Dynamics of kahikatea forest remnants in middle North Island: implications for threatened and local plants

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CONTENTS

Abstract

A suite of threatened and local plant species is associated with some lowland kahikatea-dominated forest stands on alluvial plains, but many seemingly similar stands do not contain these feature species. We collected data from 8 stands of kahikatea, 3 with threatened or local species and 5 without, to investigate this difference. The stands sampled, though outwardly similar in appearance, showed considerable difference in species composition, hydrology and climate. The large number of threatened and local plants at Paengaroa Scenic Reserve is attributable to an uncommon climate selecting for light-canopied, semi-deciduous canopy species associated with kahikatea, and an unusually diverse regional species pool. At Mapara and Mangapu, threatened or local plants are associated with sites that possess high soil moisture and/or high fertility. Analysis of stand development suggests that whereas the Paengaroa, Mapara, and Mangapu stands are fragments of the forest cover present at the time of European settlement (sometimes modified by partial logging), stands in the Waikato are younger and are artefacts of European settlement. The probability that threatened or local plant species will be present in any stand depends on the historically-determined regional species pool, whether the stand fulfils the often specific requirements of candidate species, and on whether the stand has been a persistent part of the landscape or is a recent product of landscape history.

1. Introduction

In April 1998, two kahikatea[1]-dominant forest remnants containing threatened or local plant species (Paengaroa Scenic Reserve, Rangitikei Ecological District, and Mapara Scenic Reserve, Waitomo Ecological District) were surveyed by Landcare Research, Hamilton, for Science & Research Unit of the Department of Conservation, and the results compared with surveys of similar forest remnants with and without threatened or local species mostly within the Waikato Ecological Region (Burns et al. in press; unpubl. data).

2. Background

A suite of 'threatened' or 'local' plant species (as defined in Cameron et al. 1995 but see de Lange & Norton 1998 for an alternative classification system of uncommon plants) is associated with some lowland kahikatea-dominated forest

[1] Scientific and common name equivalents are given in Appendix 1.

stands on alluvial plains in New Zealand (e.g. *Coprosma obconica*, *Myriophyllum robustum*, *Mazus novaezeelandiae* subsp. *novaezeelandiae* (Heenan 1998), *Pittosporum obcordatum*). However, many seemingly similar stands do not contain these feature species. Have these species been lost from these latter stands, and should conservation management seek to restore populations, or are there fundamental differences in stand ecology which limit the types of stands in which such threatened or local species occur ?

This research addresses the following questions:

- Does the structure and dynamics of kahikatea forest stands without threatened or local species differ from those of kahikatea stands elsewhere containing these species?
- What are the implications for threatened plant management of continuing successional trends in kahikatea stands (i.e. self-thinning of kahikatea, invasion by shade-tolerant species)?
- What are appropriate restoration goals for alluvial kahikatea stands?

3. Objectives

- To compare the species compositions and stand age- and size-structures of kahikatea-dominated forest stands with and without populations of threatened or local plant species.
- To determine the implications for threatened plant management and the design of appropriate restoration goals of compositional variation and continuing stand development of this forest type.

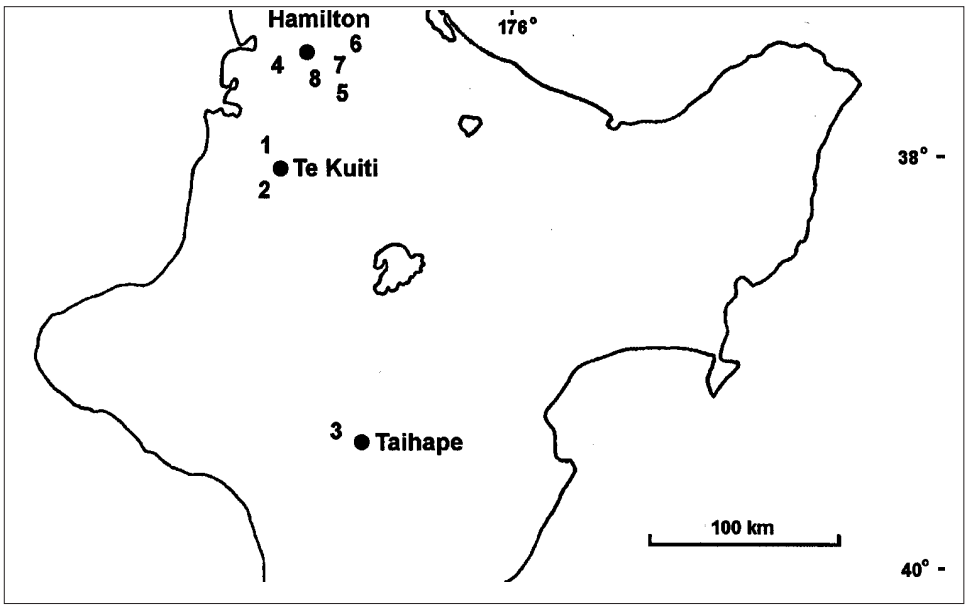

Figure 1. Location of study sites in North Island. 1. Mangapu River Forest, 2. Mapara Scenic Reserve, 3. Paengaroa Scenic Reserve, 4. Frontier Rd Bush, 5. Garrett Open Space Covenant, 6. Marychurch Rd Bush, 7. Whewell's Bush Scientific Reserve, 8. Yarndley's Bush.

