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DYNAMICS OF KANUKA (*KUNZEA ERICOIDES*) FOREST ON SOUTH KAIPARA SPIT, NEW ZEALAND, AND THE IMPACT OF FALLOW DEER (*DAMA DAMA*)

Summary: Exclosure plots established in three separate areas of kanuka (*Kunzea ericoides* var. *ericoides*) forest on south Kaipara spit in 1983 to assess the impact of introduced fallow deer (*Dama dama*) were remeasured in 1993. Kanuka shared canopy dominance with mapou (*Myrsine australis*), houpara (*Pseudopanax lessonii*) and mahoe (*Melicytus ramiflorus* ssp. *ramiflorus*) in relatively old forest in Lookout Bush, Woodhill, and dominated exclusively in two younger stands at South Head; *Coprosma rhamnoides* dominated understories throughout. At Lookout Bush cohort senescence continued in kanuka and began in mapou and houpara during the period of the study. Seedling thickets of kanuka self-thinned and were also likely to have been smothered by other species. Massive recruitment of mahoe occurred inside the exclosure, and continued in houpara, mostly outside. Mahoe and another generation of houpara are replacing the existing canopy in the absence of deer, and another generation of kanuka and houpara elsewhere in a partially stalled succession. Canopies are still intact at South Head, and there were no major changes in populations of canopy species. However, similar successional pathways are likely to occur there in future.

An influx of highly palatable shrubs, e.g., coastal karamu (*Coprosma macrocarpa*) and hangehange (*Geniostoma rupestre* var. *ligustrifolium*), into collapsing forest in the absence of deer, and their scarcity or absence elsewhere, indicates continuing impoverishment of the understorey as well as the canopy by deer. In the long term it is likely that a variety of broadleaved trees will invade these stands and that tall semi-coastal forest, similar to extant relics on the dunes, will develop. In the meantime, the high conservation value of these stands suggests that a major reduction in the deer population - sufficient to allow natural successional changes to proceed unhindered - should be a conservation priority for the region.

Keywords: kanuka; *Kunzea ericoides* var. *ericoides*; fallow deer; *Dama dama*; primary succession; south Kaipara spit; North Island; New Zealand.

Introduction

The decimation of forest understories (and more recently, canopies) by introduced mammals has been a prevailing theme in New Zealand ecology (Wardle, 1991). The impacts of the most widely dispersed mammals, i.e., red deer (*Cervus elaphus scoticus* Loennberg) and brushtail possum (*Trichosurus vulpecula* (Kerr)), have received considerable attention (e.g., Veblen and Stewart, 1982), but those of more restricted species such as fallow deer (*Dama dama* (L.)), relatively little (Nugent, 1990). Fallow deer were released at Lake Ototoa near South Head, south Kaipara spit, in 1900 (Davidson and Nugent, 1990), and now occupy some 5400 ha of sand dune, pine plantation and native forest on south Kaipara spit, at overall densities last estimated to be 0.11-0.1 ha^{-1} (Broome, 1985). They have been hunted for some 70 years, and now constitute the most important actively managed recreational 'big game' hunting resource in the Auckland region (Broome, 1985).

Like many other native plant communities on sand dunes, kanuka (*Kunzea ericoides* var. *ericoides* (A. Rich.) J. Thompson) forest is now extremely rare in the North Island outside of the Far North (Smale, 1994). Stands of kanuka forest here support moderate densities of fallow deer, and in 1983 an exclosure study was set up to monitor the impacts of fallow deer on these areas. Exclosures are a standard way of assessing the impacts of introduced browsing mammals on New Zealand forests (Payton, 1986). Remeasurement in 1993 has allowed these impacts to be assessed, along with natural successional changes in the absence of introduced mammals, and the adequacy of existing hunting pressure to maintain conservation values.

In this paper we examine the dynamics of kanuka forest on the dune systems of south Kaipara spit and the impacts on it of fallow deer. In this study, time-series data from permanent exclosure plots and adjacent controls provide the opportunity "to separate natural from [introduced] animalinduced changes in the vegetation" (Veblen and Stewart, 1982).

Study area

The former Woodhill State Forest occupies the western edge of the south Kaipara spit, northwest of Auckland City. Before its conversion from 1936 onwards to exotic conifer plantation (New Zealand Forest Service, 1970), its semi-natural vegetation consisted of a mosaic of open sand dune vegetation, wetland communities, scrub and forest. Climate is mild and humid, with a well-distributed mean annual rainfall of 1300 mm, a mean annual temperature of approximately 14∞C, a mean midsummer (January) temperature of 18∞C and a mean midwinter (July) temperature of 10∞C (New Zealand Meteorological Service, 1980). Winds have a slight southwesterly predominance (Tomlinson, 1976). Soils are mapped as yellow-brown sands, excessively to somewhat excessively drained in Lookout Bush (Sutherland *et al.*, 1985), and recently stabilised sands elsewhere (Sutherland *et al.*, 1981).

