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Structure and dynamics of kanuka (*Kunzea ericoides* var. *ericoides*) heaths on sand dunes in Bay of Plenty, New Zealand

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Abstract The structure, composition, and dynamics of a rare coastal community, kanuka (*Kunzea ericoides* var. *ericoides*) shrub- and tree-heaths on sand dunes, were studied on Whale Island and at Thornton, in Bay of Plenty. Both multi-stemmed, semi-prostrate and erect kanuka is present in virtually pure stands on largely unconsolidated dunes on Whale Island, and multi-stemmed, semi-prostrate kanuka in nearly pure stands on consolidated dunes at Thornton. This and other studies indicate that lack of competition (i.e. establishment at low densities) is primarily responsible for the multi-stemmed habit, but interacting environmental (exposure, drought) and genetic factors may also play a part. All communities are floristically poor compared with other woody communities in New Zealand, with only widespread species present and a large proportion of adventives. Mean annual diameter growth was 3.0 mm/yr at Whale Island and 2.8 mm/yr at Thornton; mean annual height growth ranged from 29.8 cm/yr in younger stands (6–18 years) on Whale Island to 10.2 cm/yr in older stands (27–34 years), and 10.5 cm/yr at Thornton. All populations had regenerated in cohorts over periods ranging from c. 5 to c. 35 years, after fire removed previous vegetation or sand became sufficiently stable for seedlings to establish. Kanuka may replace itself indefinitely on unstable dunes on Whale Island, where the community is still expanding, and at Thornton, which is isolated from seed sources of potential successors.

Keywords kanuka; *Kunzea ericoides*; sand dunes; ecology; succession

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INTRODUCTION

Woody plant communities are rare on coastal sand dunes in New Zealand, and the study of their ecology is in its infancy here, as elsewhere in the world (Ranwell 1972). Before human settlement of New Zealand some 1000 years ago and ensuing widespread forest destruction, the sclerophyllous tree kanuka or white teatree (*Kunzea ericoides**) was largely confined to sites too dry or too frequently disturbed (e.g., sand dunes) to support high forest (Burrows 1973). Kanuka is still a frequent component of shrub- and tree-heaths on coastal sand dunes in the far north of the North Island, where var. *linearis* occurs (Cockayne 1911). Elsewhere in the island, kanuka heaths (var. *ericoides*) are now very rare on dunes but remnants survive on the South Kaipara spit (Cameron & Bellingham 1986; Cameron 1987, 1988), at Hautai near East Cape (Regnier et al. 1988), and in the eastern Bay of Plenty. Here, unusual semi-prostrate growth forms occur (Fig. 1), distinct from the fully prostrate forms known as var. *microflorum* which occur inland on hydrothermally altered soils.

Dwarfing of usually erect woody species in coastal sites can be due to a variety of factors; direct salt spray effects such as chloride ion toxicity (Boyce 1954) may be more important in determining form than wind effects *per se* (Parsons 1981). Salt spray enters plants via abrasion wounds, leading to death of leaves and stems, and hence asymmetrical growth forms (Boyce 1954). Although the exact mechanisms are not fully understood, salt spray selects for low growing forms with slow height growth.

This study describes the structure and composition of kanuka scrub and forest on sand dunes at Thornton and Whale Island, in the eastern Bay of

*Nomenclature for vascular native species apart from ferns follows Cheeseman (1925) and Allan (1961), except where updated by Connor & Edgar (1987), and for adventive species follows Webb et al. (1988). Ferns follow Brownsey & Smith-Dodsworth (1989), and mosses follow Beever et al. (1992).

Fig. 1 Multi-stemmed, semi-prostrate kanuka on old blowout dunes at Thornton, Bay of Plenty. *(Photo: G. F. Pardy)*

Plenty; uses relationships between population parameters and age (in place of unavailable time-series data) to emulate the development of individual stands over time; examines possible determinants of the semi-prostrate growth form—unusual in this species—occurring in both localities; and examines size and age data to trace the history and review the successional status of these communities.

STUDY AREAS

Whale Island (Motuhora)

The study area at the western end of Whale Island (Motuhora) (NZMS 260, W15/589643) occupies largely unconsolidated dunes behind Boulder Bay (Fig. 2), which have accumulated in the late Quaternary since the island's formation by tectonic and volcanic activity (Ramsay & Hayward 1971). It lies within the White Island Ecological District of the Northern Volcanic Plateau Ecological Region (McEwen 1987) and was purchased by the Crown in 1984 as a nature reserve. Dune soils are recent, derived from wind-blown rhyolitic pumice sand, and very free draining (Rijkse 1980). Climate is mild and humid, with a mean annual rainfall of 1200–1600 mm falling on c. 120 days with a marked winter maximum. Mean annual temperature is c. 14°C, with a mean January (midsummer) temperature of 19°C and a mean July (midwinter) temperature of 9°C (New Zealand Meteorological Service 1985). Winds of all speeds have a slight north-westerly predominance, while strong winds have a marked south-westerly predominance (Tomlinson 1976).