4. Methods

4.1 STUDY STANDS

Eight stands were sampled (Figure 1, Table 1); 3 with threatened or local species and 5 without. The 3 stands with threatened or local species were Paengaroa Scenic Reserve, Mapara Scenic Reserve, and Mangapu River Forest (Table 1). Paengaroa Scenic Reserve is renowned for its array of divaricating shrubs unparalleled elsewhere in the country (Druce & Ogle 1991, Ogle & Barkla 1995, Lake & Whaley 1995). Some 30 species are present, including 8 'threatened' species (Ogle & Barkla 1995). Mapara Scenic Reserve and Mangapu River Forest are less endowed with threatened or local species; *Teucridium parvifolium* has been recorded at Mapara (Bayfield et al. 1986) and *Myriophyllum robustum* at Mangapu (de Lange & Compton 1985). Nicholls (1975) and Champion (1988) also described the Mangapu stand. Nicholls records that this stand was logged in 1930–34 and again in 1940–41 for the larger trees.

The five kahikatea-dominated stands without threatened or local plant species are: Frontier Rd Bush, Garrett Open Space Covenant, Marychurch Rd Bush, Whewell's Bush Scientific Reserve, and Yarndley's Bush (Table 1). Previous botanical notes on Whewell's Bush Scientific Reserve are provided by Boase (1984), Irving & Skinner (1985), and Champion (1988), and on Yarndley's Bush by Edmonds (1982).

TABLE 1. TENURE, SIZE, ALTITUDE AND LOCATION OF STUDY SITES, AND PRESENCE OF THREATENED OR LOCAL PLANT SPECIES.

NAME	TENURE	SIZE (ha)	ALTITUDE (m asl)	NZMS260 GRID REF.	ECOLOGICAL DISTRICT
Sites with threatened or local plant species					
Mangapu River Forest	Private	52	50	S16 965205	Waitomo
Marpara Scenic Reserve	DOC	7	150	S17 933012	Waitomo
Paengaroa Scenic Reserve	DOC	102	530	T21 433697	Rangitikei
Sites without threatened or local plant species					
Frontier Rd Bush	Private	6	40	S15 057539	Waipa
Garrett Open Space Covenant	QEII Trust Covenant	7	50	S15237 537	Hamilton
Marychurch Rd Bush	Private	5	50	S14 228738	Hamilton
Whewell's Bush Scientific Reserve	DOC	12	50	S14 201728	Hamilton
Yarndley's Bush	Waipa District Council Reserve	15	40	S15 135552	Hamilton

4.2 FIELD SAMPLING

At each study area except Paengaroa and Mapara, a transect was established trending north-south through the widest part of each stand. Four 20m x 20m plots were then positioned along this transect, with one 10m from each of the northern and southern edges, and two others in the interior of the stand equidistantly spaced along the transect between the two edge plots (24 plots). At Paengaroa, two 30m x 30m and at Mapara two 20m x 20m plots were placed in apparently homogeneous areas of alluvial kahikatea forest (4 plots). Floristic composition and species cover abundance of all 28 plots were described using the 'reconnaissance' (RECCE) technique of Allen (1992). We then identified the species and measured the dbh of all woody stems >2.5 cm. Because of the high density of saplings (2.5–10 cm dbh) at Paengaroa, diameters of these were recorded in 10×10 m subplots. Between 8–12 kahikatea trees (and matai where this was co-dominant) were selected mostly within these plots for coring, so that ages were assessed from the full range of tree diameters. The largest kahikatea trees in the stands were also cored. Cores were mounted and surfaced by sanding to reveal growth rings. Age estimates were gained by counting these using a binocular microscope. If cores missed the pith, the age of the missing portion was estimated using the geometric model of Duncan (1989) applied to the arcs of the inner growth rings. No corrections were made to allow for growth to coring height in reported age estimates because of the absence of kahikatea seedlings growing in appropriate conditions in most stands.

4.3 DATA ANALYSIS

The stand compositional data were classified using two-way indicator analysis (TWINSPAN: Hill et al. 1975). Names for vegetation types recognised followed the conventions of Atkinson (1985). Densities and basal areas for individual species and stands were computed. Population size-class distributions for kahikatea and, where common, matai were determined.

5. Results

5.1 SPECIES COMPOSITION

We recognised 4 forest assemblages from the TWINSPAN classification of sample plots which summarise the variation in species composition encountered (Figure 2). All are dominated by kahikatea in the canopy but differ substantially in canopy associates, understorey composition and density.

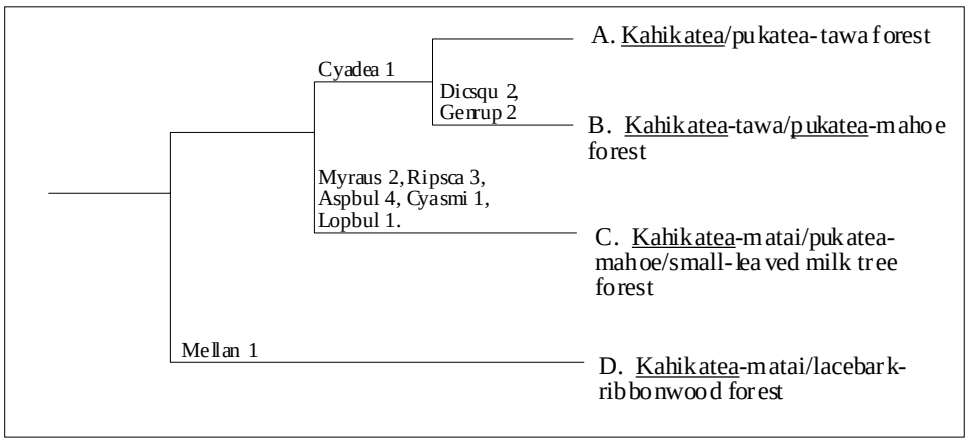

Figure 2. TWINSPAN dendrogram classifying 28 plots from 8 kahikatea-dominated forest stands into 4 vegetation associations. Indicator species names at each division abbreviated to first 3 letters of the genus and species names. Indicator species names followed by importance value on a 5-point scale of increasing abundance. Scientific and common name equivalents given in Appendix 1.

