Birds and small mammals in kanuka (*Kunzea ericoides*) and gorse (*Ulex europaeus*) scrub and the resulting seed rain and seedling dynamics

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Abstract: Native kanuka (*Kunzea ericoides*) and adventive gorse (*Ulex europaeus*) stands aged 10-14 years, and not grazed by domestic stock, were studied near Nelson, New Zealand. The aim was to determine their use by introduced small mammals, and native and adventive birds, and the effects of these animals on seed rain and seedling dynamics as factors influencing vegetation succession. Seed traps were established where they could catch only bird-dispersed or wind-blown seed, and seedling emergence and growth were monitored. Bird abundance was estimated by five-minute bird counts, and small mammal abundance by trapping. The summed frequencies of all birds, and those likely to disperse seeds, were similar in kanuka and gorse. The endemic native bird species, bellbirds (*Anthornis melanura*) which are omnivorous, brown creepers (*Mohoua novaeseelandiae*) and grey warblers (*Gerygone igata*) which are insectivorous, were more frequent in kanuka than in gorse, while fantails (*Rhipidura fuliginosa*) were equally frequent in both stands. Non-endemic silvereyes (*Zosterops lateralis*) which are omnivorous were the most abundant seed-dispersing species, and they were significantly more frequent in gorse, as were adventive California quail (*Callipepla californica*) which are granivorous. Other small adventive granivores and omnivores were either more frequent in kanuka or gorse, or equally common in both stands. Ship rats (*Rattus rattus*) and possums (*Trichosurus vulpecula*) were in low numbers throughout. Mice (*Mus domesticus*) were more frequent in the gorse, probably because of the shelter offered by the dry gorse litter, and food supply, e.g. gorse seed. More seeds of native, fleshy-fruited shrubs fell in the kanuka, largely those of *Coprosma* spp. and *Cyathodes juniperina,* which grow in the kanuka. Seed species richness was similar in kanuka and gorse. In both cases, the seed rain appeared more influenced by the local seed source than by the different bird communities. In both kanuka and gorse, the relationship between seed rain and seedling numbers was close only for the most common fleshy-fruited species. Seedling emergence and survival was greater in gorse because of openings in the canopy, and the lower density of the introduced hares and rabbits. Overall, the different morphology and structure of the adventive gorse probably have the greatest influence in seedling dynamics, and ultimately on vegetation succession.

Keywords: adventive birds; endemic birds; exotic species; *Kunzea ericoides*; seed fall; seedling dynamics; succession; *Ulex europaeus*; weeds.

Introduction

Individual plant species may have major effects on ecosystem processes, and non-native invasive shrubs can produce ecosystems with altered composition (Braithwaite *et al.*, 1989) and successional pathways (Yoshida and Oka, 2000) that function very differently from the native ecosystems they replace (Vitousek and Walker, 1989, Fensham *et al.*, 1994). Comparative studies of native and non-native communities are required if we are to understand the impacts of invasive species (Parker *et al.,* 1999).

Gorse (*Ulex europaeus*), a nitrogen-fixing shrub of European origin, has replaced native manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) as the major early successional shrub over much of the New Zealand lowlands (Blaschke *et al.*, 1981), especially following fire and the cessation of pastoralism. Before the arrival of Europeans, kanuka and manuka dominated the early phases of vegetation succession, giving way to taller broad-leaved species after about 100 years (Druce, 1957; Esler, 1967; Wilson, 1994) or longer (Allen and Lee, 1992), depending on site factors. In contrast, the process takes only about 30 years through gorse (Druce, 1957; Lee *et al.*, 1986; McQueen, 1993; Wilson, 1994). This has led to gorse being valued as a precursor to native forest in revegetation projects (Porteous, 1993; Wilson, 1994). Seed dispersal by birds is a critical part of the successional process in New Zealand woody vegetation because a high proportion of the shrubs and small trees involved have fleshy fruit (Allen and Lee, 1992; Burrows, 1994a), and soil seed banks are of minor importance (Sem and Enright, 1996). The use of kanuka and gorse vegetation by bird species, and their preferences for different fruit types (Burrows, 1994a; Williams and Karl, 1996) may influence the composition of the secondary successional vegetation. Introduced small mammals may also affect regeneration in New Zealand by either dispersing or destroying the seeds of fleshy-fruited species (Williams *et al.,* 2000), or by grazing the seedlings (Burrows, 1994b), while large grazing mammals can disrupt the process completely (Wilson, 1994).

To determine whether the habitat provided by the native kanuka and the invasive gorse differed, we investigated their use by native and introduced birds, and small introduced mammals. We compared the effects of these birds and animals indirectly by measuring seed rain into the vegetation. Seedling growth and survival were recorded and interpreted in terms of the seed rain, animal use of the understorey, and the differing vegetation structures of kanuka and gorse stands. We aimed to determine whether any observed differences might lead to different successional pathways in the native kanuka and the invasive gorse scrub.