Methods

Plot location

Permanent 20 x 20 m exclosure plots (Allen, 1993), each with an adjacent control, were established in 1983 in three separate stands of kanuka forest on the south Kaipara spit (Fig. 1), all within Woodhill Forest. The southernmost stand lies on a gentle hillslope in Lookout Bush Ecological Area (a dedicated nature conservation reserve) at 100 m a.s.l., 3 km west of Woodhill Forest village. The northern stands are at South Head, one on a hillslope in Coal Seam Ecological Area at 100 m, the other at sea level, on a dune slack beside the Waionui Inlet of Kaipara Harbour.

Plot design and data collection

Each 20 x 20 m plot was divided into 5 x 5 m subplots. All saplings (2.5-10cm diameter at breast height - dbh) and trees (>10 cm dbh), living and dead, were tagged and their diameters measured, and the numbers of large woody seedlings (<2.5 cm dbh and >1.35 m high) were recorded by species. Numbers of small woody seedlings (0.15-1.35 m high) were recorded in 24 systematically located 0.75 m^2 subplots, except in the exclosure on Coal Seam Hill, where they were recorded in 48 0.75 m^2 subplots. Five of the six plots were fully remeasured in 1993; the control at Waionui had been partially destroyed by military manoeuvres in the intervening period.

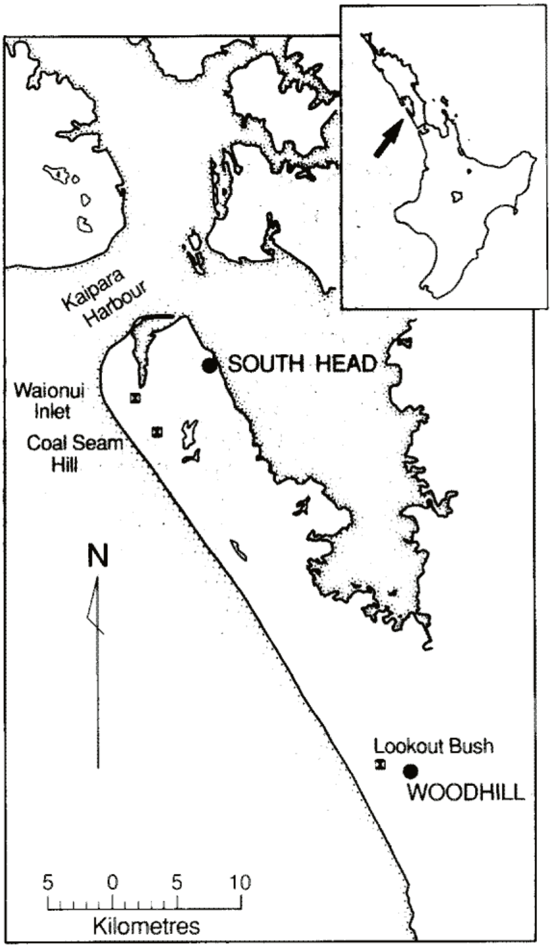

Figure 1: *Location of study areas.*

Analysis

Plant species were divided into three groups, based on their known palatability to deer: highly preferred, moderately preferred, and unpalatable. The diet of fallow deer is essentially similar to that of red deer (Davidson and Nugent, 1990). Although adaptable and opportunistic, both species have strong food preferences (Challies, 1990). Included amongst their highly preferred foods are some important or potentially important understorey and canopy species in kanuka forest on south Kaipara spit, such as large-leaved coprosmas (*Coprosma* spp.), hangehange (*Geniostoma rupestre* var. *ligustrifolium* (Cunn.) Conn), kawakawa (*Macropiper excelsum* (Forst. f.) Laing.), and mahoe (*Melicytus ramiflorus* ssp. *ramiflorus* Forst. et Forst. f.), as well as less preferred but widely eaten (moderately preferred) species such as small-leaved coprosmas, weeping mapou (*Myrsine divaricata* A. Cunn.), and mapou (*Myrsine australis* (A. Rich.) Allan) (Jane and Pracy, 1974; Allen, Payton and Knowlton, 1984; Wardle, 1984; Stewart, Wardle and Burrows, 1987). Conversely, some highly unpalatable species, e.g., prickly heath (*Cyathodes juniperina* (J.R. et G. Forst) Druce) and mingimingi (*Leucopogon fasciculatus* A. Rich.), are also locally common here. Light to moderate browse was noted in 1983 and 1993 on small-leaved coprosmas and mapou, and light browse on hangehange and houpara or coastal lancewood (*Pseudopanax lessonii* (DC.) C. Koch). Houpara was classified in this study as moderately preferred.

Because of differences in stand age and site type between study areas, plots in each locality were analysed separately. Differences in diameter growth rate of kanuka between plots were tested by *t*-test. Within plots, differences in seedling numbers between measurement years were tested by Wilcoxon signed ranks test.

