Introduced red deer reduce tree regeneration in Pureora Forest, central North Island, New Zealand

Sean W. Husheer

New Zealand Forest Surveys, 15 McElwee Street, Jervoistown, Napier, New Zealand
(E-mail: shusheer@clear.net.nz)

Abstract: This study uses data from repeatedly measured forest monitoring plots (20 × 20 m) (*n* = 32) and nine ungulate exclosures (paired fenced and unfenced plots; 20 × 20 m) to show the effects of introduced ungulates on tree regeneration in Pureora Forest Park, central North Island, between 1974 and 2002. Results show that introduced ungulates, particularly red deer (*Cervus elaphus scoticus*), have suppressed the regeneration of hardwood species such as *Coprosma grandifolia*, *Elaeocarpus dentatus*, *Griselinia littoralis*, *Melicytus ramiflorus*, *Schefflera digitata* and *Weinmannia racemosa*. These species were only common as saplings and small trees in the complete absence of ungulate browsing. The results of this study suggest that red deer will need to be culled to low densities to assure regeneration of palatable tree species in Pureora Forest.

Introduction

Many studies have shown that ungulates can modify the composition of temperate forest understoreys (for reviews see Gill 1992; Russell et al. 2001). In comparison, studies relating ungulate impacts to changes in species composition of forest overstoreys are surprisingly rare (Bradshaw et al. 2003; for the present study understorey is defined as consisting of trees <2 cm dbh (diameter at breast height) and the overstorey consisting of trees ≥2 cm dbh). In New Zealand forests, indigenous avian herbivores have largely been replaced by a suite of recently introduced mammalian herbivores (Atkinson & Greenwood 1989), and the responses of plant communities to this new form of herbivory are still occurring (Holloway 1950; Bellingham & Allan 2003). These responses are highly variable and idiosyncratic at a variety of temporal and spatial scales (Wardle 2002), so knowledge of the influence of herbivory on plant species composition over several decades is needed to understand forest dynamics in New Zealand (Bellingham et al. 2000). When indigenous herbivores are replaced by several species of introduced herbivore, relationships are even more complex as different herbivore species can have different impacts (Husheer et al. 2006a), and multi-species pest management becomes increasingly important (Simberloff 1998; Forsyth et al. 2000).

Throughout New Zealand, five common broadleaved, hardwood species (*Griselinia littoralis*,

Melicytus ramiflorus, *Pseudopanax arboreus*, *Schefflera digitata* and *Weinmannia racemosa*; nomenclature follows Parsons et al. 1995) are always palatable to red deer (*Cervus elaphus scoticus*) and goats (*Capra hircus*; Forsyth et al. 2002). Exclosure plot studies have shown that deer and goat browsing reduces the density of these five species in forest understoreys (Allen et al. 1984; Stewart & Burrows 1989; Smale et al. 1995; Wardle et al. 2001). The present study uses data from 32 permanent forest monitoring plots and nine pairs of fenced and unfenced exclosure plots to relate effects of ungulates in northern Pureora Forest Park, central North Island, New Zealand (Fig. 1; 17 380 ha; 38°S, 175°E). The study's objective was to determine if reductions in the density of introduced browsers in the past three decades have reduced or reversed their effects on forest regeneration. Alternatively, ungulate browsing may have permanently prevented the regeneration of palatable species by inducing a dense layer of browse-resistant plants (Coomes et al. 2003a). In this case even the complete removal of browsing would not lead to an increase in the density of palatable plants. If culling of ungulates has been successful there should be increased densities of deer- and goat-palatable species, such as the five listed above, in both the understorey and overstorey of affected forests.
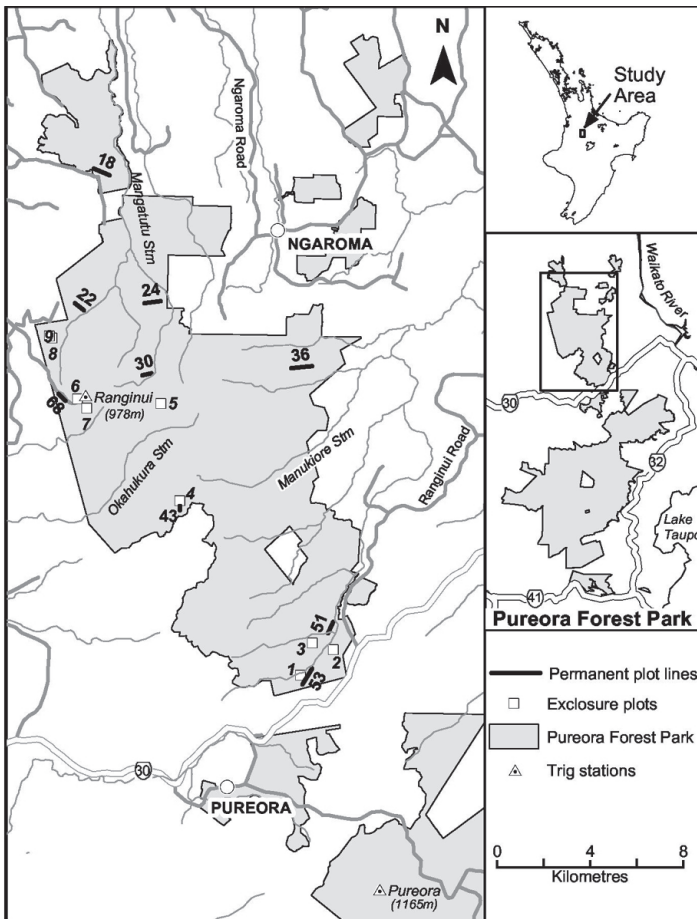
Figure 1. Map of northern Pureora Forest Park showing nine permanent-plot lines and nine paired exclosure plots.