The investigation was conducted near Nelson in stands where the gorse was collapsing with age (Druce, 1957; Lee *et al.,* 1986; Wilson, 1994) and where the adjacent kanuka was of a similar age, but with an intact canopy. The study was part of a wider investigation to determine whether there are detectable differences in ecosystem function and biodiversity between gorse scrub and the native communities it has replaced.

Study sites

The sites are near Nelson City (41°17' S, 173º15' E) in the Wakapuaka Valley. A climate station 20 km southwest of the study area has a mean annual rainfall of 968 mm and mean annual temperature of 12.5°C. The kanuka stand (NZMS 260 O16 467 015) was a *c.*10 ha area of scrub adjacent to extensive areas of similar scrub and secondary forest. It was located mid-slope on a north-west facing hill slope of 25-27^{o} between 180-205 m a.s.l. It was directly accessible from a farm vehicle track. The gorse stand (NZMS 260 O27 458 003) was a *c.*4.5 ha area of scrub surrounded by diverse secondary vegetation. It was located 1.7 km to the south-east of the kanuka stands in a valley with similar topography, but on mid-to-lower slope, at a slightly lower altitude of 90-100 m a.s.l. The gorse stand was of similar aspect and slope (north-west facing and 25-27^{o}). It was accessible via a 1 km walking track.

Adjacent remnants show the pre-European vegetation on hill slopes was dominated by *Nothofagus truncata*-*Weinmannia racemosa* forest with scattered podocarps. Much of this area was burned and cleared before 1900 and grazed until about the 1950s. The resulting land cover is a mosaic of forest remnants, secondary scrub of kanuka, manuka, and gorse, pine plantations and pasture.

The kanuka stand had a dense canopy at 5-7 m tall, and stems were 14.3±1.0 (S.D.) years old (P.A. Williams and B.J. Karl, *unpubl.*). Scattered in the understorey or canopy were *Leucopogon fasciculatus*, *Melicytus ramiflorus, Coprosma rhamnoides* and *Carpodetus serratus*. There was a thin (< 2 cm) litter layer with sparse herbs and ferns. The stand was surrounded by similar vegetation and rough pasture of *Anthoxanthum odoratum* and *Rytidosperma* spp., with *Rubus fruticosus*.

The gorse stand was 3-4 m tall and stems were 12.9±1.1 (S.D.) years old (P.A. Williams and B.J. Karl, *unpubl.*) with the oldest bushes lowest on the hill slope. The stand was collapsing with age, resulting in localised resurgence of *Pteridium esculentum* and emergence of broadleaved shrubs, such as *Melicytus ramiflorus*, *Pittosporum eugenioides, Myrsine australis* and *Carpodetus serratus*. These were more frequent on the lower slopes, but they made a negligible contribution to stand basal area. The ground was covered in a thin (< 5 cm) litter layer with scattered adventive grasses, ferns, and seedlings of woody broadleaved species. Gorse seedlings were also abundant but saplings were rare, suggesting they seldom survived more than a few years. The gorse stand was surrounded by more diverse vegetation, including *Kunzea ericoides,* young *Pinus radiata* amongst gorse, *Nothofagus* spp. forest 200 m across the valley, and scattered shrubs of *Coriaria sarmentosa* and *Leycesteria formosa* near the valley floor. Rough pasture was several hundred metres away from the gorse stand, but adjacent to the kanuka. Kanuka and gorse stands were on the same soil type.

Sheep (*Ovis aries*) were uncommon in the immediate vicinity of the study sites. They were not present beneath dense kanuka, and the gorse stand was impenetrable near the valley floor from where they could gain access. Their important influence on secondary succession in New Zealand (Wilson, 1994) was thus absent from our study. Wild pigs (*Sus scrofa*), which are renowned for living in dense scrub, were present in low numbers in both stands, as evidenced by their rootings. Rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) were uncommon in the grasslands adjacent to the kanuka, though the former were occasionally seen within the kanuka. Neither of these species, nor their faeces, were observed in the gorse during the period of the study. Possums (*Trichosurus vulpecula*) were sparse throughout, while mice (*Mus domesticus* or *M. musculus*) (Murphy and Pickard, 1990) and ship rats (*Rattus rattus*) were present.

Methods

Vegetation

Two 60-m by 20-m plots were located in each of the kanuka and gorse stands. They were laid out one above the other. The kanuka plots were about 50 m apart, whereas the limited area meant the gorse plots were contiguous. Vegetation cover was visually estimated at four heights (< 30 cm, 30 cm-2 m , 2 m-5 m, 5 m-7 m) within three 10 m diameter circular recce subplots (Allen and McLennan, 1983) within each plot. Data from the six subplots per stand were averaged.