Results

Initial composition

Forest composition differed markedly between the three study areas in 1983, although adjacent paired plots at each site were reasonably similar (Table 1). In Lookout Bush, kanuka formed a broken canopy at 12 m over a scattered subcanopy of mapou, houpara and mahoe, with a locally dense understorey dominated by *Coprosma rhamnoides* A. Cunn. On Coal Seam Hill, there was a virtually continuous kanuka canopy at 12 m over a light understorey dominated by *Coprosma rhamnoides* and *C. crassifolia* Col. The dune slack plots at Waionui also had an intact kanuka canopy at 8 m over a light understorey dominated by twiggy coprosma. Kanuka was dominant in terms of basal area (overwhelmingly so on Coal Seam Hill and at Waionui) in all plots except the Lookout Bush control, where all four canopy species shared dominance. In terms of density, however, small-leaved coprosmas (especially *C. rhamnoides*) were everywhere by far the commonest woody species, although contributing negligibly to basal area. Although manuka (*Leptospermum scoparium* J.R. et G. Forst.) was originally recorded in error in the exclosure at Waionui, it is common in the adjacent wetland, and may have been present in the control plot before it was partly destroyed.

Diameter distributions

Diameter distributions of kanuka were bimodal in both years in Lookout Bush, with peaks in the seedling/small sapling and tree classes (Fig. 2). Dead trees were present in both years, and dead saplings in the exclosure as well in 1993. Mapou and houpara had negatively-skewed diameter distributions in both years. Dead mapou was present as saplings in the exclosure in 1983, but in all sizes in 1993; in the control, dead saplings and trees were present in both years. Dead houpara was present in small numbers as large saplings in the exclosure in 1983, and as trees in 1993, but only as trees in the control in both years. Mahoe had a negatively skewed distribution in both years in the exclosure, and a bimodal distribution in the control, peaking in the seedling/small sapling and tree classes.

Kanuka had strongly negatively-skewed diameter distributions in 1983 on Coal Seam Hill and at Waionui (Fig. 3); both distributions had become more symmetrical by 1993. Large numbers

Table 1: *Composition of kanuka forest (all stems>15cm high) in three study areas on south Kaipara spit in 1983. [1] = may have included some manuka; see text.*

	Density (stems ha^{-1})		Basal area (m^2 ha^{-1})		Mean diameter (cm)	
	Exclosure	Control	Exclosure	Control	Exclosure	Control
Lookout Bush						
Kanuka	5515	14140	13.6	4.2	5.6	2.0
Mapou	2855	3980	3.5	5.8	4.0	4.3
Houpara	18495	15820	2.1	6.6	1.2	2.3
Mahoe	2760	725	<0.1	4.3	0.7	8.7
Others	68370	41380	1.2	0.9	0.5	0.5
Coal Seam Hill						
Kanuka	6160	4260	26.4	22.2	7.4	8.1
Others	64120	100250	0.8	0.3	0.4	0.2
Waionui						
Kanuka[1]	3325	4275	12.0	11.7	6.8	5.9
Others	45255	67400	0.7	2.0	0.4	0.6

