STRUCTURE AND DYNAMICS OF ALLUVIAL FOREST
IN THE POHANGINA VALLEY

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ABSTRACT

Species' population structures and replacement patterns are quantitatively described from intensive sampling of forest on alluvial surfaces of three ages. Observations and evidence from a range of other sites are incorporated to assist in tracing the development of forest on alluvial surfaces of the study area , and in examining factors influencing this development .
Cockayne's postulate that :

> " ... the most important principle underlying succession in New Zealand forests is the relation of the different species to light ."

is investigated with respect to the study area .

Relatively even-aged totara-dominant dense podocarp stands have developed on floodplain surfaces made available by progressive channel down-cutting and lateral migrations. On older surfaces these first generation stands are replaced by forests dominated principally by the angiosperms tawa , titoki and mahoe.

On a terrace surface c.2,000 - 3,000 years old , forest variation appears attributable to dynamic processes as well as differences in site drainage . On mesic sites tall tawa-dominant forest prevails , although recent windthrows have produced low groves of mahoe and other small angiosperms , and also apparently stimulated some podocarp regeneration . On xeric terrace sites , titoki and rewarewa dominate the canopy .

Low densities of podocarps on the mesic terrace sites attest to very sparse regeneration after the demise of the dense first generation stands . The discontinuous size class distributions of podocarp species on these sites appear at least partially attributable to sporadic regeneration following major windthrows .

Podocarp densities are higher on the terrace xeric sites , regeneration of matai and totara apparently being favoured by the lower vegetation density and higher understorey light levels . On these sites matai shows an all-sized stable population structure , and a cyclic discontinuous replacement of totara seems possible.

Seedling growth experiments showed both totara and kahikatea to be less shade-tolerant than two large angiosperm species (titoki and pukatea , respectively) typically seen to be replacing them in old growth forests on their respective sites. Except on the terrace xeric sites , light levels measured in forest understoreys were mainly below the compensation point experimentally estimated for totara seedlings . These findings confirm that regeneration of kahikatea and especially totara is likely to be very infrequent in old growth forest on these sites. Cockayne's postulate does not completely explain species establishment patterns within these forests . However , the findings of this study lend support to his interpretation of " light relations " as the primary influence on successional trends , and suggest that regeneration of kahikatea and especially totara is likely to be largely disturbance-dependant .

ACKNOWLEDGEMENTS

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CHAPTER ONE : INTRODUCTION

The history of New Zealand vegetation ecology has seen much dispute over the interpretation of the indigenous forests,a major difficulty being in understanding the seral status and dynamics of the large long-lived conifers of genera such as *Dacrydium*, *Libocedrus* and *Podocarpus* . Many workers have described an apparent scarcity of coniferous regeneration in high forest situations where these species are present as canopy trees or emergents ; e.g. Cockayne (1928) , Holloway (1954b) , Cameron (1954) , Nicholls (1956) , Robbins (1962) ,P.Wardle 1963b). Opinions have differed widely in attempts to explain these widespread instances of non-"accordance" (Braun 1950) , their causes and their implications.

Cockayne (1928) interpreted the podocarps and other conifers as light-demanding pioneers generally unable to regenerate in their own shade , and hence destined to be replaced by a climax forest of more shade-tolerant "dicotylous" or "broad-leaved" (angiosperm) species. This interpretation appeared consistent with the abundant establishment of various conifer species often seen in early secondary vegetation after destruction of the original forest by fire ; e.g. Cameron (1960b) , Pook (1978).

Alternative theories of mosaic or cyclical regeneration have been proposed , involving alternation of conifer and angiosperm phases ; e.g. Cameron (1954). Pronounced regeneration cycles are evident in poorly - drained Westland terrace forests (Poole, 1937) and in Tihoi forest in the Central North Island (Herbert, 1978 ; A. Katz F.R.I. ,unpub.report). However there is a lack of published evidence for more widespread occurrence of such cycles.

Robbins (1962) later extended Cockayne's linear successional replacement concept onto an evolutionary scale. He suggested that the "ancient" coniferous element of New

Zealand's vegetation was in the process of extinction , as a result of gradual displacement by angiosperm species better adapted to the modern environment .

Holloway (1954b , 1964) also rejected orthodox successional interpretations of the apparent instabilaties , instead suggesting that forest dynamics have been profoundly influenced by climatic change within the last millenium . He claimed that conifer regeneration failure was one of several broad vegetation patterns and trends best explained by a postulated change to a cooler , and probably generally drier climate beginning c.1200 A.D. Holloway's much-debated theory arose primarily from observations of the Western Southland forests , but gained almost immediate support from several other New Zealand workers who found that it offered satisfying explanations for forest patterns and "anomalies" in other regions , e.g. McKelvey (1953), Nicholls (1956), P.Wardle (1963b)

Geophysical evidence suggests mean temperature fluctuations of 0.5 to 1.0 degrees C in New Zealand within the last millenium , but there is little agreement on the ecological significance of such small changes (Fleming 1963 ; Molloy 1969 ; Burrows and Greenland 1979 ; P.Wardle 1979) . The climatic change school of thought has been increasingly criticised by a number of recent authors who have stressed the role of natural and anthropogenic disturbances in shaping New Zealand's vegetation within the last millenium and questioned the need to invoke climatic change as a major influence , e.g. Cumberland (1962) , Molloy (1969) , Veblen and Stewart (1982) , Norton (1983).

A variety of factors have probably contributed to the difficulties experienced in interpreting forest dynamics in New Zealand. The lack of historical records from the centuries of Polynesian settlement means that there is still much uncertainty about the role of anthropogenic disturbances in influencing New Zealand's present vegetation patterns. While there is clear evidence of extensive fires in several districts during this period (e.g. Molloy et al.,1963 ; Esler, 1963) at least two prominent authors have suggested that the impact of prehistoric man on the vegetation , particularly of the Central North Island, is possibly still being underestimated (McKelvey,1973 , p.23; P.Wardle 1973, p. 163.

There is also a lack of reliable accounts of the vegetation from the early days of European settlement, and much of the lowlands was cleared before the forests came under the scrutiny of modern science.

The generally slow development rates of New Zealand forest systems, and the great ages attained by many of the coniferous species, add an awkward dimension to the study of forest dynamics ; this is accentuated by the short time span of New Zealand's recorded history. The problems of time scale are certainly not peculiar to New Zealand (cf Horn 1975); Franklin and Hemstrom 1981), but I suggest that they are acutely compounded in this country.

Nevertheless, it could be argued that our poor understanding is partially attributable to a lack of experimental investigation, which has allowed the accumulation of numerous untested assumptions and hypotheses , and meant that theories of forest dynamics have developed in the absence of adequate autecological knowledge of indigenous species. Several authors have recently provided examples of how deficiencies in autecological knowledge currently impose major limitations on progress in a variety of research avenues , and appear to be immediate obstacles to the resolution of problems concerning conifer regeneration (Burrows and Greenland 1979, p.323; Dunwiddie 1979, p.258; P.Wardle 1979, p.139).

Assessments of the ecophysiology and critical establishment factors for various species have been made almost entirely from field situations , where spatial and temporal comparisons confound the effects of a multitude of variables. The New Zealand literature reveals that conclusions drawn largely from subjective field observations have led to some widely divergent claims from different authors , as to the ecological characteristics of various species. For example, Cockayne (1928) believed matai (Podocarpus spicatus)[1] to be "the least light-demanding" of the podocarps. However , Cameron (1960a) and McKelvey (1963) both grouped matai with true totara (P. totara) as the most light-demanding of the podocarps and rated rimu (Dacrydium cupressinum) and miro (P. ferrugineus) as the most "shade-bearing" of the group.

Hinds and Reid (1957) asserted that matai and (true) totara "... must be considered as belonging to the warmest New Zealand climates ... i.e. warm temperate to sub-tropical." But in an attempt to interpret forest patterns in the Tauranga stream basin of Whirinaki State Forest, A.Katz (Forest Research Institute ,unpublished report) operates on a premise that matai and totara are the most "cold-tolerant" of the large lowland podocarp species.

In discussing differential species' responses to a postulated climatic change, Holloway (1954b) referred to matai and totara as the "more mesophytic podocarps" ,compared with rimu. This description is certainly not consistent with the widespread occurrence of the two forenamed species on free-draining and drought-prone sites where rimu is rare or absent.

Besides demonstrating a lack of agreement as to various species' ecological characteristics, examples such as these also show the imprecise terminology and lack of quantification that has prevailed , and has only added to the confusion. Terms such as "shade tolerance" , "cold tolerance", "mesophytic" - used, as they generally have been , without accompanying definition of quantification,are open to a wide

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1. Unless otherwise indicated, nomenclature follows Allan (1961), Edgar (1973) and Moore and Edgar (1970). Appendix 1 provides scientific names for those species referred to by common names after their first appearance in the text.

range of interpretation.

The theorising of earlier decades has been followed by little in the way of experimental studies or tests. Cockayne (1928) postulated that "the most important principle underlying succession in New Zealand forests is the relation of the different species to light." And, as observed by Pook (1979) , "This hypothesis has seldom been critically examined since it was first enunciated."

Cockayne (1928) considered that poor self-replacement in many stands of species such as rimu, totara and kauri (Agathis australis) was due to the conifer seedlings being "strongly light-demanding" and unable to establish readily in the shade of mature forest. He considered that on most sites, conifer stands represented seral stages leading to a climax forest of "shade-tolerating" and "shade-demanding" angiosperm species.

Papers by Bieleski (1959) and Pook (1979) appear to be the only published New Zealand studies that have examined Cockayne's interpretation by means of experimental investigation of factors affecting seedling establishment and growth. Bieleski conducted a thorough investigation into factors affecting growth and distribution of kauri, with a thoughtful integration of field work and seedling growth experiments. His results suggested that kauri seedlings were in fact "decidedly shade-tolerant" , and Bieleski concluded that Cockayne's "light relation" hypothesis did not explain the dynamics of kauri forests. However, Bieleski's experiments did not include any other ecologically associated species for comparison with kauri's performance. It seems fair to suggest that such an inclusion would have greatly enhanced the value and applicability of the study, and might well have led its author to a rather different interpretation of his results obtained for kauri.

Pook's work was less comprehensive in his analysis of site factors , concentrated solely on the effects of light intensity , but this study included the comparative dimension overlooked by Bieleski. Pook (1979) compared seedling growth responses of kauri , tanekaha (Phyllocladus trichomanoides) and two commonly associated small angiosperms , under four different light levels. These experiments confirmed the generally slow growth rates of indigenous conifers in comparison with those of many " shrub hardwood " species , and on the basis of his results , Pook was less inclined to challenge Cockayne's interpretation . He suggested " that the very slow growth rates of the softwoods under shaded conditions , compared to many hardwoods , partly explain the general failure of softwood regeneration in mature primary forest and their patterns of establishment in secondary scrub and forest communities . "

The studies by Bieleski and Pook were concentrated on species of restricted northerly distributions. Despite the fact that experimental studies of comparative growth responses to controlled environmental variables are of proven value in plant ecological research (Grime,1965), there has been no similar published work on principal species of the more widespread podocarp broadleaf lowland forest types. Some understanding of causal factors operative in the mechanisms of vegetation dynamics is clearly necessary for successful management of complex forest ecosystems (Spurr and Barnes , 1973,p.10). So in view of the attempts in recent decades at so-called sustained yield management of the indigenous conifer-angiosperm forests , the lack of experimental research is surprising.

Therefore it seems fair to suggest that Cockayne's light relation hypothesis begs further investigation , by the integration of appropriate experimental work with field studies of vegetation dynamics. Pook (1979) concluded that : " There is little difficulty in accepting that other factors besides shade influence the regeneration of forest tree species . However, until a good deal more information is available on the growth responses and behaviour of many more forest components in respect of this attenuation of the primary energy source , knowledge of the effects of other factors could be greatly limited in its application . The assessment of responses of many forest components , both dominant and subordinate , to shade , would appear to be fundamental to understanding the dynamics of most indigenous forest communities and for resolving some of the problems of failure in natural maintenance of some species ."

It is to Pook's rationale that this thesis particularly relates.

CHAPTER TWO : AIMS.

The aims of this study were twofold :

(1) To describe structure and dynamics of lowland alluvial forest in the Pohangina Valley.

(2) To evaluate Cockayne's "light relation" successional mechanism hypothesis (see Chapter One p. 5)with respect to these forests.

It was intended to obtain quantitative descriptions of the vegetation on a series of different-aged alluvial surfaces. By examination of species' population structures and the successional patterns evident on each of these surfaces (i.e.the recent historical development of each sampled forest), it was hoped to (a) demonstrate the establishment/regeneration modes of the principal species; (b) trace a sequence of forest development on alluvial surfaces of the lowland Pohangina Velley.

Pursuit of the second aim involved comparison of (a) various species' performance under a range of light intensities in seedling growth experiments, with (b) species recruitment patterns observed in measurement field light environments. From this integration of field and glasshouse work it was hoped to make an assessment of the influence of light relations on establishment behaviour of some principal lowland alluvial forest species, and hence on succession in these forests. For example : Can the scarcity of totara regeneration in both flood plain and terrace forests be attributed to inability of totara seedlings to grow at the light levels currently prevailing in the understoreys of these forests?

While undertaken primarily as an investigation of causation for observed species replacement patterns, the experiments might possibly also have some predictive value. For example : if totara seedlings were found to be incapable of growth at light intensities typical of forest understoreys, then it would seem fair to suggest that totara regeneration is not to be expected (or at least rarely so) in old growth situations on sites such as these.

The choice of seedlings, as opposed to later growth stages, for the experimental subject was primarily for reasons of practicality. However this choice is consistent with a general belief among plant ecologists that the abundance and distribution of mature individuals is strongly dependant upon the factors affecting the seedling stage (Sagar and Harper, 1961). Studies of plant population dynamics suggest that for most species, the seedling shortly after germination is the most susceptible phase in the ontogeny of the individual (Cook, 1979).

Overall, it was hoped to gain some understanding of alluvial forest dynamics and of the factors affecting establishment and regeneration of some principal species. This study was motivated by the general issues discussed in the introduction. The study area was seen as offering specific examples fairly typical of some general questions posed by many New Zealand lowland forests.

CHAPTER THREE : THE STUDY AREA.

3.1 THE PHYSICAL ENVIRONMENT

The Pohangina River drains the south-west flanks of the Ruahine Range, and flows in a generally south-west direction to join the Manawatu River at Ashhurst (Fig.1) The river's length is 62 km and the total catchment area is about 536 km^2 (Brougham and O'Connor, 1982) This study is concerned primarily with the lower reaches, i.e. below the termination of the lower gorge at the Konewa Stream junction (NZMS 1, N 144/376 679) Below the gorge the river occupies a flood plain generally 500-700 metres in width, but occasionally restricted to less than 200 metres (Brougham and O'Connor,1982). At Totara Reserve, which contains the main study sites, the river level is at an elevation of about 150 metres a.s.l.

The terraces of the Pohangina Valley were mapped by Challands (1976), who identified three major terrace levels. The lowest major terrace is believed to be co-eval with the Ashhurst Terrace of the Manawatu Valley (age estimated at 18,000 to 21,000 years; Fair 1968) and with the Ohakea Terrace of the Rangitikei Valley (dated at 12,000 to 25,000 B.P.; Te Punga 1953, Cowie and Wellman 1962). However, several "minor terraces" (Challands,1976) are present below the Ashhurst Terrace along most of the lower reaches of the Pohangina River.

* The soils of the "river flats" (i.e. flood plain and minor terraces) are formed from recent sediments,derived from greywacke,sandstones, and siltstones,brought down by the river and deposited during flooding (Rijkse,1977). These recent soils, classified as Rangitikei,Manawatu and Kairanga Series, have generally high nutrient status as they are only weakly weathered. The Wakarara and Ruahine greywackes forming most of the Ruahine Range and closely jointed and in many places also sheared by faults, therefore eroding easily and supplying the rivers with an abundance of debris (Rijkse, 1977).

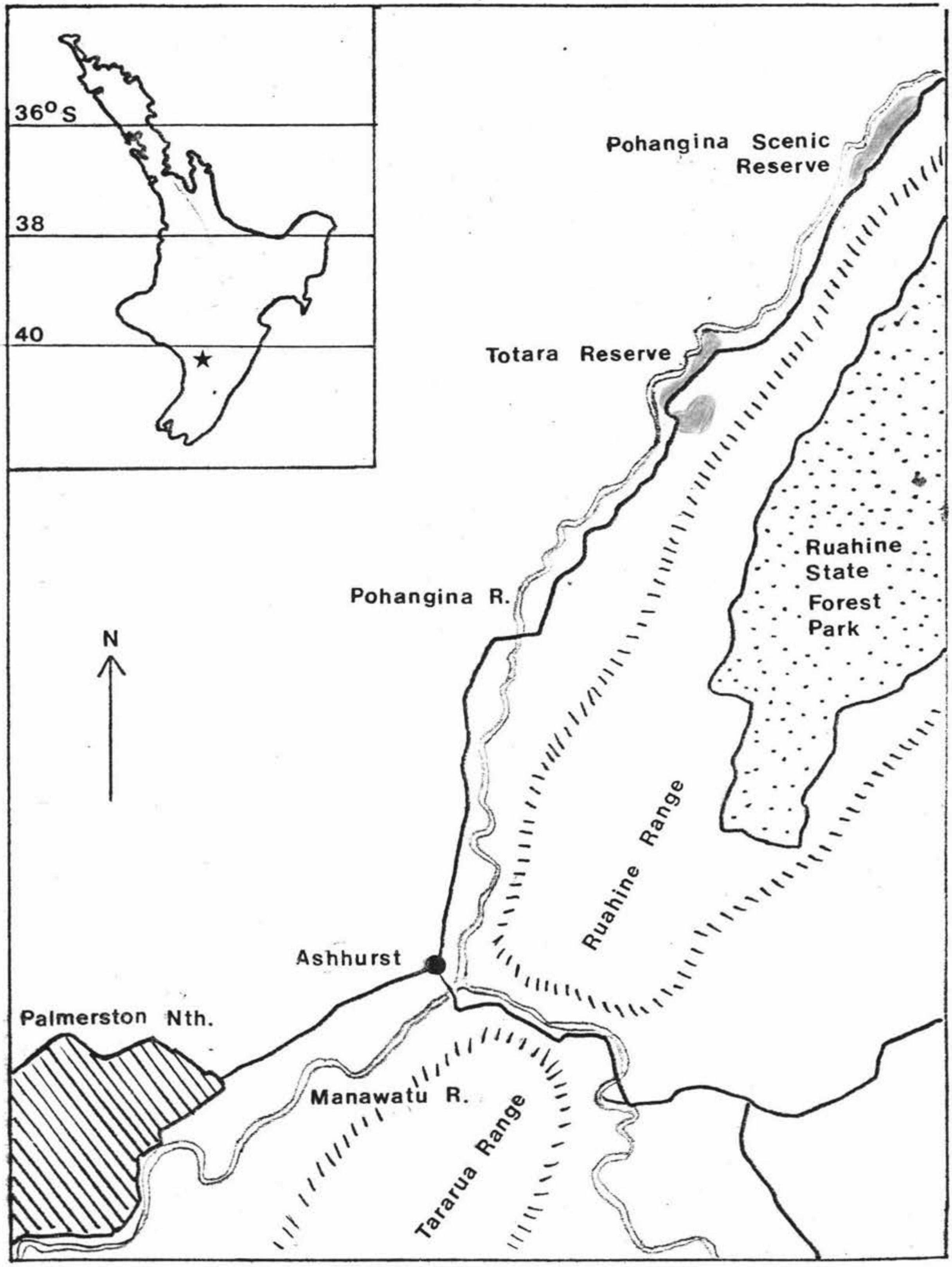
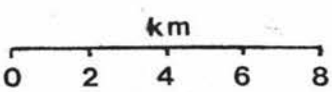


FIG. 1 Location of Pohangina Valley, North Island, N.Z.



3.2 CLIMATE

The climate of the Pohangina Valley is chacterised by warm summers and cool winters (Rijkse, 1977). Because the Pohangina Valley has no Meteorological Stations collecting comprehensive weather records, detailed and accurate local climatic data, other than rainfall records, are unavailable.

The rainfall pattern of the valley is largely controlled by the orographic effect of the Ruahine Range, which causes precipitation of moisture carried by westerly crosswinds, Annual rainfall averages 1145 mm at Totara Reserve (New Zealand Meteorological Service, 1973); but rainfall figures increase further up the valley and closer to the ranges (e.g. c.1300 mm at the Pohangina Scenic Reserve), rising to about 4000 mm in the headwaters (Brougham and O'Connor, 1982). The annual rainfall variability [1] at Totara Reserve is 174 mm (N.Z.M.S.data; A.W. Dyke pers.comm.) indicating a low drought risk.

Over the whole of the Manawatu area winds are predominantly from the west and north-west e.g. the most frequent wind directions recorded at Ohakea Airfield are N.W. (37%) and W (18%). In the Pohangina Valley, channelling by the topography produces a local dominance from the north-west and south-west directions (Wright, 1968). Gales are "relatively frequent", (Rijkse, 1977).

3.3 THE PRIMITIVE VEGETATION.

Before European settlement began last century, most of what is now Pohangina County was apparently clad in forest. Most of the lowland area was cleared between 1880 and 1920 and a reconstruction of the primitive vegetation necessarily involves some speculation. Nevertheless, the remnants

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[1] The standard deviation of annual totals.

of Totara Reserve, the Pohangina Scenic Reserve and a few smaller relicts, together with information from old maps, are sufficient to enable a reasonable appreciation of the vegetation pattern at the time of European settlement.

J.T.Stewart's map, produced from his 1859 survey along the rivers (Stewart, 1859) provides probably the earliest known useful vegetational information for the district. This is in the form of brief comments written directly on the map at many localities. "Totara" and "totara timber" are marked abundantly along the banks of the Manawatu, Oroua and Pohangina Rivers, suggesting that as in many other lowland districts throughout the country, this species was a characteristic and probably dominant component of flood plain forests. "Kahikatea" and "tawa" are also commonly marked close to the rivers.

Further away from the rivers, "rimu", (northern) "rata", "kahikatea", "matai", "tawa" and sometimes "totara" were recorded on Stewart's map, suggesting these species as conspicuous elements of the forests on the terraces. Labels of "tawhai" (= *Nothofagus* spp.) are abundant along the middle and upper reaches of the Pohangina River. Several pockets of black beech (*Nothofagus solandri* var. *solandri*) still remain in the valley, in Totara Reserve and as unfenced remnants on farmland. These are mainly on the crests of ridges and spurs (Greenwood, 1949); but two isolated black beech among tawa (*Beilschmiedia tawa*) dominant river flat forest in Totara Reserve attest to more recent riparian dispersal of this species.

The lack of references by Stewart to titoki (*Alectryon excelsus*), mahoe (*Melicytus ramiflorus*) and rewarewa (*Knightia excelsa*) contrasts markedly with the virtually ubiquitous occurrence of these species as principal canopy components in the extant remnants. Species composition has undoubtedly been modified, to varying degrees in different remnants; e.g. extraction of podocarps which appears to have often induced development of low mahoe-dominant groves. Local concentrations of rewarewa in the Pohangina Scenic Reserve are at least partially attributable to several fires within historic times. But even in patently virgin areas of Totara Reserve, these three species are usually among the principal components of an angiosperm-dominated canopy on the terraces, where the podocarps generally form a scattered emergent overstorey.

It is quite apparent from the nature of Stewart's notes that his interest in the vegetation was primarily in recording potential timber resources, and so these notes cannot be regarded as reliable indicators of species composition. Smaller (and hence less conspicuous) tree species, and those not sought for timber, are rarely specifically named anywhere on the map; but Stewart did write labels such as "mostly inferior timber" in some places. Some of the tree names marked on Stewart's map probably represent individual trees that were used for bearing trees or markers of surveyed corners. Such records do not constitute a random sample of the forest, as the surveyor would tend to choose trees of large size and (for marker trees) those having a durable wood (Spurr and Barnes, 1973). Therefore, lack of reference, particularly to mahoe and titoki, rather than establishing that these species were not among the principal canopy components of the primitive vegetation, probably results from what is, in effect, a selective, unbalanced description of mixed conifer-angiosperm forests.

Further information is furnished by a later s ale plan (Lowe, 1889). This plan has copious vegetation labels on the terraces and hill country of the Pohangina Valley. Rimu, rata, "black birch", tawa and hinau are the most frequently named species; and "tawhero" (=kamahi, <u>Weinmannia racemosa</u>) titoki, rewarewa and miro are also listed.

Totara Reserve must serve as the principal record of the primitive vegetation of the Pohangina Valley, with due allowance made for the various modifying influences outlined in the next three sections of this chapter. The reserve contains only about 300 hectares of forest, some of which is much modified. But as illustrated by Greenwood's (1949) description, this remnant is of great value as it includes considerable diversity of forest types on a variety of sites and soils.

3.4 IMPACT OF THE MAORI CULTURE.

J.T.Stewart's 1859 survey map of the Ahautaranga Block recorded no occupied Maori settlements in the Pohangina Valley (Stewart, 1859).Stewart recorded only four abandoned village sites in the valley, although an earlier visit by William Colenso in 1848 had noted a small village of nine to eleven people,which "... comprised the whole population on the banks of that river" (Bagnall and Petersen, 1948).

Although the inhabitants of the abandoned villages were probably wiped out by tribes invading from other districts, it is quite possible that these villages were never occupied on a permanent basis (Wright, 1968). Buick (1903) notes, for instance, several villages in the upper Manawatu which were used as seasonal homes. They were probably occupied only in summer to snare birds and gather berries. Mr. F.Wagstaff, who came to the Pohangina Valley as a child in 1895, recalled parties of Rangitane Maoris travelling from Palmerston North and Rangiotu to visit the valley (I.Mathieson, pers.comm.). They came to collect edible fungi (for sale) and to shoot pigeons,but never stayed more than a few days. A total of five stone adze finds are recorded from four localities within the valley.(I.Mathieson,pers.comm.) The antiquity of these adzes is not known,and these finds alone cannot be regarded as convincing evidence of more intensive Maori activity in earlier times.

The Maori made significant use of the Pohangina and Oroua Valleys for purposes of communication, if not for settlement (Wright,1968). Both these river systems were used for water transport, being linked with the Manawatu River,the main outlet to the coast. Several saddles across the Southern Ruahine Range were apparently used as overland routes to and from Hawkes Bay and the Wairarapa (Stewart 1859 ; Elder 1965).

From the evidence of very limited or sporadic use of the Pohangina Valley, it seems probable that the Maori had little direct influence on the vegetation - at least post - C. 1800. This contrasts markedly with the accounts of much vegetation destruction or modification recorded in districts supporting large Maori populations in the 19th. century (e.g. Cameron, 1964).

However a small dense stand of pole-sized totara in the Pohangina Scenic Reserve (NZMS 1, 144/387 696 quite possibly indicates a site of localised anthropogenic vegetation disturbance some time last century. This stand, with associated rewarewa and large kanuka (Leptospermum ericoides), probably corresponds with the site of a clearing in the forest noted by European settlers in that area late last century (H.Rutherford, J.Enright; pers.comm.). This was probably a clearing of Maori origin, perhaps created for cultivation of fern root. The site is about three kilometres from the site of an abandoned village ("Te Haha") noted by Stewart in 1859.

3.5 IMPACT OF THE EUROPEAN CULTURE.

After Stewart's survey in 1859, the Ahautaranga Block was purchased from Maoris in 1864, but the major phase of European settlement in the Pohangina Valley did not begin until the 1880's. The dramatic transformation of the landscape by the European culture has been described by Wright (1968). The period of most rapid forest clearance was from 1896 to 1906 during which 21.9% of the total area of Pohangina County was cleared. Accounts of forest clearance methods employed by the settlers were researched and collated by Wright (1968)

At least five sawmills were operating in Pohangina County in 1905 (N.Z.. Parliament.H.of R., 1905), and probably a greater number for a brief period after this date. But during the main phase of settlement timber supply greatly exceeded demand, and great wastage is apparent from all accounts (Wright, 1968). Most of the angiosperm tree species were not in demand for timber, and much podocarp timber was also destroyed by primitive "cut and burn" clearance methods.

But fortunately a little of the lowland forest was spared. In 1886, Section 48 , Block VII ("approximately 1,000 acres") of the Pohangina Survey District, on the east bank of the river, was reserved as State Forest (N.Z.Gov't.Gazette, 1886). In 1897 an adjoining area of 96 acres (Section 62, Block VII) was gazetted as "permanently reserved for the preservation of timber and river conservation" (N.Z.Gov't.Gazette, 1987).