Introduced small mammal abundance

Small mammal presence in kanuka and gorse stands was determined from trap lines set for rodents in March, April and May 1998, and for possums in November 1997, March and July 1998. A single line approximately 120 m long was located in each stand at least 20 m from the boundary of the vegetation type and extending up slope through both plots. Ten pairs of mouse snap traps and rat snap traps were laid adjacent to each other, 10-20 m apart, and a few metres beyond the line depending on ground conditions on the steep slopes, in each vegetation type. Traps were baited with a mixture of rolled oats and peanut butter, set overnight and cleared the next morning for 2 days per month. Ten Victor #1 traps baited with a mixture of flour and icing sugar were set for possums along the same line. Numbers of animals caught in each trap were summed for stand comparisons. For comparison with published studies, data for mice and rats were summed across all months and expressed as catch/100 trap nights (C/100 TN), with the rat traps considered as potential mouse traps (Nelson and Clark, 1973). The absolute numbers of possums caught, or cases where only fur remained in the traps, were used as an index of possum numbers.

Native and adventive bird abundance

Bird numbers were indexed from five-minute bird counts by one of us (B.J.K.) on 2 consecutive days in the months November 1997, February-May 1998 and July 1998, at 6 stations approximately 20 m apart along the line, independent from the animal traps but on the days these traps were set. Counts were taken on fine days between 0900-1200 hrs in either kanuka or gorse, and from 1300-1600 hrs in the other stand, and conversely on day 2. Judgement was used to exclude birds heard outside the respective stands, but the close proximity of the stations within each vegetation type meant records may not have been independent. Counts were summed across all months for each station.

Seed fall and seedling dynamics

Seed fall of wind- and bird-dispersed seeds was collected with the litter in circular funnels 0.1 m^2 and 0.30 m deep, constructed of heavy nylon shade cloth (0.5 mm mesh) tied at the bottom for access. Nine funnels were used per plot. Each was attached to three stakes at 1 m above ground level. No seed funnels were located beneath seeding shrubs other than kanuka and gorse. Traps were set in November 1997 and emptied approximately monthly until April 1999. Litter was oven-dried at 80^{o}C for 2 days and the fruit and seeds extracted. Seed fall data were combined for the different months into an annual figure for each trap. No rodent droppings were found in the samples and we assume that no seeds were removed from the traps.

Identity and density of seedlings (2-30 cm high) were recorded in June 1998 from within nine 1-m^2 subplots located randomly in each of the two plots in each vegetation type. Seedling dynamics were recorded from eighteen 0.5-m^2 subplots containing at least five seedlings of broadleaved species, within each type. The smaller subplot size was dictated by the need to have regular access to the seedlings without disturbing their environment. Subplots were laid out in October 1997 and all woody seedlings apart from gorse were tagged and their heights measured to the nearest 2 mm in October 1997 and June 1998. Seedlings were counted monthly, dead seedlings were recorded, and new seedlings were tagged as they reached 2 cm. The seedling environment beneath kanuka was not modified by the sampling regime because of the open sub-canopy space but, despite due care, disturbance to the dense gorse vegetation exposed the seedlings to some additional light.

All statistical tests were made using the Kruskal-Wallis approximation of the chi-squared test for two groups.

Results

Vegetation structure

The kanuka had 53.3% cover between 5-7 m, whereas the gorse did not reach this height (Table 1). The kanuka 2-5 m layer had a cover of 85.2±4.1% (= mean ± SD for this and all subsequent values in Results) with a CV of 4.9%, indicating a uniform dense canopy. The

Table 1. The estimated cover percentage (mean ± S.D.) and coefficient of variation (C.V.) for all species in four height tiers, litter, and bare ground, in kanuka and gorse stands at Nelson. K.-W. is the significance level of the Kruskal-Wallis test comparing mean percent cover between the kanuka and gorse stands. NS = not significant ($P > 0.05$).

	Vegetation cover %				Litter	Bare ground
	7-5m	5-2m	2m-30cm	< 30cm		
Kanuka	53.3 ± 39.0	85.2 ± 4.1	53.2 ± 7.5	11.7 ± 1.5	91.7 ± 2.4	8.3 ± 2.4
C.V.%	73.1	4.9	14.9	12.8	2.6	28.9
Gorse		47.2 ± 35.6	85.3 ± 14.9	33.2 ± 9.2	65.0 ± 15.0	7.5 ± 2.5
C.V.%		83.3	17.5	27.7	0	33.3
					23.1	
K.-W.		NS	NS	0.01	0.01	NS

gorse upper layer was not significantly different in cover % from the kanuka, with a mean of 47.2±35.6%, whereas it had a CV of 83.3%. This variation was a result of the senescing gorse crowns, which also contributed to the 85.3±14.9 % cover of the 30 cm-2 m layer and 33.2±9.2% cover of the < 30 cm layer. The significantly lower litter cover in the gorse (65.0±15.0) compared with kanuka (91.7±2.4) (Table 1) was partly because of the root mounds of the fallen gorse bushes, and the crowns themselves, covering the ground.

