numerous wind-dispersed seeds or spores, a form of regeneration that is primarily adapted to exploit forms of disturbance which are spatially unpredictable (Grime, 1979, pp. 100) and which are of severe intensity (Oliver, 1981). Notably 10 out of the 27 species listed in Table 4.19 belong to the Asteraceae, the best-represented family in the 10-year-old stand. In this family, efficient wind-dispersal of seeds is facilitated by a pappus which increases buoyancy. Similarly, in the genus *Epilobium* a plume of hairs aids dispersal and has enabled this genus to rapidly colonise open habitats all over the world (Raven et al., 1976, p. 74). Although the spores of *Lycopodium* species lack special buoyancy structures, they are also capable of long-distance transport in air currents because they are exceedingly small and light.

All of the species listed in Table 4.19 are members of the ground cover and most of them are herbaceous. Two exceptions are *Cassinia vauvilliersii* and *Coriaria pteridoides*.

The species listed in Table 4.19 characteristically colonise disturbed habitats at this altitude on Mt Taranaki. They can be commonly found on recent-exposed landslide surfaces, stream margins, track edges and roadsides. Hence they can be categorised together as disturbance-adapted species (White,1979,p252).

Using the concepts of Grime (1979), most of these species appear to possess a ruderal type of primary strategy in the established phase of their life-history. However, Grime (1979) points out that his concepts of three primary strategies represent the three extremes of adaptation to competition, stress and disturbance. For intermediate intensities of these three factors he has formulated a suite of secondary strategies. Using these concepts of secondary strategies, several of the species listed in Table 4.19 are competitive-ruderal perennial herbs. They are: *Cotula squalida* subsp. *squalida*, *Gunnera monoica* var. *monoica*, *Helichrysum* sp. (unnamed; aff.*H. bellidioides*), *Raoulia glabra* and *R. tenuicaulis*. All are mat-forming species which have a capacity for rapid vegetative spread via stolons or rhizomes

Table 4.20 Summary statistics of species complements of 10- and 170-year-old stands.

	No. Spp.	%
10-yr stand only	32	41
170-yr stand only	14	7
Common to both stands	32	41*
10-yr stand total	64	82
170-yr stand total	46	59
Combined total for both stands	78	100

* Jaccard's similarity index

Table 4.20 shows some summary statistics of the species complements of the two younger stands. Eighty-two per cent of the combined species complement of the 2 stands was found in the 10-year-old stand and 59 per cent in the 170-year-old stand. All the species found only in the 10-year-old stand are ground cover members, no other stratum being recognised in this stand.

Table 4.21 Summary of Jaccard's and Sorensen's similarity indices.

Comparison of:	IsJ (%)	IsS (%)
170-yr and 10-yr stands	41	58
350-and 170-yr stands	63	77
640-yr and 350-yr stands	75	85

Table 4.21 shows that the 10- and 170-year-old stands are less similar floristically than the 170 and 350-year-old stands and the 350- and 640-year-old stands.

Another measure of the floristic distinctiveness of the 10-year-old stand relative to that of the other stands can be gained by further analysis of Appendix 15, to determine the number of species exclusive to each stand. Whereas the 10-year-old stand supports 27 species not found in the other stands (Table 4.19), only 2 exclusive species occur in the 170-year-old stand, 4 in the 350-year-old stand and 7 in the 640-year-old stand (see Table 4.22).

Table 4.22 Vascular plants exclusive to various stands.

Exclusive to: 640-yr	350-yr	170-yr
Alseuosmia pusilla	Epilobium pedunculare	Blechnum penna-marina
Blechnum chambersii	Parsonsia capsularis	Lycopodium australianum
B. colensoi	Pittosporum tenuifolium var. tenuifolium	
Gahnia procera	Pterostylis banksii	
Hymenophyllum pulcherrimum		
Microlaena avenacea		
Phymatosorus diversifolius		
Spp. Totals: 7	4	2

An element of the floristic distinctiveness of the 10-year-old stand is the presence of three adventive species - *Anthoxanthum odoratum*, *Hypochoeris radicata* and *Sagina procumbens*. No adventives were recorded in the other three stands.

4.8 The replacement sequence apparent in nearby debris-fan vegetation

To gain further insight into the successional sequence of species apparent from comparison of the 4 slip-face stands, the debris-fan vegetation at the base of the 10-year-old stand and that below the 640-year-old stand on a 1977 landslide deposit were examined in June 1985. The observations made then are recorded here.

In the debris-fan vegetation below the 10-year-old stand, *Hebe stricta* var. *egmontiana* dominated the canopy (Fig. 4.29). *Brachyglottis rotundifolia* var. was coming up below, throughout, amongst *Astelia* sp. (unnamed aff. *A. nervosa*) and *A. fragrans*. On the edge of this stand seedlings of kaikawaka occurred beneath *B. rotundifolia* var. This stand was 15.5-years-old in June 1985 (age established in sections 3.1.4, 4.2.4).

Below the 640-year-old stand, the 8-year-old debris-fan vegetation was also dominated by *Hebe stricta* var. *egmontiana* (Fig. 4.32) but these individuals were shorter, had crowns which were more close-knit and the spaces between individual plants were larger.

Fig. 4.32 Eight-year-old debris-fan vegetation (June, 1985)

Brachyglottis rotundifolia var. was again found beneath the canopy but less frequently than in the 15.5-year-old debris-fan vegetation.

When these observations are considered together with the slip-face results reported previously, the successional sequence of dominants becomes apparent as:

Raoulia glabra and other dicot herbs to *Hebe stricta* var. *egmontiana* which then opens up with time and nurses *Brachyglottis rotundifolia* var. This in turn nurses kaikawaka as observed in the 170-year-old stand.

Other older debris-fan vegetation dominated by full-crowned kaikawaka and adjacent to the tributary of the Ngatoro Stream occurs in 3 locations:

1) On the true left bank of the tributary, immediately above the 8-year-old stand.

2) On either side of the Translator Road in the Upper Ngatoro Valley just above where the road crosses the stream (photo in Clarkson, 1986, p10).

3) On either side of the Ngatoro-Walk Track at its Translator Road end.

CHAPTER 5: DISCUSSION AND CONCLUSIONS

5.1 THE CROSSDATING PATTERN AND ANOMALOUS RINGS

5.1.1 Introduction

The first specific objective of this research (section 1.2) was to establish the crossdating pattern in kaikawaka and describe anomalous ring features. Stand age estimates (objective 2) and age-size relationships (objective 3) could then be determined using these rigorous dendrochronological procedures. The crossdating results and their dendroclimatic and volcanic-eruption-date implications are discussed below and the anomalous ring features are discussed in section 5.1.2.

5.1.2 Crossdating

The crossdating pattern found in the present study confirms by the synchronous placement of 5 ring signatures over the 1625-1976 time span, the pattern reported for kaikawaka at a nearby (<1 km) lower-altitude (991 m) valley-bottom site in the same study area (LaMarche et al., 1979, p25).

These 5 signatures can also be found in the chronology of tree-ring indices for kaikawaka tabulated by LaMarche et al. (1979, p23) for a site at 1050 m near Dawson Falls, 5 km south of the study area on the southeastern slopes of Mt Taranaki.

The synchronous occurrence of these ring signatures in kaikawaka at 3 different sites on Mt Taranaki establishes confidence in the crossdating procedure used in the present study. Many of the narrow rings which form the 5 signatures mentioned have been found in kaikawaka elsewhere in the North Island (e.g. Urewera National Park, Ruahine Range) and also in the South Island (e.g. Banks Peninsula) (LaMarche et al., 1979). This synchronous response over large areas indicates influence by large-scale weather patterns and forms the basis for paleoclimatic inferences from ring-width variations.

The absence of the 1934 to 1938 signature in cores from the 170-year-old stand suggests the climatic signal is being suppressed in younger trees by biological processes e.g. faster radial growth. This observation adds weight to the suggestion of Ogden (1982) that a policy of analysing samples from different age-classes separately is to be preferred when constructing chronologies to avoid blurring the climatic signals from older-generation trees.

The Dawson Falls and Jacksons Lookout study sites of Druce (1966a) are situated between the Dawson Falls chronology site of LaMarche et al. (1979) and the present study site. Also the time span covered by tree-ring series from the latter 2 sites includes the dates Druce (1966a) gave, based on tree-ring counts, for the recent eruptions of the Burrell (1655 A.D.) and Tahurangi (1755 A.D.) formations. By inference then the crossdating pattern found in the present study should also exist in kaikawaka at Druce's sites and in the cores he collected. However, he did not report any such pattern although cites a paper (Glock and Agerter, 1963) which describes the crossdating principle and procedure.

The effects of the recent eruptions on tree-ring width therefore have not yet been isolated from the synchronous climatic variation in ring widths that crossdating has shown, and the opportunity now exists to test the putative eruption dates given by Druce (1966a).

Given the strong south-easterly direction of the Burrell lapilli eruption and the variable impact over the area as shown by isopach maps of tephra (Druce, 1966a; Topping, 1972) one can theoretically use the North Egmont tree-ring series (LaMarche et al., 1979, and the present study) as experimental-control data to distinguish eruption from background climatic effects on tree-ring width. The North Egmont area received < 10 cm of Burrell lapilli compared to 23-38 cm for the Dawson Falls area.

A comparative examination of the 1650's period in the chronologies for Dawson Falls and North Egmont shows a sharp reduction in ring index for the year 1652 at Dawson Falls only. However, this reduction is clearly evident in cores from 4 pre-Burrell kaikawaka from the 640-year-old stand. It can also be seen in chronologies of LaMarche et al. (1979) for kaikawaka sites in the Ruahine Range (Takapari site) and on Banks Peninsula (Armstrong Reserve site) so is likely to be of climatic origin. Nevertheless, further comparisons of other decades using statistical filtering techniques to examine short-term (high-frequency) variations (Fritts, 1976) are warranted.

5.1.3 Anomalous rings

5.1.3.1 False rings

Lack of detection or recognition of false rings can lead to overestimates of age, spurious dates for particular events and frustrated attempts to achieve crossdating and climatic reconstruction.