Around 1900 a fire damaged forest on about 250 acres of this reserved area (part of Section 48). A Department of Lands and Survey notice and map dated February 14th.1901 (L & S.File 8/5/288, Wgton.),shows that timber on the damaged areas was to be sold at auction on March 26th.of that year. Part of Section 48 (recorded as 317 acres) was sold in 1906 (N.Z.. Laws,Statutes, etc.,1946) and subsequently converted to farmland; sale included most of the burnt-over area. However,it appears that this sale also included over 100 acres that were still in virgin forest at that time.

The remainder of the two reserved sections came to be popularly known as "Totara Reserve". They have remained to the present day almost entirely in forest, but not without further degradations.

In 1918, the Commissioner of Crown Lands granted permission for the Pohangina County Council to take "dead timber" from the reserves of the valley.[2] This licence applied to both Totara Reserve and the Pohangina Scenic Reserve, a separate section of mostly cutover forest further up the valley.

In 1922, most of Totara Reserve (Part Section 48) came under the administration of the newly-created New Zealand Forest Service, and was designated as State Forest No.89. In February 1936 a severe gale badly damaged some parts of the forest. Worst affected was a kahikatea (Podocarpus dacrydioides) - dominant dense podocarp stand on the flats at the southern end of the reserve, about 25 acres of which were "extensively smashed" (Greenwood, 1949). In the wake of the gale, 204 fallen trees (85% kahikatea) were recovered and milled. The Forest Service planted several thousand kahikatea seedlings among the shattered stand, but most of these appear to have perished. In addition to the damage inflicted by the storm and timber extraction, this area has suffered considerably from cattle browsing and trampling, and from subsequent invasion of exotic weeds and grasses.

Mr.K.B.Caldwell, now of Ashhurst, worked at a sawmill near Totara Reserve in the 1930's. He recalled (pers.comm.) that the mill owners obtained permission from the local Forest Service senior ranger to remove "dead standing" trees from any accessible part of the reserve. Apparently this term ("dead standing") was given a rather liberal interpretation, by both the ranger and the mill owners, and totara with deteriorating crowns were occasionally felled.

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[2] Dept.of Lands and Survey files for Section 61, Block VII Pohangina Survey District (correspondence).

In 1946 the two sections of Totara Reserve were constituted as the PohanginaValley Domain (N.Z..Laws,statutes, etc., 1946). The total area of about 740 acres (c.300 ha) has since then been administered by the Palmerston North City Council.

3.6 IMPACT OF THE INTRODUCED FLORA AND FAUNA.

It is probable that a century or more of interaction with new floral and faunal arrivals has significantly affected the dynamics of the indigenous vegetation, especially in insular remnant communities. For the present study, some consideration must be given to the effects of :

(a) the selective depredations of introduced mammals.

(b) the invasion of certain introduced plants into forest margins and seral vegetation communities.

It is also possible that earlier faunal changes wrought by the impact of the Polynesian culture (e.g. moa extinctions) have had far-reaching effects on the dynamics of New Zealand forests (Fleming 1977; Greenwood and Atkinson 1977; P.Wardle 1979).

Brush-tailed possums (*Trichosurus vulpecula*) were liberated at a number of localities in the Pohangina Valley and adjacent areas. The earliest of the recorded introductions to the valley was in 1983 (Pracy, 1962), but information about the liberation and spread of the species is almost certainly confused by private liberations (Elder ,1965). Although control measures are carried out by the caretaker of Totara Reserve, faecal pellets are common in most parts throughout. Heavy possum browse has been noted on five-finger (*Pseudopanax arboreus*), pate (*Schefflera digitata*), mahoe and titoki. Heavy browsing of hangehange (*Geniostoma ligustrifolium*) is probably also partially attributable to possums. Many of the northern rata (*Metrosideros robusta*) trees in the reserve are now either dead or else have very little foliage ; the decline of this species throughout forest remnants of the Manawatu region and in the Tararua and Ruahine Ranges has been largely attributed to possum browsing (Elder 1965 ; Elser 1978). In contrast, the

Pohangina Scenic Reserve still retains a fair number of rata in healthier condition.

As the forests of Totara Reserve have probably been subjected to at least 80 years of possum browsing, this agent has possibly contributed to the present scarcity therein of certain susceptible species, notably five-finger, kamahi and kotukutuku (Fuchsia excorticata). However, kamahi does not appear to be currently suffering severe browse, either within the reserve or in scrub-filled gullies on surrounding farmland. Its present restricted distribution probably reflects competition from species more characteristic of lowland alluvial sites, and it probably never was a major component of either the flood plain or the terrace forests.

In 1922, red deer (Cervus elephus) were liberated at Delaware in the foothills flanking the valley, about 12 km north-east of Totara Reserve. By the early 1940's, a "heavy concentration" of deer was reported in the upper Pohangina Valley, but few were recorded further south at that time (Elder,1965). K.B.Caldwell, a life-long resident of the valley, considered (pers.comm.) that it was not until the mid-1950's that deer first reached Totara Reserve, which is isolated from Ruahine State Forest Park by about three kilometres of farmland. This date corresponds roughly with the period when deer numbers were thought to have peaked in the southern Ruahines (Elder, 1965).

Although no quantitative animal surveys were attempted in this study, the distributions of deer sign suggested different utilisation intensities for various sites. Deer sign was only rarely encountered in the flood plain totara forests. Pellets were occasionally found on the minor terraces of the "Old Coach Road" block of the reserve (see Fig.2,Fig.3) and browsing of hangehange often noticed in these forests (especially along stream banks) is probably attributable to deer. An abundance of deer and possum sign was found on steep north-west facing slopes (the Ashhurst terrace scarp) in the southern ("Fern Walk") block of the reserve, suggesting this to be the area most heavily used by both these animals. The only deer to be heard in over 70 visits to the reserve (spanning 19 months of field work) was encountered here on 11.7.82.

There is no evidence of pigs or goats in Totara Reserve, but at earlier times stock have been "plentiful" in the totara and kahikatea stands on the flats (Greenwood, 1949). K.B. Caldwell (pers.comm.) recalled that prior to 1924, sheep were grazed on the river flats fronting the then-unfenced forest. He also claimed that cattle were wintered in the (totara) forest on the flats c.1924-35. The reserve is now fenced on all boundaries accessible to stock; although some of the fences are in poor order, only occasionally are sheep now encountered within the reserve.

Black rats (Rattus rattus), being virtually ubiquitous throughout New Zealand's forests (Taylor, 1978) are undoubtedly present in Totara Reserve. Like their predecessor Rattus exulans , they are likely to be a significant influence on long-term trends in plant species composition and recruitment (Beveridge 1964; Campbell 1978). However, no observations on rats or their effects were made during this study, and the influences of rats on vegetation are complex and not easily determined.

Cockayne (1900) asserted that modification of the indigenous forest by man and animals was a prerequisite to entry and establishment of alien plants, and later works have generally supported this view e.g. Thomson (1922), Skipworth (1982). However, it must be realised that few if any communities on the main islands of New Zealand now remain in a truly un-modified (i.e. pre-human) condition. Even the most remote and rugged areas are likely to have been subtly affected by man or his faunal introductions.

Most lowland forest remnants have undergone more conspicuous modifications, and the vulnerability of small remnants to invasion by a range of exotic plants is well documented e.g. Esler (1962, 1978); Healy (1973). Most of the exotic species present in the two main reserves of the Pohang-Valley are confined to the forest margins and clearings e.g. Acacia dealbata Link, Clematis vitalba Linn., Leycesteria formosa Wallr., Lonicera japonica Thunb., Rubus fruticosus agg., various grasses. A few bird-dispersed Prunus cerasifera up to two metres tall have been found inside the forest, but none was seen to flower or fruit in these shaded situations. Ivy (Hedera helix Linn.) has formed a dense vigorous colony at one site in the Pohangina Scenic Reserve. The advance of flowering ivy stems some distance into the reserve, and the local abundance of seedlings on the forest floor suggest that this species has some ability to invade relatively un-modified forest.

But the most potentially influential forest invader is almost certainly Wandering Willie (Tradescantia fluminensis Vell.) which can form a dense carpet up to 60 cm high on the forest floor, stifling all regeneration. The dense rank growth of Tradescantia found in many smaller forest remnants of the Manawatu region has not yet occurred in either Totara Reserve or the Pohangina Scenic Reserve. The small patches that have established in the flood plain forests of the former do not at this stage appear to be sufficiently dense or vigorous to prevent regeneration. The results of a study by Kelly (1977) lend support to Esler's view that growth of Tradescantia in Manawatu remnants has been promoted by the increased forest interior light levels resulting from human-related modifications and edge effects in these small relicts (Esler, 1962). It is likely that Tradescantia poses less of a threat to larger, less-modified forests such as Totara Reserve.

A number of exotic plant species are now vigorous colonisers of riverbeds, and their possible influences on forest development will be discussed briefly in Chapter Five (Section 5.1.1 (c)).

CHAPTER FOUR : METHODS.

4.1 FOREST STRUCTURE AND DYNAMICS.

4.1.1 Selection of study sites.

It was initially hoped to describe vegetation on a chronosequence of many surfaces. Observations suggested that Totara Reserve includes at least six distinct surface levels [1], the highest of these being the Ashhurst Terrace (Challands, 1976.). However, some of these levels are represented by very small areas within the reserve , and on some surfaces the vegetation has been greatly modified by logging, roading or tracks.

The middle ("Old Coach Road") block of Totara Reserve appeared to offer the best prospects of sizeable areas of largely un-modified forest on flood plain and "minor terrace" (sensu Challands, 1976) surfaces. So a preliminary survey of most of this block was made, using a series of parallel line transects to prepare a map of physiography and (qualitatively-described) broad vegetation types. (Fig.2) A rather complex pattern emerged , the main features being :

- Totara-dominent forest on the flats and levees of the flood plain. Rijkse (1977) indicates Rangitikei series soils for these surfaces.
- A complex of swamp and semi-swamp vegetation types associated with abandoned river channels and areas affected by seepage ; pukatea (*Laurelia novae-zelandiae*) being the most consistently present tree species.
- Forests dominated by a variety of angiosperms (especially tawa, mahoe and titoki, with emergent scattered podocarps and very occasional Northern rata on the Manawatu series soils (Rijkse,1977) of the higher flats.
- A gently-sloping fan deposited into the main river valley by the Mangatukura tributary stream; plus a

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[1] Not including sloping fan surfaces.

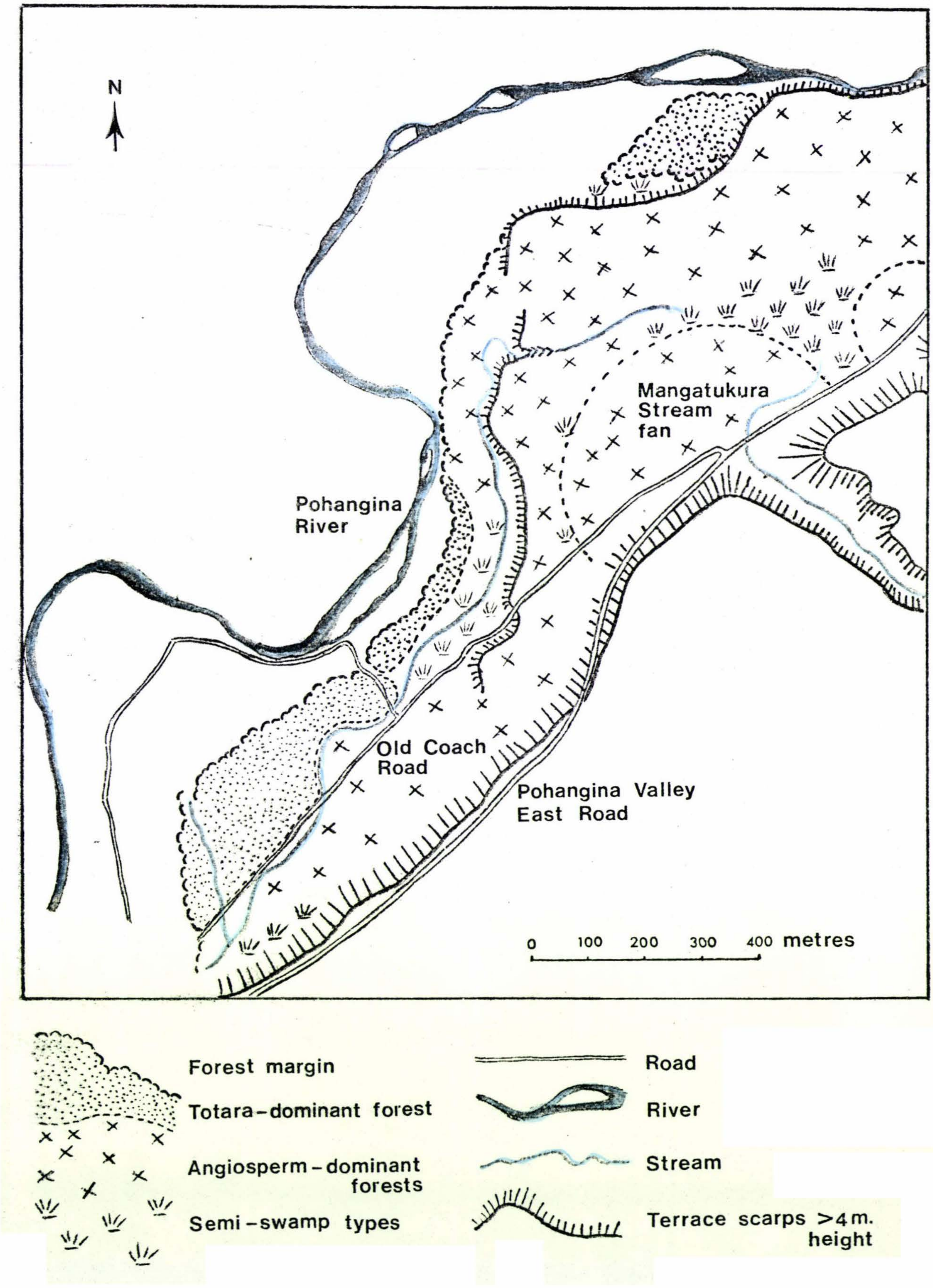


FIG. 2 OLD COACH ROAD BLOCK, TOTARA RESERVE

smaller steeper fan deposited by a periodically active run-off channel. An area of Utuwai series soil (alluvial - colluvial origin) mapped by Rijkse appears to correspond with the larger of these fans. Pukatea - kahikatea semi-swamp forest occurs between these two fans, and around their bases.

It was decided to restrict this study to one of forest development on well-drained recent alluvial surfaces only; consistency of soil character and origin being essential for time specific "side-by-side" successional comparisons (Mueller-Dombois and Ellenberg, 1974). Therefore this study was confined to soils of the Rangitikei and Manawatu series, the latter regarded as a maturational development of the former (J.Pollok, pers.comm.).

These constraints meant that only small portions of Totara Reserve were actually sampled, although observations were drawn from throughout the Manawatu-Pohangina and Rangitikei catchments. The areas selected for sampling were :

(i) Areas of totara-dominant forest on or slightly above the present flood plain.

(ii) A terrace surface about eight metres above the present river level, indicated as a "minor terrace" by Challands (1976). This terrace remnant, about 13 hectares in total area, appeared to be the largest continuous flat surface bearing largely un-modified forest on well-drained soils.

These selected areas are shown in Figures 3 and 4.

4.1.2 Vegetation Sampling.

(a) Flood Plain Forests.

The two totara dominant stands sampled are on slightly different levels designated "C" and "D" ; the latter surface being about 80 cm higher on average (see Fig. 5), and clearly bearing an older generation of forest with larger totaras. These stands form a continuous block of forest, the two separated only by a sluggish creek in an old river channel. The immediately adjacent surface "E" is about 1.5 m higher than "D", and bears the remnants of a generation of larger and presumably older totaras. However this forest appeared to have been considerably modified by road construction and some logging, and so was not sampled.

Most of the scrub and seral forest bordering the totara stands appeared to be of secondary origin, and was not sampled.

The younger stand on level "C" is about one hectare in area, and the older stand on "D" is about six hectares. These stands were sampled with a system of 400 m^2 plots sited regularly on a 100 meter square grid ; i.e. a 4% area sampling regime, with one plot in the younger "C" stand, and six plots in the older "D" stand. An elongated strip of totara forest nearby was not sampled because of edge effects. However, another totara stand (c. 1.5 ha in area), in the "Y.M.C.A." block of the Reserve further upstream, appeared to have species size distributions very similar to those of the "Old Coach Road" block younger (C) stand. Therefore , two 400 m^2 plots were sited in the "Y.M.C.A." stand, and the data from these pooled with that from the single plot in the "Old Coach Road" C stand. Ring counts on increment cores later confirmed the very similar ages of these two separate stands.

From these sample plots, a detailed analysis of stand structure was made, data-gathering procedure being similar to that described in New Zealand Forest Service (1978). A completed data sheet is included in Appendix II. All individuals rooted within the plot, and attaining or exceeding breast

Fig. 3 : Copy of aerial photograph of Totara Reserve (S.N. 2992, F/18).
Photo credit : Dept. of Lands and Survey, N.Z.
Outlines of the floodplain stands sampled are shown in blue, and the area of terrace forest is outlined in green. The survey line P - Q , from which the floodplain profile (Fig. 5) was prepared , is shown in red.
Scale c.1 : 9600

P
Q

height, were identified and recorded. For each individual, stem circumference at breast height, height tier, and if over-topped the canopy species directly overhead were recorded, A four-tier height classification was used :

T_0	Emergents	> 25 m
T_1	Canopy	> 15 m, and emergents 15-25 m
T_2	7 - 15 m	
T_3	1.4 - 7 m.	

It was attempted to assess the number of individual plants, so only the largest live stem was recorded on multi-stemmed trees. In some species (e.g. mahoe) the largest stem sometimes forked below breast height, and was accordingly measured below breast height (immediately below the fork). Strongly-buttressed stems were measured immediately above the root flanges , i.e. sometimes above breast height.

Within each plot, any dead standing trees, fallen logs or windthrow marks were also recorded.

16 1 m^2 understorey sub-plots were sited on a regular grid within each plot. Within each of these sub-plots, all seedlings of woody species were counted in three height classes : < 15 cm , 15 -50 cm , and 50 - 140 cm. First-year cotyledonary seedlings were recorded by presence alone. The proportions of ground covered by fern, grass and herb species were assessed on crude three-point scales for each sub-plot, and the species of canopy vegetation directly overhead was also recorded.

For each species, stems were tallied in the following diameter classes : $0 < x < 2.5$ cm d.b.h.

$2.5 \leqslant x < 10$ cm "

$10 \leqslant x < 20$ cm "

$20 \leqslant x < 30$ cm " etc., in 10 cm classes.

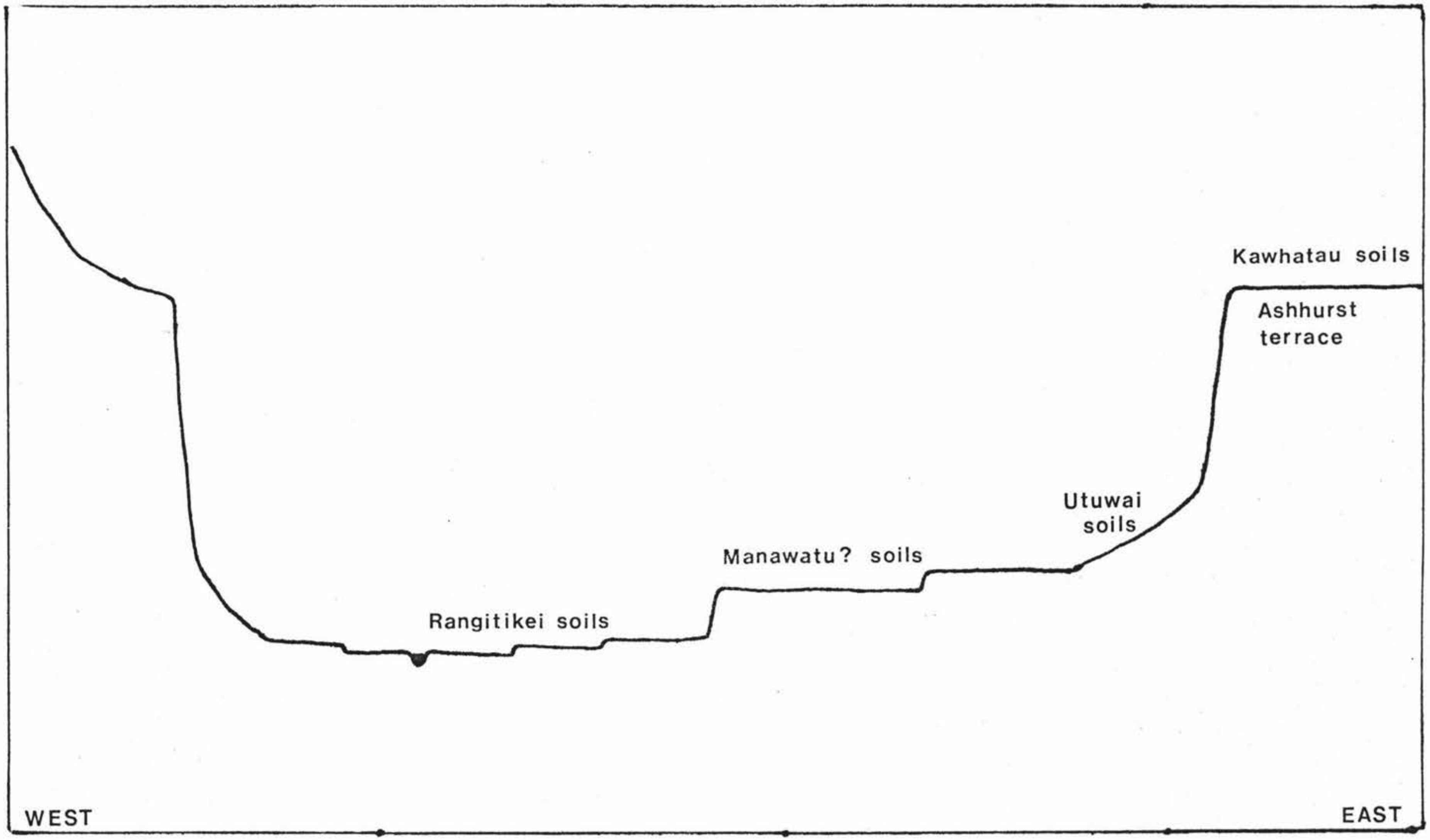


FIG 4 Idealised cross-section of Pohangina Valley at Totara Reserve

The diameter distributions obtained are a useful basis for interpretation of a stand's development history, and of the regeneration modes followed by the component species. (Hett and Loucks, 1976 ; Veblen , Schlegel and Escobar , 1980 ; Veblen and Stewart, 1980, 1982 ; Stewart and Veblen , 1982) .

Increment borings : More precise information was sought on the age structures of totara populations in these flood plain stands, and so increment borers were used to obtain ring counts. In view of the risk of damage to trees, and the technical difficulties associated with this procedure, only a small sample of totaras were bored, including a wide range of diameters. An estimated 37% of the totaras in the older stand (i.e. those > c. 71 cm d.b.h.) were too big to accurately age with the 40 cm borer used.

Several borings of each tree were usually required to obtain a core that was central enough to enable an accurate age estimate. A simple pith locator described by Applequist (1958) was used to estimate the number of rings missing from off-centre cores. However, for the majority of the trees bored (51.7% overall) all of the cores extracted were deemed too wayward to permit an accurate age estimate, and so data from these trees were not used. The proportion of "good" cores obtained was initially very low, but improved considerably with experience.

The cores were extracted at either 70 or 140 cm height; so three small totara saplings growing at the forest margin were cut and sectioned to obtain estimates of the respective ages required to reach these heights. (Appendix V).

The cores were carried and stored in a simple case made from two blocks of expanded polystyrene. After drying, the cores were glued into grooves chiselled in "Pinex" or similar softboard, and sanded to a smooth level surface. Annual rings were counted with the aid of a binocular dissecting microscope. Growth rings which showed a clear and abrupt transition to large diameter tracheids (earlywood) after the preceding latewood were interpreted as true annual rings.

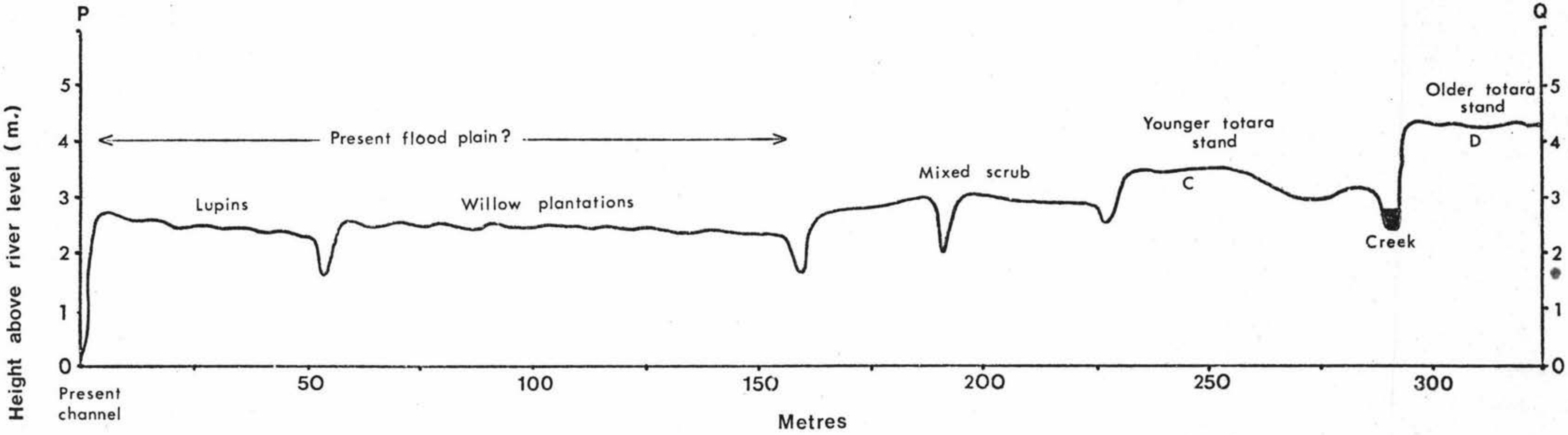
A small number of less distinct rings, which showed a gradual increase in tracheid diameter after a zone of suppressed growth , were interpreted as false rings representing intra-annual growth checks.

(b) Terrace Forest.

It was hoped that this terrace surface could be radio-carbon dated , but unfortunately no suitable dating material could be found. The elevation of about eight metres above the river level (c. 5.5 m above the present flood plain) suggests an age for this surface of at least c. 2,000 years (M.Shepherd, pers.comm.). This level is very much higher than any flood ever recorded by the Manawatu - Oroua Catchment Board, and so it is likely that soil and vegetation development on this terrace has not been influenced by major alluvial erosion or deposition for many hundreds (and possibly thousands) of years. It is noted that the mapping of "Manawatu" series soils for this surface (Rijkse, 1977) therefore appears inconsistent, since this series is defined as still subject to occasional inundation ("slowly accumulating"). Therefore, it is likely that the soils on this particular terrace surface would more appropriately be classified in the more mature "Karapoti" series. (H.Wilde , pers.comm.). Karapoti series soils have not been mapped in Pohangina County, but are found on the higher flats and levees of the Rangitikei River, above the reach of present day flooding (Cowie, Fitzgerald and Owers, 1967).

Inspection revealed considerable spatial variation in the structure and composition of the forest on this terrace. Rather than a mosaic of relatively even-sized units , there appeared to be several different vegetation types distributed in patches and belts of rather variable shape and size; the area of the individual units ranging from c.0.1 hectares to several hectares. In view of this small scale variation, plot size was reduced from 400 m^2 to 150 m^2. It was felt that a large number of regularly-spaced small

FIG. 5 FLOOD PLAIN PROFILE, TOTARA RESERVE



Prepared by Dr. M. Shepherd, Geography Dept.. Position of the survey line P–Q is marked on Fig. 3.

plots was the best method of analysing and illustrating this small-scale variation, while avoiding subjective bias in selection of sample sites. For additional sensitivity, the basic sampling unit area was further reduced by subdividing each plot into four quarters. By examination of species diameter distributions and replacement patterns it was intended to establish the nature of the relationships between the different vegetation types on the terrace , i.e. dynamically related phases (e.g. Watt 1947 ; Daubenmire 1968, pp 224-228 ("microseres" or " serules"); Knapp 1974), or static site-specific associations.