A. Kahikatea/pukatea-tawa forest

This association occurred on the edges of five of the Waikato study sites and in the interior of the grazed Marychurch Rd Bush. Kahikatea forms a dense canopy over a sparse subcanopy of pukatea and tawa. The open shrub tier is dominated by mahoe, the adventives Jerusalem cherry and Chinese privet, and the ferns *Hypolepis ambigua* and *Histiopteris incisa*. *Blechnum filiforme*, *Deparia petersenii*, and Jerusalem cherry are important as groundcover species. Notable features of this association are the open understorey and high diversity and abundance of adventive species compared to the other associations sampled. We found 28 adventive plant species in plots classified in this association and only 10 in the other three associations combined (Table 2). Species such as Jerusalem cherry and Chinese privet contribute significantly to the biomass in this association but adventives are insignificant components in all other associations.

B. Kahikatea-tawa/pukatea-mahoe forest

In contrast to the previous association, this forest association summarises the composition of the interior of the Waikato study sites. Kahikatea again forms a dense canopy in association with tawa and occasional pukatea and titoki. Pukatea and mahoe form the subcanopy with the shrub tier dominated by seedling pukatea and mahoe, the tree ferns ponga and wheki, and by the ferns *Diplazium australe* and hen and chickens fern. Groundcover is dominated by *Blechnum filiforme, Phymatosorus scandens, Diplazium australe* and *Metrosideros diffusa*.

TABLE 2. PLOT NUMBER AND SIZE, PLANT SPECIES RICHNESS PER PLOT, AND INDIGENOUS, ADVENTIVE AND TOTAL PLANT SPECIES RICHNESS OF ALL PLOTS FOR KAHIKATEA-DOMINATED FOREST ASSOCIATIONS.

				PLANT SPECIES RICHNESS IN ALL PLOTS		
ASSOCIATION	NO. OF PLOTS	PLOT SIZE	SPECIES/PLOT	INDIGENOUS	ADVENTIVE	TOTAL
A	9	20 m x 20 m	37.4	93	28	121
B	13	20 m x 20 m	30.9	87	9	96
C	4	20 m x 20 m	43.8	95	0	95
D	2	30 m x 30 m	54.5	65	2	67

C. Kahikatea-matai/pukatea-mahoe/small-leaved milk tree forest

Plots classified into this association were those at Mapara and one each from Mangapu and Frontier Bush. Soils of all these plots are persistently wet, with some having permanent shallow pools of water present. The vegetation comprises a dense stand of kahikatea with some matai over a sparse subcanopy of pate, mahoe, swamp maire, and small-leaved milk tree. Pukatea and swamp maire were also components of the subcanopy at Mangapu and Frontier Bush. The dense shrub tier is dominated by *Coprosma grandifolia* but also includes *Melicytus micranthus*, horopito, hen and chickens fern, and pigeonwood. Groundcover species include *Phymatosorus scandens*, *Uncinia uncinata*, *Hydrocotyle* spp., *Leptopteris hymenophylloides*, and *Microlaena avenacea*. Despite careful searching, the threatened shrub *Teucridium parvifolium* was not relocated during fieldwork at Mapara, although it may still be present.

D. Kahikatea-matai/lacebark-ribbonwood forest

This association only occurred at Paengaroa. It consists of kahikatea and matai emergent above a scattered subcanopy of lacebark, kohuhu, and ribbonwood and a dense shrub tier of divaricates dominated by *Coprosma rotundifolia*, weeping mapou, and poataniwha. Groundcover was provided by *Mycelis muralis, Polystichum vestitum, Poa anceps, Asplenium gracillimum, Uncinia* spp., and *Hydrocotyle elongata*.

Stands with threatened or local species generally occurred in associations C and D of this classification. These two associations had high levels of species richness per plot and low numbers of adventive species (Table 2). Association D at Paengaroa had the highest number of species per plot.

5.2 DENSITIES AND BASAL AREAS

Densities of stems >2.5 cm diameter ranged from 706–6839 stems per hectare (Table 3) and basal areas from 48.5–116.9 m^2 ha^{-1} (Table 4). However, those stands with threatened or local species (Mangapu, Mapara, Paengaroa) had higher stem densities and lower basal area than those stands without these species. High stem density at Mangapu, Mapara and Paengaroa is attributable to high densities of understorey species, e.g mahoe, *Coprosma grandifolia*, pate, *Hoberia angustifolia*, *Coprosma rotundifolia*, weeping mapou, and poataniwha. Low basal area at these same 3 stands generally correlates with lower kahikatea basal area relative to the 5 other stands sampled. Tables 3 and 4 also emphasise the differences in associated species composition between stands, with Mapara and Paengaroa particularly different.

TABLE 3. DENSITY (STEMS/ha >2.5 cm dbh) OF MAJOR SPECIES IN KAHIKATEA-DOMINANT STANDS WITH (MANGAPU, MAPARA AND PAENGAROA) AND WITHOUT (FRONTIER, GARRETT'S, MARYCHURCH, WHEWELL'S AND YARNDLEY'S) THREATENED OR LOCAL SPECIES BASED ON SAMPLE PLOTS. * = SPECIES PRESENT IN STAND OUTSIDE SAMPLE PLOTS.

