Fallow deer impacts on Wakatipu beech forest

Sean W. Husheer[1] and Chris M. Frampton[2]
[1]New Zealand Forest Surveys, 15 McElwee Street, Napier, New Zealand (E-mail: shusheer@clear.net.nz)
[2]Department of Medicine, University of Otago, P.O. Box 4345, Christchurch

Abstract: This study uses data from forty-nine 20 m × 20 m permanent plots measured in 1976, 1982, 1989 and 1997-2002 in Wakatipu Forest, western Otago. We relate changes in red (*Nothofagus fusca*), silver (*Nothofagus menziesii*) and mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest vegetation to the presence of fallow deer (*Dama dama*). Vegetation composition is likely to have been altered prior to plot establishment, and results show that there was little change in vegetation composition during the study. There are some signs of fallow deer reducing silver beech seedling abundance at some plots, but most beech stands appear to be in the late phase of development and undergoing self thinning, so are probably not immediately vulnerable to suppression of canopy regeneration. In the future, widespread disturbance is likely to release plants in the understorey from competition for light and nutrients, and at that stage fallow deer browsing of beech species may be able to alter successional pathways more than has occurred over the past two decades. Seedling and sapling density of the palatable *Griselinia littoralis* (broadleaf) was probably insufficient to ensure successful regeneration. Comparisons of seedling densities with other mixed beech forests throughout New Zealand suggest that fallow deer density will need to be nearly zero in Wakatipu Forest before regeneration of all palatable subcanopy hardwood species is assured.

Keywords: *Dama dama*; herbivory; *Nothofagus;* regeneration; browsing

Introduction

Soon after the multiple introductions of deer into New Zealand in the late 19th century, it was recognised that selective browsing was capable of eliminating subcanopy hardwood species from forest understories (Walsh, 1892; Cockayne, 1926). Later studies of the post-irruptive phase of deer colonisation showed that browsing was also capable of suppressing the regeneration of beech (*Nothofagus* spp.[1]) forest canopies in some regions (e.g. Holloway, 1950; Riney *et al.*, 1959). Beech species are regarded as being more browse resistant than common subcanopy hardwood species such as *Griselinia littoralis* (broadleaf) and *Raukaua simplex* (threefinger; Forsyth *et al.*, 2002; Husheer, Coomes and Robertson, 2003). Beech forests are also less vulnerable to other introduced browsers such as brushtail possums (*Trichosurus vulpecula*), which tend to browse on flowers, fruits and foliage of adult trees other than beech (Cowan, 2001). In podocarp forest in Pureora Forest Park, central North Island, which was colonised by possums and deer in the mid 20th century, Nugent, Fraser and Sweetapple (2001) showed that even where deer and possums browsed on the same species, deer had greater impacts on regeneration by preferentially browsing on entire cohorts of seedlings rather than less vulnerable trees. It is now widely recognised that the composition and regeneration of most New Zealand forests reflects decades of preferential browsing of palatable species by deer (Veblen and Stewart, 1982). While previous research has shown how biological and environmental influences affect beech forest composition (for reviews see Wardle, 1984; Ogden, Stewart and Allen, 1996; Leathwick and Austin, 2001) the ongoing effects of deer on forest regeneration are still poorly understood (Rogers and Leathwick, 1997; Coomes *et al.*, 2003). For instance guidelines indicating maximum threshold deer densities that allow for the regeneration of palatable plant species are still not known. This lack of fundamental knowledge is a clear impediment to setting specific management targets (Choquenot and Parkes,

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[1] Nomenclature follows Parsons, Douglass and Macmillan (1995), Edgar and Connor (2000), and Brownsey and Smith-Dodsworth (2000). *Raukaua simplex* is described by Mitchell, Frodin and Heads (1997). *Nertera villosa* is described by Macmillan (1995). *Coprosma* sp. "t" is referred to by Eagle (1986), and *Halocarpus biformis*, *Phyllocladus alpinus, Podocarpus hallii* and *Podocarpus nivalis* by Wilson and Galloway (1993).

2001; Department of Conservation, 2001). Wardle *et al.* (2001) and Wardle, Bonner and Barker (2002) showed that at some sites deer can alter ecosystem processes by modifying nutrient cycling pathways, but that this modification appears dependent on as yet unidentified influences among sites, so deer-plant interactions are likely to vary spatially and temporally (Wardle, 2002). This inability to make sitespecific predictions on deer-forest relationships means that long term monitoring studies in individual forests are often the only means of producing appropriate data to guide effective conservation management.

At Wakatipu Forest, western Otago (Fig. 1), the abundance of the dominant deer species, fallow deer (*Dama dama*), has been managed exclusively by recreational hunting for two decades. Previous unpublished studies have stated that highly palatable, subcanopy hardwood species had declined in density within several decades of the introduction of fallow deer at Wakatipu Forest in 1887 (Davidson and Nugent, 1998) and farming in 1868 (Hayward, 1971; Rose, 1977; Chisholm, 1991; Golding, 2000). Evidence of high levels of fallow deer browsing on *Carpodetus serratus* (marbleleaf), *Griselinia littoralis* and *Raukaua simplex* was noted in these studies. These three species have been identified as palatable to deer by Forsyth *et al.* (2002), and are potentially vulnerable to fallow deer suppressing their regeneration.