Small mammal abundance

There were 1.4±1.0 mice caught per trap in the gorse and 0.5±0.6 in the kanuka which was significantly fewer (Table 2). Ship rat numbers were similarly low ($P < 0.05$ per trap) in kanuka and gorse. A total of 5 possum records were made in kanuka, and 3 in gorse, but these low numbers are inconclusive (Table 2). The catch rate for mice (C/100 TN) averaged 6.3±4.5 in kanuka and 14.3±6.6 in gorse (Table 2). Ship rat numbers (C/100 TN) were 1.9±2.7 in kanuka and 1.7±2.4 in gorse.

Native and introduced bird abundance

The bird frequency index summed from the five-minute counts for all bird species was 60.8±8.0 in kanuka and 54.2±10.0 in gorse indicating similar total numbers of birds in each stand (Table 3). The frequency of birds likely to disperse seed was also similar in kanuka (33.9±6.0) and gorse (35.6±7.1). Silvereyes were the most frequent, and they were significantly more frequent in gorse (34.2±1.3) than in kanuka, (20.5±6) (Table 3). Bellbirds were 10 times more frequent in kanuka (11.4±1.8) than in gorse (1.1±0.9). Blackbirds were infrequent, although they were significantly more frequent in kanuka (2.0±0.9) than in gorse (0.25±0.43). Insectivorous birds unlikely to disperse seed were more frequent in kanuka (14.7±3.3) than in gorse (3.9±1.3) (Table 3). Brown creepers were present in the kanuka and absent from the gorse, grey warblers were significantly more frequent in kanuka, while fantails were of similar frequency in both. These species, together with bellbirds, are all endemic species. The sum of the indices for seed predators was similar in kanuka and gorse. California quail were significantly more frequent in the gorse, where they utilized the open patches. Other small adventive granivores and omnivores were either more frequent in kanuka (yellow hammer) or gorse (green finch), or equally common in both vegetation types (chaffinch, goldfinch, redpoll) (Table 3).

Seed fall

A total of 634 seeds were collected from seed fall traps in kanuka, from 7 species or groups, and 115 seeds from 13 species or groups in gorse (Table 4), where there were also 5550 gorse seeds. Overall, 68 percent of seed species or groups were bird and animal dispersed. Many bird-dispersed seed species or groups were uncommon, and the number per trap over the collection period was similar in kanuka (1.3±0.4) and gorse (0.7±0.6) indicating that species richness was similar (Table 4). There were significantly more native bird-dispersed seeds of woody shrubs and vines in kanuka (4.7±3.4 m^2 yr^{-1}) than in gorse (1.9±2.4 m^2 yr^{-1}). The number of adventive bird-dispersed species was similar in kanuka (1.9±2.8) and gorse (2.6±4.5) (Table 4).

Wind blown *Clematis vitalba* and unidentified herbaceous Asteraceae seeds were the most common seeds in kanuka (Table 4). The most common bird-dispersed seeds were *Coprosma* spp., which were mostly the small seeds of *C. rhamnoides*. Similarly, the main *Cyathodes* spp. was *C. juniperina*, which, together with *Coprosma rhamnoides*, were uncommon understory shrubs in kanuka. *Rubus fruticosus* seeds were the most common adventive fleshy-fruited species

Table 2. Small mammals trapped in kanuka and gorse scrub near Nelson (1997-1998). For mice and rats, data are total numbers caught, and a mean monthly density estimate (C/100TN). For possums the data are absolute numbers and fur-only records combined. K.-W. is the significance level of the Kruskal-Wallis test comparing mean number of animals per trap in the kanuka and gorse stands. NS = not significant (*P* > 0.05), NA = not applicable.

		Kanuka		Gorse		K.-W.
		n	Mean ± S.D.	n	Mean ± S.D.	
Total per trap	Mice	5	0.5 ± 0.6	14	1.4 ± 1.0	0.05
	Rats	1	0.1 ± 0.3	2	0.2 ± 0.4	NS
Density (C/100TN)	Mice		6.3 ± 4.5		14.3 ± 6.6	NA
	Rats		1.9 ± 2.7		1.7 ± 2.4	NA
Total	Possums	5		3		NA

in the kanuka. This species grew on the forest margins. No kanuka seed was released during the study.