Sheep (*Ovis aries*) were grazed on the island during the Second World War; goats (*Capra hircus*) were present in considerable numbers for at least a century until 1977 (Jordan 1989; Ogle 1990). Rabbits (*Oryctolagus cuniculus*), present since 1968, have now all but disappeared (Ogle 1990).

Pah Hill, at the western end of the island, was earlier occupied periodically by Maori (Hayward 1971), and a number of middens have been identified near the study area (Hayward et al. 1990). From 1838, the island was occupied sporadically for nearly a century. Accommodation huts built in the study area during the First World War were removed in 1924 (Garaway 1976; Moore 1987); European artifacts were found during the present study. A fire in January 1975 at the western end of the island burnt

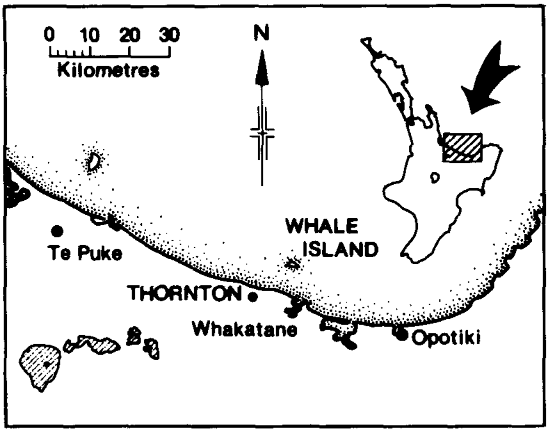

Fig. 2 Location of the study areas.

some of the study area (Ogle 1990); another, smaller fire in 1978 also burnt part of the study area.

The vegetation of the study area in 1970 was silvery sand grass (*Spinifex sericeus*) with kanuka locally important (Parris et al. 1971); two sizeable patches of kanuka scrub were mapped. Photographs in Ogle (1990) show the expansion of kanuka between 1970 and 1986, to cover a present area of c. 3.5 ha.

Thornton

The study area at Thornton (NZMS 260, V15/ 483593) occupies consolidated foredunes that have been formed by coastal progradation since the Kaharoa eruption c. 700 years ago (Pullar & Selby 1971) and older blowout dunes behind them. It falls within the Te Teko Ecological District of the Whakatane Ecological Region (McEwen 1987). Soils are recent, derived from wind-blown sand, itself derived from rhyolitic pumice, and overlain by a very thin, patchy layer of basaltic ash (Tarawera Ash, 1886). They are very free draining and have sandy textures throughout. Up to five buried soils occur within the top metre in some swales, indicating a long history of instability (Pullar 1985). Climate is mild and humid, with a mean annual rainfall of 1300–1350 mm falling on c. 120 days with a marked winter maximum. Mean annual temperature is about 14°C, with a mean midsummer temperature of 18°C and a mean midwinter temperature of 8°C (New Zealand Meteorological Service 1985; Pullar 1985). Prevailing winds are similar to those at Thornton. Thus, soil and climate are very similar at the two study areas, although soils may be somewhat more fertile at Thornton because of the presence of basaltic ash.

The central Bay of Plenty coastline has a long history of Maori presence, with evidence of human occupation around A.D. 1300 less than 2 km from the study area (Pullar 1961); an 1867 map of the district shows several pa sites on the dune system. Cultural artifacts and charcoal are common in the locality (A. Moore pers comm.) and, together with the eroded nature of the blowout dunes, which is thought to have been accelerated by Polynesian and early European burning (Pullar 1961; Pullar & Selby 1971), suggest a long fire history. The most recent fire, in the mid 1940s, destroyed some kanuka scrub to the east of the reserve before being extinguished (A. Moore pers. comm.).

Agricultural development began in the locality after the First World War, and the study area was grazed by domestic stock until very recently. Kanuka forest (var. *ericoides*) presently occurs on c. 25 ha of consolidated foredunes, mostly in fenced Crown reserve, and on c. 20 ha of older blowout dunes on grazed freehold land behind them, and has been described briefly by Beadel (1987).

METHODS

Data collection

Whale Island

In the absence of long-term plots, 14 temporary square plots ranging from 1.5 × 1.5 m to 10 × 10 m were systematically placed in homogeneous stands of kanuka scrub and forest, of varying ages, which initially were broadly estimated by canopy height and the range of diameters present. All plots were on flat ground, within 200 m of the sea. Plot size was variable and chosen so as to include at least 15 kanuka plants in each. Diameters and heights of all stems, living and dead, were recorded in each plot. The largest stem of each of c. 10 plants (covering the entire diameter range of the plot) was cut and a basal (above-ground) section obtained for aging. Discs were sanded to clarify ring boundaries, and rings were counted under a binocular microscope. Kanuka has moderately distinct to distinct growth rings (Meylan & Butterfield 1978), assumed to be annual. Some problems were encountered with false (intra-annual) rings. Ground cover of each plot was estimated using seven semi-quantitative cover classes (0–1, 2–5, 5–25, 25–50, 50–75, 75–95, 95–100%).