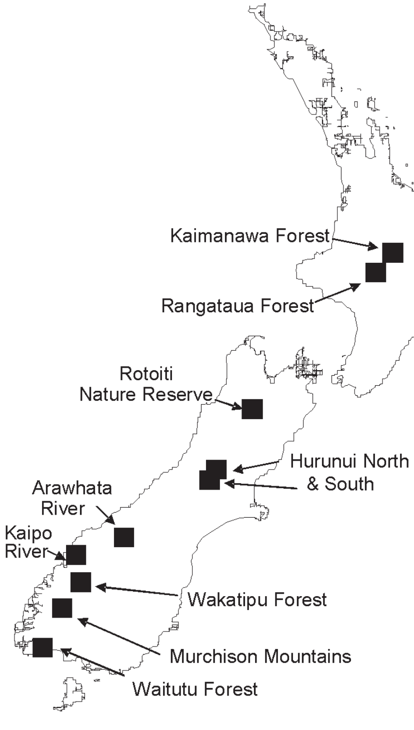

Figure 1. Location of Wakatipu Forest and nine other mixed beech forests throughout New Zealand where 20 m × 20 m permanent plot surveys have been undertaken in the past decade.

We use data from forty-nine 20 m × 20 m permanent plots (Allen, 1993), established by Rose (1977) in Wakatipu Forest in 1976 and remeasured in 1982, 1989 and finally between 1997 and 2002, to relate changes in plant species composition over two decades to ongoing browsing by fallow deer. We predicted that if restricted recreational hunting had lowered fallow deer densities sufficiently to allow recruitment of palatable subcanopy hardwood species in the understorey, that the densities of *C. serratus*, *G. littoralis* and *R. simplex* as seedlings and saplings would increase to exceed their respective densities as trees. To provide a national context on the density of these species as seedlings (with more intensive deer management regimes), we collated and compared data from 20 m × 20 m permanent plot surveys from nine other mixed beech forests throughout New Zealand. This approach provides the only possible comparative benchmark in the absence of data from replicated exclosure plots, or from permanent plot surveys that were established before the introduction of fallow deer to Wakatipu Forest.

Browsing by fallow deer could also have affected canopy regeneration in this mixed mountain (*Nothofagus solandri* var. *cliffortioides*), red (*Nothofagus fusca*) and silver beech (*Nothofagus menziesii*) forest. A secondary objective was to examine impacts of fallow deer on beech canopy regeneration, in the post-irruptive phase of deer colonisation. If fallow deer have reduced beech regeneration over the past three decades we would expect beech seedling abundance to be negatively related to fallow deer density, and for beech seedlings and saplings not to have increased in abundance over the course of this study.

Methods

The Greenstone and Caples Valleys (45°S, 168°E) are located in Wakatipu Forest (28 425 ha) and drain the eastern Southern Alps of Otago. The glacially formed valleys have extensive alluvial flats (330–610 m.a.s.l). Valley sides are dominated by mountain, red and silver beech forests from valley floors to treeline at 1000–1100 m.a.s.l. Above the treeline, subalpine shrub and tussock-land extends to the ridgeline at 1500–2000 m a.s.l. Since the introduction in 1981 of the Greenstone/ Caples Recreational Hunting Area in Wakatipu Forest, commercial hunting has not been permitted, and recreational hunting is restricted to between April and September. Department of Conservation huts and a track system provide accommodation and access for recreational hunters who were each permitted to shoot two fallow deer in any one trip.

The 49 permanent forest plots in this study were established in November 1976 and follow a standardised method used to establish over 5000 such plots in New Zealand (Allen, 1993). All 49 plots were re-measured in three surveys during October–December 1982, November–December 1989, and November 1997–April 2002. Measurements are referred to as the 1976, 1982, 1989 and 1999 surveys. On 16 randomly located transect lines that ran from streams or valley floors to the nearest tree line, plots were systematically located at 200 m intervals from line origin, except for the first plot which was 40 m from origin. In each 20 m × 20 m plot, all trees ≥ 2 cm diameter at breast height (DBH = 1.35 m) were identified by species, tagged and the diameter over bark at breast height measured. All saplings (>135 cm high, <2 cm DBH,) were counted and identified. Twenty-four circular understorey sub plots (49cm radius) were systematically located within each plot (Allen, 1993). All established woody seedlings (15–135 cm high) were identified and counted in each of the sub-plots. The presence of small seedlings (<15 cm high) of vascular plants in the sub-plots was also recorded, and their species identified. Altitude at each plot was measured to the nearest 10 m; slope was measured to the nearest 5°; and aspect to the nearest 5°. For analysis, aspect was converted to degrees from true north.