SPECIES	MANGAPU	MAPARA	PAENGAROA	FRONTIER	GARRETT'S	MARYCHURCH	WHEWELL'S	YARNDLEY'S
Melicytus ramiflorus	1638	329	0*	244	450	194	219	950
Laurelia novae-zelandiae	850	0	0	763	88	88	213	188
Dacrycarpus dacrydioides	844	288	328	444	275	250	138	388
Alectryon excelsus	419	0*	0	0*	6	0*	38	0*
Beilschmiedia tawa	75	38	0	63	0*	75	263	6
Dicksonia squarrosa	31	13	0	6	44	0*	25	69
Streblus heterophyllus	31	325	0*	0	0	0	56	0*
Prumnopitys taxifolia	6	250	577	0	0*	6	0*	0*
Coprosma grandifolia	0*	488	0*	6	0*	0	0	0
Schefflera digitata	0*	338	0*	56	331	0	0*	0*
Dicksonia fibrosa	0*	213	61	0	0	0	0	0*
Hoberia sexstylosa	0	0	622	0	0	0	0	0
Pittosporum tenuifolium	0*	0*	228	0	0	0	0	0
Coprosma rotundifolia	0*	0*	1500	0	0	0	0	0
Myrsine divaricata	0	13	678	0	0	0	0	0
Melicope simplex	0*	13	650	0	0	0	0	0
Others	412	880	2195	62	75	93	104	74
Total	**4306**	**3175**	**6839**	**1644**	**1269**	**706**	**1056**	**1675**

TABLE 4. BASAL AREA (m2/ha, STEMS >2.5 cm dbh) OF MAJOR SPECIES IN 8 KAHIKATEA-DOMINANT FOREST STANDS WITH (MANGAPU, MAPARA AND PAENGAROA) AND WITHOUT (FRONTIER, GARRETT'S, WHEWELL'S AND YARNDLEY'S) THREATENED OR LOCAL PLANT SPECIES ON SAMPLE PLOTS. * = SPECIES PRESENT IN STAND OUTSIDE SAMPLE PLOTS.

SPECIES	MANGAPU	MAPARA	PAENGAROA	FRONTIER	GARRETT'S	MARYCHURCH	WHEWELL'S	YARNDLEY'S
Dacrycarpus dacrydioides	63.8	31.2	45.1	108.5	91.3	77.3	57.3	111.8
Laurelia novae-zelandiae	15.3	0	0	3.2	8.3	10.4	6.7	1.5
Melicytus ramiflorus	4.4	0.4	0*	0.7	0.8	0.9	2,5	2.1
Alectryon excelsus	2.9	0*	0	0	0.4	0*	5.7	0*
Syzgium maire	2.7	0	0	<0.1	0	0	0	0
Dicksonia squarrosa	0.5	0.2	0	<0.1	0.5	0*	0.3	0.8
Beilschmiedia tawa	0.4	<0.1	0	0.4	0*	2.8	17	0.1
Prumnopitys taxifolia	0.4	3.4	17.2	0	0*	<0.1	0*	0*
Dicksonia fibrosa	0*	6.8	4.9	0	0	0	0	0*
Plagianthus regius	0*	0*	3.3	0	0	0	0	0
Schefflera digitata	0*	0.5	0.1	<0.1	0.5	0	0.1	0*
Cyathea dealbata	0*	0*	0*	0*	0.4	0*	1.1	0*
Knightia excelsa	0*	0*	0	0	0	0	0.8	0
Others	0.8	5.9	18.1	0.5	0.1	0.9	0.4	0.6
Total	**91.2**	**48.5**	**88.6**	**113.3**	**102.3**	**92.4**	**91.9**	**116.9**

5.3 SIZE AND AGE DISTRIBUTIONS

Kahikatea size distributions were mostly dominated by stems between 20–90 cm diameter and a much smaller number of stems >100 cm in diameter (Figures 3, 4). Mangapu, Mapara, and Paengaroa were exceptions to this pattern. Mangapu was dominated by stems 0–50 cm diameter with no larger stems (Fig. 3). Mapara and Paengaroa had the majority of kahikatea stems <20 cm and infrequent larger stems up to 160 cm in diameter (Fig. 4).

There was much less variation in age than for size of kahikatea stems (Figs 3, 4). At Frontier Rd Bush, Garrett OSC, Yarndley's Bush, and Whewell's Bush Scientific Reserve, the majority of stems were even-aged at 80–120 years old with the few larger stems much older (200–500 years). Mangapu River Forest also had a cohort of stems approximately 100 years old along with a group of younger stems 30–70 years old. Most stems at Marychurch Rd Bush were also even aged although here most stems were about 200 years old.

In contrast, kahikatea at Paengaroa and Mapara did not show such a clear cohort structure, with many ages represented. At Paengaroa, kahikatea stems ranged in age from 76 to 716 years old and at Mapara from 48 to 316 years old (Fig. 4).

Matai was only common at Paengaroa and Mapara with populations dominated by stems <20 cm diameter and <100 years old (Figure 5). However, larger matai (60-100cm diameter) were much older (up to an estimated 1358 years at Paengaroa).

Growth rates of kahikatea in most of the Waikato stands (Frontier, Garrett OSC, Whewell's Bush, and Yarndley's) were significantly higher than those stands with threatened or local species (Mangapu, Mapara, and Paengaroa) and Marychurch Rd Bush (Table 5). The fastest growing stands of kahikatea had high diameter growth rates compared to published rates for native species (Wardle 1991, p. 478–479). Matai grew more slowly than kahikatea at Mapara and Paengaroa.

TABLE 5. MEAN DIAMETER GROWTH RATES OVER THE WHOLE LIFE OF TREES FOR KAHIKATEA AND MATAI IN 8 FOREST STANDS.