Thornton

Because of very difficult internal access within much of the kanuka community here, individual plots were not sampled. Instead, a temporary linear transect, 2 m wide, was placed in the widest part of the stand, perpendicular to the shoreline, beginning at mean high water mark and running 600 m inland. In order to examine the relationship between canopy height and topography, the transect was divided into 37 sections of uniform slope, slope angles being measured by hypsometer, and distances inland also recorded. Within each section, species, basal diameters, heights, and crown dimensions (longest axis and axis perpendicular to it) of all stems >2.5 cm dbh living and dead were recorded, along with number of stems per plant and number of plants per section. The largest stem of each plant was cut and a basal section obtained for aging. Canopy height was recorded at the section junctions. Ground cover of individual species was estimated in each section (within the ungrazed reserve only) as at Whale Island.

Analysis

Linear regressions of mean largest diameter (i.e. the mean diameter of the largest stem of each plant) on mean age did not differ significantly between semi-prostrate and erect stands on Whale Island, so a single line was fitted over all plots. The nature of the basal area/age relationship (none) and of the diameter/age relationship (a linear fit) implied a relationship between stand density and mean age of the form:

$$\text{Density} = \frac{a}{\text{Age}^2}$$

where a is a constant.

At Thornton, crown dimensions indicated that most were more-or-less elliptical in shape, so crown areas were calculated using the formula for an ellipse:

$$\text{Area} = \frac{\pi AB}{4}$$

where A = longest diameter and B = diameter perpendicular to it.

Relationships between plant statistics (age, number of stems, diameter, length, basal area, crown area) and distance inland were examined by fitting quadratic functions, and tested using Mann-Whitney tests.

RESULTS

Whale Island

The kanuka communities at Boulder Bay consist of a mosaic of small stands of different ages, both multi-stemmed, semi-prostrate and erect kanuka now forming a more-or-less continuous low canopy of variable height. Multi-stemmed, semi-prostrate populations with an overall average of 5 stems/plant occur on much of the dunes, while erect populations, with an overall average of c. 2 stems/plant, occur on more consolidated sand towards the eastern end of the bay. There is virtually no understorey. Ground vegetation is almost entirely herbaceous—in young stands, mainly leaf litter with occasional dead leafless sedge (*Isolepis nodosa*), and in older stands, abundant mosses (especially *Campopylus introflexus*, *Ceratodon purpureus*, *Bryum campylothecium*, and *Hypnum cupressiforme*; Beever & Brownsey 1990), with some live leafless sedge and a range of native and adventive herbs and grasses (see Appendix 1).

Almost all plots had a single cohort age structure (Fig. 3), which is more pronounced (i.e. the age range is narrower) in younger stands. Recruitment of multi-stemmed, semi-prostrate kanuka populations has mostly occurred over periods in excess of c. 20 years, whereas erect populations have mostly established in <15 years. The coincidence of age with the multi-stemmed, semi-prostrate habit and the narrower age range of erect stands are both largely sampling artifacts. The oldest stands are all semi-prostrate, and although some younger semi-prostrate stands exist, they are impossible to sample non-destructively.

Diameter distributions are unimodal in semi-prostrate plots and of the reverse "J" form in erect plots, largely a reflection of the age difference between them (Fig. 4). Dead plants were present only in one relatively old semi-prostrate plot (mean age of 26.5 years) and were no smaller on average than living ones. In contrast, dead plants were common in the smallest (0–5 cm) diameter class in all erect plots, together with the diameter distribution suggesting self-thinning of fully stocked stands. Mean diameter of largest stem increased linearly with plot mean age ($r^2 = 0.71$, $P < 0.01$, $n = 14$), with an overall mean annual diameter increment of 3.0 mm (Fig. 5) and no sign of an age-related decrease in diameter increment. Diameter increment was also inversely related to stand density ($r^2 = 0.37$, $P < 0.05$, $n = 14$), reflecting higher levels of intraspecific competition in more densely stocked stands.