Plot tree stem, sapling and woody seedling densities, basal area, and relative frequency of occurrence of small seedlings of vascular plants (<15 cm high) in 24 sub-plots in each plot, were summarised by species for each survey. To determine changes in basal area, and the density of common tree species (≥5 stems ha^{-1}) as seedlings, saplings and trees, summaries were compared using repeated measures ANOVA for beech species and Bonferroni-corrected paired *t*-tests for other species in SYSTAT 10 (Sokal and Rohlf, 1995; SPSS, 2000). Tree species were defined as species capable of growing ≥5 m in height according to Poole and Adams (1994), and large tree species were defined as those present as trees >15 cm DBH. Aspect, altitude and slope were included as between plot factors in a repeated measures ANOVA to determine whether patterns of change were consistent through these environmental gradients. A repeated measures metric of the year of survey allowed for unequal intervals between surveys. Because the last survey spanned four years a midpoint of 1999 was used. There were some inconsistencies in the recording of tree tag data between surveys, so calculation of recruitment, mortality and growth was not undertaken. Changes in species composition over time were determined with Canonical Correspondence Analysis (CCA) in CANOCO 4.0 (Ter Braak and Smilauer, 1998). In CCA, an automatic forward selection procedure was used to test for the effect of time between surveys and altitude on overstorey, sapling, seedling and groundcover (vascular plants <15 cm high) composition. Importance values for species were calculated using density data for trees, saplings and seedlings, and frequency of vascular plant occurrence in seedling sub-plots for ground cover data. A plot identifier variable was treated as a blocking covariate to reduce unexplained spatial variation in CCA. For all statistical tests a threshold Type I error probability level of ≤0.05 was used.

To compare the densities of *C. serratus*, *G. littoralis* and *R. simplex* seedlings between the 1999 Wakatipu survey and other surveys in mixed red, silver and mountain beech forest throughout New Zealand we searched the National Vegetation Survey databank (Wiser, Bellingham and Burrows, 2001) for 20 m × 20 m plot surveys undertaken within the last decade. These three species were selected for comparisons because they were common in Wakatipu Forest as trees and previous studies have shown that they are preferentially selected by deer in New Zealand (Stewart, Wardle and Burrows, 1987; Nugent and Challies 1988; Stewart and Burrows, 1989; Forsyth *et al.*, 2002). The nine surveys selected were undertaken by the New Zealand Department of Conservation in Waitutu Forest (46° S, 167° E), Murchison Mountains (45° S, 167° E), Kaipo River Valley (44° S, 168° E), Arawhata River Valley (44° S, 169° E), North and South branches of the Hurunui River, (43° S, 172° E), Rotoiti Nature Reserve (42° S, 173° E), Rangataua Forest (39° S, 175° E), and Kaimanawa Forest Park (39° S, 176° E). The regions vary in the way deer have been managed. In the Murchison Mountains intensive subsidised commercial and government funded hunting has been undertaken to lower red deer (*Cervus elaphus*) abundance. Intensive unsubsidised commercial red deer hunting has occurred in the Arawhata, Kaipo, Hurunui north and south branches, and Waitutu study areas for the last three decades, following the establishment of a venison recovery industry in the late 1960s and early 1970s. In Wakatipu Forest, Rangataua Forest and Rotoiti Nature Reserve deer have been managed using unsubsidised recreational hunting. In Kaimanawa Forest Park management also consisted of recreational hunting, and red and sika deer (*Cervus nippon*) have been at high enough densities over the past few decades to induce compositional shifts in the overstorey and suppress beech canopy regeneration in some stands (Husheer *et al.*, 2003). We expected plot altitude and basal area and the tree stem density of *C.*

serratus, *G. littoralis* and *R. simplex* to have an influence on the seedling densities of these species. These variables were manually included in ANCOVAs comparing seedling densities among regions, with a threshold probability level to include each variable of $P \leq 0.05$.

Trends in fallow deer densities were assessed by compiling results from seven unpublished pellet frequency of occurrence surveys (1976-1999) in Wakatipu Forest. These surveys used repeatedly measured, randomly located transect lines, some of which were also used to establish the permanent plots used in this study. At intervals of 20 m on transect lines, the presence or absence of intact fallow deer pellets (no sign of breaking up) in 114-cm radius plots were recorded using the protocol described by Baddeley (1985). Pellet occurrence was determined by calculating the proportion of times that fallow deer pellets were recorded in plots on individual transect lines. Pellet data from eight lines in the Caples River, where permanent plots were also established, were extracted from Golding (2000) to test for the relationship between pellet frequency in 1998/99 and small beech seedling (<15 cm high) frequency of occurrence and woody seedling (15–135 cm high) densities in 1999 from plots on these lines.

Results

Overstorey

Between the 1976 and 1999 surveys there was a significant decline in tree stem density for all species combined, while there was a corresponding increase in overall basal area for all species combined (Table 1). While there was no statistically significant change in the basal area of any individual beech species, all three species contributed to the overall increasing trend. In comparison to red beech, which did not change significantly in tree stem density, silver and mountain beech both showed significant decreases in tree stem density. Despite these changes in the density of individual tree species, canonical correspondence analysis showed no significant changes in overall overstorey species composition between the four surveys using species importance values calculated from density summaries ($\lambda < 0.001$, $F = 0.027$, $P = 0.995$).

Understorey

There were limited changes in beech species composition in the understorey between the 1976 and 1999 surveys (Table 1). Changes that did occur were not consistent among beech species, surveys or plots.

Table 1. Mean basal area (m^2 ha^{-1} ± SEM), tree density (> 2 cm DBH, stems ha^{-1} ± SEM), sapling density (> 135 cm tall < 2 cm DBH, stems ha^{-1} ± SEM), established seedling density (15–135 cm tall, stems ha^{-1} ± SEM) and small seedling frequency of occurrence (<15 cm) with repeated measures ANOVA tests for differences in means between 1976, 1982, 1989 and 1999 surveys.