Methods

Study area description

Northern Pureora Forest Park is dominated by indigenous, podocarp-tawa-kāmahi forest (Podocarpaceae – *Beilschmiedia tawa* – *Weinmannia racemosa*; Wardle 1991). Limited logging of podocarps, especially *Dacrydium cupressinum*, occurred on the flatter, more accessible periphery of the study area until 1978. Unlogged forests dominate the steeper, higher altitude Rangitoto Range in the centre of the study area, where stands of emergent podocarps (*D. cupressinum*, *Podocarpus hallii*, *Prumnopitys ferruginea, P. taxifolia*) give way to lower-stature stands dominated more by *B. tawa* and *W. racemosa,* particularly over 600 m. Soils are derived from ignimbrite from the Taupo volcanic eruption (c. l800 years BP; Wilson 1993), which destroyed most of the forest. Annual rainfall is likely to be in excess of 1770 mm (New Zealand Meteorological Service 1973).

Four species of introduced herbivore were present in northern Pureora Forest Park when this study was initiated in 1974. Feral pigs (*Sus scrofa*) and goats had been present for over five decades and brushtail possums (*Trichosurus vulpecula*) and red deer probably colonised in the 1960s (Wodzicki 1950; Elder 1956; New Zealand Forest Service 1981; Broome & Clegg 1990; Sweetapple & Fraser 1997; Cowan 1990). This makes Pureora Forest one of the last large tracts of indigenous forest in the central North Island to be colonised by brushtail possums and red deer. There may have been insufficient time between colonisation and the onset of a period of intensive commercial hunting in the 1970s for red deer and brushtail possum populations to reach an irruptive peak (Caughley 1983). This may have limited the effects of introduced herbivores on forest dynamics, in comparison with other forests.

Frequency of deer faecal pellet occurrence on monitoring transects in 1975 and 1990 was 10% and 11% respectively in 114-cm-radius subplots spaced at 20-m intervals on transects (Broome & Clegg 1990). This suggests that the red deer population did not undergo large changes in density during this time. Although densities would have fluctuated, red deer have probably ranged in density between 2 and 5 deer per square kilometre in Pureora Forest over the last three decades (Nugent et al. 1997; Sweetapple & Fraser 1997). Intensive aerial and ground-based brushtail possum culling was progressively implemented from 1987, and by 1993 the entire area had been treated at least once (Moorcroft et al. 2000; Moorhouse et al. 2003). Culling of remaining goat and pig populations was initiated in 1981, quickly reducing densities of both of these species to very low levels (<1 animal km^{-2}; New Zealand Forest Service 1981; Clegg 1987). Since the introduction of the Pureora Recreational Hunting Area in 1981, recreational hunting has been encouraged and commercial hunting has not been permitted.