The 150 m^2 plots were sited regularly on a 75 m square grid, i.e. a sampling regime of about 2.7% . Data gathering within plots was basically the same as for the larger plots used in the flood plain forests ; in accordance with the reduced plot size only six understorey subplots were sampled in each plot.

However, the plot sampling system was found to yield inadequate data for analysis of the population structures and establishment sites of the podocarps, which were rare in comparison with the principal angiosperm species of the terrace forest. It was decided to attempt a census of all podocarp stems attaining breast height; this was accomplished by cruising the terrace with contiguous parallel belt transects. A transect width of 14 metres was employed for most of the work, i.e. the forest was scanned to a range of seven metres either side of the observer following a compass bearing. For each podocarp stem, the following were recorded

- species
- circumference at breast height
- height tier
- surrounding forest micro-type
- (if overtopped) the canopy species directly overhead.

The assistance of a second "roving" observer was of great value in sighting the smaller stems. However, some transects had to be cruised alone, necessitating cautious slow progress, especially where undergrowth was dense.

Although this was a thorough attempt to census 100 per cent of podocarp stems, the juveniles of these species can be rather inconspicuous and so it is possible that some were overlooked.

At the terrace margin the vegetation was distinctly influenced by the abundant side-light , and probably also by the extreme drainage conditions, This was regarded as a distinctive edge community and so a 20-metre wide marginal strip was excluded from this study, effectively reducing the area of terrace forest from c. 13 to c. 11 hectares.

4. 2 LIGHT RELATIONS

4.2.1 Seedling Growth Experiments

The aim of these experiments was to grow seedlings of several principal species from the Pohangina flood plain and terrace forests , under a variety of different light levels, while attempting to minimise differences in other variables between treatments. This was to enable comparisons of these species' seedlings growth rates under a variety of known light levels, and to assess the importance of light levels in determining species' recruitment patterns observed in the field.

The experiments were begun in the Botany and Zoology Department glasshouse, but this was an unsatisfactory environment as temperatures frequently reached 25 - 30 degrees C on clear sunny days. After a few weeks, a cooler glasshouse at the Massey Plant Growth Unit became available, and the experiments were transferred. The minimum and maximum temperature thermostat controls were set at 6 and 16 degrees C respectively, but in reality the air temperatures inside this glasshouse frequently exceeded 20 degrees C on clear sunny days. This compares with minimum and maximum temperature values of 3.5 degrees and 17.5 degrees respectively, obtained from a thermometer left on the floor in terrace forest from 25-4-82 to 7-5-82. Thus,temperatures in the experimental treatments were slightly higher than those experienced (in autumn months) by seedlings in the forest understorey environment.

The glasshouse roof slightly reduced light levels in the visible wavelengths, to about 80% of values obtained outside. This 80% relative irradiance level was used for the first treatment (A). Shade houses, constructed of nylon netting and bitumen paper screens on light wooden frames, were used for the other three treatments : B (24% relative light intensity), C (6.2%) and D (1.8%). (Fig. 7).

The species initially selected for the experiments were totara, kahikatea, titoki and tawa. However a variety of difficulties experienced in growing tawa led to the rather belated realisation that valid results were not likely to be obtained for this species. Therefore, seedlings of another large angiosperm (pukatea) were later added to the experiment. Although more site specific than tawa , and not a principal species on well-drained sites, pukatea provides a very useful comparison with its frequent associate kahikatea , also grown in this experiment.

Relevant details about the source and growth times of the various species seedlings are shown below in Table I.

TABLE I : SOURCES AND GROWTH PERIODS OF SEEDLINGS

SPECIES	SEEDLING SOURCE	INITIAL NO. PER TREATMENT	APPROX AGE AT COMMENCEMENT DATE	GROWTH PERIOD (approx)
Totara	Courtesy of Mc Murray's Nursery Woodville.	16 - 17	6 months (8-5-82)	270 days
Kahikatea	Germinated from NZFS seed.	21	$3\frac{1}{2}$ months (28-6-82)	220 days
Titoki	Wildlings Pohangina Valley	16	$2\frac{1}{2}$ - 3 months (8-5-82)	270 days
Pukatea	Wildlings Pohangina Valley	11	$1\frac{1}{2}$ months (28-7-82)	190 days

Batches of fairly even-sized seedlings of each species were individually potted in a free-draining potting mixture consisting of equal proportions of peat, pumice and sand . Slow-release "Osmacote" fertiliser pellets provided a balanced nutrient supply.

In all cases,seedlings were allowed at least two weeks to recover from transplanting,before the commencement of the experimental growth period. At the start of the growth periods a small sample of each species was harvested to obtain the initial average dry weight values.

The roots of the totara seedlings were already well nodulated when obtained from the nursery seedbed at less than five months age. The kahikatea seedlings, germinated in trays of sterile "Vermiculite", showed very little root nodulation at roughly two months age - at the starting date for totara, titoki and tawa seedlings. This lack of development prompted the innoculation of the kahikatea seedling trays with litter and chopped roots from kahikatea forest. Potting-up and subsequent addition of the kahikatea seedlings to the experimental treatments was delayed until root nodule development had become more pronounced.

Humidity and temperature were monitored in the four treatments over a three week period. Differences between treatments B, C and D were found to be minimal ; in these three treatments the humidity fluctuated between 70 and 80 per cent for most of the time. But, as expected, treatment A (with no shade covering) experienced wider fluctuations in both temperature and humidity. The protection of treatment A with a ventilated clear cellophane tent on a wire frame was at least partially successful in rectifying this without significantly affecting light intensity. However, treatments B and (especially) A required more frequent watering than the other two. Seedlings in each treatment were occasionally shifted , as a precaution against positional effects.

Seedling mortalities appeared to be due mainly to pathogens rather than treatment effects. A probable exception was the rather high mortality of totara in the darkest treatment (d), during the later stages of the growth period. Growth results indicated that this treatment (1.8% relative light intensity) closely approximated the light compensation point for totara seedlings. The effects of different treatments on leaf form and colour were noticeable in all species. The chlorotic appearance of the leaves of some pukatea seedlings in treatment A suggested some damage from the high level of solar radiation.

Tawa and titoki suffered from a scale insect infestation, which killed or weakened several plants, especially of the former species. Titoki were also infected by a powdery mildew (P.Long, pers.comm.), but this was largely overcome by painting the leaves with a solution of Benlate fungicide. In comparison with the angiosperms, the seedlings of the two podocarp species appeared relatively free of pathogenic attacks.

The seedlings were harvested in early February 1983. After the roots had been carefully washed free of potting mix, the seedlings were dried for approximately 48 hours at c. 95 degrees C. Root and shoot dry weights were determined, and average total dry weight increases calculated for each species in each treatment.

4.2.2 Forest Light Environments.

Accurate measurement of light in the field poses considerable problems, especially if measurements are required simultaneously at many sample points. Natural light levels often undergo rapid temporal fluctuations, and the relative illumination of understorey sites with different aspects of exposure to canopy gaps will change with the angle of the sun throughout the day. Instantaneous light measurements are therefore of limited value in ecological studies. Integrated measurements of total light quanta received over a period of at least one day are more desirable for comparing average light conditions at a number of sites.

While photo-electric integrating light metres have found use in some ecological work and can give highly accurate measurements, the expense of providing a number sufficient for adequate simultaneous sampling of habitats is prohibitive (Friend, 1961). Several chemical photometer methods have been used in biological work e.g. Pearsall and Hewitt (1933),Heinicke (1963), but most of these methods have been shown to have serious drawbacks, e.g. Braid (1923).

A photographic technique based on the bleaching of photosensitive ammonium diazo paper was first described by Friend (1961), and found to be very useful for measurement of forest understorey light environments by Young and Whitehead (F.R.I., unpub.report). This method was selected as the most suitable for the present study. Its main advantages are :

(i) Cheapness and simplicity allow the use of large numbers of replicates.

(ii) Slow speed of response, which minimises errors resulting from "handling time ".

(iii) Reliability over a wide range of light intensities.

(iv) The sensor units are robust under field conditions, and easily transported, set up and collected.

(v) Development of the papers is rapid, simple and foolproof, avoiding the tedious titrations required for analysing most photochemical solution methods.

A stack of the photosensitive paper is exposed, usually for a period of several days ; the total light integral received is estimated from the number of layers of paper penetrated by light, revealed after a dry development with amonia vapour. The number of layers bleached is proportional to the logarithm of the light integral received, (Friend ,1961) the precise relationship being determined by calibration with a photo-electric integrating meter. The assessment of partially exposed papers on a scale 1/10th. to 9/10ths (by visual comparison with a set of prepared standard integrades) provides adequate precision of measurement.

The ammonium diazo paper is sensitive mainly to the blue-violet region [2] of the visible spectrum, with peak absorbtion at 410 microns (Friend,1961). Forest under - storey light tends to be weaker in blue-violet (and red) wavelengths and relatively rich in green wavelengths, and so this method may produce slight under-estimates of the total light available for photosynthesis in understorey situations. Ultra-violet wavelengths are effective in bleaching the ammonium diazo compound, but are largely filtered out by the paper, and by the plastic of the petri dishes used to hold the paper booklets.

The method is described in detail by Friend (1961), and Young and Whitehead (F.R.I., unpub.report). The simple construction of the sensors used is shown in Fig.6 reproduced from Young and Whitehead. Sensors were attached to bamboo stakes at about 1.4 m height, at pre-determined sites (above under-storey sub-plots) in

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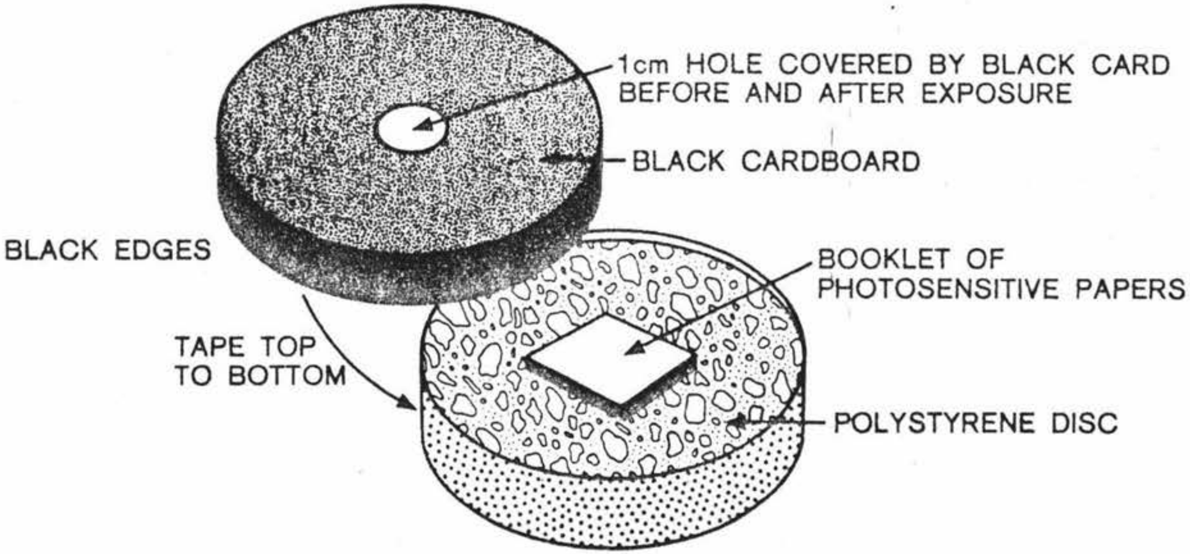
[2] This chacteristic is shared by most photo-activated chemical reactions used for light measurements.

FIG. 6 : PREPARATION OF SENSORS USING PLASTIC PETRI DISHES



Reproduced from S.C. Young and D. Whitehead, Forest Research Institute, unpublished report flood plain and terrace forests. Exposures were taken over three to five day periods ,and after development of the papers, light integrals (in moles / m^2) calculated from the logarithmic relationship shown in Appendix III. The light integral values obtained from forest understoreys were then expressed as percentages of the " full sunlight " value obtained from sensors exposed over the same period at open sites outside the forest. The logarithmic relationship shown in Appendix III was determined by calibration with an LI-COR Solar Monitor (with quantum sensor) , made available by Plant Physiology Division D.S.I.R.

The ammonium diazo paper was supplied courtesy of F.R.I. Production Division, Rotorua.

Fig. 7 : Seedling growth treatments in glasshouse.

Fig. 8 : Overview of "Y.M.C.A." block
younger (C) floodplain stand.

CHAPTER FIVE : RESULTS AND INTERPRETATION

5. 1 FOREST STRUCTURE AND DYNAMICS

5.1.1 Flood plain forest.

The forests on surfaces "C" and "D" are described in this section (see Figures 3, 4, 5).

(a) Younger stands

In the younger stands on surface "C" a dense generally continuous canopy c.15 - 25 metres high is dominated by totara. Matai occur throughout in lesser numbers, and kahikatea is locally co-dominant in some hollows. Rimu and miro are rare in the flood plain stands . Total canopy cover was estimated at 100% , from the small sample of 48 line intercepts above understory sub-plots. Podocarp species contributed 81% of this total canopy cover.

A range of angiosperm species are also present in the canopy : principally tawa and titoki , with occasional kowhai (Sophora microphylla) , lancewood (Pseudopanax crassifolius) , lemonwood (Pittosporum eugenioides) , maire (Nestegis cunninghamii and N.lanceolata (Hook.f.) L. Johnson), rewarewa and ribbonwood (Plagianthus betulinus). Low groves of smaller angiosperms (principally kaikomako (Pennantia corymbosa) and mahoe form the canopy in a few places. The forest margins form a distinct community in which kanuka , kowhai , lacebark (Hoheria sexstylosa), lancewood , ribbonwood and cabbage trees (Cordyline sp.) are prominent.

Only a very sparse sub-canopy is generally present in the T_2 height range (7 - 15 m), composed mainly of sapling and pole-sized[1] maire, matai , tawa and titoki. Where the canopy is densest the understorey is only moderately developed.

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[1] "sapling refers to stems from 2.5 to < 10 cm diameter (over bark) at breast height (140 cm), and "pole" to stems from 10 to <30 cm d.b.h..

But under less dense parts of the canopy, T_3 is occupied by a profuse growth of understorey species ; mainly hangehange, kawakawa (Macropiper excelsum) , mahoe and pigeonwood (Hedycarya arborea). There is also an abundance of both rewarewa and titoki "spindlings".[2] Throughout both flood plain stands sampled, growth of supplejack (Ripogonum scandens) is generally plentiful, but rarely impenetrable (not recorded quantitatively) .

The diameter distributions of the principal tree species only are shown in the text (Fig. 9). The comprehensive size class data for all tree and shrub species in each forest type are tabulated in Appendix IV.

The diameter distribution of totara is strongly normal, with 80% of live stems in the 20 - 50 cm d.b.h. range (mean d.b.h. 37.5 cm , s = 10.8 cm). This suggests a strongly even-aged population ; i.e. a very short period of mass establishment , with little or no subsequent effective recruitment. The present "even-aged" nature of this stand was con - firmed by the results of increment borings . (Table II). The estimated ages of seven totara between 21 and 57 cm d.b.h. (o.b.) ranged from 132 to 157 years (mean 147 years).

TABLE II : Age estimates from increment borings of totara, younger flood plain stands.

Diameter at breast height	Estimated total age (yr)	Mean diameter increment at breast height (mm yr^{-1})
21.0	132	1.77
26.0	142	2.04
30.5	145	2.34
30.5	149	2.26
37.0	148	2.78
41.5	157	2.92
57.0	155	4.06
Mean 35.0	147	2.60

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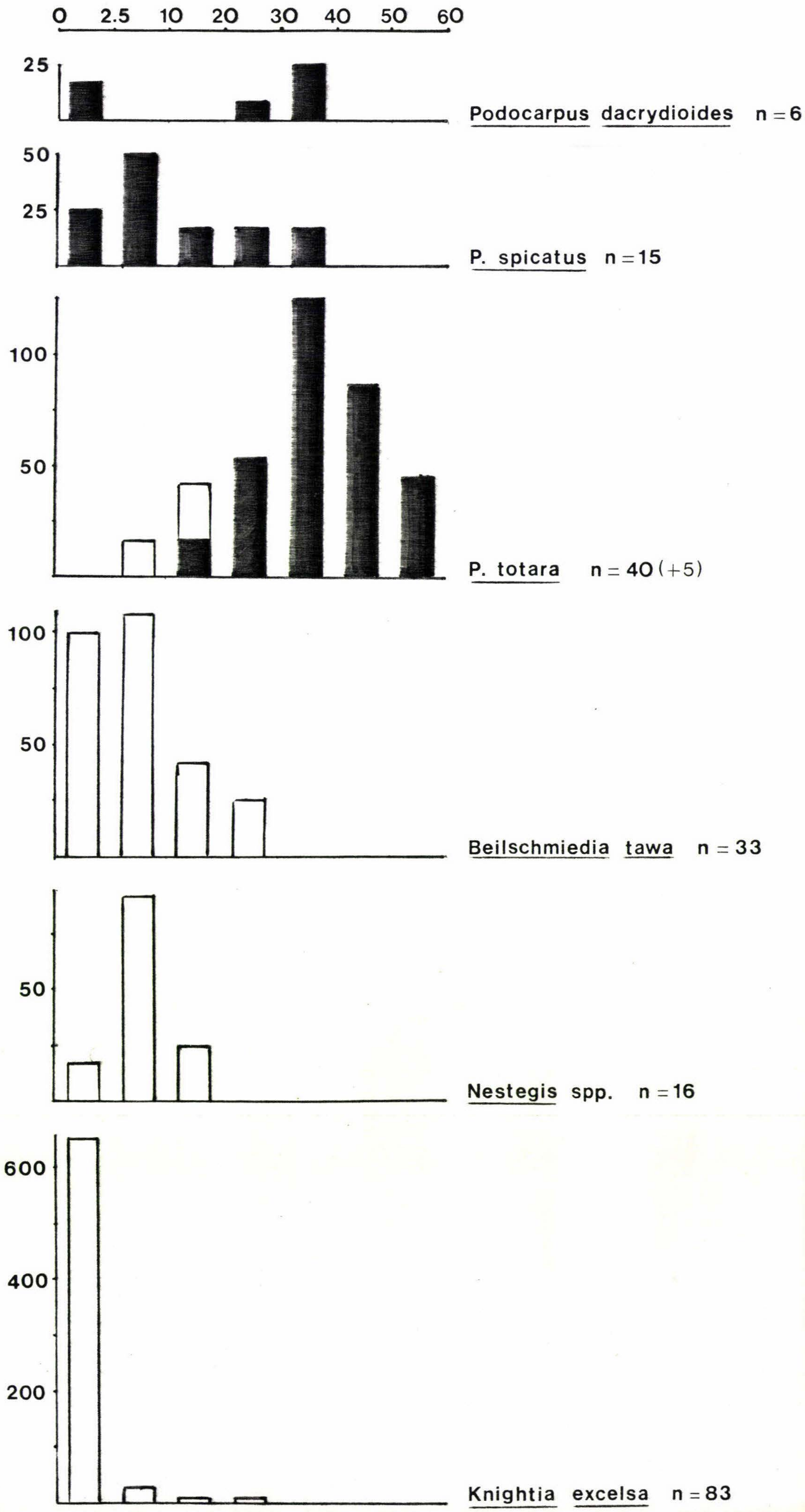
2 "Spindling" refers to stems reaching breast height, but < 2.5 cm d.b.h. (after Nicholls 1963).

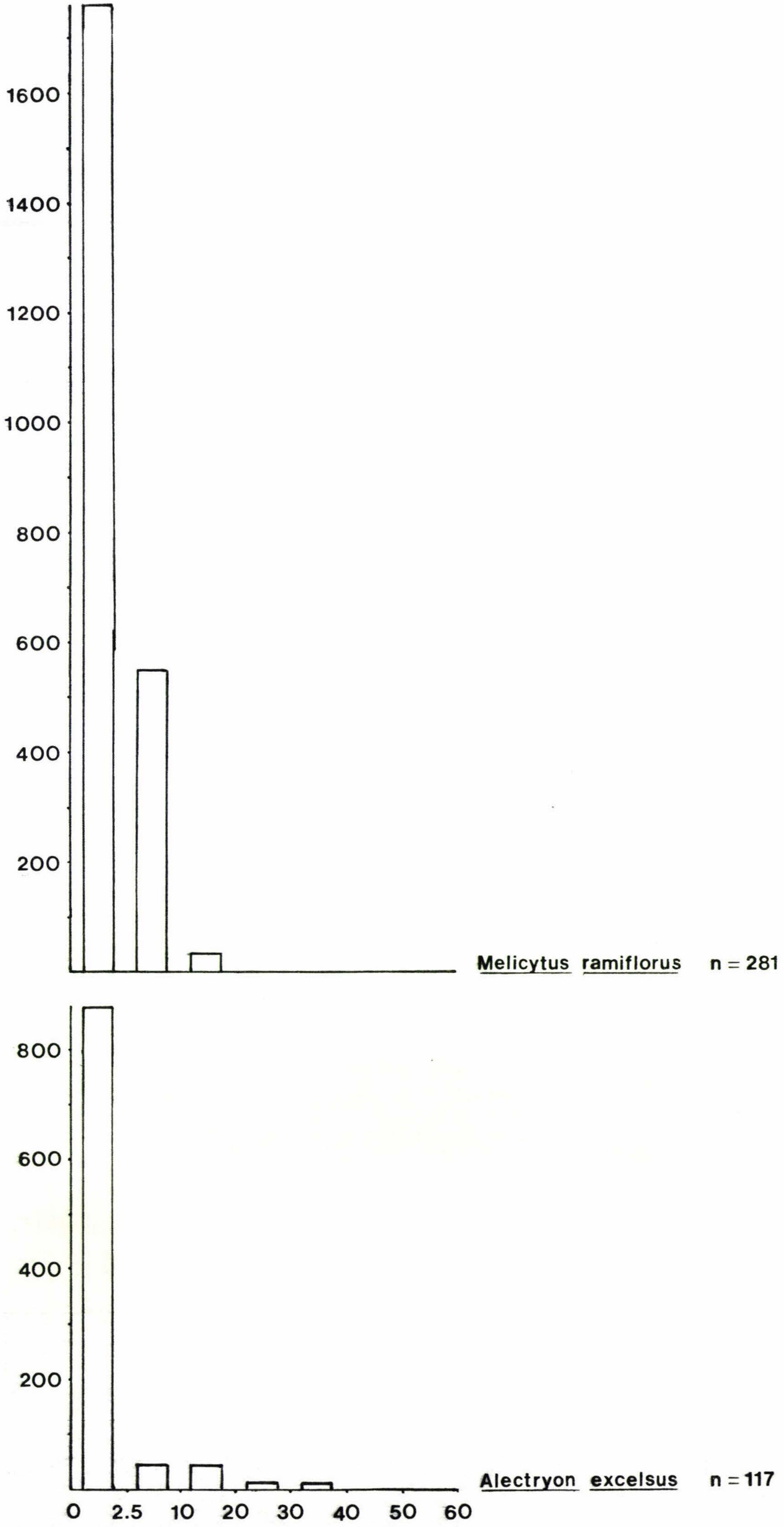
Fig. 9 : Diameter distributions for principal species in the younger (c) floodplain stands.

X - axis shows breast height diameter classes (cm) , and Y - axes show numbers of stems per hectare for each species. Note that Y - axis scale for rewarewa , mahoe and titoki differs from that used for the other species.

Podocarp species are shown by filled columns, except for dead standing totara stems which are denoted by open columns and numbered in parentheses.



0
2.5
10
20
30
40
50
60
25
Podocarpus dacrydioides n = 6
50
25
P. spicatus n = 15
100
50
P. totara n = 40 (+5)
100
50
Beilschmiedia tawa n = 33
50
Nestegis spp. n = 16
600
400
200
Knightia excelsa n = 83


1600
1400
1200
1000
800
600
400
200
Melicytus ramiflorus n = 281
800
600
400
200
Alectryon excelsus n = 117
0
2.5
10
20
30
40
50
60

A total of five over-topped dead standing totara stems (8 to 15 cm d.b.h.) recorded in the three plots are shown in Figure 9 , and these indicate a continuing thinning of this totara stand. This process , acting primarily against the smaller and generally (but not invariably) younger classes , will tend to reinforce the even-aged nature of the stand (cf. Lloyd, 1960). The very few live totara spindlings and saplings seen in these stands invariably appeared unthrifty : sparse foliage , die-back of shoot tips and weak attenuated stems were characteristic.

No age estimated from ring counts were obtained for other species. But in contrast to totara (and kahikatea), a number of angiosperm species are well represented by smaller size classes in this stand , suggesting a current active invasion . For example , rewarewa and titoki have strongly "inverse J " type diameter distributions (Leak, 1965), characteristic of stable or expanding populations.

The all-sized representation of matai suggests continuing recruitment long after effective entry of totara virtually ceased . But this is not a classic inverse J-shaped structure . The diameter distributions of matai and maire (and to a lesser extent tawa) in this stand suggest waves or pulses of establishment , rather than continuous recruitment at either constant or steadily increasing rates.

Several of the less numerous angiosperm species in the canopy (not shown in Fig. 9) show size class structures akin to that of totara , probably reflecting similar episodic establishment : kowhai , ribbonwood , lancewood , and lemonwood are represented by a few stems in the 20 - 40 cm diameter range , but smaller stems (especially for the first two species) are rare within the stand . These trees are typically of slightly lesser diameter than most of the totaras , and therefore likely to have established later. However, heart rot and indistinct growth rings thwarted attempts to age these species .

The composition of the seedling layer sample (Appendix IV) shows a current lack of podocarp entry ,and suggests a continuing influx of angiosperm species (especially titoki) into this stand.

(b) Older Stand.

In this stand , totara and the other less numerous podocarps form a rather less dense upper canopy c. 23 - 33 metres high ; overtopping most of the large angiosperms (maire , tawa , titoki) which form a patchy lower canopy up to 25 metres high . Podocarp species' crown cover was estimated at 75% , and a total canopy cover at 97% . The density of podocarp trees $\geqslant$ 30 cm d.b.h. was estimated at c. 188 ha $^{-1}$, c. 158 of these (84%) being totara.

Below this the understorey layers are rather variable. T_2 is in most parts rather sparsely occupied except for tawa (saplings and poles), titoki (saplings) and a few large mahoe and pigeonwood. On most sites kawakawa , mahoe, pigeonwood and small tawa dominate a generally dense T_3 layer . Other numerous species of this tier include Coprosma australis , hangehange , rohutu (Lophomyrtus obcordata), titoki and turepo (Paratrophis microphylla).

On the dampest sites, pate and (spindling to pole) pukatea locally dominate the understorey layers , with Syzygium maire (A.Cunn.) Sykes et Garnock-Jones appearing very occasionally. On the very driest sites tawa is almost absent , except for a few seedlings and spindlings which often die back in summer.

On a few sites, groves of small angiosperms (mainly mahoe) less than 10 m tall locally form most of the canopy ; e.g. where some totaras have died , or where the original podocarp strike was apparently not dense ;and on one site where three podocarps have been logged , In one of the sample plots fully half the standing totara were either dead or moribund , apparently due to water-logging resulting from changing patterns of drainage.In contrast, the matai on this site appear unaffected. There are no.

Fig. 10 : Overview of " Old Coach Road " older (D) floodplain stand.

Fig. 11 : Interior of older floodplain stand.

kahikatea among the other podocarps in the canopy on this particular site , which tends to confirm that formerly it was better drained. Beneath the opening canopy a very lush growth has developed in the T_3 layer , comprised mainly of hangehange , mahoe , pate , pigeonwood , pukatea and tawa.

The diameter distributions of the principal tree species are shown in Figure 12 . Totara shows a wide spread of size classes ($\bar{x} = 61.6$ cm d.b.h., s = 20.8 cm). But as in the younger stand , the paucity of stems $<$ c.20 cm d.b.h. attests to a lack of recent establishment. The spread of diameters though , is sufficiently wide (range 19 - 104 cm) to superficially suggest that this is not an even-aged population ; perhaps developed from several episodes of establishment , in similar manner to the " rejuvenation " of alluvial kahikatea stands described by P.Wardle (1974) .