Mean length of largest stem was not related to plot

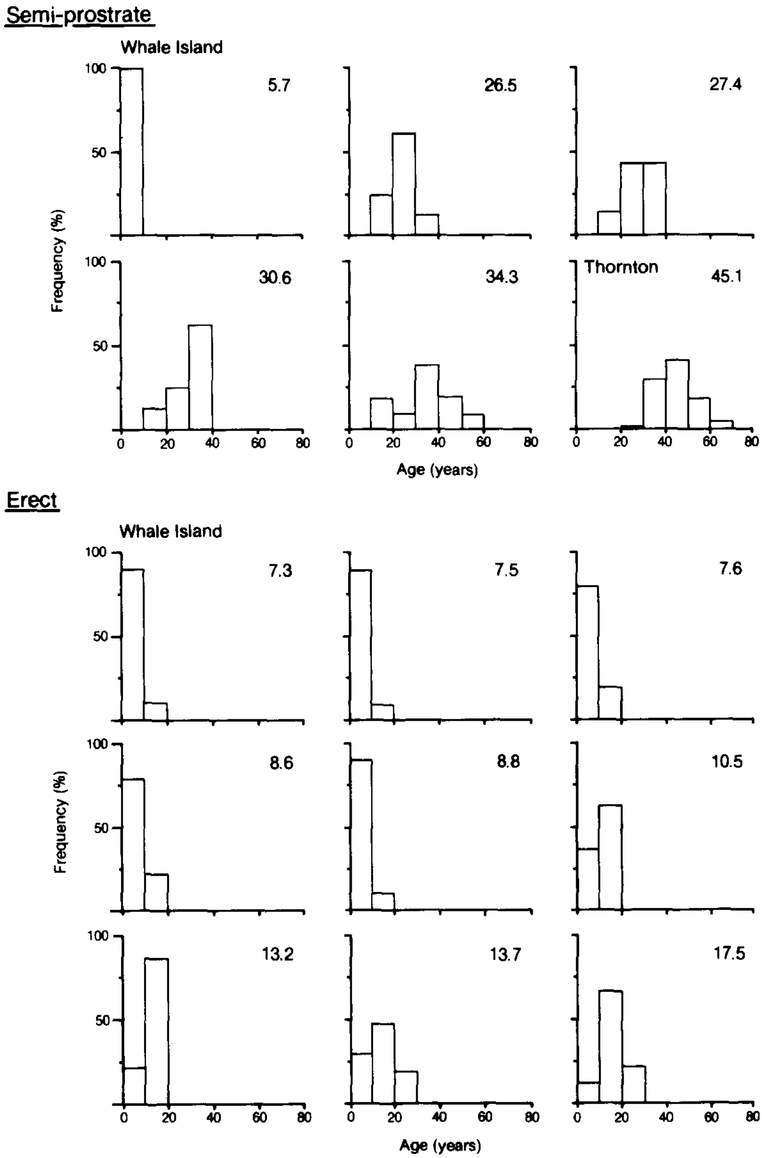

Fig. 3 Age/frequency distributions of kanuka in kanuka forest and scrub on sand dunes at Boulder Bay, Whale Island (individual plots) and Thornton (single transect). Mean plot ages in years.

mean age, implying annual height growth of c. 25 cm over the first c. 10–15 years. Mean stand height was 3.2 m, varying from 0.5 m in a very young stand (mean age 6 years), to c. 3.7 m in some other stands (7–18 years).

No relationship between stand basal area and mean age was evident, implying rapid early basal area increment (Fig. 6). Mean basal area was 42 m^2/ha, ranging from 8 m^2/ha in one young stand (mean age 6 years) to 70 m^2/ha in another (mean age 8 years). Semi-prostrate stands had c. 60% of the basal area, on average, of erect stands (Table 1).

Densities vary greatly with stand age, being very high (>100 000 stems/ha in some instances) in young stands, and <1000 stems/ha in older ones (Fig. 7). Intense self-thinning was evident in the younger stands sampled but is largely complete by the time mean age reaches c. 20 years. As with basal area, stand densities are somewhat lower, on average, in semi-prostrate than erect populations. The wide-