The most common bird-dispersed seeds in gorse were *Coprosma* spp. (mostly *C. robusta*), *Leycesteria formosa* and *Melicytus ramiflorus,* with a few seeds of *Coriaria arborea, Cyathodes* spp., *Muehlenbeckia australis* and *Rubus fruticosus.* These species were represented within the gorse by scattered fruiting plants, with the exception of *L. formosa* that must have been carried for several hundred metres. The *Clematis vitalba* seeds could have originated near the traps, but the two seeds of *Nothofagus solandri* must have been blown

Table 3. Estimate of birds in kanuka and gorse scrub near Nelson. Data are the summed 5-minute bird counts per station (n = 6) recorded for two days per month between November 1997 and July 1998, giving a total of 12 counts. K.-W. is the significance level of the Kruskal-Wallis test comparing mean number of counts per station in the kanuka and gorse stands. The data divided by 54 gives the mean number per 5-minute count. NS = not significant (*P* > 0.05), NA = not applicable.

Bird species	Kanuka Mean ± S.D.	Gorse Mean ± S.D	K.-W.
Total seed dispersers (omnivorous)	33.97 ± 6.02	35.62 ± 7.12	NS
Bellbird (*Anthornis melanura*) (e)[1]	11.42 ± 1.89	1.17 ± 0.99	0.01
Blackbird (*Turdus merula*) (i)	2.0 ± 0.95	0.25 ± 0.43	0.01
Silvereye (*Zosterops lateralis*) (n)	20.50 ± 6.06	34.25 ± 7.90	0.01
Total dispersal neutral (insectivorous)	14.75 ± 3.32	3.92 ± 1.37	0.01
Brown creeper (*Mohoua novaeseelandiae*) (e)	4.58 ± 2.86	0	NA
Fantail (*Rhipidura fuliginosa*) (e)	4.83 ± 2.21	3.17 ± 1.86	NS
Grey warbler (*Gerygone igata*) (e)	5.33 ± 2.02	0.75 ± 0.83	0.01
Seed predators (granivorous/omnivorous)	12.67 ± 4.61	11.08 ± 3.01	NS
California quail (*Callipepla californica*) (i)	0.67 ± 1.11	3.0 ± 3.0	0.05
Chaffinch (*Fringilla coelebs*) (i)	3.67 ± 1.83	3.25 ± 1.42	NS
Goldfinch (*Carduelis carduelis*) (i)	1.83 ± 1.21	2.08 ± 1.66	NS
Greenfinch (*Carduelis chloris*) (i)	1.75 ± 1.82	3.0 ± 1.22	0.05
Hedge sparrow (*Prunella modularis*) (i)	0.67 ± 1.01	2.50 ± 1.26	0.01
Redpoll (*Carduelis flammea*) (i)	0.17	0.08	NA
Yellowhammer (*Emberiza citrinella*) (i)	2.33 ± 0.62	0.58 ± 0.49	0.01
Weka (*Gallirallus australis*) (e)	0.8	0	NA
Other			
Harrier hawk (*Circus approximans*) (n)	0	0.8	NA
Total	60.8 ± 8.0	54.2 ± 10.0	NS

[1] Endemic (e), non-endemic native (n), and introduced (i) birds.

Table 4. Total seed fall (No. m^{-2} yr^{-1}) from 18 traps, and woody/vine seedlings (No. m^{-2}) from 18 quadrats (gorse seedlings excluded) in kanuka and gorse stands at Nelson, and woody bird-dispersed native and adventive species, and their sum (mean ± S.D.). K.-W. is the significance level of the Kruskal-Wallis test comparing mean number of seeds, or seedlings, per trap or quadrat, in the kanuka and gorse stands. NS = not significant ($P > 0.05$), ND = not determined.

	All seeds			Woody seedlings		
	Kanuka	Gorse	K.-W.	Kanuka	Gorse	K.-W.
Aristotelia fruticosa (b)[1]					0.07	
Clematis vitalba (w)	15.76	1.59	0.01		0.12	
Asteraceae (unidentified) (w)	4.75	0.30	0.01			
Coprosma rhamnoides (b)	ND	ND		0.03	0.03	NS
Coprosma robusta (b)	ND	ND			0.22	
All *Coprosma* spp. (b)	2.37	0.65	0.01			
Coriaria arborea (b)		0.06				
Cyathodes juniperina (b) (some *Leucopogon fasciculatus*) (b)	1.40	0.24	0.01			
Dodonaea viscosa (b)		0.50				
Leycesteria formosa (b)	0.06	1.26	0.01			
Melicytus ramiflorus (b)		1.10		0.06	0.18	0.05
Myrsine australis (b)					0.10	
Muehlenbeckia australis (b)		0.05				
Nothofagus solandri (o)		0.06				
Pittosporum eugenioides (b)					0.02	
Pseudopanax arboreus (b)					0.02	
Rubus fruticosus (b)	1.89	1.34	NS		0.07	
Ulex europaeus (o)		402.0			ND	
Uncinia sp. (o)		0.11				
Unidentified	0.36	0.06				
Total woody bird-dispersed plants						
- native	4.7 ± 3.4	1.9 ± 2.4	0.05	0.10 ± 0.30	0.63 ± 0.83	0.01
- adventive	1.9 ± 2.8	2.6 ± 4.5	NS		0.06 ± 0.0	
- sum	6.6 ± 4.2	4.5 ± 5.4	NS	0.10 ± 0.30	0.73 ± 1.05	0.01