In the present study several false rings were detected in cores with numbers of annual rings varying from 198 to 453 (Table 4.1). However, Dunwiddie (1979) after a nation-wide collection of kaikawaka cores reported false rings are virtually non-existent in kaikawaka except in some very young trees. Dunwiddie (1979) may have used a narrower definition for false rings, classifying only type 1 false rings of the present study as such. The broader definition I adopted is modified from Kuo and McGinnes (1973). Kawana and Kawaguchi (1957) also found concentric circles of resin cells which macroscopically resembled false rings (type 2 false rings of the present study) in *Cryptomeria japonica* trees.

In the present study, permanently-mounted cores progressively sanded with finer-grit paper were used and unusually narrow rings compared with those either side were recognised as marker rings, key elements in the crossdating sequence (Fig. 4.1). This recognition is in contrast to the treatment of Druce (1966a) who classed such narrow rings in kaikawaka cores from Southeast Egmont as false during tree-ring counts on blade-surfaced cores impermanently mounted. Likewise Clayton-Greene (1977) followed Druce (1966a) in respect to surfacing method, lack of permanent mounts and classification of very narrow rings as false for kaikawaka cores collected from Mt Pirongia and Mt Te Aroha. In the present study no anatomical evidence was detected to justify such a classification. The lack of recognition of such rings as markers by Druce (1966a) and Clayton-Greene (1977) is probably attributable to their poor surfacing and core orientation methods which obscured cellular detail and consequently lead to a lack of detection of crossdating patterns.

5.1.3.2 Damaged rings

Although many studies have used core samples taken from kaikawaka throughout New Zealand (Druce, 1966a; Clayton-Greene, 1977; Wardle, 1978; Dunwiddie, 1979; Norton, 1983; Veblen and Stewart, 1982; Haase, 1986a) the presence of damaged rings, their synchronous occurrence within a tree, in different trees (4) and with false rings (section 4.1.2.2) have not been previously reported.

In the present study damaged rings were located in the earlywood (mostly pocket damage - 87 %) and at the earlywood-latewood (EW-LW) transition, again mostly pocket damage (53 %) but with a higher frequency of zone damage (27 %) and some hole damage (20 %). The earlywood (EW) location corresponds to the start of the growing season suggesting spring frost and the latter to the late-summer, early-autumn time of year suggesting early autumn frost. However this hypothesis does not account for the false ring observed later in the season in one instance (Fig. 4.3). One would expect cold hardening and resistance to further frost injury after a period of temperature-induced latewood formation. Nevertheless, unseasonally warm weather extending the growing season could reduce frost hardiness making the plant more susceptible to another abrupt onset of cold weather and result in false ring formation. That Haase (1986b) found continuation of wood increment (cambial activity) throughout the winter in younger trees of subalpine *Olearia ilicifolia*, a kaikawaka associate at Arthur's Pass, South Island offers some supporting evidence for this hypothesis. In those less-susceptible individuals the frost event could cause a false ring rather than a frost ring and the second event have no effect.

LaMarche (1970) reports the occurrence of frost-damage rings in subalpine conifers in the United States, both early and late in the growing season. Studies by Fritts (1969) on bristlecone (*Pinus aristata* Engelm.) indicates differences in the length and duration of the growing season may be largely responsible for the pattern of late-season frost damage. Cambial activity began about a week earlier and ended as much as two weeks later in young trees as compared with older trees on the same site and cambial activity began and ended at least a week later at high elevations during a given growing season. Stems of young trees can also be frozen more frequently because of their relatively thin bark (LaMarche, 1970).

Ogden (1978) found synchronous frost rings in Pencil Pine (*Arthrotaxis cupressoides*) in Tasmania. They appeared to be of local rather than regional significance, affecting mainly younger trees which grew in relatively open situations.

The damaged rings (mostly zonal type) and false rings found in ring 204 were formed in 1775, the date Druce (1966a) tentatively estimated for the Tahurangi eruption, based on an indirect method using kanuka. The study area received between 8 and 13 cm of Tahurangi Ash as did other areas of the mountain at this altitude (Druce, 1966a Fig. 16). Hence direct impact of hot ash on cambial layers of kaikawaka or, more likely, indirect effects through defoliation of the crown and disruption of downward translocation of plant growth regulators, and/or burial of root systems may be involved in the ring features described. Defoliation of surrounding plants and greater exposure to frost events is also a feasible cause.

Another related damage mechanism possibly operating in this case is that of volcanic-eruption induced frost damage (LaMarche and Hirschboeck (1984). They found that major eruptions are likely to be closely followed by frost events at better than the 99.9 % confidence level. Noteworthy is the observation that damage was most extensive laterally in ring 204 (1775) except in one instance (core 51B) where ring 205 (1774) showed a similar amount of damage.

The coincidence of damaged rings of the zone type and false rings of both types, in the same year, within a tree and in different trees suggests that in some instances these rings provide an internal time datum i.e. are a type of marker. They therefore have value for crossdating purposes and can be used for independent verification of dates assigned on the basis of patterns of ring-width variation.

The presence of pockets or zones of damaged cells in 6 rings of core 51B (in the EW in 2 instances) and multiple occurrence in some cores of the pre-Burrell set suggests multiple events of varying intensity at different times of the year by the same agent e.g. frost or, less likely, similar damage being caused by different agents. Hole damage is distinctive from the other two types because of the curvature of the radial files of cells around a hole suggesting a different damaging agent.

Further examination of the distribution of damaged rings in kaikawaka on Mt Taranaki, in relation tree age, elevation above sea level, core height and exposure to known frost events is warranted.

5.1.3.3 Partially absent rings

Some forty different terms have been used in the literature as synonyms for partially absent xylem rings according to Studhalter et al. (1963). An unbalanced or physiologically inefficient crown limits production or downward translocation of plant growth regulators resulting in local cambial dormancy, lobate growth and eccentric centres. As distance from the crown increases down the stem, partially absent rings occur more commonly. They are commonly found in overmature trees, trees heavily defoliated by insects or other agents, suppressed trees of the understorey, senescing branches and stems of trees with flag-formed or one-sided crowns (Kozlowski, 1971).

In the present study, two types of partially absent rings were identified in core samples of kaikawaka and described. These types can be classified further using the system described and illustrated by Glock et al. (1960). They described 3 major categories of partially absent rings - lenses, half-lenses and arcs.

5.1.3.4 Absent rings

Dunwiddie (1979) found that in datable material from kaikawaka, absent rings were most frequently noted in older trees, but did not exceed 2 % along any single radius. In the present study the highest frequency observed in datable cores was 3.4 % suggesting more intense environmental stresses operated on the material dated.

Norton (1986) notes that the mean percentage of absent rings from a large number of kaikawaka trees was 0.28 % compared with 1.35 % in

Nothofagus solandri. In the present study (Table 4.1) the mean percentage of absent rings in 25 kaikawaka trees (4924 rings) from the 3 older stands was 0.59 % ranging from 0 % in the youngest stand to 0.72 % in the oldest. This low mean percentage supports the finding of Norton (1986) that in datable material of kaikawaka, absent rings occur less frequently than in datable material of *Nothofagus solandri*. The higher percentage in the oldest stand of kaikawaka confirms the observation of Dunwiddie (1979) that in datable material of kaikawaka absent rings are most frequent in older trees.

Data from two trees, 5 cores per tree (Table 4.2) suggests cambial activity in kaikawaka at this study site varies considerably with sampling height and radial position making determination of the exact year any tree, as an entity, died difficult.

5.1.3.5 Displaced marker rings

The phenomenon of marker-ring displacement (section 4.1.2.5) highlights the importance of using more than 1 core per tree when crossdating. Also displaced marker-rings can only be detected and the spurious invoking of an absent ring avoided by matching patterns of ring characteristics (not just width) over regions (ring signatures) rather than of narrow rings singly.

Marker-ring displacement can be explained by two growth characteristics of this species which are most easily observed using discs, and by a statistical feature of chronologies.

The growth characteristics are compression wood formation particularly noticeable near core centres and lobate growth (see Fig. 4.5). Both involve areas of locally accelerated and suppressed growth in various parts of the tree. In these regions the relative widths of rings do not display circuit uniformity i.e. a relatively narrow ring can become wide and the adjacent wide ring narrow as one traces their width around the tree. Partially absent and absent rings also occur in suppressed regions where rings wedge out. Dunwiddie (1979) notes that areas of locally suppressed and accelerated growth in kaikawaka at some stressed sites can migrate around a tree as it grows but may not necessarily be evident as lobes on the outside of the trunk. Ogden (1978) noted considerable radial variation in growth rates for King Billy Pine (*Arthrotaxis selaginoides*) in Tasmania with the fastest growing radii changing from time to time and suggested this was in response to branch development, shading and abscission in the crown. Such explanations may also account for lobate growth in kaikawaka.

The statistical feature of chronologies of tree-ring indices that may account for the special case of marker-ring displacement is that averages can mask individual values. The NET189 chronology was constructed using ring-widths from 53 radii from 14 trees (LaMarche et al., 1979) and on average ring 130 was narrowest even though some subsets of cores probably showed ring 129 to be.

5.2 Age estimates of the four stands

5.2.1 Introduction

To establish that the four stands form a vegetation chronosequence (objective 2), it was necessary to determine time-zeros - the estimated dates when landslides occurred and new surfaces became available for colonisation. For this purpose the oldest kaikawaka in each stand were selected and dated using rigorous dendrochronological procedures. Results revealed the landslide events occurred around 1333-1343 A.D. (640-yr stand), 1625 A.D. (350-yr stand), 1811-1817 A.D. (170-yr stand) and 1968-1971 A.D. (10-yr stand).

Stand-age estimates are made up of a number of components, each of which has an error associated with its determination. Attempts have been made to minimise and estimate the size of errors. In the following sections, the 4 components of the stand-age estimates - crossdating, centre estimates, coring-height adjustments and invasion-lag periods are briefly discussed and consideration is given to errors.