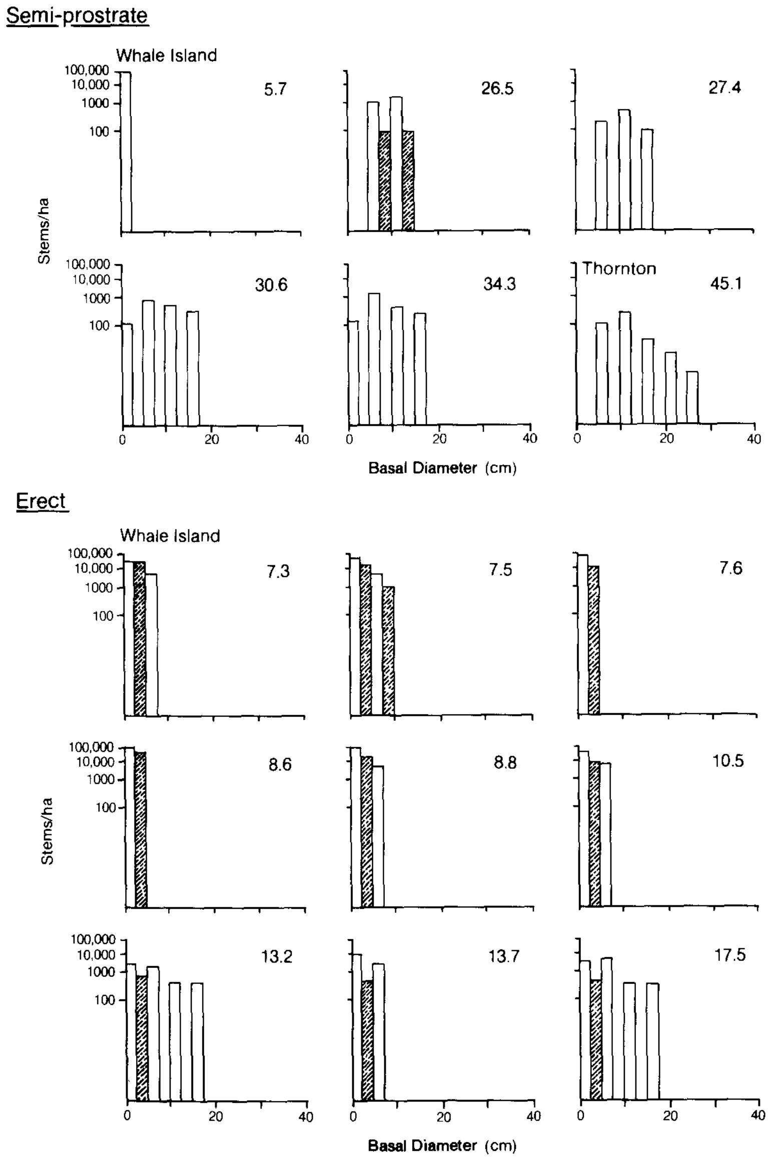

Fig. 4 Diameter distributions of kanuka in kanuka forest and scrub on sand dunes on Whale Island and at Thornton. Mean plot ages in years. Hatched bars represent dead plants.

spreading crowns of semi-prostrate plants suggest that they have not been subject to the same degree of competition and self-thinning as erect plants.

Thornton

Multi-stemmed, semi-prostrate kanuka form a more-or-less continuous canopy, of variable height, with occasional akeake (*Dodonaea viscosa*), mingimingi (*Leucopogon fasciculatus*), and adventive boxthorn (*Lycium ferocissimum*). Almost all kanuka plants are multi-stemmed from the base, with a peculiar candelabra-like form and wide flat-topped crowns. Predominant canopy height varies from 1 m on the most exposed sites (e.g., the crest of the main foredune ridge) to 6 m on the most sheltered sites (e.g., in the lee of the main foredune ridge, and in hollows in the blowout dunes). Thus, the smooth wind-shorn canopy tends to obscure the topography, particularly in the foredune system. Canopy height generally increases from the foredunes to the inland blowout dunes. Within the fenced foredunes, ground cover is predominantly meadow rice grass (*Microlaena stipoides*), pohuehue (*Muehlenbeckia complexa*), and several mosses including *Bryum campylo-*

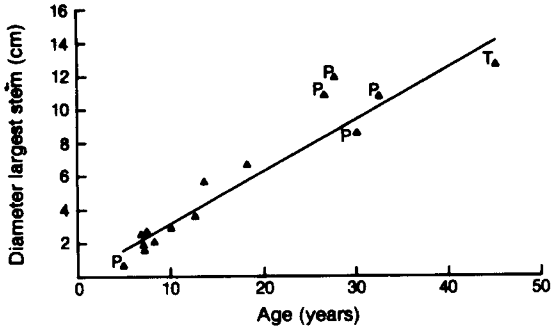

Fig. 5 Mean largest kanuka diameter (see text) versus plot mean age in kanuka forest and scrub on Whale Island (individual plots) and at Thornton (whole transect). Line (mean largest diameter = 0.3 age) represents diameter growth rate over all plots (Whale Island and Thornton). P, multi-stemmed, semi-prostrate stands; T, Thornton.

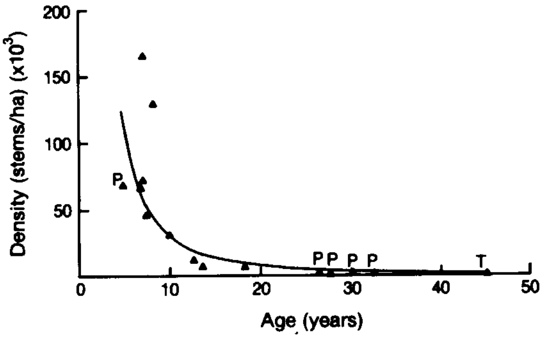

Fig. 7 Stand density versus plot mean age in kanuka forest and scrub on Whale Island (individual plots) and at Thornton (whole transect). Fitted curve represents density in relation to age over all plots. P, multi-stemmed, semi-prostrate stands; T, Thornton.

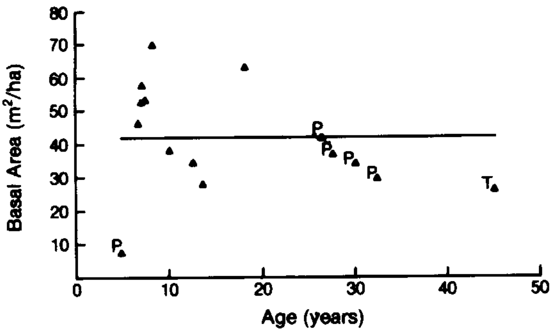

Fig. 6 Stand basal area versus plot mean age in kanuka forest and scrub on Whale Island (individual plots) and at Thornton (whole transect). Line represents mean basal area of all plots. P, multi-stemmed, semi-prostrate stands; T, Thornton.