However the results of increment borings do not appear to support this hypothesis . As mentioned in Chapter Four , an estimated 37% of the totara in this stand were too large to age accurately with the available equipment . Therefore the sample of increment cores is likely to be biased in favour of the younger stems in this stand. Six stems (35 - 71 cm d.b.h.) showed ages ranging from 231 to 263 years (Table III). The smallest totara that ~~was~~ aged (29 cm d.b.h., 208 years) ~~,~~ was growing beside a small creek flowing in an old river channel which forms the " inland " boundary of the stand . Its late establishment was probably permitted by side light from the formerly open channel , before it became overgrown with its present cover of small angiosperms.

TABLE III : Age estimates from increment borings of totara , older flood plain stand.

Diameter at breast height (cm)	Estimated total age (yr)	Mean diameter increment at breast height (mm yr^{-1})
29.0	208	1.49
34.5	234	1.57
41.5	239	1.85
47.0	231	2.16
58.0	263	2.33
63.0	257	2.59
70.5	234	3.21
Mean 49.0	238	2.17

Although the range of totara ages is evidently wider than in the younger stand examined , the results suggest a unimodal age structure for this stand too . The largest trees (> 71 cm d.b.h.) are likely to be older on average than the smaller totaras. However, considerable growth rate variation and a poor age diameter correlation within this stand are apparent from the data in Table III. I therefore believe that most of the extant totara in this stand germinated between about 230 and 270 years ago i.e. a single episode of establishment . The partially-buried root flanges of many of the totara show that there has been some sedimentation on these sites since the stand was initiated .However soil profiles reveal no evidence of topsoil burial which might be expected if this stand had been subject to partial destruction and rejuvenation by catastrophic siltation .[3]

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[3] However the structure of another smaller flood plain stand (not sampled) is suggestive of partial destruction by flooding : among totara of similar size to those in the younger "C" stand (30 - 50 cm dbh),clumps of younger kanuka have established.

Although matai is again better represented (compared with totara) in the smaller size classes , small stems of this species are less common than in the younger stand . The diameter distribution of matai is paralleled by that of maire , which also suggests a decline (but not cessation) of effective recruitment after an earlier period of more abundant establishment .

In contrast, most of the angiosperm tree species (as distinct from understorey shrubs) show " inverse J " type distributions characteristic of stable or expanding populations. Hett and Loucks (1976) showed that the power function [4] $y = y_0 x^{-b}$ provides a model approximating the age structures of stable continuously-regenerating tree species populations . The diameter distribution of turepo is well described by the power function model ($r = -0.97$, $P < 0.01$) suggesting that this species has a stable, all-aged population structure in this stand. The diameter distributions of tawa ($r = -0.93$, $P < 0.05$) and titoki ($r = -0.90$, $P < 0.05$) fit the model significantly, but not well as that of turepo . The tawa distribution in this stand is skewed in favour of the smaller classes ,suggesting that this is an invading (rather than stable) population. Mahoe and pigeonwood also show "inverse J " type diameter distributions , but the number of size classes present is insufficient for application of the power function model.

The tree species well represented by seedlings are mahoe , pigeonwood , pukatea (localised) ,tawa , titoki and turepo (see Appendix IV.) Although the totara trees of the canopy can be expected to outlive most of the present angiosperm trees beneath them, a continuation of the current recruitment trends within this stand would result in development of an angiosperm-dominated canopy within a few hundred years.

Several small stands of larger,more widely-spaced podo-

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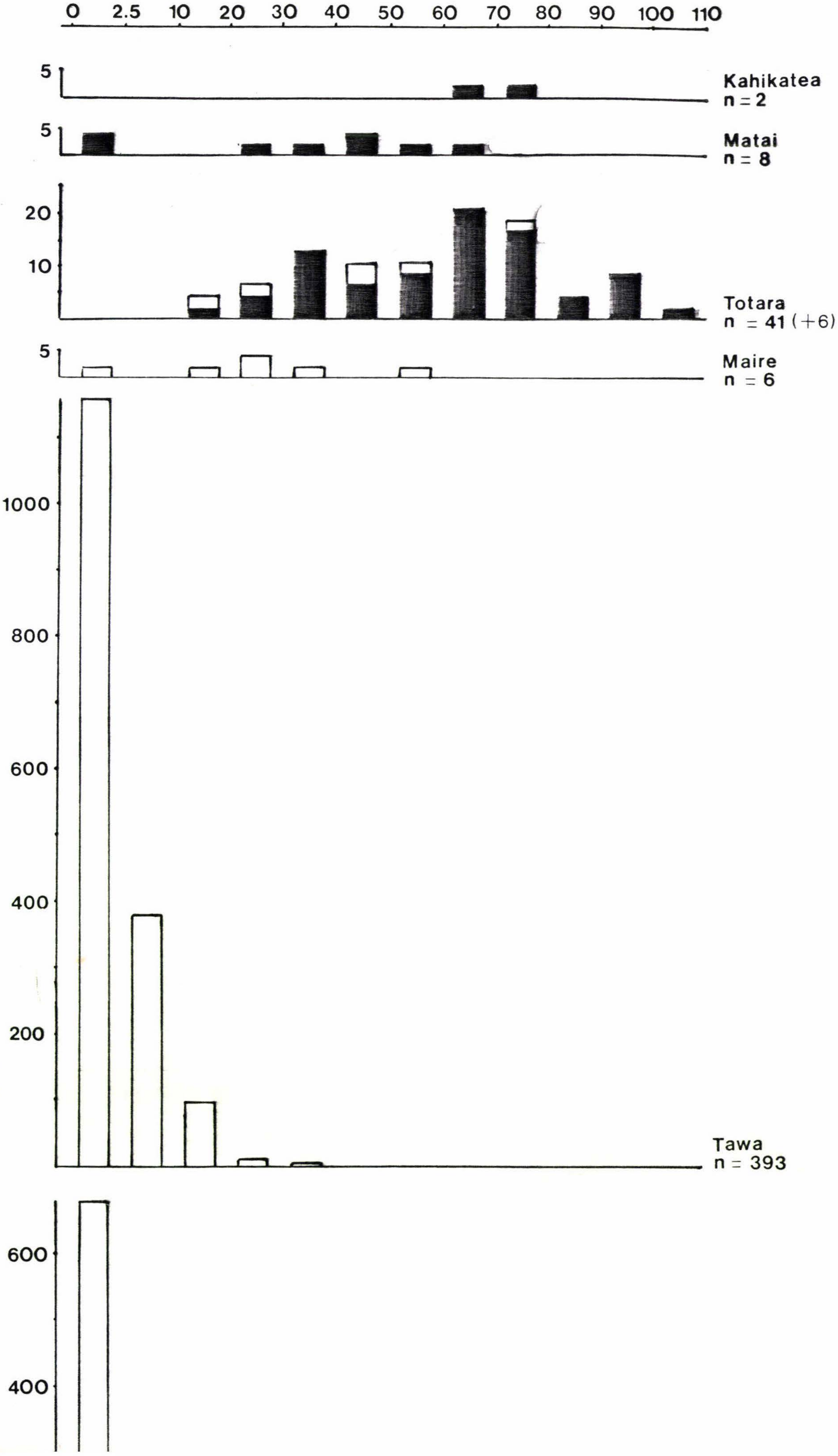
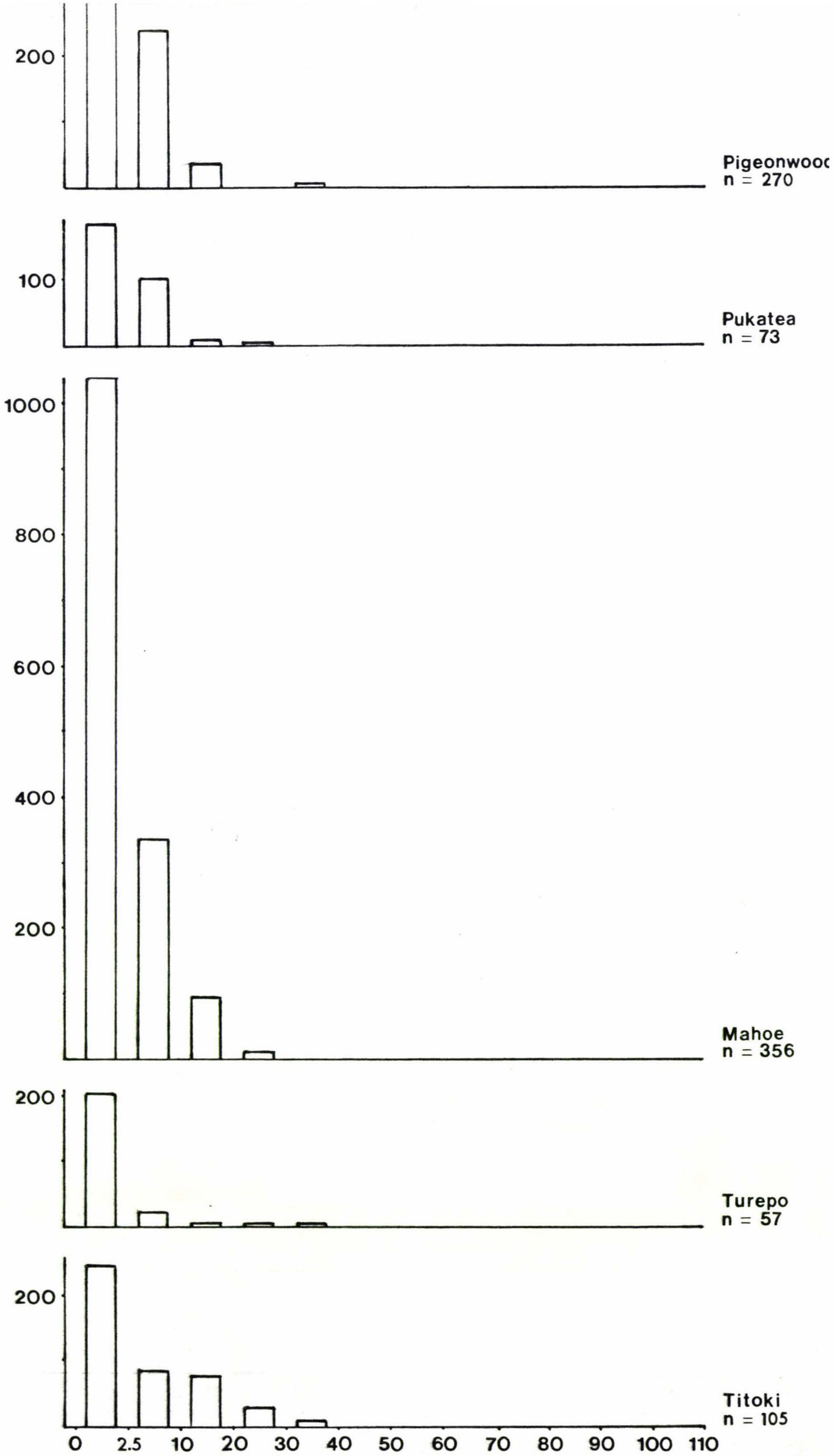
[4] Where y is the number in any age class x , y_0 is the initial input into the population at time zero, and b is the mortality rate.

Fig. 12 : Diameter distributions for principal species in the older (D) floodplain stand.

X-axis shows breast height diameter classes (cm), and Y-axes show numbers of stems per hectare for each species. Note that Y-axis scale for podocarp species and maire differs from that used for the other species.

Dead standing totara stems are denoted by open columns and numbered in parentheses.


0
2.5
10
20
30
40
50
60
70
80
90
100
110
5
Kahikatea
n = 2
5
Matai
n = 8
20
10
Totara
n = 41 (+6)
5
Maire
n = 6
1000
800
600
400
200
Tawa
n = 393
600
400


200
Pigeonwoo
n = 270
100
Pukatea
n = 73
1000
800
600
400
200
Mahoe
n = 356
200
Turepo
n = 57
200
Titoki
n = 105
0
2.5
10
20
30
40
50
60
70
80
90
100
110

carps are present on slightly higher surfaces in Totara Reserve. These have undergone some modifications, but are probably remnants of older first generation stands. In an unusually mixed stand (similar numbers of kahikatea, matai and totara, with a few rimu) near the southern end of the Reserve, a totara of about 125 cm d.b.h. was recently felled after dying about ten years earlier. Cut at about 60 cm height , the stump appeared to contain very approximately 440 rings , suggesting an age in the region of 450 years.

(c) Initiation of Flood Plain Stands.

Surface Availability A flood plain surface profile was prepared from a survey line marked on Figure 3. This profile (Fig. 5) suggests that surfaces "C" and "D" ,now occupied by the totara-dominant stands described earlier , became available for vegetation development by progressive lowerings of the channel level. Degradation such as this may result from tectonic changes, or from changes in the hydrologic regimen e.g. reduced sediment yield (Leopold et al., 1964).

Grant (1981a) produced evidence for the occurrence throughout the last millenium of five major erosion periods in the Ruahine Range (part of which is drained by the Pohangina River).Grant postulated that " each erosion period resulted primarily from a sustained increase in the frequency of major rainstorms". Aggradation of river flood plains downstream could be expected during such erosion periods. The reduction in sediment transport at the close of each erosion period would be expected to cause downcutting by rivers during the subsequent "tranquil interval", leaving the recently deposited alluviem available for colonisation by vegetation.

The closure date (c.1800) [5] of the "Wakarara" erosion period proposed by Grant correlates closely with the age of the young forest on surface "C" - if an allowance is made

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[5] Grant (pers.comm.,1983) has recently slight revised his postulated closure date for the "Wakarara" erosion period, from 1830 (as in Grant,1981a) to 1800 A.D..

for several decades of seral vegetation development prior to the entry of totara. However, the age of the older forest on surface "D" does not correlate closely with the closure dates of any of the earlier periods proposed by Grant. This suggests that Grant's erosion chronology does not identify the event(s) responsible for development of this older surface.

Progressive channel migrations ,probably effected largely during high floods, are also evident from Figure 5. It therefore appears that changes in course as well as level of the river are likely to have been significant in releasing areas of flood plain from chronic inundation and sedimentation , hence permitting the commencement of forest development .

Colonisation by seral communities . The largest and almost certainly oldest extant trees on surfaces "C" and "D" are podocarps , mainly totara . However it is highly improbable that these were the first woody pioneers of fresh alluvium. Rather,it seems likely that the present relatively even - aged stands of totara established under a pioneering scrub community , probably dominated by kanuka. This type of development is suggested by the growth of seedling and sapling totara in the kanuka-dominated ecotonal fringes on some margins of the present stands. Developing totara seedlings were also occasionally found under willows. But seedlings do not appear to establish on the open riverbed ; this is no surprise as totara seedlings are known to be rather frost-tender (Beveridge, 1973). Cameron (1960b) found that on young pumice soils of the Volcanic Plateau, 40 - 60 years was typically required for abandoned burnt clearings to develop a Leptospermum -dominant "nurse" vegetation under which podocarp regeneration could become established.

An old sale notice and map dating from 1901 (L & S File 8/5/288, Wgton.) affords an indication of the nature of the seral scrub community that probably preceded the present totara stands. The map has a number of useful vegetation labels and notes : "Tree manuka,matipo,tuwhiri &c"

and "Manuka and dwarf totara", are marked on areas of flood plain in the "Old Coach Road" block of Totara Reserve. Unfortunately the map is rather ill-proportioned (i.e. scale is erratic) and it is difficult to relate the positions of these labels to the present day vegetation distribution ; but both areas labelled appear to have since been cleared.

The three names in the first-mentioned label correspond to kanuka, mapau (Myrsine australis) and kohuhu (Pittosporum tenuifolium) respectively (Allan,1961), and so a scrub community dominated by these species was present on at least some flood plain surfaces. Clumps of kanuka and manuka are found among the present predominant cover of lupin (Lupinus arboreus Sims) and exotic grasses; many of these are patently a secondary development after clearance.

The reference to "Manuka and dwarf totara" suggests that another generation of totara (of more recent origin than the extant stands) was developing on an adjacent younger surface (since cleared). But it is quite possible that this label was inaccurately positioned. It may , in fact, refer to the younger of the two present stands ,at an early stage of development.

The primitive seral riverbed vegetation has been much modified by Man and his introductions. Pasture and Catchment Board plantations (mostly Salix and Populus spp.) now cover much of the flood plain in the lower reaches of the Pohangina River, Areas of the riverbed not currently under such management support a highly variable admixture of exotics and indigenes . Prominent among these are Buddleia davidii Franch ., both species of Leptospermum , Leycesteria formosa , lupin , toetoe (Cortaderia toetoe Zotov) , tutu (Coriaria arborea), willows (Salix spp.) and various exotic grasses.

Totara seedlings appear to find few opportunities for establishment in these communities, probably as a result of increased competition from exotic species .

Dense rank growth of exotic grasses in many places undoubtedly impedes establishment of woody plants. It may be that interruptions due to landuse changes rarely permit development of the new vegetation to a stage suitable for entry of totara seedlings. Lack of seed dispersal into these communities seems an unlikely explanation : a variety of exotic and indigenous passerines are abundant, and these would be expected to bring in seed of many trees and shrubs from the forest remnants nearby.

However, conditions locally favourable to entry of podocarps do occasionally arise, as illustrated by a spectacular strike of totara and kahikatea seedlings under a Populus alba plantation on the Rangitikei riverbed (Figure 14). The plantation is on a bank of sand and silt bordering the main river channel. The surface is c 2.5 - 3 m above the river level, and Rangitikei-Wanganui Catchment Board data suggest that it is likely to be flooded about once a year on average. Although deposition of seed by a flood was first suspected, no likely seed sources have been found further upstream on the flood plain. The intense localised concentration of seedlings suggests that a large flock of starlings roosting in the Populus trees may have been responsible for seed deposition. Most of the totara and kahikatea seedlings are now three years old (Nov.1983) and some are over 30 cm tall. Mahoe seedlings are also abundant on this site ; their much faster growth rates are already apparent (Fig.14). Other species seedlings present in lesser numbers include Coprosma spp., kaikomako, mapau, matai and pigeonwood. There is very little undergrowth under the plantation, and the resulting lack of competition has undoubtedly aided the growth of these seedlings. It is perhaps noteworthy that freshly fallen leaf litter of another Populus species (P. tremuloides Linn.) has been found to produce phyto-toxic effects on certain grass species (Younger et al., 1980). A similar allelopathic effect is possibly responsible for the paucity of undergrowth beneath Populus alba plantations .

Fig. 13 : Pohangina River Valley , showing prominence of the exotics Acacia dealbata (yellow flowers) and lupin in riverbed vegetation.

Fig. 14 : Kahikatea , totara and mahoe seedlings under Populus alba , Rangitikei River.

(d) Sustainability of reserves.

The seral status of floodplain dense totara stands and the dynamic nature of fluvial systems are vital considerations affecting reserves of these communities. The same problems were discussed by P. Wardle (1974) in relation to kahikatea forests in South Westland.

The very essence of these communities militates against their adequate conservation. They have all but disappeared from most of New Zealand , as the sites they occupied were those most valued for intensive agriculture. While totara - matai stands appear more tolerant than kahikatea of sedimentation (Foweraker 1929), they are still liable to destruction by channel course changes and erosion , such as occurred on the Rangitikei River near Bulls c. 1890 (J.Dwyer , pers.comm.) The initiation of new stands is dependant on the availability for colonisation of fresh alluvial surfaces (McSweeney, 1982). However , modern land-use patterns and management of river courses by Catchment authorities greatly restrict such opportunities . This certainly applies to the reserves of the Pohangina Valley , where no new stands of any extent appear to have established within the last 150-odd years.

The endangered position of floodplain dense podocarp forest communities clearly means that thoughtful conservation measures are a matter of urgency (McSweeney ,1982). A serious attempt to ensure a sustainable representation of these communities must involve reservation of as much floodplain area as is possible adjacent to present stands , and probably also release of such areas from catchment control. In this way a dynamic equilibrium of successional stages could be attained . As illustrated by McSweeney , the best remaining opportunities for such reservation are in South Westland.

5.1.2 Terrace Forest.

The results from 19 150 m^2 plots confirmed the distinct spatial variation in structure and species composition that was apparent from the initial inspection of this terrace. Overall, the forest on this surface is dominated by three angiosperm tree species (mahoe , tawa , titoki) seen to be among the most abundant invaders of the older flood plain stand described earlier. The forest pattern is partly attributable to edaphic heterogeneity , in that distinct local floristic differences appeared to result from variation in site drainage conditions.

(a) Xeric sites

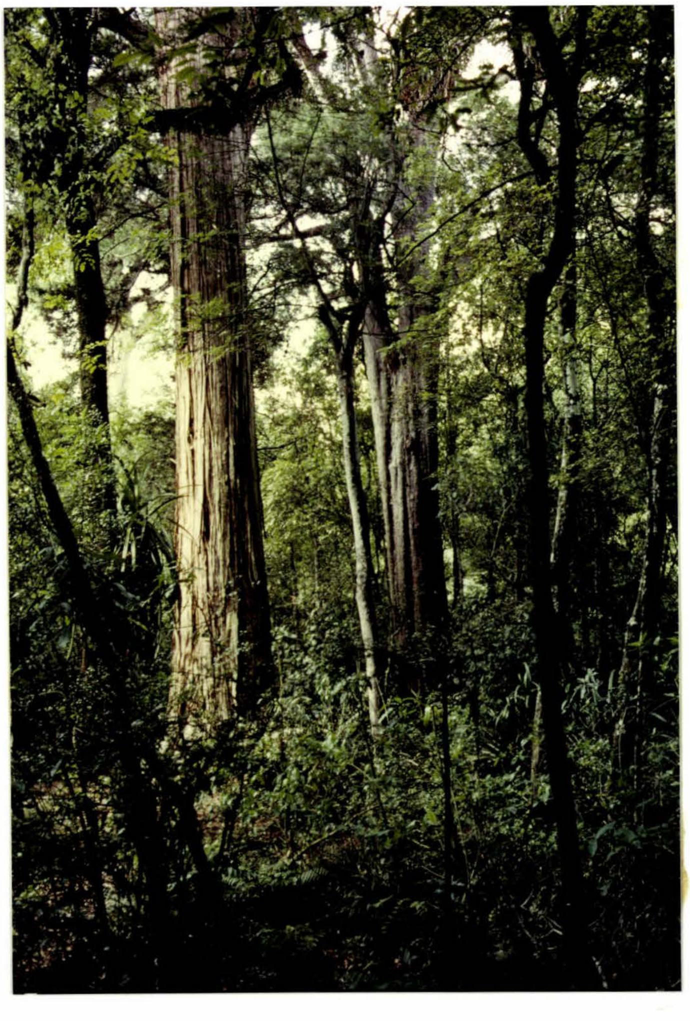
A"microtype" in which drought-tolerant species (cf. Atkinson and Greenwood 1972; Ogden 1976) are prominent is present on sites mainly toward the outer margin of this terrace. The light canopy , sparse undergrowth and generally poor representation of drought-sensitive species all attest to the excessive drainage of these sites.

This "xeric sites" microtype could be referred to as a "rewarewa - titoki - totara" forest , after the three species which dominate its appearance. Of the 76 plot quarters sited on this terrace , 20 (26.3%) were classified as occupying xeric sites.

Titoki typically forms most of the canopy at c.10-12m, with rewarewa generally emergent. Other less numerous canopy species are mahoe , maire , mapau (Myrsine australis) and tawa. Large emergent totara (and fewer matai) over 25 m tall, are scattered throughout . Tawa is much less abundant, and of smaller stature, than on immediately adjacent sites where slower drainage allows this species to dominate.

The most numerous species in the sparse understorey are kawakawa , mahoe , pigeonwood rangiora (Brachyglottis repanda)and small rewarewa and titoki. In addition , several small-leaved species less commonly found on the more mesic terrace sites are quite well represented e.g. Melicope simplex

Fig. 15 and 16 : Interior of terrace xeric forest, showing titoki-dominant canopy with emergent totara and matai.



rohutu , turepo. In contrast, supplejack is much less plentiful than on adjacent mesic sites.

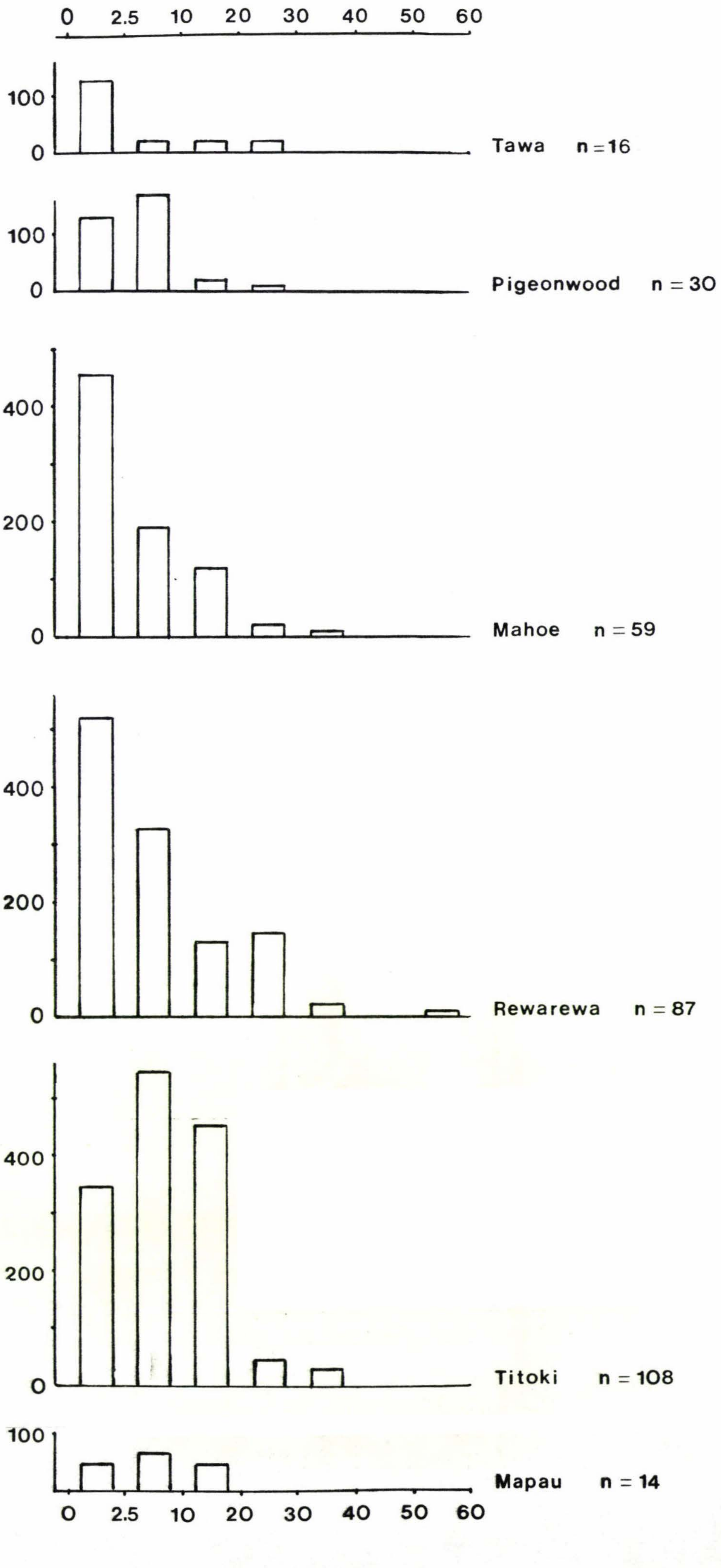
The diameter distributions for this xeric microtype (Fig. 17) generally confirm that it is a self-perpetuating site specific forest ; i.e. most of the principal species appear to be replacing themselves on these sites. The power function model significantly fits the diameter distribution of rewarewa ($r = -0.87$, $P < 0.05$), and barely does so for mahoe ($r = -0.86$, $P < 0.1$).

But for titoki there is no significant fit ($r= -0.62$). A glut of titoki stems between 2.5 and 20 cm d.b.h. (and relative scarcity in the < 2.5 cm class) has produced this departure from the model , and this distribution suggests a fluctuating regeneration rate. This is possibly an example of a self-perpetuating regeneration oscillation , as discussed by Hett and Loucks (1976). Observations suggest that regeneration of titoki on both xeric and mesic sites is inclined to follow a gap-phase mode. Dense thickets of large titoki seedlings are commonly found under small gaps and under thinning canopies. The crowded,relatively even - aged stands of titoki which develop suppress subsequent regeneration , but as these stands mature and open up another phase of intensive recruitment begins. Many (but not all) stands of titoki throughout this microtype are currently at approximately the same developmental stage, with a resulting overall appearance of an unbalanced population structure. This widespread "in phase" development throughout several separate pockets of this microtype could be the result of synchronisation by exogenous disturbance at some time in the recent past. Similar self-perpetuating cycles of senescence and regeneration are described for stands of Nothofagus spp. by J.Wardle (1969 and Ogden (1971).