5.2.2 Crossdating

The crossdating procedure when applied correctly assures the proper placement in time of each ring through the matching of variations in ring characteristics among all samples and through detection of anomalous rings (section 3.2.3). The error associated with this procedure is largely dependent on the climatic sensitivity of the material. If the material is sensitive enough without being too difficult to crossdate, there is no error. Core samples from the 640- and 350-year-old stands were sufficiently sensitive for sound crossdating including accommodation of displaced marker rings, and cores from the 170-year-old stand although less sensitive displayed low incidence of growth suppression and were therefore easily dated (section 4.1.1).

5.2.3 Centre estimates

Ogden (1985) notes that most studies do not mention the methods used and assumptions made in calculation of centre estimates for any missing radius, when a core does not bisect the pith. In the present study, the method used has been set out explicitly in section 3.2.4 and 95 % confidence limits for the centre estimate were calculated. These ranged from 0 to 3 % of core age for those cores used in estimating the ages of the 3 kaikawaka stands, suggesting the method is acceptable for this purpose.

For absolute dating purposes much more work is required to determine the types of radial growth patterns that occur near the centre of young kaikawaka of various ages and at various heights. Two types were seen in the present study - cores with very slow growth rates (narrow rings) and those with very fast rates (wide rings). The method also requires testing using discs with chronological centres to examine the size of errors associated with predictions as each component of the method is varied and to determine at what point e.g. distance from the centre, errors become unacceptably large. Heath (1959) in dating an avalanche deposit in Lassen Volcanic National Park (species of conifer not given) found five or fewer missing rings could be estimated with moderate accuracy but greater departure from the pith seriously diminished the value of the core.

5.2.4 Coring-height adjustments

The height growth rate used to adjust tree-age estimates from coring height to the ground level (downslope datum) was assumed to average 1 cm yr^{-1} over the coring height range 21-124 cm. The basis of this assumption is set out in section 3.2.5.

It is of interest to compare this rate with other values reported in the literature, in order to estimate the variability in height growth rate of kaikawaka at the upper altitudinal limits of its subalpine ecological range.

Wardle (1963a, p35) measured annual growth in length of upper shoots from healthy adult plants of kaikawaka in the ToAroha Basin, 854-976 m, western side of the Southern Alps. He reported a representative annual shoot growth of between 0.9-1.1 cm and notes that growth in the canopy shoots and crown of adult trees reflects height growth rates of young plants of the same species and that the latter is of greater ecological significance. Wardle (1963a, p36) comments that the relatively slow growth of kaikawaka may reflect the ability of its seedlings to grow slowly but consistently under a closed canopy.

At lower altitudes (610-701 m) of the same study area, Wardle (1963a) found shaded but healthy kaikawaka seedlings had height growth rates ranging from 1.1 to 2.3 cm yr^{-1} and averaging 1.86 cm yr^{-1} over the height range 33 to 150 cm above ground level.

Druce (1966a, p22) provides data for kaikawaka cored from Southeast Egmont between 915-1037 m which enables height growth rate to be calculated for 1 individual at 1.5 cm yr^{-1}.

Obviously height growth rate of kaikawaka varies, with faster rates being reported at some lower-altitude sites. The available data suggests 1 cm yr^{-1} is a reasonable estimate to use as the average for kaikawaka at its upper altitudinal limits. Between-tree (within site) variation has been reported for this species by Norton (1983) in a study of 4 sites over the altitudinal range 770-1000 m in Westland. He found for 5 seedlings a mean height growth rate (up to 1 m) of 1.54 cm yr^{-1} with a range from 0.77 to 2.86 cm yr^{-1} reflecting differences in microsite conditions. Further work is required to assess between-tree variation in height growth rates of kaikawaka on a stand basis within the site of the present study.

5.2.5 Invasion-lag periods

From field observations on kaikawaka colonization or lack thereof of open slip-faces and debris-fans of known ages, the invasion-lag period for this study site was estimated to range from 20-30 years and average 25 years. Calder and Wardle (1969) note that kaikawaka seedlings may appear within 40 years of a fire in low subalpine forest, a comparable type, at Arthur's Pass, South Island. To the best of the authors knowledge no other information on the invasion-lag period for this species occurs in the literature. Obviously further work is required.

5.3 Age versus size relationships

The third objective of this research was to examine the age versus size relationships of kaikawaka using the crossdating procedure with a view to predicting age-class structures from DBH measurements.

A linear relationship between tree age at 0 cm downslope and DBH of kaikawaka was found to be significant at the 0.1 % level (r= 0.97 ± 0.1). Studies of this species at other sites both in the North and South Islands have also demonstrated high correlation between tree age and DBH. Clayton-Greene (1977) using combined data from Mt Pirongia and Mt Te Aroha found a linear relationship significant at the 0.1 % level (r not given) and Norton (1983) using data from 3 study sites in Westland found linear relationships also significant at the 0.1 % level (r= 0.71, 0.88, 0.90).

However, as in those studies the present study revealed a wide variation of age within any one size class even after the exclusion of data from double-leadered trees (3) and unusually small-diameter old trees (1). For example, the 36-45 cm size class in the 640-yr stand shows an age variation of 206 years from 355 to 561 tree nos 96 and 45, Appendix 16). Such variation suggests ages predicted from DBH data using the regression equation may be misleading.

The wide age variance within any size class indicates a highly variable radial growth rate (RGR), a characteristic evident visually on the core surfaces. For example, core 49C (40.7 cm DCH, 438 years) showed an average RGR of 0.46 mm yr^{-1} compared to 0.79 mm yr^{-1} for core 36C (36.3 cm DCH, 231 years), 1.7 times greater.

Similar variation was reported by Druce (1966a) for two kaikawaka trees at Southeast Egmont. Situated a few metres apart and of similar DBH (61 and 55.9 cm), these trees were aged at approximately 464 and

227 years respectively. Corresponding average RGR's are 0.66 mm yr^{-1} and 1.26 mm yr^{-1}, a RGR factor of 1.9 times.

Individual ring width values are dispersed over a greater range than the average values given above with some rings being only 2-3 cells wide (0.160 mm) and others being > 2.06 mm wide (core 49C).

This variation in RGR is partly due to age, local site factors and relationships with neighbouring trees (Ogden, 1978). Radial growth rate is a trait with substantial phenotypic plasticity which enables trees to respond to open spaces as occurs when suppressed individuals are suddenly released from the understorey (Knowles and Grant, 1983).

Growth variability in annual increments associated with genetic patterns has been examined for *Pinus ponderosa* in the upper montane region of the Front Range in Colorado (Knowles and Grant, 1981). They measured ring widths and estimated the level of heterozygosity by resolving electrophoretically four isozyme systems from pollen samples. A significant positive association between level of heterozygosity and growth variability was found with predominantly heterozygous individuals having markedly greater variation in annual radial increment than predominantly homozygous individuals. No significant differences in a comparison of average annual increments between these two groups occurred.

From this perspective it would be of interest to examine the within-tree variability in radial growth increments of the unusually small-diameter old kaikawaka excluded from the regression (e.g. core 49C), in comparison with that of nearby trees which were included (e.g. 45E).

Druce (1966a) reported a DBH size range for pre-Burrell kaikawaka from Southeast Egmont of 45.7 to 124.5 cm. Tree number 49 in the present study extends that range to a DBH size 6.8 cm smaller at 38.9

cm. This individual qualified as a pre-Burrell tree on unadjusted core age alone (390 years). When the 48 ± 13-yr centre estimate and 173-yr core height adjustment are added, the age estimate for this individual becomes 611 yrs (1368 A.D.) which gives it a pre-Newall status (before 1500-1550 A.D.).

5.4 Successional pattern in floristic and life-form composition

The fourth objective of this research was to describe for the study site the successional pattern in floristic and life-form composition on a stratum basis.

From cover ratings of species in the slip-face stands (sections 4.4.1.1, 4.5.1.1, 4.6.1.1 and 4.7.1.1) and observations of the replacement sequence in nearby debris-fan vegetation (section 4.8), the species replacement sequence in the top layer of the slip-face stands is most probably as follows: *Raoulia glabra* and other dicot herbs to *Astelia* sp.(unnamed; aff. *A. nervosa*) and *Astelia fragrans*, to *Hebe stricta* var. *egmontiana* and *Dracophyllum longifolium* var., to *Brachyglottis rotundifolia* var.. These latter 3 species become less important with time and the cover of the small-tree canopy members *Griselinia littoralis* and *Pseudopanax simplex* increases with time (350-yr stand). Kaikawaka and *Podocarpus hallii* are nursed under the dicot shrub canopy (170-yr stand) and emerge with time (350-yr stand) to dominate the stands physiognomically (640-yr stand). Thus the trend is a sequential physiognomic dominance of the site with time by species with larger size at maturity.

In the understorey *Pseudowintera colorata* becomes dominant in the subcanopy with time (640-yr stand) as does *Astelia fragrans* in the ground cover.

Comparison of species totals per stratum for each stand show that the ground cover strata are the most diverse in all 4 stands and the major differences in species composition of the 4 stands occur in this stratum.

The comparison of Jaccard's and Sorenson's similarity indices (Table 4.21) show the 10-year-old stand was most distinctive floristically.

The life-form composition analysis for the 3 older stands (sections 4.4.1.2, 4.5.1.2, 4.6.1.1) indicated they were similar in many respects: ferns dominated the ground cover and epiphytic category, dicot shrubs the canopy and subcanopy strata with dicot trees also well represented here. The emergent stratum was composed entirely of 2 gymnosperm trees. A special feature of the 640-yr stand was the presence of hemi-epiphytes (section 4.4.1.1). This type of forest is most appropriately called subalpine low forest (Mueller-Dombois and Ellenberg, 1974) and is similar in life-form composition to the type described by Haase (1986c).

By contrast the only stratum recognised in the 10-year-old stand (the ground cover) was dominated by dicot shrubs, dicot herbs other than composites, composite herbs and ferns (section 4.7.1.2).