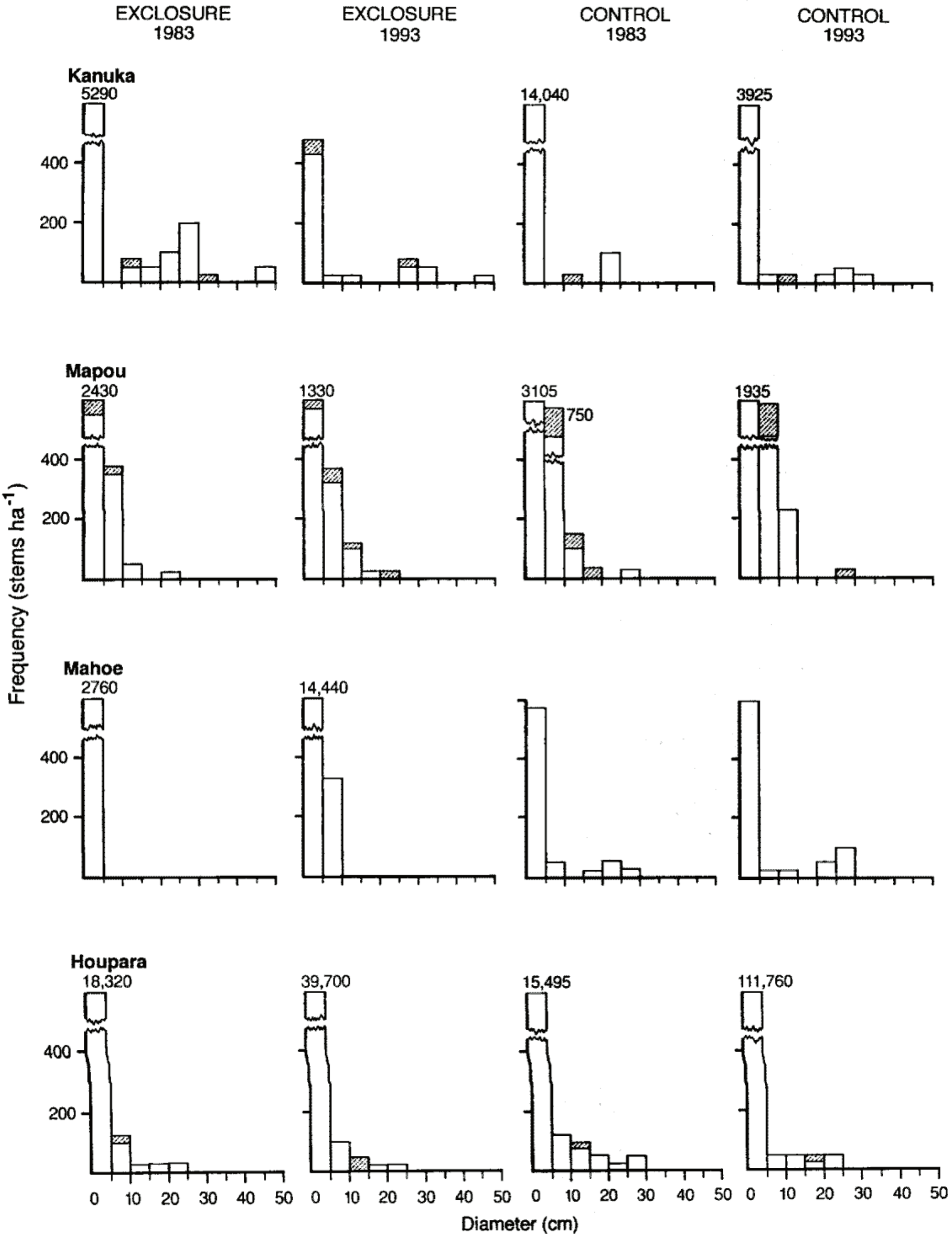

Figure 2: *Diameter distributions of major woody species in kanuka forest in Lookout Bush, south Kaipara spit, in 1983 and 1993. Hatched bars represent dead individuals.*

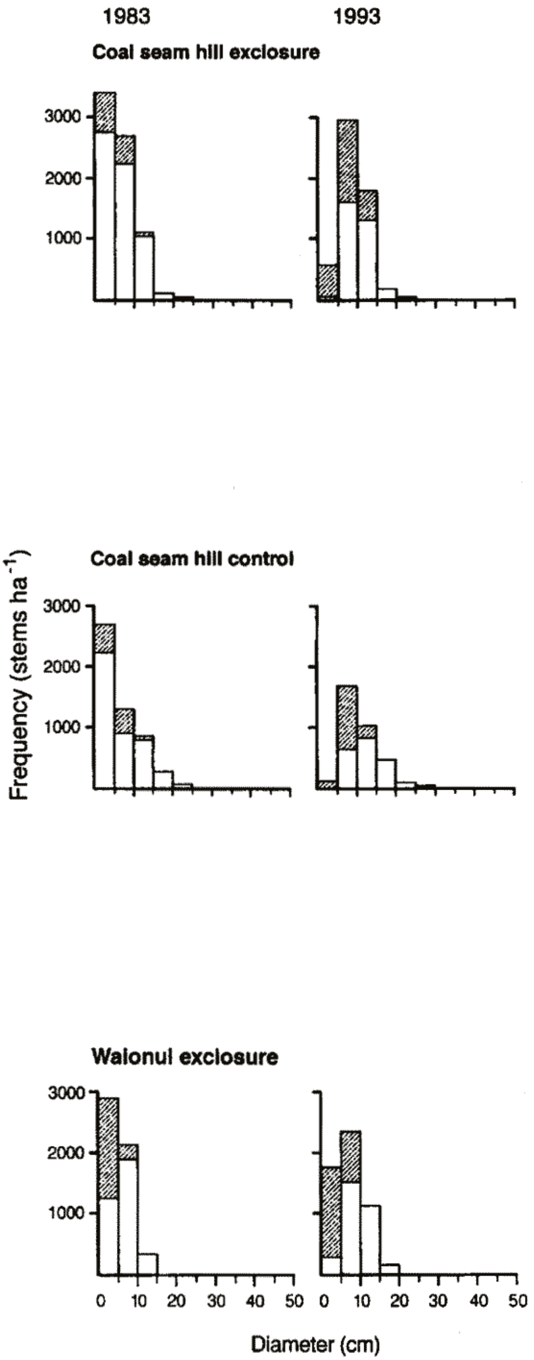

Figure 3: *Diameter distributions of kanuka in kanuka forest on Coal Seam Hill and at Waionui Inlet, south Kaipara spit, in 1983 and 1993. Hatched bars represent dead individuals.*

of dead stems were present as saplings and smaller trees on Coal Seam Hill in both years, and even larger numbers at Waionui, but only as saplings.

Diameter growth rates of major species

Diameter growth rates of kanuka over the past 10 years were similar in Lookout Bush and on Coal Seam Hill, in spite of gross differences in average size, but significantly faster (P<0.01) at Waionui than on Coal Seam Hill (Table 2). Mapou, houpara, and mahoe in Lookout Bush had similar growth rates to kanuka.