Canopy - understorey association tables were compiled with the aim of revealing any species replacement trends or cycles within this microtype (Appendix VIa). For the principal species attaining canopy stature , the tables show the distributions of the smallest size class (spindlings) under different species' canopies. The "expected" values were

Fig. 17 : Diameter distributions for principal species of the terrace xeric sites.

X-axis shows breast height diameter classes (cm) , and Y-axes show numbers of stems per hectare for each species.


0
2.5
10
20
30
40
50
60
100
0
Tawa n = 16
100
0
Pigeonwood n = 30
400
200
0
Mahoe n = 59
400
200
0
Rewarewa n = 87
400
200
0
Titoki n = 108
100
Mapau n = 14
0
2.5
10
20
30
40
50
60

calculated on the basis of species' canopy cover percentage estimates. For example, if rewarewa comprises 25% of canopy cover in a certain forest type ; then under the null hypothesis, that establishment and survival (and hence spatial distribution) of juveniles in the understorey is not influenced by the species of present canopy trees, one would expect to find approximately 25% of the spindlings of any given species beneath rewarewa.

The only trends that show up significantly ($P < 0.05$) for this microtype are : (i) a lack of mahoe establishment beneath rewarewa ; (ii) poor self-replacement by titoki . In the cases of the other trends suggested by the data, either the deviations are not statistically significant, or the "expected" values are too small to permit Chi^2 tests (Greig-Smith, 1964, p.61). The sample sizes are too small to permit any definitive conclusions as to the existence of regeneration cycles, or species alterations as discussed by Fox (1977). Nevertheless, it is probably noteworthy that most of the principal species show poor self replacement ; regeneration of any given species tends to occur preferentially beneath one or more of the other associates, or in the case of rewarewa, in open gaps.

Although the large emergent totara are a major physiognomic feature of this microtype, only one totara stem (126 cm d.b.h.) fell within the 20 plot quarters classified as xeric sites (total 750 m^2). Regeneration of totara appeared very scarce . Small stems of matai appeared to be better represented, and three spindlings of this species were recorded in the plot samples from xeric sites (Appendix IV).

(b) Mesic Sites.

On the remainder of the terrace, where drainage is neither excessive nor impeded , the forest consists mainly of a mosaic of two distinguishable structures. Tall tawa - dominant forest occupies the greater area ; 36 (47.4%) of the terrace plot quarters being assigned to this microtype. Low groves of mahoe and other small angiosperms form the canopy

Fig. 18 and 19 : Overview of terrace forest .

in most of the remainder ; 18 (23.7%) of the plot quarters were assigned to this microtype . Two other plot quarters were classified as "mesic open" ; i.e. with no closed canopy. The low mahoe microtype occurs as small groves scattered throughout the tawa-dominant forest , and also forms two more extensive tracts over one hectare in area.

Tall tawa-dominant microtype. In the tall forest tawa up to 80 cm or more d.b.h. invariably forms most of the canopy at c. 15 - 25 m (T_1). Titoki is typically the most common upper tier associate of tawa, and rewarewa is also a frequent canopy component .Hinau (*Elaeocarpus dentatus*) ,mahoe and pukatea also occasionally contribute to the canopy. Emergent podocarps are scattered sparsely throughout, and a mere handful of living northern rata is present.

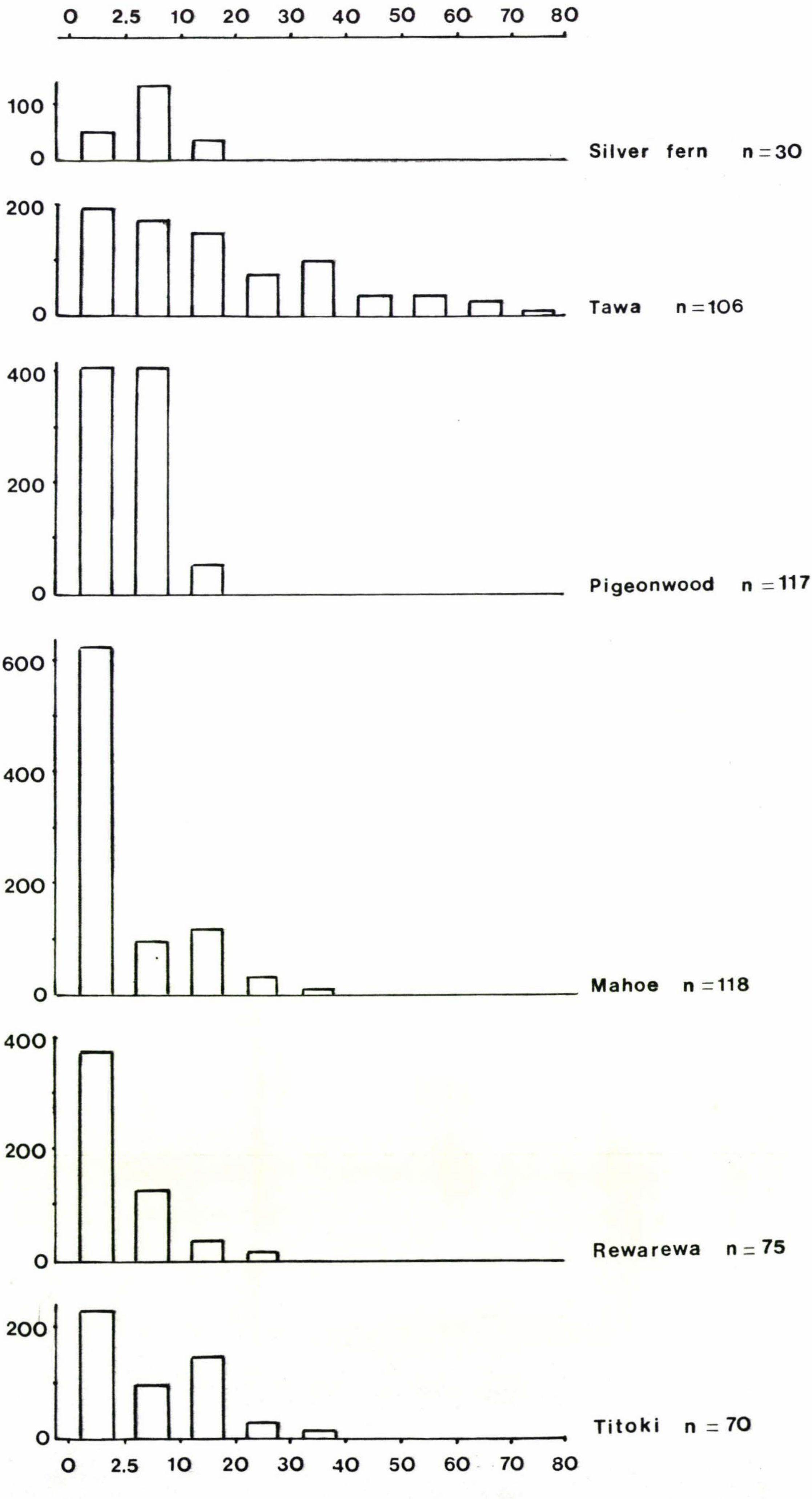
The most abundant species in the understorey are hangehange, kawakawa , mahoe , pigeonwood and silver fern (*Cyathea dealbata*), as well as juveniles of the canopy species rewarewa , tawa and titoki. Podocarp juveniles are rare .

The diameter distributions for the principal three species of this microtype are shown in Fig. 20. Mahoe, tawa and titoki are present in a sufficient number of size classes for application of the power function model. The model fits the diameter distribution of tawa only moderately well , but significantly. ($r = -0.77$, $P < 0.02$).The fits for mahoe ($r = -0.81$) and titoki ($r = -0.83$) are only barely significant ($P < 0.1$).Although the diameter distributions of all three species show some suggestion of wave-like departures from steady replacement , the overall picture is one of "accordance" (Braun , 1950), and relatively stable species composition .

Low mahoe groves microtype. In these low groves mahoe invariably forms most of the canopy at c. 4 - 8 m high. Pigeonwood and occasionally other small angiosperms such as lemonwood and pate are also canopy components. Larger species such as tawa and titoki are also occasionally present in the canopy or as emergents. Tree ferns and more rarely cabbage trees and nikau (*Rhopalostylis sapida*) add to the diversity. Dense tangles of supplejack are abundant.

Fig. 20 : Diameter distributions for principal species of tall tawa-dominant microtype, terrace forest.

X-axis shows breast height diameter classes (cm) , and Y-axes show numbers of stems per hectare for each species.


0
2.5
10
20
30
40
50
60
70
80
100
0
Silver fern n = 30
200
0
Tawa n = 106
400
200
0
Pigeonwood n = 117
600
400
200
0
Mahoe n = 118
400
200
0
Rewarewa n = 75
200
0
Titoki n = 70
0
2.5
10
20
30
40
50
60
70
80

On any one site, most of the mahoe stems are of similar diameter. The diameter distributions for this microtype (Fig.21) show a relative scarcity of mahoe stems in the smallest size class , indicating a current lack of replacement (from seed) on these sites. Mahoe's poor self-replacement is indeed the most significant ($P < 0.001$) trend apparent from the canopy-understorey association data for the mesic sites (Appendix VIb). In contrast, spindlings of larger angiosperms such as rewarewa , tawa and titoki are well represented on most of these sites. Some saplings of these species are in the process of breaking through the low canopy. But where it remains dense and vigorous, this canopy is a considerable barrier to penetration , and many saplings are bound and deformed by lianes . Podocarp spindlings are frequent on some sites in this microtype.

Under these low mahoe groves there is an abundance of windthrow scars , many still with associated log remnants. Eight of the 18 plot quarters contained either wind-throw scars or broken-off stumps ; in contrast , similar evidence of recent violent deaths was found in only four of the other 54 terrace plot quarters . Therefore it appears that most of these groves have developed after windthrow of patches of tall forest.[5] The majority of the logs are too far decayed to permit specific identifications in the field, but both podocarps (rimu) and tall angiosperm species appear to have been windthrown. It appears that some logs were salvaged for timber.

The mahoe are typically multi-stemmed , forking at or near ground level. Some clearly established on fallen logs that have since largely rotted away (Fig. 23).But on some sites there are a few larger mahoe which undoubtedly pre-date windfall. The form of some mahoe suggests they have produced new shoots after being smashed , or toppled and partially uprooted - probably by larger trees falling on top of them.

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5 Logging appears to have induced similar development at one site on this terrace,and at several other sites in the reserves of the valley.

Fig. 21 : Diameter distributions for principal species of low mahoe-dominant microtype, terrace forest.

X-axis shows breast height diameter classes (cm), and Y-axes show numbers of stems per hectare for each species.

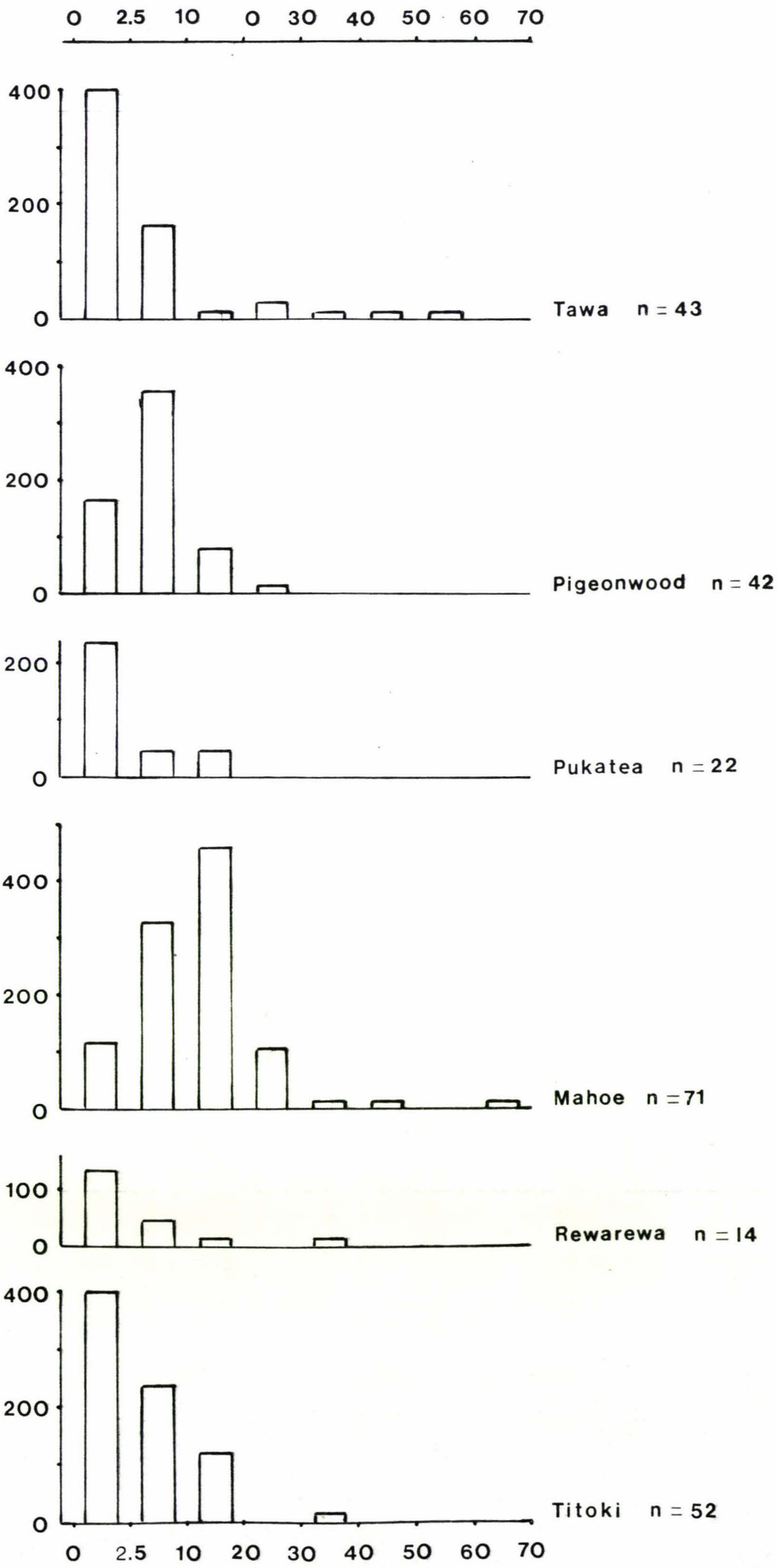

0
2.5
10
0
30
40
50
60
70
400
200
0
Tawa n = 43
400
200
0
Pigeonwood n = 42
200
0
Pukatea n = 22
400
200
0
Mahoe n = 71
100
0
Rewarewa n = 14
400
200
0
Titoki n = 52
0
2.5
10
20
30
40
50
60
70

Fig.22:Interior of low mahoe grove , terrace forest; showing mahoe growing on windthrow mound.

Fig. 23 : Mahoe stems established on decaying fallen log.

It is likely that some of the windthrows were produced by the 1936 gale which caused much damage in other parts of the reserve (see section 3.5; also Greenwood 1949) and in other forests of the region (Elder 1965 ; Esler 1978). Increment borings were made on several mahoe stems on one site. The growth rings were indistinct , but 31, 33 and 36 rings appeared to be present on three stems ranging from 10 to 12 cm d.b.h. Although the periodicity of ring formation in mahoe is unknown, this does suggest that the windthrows on this particular site occurred more recently than 1936.

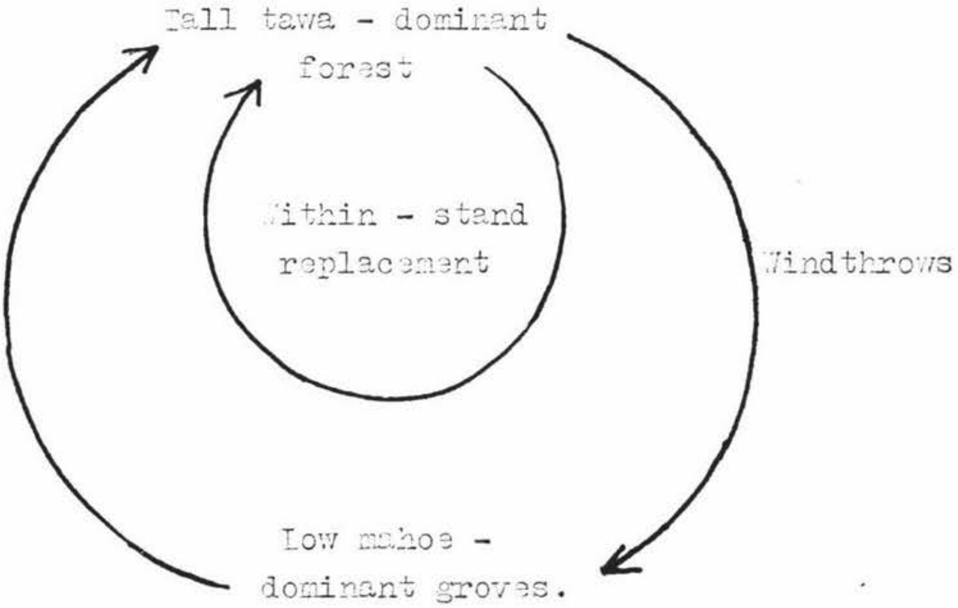
One of the sample plots covered part of a recently opened small windthrow gap in the forest. Here the canopy was apparently initially opened by the fall of a single unidentified podocarp , perhaps around 20 years ago. This gap has been enlarged by the much more recent windthrow of a tall rimu, which also brought down a tawa and damaged several other trees.

One quarter of this plot was classified as "mesic open" , as no canopy was present over most of it.In another quarter of the plot, young mahoe have already formed a light canopy up to 3 m high in the clearing. This quarter was accordingly classified as belonging to the low mahoe grove microtype. Two wineberry (Aristotelia serrata) up to 5 m tall had evidently been among the earliest colonists of the gap. Seedlings and spindlings of pigeonwood and rewarewa are also well represented in the gap , and there is a little coppice growth of mahoe , pigeonwood and tawa .

This example demonstrates the mechanism of gap opening and colonisation on the "mesic" (but still well-drained) sites. However, most of the earlier windthrows (that produced the present mahoe-dominant groves) were apparently on a larger scale than this fairly small example.

Canopy penetration by saplings of taller species observed in some groves presages the redevelopment of high forest on these sites. This development is inevitably proceeding in rather patchy fashion, giving rise in the short-term to uneven heterogeneous canopies. But as a higher canopy gradually coalesces one would expect young tawa to be drawn up beneath to form tall stands similar to those now present on the terrace.

Thus, on the mesic sites of this terrace there appears to be a cyclic pattern of forest development similar to the "microseres" or "serules" described by Daubenmire (1968) for tropical and sub-tropical rain forests. The species diameter distributions for the tawa-dominant tall stands (Fig. 20) suggest that in the absence of major windthrows this microtype is likely to be self-replacing, as small tawa stems are generally well represented in the understorey layers of these stands. But future windthrows of suitably pre - disposed stands (e.g. groups of large-crowned decadent tawa) would be expected to initiate further "microseres".



(C) Status of Podocarp Species in Terrace Forest.

As explained in Chapter Four, the low densities of podocarps in this terrace forest (except at the margin) meant that the plot sampling system employed produced very scant data for these species. It was decided to cruise the entire terrace with contiguous parallel transects in an attempt to census all podocarp stems ≥ breast height tall.

A total of 251 stems of five podocarp species were recorded in the total area of about 11 hectares of forest. 167 (66.5%) of these were in the smallest (spindling) size class ; i.e. $<$ 2.5 cm d.b.h. Densities of podocarp "trees" ($\geqslant$ 30 cm d.b.h.) were much higher on xeric than on mesic sites (Table IV). However, the densities of podocarp spindlings were on average very similar for xeric and mesic sites. On face value this suggests that rates of spindling survival and recruitment to larger classes are significantly higher on xeric sites.

TABLE IV : Numbers of live podocarp trees ($\geqslant$ 30 cm d.b.h.) in terrace forest.

	Xeric sites	Mesic sites	Overall
Rimu		4	4
Kahikatea		7	7
Matai	6	11	17
Miro		1	1
Totara	27	9	36
Total	33	32	65
Density (ha^{-1})	11.42	3.95	5.91

The diameter distributions of the podocarp species are shown in Figure 24. Differences in site moisture status are likely to affect both establishment behaviour and growth rates ;accordingly data for xeric and mesic sites are shown separately. The data are probably most appropriately treated as eight separate populations.

No increment cores were taken from the podocarps on the terrace , and so age-diameter relationships are unknown. A poor age-diameter correlation was found for totara within both the dense podocarp flood plain stands , with diameter growth rates in the younger stand ranging from 1.77 to 4.06 mm per annum (Table II). A.Katz (F.R.I.,unpublished data) also found a poor age-diameter correlation in the Okurapoto dense podocarp stand in Whirinaki State Forest. However, most New Zealand studies indicate that in forests where conifers are present at lower densities , diameter is a more reliable indicator of age ; e.g. Nicholls (1956), P.Wardle 1963a), Veblen and Stewart (1980,1982). In these types of forest, diameter distributions can therefore be more confidently used to approximate podocarp population age structures.

The overall picture superficially suggested by the diameter distributions is one of non-equilibrium population structures and discontinuous establishment. The exception to this is that of matai on xeric sites , which is the only diameter distribution approximating an inverse - J type structure. This distribution is well described by the power function model ($r = -0.91$) , and the fit is highly significant ($P < 0.001$).This suggests a stable matai population structure on these sites .

The totara diameter distribution for xeric sites suggests a very different population structure. There is a massive discontinuity of size classes between 10 and 80 cm d.b.h.,[6] suggesting a "regeneration gap" of several centuries. 22 (81%) of the 27 live totara trees are clumped between 110 and 170 cm d.b.h.;this distribution is sufficiently normal in nature to suggest a relatively even-aged population. On the questionable basis of extrapolation from growth rates in flood plain stands, one might expect that most of the extant totara trees germinated sometime around 500 - 650 years ago.

Such an interpretation must be applied with caution, as normal diameter distributions can arise in stands that are other than even-aged. For example, Herbert (1980) found that "despite the superficially even-aged appearance" , the

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[6] One dead standing totara 51 cm. d.b.h. was found, its top completely shattered, as if by a lightning strike.

dominant rimu component of a dense podocarp stand in Tihoi State Forest actually included an age range of over 350 years. This "even-aged aspect" condition was described by Jones (1945) as commonly occurring in forests of the northern temperate zone. However, this condition (reflecting a poor age-diameter correlation) appears to be associated more with forests where the species concerned occurs as dense stands , rather than as a more scattered emergent component.

Even if one cannot be confident of an even-aged veteran population, the diameter distribution of totara clearly attests to a lengthy "regeneration gap" , after a period of relatively frequent establishment on these sites. Rather than randomly scattered over the xeric sites , the totara trees tend to be clustered, and their crowns sometimes meet. Their boles are of only moderate height (typically 10 - 15 m to the first major branch), with broad spreading crowns. This form suggests that these totara did not develop in very dense stands of other tall trees. However, totara density on these sites has in the recent past been significantly higher than the present stocking. This is clear from the presence of two dead standing trees, four cut stumps and probably at least four fallen totara logs.[7]

Many of the present meagre stocking of spindlings and saplings appear unthrifty (as described for the flood plain stands, section 5.1.1 (a)). Even on these xeric terrace sites, totara seems to be a poor competitor in the forest understorey. Nevertheless, some of these juveniles, developing beneath a light canopy of mature titoki, look certain to progress further and emerge - thus representing effective regeneration in progress.

Most (73%) of the totara spindlings and saplings are concentrated in two small (widely-separated) clusters.

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7 Two of these logs were unmistakably totara , but the state of decay of the others prevented positive identification in the field.

Probably significant is the fact that these sites of regeneration are away from the present main concentrations of adult totara trees. There is only one standing totara within about 100 m of the larger "regeneration cluster ". Similarly a solitary veteran totara about 25 - 30 m away is the only adult conspecific within 60 m of the other regeneration site. No totara spindlings or saplings are present beneath the crowns of any of the adult trees.

A self-suppression effect on regeneration therefore seems distinctly possible. Fox (1977) discusses several examples of "auto-inhibition" effects , the precise causes of which are generally not well understood. Such an effect, resulting from the occupancy of these sites by the present generation of totara, could be at least partially responsible for the "regeneration gap" of recent centuries. The current pattern may reflect development of conditions more favourable to regeneration on those sites where the densities of the veteran totara have declined by natural attrition and a little logging. Under this scenario, one would predict a more widespread upsurge of totara regeneration on the xeric sites in the near future, as more of the present trees die . Totara might not be able to vigorously re-invade until the present soil and litter conditions produced by the mature trees have been altered by a period of angiosperm site occupancy . Such a cycle was proposed by Bieleski (1959) for regeneration of kauri .

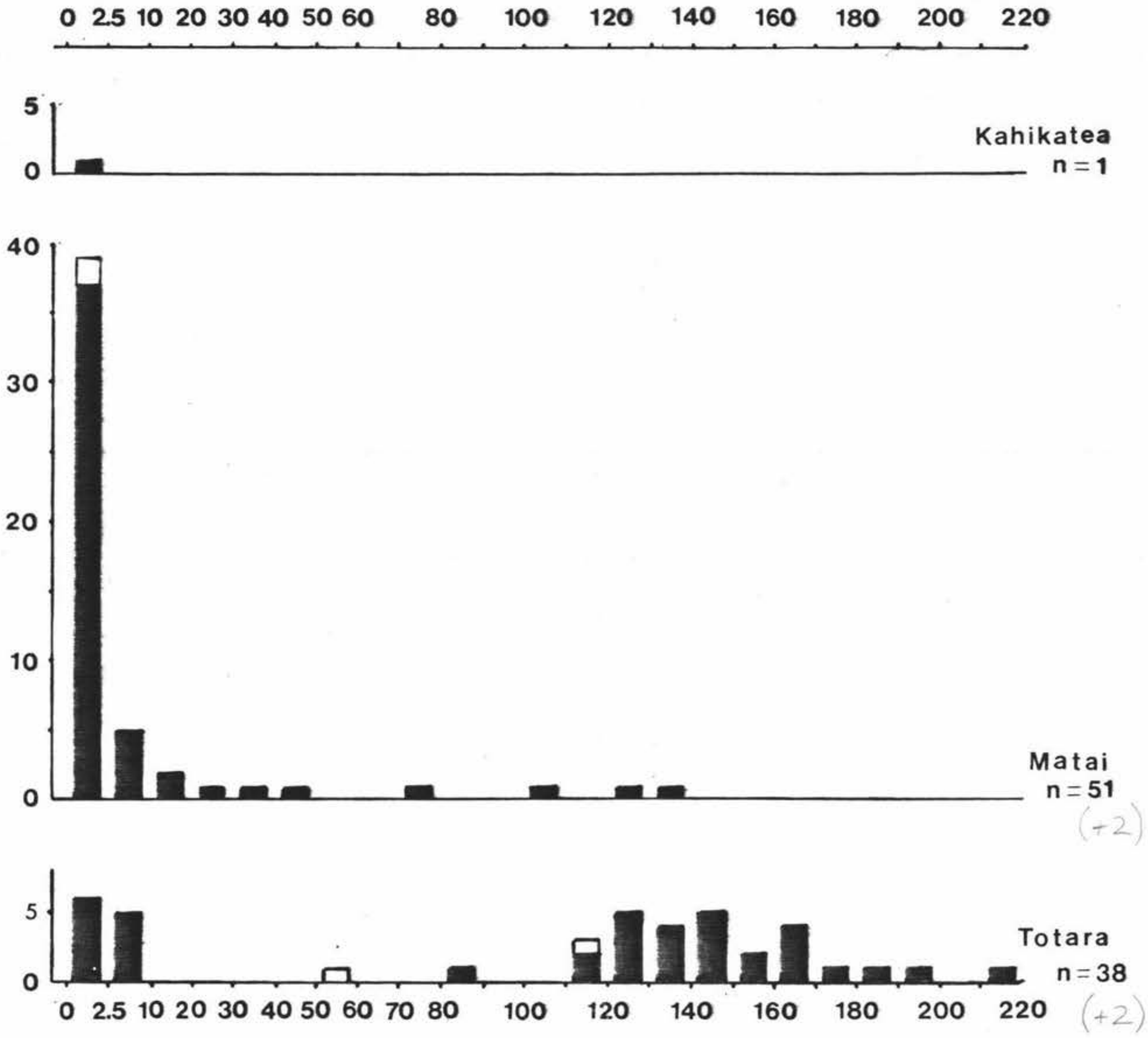
Thus a discontinuous cyclic pattern of totara regeneration on the terrace xeric sites can be envisaged as possible, with lengthy natural "regeneration gaps" resulting from auto-inhibition during phases of site domination by mature to old totara trees. Such a cycle, once initiated by major disturbance affecting the whole forest, could be perpetuated for many generations (Jones 1945 ; Ogden 1971); although a gradual decay of synchronism throughout the forest would be expected.