[1] Dispersed by birds or animals (b), wind (w), other (o).

several hundred metres. Several fruiting *Podocarpus totara* and *Prumnopitys taxifolia* trees are present within 0.5 km of the kanuka traps, and 0.5 km of the gorse traps, but their seeds were not recorded.

Seedling dynamics

Density of woody seedlings averaged only 0.10±0.3 per m^2 beneath the kanuka, and there were significantly more (0.70±1.0) beneath the gorse (Table 4). The two species beneath kanuka were *Coprosma rhamnoides* and *Melicytus ramiflorus*, and the main species beneath gorse were *Coprosma robusta* and *M. ramiflorus*. The ratio of woody seedlings to seed fall was 0.015 in the kanuka and 0.16 in gorse (from Table 4), indicating a much lower seedling establishment in kanuka.

Woody species recorded in the seed rain, but not as seedlings, were *Rubus fruticosus* (only semi-woody) in the kanuka, and *Coriaria arborea, Dodonaea viscosa, Leycesteria formosa* and *Nothofagus solandri* in the gorse, although *D. viscosa* was present as saplings. *Aristotelia serrata, Myrsine australis, Pittosporum eugeniodes* and *Pseudopanax arboreus* were recorded as seedlings but were not recorded in the seed rain.

There was no net increase in seedling numbers between October and June in the kanuka, whereas the number of seedlings in the gorse increased from 26 to 42, when there were significantly more seedlings in the gorse (Table 5). Turnover of seedlings was 50 percent in the kanuka, significantly higher than the 27 percent turnover in gorse. This indicated a higher seedling survivorship in the gorse (Table 5). There was no net gain in seedling height over the period in either kanuka or gorse. Browse damage was recorded only in the kanuka. As sheep were absent, and possum numbers were similar in both kanuka and gorse, browsing was most likely by hares and rabbits (a very young rabbit was found in the kanuka, but no burrows were located).

Table 5. Total number of native hardwood seedlings in 18 0.5m^2 subplots, and their mean height (cm) (mean ± S.D.) in October 1997 and June 1998, and the number appearing over that period, in kanuka and gorse stands near Nelson. Turnover (%) is the number of seedlings dying in that period, divided by the number of seedlings present in October plus the number appearing over the period, x 100. K.-W. is the significance level of the Kruskal-Wallis test comparing mean number of seedlings in kanuka and gorse. NS = not significant ($P > 0.05$), NA = not applicable.

	Seedlings					
	Present October 1997		Appearing October 97-June 98	Present June 1998		Turnover %
	n	Mean ± S.D.	n	n	Mean ± S.D.	
Kanuka	20	9.7 ± 7.6	14	17	8.8 ± 7.2	50
Gorse	26	9.1 ± 7.6	32	42	14.8 ± 11.3	27
K.-W.	NS	NS	NA	0.01	NS	0.05

Discussion

The presence of weeds indicates that a site has a different history, and possibly other different characteristics, from one supporting native vegetation. Conclusions regarding the differences between kanuka and gorse that may be drawn from our study, or similar comparative studies (e.g. Eugunjobi, 1971) are therefore speculative (Adair and Groves, 1998). Kanuka and gorse scrub was extensive in the Nelson-Marlborough region 20 years ago (Blaschke *et al*., 1981), but most stands have since been converted to exotic forestry. We located only two stands within 100 km of Nelson city that largely satisfied our requirements. The stands' approximate histories were known, for example, we knew that the kanuka had not evolved through gorse. They were of similar age, which meant we were not studying simply the effects of time (*sensu* Jenny, 1941) that operate in kanuka and gorse successions (Druce, 1957). They were within a few kilometres of each other, on similar slopes, with the same aspect and soil type, and at similar altitudes. The stands were large enough to accommodate a number of bird and animal recording stations. They were not grazed by domestic stock. This eliminated a major influence on vegetation succession (Wilson, 1994). The stands were preserved on private land, as part of an outdoor tourism venture, so the field equipment was secure from human interference. One condition for an ideal study was not satisfied: there was grassland adjacent to the kanuka and native forest was nearer the gorse.