Table 1 Plant statistics and population parameters of kanuka forest on sand dunes at Thornton (standard errors in brackets). Data from the entire transect.

Mean age (years)	45.1	(±1.4)
Mean number of stems per plant	8.9	(±1.9)
Mean basal diameter of the largest stem (cm)	12.6	(±0.6)
Mean length of longest stem (m)	4.7	(±0.2)
Mean plant basal area (m^2)	0.052	(±0.01)
Mean plant crown area (m^2)	29.5	(±3.4)
Mean annual diameter increment (mm/yr)	2.8	(±0.01)
Mean annual height increment (cm/yr)	10.5	(±0.5)
Stand density (stems/ha)	495.0	
Stand basal area (m^2/ha)	25	

thecium and *Hypnum cupressiforme*. A number of adventive herbs and grasses occur sporadically (see Appendix 1).

The kanuka population has a distinct single cohort structure (Fig. 3), with a mean age of 45 years (Table 2); age was not related to distance inland. Recruitment occurred over a protracted period, beginning c. 70 years ago when agricultural development began in the district and uncontrolled fires ceased. Diameter distribution is also unimodal (Fig. 4). Diameter of largest stem and age were weakly, though significantly, linearly related ($r^2 = 0.26$, $P < 0.01$, $n = 44$), with an overall mean annual increment of 2.8 mm, and no sign of an age-related decrease in diameter increment. Diameter growth-rates were similar on dune ridges (0.29 ± 0.01 cm/yr) and in swales (0.28 ± 0.01 cm/yr).

No other plant characteristics (length of largest stem, basal area, crown area) were related to age or topographic position (ridges versus swales). However, there are indications of somewhat slower height growth on ridges (8.5 ± 1.1 cm/yr) than elsewhere (11.1 ± 0.5 cm/yr), not statistically significant probably because of an inadequate sample of plants on ridges.

Basal area (ranging from 0.035 m^2 to 0.095 m^2) and crown area (from c. 20 m^2 to c. 65 m^2) of individual plants tended to be higher in the central portion of the transect. Lying between the linear foredune system and the blowout dunes behind them, this is the most sheltered and also the lowest lying part of the stand. No other plant characteristics were related to distance inland.

DISCUSSION

Only 42 vascular species were recorded from kanuka heaths on Whale Island and at Thornton. Nearly half of them are adventive (mostly grasses and annual herbs) and all of them, as well as the mosses, are widespread plants. Thus, the flora is depauperate in comparison with widespread woody communities in New Zealand, reflecting in part the harsh edaphic and climatic conditions, the long fire history at both sites, and the general fragility and susceptibility to modification of plant communities on sand dunes (Ranwell 1972; Healy 1973). The marked differences in floristic richness between younger (<18 years) and older stands on Whale Island (Appendix 1) probably reflect the much higher light levels beneath older, less dense stands, and the development of significant organic horizons in them.

Faster early growth (c. 40–50 cm/yr in height, 6–7 mm/yr in diameter) than found here has been recorded in kanuka planted on fertile lowland sites in North Island and northern South Island (G. F. Pardy pers. comm.). Growth-rates more comparable with those presented here have been recorded in secondary kanuka forest elsewhere in the country (Esler & Astridge 1974; Allen et al. 1992; Smale 1993a). Slower height growth in the older stands on dunes is likely to result at least partly from their growth in very exposed conditions; canopy height at Thornton is clearly related to topographic position and hence degree of exposure to the prevailing wind, and there are indications of slower height growth on ridges. Elevated sites (e.g., dune ridges) are also the driest and most drought-susceptible, so moisture stress may also be involved, especially on very free draining sandy soils which have low moisture-holding capacity. Kanuka normally lives for 80–150 years (Burrows 1973) but occasionally much longer (see Druce 1966). At Thornton, the absence in individuals up to 65 years old of the reduced diameter growth and marked crown decline characteristic of old to senile trees (Gatsuk et al. 1980), suggests that kanuka may have normal longevity on sand dunes. Basal areas in sand dune kanuka communities are rather low in comparison with those in high forest generally in New Zealand (see Ogden 1983), but are similar to those in seral kanuka forest elsewhere (Smale 1993a, b).

The semi-prostrate "candelabra" habit can be evident by as early as 6 years. Although the mean number of stems per plant is significantly correlated with plot age ($r^2 = 0.71$, $P < 0.01$), reflecting the coincidence of age with stand type (erect versus semi-prostrate), other evidence from this and studies elsewhere indicates that this is more likely to be a sampling artefact. Bellingham (1956) noted that the growth form of kanuka depended on stand density at crown height in relation to the potential spread of unrestricted individuals, an observation confirmed by Esler (1967) and Kirschbaum & Williams (1991) and supported here by lower basal areas and somewhat lower densities in semi-prostrate than erect stands. On Whale Island, erect kanuka is restricted to sheltered sites between older semi-prostrate stands, and to the sheltered eastern end of the dune system where it abuts the adjacent hillslope, suggesting that exposure to wind (see Cockayne 1911) and probably salt spray as well (Boyce 1954) may cause the semi-prostrate habit. However, kanuka has established at high densities in the erect stands here, with intense self-thinning occurring between and within individuals (Esler 1967), suggesting again that lack of competition may be important for the semi-prostrate habit. The dune soils at both localities are undoubtedly droughty (see also Dobson 1979), so exposure and drought may also be involved. Environmental and biotic factors may well be linked, with èxposure and drought lowering the rate of successful establishment and thus reducing competition.