The carriage of fire on these dry sites is quite conceivable, and so there is the possibility that past burns may have influenced vegetation development. The prominence of

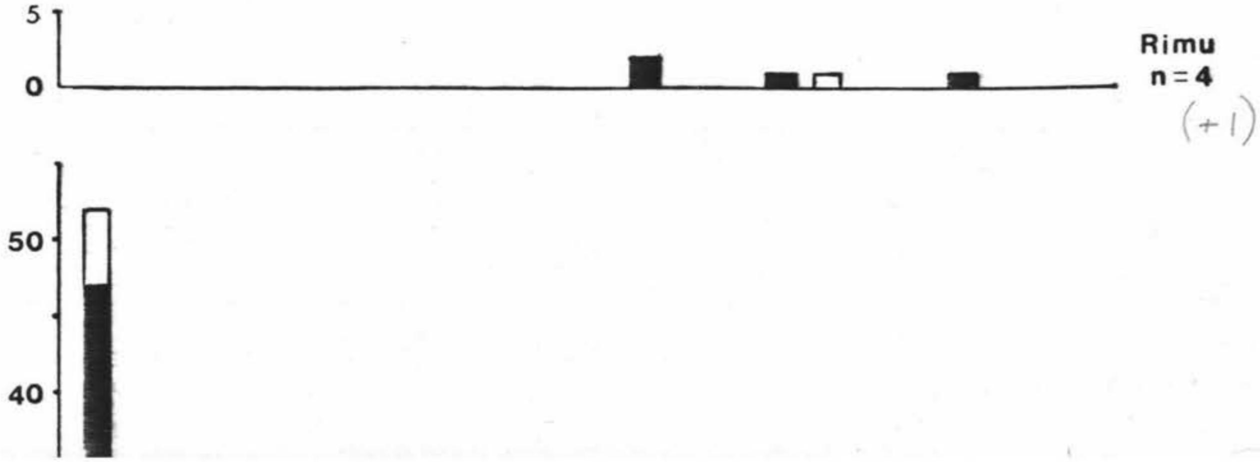
Fig. 24 : Diameter distributions of podocarp species in terrace forest.

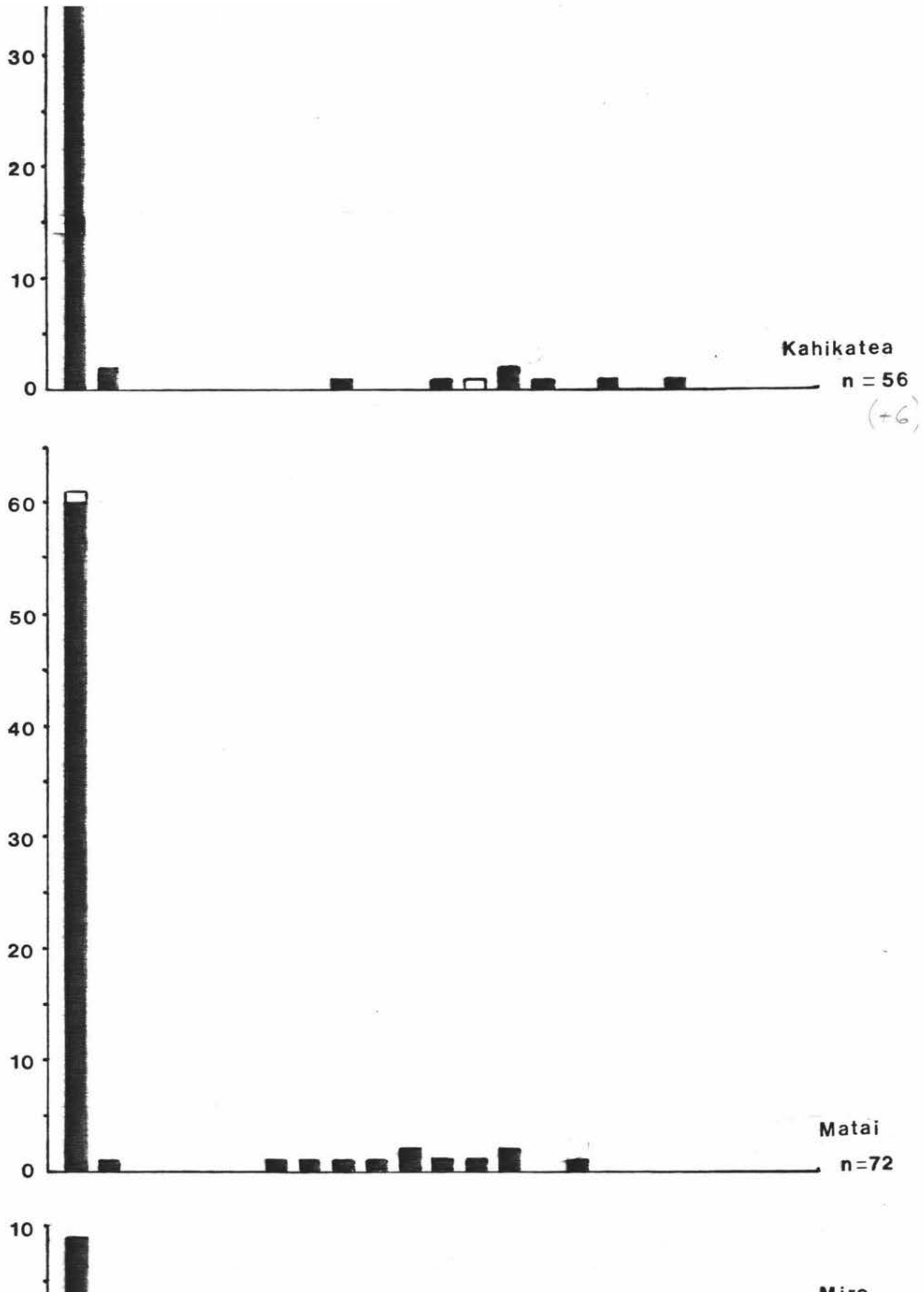
X-axis shows breast height diameter classes, and Y-axes show numbers of stems (**not** density) for each species . Dead standing stems are denoted by open columns and by figures in parentheses.

XERIC SITES



MESIC SITES




30
20
10
0
Kahikatea
n = 56
(+6)
60
50
40
30
20
10
0
Matai
n=72
10
0
Miro
n = 12
5
0
Totara
n=17
0 2 5 10 20 30 40 50 60 70 80 100 120 140 160 180 200 220
(+2)

rewarewa is perhaps suggestive of fire (McKelvey,1963). However the only direct evidence of burning is a solitary burnt-out bole, and the presence of large apparently unscarred totara within c.40 m of this site tends to discount the possibility of an extensive recent conflagration.

Mesic Sites . Marked discontinuities also occur in the diameter distributions for all podocarp species on mesic sites.

Although matai, miro and kahikatea are relatively well-represented by spindlings (compared to the numbers of mature trees), there are no stems of any of these species in the 10 - 50 cm diameter range. This seems to indicate a current upsurge in regeneration of these species, after probably at least two centuries of nil effective establishment.

Alternatively, this interpretation may be incorrect , and the "regeneration upsurge" may be an apparent rather than a real phenomenon. It is possible that few of the present set of matai and kahikatea spindlings will develop further and contribute to effective regeneration. Current mortality among the kahikatea does appear to be fairly high,[8] and many individuals of both species appear unthrifty. Similar stockings of podocarp spindlings might have been present throughout the last few centuries , during which time there was apparently no effective recruitment to the larger size classes.

Totara is much more sparsely distributed than on the xeric sites . There are nine extant (and two dead) stems between 90 and 170 cm d.b.h. but no stems in the 10 - 90 cm range ; once again indicating a lengthy regeneration gap. Juveniles are very rare , but some appear very healthy.

The regeneration gap is most pronounced and least fathomable in the case of rimu. This species is represented on this terrace solely by large trees , with a complete

[8] Five dead standing kahikatea stems < 2.5 cm d.b.h. were recorded (see Fig. 24).

absence of stems of less than 110 cm d.b.h. Two recently fallen stems and two more decayed logs are recognisable as rimu , there is one massive dead standing tree, and one of the four remaining live rimu is a moribund fast-disintegrating specimen. The picture is clearly that of a senile population experiencing heavy mortality, with no replacement. Observation suggests that the rimu population throughout other parts of Totara Reserve is in similar condition, and it appears that the mere handful of young rimu in the dense podocarp flood plain stands represent virtually the only effective establishment of this species for several hundred years.

Although seedfall and germination were not specifically monitored, no rimu seedlings (even of the cotyledonary stage) were seen in the intensively-studied Old Coach Road block of Totara Reserve , suggesting that at least currently there is little or no local supply of viable seed.Although it would seem highly improbable that most of the rimu in the reserve are actually too old to produce viable seed , it is conceivable that perhaps copious quantities of pollen may be required to ensure a good seed set in this species , and that the present low density of trees militates against adequate pollen transfer (M.McEwan, pers.comm.). However, this explanation appears unsatisfactory in view of evidence for a similar lack of recent viable seed production in nearby "Keebles Bush", where rimu trees are present at much higher density . R.M. Greenwood (pers.comm.) has collected litter from Keebles Bush since 1979, and from these samples has successfully raised seedlings of many species. But no germination of rimu seedlings was found in any of the samples.

Rimu is regarded by Beveridge (1980) as the podocarp with the most irregular seed crops, and is also known to show a high incidence of empty or undeveloped seed. However, there is little understanding of the environmental stimuli and/or physiological mechanisms controlling podocarp seed crop periodicity. (e.g. Beveridge 1973,1980). From the evidence described above, it appears likely that the rimu populations in both Totara Reserve and Keebles Bush (separated by about **38** km) are subject to the same regional periodicity , and that heavy seed crops are infrequent throughout the Manawaṭu region.

No rimu spindlings accompany the present stockings of juvenile matai and kahikatea concentrated on certain sites (described later in this section) in Totara Reserve. This may merely have resulted from a lack of rimu seed production during the few years that these particular sites were in a condition receptive to podocarp establishment.

Establishment Sites . Analysis of the establishment sites of the podocarps, i.e. the sites occupied by the smallest size class (spindlings), appears to offer some insights on regeneration mechanisms.

For each of the 167 (live) podocarp spindlings found during the cruising of the terrace, the immediate environment of the site was classified in the same categories used for the plot samples :- xeric forest microtype
- xeric open (canopy gap $\geqslant$ c. 40 m^2)
- tawa forest microtype
- low mahoe grove microtype
- mesic open (canopy gap $\geqslant$ c. 40 m^2)

The results show marked differences between the three main site vegetation microtypes (Table V). The lack of rimu, kahikatea and miro spindlings on xeric sites is consistent with the absence there of adult conspecifics (Table IV).

An interesting feature is the much higher average density of podocarps in the low mahoe groves , than in the tall tawa forest microtype. This is particularly so for kahikatea and matai . Chi-square tests were used to establish the significance of these differences (Table VI). The "expected" values for the tests were derived from the estimated areal proportions of the three site vegetation types found on mesic sites. In order to fulfill the general recommendation that no expected value should be less than 5 , the scant "mesic open" category data were included in the " mahoe groves" category. The pooled data for all podocarp species' spindlings were tested ; kahikatea and matai were also tested independently.

The test results are highly significant in all cases ($P < 0.001$). This clearly demonstrates that the sites now occupied by low mahoe groves have recently provided conditions more conducive to podocarp establishment than those sites currently occupied by tall forest.

As explained earlier, most of these mahoe groves have arisen after extensive windthrows. On one site where three mahoe stems appeared to contain 31, 33 and 36 rings, one kahikatea and one matai spindling were cut at ground level. 31 and 32 rings respectively were counted on these basal sections . It therefore seems probable that many of the podocarp spindlings are of similar age to the present mahoe stems. Their germination (or release of existing small seedlings) was probably induced by the massive canopy opening and soil disturbance resulting from windthrow. But the podocarps have subsequently been overtopped by mahoe and other fast-growing angiosperms which now form the canopy. Smaller podocarps (seedlings , < breast height)also present in these stands may be of lesser age.

It is difficult to assess the extent of effective regeneration that will develop from the present juveniles. The basal section cut from a matai spindling revealed fairly steady growth continuing through to the present. In contrast the kahikatea showed recent suppression, after a burst of six or seven years of rapid highly eccentric growth which was presumably related to side light from a small transient gap. But this sample of growth patterns is too small to be useful in its own right in assessing the status of the present spindling crop , especially in view of the variation within the low mahoe microtype. Some spindlings are clearly struggling ; very sparsely-foliaged , tangled by lianes and overtopped by dense canopies. But a good proportion appear healthy and uncluttered. Some of these are well positioned to take advantage of small gaps and areas of lighter canopy.

Beveridge (1980) stated that windthrow gaps on well - drained sites are often invaded by fast-growing small angiosperms which "generally inhibit development of young podocarps

TABLE V: Distribution of podocarp spindlings among terrace forest microtypes.

Microtype	Species						
	Kahikatea	Matai	Miro	Totara	Total	Density/ha.	
Xeric sites	1	37	0	6	44	15.2	
Tall tawa-dominant	12	24	8	4	48	9.2	15.2
Low mahoe-dominant	33	33	1	3	70	26.9	
Mesic open	2	3	0	0	5	-	
TOTAL	48	97	9	13	167	15.2	

TABLE VI: Chi^2 tests on distribution of podocarp species spindlings on mesic sites.

(a) Kahikatea

Microtype	No. of spindlings		X^2	
	Observed	Expected*		
Tall tawa-dominant forest	12	30.21	10.38	
Low mahoe + mesic open	35	16.79	18.68	
TOTAL	47	47	29.36	$P<0.001$

* "Expected" values calculated on the basis of the estimated areal proportions of the various microtypes on the terrace.

Table VI continued on P. 83

TABLE VI: Continued

(b) Matai

Microtype	No. of spindlings Observed	 Expected	X^2*
Tall tawa-dominant forest	24	38.58	5.14
Low mahoe + mesic open	36	21.43	9.24
TOTAL	60	60	14.38 $P<0.001$

(c) All Podocarp Species

Microtype	No. of spindlings Observed	 Expected	X^2*
Tall tawa-dominant forest	48	79.07	11.82
Low mahoe + mesic open	75	43.93	21.27
TOTAL	123	123	33.09 $P<0.001$

For each of the three tables, the calculated X^2 value exceeds the tabulated value for $P= 0.001$ i.e. highly significant differences in podocarp spindling densities between microtypes.

* Yates correction employed in calculation of X^2 values.

while they remain vigorous". In this case it is not known how long the mahoe canopies can be expected to remain vigorous. Grant (1981b) obtained age estimates of about 100 years from ring counts on "large mahoe" growing on alluvium in the West Tamaki catchment of the Ruahine Range (450 m a.s.l.). I am in no doubt that massive "old man" Mahoe are often over 100 years old. Mahoe appears to replace old dying limbs by new shoots growing up from near the base of the stem (Esler,1962). Although the absolute longevity of mahoe is unknown, the typical life span of most limbs is almost certainly more in the order of decades than centuries. This is suggested by the number of decadent and dead limbs already present in some of the mahoe groves. An increasing incidence of small canopy gaps throughout a mahoe grove can be envisaged from such a process of limb senescence and replacement. Thus, complete death of canopy mahoe individuals is probably not necessary for release of many of the podocarp (and angiosperm) juveniles beneath.

The process described above - that of podocarp seedling recruitment in large windthrow gaps , suppression for several decades beneath small fast-growing angiosperms, with subsequent release and emergence through thinning canopies - is apparently in progress on this terrace at present. Needless to say, such a process cannot be proven to represent the major regeneration mechanism responsible for establishment of most of the extant podocarp trees on the mesic sites of this and other terraces. But developments similar to those currently in progress ,including regeneration of some podocarps, could be expected to follow similar future windthrows. The size and species composition of podocarp cohorts initiated in this manner could depend on a range of factors e.g. seed availability, weather conditions, soil and litter conditions created by the previous site occupants.

It must be re-emphasized at this stage that the particular condition of most of the present mahoe groves appears to be the result of windthrow of sizeable groups of tall trees. It appears that massive opening of the forest has created conditions favouring rapid site capture by mahoe and other small angiosperm species that although often confined to the understorey of tall forest, show rapid growth in open situations. These openings have also permitted establishment of podocarps. Smaller scale canopy mortality (e.g. single tree falls) or gradual openings (standing deaths) favour recruitment to the canopy of the taller angiosperm species such as rewarewa , titoki and especially tawa , which are well represented in the understoreys of most of the tall tawa-dominant stands. Similar within-stand replacement by the canopy dominants appears to be typical of forests where intervals between disturbances are generally longer than the generation time of the canopy dominants (e.g. Jones, 1945 ; Fox, 1977).

5.2 Light Relations.

5.2.1 Seedling Growth Experiments.

The seedlings were harvested and dried after growth periods ranging from 190 days (for pukatea) to 270 days (titoki and totara). The relationships between dry weight increment and relative light intensity are shown in Fig.25. None of the four species grown showed a linear relationship throughout the full range of light intensities (1.8 to c.80% r.l.i.). Only for totara was there a statistically significant difference between the mean final dry weights in Treatments A and B. (Table VII) , and in all species it appears that photosynthesis becomes saturated at light levels below 80% r.l.i.

Judging from the slope of the lines between the 24% and 80% points (Fig.25) , the totara seedlings show the highest saturation level - perhaps at around 40% relative light intensity. Kahikatea and titoki both appear to reach saturation point at slightly above the 24% level. Pukatea appears to reach saturation at or below the 24% level ; but the sample was very small for this species , and so the results for pukatea can be expected to be the least reliable.

Earlier Northern Hemisphere studies have found that pioneering tree species generally show higher saturation levels than late successional species. For example , both Kramer and Decker (1944), and Kozlowski (1949) found that seedlings of Lobolly pine (<u>Pinus taeda</u>) showed increased photosynthesis for increased illuminance at all levels up to full sunlight . In contrast , the associated hardwood species found to be invading pine stands reached their maximum photosynthetic rate at 30% or less relative illuminance. Thus the photosynthetic response of pukatea appears typical of a late succession or climax species , whereas that of totara is suggestive of a more pioneering nature.

The saturation levels suggested by the results of the present study are lower than those typically found by most authors , e.g. Kramer and Decker (1944), Kozlowski (1949) , Bieleski (1959). This may indicate that factors other than photosynthetic saturation contributed to the levelling off of the increment graphs for all species grown in the present study e.g. effects of heating associated with higher light intensities .

Growth rates for each species in each treatment were calculated from mean dry weight increases according to the "compound interest " growth rate formula (V.H. Blackman , 1919) :

$$r = ({}^{1}/_{t}) \log_e W2 / W1 ,$$

where r is the geometric growth rate ; t the number of days between weight measurements ; W1 the mean dry weight of the initial sample ; and W2 the final mean dry weight.

Figure 26 shows the relationship between $\log_{10}$ per cent relative light intensity and growth rate for the four species. It is apparent from this that with <u>decreasing</u> light intensity , the performance of the two podocarp species declined relative to that of their angiosperm competitors . This relationship is also demonstrated by visual comparisons of totara and titoki seedlings from treatments A and D (Fig. 27, 28).

The virtually nil growth of totara in treatment D indicates that this light level (1.8% r.l.i.) approximates the compensation point for the species. The high mortality of totara seedlings in treatment D (from Table VII) is consistent with this. Extrapolation of the graphs back to the "X" intercept suggests compensation points $\leqslant$ 1.0% r.l.i. for both kahikatea and titoki , and in the region of 0.7% r.l.i. for pukatea .

This pattern among the four species parallels that found earlier for light saturation levels ; i.e. photosynthetic compensation points appear to show a positive correlation with saturation levels. Thus an adaptive gradient is apparent among the light requirements of the four

TABLE VII: Seedling Growth Results

Treatment	n initial	n final	Mean dry wt. (mg) initial	Mean dry wt. (mg) final	★	Mean daily increment (mg)	Growth rate (mg/g/day)	Shoot/root ratio (final)
Totara								
A	16	15	71	2319	P< 0.001	8.33	12.91	2.50
B	16	16	71	1529	P<0.001	5.40	11.14	3.15
C	16	15	71	296	P<0.001	0.84	5.29	3.63
D	17	13	71	74		0.01	0.02	3.93
Kahikatea								
A	21	20	22	978	N.S.	4.30	17.25	2.20
B	21	19	22	835	P<0.001	3.74	16.53	2.44
C	21	20	22	232	P<0.001	0.95	10.71	2.74
D	21	20	22	52		0.14	3.91	3.07
Titoki								
A	16	13	78	1872	N.S.	6.64	11.77	2.71
B	16	14	78	1716		6.07	11.45	2.92
C	16	13	78	672	P<0.001	2.20	7.98	3.42
D	16	14	78	170	P<0.001	0.34	2.89	4.63
Pukatea								
A	11	7	18	444	N.S.	2.24	16.87	1.43
B	11	9	18	443	P<0.005	2.24	16.86	1.66
C	11	9	18	222	P<0.001	1.05	13.22	2.16
D	11	7	18	69		0.27	7.07	2.95

★ T-test for significance of differences between final dry weight treatment means. N.S. = difference <u>not significant</u> at P=0.05 level.

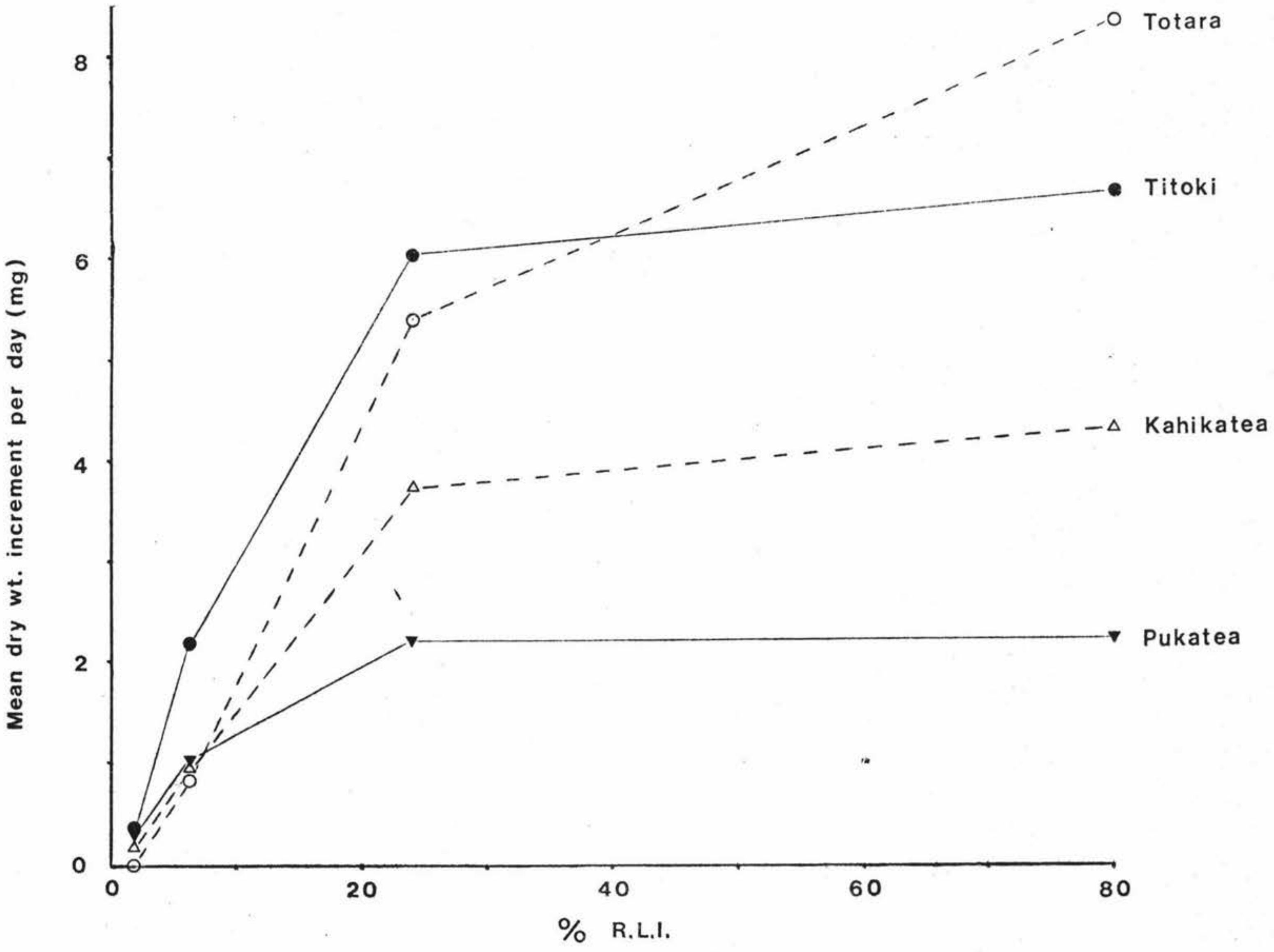
species : the adaption of photosynthetic and respiration mechanisms of shade intolerant species for maximum utilisation of strong sunlight is achieved at the cost of lowered efficiency under shade conditions (Spurr and Barnes , 1973).

A possible limitation to the usefulness of the experimental results must be mentioned. There were considerable differences between the initial mean seedling weights of different species , and there is some evidence that this might limit the validity of interspecific comparisons of growth rates and compensation points. G.E. Blackman and Wilson (1951 a,b) found that relative growth rates (g / g / day) for Helianthus seedlings declined with increasing age , and this appeared to be due to a gradual diminution of leaf-area to plant weight ratio , with increasing plant size. I might add that self-shading effects are also likely to contribute to this decline .Similar observations on trends in growth of Cannabis and Helianthus seedlings were discussed by V.H. Blackman (1919). Thus there is evidence that certain annual plants become less efficient energy transducers as they grow larger , as a consequence of morphological development . Intuitively , one would expect this law to apply to most plants , although to my knowledge the significance of the effect in forest tree seedlings has not been studied .

Fortunately , the titoki and totara seedlings had very similar initial mean dry weights (Table VII) , and so comparisons can be safely made between these two species which are commonly associated on well-drained sites. The same can be said for the other pair of intimate ecological associates , kahikatea and pukatea . The results of this section suggest that seedlings of both podocarp species grown have higher compensation points and inferior growth rates at low relative light intensities , in comparison with two principal angiosperm associates which typically appear to be replacing them on their respective sites.

It is perhaps regrettable that certain other species were not grown in these experiments . Comparable information

FIG. 25 SEEDLING INCREMENT RATES vs RELATIVE LIGHT INTENSITY



on the light responses of matai , rimu and especially mahoe seedlings would have been useful . Mahoe is abundant throughout the forests studied and appears to be a much more important element in forest dynamics than was initially realised by this author .

Caution must be exercised in comparing the growth rates and estimates of compensation points with those obtained for other species seedlings by other workers. For example ,Bates and Roeser (1928) estimated compensation points for seedlings of some North American conifers :

Pseudotsuga taxifolia	3%, r.l.i.
Pinus ponderosa	2% "
Sequoia sempervirens	1.5% "

Bieleski (1959) estimated a compensation point of 0.9% r.l.i. for kauri seedlings . Pook (1979) infers values in the region of 1% for all four species grown in his study : kauri , tanekaha , lancewood and mapau .

Most workers appear to have obtained their results using instantaneous measurements of light intensity (although unfortunately this is sometimes not made/clear); whereas all light measurements made in the present study were integrated (long term , cumulative) values. Average light conditions in the four growth treatments were measured using integrating light meters over a 24 hour period. Such a method is likely to produce lower values for relative light intensity (% of full daylight) than instantaneous measurements made in the middle hours of the day when the sun is high.

This distinction is more important in the field. Under canopy gaps, very significant differences may arise between instantaneous and integrated measurements on the same microsite. Instantaneous measurements made toward the middle of the day, during clear or light overcast conditions, may produce figures as high as 10 - 20% r.l.i. under even a small (single tree) canopy gap. But the average light conditions for such a site throughout a full day are unlikely to be higher than c. 5% of total irradiance received outside the forest.