Population dynamics of major species

Between 1983 and 1993 nearly half of the tagged kanuka saplings and trees (>2.5 cm dbh) in the Lookout Bush exclosure died (mean diameter of dead stems 9.3 cm *cf.* stand mean 15.6 cm), and a quarter of those in the control (mean diameter of dead stems 22.5 cm *cf.* stand mean 22.5 cm), creating gaps too large to be filled by lateral crown expansion of surviving trees. There were a small number of 'ingrowths' (individuals growing into a larger size-class over a measurement interval) - presumably from the seedling population - in the exclosure. In the control, however, the population of larger (>2.5 cm) stems increased (Table 3), with over two-thirds of the saplings and trees present in 1993 presumed to be ingrowths from the 1983 seedling population. In both plots there was a significant (P<0.05) order-of-magnitude reduction in kanuka seedling populations, due to self-thinning of thickets and perhaps smothering by seedlings of large-leaved species as well. One quarter of the tagged mapou died in both the exclosure and control, dead trees being of somewhat larger diameter, on average, than in the stand as a whole (10.3 *cf.* 7.4 cm in exclosure, 8.6 *cf.* 7.4 cm in control); ingrowths were insignificant. A third of the tagged houpara died in the exclosure, and half in the control, with mean diameters of dead stems similar to the stand mean in both plots (9.2 *cf.* 10.1 cm in exclosure, 15.3 *cf.* 13.7 cm in control). There was significant recruitment of houpara inside the exclosure, and highly significant (P<0.01) recruitment outside, giving a sevenfold increase in the number of seedlings. The mahoe population also increased significantly inside the exclosure (a fivefold increase in seedling numbers), but not outside.

Amongst understorey species in Lookout Bush, coastal karamu (*Coprosma macrocarpa* Cheeseman) and to a small extent kawakawa, invaded the exclosure, but remained absent outside (Table 4). Hangehange invaded both plots, but the exclosure much more abundantly. There was a highly

Table 2: *Periodic mean annual diameter increment 1983-1993 (cm yr^{-1}) of major canopy species (>2.5 cm dbh) in kanuka forest in three study areas on south Kaipara spit.*

	Lookout Bush			Coal Seam Hill			Waionui		
Species	n	mean	range	n	mean	range	n	mean	range
Kanuka	12	0.04	0-0.47	182	0.07	0-0.19	121	0.20	0.11-0.34
Mapou	55	0.09	0.05-0.24	-	-	-	-	-	-
Houpara	13	0.09	0.03-0.25	-	-	-	-	-	-
Mahoe	6	0.27	0.10-0.41	2	0.18	0.15-0.20	-	-	-

Table 3: *Changes in density (stems ha^{-1}) and basal area (m^2 ha^{-1}) of saplings and trees (>2.5 cm dbh) in kanuka forest in Lookout Bush, Woodhill and on Coal Seam Hill and Waionui, South Head, between 1983 and 1993. "Others" are for Lookout Bush exclosure:* Coprosma crassifolia, *cabbage tree (*Cordyline australis *(Forst. f.) Endl.), and in 1993 only, kawakawa; for Lookout Bush control:* C. crassifolia*, cabbage tree, akeake (*Dodonaea viscosa *Jacquin); for Coal Seam Hill* Corokia cotoneaster *in 1983, and hangehange in 1993. Waionui - Control plot now partly destroyed.*

	Exclosure				Control			
	Density		Basal area		Density		Basal area	
Species	1983	1993	1983	1993	1983	1993	1983	1993
Lookout Bush								
Kanuka	425	250	13.6	12.1	100	250	4.2	6.0
Mapou	625	500	3.5	2.8	1200	925	5.8	4.3
Houpara	225	650	2.1	2.3	350	275	6.6	3.3
Kohuhu	50	0	0.6	0	0	25	0	0.1
Mahoe	0	1325	0	1.9	175	200	4.3	8.6
Coastal karamu	0	100	0	0.1	25	25	<0.1	<0.1
Hangehange	0	50	0	<0.1	0	0	0	0
Others	50	75	0.6	<0.7	75	75	<0.8	<1.0
Total	1375	2950	20.4	20.0	1925	1775	21.8	23.4
Coal Seam Hill								
Kanuka	3675	3150	26.4	29.0	2050	2075	22.2	28.3
Coastal karamu	125	125	0.4	0.6	0	0	0	0
Coprosma crassifolia	100	100	<0.1	<0.1	75	50	<0.1	<0.1
Mahoe	50	50	0.3	0.4	0	0	0	0
Weeping mapou	50	75	<0.1	<0.1	25	0	<0.1	0
Brachyglottis repanda	0	50	0	0.1	150	175	0.2	0.3
Others	25	25	<0.1	<0.1	0	0	0	0
Total	4025	3575	27.2	30.3	2300	2300	22.5	28.7
Waionui								
Kanuka	3125	2600	12.0	17.5				
Mingimingi	125	25	0.4	<0.1				
Cabbage tree	75	75	0.3	0.4				
Prickly heath	75	0	<0.1	0				
Total	3400	2700	12.7	18.0				

significant decline in small-leaved coprosmas inside the exclosure, and a significant decline in prickly heath outside.