	MEAN DIAMETER GROWTH RATE (cm/yr)	
NAME	KAHIKATEA	MATAI
Mangapu River Forest	0.39	-
Mapara Scenic Reserve	0.31	0.18
Paengaroa Scenic Reserve	0.19	0.11
Frontier Rd Bush	0.60	-
Garrett Open Space Covenant	0.78	-
Marychurch Rd Bush	0.30	-
Whewell's Bush Scientific Reserve	0.49	-
Yarndley's Bush	0.56	-

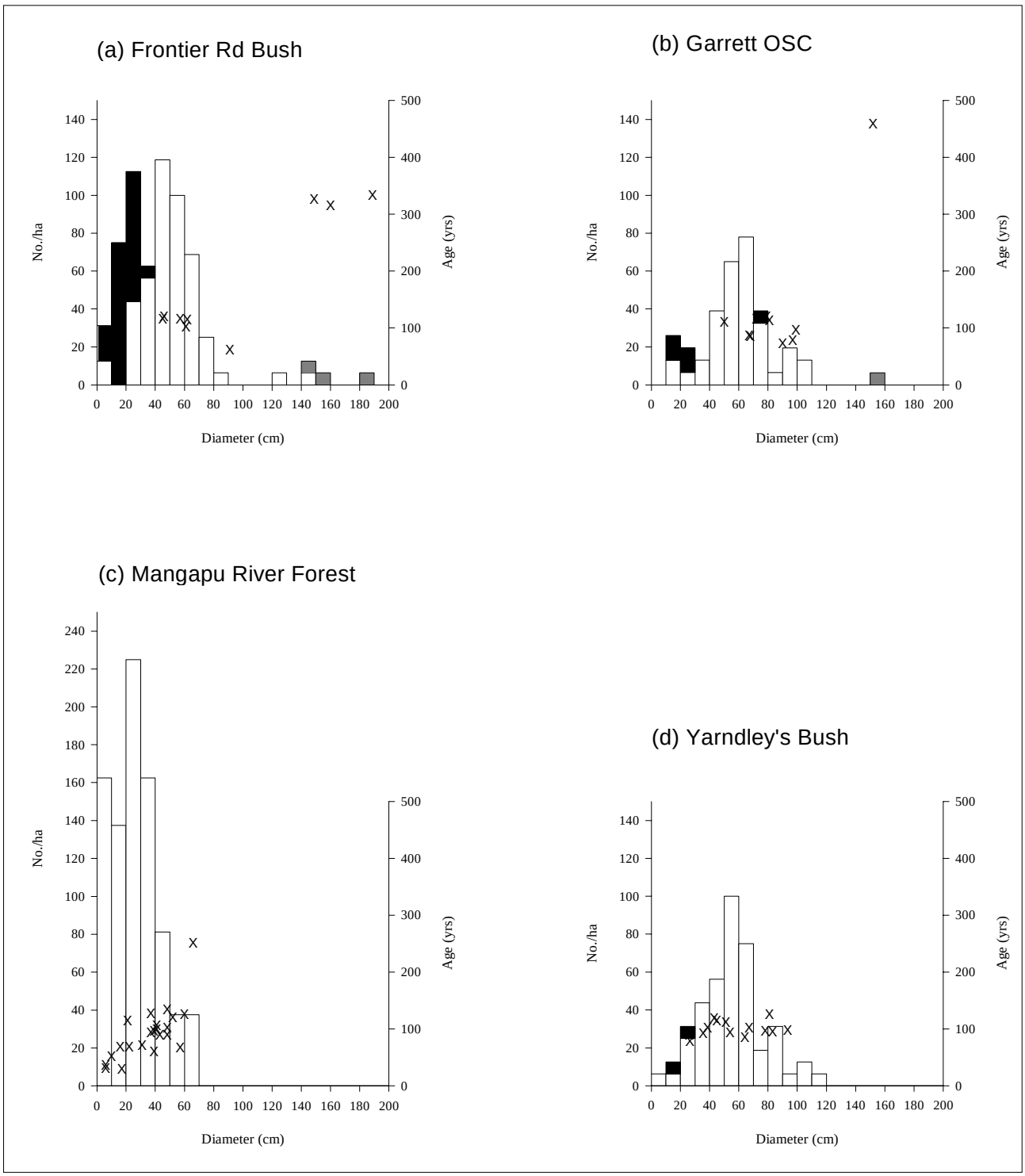

Figure 3. Size-class frequency distributions of stem diameter and plots of age versus diameter for *Dacrycarpus dacrydioides* populations at (a) Frontier Rd Bush, (b) Garrett Open Space Covenant, (c) Mangapu River Forest, and (d) Yarndley's Bush.