Within these constraints, we believe many of the differences we studied were due to the dominant species. Kanuka and gorse scrub of the same age had different structures. Kanuka was taller with a dense, even canopy, and while the margins of the gorse stand were armoured, there were large canopy gaps within the stand where the sun reached the ground. These structural differences probably influenced the size and composition of the bird communities. Californian quail utilized the gaps in the gorse. The taller crowns of kanuka, with a greater abundance of fine branches for gleaning, may have offered sites preferred by some of the omnivorous and insectivorous species. Bellbirds, brown creepers and grey warblers occupy higher parts of the vegetation than silvereyes within podocarp/ angiosperm forest (Fitzgerald *et al*., 1989; Spurr *et al.,* 1992) and kanuka forest (Gill, 1980). Kanuka flowers have an abundance of nectar (Molloy, 1975) whereas gorse produces very little (Sandry, 1985). Nectar abundance presumably influences the composition of the invertebrate fauna while these species are flowering, as they were during the study period. Dietary studies would be required to elucidate the effect of these differences on bird numbers. Whatever the underlying interactions (and based simply on bird frequency counts) the lower number of bellbirds, brown creepers and grey warblers in gorse suggests that this invasive plant species provides poorer habitat than does kanuka for endemic birds. On the same basis, gorse may offer superior habitat for some adventive birds (Californian quail, green finch, yellow hammer), and also for the recently self-introduced silvereye. This illustrates the positive and negative interactions that can occur between invaders and native species (Simberloff and Holle, 1999).

The dietary preferences of foraging birds will influence the seed rain composition. The low use of gorse by bellbirds could have potentially reduced the input of native seeds as bellbirds prefer native plant foods (Williams and Karl, 1996). In our study, however, seed fall species richness was similar, and there were significantly more native woody seeds deposited in the kanuka. Both kanuka and gorse had an abundance of silvereyes. These birds were likely to disperse a wider range of plant species and they were the only abundant seed-dispersing bird in the gorse. All the plant species deposited in the kanuka and gorse had fruits < 6 mm diameter, small enough to be dispersed by silvereyes (Burrows, 1994a; Williams and Karl, 1996). [In this respect, we disagree with the classification of Bray *et al.* (1999), in which *Coprosma robusta* and

Pseudopanax arboreus were described as having large fruit, unlikely to be distributed by silvereyes, as we have noted the presence of these seeds in silvereyes' faeces (Williams and Karl 1996, p. 131).] New Zealand pigeons (*Hemiphaga novaeseelandiae*) are important dispersers of larger seeds but they were not seen in either kanuka or gorse. Starlings (*Sturnus vulgaris*) were absent from our early secondary successional stands presumably because of the absence of woody species with large fruit displays, e.g., *Sambucus nigra,* to which they are attracted in other vegetation (Williams, 1983; Allen *et al.,* 1992; Burrows, 1994a; Williams and Karl, 1996). Seed dispersal into the earliest stages of regenerating gorse is therefore particularly dependent on silvereyes and the occasional bellbird, or blackbird (Burrows, 1994a; Williams and Karl, 1996). Woody plant species capable of establishing in gorse are therefore dependent largely on recently self-introduced birds and less so on other native birds or adventive birds.

These birds, and other animals to an unknown extent, account for 68 percent of seed species or species groups deposited in the kanuka and gorse, which is comparable to the 54 percent recorded in manuka-kanuka stands in Golden Bay (Bray *et al*., 1999). All the fleshy-fruited species whose seeds were trapped in kanuka occurred within 100 m of the traps. Similar distances applied to seeds of fleshy-fruited species recorded in gorse, with the exception of the abundant *Leycesteria formosa* seeds, which must have been carried about 200 m from the valley floor to the traps. Several bird species disperse these very small seeds (Williams and Karl, 1996). Silvereyes dispersed *Asparagus asparagoides* seeds an average of 90.5 m, and a maximum theoretical distance of 12 km based on gut passage rate and flight speed (Stansbury 2001). *Leycesteria formosa* fruits are also palatable to possums and rats, and large numbers of viable seeds pass through these animals (Williams *et al.*, 2000). Wind dispersal accounted for only 23 percent of seed species or groups, even though seeds of the wind-dispersed *Clematis vitalba* were the most abundant. This reflected the large seed production and wide distribution of *Clematis vitalba* in the study area. Wind-dispersed seeds of potential canopy trees were represented by only a few *Dodonaea viscosa* that probably dispersed at least 100 m from their nearest source.