On Coal Seam Hill, 15% of larger (>3 cm) kanuka died over the period in the exclosure and control plots (mean diameter of dead stems 7.4 *cf.* stand mean 9.1 cm), and 25% in the control (8.0 *cf.* 11.1 cm) (Table 3). The small number of ingrowths into this size class were likely to be pre-existing suppressed seedlings. Weeping mapou increased significantly in both plots. Mingimingi decreased significantly inside, while prickly heath increased significantly outside (Table 4). In the exclosure at Waionui, 13% of tagged kanuka died (mean diameter 5.9 cm *cf.* stand mean 7.2 cm), and there were a small number of ingrowths (Table 3). There were no significant changes in understorey species (Table 4). At both Coal Seam and Waionui, gaps are

Table 4: *Changes in density (stems ha^{-1}) of established seedlings (>15 cm high, <2.5 cm dbh) in kanuka forest in Lookout Bush, Woodhill, and on Coal Seam Hill and at Waionui, South Head, between 1983 and 1993. "Others" for Lookout Bush exclosure:* Olearia furfuracea *(A. Rich) Hook. f., and in 1993 only:* Carmichaelia cunninghamii *Raoul,* Cordyline australis, Corokia cotoneaster *Raoul*, Hebe stricta *var.* stricta *(Benth.) L.B. Moore,* Knightia excelsa, Macropiper excelsum, Pittosporum tenuifolium*; for Lookout bush control in 1993 only:* C. cunninghamii, K. excelsa, M. excelsum, Pseudopanax crassifolius*; for Coal Seam Hill exclosure:* Carmichaelia cunninghamii, Corokia cotoneaster*, and in 1993 only:* Brachyglottis repanda *J.R. et G. Forst.,* Olearia furfuracea*; for Coal Seam Hill control:* Olearia furfuracea *in 1983 only, and* Brachyglottis repanda, Cyathea dealbata *Swartz in 1993; for Waionui:* Carmichaelia cunninghamii*, and in 1993 only* Cordyline australis *and* Corokia cotoneaster. *Large-leaved coprosmas:* C. macrocarpa *and some* C. lucida *J.R. et G. Forst.*

	Exclosure		Control	
Species	1983	1993	1983	1993
Lookout Bush				
Kanuka	5090	350	14040	3500
Mapou	2230	1280	2780	1710
Houpara	18270	39200	15470	111660
Mahoe	2760	13440	550	620
Prickly heath	1140	320	3830	1400
Small-leaved coprosmas	66580	20230	37450	36450
Large-leaved coprosmas	0	1300	0	0
Hangehange	0	5340	0	1120
Others	550	1270	0	1770
Total	96620	82730	74120	158230
Coal Seam Hill				
Kanuka	2485	0	2210	550
Mapou	275	600	0	0
Houpara	275	350	550	550
Mahoe	275	115	0	0
Small-leaved coprosmas	47230	33965	74290	110870
Coastal karamu	825	390	0	0
Prickly heath	830	1295	550	3440
Weeping mapou	8840	21055	5620	25960
Hangehange	275	930	0	0
Mingimingi	4695	640	13410	5040
Others	550	680	2270	620
Total	66555	60020	102210	147030
Waionui				
Kanuka	200	0		
Prickly heath	1300	3260		
Mingimingi	1370	70		
Small-leaved coprosmas	35300	17570		
Hangehange	7800	8380		
Others	0	170		
Total	45810	29450		

being filled by lateral crown expansion of surviving trees (*pers. obs.*). Total basal area remained more-or-less stable in Lookout Bush, but increased substantially (by 0.5 m^2 ha^{-1} yr^{-1}) on Coal Seam Hill and at Waionui.

Changes in seedling populations of species grouped by palatability

There was a highly significant (P <0.01) increase in seedlings of highly preferred species inside the Lookout Bush exclosure, but not outside it. Moderately preferred species declined significantly (P <0.05) inside, and increased significantly outside. Unpalatable species declined significantly inside, but not outside. On Coal Seam Hill, seedling populations of highly palatable species remained stable inside the exclosure, and absent outside. Moderately preferred species also remained stable inside, but showed a highly significant increase outside. Unpalatable species declined significantly inside, but not outside. Seedlings of highly palatable species increased significantly inside the Waionui exclosure.

Discussion

Kanuka stand development is well documented (e.g., Esler and Astridge, 1974; Smale, 1994), with rapid early basal area increment and inexorable declines in density: “The thinning process continues plant by plant and limb by limb for the whole life of the stand” (Esler and Astridge, 1974). Basal areas here, particularly at Waionui, are low in comparison with those of mature kanuka forest elsewhere, where values of around 40 m^2 ha^{-1} are more common (Smale, 1994).The earliest aerial photographs of Lookout Bush, taken in 1940, show mature kanuka forest with discrete well developed crowns; and stable basal area - as in Lookout Bush - is typical of mature forest (Whitmore, 1983). Kanuka has a normal lifespan of 80-150 years (Burrows, 1973); bimodal diameter distributions, slow diameter growth rates in trees, the relatively low density of trees, their generally moribund state, and the presence of large gaps unable to be filled by surviving trees suggest two cohorts: a senescent pioneer one perhaps a century old and a young (10-15 year) regenerating one coinciding with the onset of senescence of the original cohort.