= live stem = dead stems = supplementary stems sampled outside plots

X = age estimates of cored trees

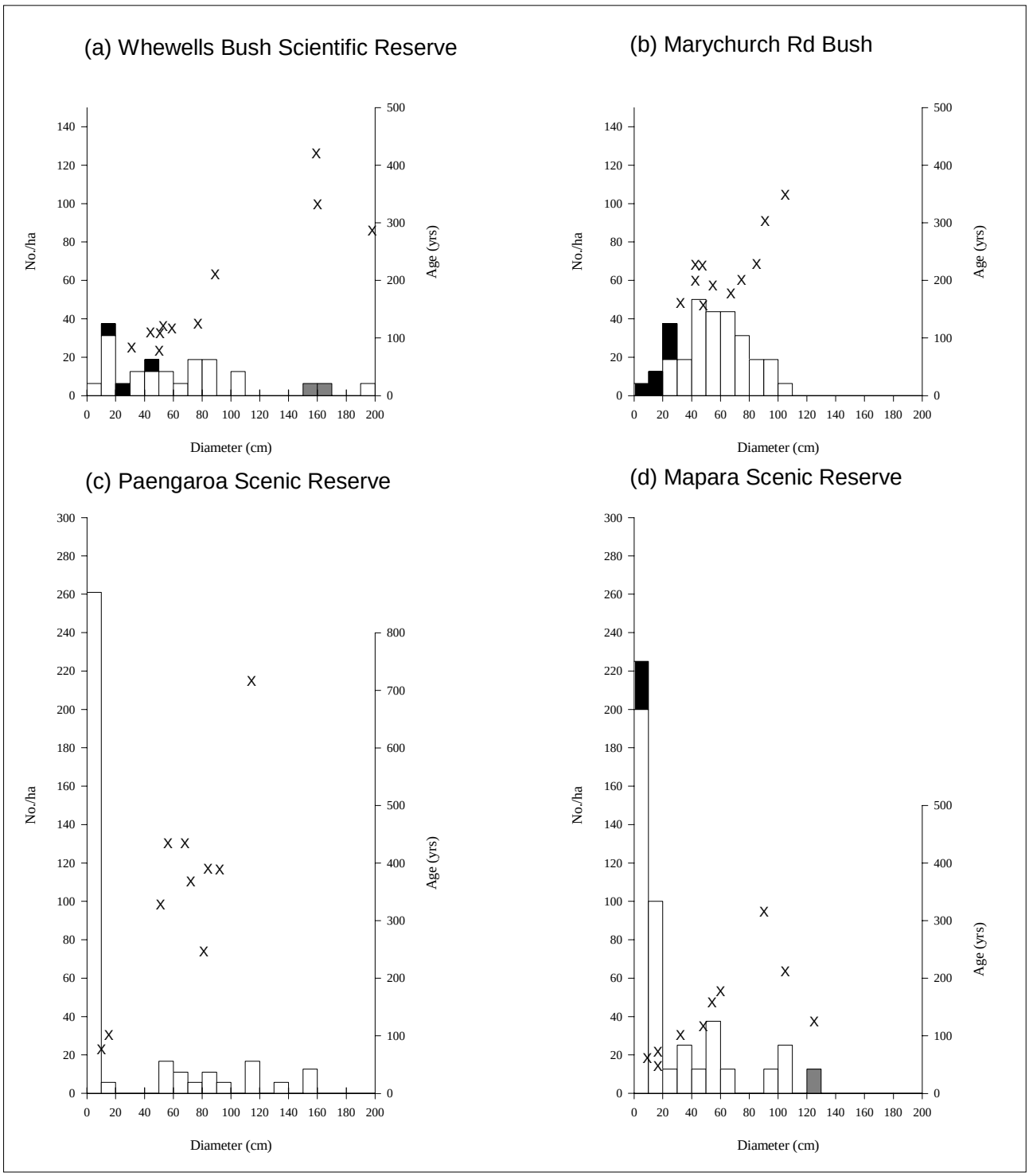

Figure 4. Size-class frequency distributions of stem diameter and plots of age versus diameter for *Dacrycarpus dacrydioides* populations at (a) Whewell's Bush Scientific Reserve, (b) Marychurch Rd Bush, (c) Paengaroa Scenic Reserve, and (d) Mapara Scenic Reserve.