Species	1976	1982	1989	1999	$F_{3,46}$	*P*
Basal area (m^2 ha^{-1})						
red beech	18.0±3.6	18.2±3.7	20.2±3.9	19.8±3.8	2.042	0.121
silver beech	22.2±3.9	22.6± 4.1	23.0±4.2	23.4±4.3	1.492	0.229
mountain beech	15.8±3.1	16.3± 3.1	16.7±3.2	17.1±3.3	1.315	0.281
All other species	1.3±0.4	1.5±0.5	1.4±0.4	1.1±0.3	1.541	0.217
All species	57.3±3.0	58.7±3.3	61.2±3.2	61.4±3.0	4.949	0.005
Tree stem density (stems ha^{-1})						
red beech	188±43	189±43	176±38	174±39	1.196	0.322
silver beech	840±152	813±146	714±121	608±95	3.857	0.015
mountain beech	566±109	548±106	495±96	451±87	5.309	0.003
All other species	257±70	255±65	234±64	224±60	0.839	0.479
All species	1852±143	1806±136	1618±115	1456±99	12.522	<0.001
Sapling density (stems ha^{-1})						
red beech	76±32	91±53	65±26	336±148	1.358	0.267
silver beech	210±55	102±31	140±52	98±36	4.468	0.008
mountain beech	67±27	34±16	29±12	207±106	2.973	0.041
Seedling density (stems ha^{-1})						
red beech	451±270	2164±940	11837±5655	7384±2570	2.500	0.071
silver beech	496±186	744±233	2063±575	2119±595	4.334	0.009
mountain beech	327±145	3438±1970	11938±5265	12592±5378	2.119	0.111
Frequency of occurrence of <15 cm seedlings (%)						
red beech	27±5	35±6	32±5	29±5	3.808	0.016
silver beech	19± 3	22±3	29±4	18±3	5.440	0.003
mountain beech	43±6	50±6	47±6	46±6	4.255	0.010

Table 2. Density of seedlings (15–135 cm high), saplings (> 135 cm high, < 2 cm DBH) and trees (≥ 2 cm DBH). Values are (stems ha^{-1} ± SEM) of common (≥ 5 stems ha^{-1}) subcanopy hardwood trees from the 1999 survey. Sapling density of these species in 1976 is also listed with a series of paired *t*-tests comparing 1976 and 1999 sapling densities.

Species	1999		Saplings			
	Seedlings	Trees	1976	1999	t_{48}	*P*
Carpodetus serratus	248±226	5±3	<0.1	7±6	1.163	0.175
Griselinia littoralis	<0.1	8±4	<0.1	1±1	1.429	1.000
Myrsine divaricata	282±111	30±13	15±7	16±10	0.260	1.000
Phyllocladus alpinus	688±361	67±41	29±20	76±29	2.441	0.126
Podocarpus hallii	1939±1109	45±16	21±11	47±18	1.524	0.938
Pseudowintera colorata	56±46	13±10	17±14	82±79	1.000	1.000
Raukaua simplex	101±47	10±6	<0.1	5±2	2.112	0.280

Repeated measures ANOVA showed a general decline in silver beech sapling densities, while mountain beech sapling densities first declined, then increased. Red beech declined at high altitude plots ($F_{3,45}$ = 3.063, *P* = 0.038), but not overall. For mountain beech, increases in sapling densities were greatest at low altitudes ($F_{3,45}$ = 4.070, *P* = 0.012). Repeated measures analysis also showed that there was no statistically significant effect of aspect or slope on changes in red beech, silver beech and mountain beech sapling densities (*P* > 0.079).

There was no significant change in the sapling densities of common tree species (≥5 tree stems ha^{-1}) between 1976 and 1999, but species known to be unpalatable to deer (*Podocarpus hallii*, *Phyllocladus alpinus*, *Pseudowintera colorata*; Forsyth *et al.*, 2002) were more common than palatable species (Table 2). CCA showed significant changes in sapling species composition with altitude (λ = 0.59, *F* = 19.86, *P* = 0.005), but only marginally significant changes between the four surveys (λ = 0.07, *F* = 2.15, *P* = 0.050). There was some evidence of regeneration failure of *G. littoralis*, *M. divaricata* and *R. simplex*, with all three species having higher tree than sapling densities (Table 2).

There was no significant change in the densities of red beech or mountain beech seedlings between surveys, but silver beech seedling density increased substantially between 1976 and 1999 (Table 1). Large standard errors of means indicate that there was considerable variability in seedling densities among plots. Repeated measures analysis showed that altitude, aspect and slope had no significant effect (*P* > 0.05) on changes in densities of beech seedlings between surveys. Paired *t*-tests of seedling (15–135 cm high) densities of large tree species (present as trees > 15 cm DBH) showed that *Coprosma pseudocuneata* decreased in mean (± SEM) density between 1976 (2481±142 stems ha^{-1}) and 1999 (507±217 stems ha^{-1}; *t* = 2.511, *P* = 0.015) while there was no significant change in the seedling density of *C. serratus*, *G. littoralis*, *P. alpinus*, *P. hallii* or *R. simplex* (*P* > 0.05). Densities of *G. littoralis* seedlings were also very low in comparison to tree stem density, indicating selective browsing of seedlings by fallow deer may have induced regeneration failure.