Sampling approach

Methods used to establish paired fenced and unfenced plots at nine sites and 32 unfenced permanent monitoring plots in this study followed a protocol used by the New Zealand Forest Service to establish a network of permanent plots (20×20 m) throughout New Zealand in the late 1970s and early 1980s (Allen 1993). Data for Pureora Forest measurements have been stored in the National Vegetation Survey databank (Wiser et al. 2001).

Paired unfenced and fenced plots (20×20 m) were established between January and March 1984 (540–940 m a.s.l.), and were remeasured in four surveys: in February 1986; May–July 1989; January–March 1993; and most recently between November 2001 and January 2003. Fences surrounding one of the paired plots at each of the nine sites were designed to exclude deer and goats, while at most only deterring the access of smaller browsers (<30 cm high) such as brushtail possums and pigs. Paired-plots were subjectively located at sites that: (1) field staff considered were generally representative of canopy gaps, (2) appeared to have high levels of ungulate browsing, and (3) where two similar paired-plots could be established, and one of the pair then selected for ease of fencing to exclude goats and deer. Exclosure plot measurements are referred to hereafter as the 1984, 1986, 1989, 1993 and 2002 paired-plot surveys.

To provide a representative sample of changes in forest composition and structure, 32 permanent plots (20×20 m) were located systematically at 200-m intervals on nine lines. These lines originated at randomly selected points along watercourses and ran to nearest ridge-tops, providing a range of plot altitudes

(360–960 m). Plot establishment occurred over 3 months commencing in November 1974. Plots were remeasured in four following surveys between November 1981 and January 1982, February and March 1986, January and March 1993, and most recently between November 2001 and February 2003. Enumerations are referred to hereafter as the 1975, 1981, 1986, 1993 and 2002 permanent-plot surveys.

Plot measurement procedures

To measure overstorey composition in each permanent plot, all stems for each tree species (>5 cm dbh in permanent plots, >2 cm dbh in paired-plots) were identified, tagged, and the diameter over bark at breast height (135 cm) measured. To measure forest understorey composition, 24 circular subplots (49-cm radius) were systematically located according to Allen (1993) within each plot. All established woody seedlings (15–135 cm high) were identified and counted in each of the subplots. All saplings (>135 cm high, <2 cm dbh) were counted and identified. Only overstorey measurements (tree diameters) were obtained from the 1975 permanent-plot survey, and only understorey (seedling and sapling) measurements for the 1986 permanent- and paired-plot surveys.

Data analysis

Analyses of seedling, sapling and tree stem densities were undertaken on the 28 most common tree and shrub species. These were species with mean stem densities in any one paired-plot or permanent-plot survey of either >1000 seedlings ha^{-1}, >100 tree stems or saplings ha^{-1}, or with mean basal area > 1 m^2 ha^{-1}. Plot basal area, tree stem and sapling densities in each plot and seedling densities from 24 subplots in each plot were summarised for each survey. Comparisons of changes in mean densities over time were made using repeated measures ANOVA in SYSTAT 10 (SPSS 2000). Bonferoni corrections of P-values were applied when repeated comparisons of individual species were made (Sokal & Rohlf 1995). Detrended Correspondence Analysis (DCA) scores for seedlings, saplings and trees were calculated to summarise species composition for all surveys. Mean scores were compared using repeated measures ANOVA to test for changes in species composition in both understorey and overstorey. Results are presented as mean ± SE.

For paired-plots, the effects of time, fencing, and their interactions on species composition were analysed using a randomised permutation procedure in Canonical Correspondence Analysis (CCA), using default procedures in CANOCO 4.0 (ter Braak & Šmilauer 1998). Importance values were calculated using densities for tree stems, saplings and seedlings. A dummy variable was used for fencing (fenced = 1,

unfenced = 0). Because plots were repeatedly measured, and fenced and unfenced plots were paired at nine sites, a site-identifier variable was treated as a blocking covariate to reduce unexplained variation in CCA. Changes in seedling, sapling and tree stem densities of individual species were tested using repeated measures ANOVA. Species absent from most plots in 1984, but common in fenced plots in 2002, confounded ANOVA, so paired *t*-tests of differences in abundance between fenced and unfenced plots in 2002 were employed. Inconsistencies in the recording of tree-tag data between permanent-plot and paired-plot surveys were detected during a thorough data-checking procedure. Therefore, calculations of tree recruitment and mortality were not undertaken. Inconsistent identification and counting of tree ferns and other herbaceous plants between surveys precluded the use of data from these species.