5.5 Relay floristics and initial floristic composition

The fifth objective of this research was to assess the relative importance at the study site of the relay-floristic principle (successive appearance and disappearance of groups of species) versus the initial-floristic composition principle (vegetation development from initial flora without additional increments by further invasion), (Egler,1954; Finegan 1984).

In the 10-year-old stand primary succession is taking place after removal of the soil in a severe disturbance. The early-successional or pioneer species of vascular plants do not include kaikawaka - only 1 prostrate, deformed individual was found and it has not survived.

The main pioneers are dicot herbs, many in the Asteraceae, dicot shrubs and ferns (section 4.7.1.2). Twenty-seven species of vascular plants (Table 4.19) were exclusive to this stand. All were ground cover members that are likely to be overtopped and shaded out by the next relay of species within 170 years.

By contrast in the 3 older stands, few exclusive species were found 2 in the 170-yr stand, 4 in the 350-yr stand and 7 in the 640-yr stand (Table 4.22). These species are mostly ground cover members which may invade after minor disturbances. However, 11 species were exclusive to the two older stands (640-yr and 350-yr), 5 to the two younger stands (170-yr and 10-yr), 10 to the 3 older stands, 3 to the 3 younger stands and 25 species occurred in all 4 stands (section 4.6.1.2 and Appendix 15).

These observations can be interpreted using a combination of the relay-floristic and initial-floristic-composition models. Some early-successional species persist for a period less than 170 years, others invade throughout the period of the chronosequence and another group are part of the initial flora yet persist throughout.

The observations of numerous kaikawaka seedlings in the 170-yr and 350-yr stands under a shrub, small-tree canopy indicates periodic colonization and establishment. This recent regeneration with reduced recruitment into the larger-DBH size classes is evidenced by the reverse-J-shaped DBH size-class frequency distributions of kaikawaka in these 2 stands and the seedling height-class distribution in the 350-yr stand. This stand also displays a clustered spatial distribution of seedlings and poles around larger and taller trees suggesting pulses of regeneration from these as they reach reproductive maturity. Similarly the 640-yr stand contains at least 2 pulses of regeneration (discussed further in section 5.6). The implication from these observations is that kaikawaka at this site can invade and regenerate in existing vegetation i.e. participate in secondary succession.

5.6 Population size structures of kaikawaka

Life history analysis is historically cast in terms of animal populations where heavy emphasis was correctly placed on age as the biological attribute of most significance, reflecting the strong link between age and reproductive output (Knowles and Grant, 1983). However that link appears much weaker in plants and plant biologists have recently suggested that size may be a better predictor of reproductive output than age (Harper, 1977). Hence there are sound ecological reasons for emphasizing size distributions in the analysis of forest tree populations in addition to the practical one that size is more easily measured. Consequently DBH size-class frequency distributions were constructed for each of the 3 kaikawaka populations (sections 4.4.2, 4.5.2, 4.6.2).

The general shape and cluster pattern in these distributions has been confirmed using histograms, dotplots and stem-and-leaf displays available in the general purpose statistical computing system, Minitab (Ryan et al., 1985). While histograms show general shape better, dotplots show more detail in the data by grouping it less - the x axis is divided into many more divisions. The ideal of having each distinct data value with its own plot position is approximated by using each printer position to represent a small range of data values (Bray et al., 1987).

Figure 5.1 shows dotplots of kaikawaka DBH on a common axis for the 3 older stands. These dotplots display dissimilar DBH distributions and indicate more clearly than the histograms (Chapt.4) that waves or pulses of regeneration have occurred rather than continuous recruitment. Although seedlings and poles were relatively under-represented in the oldest stand at the 16 % level, abundant regeneration (50-52 %) was apparent in the adjacent 350- and 170-year-old stands.

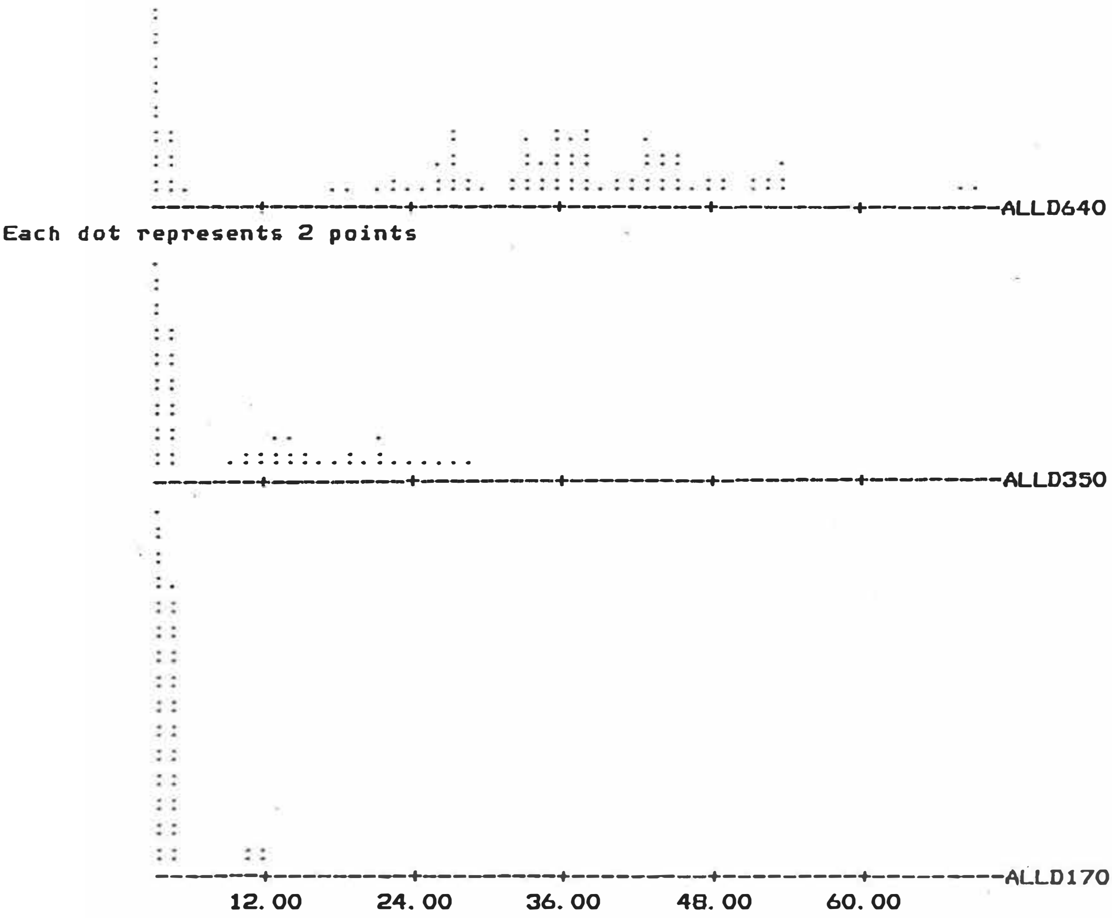


Fig.5.1 DBH dotplot distributions of kaikawaka for the 3 older stands, 640-yr, 350-yr and 170-yr, top to bottom. X axis = DBH, Y axis = no. of individuals.

A combined DBH dotplot distribution for the site (3 stands - Fig. 5.2) shows no real regeneration gaps, after taking into account the faster radial growth rates of double-leadered, twin-crowned trees. In fact this site DBH distribution tends to follow the negative exponential form generally expected for self-replicating mixed age populations (Meyer, 1952).

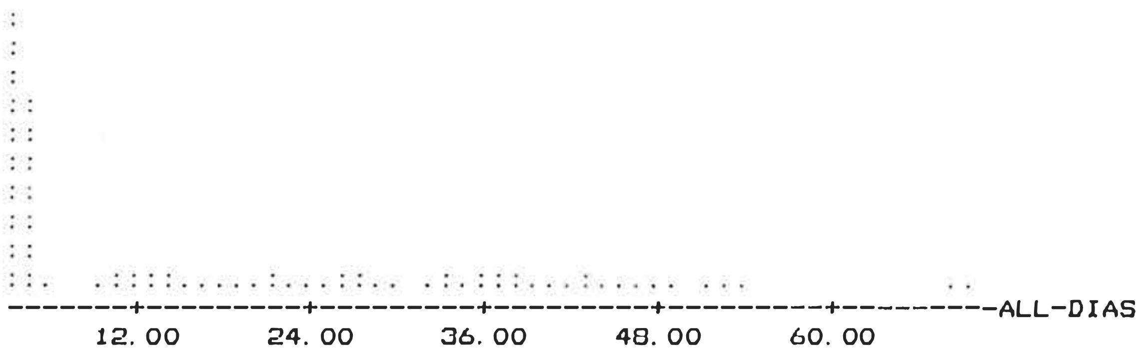


Fig. 5.2 Combined DBH dotplot distribution of the 3 kaikawaka populations. Axes as in Fig. 5.1. Total count = 259.

These results are in contrast to the findings of Wardle (1963b, 1978) in which larger DBH size-classes at several sites were adequately represented but smaller DBH size-classes inadequately so. Wardle (op.cit.) interpreted such distributions to represent synchronous regeneration failure, a regeneration gap attributable to regional climatic change. Such an interpretation was in accordance with the hypothesis of Holloway (1954) on the effects of climatic change in forests of the South Island.

Results of the present study are in agreement with the conclusions of Clayton-Greene (1977), Veblen and Stewart (1982), Norton (1983) and Haase (1986a). The population size structures of kaikawaka in 3 adjacent stands on the sideslope of the Razorback Ridge, Upper Ngatoro Valley, reflect an intermittent mode of regeneration which is explainable in terms of initiation by disturbance of various kinds over a range of scales (Druce, 1966b; White, 1979; Oliver, 1981).

The major initiating disturbances were undoubtably infrequent catastrophic landslides, exposing slip-faces for recolonisation and depositing debris into the Ngatoro Stream tributary below. On the slip-faces subsequent minor disturbance has been caused by windstorms which can uproot and overturn small trees such as *Pseudopanax simplex* and *Griselinia littoralis* (pers. observ., 15.9.85, 350-year-old stand). Minor disturbance is also evident in the 640- and 10-year-old stands caused by the trampling, camping and browsing of goats.