CCA showed no significant changes in composition of ground cover species (<15 cm high) over time (λ = 0.030, *F* = 1.230, *P* = 0.135) or of changes in the eight ground cover species that had a mean occurrence in 1999 > 5% (*Grammitis billardieri*, *Hymenophyllum* spp., *Nertera villosa*, *Polystichum vestitum*, *Uncinia* spp., and red, silver and mountain beech; λ < 0.001, *F* = 0. 150, *P* = 0. 960).

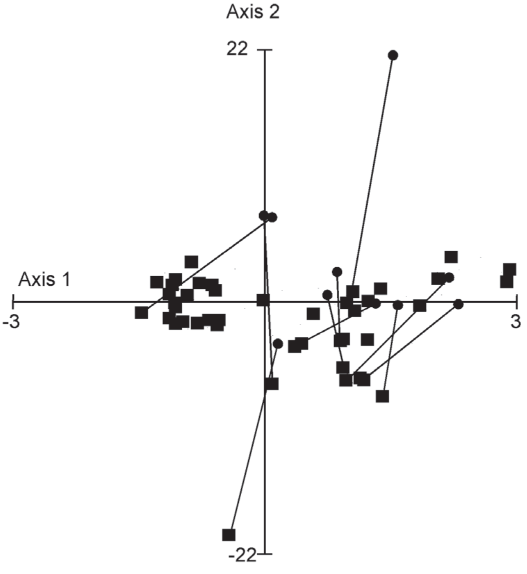

Figure 2. Plot scores from woody seedling (15–135 cm high) CCA ordination from the 1999 (■) survey from plots with seedlings present (*n* = 47). Ten individual plots showing large changes from 1976 (●) to 1999 are linked.

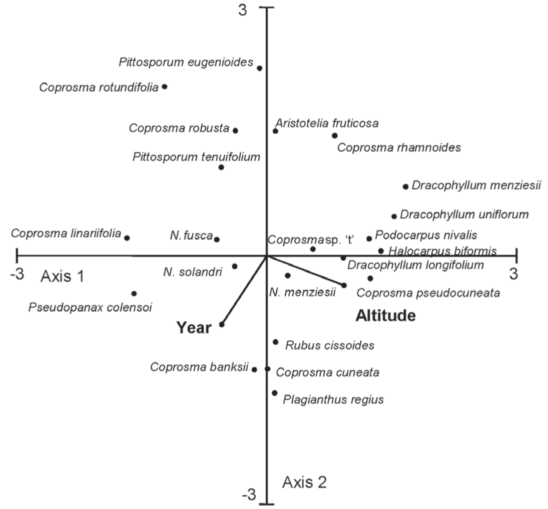

Figure 3. CCA diagram of woody seedling (15-135 cm high) species scores for the effects of year of survey and plot altitude. Only species scores for *Nothofagus* and species with high or low (≥ 1 or ≤ –1) axis 1 and axis 2 scores are displayed.

There was some evidence that woody seedling composition did change between surveys at some high altitude plots. CCA showed significant changes in woody seedling species composition with altitude (λ = 0.38, F = 8.51, P = 0.005) and over time (λ = 0.11, F = 2.58, P = 0.010), that was particularly evident for 10 of the 49 plots (Fig. 2). These plots were significantly higher (mean = 815 m a.s.l.) than the remaining 39 plots (mean = 696 m a.s.l., t_{48} = 2.553, P = 0.017) and marginally more north facing (24° from north) than remaining plots (21° from north; t_{48} = 2.122, P = 0.050), but there was no difference in plot slope (t_{48} = 0.942, P = 0.361). Close examination of data revealed that these ten plots had inconsistent and sometimes large changes in the densities of silver beech seedlings. There was a trend for *Podocarpus nivalis, C. pseudocuneata* and *Coprosma* sp. "t" to increase and *Coprosma cuneata* to decline in these ten plots over time. When all plots were considered, there appeared to be changes in seedling composition from *Aristotelia fruticosa*, *Coprosma rhamnoides*, *Coprosma robusta*, *Coprosma rotundifolia*, *Dracophyllum* spp., *Pittosporum* spp. towards *Coprosma banksii, Coprosma cuneata, Plagianthus regius, Pseudopanax colensoi* and *Rubus cissoides* (Fig. 3). More common species including red, silver and mountain beech contributed little to overall compositional shifts.