□ = live stem ■ = dead stems ▨ = supplementary stems sampled outside plots

X = age estimates of cored trees

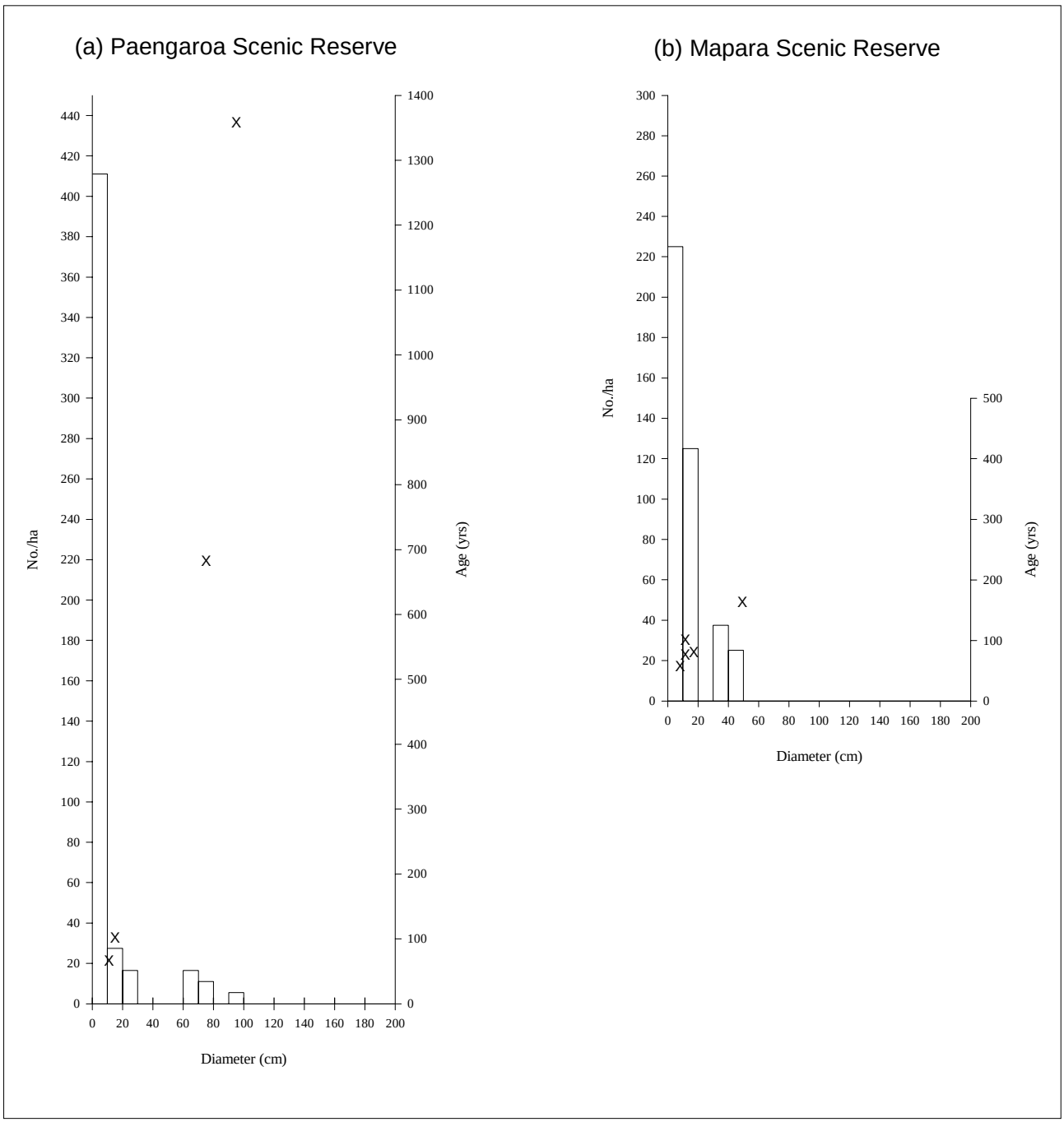

Figure 5. Size-class frequency distributions of stem diameter and plots of age versus diameter for *Prumnopitys taxifolia* populations at (a) Paengaroa Scenic Reserve and (b) Mapara Scenic Reserve. X = age estimates of cored trees.

6. Discussion

The kahikatea stands sampled, though outwardly similar in appearance, show considerable differences in species composition. Some of these differences in species composition can be attributed to differences in the physical environment. For example, Paengaroa is at much higher altitude (Table 1) and has a cooler and drier climate than the other remnants, also experiencing frequent, extreme frosts (Table 6). In contrast, Mapara and Mangapu (and parts of Frontier Bush) have wetter soils, with areas more subject to prolonged and, perhaps, permanent inundation than the other remnants. These specific combinations of environmental conditions form habitats which can be suitable for the often particular requirements of threatened or local species.

At Paengaroa, some tree species typically associated with alluvial kahikatea in the middle and northern North Island, i.e. pukatea, tawa, and titoki, are absent because of the dry and/or cool conditions. Their place is taken by ribbonwood and lacebarks. These species cast less shade and are also semi-deciduous compared to the dense shade characteristic of the absent evergreen broadleaved trees. The consequent higher light levels in the understorey allows a range of threatened or local plants that are relatively light-demanding yet frost-tolerant to exist in the understorey, e.g. *Pittosporum obcordatum, Coprosma obconica* (Ogle & Barkla 1995). The presence of kohuhu, a seral species characteristic of early successional stages to tall forest in much of the North Island, in the subcanopy and understorey also indicates unusually high light levels within the forest here. The semi-swamp forests at Mapara and Mangapu also provide habitat for threatened or local species, although these are associated with wetland forest and/or high-fertility alluvial soils. For example, the aquatic herb, *Myriophyllum robustum* occurs in permanent pools of stagnant water at Mangapu and *Teucridium parvifolium* occurs on high-fertility alluvial soils at Mapara.

Differences in species composition between stands can also be attributed to the historical biogeography of the regions in which they occur. This determines the regional species pool or pools from which the component species of each stand

TABLE 6. MEAN ANNUAL TEMPERATURE, MEAN ANNUAL PRECIPITATION, AND AVERAGE DAYS OF GROUND FROST FOR CLIMATIC STATIONS CLOSEST TO WAIKATO (RUKUHIA), KING COUNTRY (TE KUITI) AND PAENGAROA (HIWI, TAIHAPE) STANDS.

CLIMATE STATION	MEAN ANNUAL TEMPERATURE (°C)	MEAN ANNUAL PRECIPITATION (mm/yr)	AVERAGE DAYS OF GROUND FROST (days/yr)
Rukuhia	13.7	1240	29.5
Te Kuiti	13.5	1531	47.3
Taihape	10.4	941	63.4

can possibly be drawn. At Paengaroa, Ogle & Barkla (1995) argue that historical links with the eastern North Island, since broken, allowed this area to accumulate species characteristic of this regional species pool, as well as species of the western forests. With forests of the eastern North Island now greatly reduced in extent (Grant 1996), many species characteristic of this region are considered threatened.

Other differences in composition may be attributable to the effects of surrounding land use. Plots established on the edges in the Waikato stands consistently had different composition than plots in the interior of the same stands. Edge plots had higher diversity and abundance of adventive weed species, higher light levels and a poorly developed understorey. Some of these differences are caused by trampling and grazing by cattle around the edges of stands, as stands where cattle had access to the interior had species composition similar to edge plots.

The population size- and age-structures of kahikatea and matai suggest three different patterns of stand history and development occurring at Paengaroa, King Country (Mapara and Mangapu), and in the Waikato (Frontier, Garrett OSC, Marychurch, Whewell's, and Yarndley's).

At Paengaroa, the high understorey light levels already referred to have allowed kahikatea and matai, among the more light demanding of the tall New Zealand conifers, to establish and survive abundantly as saplings and small trees. The larger trees in the forest probably represent successful saplings that have grown slowly to maturity over centuries without the need for clearly-defined canopy gaps. Therefore, we interpret the population structure of kahikatea and matai at Paengaroa as indicative of 'old-growth' forest that regenerates by continuous replacement. The forest at Paengaroa is certainly 'old-growth'. The maximum estimated age recorded for kahikatea was 716 years, and 1358 years for matai at Paengaroa Scenic Reserve. Normal longevity is 450 years in kahikatea and 600 years in matai (Enright and Ogden 1995).