Kaikawaka has also colonised debris-fans adjacent to the tributary of the Ngatoro Stream (detailed locations given in section 4.8). These were deposited after heavy rains and catastrophic up-valley erosion. Similarly, Veblen and Stewart (1982) found stands of kaikawaka with *Podocarpus hallii* on poorly drained debris fans in central Westland, South Island.

The results of the present study support the conclusions of Allen and Wardle (1984) who considered disturbance of varying scales plays a major role in determining vegetation structure and species composition in New Zealand's montane and subalpine vegetation.

5.7 Canopy dieback, forest life-cycle phases and cohort senescence

Stand structure and succession is one of five research areas identified by Mueller-Dombois (1983) as currently being investigated to explain widespread canopy dieback of a range of species, in montane and subalpine forests both in the Pacific, including New Zealand (Mueller-Dombois, 1983) and in Europe (Mueller-Dombois, 1987).

The present study examines stand structure and succession of kaikawaka on a sideslope of the Razorback Ridge, Upper Ngatoro Valley, Mt Taranaki. Tree-group dieback of kaikawaka was evident in the 640-year-old stand (section 4.4.2) and stand-level dieback of kaikawaka and *Podocarpus hallii* occurs on an adjacent, presumed-older surface (> 640 yrs) (Fig. 2.2). In many places elsewhere on Mt Taranaki but particularly noticeable between Ahukawakawa Mire and North Egmont, extensive stand-level dieback of kaikawaka (> 200ha) is evident (Figs 4.20, 4.21). This dieback phenomenon warrants an explanation from a conservation management viewpoint since apparently deteriorating indigenous forest raises public concern and suggests poor management.

Mueller-Dombois (1987) has recognised a number of features common to dieback stands in Hawaii and New Zealand: 1) regeneration occurs in waves rather than in the form of continuous recruitment, 2) in all cases examined there was an association between stand-level dieback and stand recovery and 3) dieback was limited to the canopy population and did not extend to its seedlings. These features are also characteristic of the kaikawaka populations on the sideslope of the Razorback Ridge and suggest the cohort-senescence dieback theory (Mueller-Dombois, 1983; 1987) and the European forest life-cycle theory (Jones, 1945; Watt, 1947) are applicable in most respects to the study area.

According to these theories an initial catastrophic stand-destroying disturbance such as a landslide gives rise to cohorts of physiologically and genetically similar individuals of a pioneering species which then pass cyclically through various forest life-cycle phases or structural variations. These structural variations have been labelled in self-explanatory terms, namely the regeneration phase, the building phase, the optimal phase, the terminal or aging phase and the breakdown or dieback phase. A short-circuit regeneration/mixed-structure phase has also been recognised (Mueller-Dombois, 1987). Over areas ranging from half a square kilometre in European virgin forests to 100 km^2 on the the island of Hawaii, forests comprise a spatial mosaic with all forest life-cycle phases repeatedly represented. This mosaic is called Waldtexture in Europe and only on this scale do forests form dynamic systems that are in a state of equilibrium.

In some respects the European Waldtexture mosaic as explained by the forest life-cycle theory in conjunction with the cohort senescence theory parallels the model Cameron (1954) proposed to account for a mosaic of podocarp-dominated and hardwood-dominated communities in Whirinaki Valley, North Island, New Zealand. It differs however in that the initial colonisation is by a pioneer species after catastrophic disturbance.

Whitmore (1985) terms the latter ecological process succession, or directional change in time, following Finegan (1984). The former ecological process where climax ecosystems are maintained in the absence of catastrophic disturbance is termed cyclic replacement (Whitmore, 1985). Pioneer trees participate only infrequently in this process (Finegan, 1985).

Oliver (1981) also describes a chain of general physiognomic stages which forests develop through after disturbance. These stages are: stand initiation, stem exclusion, understory reinitiation, and old growth. He concluded disturbance severity determines which species will dominate the forest afterward and notes the importance of disturbance frequency in determining the general forest type over a large area. This is recognising that species dominance and stand physiognomy change with time (i.e. succession occurs) following disturbance.

In the case of kaikawaka described on Mt Taranaki the stands situated on the steep Razorback Ridge sideslope are representative of a full range of forest life-cycle stages (Fig. 2.2) in a relatively small area (< 5ha). The 170-yr stand equates to the rejuvenation phase, the 350-yr stand the building phase, the 640-yr stand the optimal phase progressing to terminal phase and the adjacent stand above, the dieback phase.

However only the dieback phase is evident in a much larger area (> 200ha), part of a debris-fan off Mt Taranaki situated between Ahukawakawa Mire and the Kokowai Track (Department of Lands and Survey, 1986; Figs. 4.20, 4.21).

The difference in areal extent and spatial distribution of the forest life-cycle phases mentioned above reflects the dependence of disturbance within one landscape on topography, substrate and vegetation (White, 1979). A different disturbance regime is clearly operating in the two areas.

Because at a given site catastrophic stand-destroying disturbance maybe less frequent than the normally attainable age (Harper and White, 1974, p434) of the dieback species, cohorts of individuals predispose the stand to canopy dieback in the dieback phase of the forest life-cycle. Such an interpretation is clearly applicable to the sideslope stands of kaikawaka in the study area and is probably applicable to the other dieback stands described.

The features of the four-level causal chain in the cohort senescence dieback theory are similar to the three-step chain reaction model proposed by Manion (1981) for decline diseases. These diseases are now seen as symptoms of forest decline rather than as causes. Manion's model involves disease-initiating or predisposing factors such as age or site, initiating factors such as drought or wind and contributing factors such as secondary attack by insects and fungi.

The cohort senescence dieback theory (Mueller-Dombois, 1983) involves: 1) a catastrophic disturbance such as a landslide which permits a relatively large cohort of an opportunistic species to become established; 2) stand development during which some individuals become suppressed or are thinned out but many trees develop uniformly into maturity and enter the senescing life stage together; 3) vigour of the cohort stand decreases in the senescing life stage and a fluctuating site factor such as transient soil drought may trigger stand-level dieback; 4) insect population buildup or increased fungal attack by weak pathogens hasten decline after initial breakdown of the canopy.

The cohort senescence dieback theory differs from the decline-disease model in emphasizing cohort senescence and by considering successional implications.

Some successional implications observed in Hawaiian rain forest are that the breakdown of the canopy following cohort senescence may permit invasion or stimulate development of a new cohort i.e. cyclic stand redevelopment on the same area unless undergrowth species interfere, or replacement dieback. With each generation turnover, cohort sizes become smaller more disjunct, and/or irregular. Alternatively, displacement dieback may occur where another potential canopy species is favoured by the canopy breakdown (Mueller-Dombois, 1987).

Further investigation is needed to ascertain which type of stand redevelopment in dieback areas if any, is occurring on Mt Taranaki.

Appendix 1 List of native vascular plants of the 640-year-old stand, arranged in life-form groups.

FERNS (18)

*Asplenium bulbiferum
*A. flaccidum (e)
*A. terrestre subsp. terrestre
*Blechnum chambersii
*B. colensoi
*B. fluviatile
*B. sp.(a) (B. capense agg.) (common sp.; lower pinnae reduced in length)
*Cyathea smithii
*Grammitis billardieri (e)
*Histiopteris incisa
*Hymenophyllum multifidum (e)
*H. pulcherrimum
*H. sanguinolentum (inc. H. villosum) (e)
*Hypolepis rufobarbata
Leptopteris superba
Phymatosorus diversifolius (e)
*Polystichum silvaticum
P. vestitum

GYMNOSPERM TREES (2)

Libocedrus bidwillii
*Podocarpus hallii

DICOT TREES (8)

Carpodetus serratus
Fuchsia excorticata
*Griselinia littoralis
Melicytus lanceolatus
Myrsine salicina
Pseudopanax colensoi s.s.
*P. simplex
*Schefflera digitata

DICOT LIANES (2)

Clematis paniculata
*Rubus cissoides var. cissoides

DICOT HERBS (other than composites) (6)

*Cardamine debilis agg.
*Ourisia macrophylla var. macrophylla
Oxalis lactea
*Ranunculus hirtus s.s.
*Stellaria parviflora
*Viola filicaulis

MONOCOT TREES (1)

Cordyline indivisa

ORCHIDS (1)

*Corybas trilobus

GRASSES (2)

Microlaena avenacea
*Poa laevis var. (P. caespitosa var. leioclada)

SEDGES (3)

*Gahnia procera
*Uncinia banksii
*U. clavata

MONOCOT HERBS (other than orchids, grasses, sedges and rushes) (3)

*Astelia fragrans
*A. sp. (unnamed; aff. A. nervosa)
Luzuriaga parviflora (e)

DICOT SHRUBS (13)
 Alseuosmia macrophylla
 Brachyglottis rotundifolia var.(B. elaeagnifolia)
*Carmichaelia arborea var. (C.egmontiana)
*Coprosma grandifolia
 Coprosma lucida s.s. (incl.C. australis)
*C. pseudocuneata
*C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
*C. tenuifolia
 Gaultheria antipoda
*Hebe stricta var. egmontiana
*Myrsine divaricata var. divaricata
 Olearia arborescens
*Pseudowintera colorata

Total No. of species = 59

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*specimens lodged in personal herbarium
(e) = epiphytic only
(s) = seedling

Appendix 2 List of epiphytes and lianes of the 640-year-old stand, arranged in life-form groups.

FERNS (5)
Asplenium flaccidum
Grammitis billardieri
Hymenophyllum multifidum
H. sanguinolentum
Phymatosorus diversifolius

DICOT TREES (3)
Griselinia littoralis
Melicytus lanceolatus
Pseudopanax simplex

DICOT SHRUBS (3)
Brachyglottis rotundifolia var.
Coprosma "taylorae"
Myrsine divaricata var. divaricata

DICOT LIANES (2)
Clematis paniculata
Rubus cissoides var. cissoides

MONOCOT HERBS (1)
Luzuriaga parviflora

Total No. of species = 14

Appendix 3 List of native vascular plants of the 640-year-old stand, arranged alphabetically.