Conversely, increasing basal area (as at South Head) is characteristic of forest in the building phase, and strongly negatively skewed diameter distributions becoming more symmetrical over time, faster diameter growth rates (Waionui only), relatively high densities of live stems, large numbers of dead stems, and intact canopies suggest younger cohort ages at South Head. The earliest aerial photographs of Coal Seam Hill in 1953 show a smooth-textured closed canopy characteristic of dense younger stands, and those of Waionui in 1952 show scattered kanuka shrubs with separate individual crowns. A predominant ground cover at Waionui of *Baumea juncea* (R. Br.) Palla, a common species of the adjacent saltmarsh, suggests that this stand is an early stage of a primary sere from open dune slack to closed forest. At both sites, the mean diameter of dead kanuka was larger in 1993 than in 1983, indicating self-thinning eliminating progressively larger stems over time. Similar diameter distributions in kanuka, initially negatively skewed but becoming more symmetrical with time, and with high proportions of dead stems in the smaller size classes, occur in approximately 100 year old kauri (*Agathis australis* (D.Don.) Lindley) dominant secondary forest northwest of Auckland (Ogden, 1983).

Most of the remaining larger kanuka in the Lookout Bush plots can be expected to die in the next few decades. With maximum recorded diameters of less than 30 cm and cohort senescence now occurring, mapou and houpara appear to have lifespans similar to or shorter than that of kanuka. Two markedly different successional pathways are evident. Within the exclosure (i.e., in the absence of deer), kanuka and its associated subcanopy species are being replaced by mahoe and another generation of houpara, and outside by another generation of both kanuka and houpara - an example of a partially “stalled succession” (Connell and Slatyer, 1977). Mapou seems likely to be but a minor component of any future canopy. Successions similarly stalled by red deer have been reported in secondary kanuka forest in the northern Urewera country by Payton, Allen and Knowlton (1984). Successional trends are harder to predict in the younger stands at South Head, where existing canopies are still intact. Again, however, mahoe and houpara seem likely successors to kanuka inside the exclosure on Coal Seam Hill, and houpara and another generation of kanuka outside. Current and immediate future canopy species are all relatively short-lived, implying frequent canopy turnover and hence susceptibility to invasion by aggressive adventive weeds, foremost of which are the locally abundant pampas grasses (*Cortaderia* spp.).

Allen *et al.* (1984) distinguished four patterns of response to the exclusion of browsing mammals in a variety of primary and secondary forest types in the Urewera country. Some species, including prickly heath, were common both inside exclosures and outside; others (e.g., mapou, mahoe) were more common inside than out. Another group, including large-leaved coprosmas and hangehange, was virtually confined to exclosures, while the remaining group of species was virtually absent from exclosures. Similar patterns occurred on south Kaipara spit, with prickly heath common throughout (although more common outside exclosures), mahoe and hangehange more common inside than outside, and large-leaved coprosmas confined to exclosures.

Changes in understorey species populations reflect not only their differing palatability to deer but also their innate biological attributes, and the direct and indirect interactions of these between species. For example, the decline in small-leaved coprosmas in the Lookout Bush exclosure, where the growing space vacated by kanuka is mostly being captured by other canopy species, is largely due to their being outcompeted by taller, larger-leaved species like mahoe whose establishment has been facilitated by the absence of deer. At South Head the growing space vacated by kanuka is still being occupied by surviving individuals of the original cohort. Large-leaved canopy-forming species have not invaded the exclosures, allowing an increase in short-stature weeping mapou inside the exclosure on Coal Seam Hill. Nevertheless, the present scarcity or absence of younger mahoe and coastal karamu, hangehange and kawakawa in much of the kanuka forest on the south Kaipara spit is directly attributable to the influence of a moderate fallow deer population. Although no change in deer numbers was evident between 1982 and 1985 (Broome, 1985), significant increases in moderately preferred species in both remaining control plots since 1983 suggest that browsing pressure may have diminished over the past decade. The continuing impact of fallow deer is still considerable, altering the composition not only of the current understorey, but also of the future canopy. Apart from coastal karamu, all the highly palatable species have small, fleshy fruits allowing dispersal by common introduced passerines, and thus widespread and rapid establishment should deer populations decline or disappear.

Ground uprooted by pigs (*Sus scrofa* L.) was locally evident on Coal Seam Hill in 1993, although they have not previously been recorded from the district (McIlroy, 1990). With mid-nineteenth century liberations on the Auckland isthmus (Cowan, 1990), possums have probably long been present in Woodhill Forest; faecal pellets were present in every plot in 1993, including the exclosures. Like deer, they are opportunistic feeders but also have strong preferences (Cowan, 1990), some of which overlap with those of deer. Of current canopy species, only mahoe is moderately to highly preferred by both possum and deer, and of understorey species, only coprosmas and hangehange. Some of the potential future canopy species of the kanuka forests - e.g., kohekohe (*Dysoxylum spectabile* (Forst. f.) Hook. f.) and titoki (*Alectryon excelsus* Gaertn.) - are also highly preferred foods of possum, and their future spread may at least be slowed by the presence of possums. While experiments of this kind cannot directly assess the effects on successional processes of the removal of possums but not deer, or of both, the invasion of the Lookout Bush exclosure by possum and deer-preferred species (mahoe and to a lesser degree large-leaved coprosmas and hangehange) in the presence of possum but absence of deer suggests that the latter are having the more critical impact here. A similar conclusion has been drawn from other exclosure studies in New Zealand (Nugent and Fraser, 1993).