Results

Paired fenced and unfenced plots

Unfenced plots in 1984 and 2002 had similar CCA axis 1 sapling scores to fenced plots in 1984, confirming baseline comparability. By 2002, fenced-plot sapling scores increased substantially, while there was little change in unfenced plots (Fig. 2). Analysis showed that there were significant changes in sapling species composition in paired deer exclosure plots from 1984 to 2002 ($\lambda = 0.16$, $F = 3.2$, $P = 0.005$) that varied significantly between fenced and unfenced plots ($\lambda = 0.16$, $F = 5.4$, $P = 0.005$). Changes were mostly due to increases in densities of six deer-palatable hardwood species: *Coprosma grandifolia*, *Elaeocarpus dentatus*, *Griselinia littoralis*, *Melicytus ramiflorus*, *Sschefflera digitata* and *Weinmannia racemosa* in all nine of the fenced plots.

There was no significant difference in the pooled density of these six palatable species between fenced and unfenced plots upon plot establishment in 1984 (pooled fenced 1984 = 36 ± 17 vs unfenced 1984 = 44 ± 21 saplings ha^{-1}, paired-t_8 = 0.2, $P = 0.834$). By 2002, the pooled density of these six species as saplings had increased by an average of 20 times inside fenced plots, along with increases in individual species, but had not significantly changed in adjacent unfenced plots (Table 1; pooled fenced 2002 = 717 ± 64 vs unfenced 2002 = 63 ± 28 saplings ha^{-1}, paired-t_8 = 12.7, $P < 0.001$).

This was related to an increase in the number of sapling species present inside fenced plots. The mean number of sapling species present was not significantly different between fenced and unfenced plots in 1984 (fenced = 5.8 ± 1.4 vs unfenced = 6.0 ± 1.1; paired-t_8 = 0.2, $P = 0.813$). By 2002, the mean number of sapling species was significantly higher in fenced plots
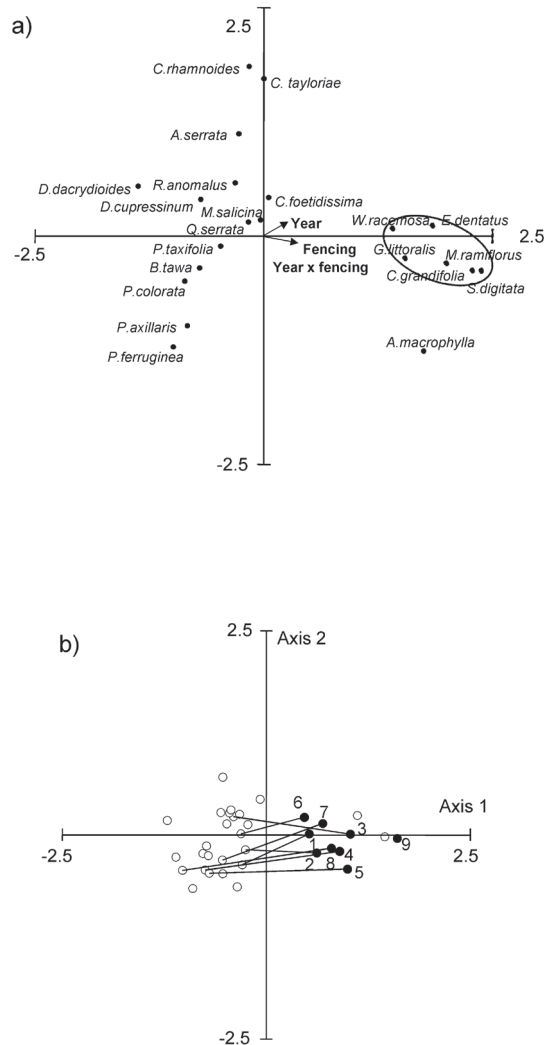

Figure 2. Sapling (>135 cm high, <2 cm dbh) Canonical Correspondence Analysis ordination diagrams of (a) species scores for the effects of year and fencing and their interactions (year × fencing) on species composition and (b) plot scores from 1984 and 2002 from paired fenced and unfenced plots at nine sites. Individual fenced plots are linked between 1984 (○) and 2002 (●). There is no score for the fenced plot at site nine in 1984, due to an absence of saplings. Species names are: *Alseuosmia macrophylla, Aristotelia serrata, Beilschmiedia tawa, Coprosma foetidissima, C. grandifolia, C. rhamnoides, C. tayloriae, Dacrycarpus dacrydioides, Dacrydium cupressinum, Elaeocarpus dentatus, Griselinia littoralis, Melicytus ramiflorus, Myrsine salicina, Prumnopitys ferruginea, P. taxifolia, Pseudowintera axillaris, P. colorata, Quintinia serrata, Raukaua anomalus, Schefflera digitata* and *Weinmannia racemosa*.