FIG. 26 SEEDLING GROWTH RATES vs LOG (% RELATIVE LIGHT INTENSITY)

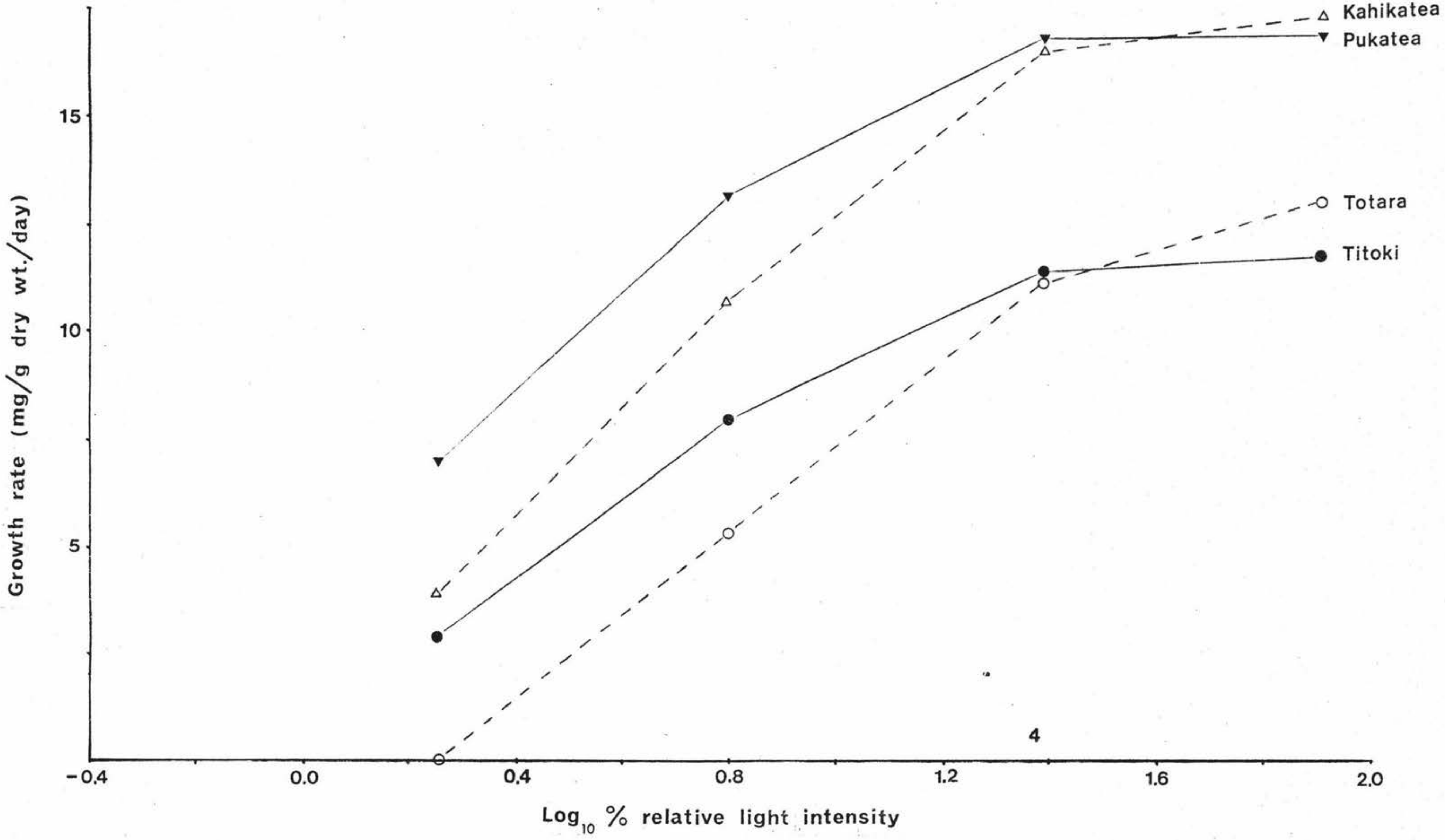


Fig. 27 : Comparative development , at time of harvest , of totara seedlings from treatment A (left) and treatment D.

Fig. 28 : Comparative development of titoki seedlings from treatment A (left) and treatment D.

5.2.2 Forest Light Measurements.

Measurements of relative light intensities (r.l.i.) were obtained from small samples of points in floodplain and terrace forest understoreys (total 52 points , Table VIII). These values are expressed as percentages of the "full sunlight " values obtained from sensors exposed at open sites outside the forest , over the same period.

TABLE VIII : Forest Understorey Light Environments.

Forest Type	N	Mean r.l.i. (%)	Range	Percentage of sample below 1.8% r.l.i. *
1.Floodplain totara forest (younger "C" stand	13	1.41	0.81 - 3.07%	84.6
2.Terrace forest				
(a) Xeric sites	11	2.52	1.44 - 4.34%	27.3
(b) Tall tawa - dominant	15	1.31	0.77 - 2.29%	86.7
(c) Low mahoe - dominant	13	1.36	0.77 - 2.43%	84.6

* This figure is the experimentally-estimated compensation point for totara seedlings (Section 5.2.1).

The understorey light environments in type 1 and micro-types 2 (b) and 2 (c) were all found to be very similar. No significant differences ($P = 0.05$) were found between these three samples, using T-tests conducted according to the procedure recommended by Cochrane and Cox (1950) for comparing samples of unequal size and variance .

The xeric sites microtype (2a) showed a mean value significantly higher ($P < 0.01$) than the other three samples , as might be expected from the lower soil moisture status and consequently lower vegetation density on these sites . In addition , a wider range of light intensities was evident in the xeric sites sample . This variation within the microtype is probably an indication of the environmental heterogeneity created by the patchy distribution of the massive emergent tōtara throughout a matrix of much smaller trees.

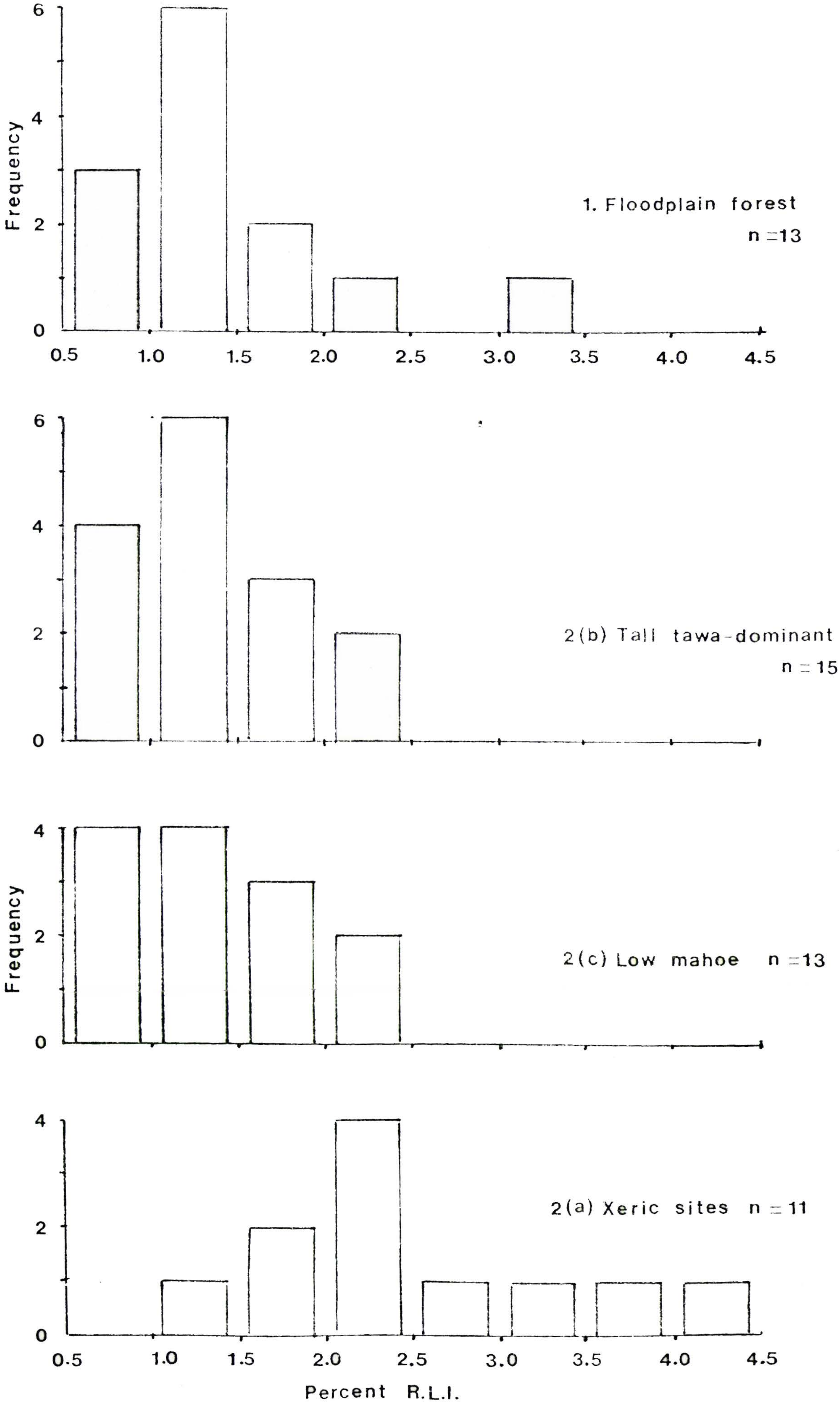


FIG. 29 UNDERSTOREY LIGHT ENVIRONMENTS

5.2.3 Influence of light intensity on seedling establishment.

In all four forest (micro) types in which light measurements were made , podocarp diameter distributions suggest that understorey establishment , survival and recruitment rates of these species are low in comparison with those of associated angiosperms such as pukatea , tawa and titoki (Section 5.1.1 , 5.1.2). These latter species are on most sites represented by all-sized populations. These circumstances are particularly so for microtype 2 (b) and type 1 , and least so for 2 (c).

In microtypes 2 (b) , 2 (c) and type 1 , present understorey light intensities on most sites are below the compensation point experimentally estimated for totara seedlings (Table VIII). Needless to say , this does not conclusively prove that light is in fact the factor currently limiting totara regeneration on these sites . A host of other site factors are potentially influential in determining understorey replacement trends (Fox, 1977), and it is possible that some other unidentified factor may be the critical limitation . But the results clearly show that present understorey light environments are inimical to totara seedlings , and confirm that totara regeneration can be expected only rarely in undisturbed old growth forests on these sites. Even though light intensities are above the compensation point on some microsites , they are still sufficiently low to render totara seedlings uncompetitive (in terms of growth rate) in comparison with titoki seedlings (Fig. 26).

It has been argued that the failure of "intolerant" species' seedlings in forest understoreys is due to the indirect effects of shade , particularly in producing inad - equate root development and consequent moisture stress (Spurr and Barnes , 1973). This effect undoubtedly does have a major bearing on understorey competition and survival ; but the results of this study suggest that the direct effect of light starvation may be sufficient to largely account for the failure of totara seedlings in type 1 and microtypes 2 (b) and 2 (c).

On the terrace xeric sites (2a) the situation is rather different in that light levels were found to be predominantly above the compensation point of totara seedlings (Table VIII). Yet while the present forest on these sites is characterised by large emergent totara , smaller stems of the species are currently very scarce in most parts. In fact, the plot sampling of the terrace recorded no totara seedlings ≥ 15 cm tall in a total of 30 1 m^2 understorey subplots on xeric sites (Appendix IVc). Thus even in what appear to be relatively well-lit understoreys on these xeric sites , totara seedlings currently show very low densities and survival rates in comparison with the principal angiosperms rewarewa and titoki.

The probably importance of forest floor cover in limiting regeneration has been discussed by a number of authors , e.g. P. Wardle (1963b), Burrows and Greenland (1979), Veblen et al. (1980). Roughly one half of the 1 m^2 understorey sub-plots in both microtypes 2 (a) and 2 (c) were assessed as predominantly covered by ferns, grasses etc. (Table IX). This ground cover would be expected to significantly reduce the forest floor light intensities from those measured at about 1.4 m above ground , for about one half of the microsites in both forests. Thus the light levels effectively available to small first year seedlings are quite possibly below the 1.8% figure over the greater extent of the xeric forest , as well as on more mesic sites. This is likely to be a vital disadvantage to species with small seed reserves , e.g. totara.

TABLE IX : Forest floor cover assessed from understorey sub-plots.

Forest (micro) type	Total no.of understorey sub-plots	No.of sub-plots with ground cover * > 50% area.
1. Floodplain totara forest	48	13 (27.1%)
2. Terrace forest		
(a) Xeric sites	30	15 (50%)
(b) Tall tawa - dominant.	54	26 (48.1%)
(c) Low mahoe - dominant.	27	7 (25.9%)
Overall	159	61 (38.4%)

* Ferns , grasses etc.

An additional factor which is likely to discriminate against the initial establishment of the young seedlings of small-seeded species such as totara is the accumulation of deep uncompacted litter on the forest floor. On dry sites this litter is slow to decay (especially totara twigs and the large coarse leaves of rewarewa) , and may be a formidable obstacle to the penetration of seedling radicles . The larger seed reserves of rewarewa and titoki are likely to be advantageous for initial growth of the radicle through this layer to reach the more reliable moisture supply of the soil below .

Cameron (1963) suggested a similar explanation as a factor contributing to the lack of rimu regeneration in many Central North Island high forest situations , on free-draining pumice soils. He considered that rimu regeneration may fail because the poorly-developed roots of seedlings growing in heavy shade are unable to penetrate the thick layer of raw humus. The rimu seedlings therefore suffer dessication as a result of competition from the spreading, shallow root systems of mature podocarps which widely pervade this raw humus.

Like rimu, totara seedlings have poor root development when grown under shade (see shoot : root ratios, Table VII). Evidence that the present scarcity of totara regeneration on xeric terrace sites may be partially attributable to some sort of self-suppression effect ,was discussed earlier in this chapter (5.1.2 (c)). Cameron reported that the shallow feeding roots of mature podocarps may extend for a radius of more than 30 feet (9m) from the bole of the tree . It seems not unreasonable to infer from this that root competition could conceivably be implicated in such an auto-inhibition effect , even when only modest densities of podocarp trees (c.11.4 / ha) are present on the terrace xeric sites . Although totara does not appear well-adapted to growth in forest understorey environments, more vigorous regeneration might occur on these sites after surface root competition is reduced by decline and death of the present generation of mature trees.

<u>Kahikatea</u>. Although more abundant in other parts of Totara Reserve, mature trees of kahikatea tend to be localised on the dampest sites of the study areas, which are predominantly well-drained. The species is absent from xeric terrace sites (microtype 2a), with the exception of ephemeral seedlings and a solitary spindling (Fig.24). Throughout type 1 and microtype 2 (b) small stems are generally scarce, although rather better represented than those of totara. Reasonable numbers of kahikatea (and matai) spindlings and large seedlings have become established on some terrace sites (2c) , apparently after windthrow - although understorey light levels on these sites are now similar to those in type 1 and microtype 2 (b). On the majority of the understorey microsites sampled , light intensities were above the compensation point of c.1.0% r.l.i. that was suggested for kahikatea

seedlings by the growth experiments. Therefore it would appear that the understorey light environments are at least survivable for kahikatea seedlings over the greater extent of all four forest microtypes.

After good seed crops, cotyledonary seedlings of kahikatea occur in profusion throughout most parts of Totara Reserve. But as in other forests, most of these do not survive more than one or two summers ; and this massive early mortality is attributed primarily to desiccation (Beveridge, 1980). Kahikatea seedlings will survive only on the least drought-prone microsites (J.Herbert,pers.comm.), and here they must compete with such species as tawa and pukatea . While understorey light levels appear to be mainly above compensation point on those microsites that are sufficiently moist for kahikatea , they are still low enough to place the species' seedlings at a competitive disadvantage relative to those of pukatea . The experimental results suggest that in the range of light intensities typical of moist site forest understoreys, the growth rates of kahikatea seedlings are inferior to those of pukatea (Fig. 26).

As was mentioned earlier in relation to totara,ground cover of ferns may be significant in limiting regeneration. This cover would be expected to further reduce light levels from those measured at breast height (possibly to levels below 1% r.l.i.) over the greater extent of the forest floor in tawa-dominant microtype 2 (b). However this effect would be less significant in type 1 and microtype 2 (c), where the proportion of forest floor cover is lower (Table IX).

Matai is a significant component of most forest types in Totara Reserve. It is consistently present on well-drained sites , and a few matai are also to be found accompanying kahikatea on more moist sites. Although this species was not grown in the seedling experiments, the field studies do suggest matai to be distinctly more tolerant than totara of understorey conditions (cf. Cameron 1960a ; McKelvey 1963), and significant differences are apparent between establishment behaviour of the two species (concurs with McSweeney, 1982).

5.2.4 Conclusions of Light Relations Investigations.

The results of the seedling growth experiments showed that the two podocarp species grown have higher compensation points and lower growth rates under shaded conditions in comparison with two large angiosperm species which tend to replace them as dominants in relatively undisturbed old growth forests. In comparison, the podocarp species perform relatively better at higher light levels (Fig. 26). These results lend plausibility to the light relation causation thesis suggested by Cockayne (1928) in explanation for seral replacement of conifers by various angiosperm species. Clearly, titoki is better adapted than totara to establishment in shaded forest environments, and the same can be said of pukatea relative to kahikatea on more moist sites.

Even though understorey light levels on many microsites appear to be at least survivable for kahikatea seedlings, there are indications that podocarp juveniles become increasingly light demanding for growth through the sapling and pole stages (Cameron 1960a ; Beveridge 1973). Therefore, rising compensation points may mean that many podocarp juveniles perish from absolute light starvation in forest understoreys.

In old growth forests, opportunities for establishment of kahikatea are therefore likely to be rare ,depending on coincidences of favourable circumstances. Consistent with this scenario are the relatively low densities of podocarps on the terrace sites , where active accumulation ceased perhaps 2,000 years ago. The association of podocarp establishment with disturbance is underlined by the higher concentrations of these species on nearby sites where geomorphic processes have intermittently been more recently active e.g. totara on steep unstable scarps , and kahikatea on the lower parts of small alluvial-colluvial fans.

The experimental results suggest that at high light intensities (> c. 25% r.l.i.) the two podocarp species have higher growth rates than their respective large ("forest") angiosperm competitors ; hence they may have a competitive edge in more open situations. But while it appears that massive canopy opening by windthrows does produce some regeneration of podocarps , these situations do not favour their abundant establishment. In windthrow gaps podocarps are likely to be overtopped and suppressed for a time by small faster-growing angiosperm species (e.g. lemonwood, mahoe, pigeonwood); as noted in this study, and earlier described by Beveridge (1980). Pook (1979) showed that growth rates of such "shrub hardwood" species were , at all light intensities, superior to those of large conifers : hence regeneration of conifers tends to be more abundant on those sites least favourable for vigorous growth of "mesophytic" [10] shrub hardwoods (Pook 1979 ; Beveridge 1980).

It is not my intention to suggest that the "light relation" thesis of Cockayne (1928) provides anything like a universal explanation for the causal mechanisms of successional trends, or for "regeneration gaps". Even within the confines of this study, there is evidence suggesting the importance of other factors in influencing the discontinuous regeneration of totara on xeric terrace sites. Additionally, the absence of rimu regeneration remains unsatisfactorily explained. But the results of this study do confirm that kahikatea and especially totara show at least some of the characteristics of light-demanding pioneer species, and are poor competitors under shade. Consequently their establishment is likely to be strongly associated with the early stages of primary successions ; although the field studies show that they will persist on edaphically extreme sites, and also by sporadic regeneration following smaller scale disturbances.

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[10] Refers to large-leaved small angiosperm species that are most competitive on moist, fertile sites e.g. fivefinger , mahoe , pate , pigeonwood .

CHAPTER SIX : SYNTHESIS

It was deemed appropriate to discuss many aspects of this study in the immediate context of the results (Chapter Five), but it remains to present a synthesis which considers the various approaches.

During the early stages of vegetation development on alluvial surfaces , successful establishment is restricted to those species tolerant of frequent flooding and sedimentation (Nanson and Beach, 1977). At Totara Reserve, the flood plain stands described in this study have developed apparently uninterrupted since their initiations - as a result of relatively rapid down-cutting by the river, and favourable channel migrations. However, at other sites on the river , disruption of forest development by sedimentation or by lateral erosion is evident (Fig. 30). The dynamic nature of flood plain ecosystems is well-illustrated by other accounts of New Zealand alluvial forests (Foweraker 1929 ; P.Wardle 1974 ; McSweeney 1982). Young forests on low-lying surfaces are at the mercy of fluctuations in the hydrologic regimen : they are "liable to be destroyed by the same forces which originated them". (P.Wardle, 1974).

The capacity for survival of deep alluviation by production of new (adventitious) root systems (Foweraker, 1929 ; McSweeney 1982) undoubtedly favours totara in these "catastrophe dominated" situations. In California, the same survival device enables redwoods (<u>Sequoia sempervirens</u>) to maintain dominance on low-lying alluvial sites where intermittent flooding and sedimentation eliminate less resilient competitors (Stone and Vasey,1968). Some degree of this capacity is apparently present in many New Zealand flood plain species (Christensen 1923 ; P.Wardle 1974; Grant 1981a,b). But it is particularly well-developed in totara, enabling the species to survive inundation of a severity sufficient to kill all other trees in a stand. Investment in such a device reflects a major aspect of totara's

Fig. 30 : Young kahikatea stand being lost to erosion , Pohangina Scenic Reserve.

ecological strategy : that of extreme site tenacity and resilience in the face of most stresses [1] and disturbances. Once lost to other species, sites are not readily regained by totara.

In the flood plain stands described in this study, totara has established en masse in the early stages of forest development ; probably beneath a gradually opening Leptospermum canopy . In both stands, the conditions favouring totara entry have persisted only briefly . Later recruitment of this shade-intolerant species has been inhibited by increasing vegetation density and competition ; although there is some circumstantial evidence of an autoinhibition effect beneath established totara trees. Matai probably began to establish at much the same stage as totara, but gradual recruitment of this species has continued beneath the flood plain forest canopy - albeit at a declining rate.

The sizes attained by the slow-growing maire [2] in the older flood plain stand suggest that some probably established with the early podocarps . It appears that maire has usually been among the earliest large "forest" angiosperm species to enter - although it has in fact been preceded by tawa throughout much of the younger stand . Maire's preference for youthful mineral soils is clear from its distribution throughout the country (e.g. McKelvey 1963,1973; Nicholls 1956). The establishment patterns in these forests suggest that these species are relatively intolerant of shady understorey environments. A noticeable tendency for maire seedlings to establish on rotting logs and stumps may indicate that root competition inhibits their development on the forest floor.

[1] With the exception of waterlogging (Section 5.1.1 (b)).

[2] Data in Patel (1976) suggest that Nestegis spp.may be among the slowest growing lowland indigenous New Zealand trees.

Titoki has apparently been a consistently early entrant ,but recruitment of this species continues unabated. Its development beneath thinning canopies and small gaps leads to its eventual canopy dominance on sites too dry for tawa.

The size distribution of tawa in the older flood plain stand suggests that this species normally enters a little later ; a strong influx developing beneath the podocarp canopy. However, small stands of tawa have already attained local canopy dominance in some parts of the younger stand , having apparently pre-empted podocarps on these sites. This suggests that tawa is capable of colonising very young mineral soils , but is usually preceded by more rapidly dispersed or faster-growing species [3]. Such an observation is **more** consistent with "tolerance" or "inhibition" successional models than those which emphasize "facilitation" (see Connell and Slatyer, 1977).

Fast growing angiosperms such as kowhai, lemonwood and ribbonwood have exploited occasional canopy gaps in the early stages of flood plain forest development. These are more typically species of seral scrub and forest margins ; their juveniles are rarely found in the forest understorey.The young stands are still subject to occasional inundation and sedimentation, and so the establishment of these trees may be attributable to deaths among some of the less alluviation - resilient canopy species - reflecting an intermittently continuing allogenic influence on canopy replacement, during the first 100-200 years of forest development. But these trees are a very transient phenomenon.They are of limited potential stature and so liable to be overtopped and suppressed by continued growth of the surrounding totaras; in any case their normal longevity probably rarely exceeds 100 years [4] .

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3. Tawa has also established surprisingly early after a fire (c.1900) on a much older terrace site (Greenwood,1949).

4. The statements regarding growth rates and longevities of these species are based on observations of trees known to have established (i) after forest clearance c.1890 near Bulls; (ii) at Totara Reserve after the 1936 gale.

The younger ("C") flood plain stand at Totara Reserve shows a stage approaching 200 years after the commencement of forest development. Nearly all the species that will be significant elements of older forests have already entered. However some of these are as yet only very minor canopy components (e.g. rewarewa , rimu), or have not yet attained canopy status (e.g. pigeonwood), or else are represented at this stage only by occasional juveniles (e.g. hinau).

With continued lowering of the river channel, inundation by floodwaters becomes less frequent , and autogenic influences on forest development gradually increase in relative importance. But floods still occasionally add fresh silt to the forest floor, and soils mature only slowly.

At the stage of the older ("D") stand, about 300 years after initiation, species diversity of the canopy has in fact declined slightly. The totara have overtopped most of their competitors ; the sheer height of the canopy combined with the reduction of flood-related disturbances has meant fewer opportunities for establishment of the seral species present in stand "C". But the understorey layers below have increased in complexity and diversity. Soil moisture retention has increased sufficiently to support a range of shade-tolerant large-leaved angiosperm species throughout most parts. On the most freely-drained sites tawa has still not entered : these probably correspond to the floristically distinctive xeric sites in the older forest on the terrace.

From this stage on the "first generation" podocarps will continue to dominate the forest for several centuries. But as their densities gradually decline, replacement of their ranks is on most sites minimal (mainly matai). This poor replacement appears largely attributable to their intolerance of shade. Small remnants of forest on older surfaces afford sparing glimpses of later stages of first generation development : an increasingly uneven canopy structure, with the gaps between the massive veterans filled mainly by tawa , titoki and mahoe .

In the absence of catastrophic disturbance, the inevitable consequence of this trend is the development of an angiosperm-dominated canopy within 1,000 years of surface initiation. But virgin-forested surfaces in the c.600 to c. 2,000 years B.P. (estimated) age range are very poorly - represented in the study areas. Therefore attempts to reconstruct forest development in this age range can only be dangerously speculative.

The present state of the rimu on the terrace shows that the species has established in significant numbers on relatively young surfaces (c.1,500 - 2,000 years old). The presence of a few massive dead standing northern rata , clearly of epiphyte origin, suggests even earlier entry of rimu. It is clear that in tall tawa-dominant forest there are very few opportunities for regeneration of podocarps, which are poor competitors in the shady understorey on these sites. Large windthrows do appear to stimulate some regeneration of podocarps. But the "regeneration gaps" of podocarp species on the mesic terrace sites remain poorly-understood , and there is no evidence indicative of the mode of establishment of the present rimu. The possibility remains that major exogenous disturbances of unknown nature may have been involved in the establishment of the extant podocarps on the terrace. Concentrations of podocarps in many situations throughout New Zealand may well be testimony to dramatic disturbances of the past, persisting after all other overt evidence of these events has been submerged. But to entertain such an explanation in the absence of independent corroborative evidence would be little more than a convenient circularity .

The picture is perhaps a little clearer for the xeric sites of the terrace. In the virtual absence of tawa ,titoki dominates the canopy , and rewarewa attains its greatest abundance on these sites. The xeric sites appear to be refugia for some flood plain species that have not maintained their position so well on the more mesic sites e.g. maire , totara, turepo. The lower vegetation density and reduced understorey competition has favoured regeneration of those podocarp species tolerant of dry conditions i.e.matai and totara.

This persistence on edaphically extreme sites appears to be a typical "alternative strategy" of shade-intolerant, typically pioneering species (Spurr and Barnes, 1973). Matai appears to be regenerating steadily if not abundantly, and a cyclic discontinuous replacement of totara on these sites seems possible. Thus the present forest structure on these sites seems largely explicable, although it is quite possible that past fires have influenced vegeta ian development.