Relics of mature semi-coastal forest on the dune systems of the Kaipara contain a variety of broadleaved trees, the most widespread of which are karaka (*Corynocarpus laevigatus* J.R. et G. Forst.), puriri (*Vitex lucens* Kirk), kohekohe, titoki, houpara, and mahoe (P.J. Bellingham and E.K. Cameron, *unpubl. data*; New Zealand Forest Service, *unpubl. data;* Reid, 1977; Mackinder, 1984). Rewarewa (*Knightia excelsa* R. Br.), mangeao (*Litsea calicaris* (A. Cunn.) Kirk), turepo (*Streblus heterophyllus* (Blume) Corner), mapou, lancewood (*Pseudopanax crassifolius* (Sol. ex A. Cunn.) C. Koch), kohuhu (*Pittosporum tenuifolium* Sol. ex Gaertn.), and wharangi (*Melicope ternata* J.R. et G. Forst.) are somewhat less widespread. Ngaio (*Myoporum laetum* Forst. f.), kowhai (*Sophora microphylla* Ait.), and narrow-leaved maire (*Nestegis montana* (Hook. f.) L. Johnson) are local, and pohutukawa (*Metrosideros excelsa* Sol. ex Gaertn.), taraire (*Beilschmiedia tarairi* (A Cunn.) Kirk), and tawa (*B. tawa* (A. Cunn.) Kirk) rare. Although all these species (apart from taraire and tawa) are present in or near Lookout Bush (E.K. Cameron and P.J. Bellingham, *unpubl. data*), many occur only occasionally or rarely. Only a few are present on Coal Seam Hill (Cameron and Bellingham, 1986) and at Waionui. Most have bird-distributed fruits, and are likely eventually to invade the kanuka stands of the south Kaipara spit, and replace them. Significantly, however, the only known disperser of several large-fruited species such as karaka, puriri, and mangeao (Clout and Hay, 1989) surviving at south Kaipara is the New Zealand pigeon (*Hemiphaga novaezelandiae*), whose growing scarcity may restrict their future dispersal.

Conifers appear to be naturally rare; totara (*Podocarpus totara* G. Benn. ex D. Don.) is locally common on dunes, as in Tapu Bush on north Kaipara spit (Reid, 1977), while matai (*Prumnopitys taxifolia* (D. Don.) de Laubenf.) occurs extremely rarely on south Kaipara spit (P.J. Bellingham, *pers. comm.*). For most this probably reflects their relative inflammability and the presumed long fire history of these areas rather than an unsuitable habitat. Totara, rimu (*Dacrydium cupressinum* Lamb.), tanekaha (*Phyllocladus trichomanoides* D.Don.) and to a lesser extent, matai, but not kahikatea (*Dacrycarpus dacrydioides* (A Rich.) de Laubenf.), planted experimentally in kanuka forest at Lookout Bush in 1961 have survived and grown well (G.F. Pardy and G.A. Steward, *unpubl. data*), and now constitute a significant seed source, albeit of foreign origin.

Kanuka tree-heaths generally occupy sites which are too dry to support taller, more diverse forest, or formerly forested sites where sundry factors are preventing its return (Wardle, 1991). Those on the south Kaipara spit fit a third category, being essentially seral and merely a stage in a primary successional pathway from open dune vegetation to forest; there is no evidence of an earlier forest at any locality here. They currently provide habitat for some local (fierce lancewood, *Pseudopanax ferox* Kirk), vulnerable (*Pimelea tomentosa* (J.R. et G. Forst.) Druce), and rare (an unnamed *Pratia*) species, and also support a regional endemic, *Hebe diosmifolia* (A. Cunn.) Ckn. et Allan, at its southern limit (Cameron and Bellingham, 1986; E.K. Cameron, *pers. comm.*), all characteristic scrub species likely eventually to disappear if natural successional changes are allowed to proceed.

Although the results of this experiment apply strictly only to the plots themselves, observation suggests that they pertain widely to kanuka stands on south Kaipara spit. It should be stressed that protection for any length of time after nearly a century of browsing cannot return seral forest to the structure and composition that would have prevailed in its absence (see also Anderson and Katz, 1993). Nevertheless, these stands are among the best remaining examples of duneland kanuka forest in the country and should be a priority for nature conservation in the region. As elsewhere in the country (e.g., Nugent, 1990), the high palatability to deer of many existing and potential canopy and understorey species means that the level of reduction (near extermination) in the deer population probably needed to allow natural successional changes to proceed unhindered is unlikely to be acceptable to the recreational hunting fraternity.

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