Established seedlings growing in quite sheltered places in the blowout dunes at Thornton lack apical

Table 2 Population parameters of semi-prostrate versus erect kanuka on Whale Island and at Thornton.

	Mean age (years)	Mean no. of stems/plant	Sampled age range (years)	Basal area (m^2/ha)
Semi-prostrate				
Whale Island	5.7	2.0	3–7	7.0
	26.5	4.1	18–35	41.4
	27.4	9.1	15–38	36.3
	30.6	3.1	18–38	29.2
	34.3	5.3	17–54	33.6
Thornton	45.1	8.9	30–65	25.7
Erect				
Whale Island	7.3	1.2	5–10	45.9
	7.5	1.7	6–10	52.8
	7.6	1.8	5–10	52.4
	8.6	1.5	4–15	57.4
	8.8	1.5	7–13	69.6
	10.5	1.9	7–15	37.9
	13.2	1.5	8–20	27.6
	13.7	2.3	6–22	34.2
	17.5	2.6	8–30	62.8

dominance and have long trailing branches, suggesting that genetic factors may be involved as well; kanuka has a relatively poor long-distance dispersal ability (Boden 1971 in Kirschbaum & Williams 1991), which favours development of local ecotypes in specific habitats. Young semi-prostrate kanuka can act as temporary sand traps, producing hummocks like those well-known in dune systems elsewhere in the world (Ranwell 1972). They are often destroyed by burial or by blowout, whereby accumulated sand is blown out from beneath the crown as it thins, exposing the root system and eventually uprooting the plant altogether.

All kanuka stands sampled appear to have arisen from invasion of open sand dune vegetation or after fire had removed previous vegetation. Kanuka is an opportunistic species with great capacity to invade bare ground (Burrows 1973), and wood anatomy indicates that it is a xeromorphic species adapted to withstand dry conditions (Johnson 1984). It establishes directly on bare sand if the sand is sufficiently stable to prevent burial or uprooting of very small seedlings. Seed is shed in the late autumn – early winter following flowering, and is viable for only a further 6 weeks (Burrows 1973). Hence, germination occurs in the cooler, wetter months of the year, with rapid growth of a taproot to moist, lower layers in the soil profile; 2 cm high seedlings can have taproots 10 cm long. Observation indicates that mortality rates of newly germinated seedlings in the following summer can be high. Isolated plants soon develop extensive lateral root systems, ultimately extending for horizontal distances of 10 m or more.

A 1909 photograph of the Boulder Bay dunes at Whale Island shows only scattered small kanuka plants and much bare sand. Aerial photographs taken in 1957 show small groves of kanuka scattered toward the eastern end of the bay. Since then it has colonised the intervening gaps and expanded southward onto unconsolidated sand and eastward onto consolidated sand. In spite of minor losses due to blowout and burial at the northern and western edges of the stand, the area of kanuka heath has more than doubled in the past 30 years. At Thornton, aerial photographs and local knowledge (A. Moore pers. comm.) indicate that there were fewer and shorter (c. 1 m tall) kanuka plants in a mosaic of bare sand on the foredunes in the 1940s. Dwarf heath (*Leucopogon fraseri*) was common then but, along with common broom (*Carmichaelia cunninghamii*), has now disappeared entirely. The severely distorted branches of some kanuka on the foredunes indicate that they have grown up in the presence of pohuehue, which climbs around branches and deforms them. Subsequent fires and land development have largely eliminated kanuka outside the present reserve.

A variety of trees, apart from kanuka, occurs on old dunes in other parts of New Zealand (Cockayne 1911; Esler 1978). The Whale Island communities are within reach of seed sources of a number of trees (e.g., karaka (*Corynocarpus laevigatus*), mahoe (*Melicytus ramiflorus* ssp. *ramiflorus*), pohutukawa (*Metrosideros excelsa*), and ngaio (*Myoporum laetum*)) and shrubs (e.g., rangiora (*Brachyglottis repanda*) and kawakawa (*Macropiper excelsum*)) which occur on dunes elsewhere in the country and are present on the island; a few established pohutukawa seedlings occur beneath the older stands. Being separated by at least 6 km of pasture from the nearest coastal forest, the Thornton stand is somewhat isolated from seed sources of other potential canopy species; only a few small fivefinger (*Pseudopanax arboreus*) seedlings have been seen within the reserve. Ephemeral kanuka seedlings are widespread in the moss carpets beneath older stands on Whale Island and on the blowout dunes, but established seedlings, up to 30 cm high, occur only occasionally.