Future attempts to elucidate the mechanisms of podocarp regeneration in old growth forests are likely to profit from placing more emphasis on understanding the dynamics of the "background" angiosperm species. In most New Zealand forests it is after all the matrix of angiosperms that is probably the major biotic environmental influence on species recruitment patterns. Research directed toward an understanding of spatial and temporal patterns of mortality and regeneration in principal angiosperm species is therefore likely to be of much value.

Status of the Podocarp Species.

It is difficult to find direct ecological equivalents of the podocarps in other forest systems throughout the world. Totara and coastal redwood do show obvious similarities in their strategies of adaption to flood plain environments ,but major differences in replacement potential (and hence successional status) are also evident (cf.Stone and Vasey 1968 ; Wright and Bailey 1982). Predictable recurrence of fire , which facilitates regeneration of various North American long-lived but shade-intolerant conifers (e.g.*Larix occidentalis* , *Pseudotsuga menziesii*) appears not to have been a natural phenomenon in pre-human New Zealand forests.

Totara exhibits many of the attributes of a pioneer species , and indeed on most sites it establishes in abundance only in the early stages of successions. While juveniles show some shade persistence , this study shows them to be shade intolerant , in that their growth rates "in suppression" (Fox ,1977) are poor relative to their principal angiosperm competitors. But even totara,by nature the most pioneering of the podocarp species, does not fit the classic stereotype of an " r-selected " (McArthur and Wilson, 1967) pioneer strategy . Totara's longevity and relatively slow growth rates are rather atypical of early successional species ; opportunities arising in secondary successions are more commonly exploited by small faster-growing angiosperms , rather than podocarps.

Other podocarp species , although also frequently achieving their greatest abundance in the early stages of successions , appear variously further along a gradient of successional character. But they rarely exhibit many-aged and all-aged stands , except on edaphically extreme sites where competition is reduced , or (in the case of rimu) in very high rainfall regions e.g. Veblen and Stewart (1980), June (1982).

Cockayne's interpretation of New Zealand forests was suggestive of coniferous decline and replacement on a grand scale , a theme later expanded by Robbins (1962). The results of recent studies (Clayton-Greene 1977 ; Veblen and Stewart 1982 ; Norton 1983) suggest that any fault in Cockayne's interpretation lay in his under-estimation of the frequency of disturbances and their role in shaping the vegetation. Even on stable flat sites where no dramatic geomorphic processes are active , disturbances by windthrow appear to provide occasional regeneration opportunities , enabling persistence of the longevous conifers as a significant component of the vegetation.

Climatically-induced regeneration failure has been widely suggested as an explanation for discontinuous or "unbalanced" population structures in a variety of situations throughout New Zealand e.g.Holloway (1954b), Nicholls (1956), P.Wardle (1963b). As noted by Norton (1983), the fundamental assumption underlying this argument is that prior to the date of the supposedly-fateful climatic change , these particular species maintained all-aged populations by continuous regeneration in old growth forests , on the sites concerned.

While admittedly of very limited application to the core of the climatic change controversy , the results of this study do suggest that in the case of totara, and probably also kahikatea ,such an explanation is unlikely. Shade - intolerant species such as totara are always likely to be poor competitors in forest understoreys. On level terrace sites opportunities for establishment are likely to be infrequent , and hence densities low. Regeneration of podo - carps following major windthrows , as seems probable for some sites in this study , would be liable to produce discontinuous age and size distributions. On sites where intermittently active geomorphic processes result in soil and vegetation disturbance ,more frequent establishment of species such as totara can be expected.

Clayton-Greene (1977), Veblen and Stewart (1982), and Norton (1983) all arrived at similar findings for kaikawaka (<u>Libocedrus bidwillii</u>), another indigenous conifer species for which climatically-induced regeneration failure has been postulated (P.Wardle 1963b, 1978). Each of these studies, in different localities , concluded that establishment of kaikawaka was associated primarily with disturbances such as windthrow and mass movement , and therefore likely to be of a periodic discontinuous nature.

Nevertheless , climatic fluctuations undoubtedly do influence vegetation dynamics , both directly and indirectly, and the possibility of significant climatic influence on conifer regeneration patterns within the last millenium cannot be discounted. The early proponents of climatic change (e.g. McKelvey 1953 , Holloway 1954, Nicholls 1956) produced very little hard data to support their arguments. But there now appears to be increasing confirmation by quantitative evidence of a generalised widespread depression of <u>rimu</u> regeneration throughout New Zealand , centred on the period c.1,600 to c.1,800 A.D. (Bathgate 1981 ; June 1982). As noted by P.Wardle (1979) there is indeed a "striking coincidence" of this regeneration depression with the climatological record of reduced temperatures within New Zealand over the same period , as established from geo - physical evidence (Burrows and Greenland, 1979).

Bathgate (1981) established a positive relationship between diameter increment of rimu in the Longwood range and recorded air temperatures since 1853. He inferred from this that depressed regeneration rates and "significantly slow" diameter growth of rimu during the 17th. to early 19th. centuries A.D. are both likely to be attributable to "a major cool period". Bathgate's work amounts to some formidable circumstantial evidence for significant recent climatic influence , but still leaves the problem of a mechanism for such an influence , in discriminating against regeneration of rimu and possibly also other conifers. It seems logical that even a slight reduction in growth rate would be a disadvantage to young rimu in the fiercely competitive environment of the forest understorey. But intuitively one would expect a temperature decline to similarly depress growth rates of the associated angiosperm species. Thus one might expect a general downhill migration of vegetation zones , rather than a widespread uni-directional shift in the competitive balance between species previously coexisting on the same sites.

It is possible that rimu and other indigenous conifers are more sensitive than are their angiosperm competitors to small changes in certain climatic factors. Bathgate's (1981) work would be complemented by an examination of the diameter increment trends of some of the longer-lived angiosperm species of the Longwood forests, to determine if their growth rates during the 17th. to early 19th. centuries suffered a decline similar to that found for rimu. But whatever circumstantial evidence is amassed ,I suggest that the problem is likely to be resolved only when comparative experiments have determined the precise effects of small changes in climatic parameters on the growth of the various species concerned.

Conclusion similar to those of Clayton-Greene (1977) and Veblen and Stewart (1982) for kaikawaka cannot necessarily be extended to populations of other indigenous conifers.There is no doubt that a range of establishment modes occurs throughout the different species; and equally that the behaviour of any one species varies with regional and site differences in soils , climate and associates .

APPENDIX I : LIST OF INDIGENOUS PLANT NAMES

Throughout the text , scientific names are generally used in the first reference to each species. Common names only are used in subsequent references , except for those species which have no well-established English or Maori name ,or which are better known by their scientific names e.g. Melicope simplex. Scientific names only are used also for certain species (e.g. Syzygium maire), in order to avoid possible ambiguities in interpretation of English or Maori names . Unless indicated otherwise , nomenclature follows Allan (1961) , Edgar (1973) and Moore and Edgar (1970) .

Common name	Scientific name
black beech (= tawhai)	Nothofagus solandri var.solandri
cabbage tree	Cordyline australis
five finger	Pseudopanax arboreus
hangehange	Geniostoma linguistrifolium
hinau	Elaeocarpus dentatus
kahikatea	Podocarpus dacrydioides
kaikawaka	Libocedrus bidwillii
kaikomako	Pennantia corymbosa
kamahi (= tawhero)	Weinmannia racemosa
kanuka (= tree manuka)	Leptospermum ericoides
kauri	Agathis australis
kawakawa	Macropiper excelsum
kohuhu (= tuwhiri)	Pittosporum tenuifolium
kotukutuku	Fuchsia excorticata
kowhai	Sophora microphylla
lacebark	Hoheria sexstylosa
lancewood	Pseudopanax crassifolius
lemonwood	Pittosporum eugenioides
mahoe	Melicytus ramiflorus
maire	Nestegis cunninghamii (Hook.f.) L.Johnson. N. lanceolata " (hook.f.)
manuka	Leptospermum scoparium

Common name	Scientific name
mapau (= matipo)	*Myrsine australis*
matai	*Podocarpus spicatus*
miro	*Podocarpus ferrugineus*
nikau	*Rhopalostylis sapida*
northern rata	*Metrosideros robusta*
pate	*Schefflera digitata*
pigeonwood	*Hedycarya arborea*
pukatea	*Laurelia novae-zelandiae*
rangiora	*Brachyglottis repanda*
rewarewa	*Knightia excelsa*
ribbonwood	*Plagianthus betulinus*
rimu	*Dacrydium cupressinum*
rohutu	*Lophomyrtus obcordata*
silver fern	*Cyathea dealbata*
supplejack	*Ripogonum scandens*
tanekaha	*Phyllocladus trichomanoides*
tawa	*Bielschmiedia tawa*
titoki	*Alectryon excelsus*
toetoe	*Cortaderia toetoe* Zotov
totara	*Podocarpus totara*
turepo	*Paratrophis microphylla*
wineberry	*Aristotelia serrata*

APPENDIX II : Samples of completed data sheets for Plot P 10 , older floodplain stand.

Plot No. P10 Dimensions 25x16 Date 3/11/82

Site OCR Dense Podocarp "250 yr". Site now quite damp - a little water standing in channel. Many totara dead/moribund - waterlogging?

Canopy Podocarps 27-35 m - crowns almost meeting

Tier Structure Sparse T_1 & T_2 under canopy. v. Dense understorey, much supplejack.

I

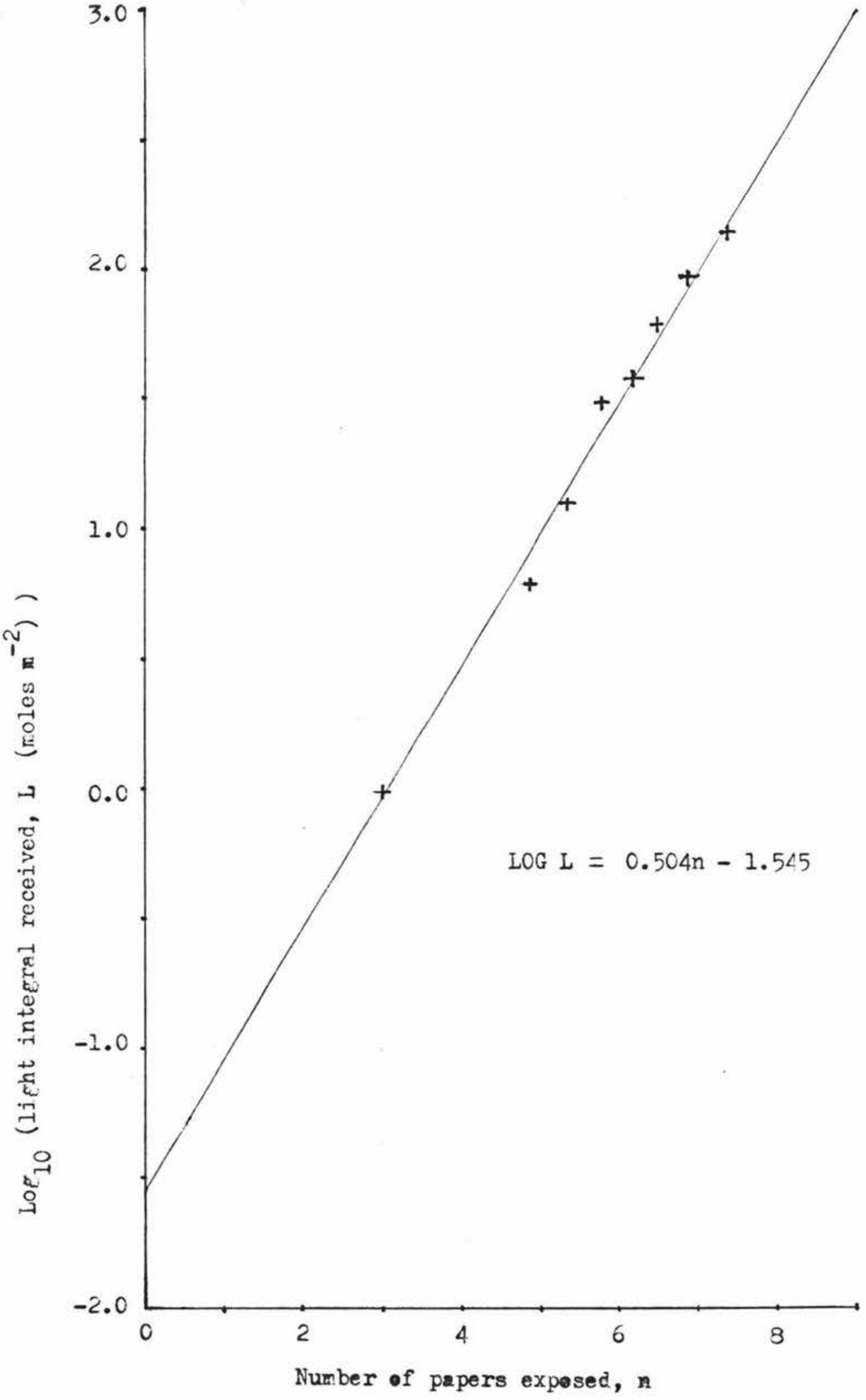
Species	Circum	Tier	Overhead	Species	Circum	Tier	Overhead
Mel ram	—	3	Bei taw	Pen cor	—	3	Pod tot
Sch dig	6	3	"	Bei taw	20	2	"
Sch dig	5	3	Pod tot	Sch dig	—	3	"
"	4.5	3	"	Bei taw	—	3	"
Sch dig	9.5	3	"	Pod tot	65	2	"
"	5	3	"	DEAD - top broken			
ulram ~~Sch dig~~	5	3	"	Bei taw	6	3	"
Sch dig	3	3	"	Mel ram	11	3	"
Cop gra	5	3	"	Mel ram	5.5	3	"
Hed arb	3.5	3	Bei taw	Ale exc	67	2	"
Mel ram	—	3	Pod tot	Mac exc	10.5	3	"
Mel ram	—	3	"	Mel ram	3	3	"
Sch dig	4.5	3	"	Mel ram	—	3	"
Mac exc	12	3	"	Hed arb	6.5	3	"
Mel ram	3	3	"	Mac exc	3	3	"
Gen lin	5	3	"	Gen lin	—	3	"
Hed arb	4	3	"	Mel ram	—	3	"
Mac exc	13.5	3	"	Cop bel	—	3	"
Gen lin	3.5	3	"	Hed arb	—	3	"
Cop gra	3	3	"	Hed arb	3	3	"
Cop gra	6.5	3	"	Bei taw	7	3	"
Kni exc	3	3	"	Mel ram	3	3	"
Ale exc	29	2	"	Mel ram	3	3	"
Mel ram	—	3	"	Pod tot	≥286	0	—
Mel ram	—	3	"	Butt rot - some wastage on			
Bei taw	4.1	2	"	one side of tree			
Pod tot	147	0	—	Hed arb	4.5	3	Pod tot
Mel ram	—	3	Pod tot	Gen lin	3	3	"
Gen lin	5	3	"	Sch dig	4.5	3	"

PLOT NO P10 DIMENSIONS 25x16 DATE 3/11/82

SITE OCR Dense Podocarp 250 yr

Seedling Sp	I		J		K		L		M		N		O		P	
	<15<		<15<		<15<		<15<		<15<		<15<		<15<		<15<	
Bel taw		1		1		0+1			1	1		1	1		1	1
Hed arb	1		2						1		2		1		3	
Asp bul		✓										✓		e		
Mac exc				0+1												
Ale exc			1	1		2					1		1		1	
Lau nov			2	1					1							
Pru mic								0+1		2						
Carex								✓								
Mac exc							4									
Dac dac							1								2	
Mel ram					1	0+1										
Gen lin						0+1			1		1					
Lop obc					1											
Ble flu						✓								✓		
Polystichum						✓				✓		✓				
Sch dig								1								
Pod spi											1				1	
Pas tet														1		1
Overhead																
T1	Pod tot		Gap/Totara		Totara		Matai / Nestegis		Light totara		Totara		Nestegis		Totara	
T2	Ale exc/Kip		–		Tawa		Tawa		Titoki		–		Tawa		–	
T3	Sch dig (dense)		Dense mixture		Light mix		Light mix		Sch dig		Mixed		Neg		Pennantia / Dense mix	
Comments																
Mk ave														✓		

APPENDIX III : Relationship between number of diazo papers exposed and $\log_{10}$ light integral received in sunlight.



APPENDIX IV : SIZE CLASS DATA FOR ALL TREE AND SHRUB SPECIES FROM PLOT SAMPLES.

IV (a) Younger flood plain stands (3 x 400 m^2 plots)

SPECIES	Stem diameter at breast height (cm)						
	0–2.5	2.5–10	10–20	20–30	30–40	40–50	50–60
Dicksonia squarrosa			1				
D. fibrosa					1		
Dicksonia sp.			3				
Cyathea dealbata	7		1				
Podocarpus dacrydioides	2			1	3		
P. spicatus	3	6	2	2	2		
*P. totara		0^{+2}	2^{+3}	7	15	10	6
Beilschmiedia tawa	12	13	5	3			
Hedycarya arborea	54	3					
Macropiper excelsum	51	67					
Melicytus ramiflorus	211	66	4				
Knightia excelsa	78	3	1	1			
Pittosporum eugenioides	1				1		
Lophomyrtus bullata	9	2					
L. obcordata	20	21					
Elaeocarpus dentatus	2	1					
Plagianthus betulinus	1						
Hoheria sexstylosa	7						
Sophora microphylla					1		
Paratrophis microphylla	15	5	1				
Pennantia corymbosa	1	1	2				
Melicope simplex	2	1	1				
Alectryon excelsus	105	5	5	1	1		
Schefflera digitata	3						
Myrsine australis	1	4					
Nestegis spp.	2	11	3				
Geniostoma ligustrifolium	65	97					

* Numbers of dead standing totara stems in each diameter class shown in superscript.

SPECIES	Stem diameter at breast height (cm)							
	0	2.5	10	20	30	40	50	60
Coprosma rotundifolia	1							
C australis	5	1						
Coprosma sp.	1							
Brachyglottis repanda	1							
Rhopalostylis sapida	1							

Seedling Samples : from 48 x 1 m^2 understorey sub-plots.

Species	Seedling Height Classes (cm)		
	<15 cm.	15 - 50	50 - 140
Podocarpus dacrydioides	5		
P. spicatus	10		
P. totara			
Beilschmiedia tawa	16	5	1
Hedycarya arborea	48	5	1
Macropiper excelsum	164	7	1
Melicytus ramiflorus	23	12	2
Knightia excelsa	2	13	2
Pittosporum eugenioides	3		
Lophomyrtus obcordata	1	1	
L.bullata x obcordata		1	
Hoheria sexstylosa		1	
Paratrophis microphylla	15	14	2
Corynocarpus laevigata		1	
Pennantia corymbosa	12	14	1
Melicope simplex	7	1	
Alectryon excelsus	103	41	11
Schefflera digitata	3		
Pseudopanax crassifolius	1		
Myrsine australis	1		
Nestegis spp.	3		
Geniostoma ligustrifolium	18		

APPENDIX IV

IV (b) Older flood plain stand.
(6 x 400 m^2 plots

Species	Stem diameter at breast height (cm)											
	0	2.5	10	20	30	40	50	60	70	80	90	100 110
Dicksonia squarrosa		3	2									
Cyathea dealbata	5		5	4								
C.medullaris		1		2								
Podocarpus dacrydioides								1	1			
P. spicatus	2			1	1	2	1	1				
P.ferrugineus		1										
P. totara			1^{+1}	2^{+1}	6	3^{+2}	4^{+1}	10	8^{+1}	2	4	1
Beilschmiedia tawa	275	92	23	2	1							
Hedycarya arborea	163	36	9	0	1							
Laurelia novae-zelandiae	45	25	2	1								
Macropiper excelsum	96	139	4									
Melicytus ramiflorus	249	81	23	3								
Knightia excelsa	14	3										
Lophomythus bullata	6	1										
L. obcordata	26	7										
L.bullata x obcordata ?	1	1										
Elaeocarpus dentatus	1											
Plagianthus betulinus	1											
Hoheria sexstylosa	4											
Carpodetus serratus	1											
Paratrophis microphylla	49	5	1	1	1							
Pennantia corymbosa	7	5	1									
Melicope simplex		2	3									
Alectryon excelsus	58	20	18	7	2							
Schefflera digitata	123	17										
Pseudopanax crassifolius		1										
Myrsine australis	1											
Nestegis spp	1		1	2	1		1					

Species	Stem diameter at breast height (cm) 0	2.5	10	20	30	40
Geniostomaligustrifolium	106	15				
Coprosma rotundifolia	2					
C. australis	30	5				
Brachyglottis repanda	2					

Seedling samples : from 80 x 1 m^2 understorey sub-plots

Species	Seedling height classes (cm) <15	15 - 50	50 - 140
Podocarpus dacrydioides	14		
P. spicatus	10		1
P. totara	1		
Pseudowintera colorata	3		
Beilschmiedia tawa	43	34	8
Hedycarya arborea	95	20	6
Laurelia novae-zelandiae	14	5	1
Macropiper excelsum	76	1	4
Melicytus ramiflorus	11	20	7
Knightia excelsa	1		
Lophomyrtus obcordata	4	3	2
Hoheria sexstylosa	6		
Plaganthus betulinus	1		
Paratrophis microphylla	16	30	7
Pennantia corymbosa	4	2	
Melicope simplex	13	4	
Alectryon excelsus	69	21	5
Schefflera digitata	2	2	3
Myrsine australis	1		
Nestegis spp.	23		
Coprosma rotundifolia	2		
C. australis	2	2	1
Coprosma sp.	2		

APPENDIX IV

IV (c) Terrace Xeric Sites
(5 x $150m^2$ plots)

Species	Stem diameter at breast height (cm)									
	0	2.5	10	20	30	40	50	60	120	130
Cyathea dealbata	3		2	1						
Podocarpus spicatus	3									
P. totara									1	
Beilschmiedia tawa	10	2	2	2						
Hedycarya arborea	10	13	2	1						
Macropiper excelsum	8	25								
Melicytus ramiflorus	34	14	9	2	1					
Knightia excelsa	39	25	10	11	2					
Lophomyrtus obcordata	6	1								
Hoheria sexstylosa	2									
Prunus cerasifera	3									
Paratrophis microphylla	7	2								
Melicope simplex	1	5								
Alectryon excelsus	26	41	34	4	3					
Pseudopanax crassifolius				1						
Myrsine australis	4	6	4							
Nestegis spp.	2									
Geniostoma linguistrifolium	5	1								
Coprosma rhamnoides	3									
C. australis	2	1								
Brachyglttis repanda	15	2								

Seedling Samples: from 30 x $1m^2$ understorey sub-plots.

Species	Seedling height classes (cm)		
	< 15	15-50	50-140
Podocarpus spicatus	2		
P. totara	3		
Hedycarya arborea	34	1	
Macropiper excelsum	12	1	
Melicytus ramiflorus	2		3
Knightia excelsa	18	1	
Pittosporum eugenioides		1	
Paratrophis microphylla			1
Melicope simplex		1	
Alectryon excelsus	25	24	3
Myrsine australis	3	2	1
Nestegis spp.	2	2	
Geniostoma linguistrifolium	3	1	
Coprosma sp.	2	2	

Appendix IV

IV (d) Terrace mesic sites
(14 x 150m^2 plots)

Species	0	2.5	10	20	30	40	50	60	70	80
Dicksonia Squarrosa	1									
Cyathea dealbata	13		21	9						
C. medullaris			1							
Podocarpus dacrydioides	1									
P. spicatus	1							1		
P. ferrugineus	1									
P. totara	1									
Beilschmiedia tawa	55	34	21	12	14	6	5	3	1	
Hedycarya arborea	72	84	13	1						
Laurelia novae-zelandiae	21	4	3	1						
Macropiper excelsum	16	17								
Melicytus ramiflorus	101	44	47	11	2	1		1		
Knightia excelsa	64	21	6	2	1					
Lophomyrtus bullata	5									
L. obcordata	2									
Elaeocarpus dentatus	1			1						
Aristotelia serrata		2								
Hoheria sexstylosa	4									
Carpodetus serratus	1									
Paratrophis microphylla	10									
Pennantia corymbosa	1									
Alectryon exccelsus	63	29	28	4	2					
Schefflera digitata	5									
Myrsine australis	6	4								
Nestegis cunninghamii	1									
Geniostoma linguistrifolium	17	6								
Coprosma australis	10	2								
C. lucida	1									
Brachyglottis repanda	4									

Seedling samples: from 84 x $1m^2$ understorey sub-plots

Species	Seedling height classes (cm) >15	15–50	50–140
Podocarpus dacrydioides	22	1	
P. spicatus	7	2	
P. ferrugineus	1		
P. totara	11		
Beilschmiedia tawa	11	9	2
Hedycarya arborea	107	17	2
Laurelia novae-zelandiae	54	2	
Macropiper excelsum	65	2	2
Melicytus ramiflorus	9	7	3
Knightia excelsa	27	2	1
Pittosporum eugenioides	1		
Elaeocarpus dentatus	6		
Paratrophis microphylla		1	
Pennantia corymbosa	4	1	
Melicope simplex		1	
Allectyon excelsus	57	49	11
Schefflera digitata	1		
Pseudopanax crassifolius	1		
Myrsine australis	6	7	1
Nestegis spp.	8	1	
Geniostoma linguistrifolium	2	1	2
Coprosma australis	5	1	1
Coprosma sp.		1	

APPENDIX V: Totara ring count data used for age estimates in Tables II and III.

Circumference at b.h. (cm)	Boring height(cm)	Rings on core	Estimated missing rings	Correction for boring height*	Estimated total age
Younger Stands					
65.5	70	113	10	9	132
82	70	128	5	9	142
96	70	140	0	9	149
96.5	70	134	2	9	145
117	70	137	2	9	148
131	70	147	1	9	157
180	70	144	2	9	155
Older Stand					
91	70	199	0	9	208
108.5	70	221	4	9	234
130.5	70	225	5	9	239
147	70	214	8	9	231
182	140	234	15	14	263
198	140	242	1	14	257
222	140	211	9	14	234

* Correction figures derived from sections of three totara saplings, which suggested on average time of about 9 years for growth to 70cm height, and an additional 5 years to reach 140 cm.

APPENDIX VI: Canopy - understorey association data, showing frequencies of principal tree species spindlings beneath different canopy trees in terrace forest.

(a) Xeric Sites

		Canopy Species						
Spindling		Totara	Mahoe	Rewarewa	Titoki	Others	GAP	TOTAL
Mahoe	0	8	1	0	18	5	2	34
	E	3.74	2.04	8.16	14.96	3.40	1.70	
	X^2	–	–	↓.005	N.S.	–	–	
Rewarewa	0	3	6	4	16	1	9	39
	E	4.29	2.34	9.36	17.16	3.40	1.95	
	X^2	–	–	N.S.	N.S.	–	–	
Titoki	0	2	5	9	4	5	1	26
	E	2.86	1.56	6.24	11.44	2.60	1.30	
	X^2	–	–	N.S.	↓.05	–	–	
Others	0	0	6	9	20	3	2	40
	E	4.40	2.40	9.60	17.60	4.00	2.00	
	X^2	–	–	N.S.	N.S.	–	–	
TOTAL	0	13	18	22	58	14	14	139

Expected values ("E") calculated on the basis of the areal proportions of the various species' canopy cover.

(b) Mesic Sites

		Canopy Species						
Spindling		Tawa	Pigeonwood	Mahoe	Titoki	Others	GAP	TOTAL
Tawa	O	19	7	14	9	4	2	55
	E	22.61	2.37	13.97	9.02	4.68	2.37	
	X^2	N.S.	–	N.S.	N.S.	–	–	
Pigeonwood	O	42	2	9	11	3	5	72
	E	29.59	3.01	18.29	11.81	6.12	3.01	
	X^2	↑.025	–	↓.05	N.S.	N.S.	–	
Mahoe	O	65	2	4	17	7	6	101
	E	41.51	4.34	25.65	16.56	8.59	4.34	
	X^2	↑.001	–	↓.001	N.S.	N.S.	–	
Rewarewa	O	39	1	8	12	1	3	64
	E	26.30	2.75	16.26	1.97	5.44	2.75	
	X^2	↑.025	–	↓.05	–	N.S.	–	
Titoki	O	29	9	17	3	2	3	63
	E	25.89	2.71	16.00	4.92	5.36	2.71	
	X^2	N.S.	–	N.S.	N.S.	N.S.	–	
Others	O	15	4	25	9	0	2	55
	E	22.61	2.37	13.97	9.02	4.68	2.37	
	X^2	N.S.	–	↑.005	N.S.	–	–	
TOTAL	O	209	25	77	61	17	21	410

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