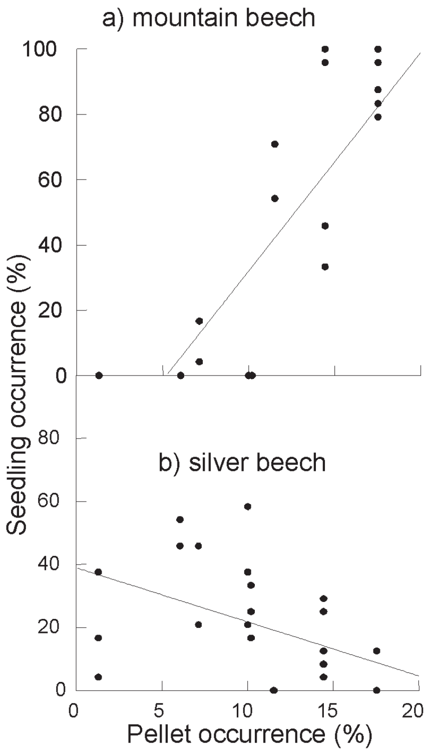

Figure 4. The relationship between seedling (< 15 cm high) frequency of occurrence of a) mountain and b) silver beech in 1999 and pellet frequency of occurrence in 1998/1999 on lines in the Caples Valley (n = 8; data extracted from Golding, 2000). Lines of best fit from linear regressions are: a) mountain beech seedling occurrence = 6.681 × pellet occurrence –34.83, R^2 = 0.655, $F_{1,\,24}$ = 45.522, P < 0.001 and b) silver beech seedling occurrence = 38.858 – 1.713 × pellet occurrence, R^2 = 0.237, $F_{1,\,24}$ = 7.465, P = 0.012.

Comparisons with other regions

There were no significant differences between the densities of seedlings (15-135 cm) of *C. serratus*, *G. littoralis* and *R. simplex* at Wakatipu Forest, in comparison to nine other regions, or between regions with and without commercial and government funded deer hunting (Table 3). ANCOVA showed that tree stem density of these species had a significant effect on their respective seedling densities.

Pellet frequency of occurrence

Pellet frequency of occurrence data indicates a substantial decline in fallow deer densities during the

Table 3. Comparisons of seedling (15–135 cm high) and tree stem densities (≥2–3 cm DBH; mean stems ha^{-1} ± SEM) for three common palatable, subcanopy hardwood species from recent surveys from Wakatipu Forest, Murchison Mountains, Kaipo Valley and Waitutu Forest, Fiordland National Park, Rangataua Forest, southern Mount Ruapehu, Rotoiti Nature Reserve, Arawhata Valley, southern and northern Hurunui Valleys, and Kaimanawa Forest Park. Data was obtained from the National Vegetation Survey databank (Wiser, Bellingham and Burrows, 2001). Linear contrasts were used to test for differences in means between Wakatipu and other regions and between regions with and without commercial deer hunting. For these contrasts, covariates of plot altitude, basal area and the tree stem density of *C. serratus*, *G. littoralis* and *R. simplex* were included when a threshold value of P ≤ 0.05 was obtained.

				Species					
Region	*n*	Years	Elevation	*Carpodetus serratus*		*Griselinia littoralis*		*Raukaua simplex*	
	(plots)		(m a.s.l)	Seedlings	Trees	Seedlings	Trees	Seedlings	Trees
Regions with no commercial or government funded hunting									
Wakatipu Forest	49	1997-2002	290-1140	248 ± 121	4 ± 3	<1 ± 84	7 ± 4	101 ± 188	10 ± 6
Kaimanawa Forest	171	1998-2001	650-1300	213 ± 65	49 ± 8	181 ± 45	54 ± 8	730 ± 100	19 ± 3
Rangataua Forest	48	1999	600-1100	380 ± 123	40 ± 10	58 ± 85	10 ± 3	380 ± 190	5 ± 2
Rotoiti Reserve	17	1997-2000	600-1100	32 ± 206	35 ± 19	65 ± 143	67 ± 24	97 ± 318	4 ± 2
Regions with recreational and commercial hunting									
Arawhata River	43	1998-2000	0-1030	128 ± 109	45 ± 14	206 ± 117	44 ± 11	938 ± 186	90 ± 6
Kaipo River	10	1999	0-95	<1 ± 226	12 ± 5	<1 ± 243	7 ± 4	<1 ± 386	0
Waitutu Forest	107	1997	20-890	36 ± 69	16 ± 4	21 ± 74	16 ± 3	299 ± 118	26 ± 4
Hurunui North	27	1999	635-1180	<1 ± 137	0	798 ± 148	45 ± 30	368 ± 235	4 ± 3
Hurunui South	25	2001	640-1130	243 ± 143	5 ± 3	199 ± 153	0	221 ± 244	0
Linear contrast between commercial and government funded hunting									
Murchison Mountains	22	1998	500-1100	<1 ± 181	5 ± 3	<1 ± 126	2 ± 2	176 ± 280	9 ± 6
Linear contrast between seedling density means of Wakatipu and all other surveys									
$F_{1, 461}$				3.284		1.179		1.522	
P				0.071		0.278		0.218	
Linear contrast between regions with and without commercial or government hunting									
$F_{1, 461}$				1.495		2.795		3.525	
P				0.222		0.095		0.061	
Covariates included in analysis									
				C. serratus tree stem density ($P = 0.001$)		*G. littoralis* tree density ($P = 0.026$)		*R. simplex* tree density ($P < 0.001$) Basal area $P < 0.001$ Plot altitude $P < 0.001$	

1980s at Wakatipu Forest. Pellet occurrence was high in 1976 (27.0 % pellet occurrence; Rose, 1977), but declined by 1980 (7.0±1.2 %; Golding, 2000), increased in 1982 (18.6±1.5 %; Chisholm, 1991), and remained low in 1986/87 (8.9±1.8 %; Golding, 2000), 1987 (10.1±1.3 %; Chisholm, 1991), 1989 (10.1±1.8 %; Chisholm, 1991) and 1998/99 (11.3±2.1 %; Golding, 2000).