There were about 5-6 seeds per m^2 yr^{-1} of fleshy-fruited woody or vine species dispersed into the kanuka and gorse stands. This compares with the 1.9 seeds per m^2 of these life forms that fell into grassland sites (distance from potential source not stated) over the peak 2 months of the fruiting season on Mana Island near Wellington (Ferguson and Drake, 1999). On Banks Peninsula there were 13 seeds per m^2 yr^{-1} in bracken-blackberry vegetation only 30 m from mixed forest where thousands of seeds fell (Burrows, 1994a). The seeds deposited in kanuka and gorse illustrate how they provide perching opportunities critical for the establishment of later successional stages (Debussche *et al.*, 1982; Kollman and Piri, 1995; Ferguson and Drake, 1999).

Seed fall would vary from year to year (Burrows, 1994b), but most species involved germinate within a year of dispersal (Burrows, 1995a,b, 1997). The fleshy-fruited species with the most frequent seed fall, *Coprosma rhamnoides* in the kanuka and *M. ramiflorus* (with *L. formosa*) in gorse, ranked first amongst the seedling species. This illustrates a tight link between seed supply from the adjacent vegetation, seed fall, and the first fleshy-fruited woody species in secondary successions, as described for manuka-kanuka forest by Bray *et al.* (1999). The abundance of *L. formosa* seeds relative to the number of seedlings (none were recorded in kanuka or gorse) is an example of an invasive weed that produces abundant fruit for dispersal when growing on a favourable site, in this case a moist toe slope, but whose seeds are carried to an unfavourable environment, in this case, gorse scrub on a dry hill slope. Similar vegetation further inland where precipitation is > 1400 mm yr^{-1} provides suitable habitat for *L. formosa.*

Seedling survival was higher in gorse than in kanuka stands of a similar age and several factors may be involved. The disappearance of some seedlings in both stands may have been caused by drought, as has been shown on Banks Peninsula (Burrows, 1994a). Grazing may have limited the abundance of native broadleaved seedlings in gorse near Dunedin as the seedlings were more abundant on steep slopes less accessible to browsers (Lee *et al.,* 1986). Woody seedlings were abundant in ungrazed gorse scrub older than 10 years (Wilson, 1994) but uncommon in dense kanuka of similar age on Banks Peninsula (Wilson, 1994) and near Dunedin (Allen *et al.*, 1992). Such vegetation provides an environment unfavourable to light-demanding broad-leaved woody seedlings, where light levels of only 2.3 percent of light in the open were recorded beneath 17-year-old manuka (Bray *et al*., 1999). This is below the levels that reduce growth for several woody species in our study (Williams and Buxton, 1989). The vegetation structure and collapsing canopy of similar-aged gorse offers a more favourable light environment earlier in the succession and, in addition, may inhibit entry of browsing hares and rabbits where the stands are not penetrated by sheep or cattle. Kanuka stand structure facilitates the entry of these animals as shrubs are not armoured, and the layer up to 1m above ground level is much less dense than in mature gorse scrub. Differential access to browsing ungulates is not apparent in open shrublands of kanuka and gorse (P.A. Williams, *unpubl.*).

In contrast to the low numbers of rabbits and hares, the numbers of mice in the kanuka (6.3 C/100 TN) and gorse (14.3 C/100 CN) were within but towards the lower end of the range of densities (0-130.2 C/100 TN) reported in New Zealand (Murphy and Pickard, 1990). Their greater abundance in gorse than in kanuka probably resulted from the favourably dense ground cover (King *et al.*, 1996) formed by the mounds of dead gorse crowns, and the food supply of 400 per m^2 yr^{-1} of gorse seeds with their associated weevil (*Apion ulicis*). Mice numbers tend to be higher where there are few rats (King *et al.*, 1996). Ship rat numbers were uniformly low in both kanuka and gorse in our study.

Mice do not appear to limit the regeneration of gorse, as there were large numbers of gorse seedlings on disturbed ground. Mice destroy a high percentage of small seeds of fleshy-fruited woody species in captivity (Williams *et al.*, 2000) but there is no published evidence of them eating such seeds in the wild (Murphy and Pickard, 1990), and they had little effect on seed removal rates in lowland forest near Wellington (Moles and Drake, 1999). This leaves open the question of whether they influence the direction of vegetation succession. The greater numbers of mice in gorse than in kanuka are nevertheless an example of an invasive mammal being more successful in association with habitats found in its country of origin than with indigenous habitats (Brown, 1989).

Overall, it appears that, in these stands of kanuka and gorse, seedling survival may be more important than seed fall in dictating the speed of secondary succession. The net effect of differing vegetation structures and stand dynamics on bird and animal communities, and seedling survival is that kanuka and gorse are likely to have differing vegetation successional trajectories. To determine what these differences might be, in the absence of history and site effects, gorse and kanuka (or manuka) stands would need to be grown experimentally adjacent to a range of native communities, and studied for at least 30 years.

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