In the King Country, both Mapara and Mangapu have high numbers of kahikatea (and matai at Mapara) <20 cm diameter and <100 years old but few older large diameter stems > 80 cm diameter (of kahikatea at Mangapu and of matai at Mapara). This pattern is probably a response to relatively recent partial logging at both sites which would have removed the larger stems, while leaving large gaps for recolonisation by light-demanding kahikatea and matai seedlings. Bayfield et al. (1986) report that Mapara was logged, and this probably occurred in the early decades of the 20th century (Roche 1990). Mangapu was logged in the 1930s and 1940s (Nicholls 1975). Therefore, both Mapara and Mangapu are examples of original 'old-growth' forest regenerating after partial logging.

The five kahikatea forest remnants in the Waikato region generally show similar size and age structures, dominated overwhelmingly by a dense cohort of trees of similar size and age. A few large (>1 m diameter) kahikatea trees usually between 350 and 450 years old are surrounded by a dense cluster of small to medium-sized (30–90 cm diameter) trees aged 80–120 years old which form the majority of the stand. This structure suggests that these forest remnants largely originated as a result of the drainage and clearance associated with land development for agriculture in the 1870s to 1890s (Burns et al. in press). Other observations related to forest development in these stands, e.g. death of the

smallest stems (self-thinning) and the invasion of more shade-tolerant species such as tawa (*Beilschmiedia tawa*) and titoki (*Alectryon excelsus*), are consistent with this interpretation. The Waikato stands, therefore, are not 'old-growth' stands but were formed by kahikatea acting opportunely to colonise large gaps created by anthropogenic disturbance. In these stands, kahikatea may have colonised habitats not normally available to it under natural disturbance regimes or in the presence of then-absent competitors.

Marychurch Rd Bush was notable amongst the Waikato stands as the cohort of kahikatea on this site all established approximately 200 years ago. The disturbance event that initiated this stand is unknown, although many stems are elevated above the ground on root plates shaped to suggest that trees established on fallen logs. This suggests that stand-initiation followed a blowdown.

This analysis of stand development suggests that whereas the Paengaroa, Mapara, and Mangapu stands are 'old-growth' and essentially fragments of the forest cover present at time of European settlement, the Waikato stands are much younger (Marychurch Rd excluded) and are essentially artefacts of European settlement.

Growth rates of kahikatea at Paengaroa, Mapara, and Mangapu are about half those in the Waikato remnants (Table 5). To some extent this may reflect the younger average age of the Waikato stands; diameter growth rates in podocarps tend to peak during the pole-small tree phase and decline somewhat thereafter (see Herbert 1980). But it may also reflect the relatively harsh climate at Paengaroa, Mapara, and Mangapu compared with that of the more equable Waikato lowlands.

Podocarps are regenerating in old-growth forest at Paengaroa, Mapara, and Mangapu and major changes in structure and composition are not expected in the foreseeable future. Thus habitat for 'threatened species' is likely to persist. By contrast, stand structure and composition is likely to change considerably in the Waikato stands as they progress through the 'understorey re-initiation' stage and into old-growth forest. An eventual decline in kahikatea dominance and concomitant increases in the importance of broadleaved species already present are likely. It is unlikely that most of the threatened or local species present at Paengaroa would be found within the Waikato stands for habitat and biogeographic reasons, and these should not be considered within any future restoration projects. However, habitats suitable for the threatened or local species found at Mapara and Mangapu may be found in parts of the Waikato stands.

Three of the stands sampled (Mangapu River Forest, Frontier Rd Bush, and Marychurch Rd Bush) are still in private ownership and depend on the goodwill of landowners and the variably-interpreted provisions of the Resource Management Act for their conservation. Proposals for the acquisition and reservation of the Mangapu River Forest have occurred several times in the past (e.g. Nicholls 1975, de Lange & Compton 1985) without success. Over that time, clearances by landowners (including loss of several hectares as recently as 1996) have decreased total area from 125 ha (Nicholls 1975) to 52 ha currently. We recommend that DOC renew investigations towards reservation of these three stands.

Dense stands of kahikatea-dominated forest were once common on alluvial surfaces throughout New Zealand (Wardle 1974). Those remnants that remain, though outwardly similar in appearance, differ substantially in species associated with the kahikatea, and in their history (reflected in population age structures). The probability that threatened or local plant species will be present in these stands also differs, depending on whether the stand fulfils the often specific requirements of the threatened or local species, on historical biogeography of the species themselves, and on whether the stand has been a persistent part of the landscape or is a recent product of landscape history.

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Appendix 1

SCIENTIFIC NAME	COMMON NAME[2]
Alectryon excelsus	titoki
Asplenium bulbiferum	hen and chickens fern
Beilschmiedia tawa	tawa
Cyathea dealbata	ponga
Cyathea smithii	soft tree fern
Dicksonia squarrosa	wheki
Dacrycarpus dacrydioides	kahikatea
Dacrydium cupressinum	rimu
Geniostoma rupestre	hanghange
Hedycarya arborea	pigeonwood
Hoheria sexstylosa	lacebark
Laurelia novae-zelandiae	pukatea
Ligustrum sinense	Chinese privet
Lophomyrtus bullata	ramarama
Melicope simplex	poataniwha
Melicytus lanceolatus	narrow-leaved mahoe
Melicytus ramiflorus	mahoe
Myrsine australis	mapou
Myrsine divaricata	weeping mapou
Pittosporum tenuifolium	kohuhu
Plagianthus regius	ribbonwood
Prumnopitys taxifolia	matai
Pseudowintera colorata	horopito
Ripogonum scandens	supplejack
Schefflera digitata	pate
Solanum pseudocapsicum	Jerusalem cherry
Streblus heterophyllus	small-leaved milk tree
Syzygium maire	swamp maire

[2] Nicol (1997)