---

*Alseuosmia pusilla
*Asplenium bulbiferum
*A. flaccidum
*A. terrestre subsp. terrestre
*Astelia fragrans
*A. sp. (unnamed; aff. A. nervosa)
*Blechnum chambersii
*B. colensoi
*B. fluviatile (occasional above cedar no. 65)
*B. sp.(a) (B. capense agg.)(common sp.; lower pinnae reduced in length
Brachyglottis rotundifolia var. (B. elaeagnifolia)
*Cardamine debilis agg.
*Carmichaelia arborea var. (C.egmontiana)
Carpodetus serratus
Clematis paniculata
*Coprosma grandifolia
*C. lucida s.s. (inc. C. australis)
*C. pseudocuneata
*C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
*C. tenuifolia
Cordyline indivisa
*Corybas trilobus
*Cyathea smithii
*Fuchsia excorticata
*Gahnia procera
Gaultheria antipoda
*Grammitis billardieri
*Griselinia littoralis
*Hebe stricta var. egmontiana
*Histiopteris incisa
*Hymenophyllum multifidum
*H. pulcherrimum
*H. sanguinolentum (incl. H. villosum)
Hypolepis rufobarbata
*Leptopteris superba
Libocedrus bidwillii
*Luzuriaga parviflora
Melicytus lanceolatus
Microlaena avenacea (uncommon, near cedars no. 62 and 47)
*Myrsine divaricata var. divaricata
*M. salicina
Olearia arborescens
*Ourisia macrophylla var. macrophylla
Oxalis lactea
Phymatosorus diversifolius (near cedar no. 110)
*Poa laevis var. (P. caesipitosa var. leioclada)
*Podocarpus hallii
*Polystichum silvaticum
*P. vestitum
Pseudopanax colensoi s.s. (uncommon)
*P. simplex
*Pseudowintera colorata
*Ranunculus hirtus s.s.
*Rubus cissoides var. cissoides
*Schefflera digitata (uncommon, near cedar no. 63)

*Stellaria parviflora
*Uncinia banksii
*U. clavata
*Viola filicaulis

Total No. of species = 59

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*specimens lodged in personal herbarium

Appendix 4 List of the native vascular plants of the 350-year old-stand, arranged in life-form groups.

FERNS (13)
Asplenium bulbiferum
A. flaccidum (e)
Blechnum fluviatile
B. sp.(a) (B.capense agg.) (common sp; lower pinnae reduced in length)
Cyathea smithii
Grammitis billardieri (e)
Histiopteris incisa
Hymenophyllum multifidum (e)
H. sanguinolentum (e)
Hypolepis rufobarbata
Leptopteris superba
Polystichum silvaticum (gc,e)
P.vestitum

GYMNOSPERM TREES (2)
Libocedrus bidwillii
Podocarpus hallii

DICOT TREES (11)
Aristotelia serrata (s)
Carpodetus serratus
Fuchsia excorticata
Griselinia littoralis
Melicytus lanceolatus
Myrsine salicina
Pittosporum tenuifolium var. tenuifolium
Pseudopanax colensoi s.s
P. simplex
Schefflera digitata
Weinmannia racemosa (sc)

ORCHIDS (2)
Corybas trilobus
Pterostylis banksii

DICOT SHRUBS (13)
Brachyglottis rotundifolia var. (B. elaeagnifolia)
Carmichaelia arborea var. (C. egmontiana)
Coprosma grandifolia
C. lucida s.s (incl. C. australis)
C. pseudocuneata
C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
C. tenuifolia
Dracophyllum longifolium var. (D.urvilleanum)(incl. D. filifolium)
Gaultheria antipoda
Hebe stricta var. egmontiana
Myrsine divaricata var. divaricata
Olearia arborescens
Pseudowintera colorata

DICOT LIANES (3)
Clematis paniculata
Parsonsia capsularis
Rubus cissoides var.cissoides

DICOT HERBS (other than composites) (8)
Cardamine debilis agg.
Epilobium pedunculare
E sp.
Ourisia macrophylla var. macrophylla
Oxalis lactea
Ranunculus hirtus s.s
Stellaria parviflora
Viola filicaulis

MONOCOT TREES (1)
Cordyline indivisa

SEDGES (2)
Uncinia banksii
U. clavata

MONOCOT HERBS (other than orchids, grasses, sedges, rushes) (3)
Astelia fragrans
A. sp. (unnamed;aff. A. nervosa)
Luzuriaga parviflora

Total No. of species = 58

*specimens lodged in personal herbarium
(s) = seedlings only

(e) = epiphytic only
(sc) = subcanopy only
(gc,e) = ground cover and epiphytic

Appendix 5 List of epiphytes and lianes of the 350-year-old stand, arranged in life-form groups.

FERNS (5)
Asplenium flaccidum
Grammitis billardieri
Hymenophyllum multifidum
H. sanguinolentum
Polystichum silvaticum

DICOT TREES (1)
Griselinia littoralis

DICOT LIANES (2)
Clematis paniculata
Rubus cissoides var. cissoides

OTHER MONOCOT HERBS (1)
Luzuriaga parviflora

DICOT SHRUBS (1)
Coprosma "taylorae"

Spp. total = 9

Appendix 6 List of native vascular plants of the 350-year-old stand, arranged alphabetically.

---

*Aristotelia serrata
Asplenium bulbiferum
A. flaccidum
Astelia fragrans
A. sp. (unnamed; aff. A. nervosa)
Blechnum fluviatile
B. sp. (a) (B. capense agg.) (common sp; lower pinnae reduced in length)
Brachyglottis rotundifolia var. (B. elaeagnifolia)
*Cardamine debilis agg.
Carmichaelia arborea var. (C. egmontiana)
*Carpodetus serratus
Clematis paniculata
Coprosma grandifolia
*C. lucida s.s. (ind. C. australis)
C. pseudocuneata
C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
*C. tenuifolia
Cordyline indivisa
*Corybas trilobus
Cyathea smithii
Dracophyllum longifolium var. (D. urvilleanum) (incl. D. filifolium)
*Epilobium pedunculare
*E. sp.
*Fuchsia excorticata
*Gaultheria antipoda
Grammitis billardieri
Griselinia littoralis
Hebe stricta var. egmontiana
*Histiopteris incisa
Hymenophyllum multifidum
*H. sanguinolentum (incl. H. villosum)
*Hypolepis rufobarbata
Leptopteris superba
*Libocedrus bidwillii
Luzuriaga parviflora
*Melicytus lanceolatus
Myrsine divaricata var. divaricata
*M. salicina
Olearia arborescens
*Ourisia macrophylla var. macrophylla
*Oxalis lactea
Parsonsia capsularis
Pittosporum tenuifolium var. tenuifolium
Podocarpus hallii
*Polystichum silvaticum
P. vestitum
Pseudopanax colensoi s.s.
P. simplex
Pseudowintera colorata
*Pterostylis banksii
*Ranunculus hirtus s.s.
*Rubus cissoides var. cissoides
Schefflera digitata
*Stellaria parvifloria

*Uncinia banksii
*U. clavata
*Viola filicaulis
*Weinmannia racemosa

Total No. of species = 58

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*Specimen lodged in personal herbarium

Appendix 7 List of those native vascular plants recorded for the 350-year-old stand but not for the 640-year-old stand, together with their life-form group and stratum or plant category.

SCIENTIFIC NAME	LIFE FORM GROUP	STRATUM OR PLANT CATEGORY
Aristotelia serrata (seedling)	Dicot tree	Ground cover
Dracophyllum longifolium var. (D. urvilleanum) (incl. filifolium)	Dicot shrub	Shrub-small tree canopy
Epilobium pedunculare	Dicot herb	Ground cover
E. sp.	Dicot herb	Ground cover
Parsonsia capsularis	Dicot liane	Liane
Pittosporum tenuifolium var. tenuifolium	Dicot tree	Shrub-small tree canopy
Pterostylis banksii	Orchid	Ground cover
Weinmannia racemosa	Dicot tree	Shrub-small tree subcanopy

Total No. of species = 8

Appendix 8 List of those native vascular plants recorded for the 640-year-old stand but not for the 350-year-old stand, together with their life-form group and stratum or plant category.

	LIFE FORM GROUP	STRATUM OR PLANT CATEGORY
Alseuosmia pusilla	Dicot shrub	Ground cover
Asplenium terrestre subsp. terrestre	Fern	Ground cover
Blechnum chambersii	Fern	Ground cover
B. colensoi	Fern	Ground cover
Gahnia procera	Sedge	Ground cover
Hymenophyllum pulcherrimum	Fern	Ground cover
Microlaena avenacea	Grass	Ground cover
Phymatosorus diversifolius	Fern	Epiphyte
Poa laevis var.	Grass	Ground cover

Total No. of species = 9

Appendix 9 List of those native vascular plants common to both the 350- and 640-year-old stands.