There was a significant positive relationship between the occurrence of mountain beech seedlings in 1999 (<15 cm high) and pellet occurrence in 1998/1999, and a negative relationship between the occurrence of silver beech seedlings and pellet occurrence (Fig. 4). High mountain beech seedling occurrence could be a response to low silver beech occurrence because the two species tended to be present in different plots (Pearson correlation = -0.620) with only 13 plots where both silver and mountain beech seedlings (<15 cm) were present. There was no significant effect ($P > 0.05$) of pellet occurrence on red beech seedling occurrence or on red, silver and mountain beech seedling (15-135 cm high) densities (stems ha^{-1}).

Discussion

Poor regeneration of deer-palatable plants

This study provides circumstantial evidence of poor regeneration of two deer-palatable subcanopy hardwood species in Wakatipu Forest between 1976 and 1999, and does not show increases in the density of deer-palatable species following the introduction of restricted recreational hunting in 1981. Instead, it appears that browsing by fallow deer has prevented recruitment of seedlings of the palatable *G. littoralis* (broadleaf) into the sapling and tree tiers. Sapling density of the palatable *R. simplex* (three finger) was lower than its tree stem density, also suggesting suppression of regeneration. In a review of ungulate diet studies in New Zealand, Forsyth *et al.* (2002) found that *R. simplex* consumption varied considerably between studies and tended to be in relation to its availability in the browse tier, whereas *G. littoralis* was consistently a highly preferred species. This preferential selection by deer increases the susceptibility of *G. littoralis* to regeneration failure, even at low deer densities. Golding (2000) found further evidence for the palatability and vulnerability of subcanopy hardwood species in the Caples Valley. *G. littoralis* and *R. simplex* seedlings were more common at sites inaccessible to fallow deer, and *G. littoralis* was also frequently found in fallow deer rumens. When considered along with the results of previous studies (e.g. Nugent and Challies, 1988; Nugent, 1990; Bellingham and Allan, 2003; Husheer *et al.*, 2003), this evidence supports a conclusion that intensive browsing by fallow deer has reduced the regeneration of *G. littoralis* and *R. simplex* at Wakatipu Forest. In contrast, the deer-palatable *C. serratus* (marbleleaf), and the unpalatable *P. alpinus* (mountain toatoa), *P. hallii* (Hall's totara) and *P. colorata* (pepperwood) had higher densities as saplings than as trees, indicating more successful regeneration.

Subcanopy hardwood species are also known to be palatable to cattle (Walton, 1972; Adams, 1975), which have been farmed for over a century in Wakatipu Forest, so cattle grazing may have contributed to the poor regeneration of palatable plants. However, it is unlikely that cattle reduce palatable species regeneration in Wakatipu Forest, because cattle concentrate grazing on grass covered river flats, avoid steep valley sides and generally use forests only for shelter (Riney, 1957; Rosoman, 1990). Several studies have shown that cattle grazing is capable of reducing the density of New Zealand forest understories (Moore and Cranwell, 1934; McKelvey, 1963; McSweeny, 1982; Timmins, 2002), so the effects of cattle grazing on regeneration should not be ruled out without exclosure plot studies.

Limited change in forest species composition 1976–1999

This study provides little evidence that browsing by fallow deer induced large changes in the structure and composition of Wakatipu beech forests over the last two decades. The limited compositional changes that were detected could be due to natural successional processes, or to the legacy of high fallow deer densities prior to plot establishment, as much as to contemporary effects of fallow deer browsing on the remaining palatable species. Factors such as plant competition, temperature, soil moisture deficit (Leathwick and Austin, 2001), restrictions on resource availability (Wardle, 1970), and external disturbance from storms, disease and earthquakes (Wardle and Allen, 1983; Harcombe *et al.*, 1998; Ogden, 1988; Vittoz, Stewart and Duncan, 2001) are also important influences on beech forest succession and regeneration. Previous studies on deer impacts in New Zealand have concluded that there was a substantial shift in understorey composition within a decade of deer reaching an irruptive peak (e.g. Jane and Pracy, 1974; Allen, Payton and Knowlton, 1984; Stewart and Harrison, 1987; Stewart and Burrows, 1989), which is likely to have occurred in Wakatipu Forest during the 1920s (Dunn, 1930). In central North Island beech forests, with considerable cyclone-induced disturbance, and where sika deer have established, historical shifts favouring browse-resistant turf communities and unpalatable seedling regeneration now seem to have been translated into shifts in the species composition of small trees (Husheer *et al.*, 2003), which will inevitably alter species composition of stand dominants in the future. Similar conclusions have also been reached in some European and American studies (e.g. Eriksson, Eriksson and Berglund 1995; Olff *et al.*, 1999; Cretaz and Kelty 2002.), but results from Wakatipu Forest do not show such ongoing deer-induced changes.