Kanuka may replace itself at both localities when the existing stands reach the end of their natural lifespan, and pronounced canopy opening and accelerated collapse (see Esler 1967) occur. Gap-phase self-replacement of kanuka occurs in seral kanuka forest on windswept ridges on Kapiti Island (Esler 1967) and in seral kanuka-kamahi (*Weinmannia racemosa*) forest in the Urewera ranges (Payton et al. 1984) after localised kamahi death. However, development of drought-prone organic horizons several centimetres deep, at the soil surface beneath sand dune kanuka stands, may preclude mass self-replacement. Continuing instability on the Whale Island dune system will ensure that fresh surfaces continue to become available for colonisation by kanuka there. The future of the young erect kanuka stands on consolidated sand at the eastern end of Boulder Bay is harder to predict. All of the species listed above, except possibly ngaio, are capable of invading these stands once self-thinning has greatly reduced stand densities, and of contributing to the future canopy. Here, biological influences are likely to be as important as environmental ones in controlling community changes (see Ranwell 1972).

Sand dune communities are highly susceptible to modification and weed invasion, and particular threats are now posed to mainland and island communities by some adventive plants. On Whale Island, pampas (*Cortaderia selloana*) could partially oust kanuka if allowed to persist and spread unchecked. At Thornton, boxthorn, a widespread invader of open coastal sites (Healy 1973), is actively regenerating and could eventually replace kanuka.

CONCLUSIONS

Important differences exist between the kanuka heaths on sand dunes at Boulder Bay, Whale Island, and at Thornton. Much of the dune system on Whale Island is unstable, with active blowout erosion occurring at the western end of the foredunes and in the hollow behind them; the dunes under kanuka at Thornton are now essentially stable. The Whale Island communities are relatively young, with a variety of ages resulting from a continuing fire history and from the unstable nature of much of the dune system; the Thornton forest contains one age class resulting from colonisation of a relatively stable substrate after uncontrolled fires ceased. Multi-stemmed, semi-prostrate kanuka communities may persist at both localities, but for different reasons (an unstable habitat on Whale Island, isolation from seed sources at Thornton). The persistence of these communities may now be jeopardised by invasive weeds.

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(Appendix 1 over page)

Appendix 1 Vascular flora of sand dune kanuka communities on Whale Island and at Thornton, Bay of Plenty (percentage frequency of occurrence/mean cover value—ground cover species only).

		Whale Island	
	Thornton	Younger (≤18 yr)	Older (≥27 yr)
Ferns			
Asplenium flaccidum ssp. *flaccidum*	–	–	50/0.1 (E)
A. oblongifolium	–	–	25/0.1
A. polyodon	–	–	25/0.1
Phymatosorus diversifolius	–	–	100/0.1 (E)
Pyrrosia eleagnifolia	5.9/0.1 (E)	–	100/4.0 (E)
Dicotyledonous trees and shrubs			
Cassinia leptophylla	–	–	100/0.1
Dodonaea viscosa	x	–	–
Kunzea ericoides var. *ericoides*	100	100	100
Leucopogon fasciculatus	x	–	–
Lycium ferocissimum†	14	–	–
Metrosideros excelsa	–	–	25/0.1 (S)
Pseudopanax arboreus	14/0.1 (S)	–	–
Dicotyledonous lianes and trailing plants			
Muehlenbeckia complexa	100/5.9	–	–
Dicotyledonous herbs			
Conyza albida†	–	–	100/0.5
Dichondra repens (Ogle 1990)	–	–	75/0.4
Galium aparine†	14/0.5	–	–
Geranium solanderi	–	–	25/0.1
Hypochaeris glabra†	–	–	25/0.1
H. radicata†	29/1.0	–	25/0.1
Lactuca virosa†	14/0.1	–	–
Oxalis rubens (Ogle 1990)	–	–	25/0.1
Phytolacca octandra†	29/0.6	–	–
Polycarpon tetraphyllum†	–	–	25/0.1
Rumex acetosella†	14/0.5	–	–
Senecio bipinnatisectus†	–	–	50/0.3
S. hispidulus	–	–	50/0.3
S. jacobaea†	–	–	75/0.4
S. lautus ssp. *lautus*	–	–	25/0.1
S. minimus	–	–	75/0.4
Solanum americanum†	–	–	25/0.1
Sonchus oleraceus†	–	–	50/0.3
Taraxacum officinale†	–	–	25/0.1
Veronica plebeia†	–	–	25/0.1
Grasses			
Bromus diandrus†	14/2.1	–	25/3.8
Dactylis glomerata†	29/9.0	–	–
Deyeuxia billardierei	–	–	25/0.1
Holcus lanatus†	14/0.1	–	–
Lagurus ovatus†	–	–	25/0.9
Microlaena stipoides	71/14.1	–	–
Oplismenus hirtellus	–	–	25/3.8
Sporobolus africanus†	14/0.1	–	–
Other monocotyledonous herbs			
Isolepis nodosa	–	80/0.7	100/6.4

†Adventive; E, also recorded as an epiphyte; x, not present in plots but recorded immediately outside them; S, present only as seedlings.