	Life-form group	Main stratum or plant category
Asplenium bulbiferum		
A. flaccidum		
Astelia fragrans		
A. sp. (unnamed; aff. A. nervosa)		
Blechnum fluviatile		
B. sp. (a) (B.capense agg.)		
Brachyglottis rotundifolia var. (B. elaeagnifolia)	Dicot shrub	Canopy
Cardamine debilis agg.		
Carmichaelia arborea var. (C. egmontiana)	Dicot shrub	Canopy
Carpodetus serratus	Dicot tree	Canopy
Clematis paniculata		
Coprosma grandifolia	Dicot shrub	Canopy
C. lucida s.s. (incl. C. australis)	Dicot shrub	Canopy
C. pseudocuneata	Dicot shrub	Canopy
C. "taylorae"	Dicot shrub	Canopy
C. tenuifolia	Dicot shrub	Canopy
Cordyline indivisa	Monocot tree	Canopy
Corybas trilobus		
Cyathea smithii		
Fuchsia excorticata	Dicot tree	Canopy
Gaultheria antipoda	Dicot shrub	Canopy
Grammitis billardieri		
Griselinia littoralis	Dicot tree	Canopy
Hebe stricta var. egmontiana	Dicot shrub	Canopy
Histiopteris incisa		
Hymenophyllum multifidum		
H. sanguinolentum (incl. H. villosum)		
Hypolepis rufobarbata		
Leptopteris superba		
Libocedrus bidwillii		
Luzuriaga parviflora		
Melicytus lanceolatus	Dicot tree	Canopy
Myrsine divaricata var. divaricata	Dicot shrub	Canopy
M. salicina	Dicot tree	Canopy
Olearia arborescens	Dicot shrub	Canopy
Ourisia macrophylla var. macrophylla		
Oxalis lactea		
Podocarpus hallii		
Polystichum silvaticum		
P. vestitum		
Pseudopanax colensoi s.s.	Dicot tree	Canopy
P. simplex	Dicot tree	Canopy
Pseudowintera colorata	Dicot shrub	Canopy
Ranunculus hirtus s.s.		
Rubus cissoides var. cissoides		
Schefflera digitata	Dicot tree	Canopy
Stellaria parviflora		
Uncinia banksii		
U. clavata		
Viola filicaulis		

Total Number of Species = 50

Appendix 10 List of the vascular plants of the 10-year-old stand, arranged alphabetically.

Acaena anserinifolia
*Anthoxanthum odoratum (Adv.)
*Asplenium flaccidum subsp. flaccidum
*A. terrestre subsp. terrestre
Astelia sp. (unnamed; aff. A. nervosa)
Blechnum fluviatile
B. sp. (a) (B. capense agg.) (common sp.; lower pinnae reduced in length)
Brachyglottis rotundifolia var. (B. elaeagnifolia)
Carmichaelia arborea var. (C. egmontiana)
Cassinia vauvilliersii
*Celmisia glandulosa var. latifolia
C. gracilenta var. (C. major var. brevis)
Coprosma grandifolia
C. lucida s.s. (incl. C. australis)
C. pseudocuneata
C. robusta
C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
C. tenuifolia
Coriaria pteridoides
Cotula squalida subsp. squalida
Dracophyllum longifolium var. (D. urvilleanum) (incl. D. filifolium)
Epilobium brunnescens
*E. rotundifolium
*E. sp.
Euphrasia cuneata
Gaultheria antipoda
Griselinia littoralis
Gunnera monoica var. monoica (incl. G. albocarpa and G. strigosa)
Hebe stricta var. egmontiana
*Helichrysum filicaule
H. sp. (unnamed; aff. H. bellidioides)
Histiopteris incisa
Hydrocotyle moschata
Hymenophyllum multifidum
H. sanguinolentum
Hypochoeris radicata (Adv.)
Lachnagrostis sp. (b) (unnamed, included in L. filiformis as var. semiglabra by Zotov 1965)
*Lagenifera pumila
Libocedrus bidwillii
*Luzula sp.
*Luzuriaga parviflora
*Lycopodium fastigiatum
*L. scariosum
*L. volubile
*Nertera ciliata
Olearia arborescens
Ourisia macrophylla var. macrophylla
*Poa anceps var. anceps
P. laevis var. (P. caespitosa var. leioclada)
Podocarpus hallii
Polystichum vestitum
Pratia angulata
Pseudopanax colensoi s.s.
P. simplex
Pseudowintera colorata
*Raoulia glabra

R. tenuicaulis
*Rytidosperma sp.
*Sagina procumbens (Adv.)
Senecio rufiglandulosus var. rufiglandulosus
*Stellaria parviflora
Trichomanes reniforme
Uncinia banksii
Viola filicaulis

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* = Specimen lodged in personal herbarium
Adv. = Adventive species

Appendix 11 List of the vascular plants of the 170-year-old stand, arranged alphabetically.

Aristotelia serrata
*Asplenium bulbiferum,
A. flaccidum
Astelia fragrans
A. sp. (unnamed; aff. A. nervosa)
Blechnum penna-marina
B. sp. (a) (B. capense agg.) (common sp.; lower pinnae reduced in length)
Brachyglottis rotundifolia var. (B. elaeagnifolia)
Cardamine debilis agg.
Carmichaelia arborea var. (C. egmontiana)
Coprosma grandifolia
C. lucida s.s. (incl. C. australis)
C. pseudocuneata
C. robusta
C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
C. tenuifolia
Corybas trilobus
Cotula squalida subsp. squalida
Dracophyllum longifolium var. (D. urvilleanum) (incl. D. filifolium)
Epilobium sp.
Fuchsia excorticata
Gaultheria antipoda
Grammitis billardieri
Griselinia littoralis
Hebe stricta var. egmontiana
*Hymenophyllum multifidum
H. sanguinolentum (incl. H. villosum)
Libocedrus bidwillii
Luzuriaga parviflora
Lycopodium australianum
Myrsine divaricata var. divaricata
Ourisia macrophylla var. macrophylla
Oxalis lactea
Poa anceps var. anceps
Podocarpus hallii
Polystichum vestitum
Pratia angulata
Pseudopanax colensoi s.s.
P. simplex
Pseudowintera colorata
Ranunculus hirtus s.s.
Stellaria parviflora
Uncinia banksii
U. clavata
*Viola filicaulis
Weinmannia racemosa

---

* = specimen lodged in personal herbarium

Appendix 12 List of the vascular plants of the 170-year-old stand, arranged in life-form groups.

LYCOPODS

*Lycopodium australianum

FERNS

Asplenium bulbiferum
A. flaccidum (e)
*Blechnum penna-marina
B. sp. (a) (B. capense agg.) (common sp.; lower pinnae reduced in length)
Grammitis billardieri (gc,e)
Hymenophyllum multifidum (gc,e)
H. sanguinolentum (e)
Polystichum vestitum

GYMNOSPERM TREES

Libocedrus bidwillii
Podocarpus hallii

DICOT TREES

Aristotelia serrata (s)
Fuchsia excorticata (s)
Griselinia littoralis
Pseudopanax colensoi
P. simplex
Weinmannia racemosa

DICOT SHRUBS

Brachyglottis rotundifolia var. (B. elaeagnifolia)
Carmichaelia arborea var. (C. egmontiana)
Coprosma grandifolia
C. lucida s.s. (incl. C. australis)
C. pseudocuneata
C. robusta
C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
C. tenuifolia
Dracophyllum longifolium var. (D. urvilleanum) (incl. D. filifolium)
Gaultheria antipoda
Hebe stricta var. egmontiana
Myrsine divaricata var. divaricata
Pseudowintera colorata

COMPOSITE HERBS

Cotula squalida subsp. squalida

DICOT HERBS

Cardamine debilis agg.
Epilobium sp.
Ourisia macrophylla var. macrophylla
Oxalis lactea
Pratia angulata
Ranunculus hirtus s.s.
Stellaria parviflora
Viola filicaulis

ORCHIDS
Corybas trilobus

GRASSES
Poa anceps var. anceps

SEDGES
Uncinia banksii
U. clavata

MONOCOT HERBS
Astelia fragrans
A. sp. (unnamed; aff A. nervosa)
Luzuriaga parviflora (e)

(e) = epiphytic only
(gc,e) = ground cover and epiphytic
(s) = seedling only

Appendix 13 List of the vascular plants common to both the 170- and 350-year-old stands.

Aristotelia serrata
Asplenium bulbiferum
A. flaccidum
Astelia fragrans
A. sp. (unnamed; aff. A. nervosa)
B. sp. (a) (B. capense agg.) (common sp.; lower pinnae reduced in length)
Brachyglottis rotundifolia var. (B. elaeagnifolia)
Cardamine debilis agg.
Carmichaelia arborea var. (C. egmontiana)
Coprosma grandifolia
C. lucida s.s. (incl. C. australis)
C. pseudocuneata
C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
C. tenuifolia
Corybas trilobus
Dracophyllum longifolium var. (D. urvilleanum) (incl. D. filifolium)
Epilobium sp.
Fuchsia excorticata
Gaultheria antipoda
Grammitis billardieri
Griselinia littoralis
Hebe stricta var. egmontiana
Hymenophyllum multifidum
H. sanguinolentum (incl. H. villosum)
Libocedrus bidwillii
Luzuriaga parviflora
Myrsine divaricata var. divaricata
Ourisia macrophylla var. macrophylla
Oxalis lactea
Podocarpus hallii
Polystichum vestitum
Pseudopanax colensoi s.s.
P. simplex
Pseudowintera colorata
Ranunculus hirtus s.s.
Stellaria parviflora
Uncinia banksii
U. clavata
Viola filicaulis
Weinmannia racemosa

Appendix 14 List of the vascular plants of the 10-year-old stand, arranged in life-form groups.

LYCOPODS
Lycopodium fastigiatum
L. scariosum
L. volubile

FERNS
*Asplenium flaccidum subsp. flaccidum
*A. terrestre subsp. terrestre
Blechnum fluviatile
B. sp. (a) (B. capense agg.) (common sp.; lower pinnae reduced in length)
Histiopteris incisa
Hymenophyllum multifidum
H. sanguinolentum
Polystichum vestitum
Trichomanes reniforme

GYMNOSPERM TREES
Libocedrus bidwillii
Podocarpus hallii

DICOT TREES
Griselinia littoralis
Pseudopanax colensoi s.s.
P. simplex

DICOT SHRUBS
Brachyglottis rotundifolia var. (B. elaeagnifolia)
Carmichaelia arborea var. (C. egmontiana)
Cassinia vauvilliersii
C. grandifolia
C. lucida s.s. (incl. C. australis)
C. pseudocuneata
C. robusta
C. "taylorae" (C. parviflora var. dumosa, Cheeseman 1906)
C. tenuifolia
Coriaria pteridoides
Dracophyllum longifolium var. (D. urvilleanum) (incl. D. filifolium)
Gaultheria antipoda
Hebe stricta var. egmontiana
Olearia arborescens
Pseudowintera colorata

COMPOSITE HERBS
Celmisia glandulosa var. latifolia
C. gracilenta var. (C. major var. brevis)
Cotula squalida subsp. squalida
Helichrysum filicaule
H. sp. (unnamed; aff. H. bellidioides)
Hypochoeris radicata (Adv.)
Lagenifera pumila
Raoulia glabra
R. tenuicaulis
Senecio rufiglandulosus var. rufiglandulosus

DICOT HERBS
Acaena anserinifolia

Epilobium brunnescens
E. rotundifolium
E. sp.
Euphrasia cuneata
Gunnera monoica var. monoica (incl. G. albocarpa and G. strigosa)
Hydrocotyle moschata
Nertera ciliata
Ourisia macrophylla var. macrophylla
Pratia angulata
Sagina procumbens (Adv.)
Stellaria parviflora (incl. S. minuta)
Viola filicaulis

GRASSES
Anthoxanthum odoratum (Adv.)
Lachnagrostis sp. (b) (unnamed, included in L. filiformis as var. semiglabra by Zotov 1965)
Poa anceps var. anceps
P. laevis var. (P. caespitosa var. leioclada)
Rytidosperma sp.