Beech canopy regeneration

On a landscape scale, there is little evidence of canopy regeneration failure at Wakatipu Forest, with little change between surveys in the density of seedlings and saplings of mountain, red and silver beech. On a plot scale, there is some evidence that regeneration of silver beech has been reduced by browsing on small seedlings at sites with high fallow deer densities. High mountain beech and low silver beech seedling occurrence was related to high fallow deer pellet occurrence, which might be caused by fallow deer preferentially browsing on silver beech, or to intraspecific competition for nutrient and light availability between silver and mountain beech. Because beech species rely on canopy disturbance for seedling recruitment, regeneration dynamics are spatially and temporally complex, and determining the sustainability of beech forest canopy regeneration requires detailed long term data on plant population dynamics (Ogden *et al.*, 1996).

Results from overstorey data indicate that most stands in Wakatipu Forest were in the late phase of development, with tree densities decreasing through a process of self thinning. In this process, catastrophic stand disturbance is low, mortality exceeds recruitment and surviving trees increase in size (Westoby, 1984; Bellingham, Stewart and Allen, 1999). Gradual increases in beech tree biomass are likely to reduce the level of nutrients available to seedlings (Allen, Clinton and Davis, 1997; Davis, Allen and Clinton, 2003), which in turn is likely to reduce the rate at which compositional shifts can occur. In the absence of disturbance, the more shade tolerant and slower growing silver beech seedlings tend to replace mountain beech through higher seedling survivorship, whereas mountain beech can be more competitive following stand collapse (Ogden, 1985). If future stand collapse at Wakatipu Forest releases nutrients, site productivity may increase thereby attracting fallow deer to these sites, as well as allowing mountain beech to increase in density at the expense of silver beech.

Palatable seedling regeneration not related to deer hunting intensity

We compared the densities of seedlings of the palatable subcanopy tree species *C. serratus*, *G. littoralis* and *R. simplex* at Wakatipu Forest with other permanent plot surveys of forests throughout New Zealand, and allowed for the influences of tree stem density of these species, and plot basal area and altitude. In forest adjacent to the Murchison Mountains, which has undergone intensive hunting, Nugent, Parkes and Tustin (1987) estimated that deer density was 3.5 deer km^{-2} in 1984. In the Caples Valley, Golding (2000) estimated fallow deer density at 10 deer km^{-2} in 1999 and Husheer and Robertson (*in press*) estimated that there were >16 deer km^{-2} in the Kaimanawa Region, which was sufficient to prevent mountain beech seedling growth. Palatable seedlings at Wakatipu Forest were at similar densities to other New Zealand beech forests, despite much higher levels of hunting intensity in other forests, and potentially large variation within and among forests in deer densities and other important environmental characteristics such as rainfall, temperature and soil development. Seedling densities for *G. littoralis* were generally lower than might be expected in the absence of deer browsing, and along with *C. serratus* and *R. simplex*, seedling densities appeared unrelated to the level of hunting intensity. Results did not show benefits for palatable species from the intensive commercial and recreational hunting that has occurred throughout New Zealand since the 1960s. Instead, regeneration of highly palatable species appeared poor in all ten forests surveyed, supporting research concluding that deer densities need to be very low, or nearly zero, to ensure that all highly palatable subcanopy hardwood species can regenerate (Nugent, Fraser and Sweetapple, 1997). Previous exclosure plot studies from these regions support a conclusion of poor palatable species regeneration in New Zealand beech forests, because once deer browsing was completely removed palatable species increased in density, often dramatically (e.g. Murchison Mountains, Burrows *et al.*, 1999; Hurunui, Wardle *et al.*, 2001; Kaimanawa, Husheer *et al.*, 2003).

Future effects of fallow deer browsing at Wakatipu Forest

There are three potential scenarios of future changes in subcanopy species composition at Wakatipu Forest. Firstly, increased hunting intensity may lower fallow deer densities sufficiently to allow recruitment of palatable species into the sapling tier. Secondly, fallow deer may continue to prevent regeneration of palatable subcanopy hardwood species. Finally, in a third scenario that is more complex, fallow deer browsing may have already shifted forest successional processes into an alternative and stable state independent of future browsing effects. Results from the present study suggest that existing levels of recreational hunting will not lead to regeneration of palatable trees. Comparisons among New Zealand forests suggests that browsing from fallow deer will need to be nearly eliminated before widespread regeneration of palatable species might occur. At some sites, fallow deer-induced ecosystem-level change may already have permanently shifted forest succession (Wardle, 2002). Exclosure plot studies have shown that complete removal of deer browsing results in rapid regeneration of palatable plants at many, but not all sites (Wardle *et al.*, 2001, 2002). It is possible that even after deer populations are removed, palatable plant species will not be completely restored to 19th century densities, because of irreversible changes in plant competition favouring unpalatable species (Coomes *et al.*, 2003), reduction of seed sources, or permanent alteration of ecosystem processes following a fallow deer induced reduction in the nutrient quality of litter fall (Wardle *et al.*, 2001). Clearly, the successional responses of forests to disturbance, and changes in resource availability, environmental variation and herbivory are complex, so the effects of deer browsing must be considered separately for individual forests. The results of this study have highlighted that when deer are present in mixed beech forests regeneration of highly palatable plants can be prevented. Unlike some other New Zealand forests, Wakatipu Forest has not shown large deer-induced changes in forest species composition in the past three decades, but may do so following future disturbance events.

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