SEDGES
Luzula sp.
Uncinia banksii

MONOCOT HERBS (other than orchids, grasses, sedges, rushes)
Astelia sp. (unnamed; aff. A. nervosa)
Luzuriaga parviflora

Adv = adventive species

Appendix 15 Comparison of the floristic composition of the four stands.

Scientific name	640	350	170	10	Family
Acaena anserinifolia				*	Rosaceae
Alseuosmia pusilla	*				Alseuosmiaceae
Anthoxanthum odoratum (Adv.)				*	Poaceae
Aristotelia serrata		*	*		Elaeocarpaceae
Asplenium bulbiferum	*	*	*		Aspleniaceae
A. flaccidum	*	*	*	*	
A. terrestre subsp. terrestre	*			*	
Astelia fragrans	*	*	*		Liliaceae
A. sp. (unnamed; aff. A. nervosa)	*	*	*	*	
Blechnum chambersii	*				Blechnaceae
B. colensoi	*				
B. fluviatile	*	*		*	
B. penna-marina			*		
B. sp. (a) (B. capense agg.) (common sp.; lower pinnae reduced in length)	*	*	*	*	
Brachyglottis rotundifolia var. (B. elaeagnifolia)	*	*	*	*	Asteraceae
Cardamine debilis agg.	*	*	*		Brassicaceae
Carmichaelia arborea var. (C. egmontiana)	*	*	*	*	Brassicaceae
Carpodetus serratus	*	*			Escalloniaceae
Cassinia vauvilliersii				*	Asteraceae
Celmisia glandulosa var. latifolia				*	Asteraceae
C. gracilenta var. (C. major var. brevis)				*	
Clematis paniculata	*	*			Ranunculaceae
Coprosma grandifolia	*	*	*	*	Rubiaceae
C. lucida s.s. (incl. C. australis)	*	*	*	*	
C. pseudocuneata	*	*	*	*	
C. robusta			*	*	
C. "taylorae" (C. parviflora var.dumosa, Cheeseman 1906)	*	*	*	*	
C. tenuifolia	*	*	*	*	
Cordyline indivisa	*	*			Agavaceae
Coriaria pteridoides				*	Coriariaceae
Corybas trilobus	*	*	*		Orchidaceae
Cotula squalida subsp. squalida			*	*	Asteraceae
Cyathea smithii	*	*			Cyatheaceae
Dracophyllum longifolium var. (D. urvilleanum) (incl. D. filifolium)		*	*	*	Epacridaceae
Epilobium brunnescens				*	Onagraceae
E. pedunculare		*			
E. rotundifolium				*	
E. sp.		*	*	*	
Euphrasia cuneata				*	Scrophulariaceae
Fuchsia excorticata	*	*	*		Onagraceae
Gahnia procera	*				Cyperaceae
Gaultheria antipoda	*	*	*	*	Ericaceae
Grammitis billardieri	*	*	*		Grammitidaceae
Griselinia littoralis	*	*	*	*	Cornaceae
Gunnera monoica var. monoica (incl. G. albocarpa and G. strigosa)				*	Haloragaceae
Hebe stricta var. egmontiana	*	*	*	*	Scrophulariaceae
Helichrysum filicaule				*	Asteraceae
H. sp. (unnamed; aff. H. bellidioides)				*	
Histiopteris incisa	*	*		*	Pteridaceae
Hydrocotyle moschata				*	Apiaceae
H. multifidum	*	*	*	*	Hymenophyllaceae

H. pulcherrimum	*				
H. sanguinolentum (incl. H. villosum)	*	*	*	*	
Hypochoeris radicata (Adv.)				*	Asteraceae
Hypolepis rufobarbata	*	*			Hypolepidaceae
Lachnagrostis sp. (b) (unnamed, included in L. filiformis as var. semiglabra by Zotov 1965)				*	Poaceae
Lagenifera pumila				*	Asteraceae
Leptopteris superba	*	*			Osmundaceae
Libocedrus bidwillii	*	*	*	*	Cupressaceae
Luzula sp.				*	Cyperaceae
Luzuriaga parviflora	*	*	*	*	Philesiaceae
Lycopodium australianum			*		Lycopodiaceae
L. fastigiatum				*	
L. scariosum				*	
L. volubile				*	
Melicytus lanceolatus	*	*			Violaceae
Microlaena avenacea	*				Poaceae
Myrsine divaricata var. divaricata	*	*	*		Myrsinaceae
M. salicina	*	*			
Nertera ciliata				*	Rubiaceae
Olearia arborescens	*	*		*	Asteraceae
Ourisia macrophylla var. macrophylla	*	*	*	*	Scrophulariaceae
Oxalis lactea	*	*	*		Oxalidaceae
Parsonsia capsularis		*			Apocynaceae
Pittosporum tenuifolium var. tenuifolium		*			Pittosporaceae
Phymatosorus diversifolius	*				Polypodiaceae
Poa anceps var. anceps			*	*	Poaceae
P. laevis var. (P. caespitosa var. leioclada)	*			*	
Podocarpus hallii	*	*	*	*	Podocarpaceae
Polystichum silvaticum	*	*			Dryopteridaceae
P. vestitum	*	*	*	*	
Pratia angulata			*	*	Liliaceae
Pseudopanax colensoi s.s.	*	*	*	*	Araliaceae
P. simplex	*	*	*	*	
Pseudowintera colorata	*	*	*	*	Winteraceae
Pterostylis banksii		*			Orchidaceae
Ranunculus hirtus s.s.	*	*	*		Ranunculaceae
Raoulia glabra				*	Asteraceae
R. tenuicaulis				*	
Rubus cissoides var. cissoides	*	*			Rosaceae
Rytidosperma sp.				*	Poaceae
Sagina procumbens (Adv.)				*	Caryophyllaceae
Schefflera digitata	*	*			Araliaceae
Senecio rufiglandulosus var. rufiglandulosus)				*	Asteraceae
Stellaria parviflora		*	*	*	Caryophyllaceae
Trichomanes reniforme				*	Hymenophyllaceae
Uncinia banksii	*	*	*	*	Cyperaceae
U. clavata	*	*	*		
Viola filicaulis	*	*	*	*	Violaceae
Weinmannia racemosa		*	*		Cunoniaceae
Stand spp. totals	59	58	46	64	

Species total = 100

Adv = adventive species

Appendix 16 Regression data components.

Tree No. and Core Label	Core Ht upslope (cm)	Dist us-ds (cm)	Core Ht downslope (cm)	Centre Estimate (Yrs+/-*)	Core Age 1=1978 (yrs+/-*)	Tree Age (ds at 0cm on DBH date)	DBH (cm)	DCH (cm)
640-YEAR STAND								
35AB	40	13	53	-	66+/-	119+/-	6.1	7.1
36CD	114	50	164	33+/- 9	231+/- 9	395+/- 9	35.6	36.3
37EE2	45	70	115	48+/-10	315+/-10	430+/-10	40.8	45.7
39CC2	76	60	136	0	395+/- 0	531+/- 0	42.9	47.8
40EE2	41	40	81	84+/-17	303+/-17	384+/-17	31.9	35.3
42EE2	43	45	88	47+/-11	367+/-11	455+/-11	36.3	40.0
45EE2	54	48	102	5+/- 0	458+/- 0	561+/- 0	45.4	48.1
51BB2	46	56	102	138+/-51	405+/-51	507+/-51	47.2	52.1
52EF	46	40	86	87+/-19	286+/-19	372+/-19	34.3	35.9
54AA2	97	46	143	77+/-20	268+/-20	411+/-20	36.9	38.0
70CD	78	30	108	50+/- 9	249+/- 9	358+/- 9	29.9	32.6
73AA2	52	43	95	0	284+/- 0	379+/- 0	37.1	39.5
80BC	88	36	124	0	333+/- 0	457+/- 0	38.2	39.8
92AA2	94	73	167	0	251+/- 0	418+/- 0	36.8	37.8
96AA2	55	63	118	5+/- 3	237+/- 3	355+/- 3	36.1	39.0
350-YEAR STAND								
56AB	87	36	123	-	96+/-	220+/-0	14.2	12.9
133AB	46	56	102	0	154+/-0	257+/-0	26.6	28.5
134AB	106	57	163	9+/-5	166+/-5	330+/-5	28.2	28.9
138AB	109	39	148	-	71+/-	220+/-	16.1	16.5
141AB	15	19	34	-	107+/-	146+/-	16.6	20.0
58A	74	49	123	-	103+/-	226+/-	21.3	22.7
137A	65	39	104	-	89+/-	194+/-	19.4	22.0
139A	95	36	131	-	125+/-	257+/-	22.3	22.9
170-YEAR STAND								
200EF	23	52	75	-	68+/-	143+/-	12.5	13.0
201AB	23	25	48	-	66+/-	114+/-	11.7	13.1

*These figures give .95 confidence limits.

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