Table 1. Mean sapling densities (saplings ha^{-1} ± SE) in 1984 and 2002 with Bonferoni-corrected paired t-tests of density between fenced and unfenced plots in 2002 at nine sites, for six selected species. Total densities of the 26 most common species and results of a paired t-test are also presented.

Species	1984		2002		t_8	P
	Fenced	Unfenced	Fenced	Unfenced		
Coprosma grandifolia	3 ± 3	0	286 ± 51	3 ± 3	5.7	< 0.001
Elaeocarpus dentatus	3 ± 3	3 ± 3	42 ± 16	3 ± 3	2.8	0.023
Griselinia littoralis	0	8 ± 6	67 ± 27	6 ± 6	2.6	0.032
Melicytus ramiflorus	3 ± 3	0	69 ± 25	11 ± 4	2.6	0.032
Schefflera digitata	3 ± 3	0	86 ± 26	3 ± 3	3.3	0.011
Weinmannia racemosa	25 ± 14	22 ± 9	167 ± 46	39 ± 24	4.0	0.004
Total	514 ± 122	536 ± 110	1444 ± 251	853 ± 197	5.0	0.001

compared with unfenced plots (fenced = 10.7 ± 1.3 vs unfenced = 7.0 ± 0.9; paired-t_8 = 5.4, P < 0.001).

The combined density of saplings of all of the 26 common tree and shrub species in paired-plots nearly trebled in fenced plots, while changing little in adjacent unfenced plots. This overall increase was largely due to the changes observed in the six most palatable species. When examined individually using Bonferoni-corrected repeated measure ANOVAs, the other 20 common tree and shrub species present as saplings did not vary significantly in density between the fenced and unfenced plots in 2002 (P > 0.104).

Changes in overstorey species composition also varied significantly between fenced and unfenced plots between 1984 and 2002 (λ = 0.12, F = 2.7, P = 0.005). In fenced plots, mean *Coprosma grandifolia* tree stem density increased by an average of 126 times ($F_{2,16}$ = 4.1, P = 0.037), *Schefflera digitata* 22 times ($F_{2,16}$ = 3.7, P = 0.047) and *Weinmannia racemosa* by 27% ($F_{2,16}$ = 8.0, P = 0.004) between 1984 and 2002. In adjacent unfenced plots there was no change in stem

density of *C. grandifolia*, a doubling of *S. digitata* density, and a 22% decline in *W. racemosa* stem density. These changes contributed to a doubling of tree stem density in fenced plots when data from all of the 23 species found as trees in fenced and unfenced plots were pooled, compared to significantly less change in unfenced plots ($F_{2,16}$ = 7.3, P = 0.006). In contrast to trees and saplings, CCA showed no significant effect of time or fencing, or their interactions, on seedling species composition (P > 0.270).

Permanent plots

Four of the 28 common species found in northern Pureora Forest Park showed significant changes in tree density between the initiation of permanent-plot establishment in November 1974 and completion of the final survey in February 2003 (Table 2), while the remaining 24 species showed no significant change in ANOVA analysis (P > 0.441). The most abundant tree species, *Beilschmiedia tawa,* steadily increased in density between 1975 and 2002 surveys by 34%.

Table 2. Mean tree stem densities in 1975 and 2002 (>5 cm dbh; stems ha^{-1} ± SE), sapling densities in 2002 (>135 cm high, <2 cm dbh; saplings ha^{-1} ± SE) and seedling densities in 2002 (15–135 cm high; seedlings ha^{-1} ± SE) in 32 plots in Pureora Forest Park. Results of a series of repeated measures ANOVAs comparing tree densities between surveys of 1975, 1981, 1993 and 2002 are also displayed.

	Trees 1975	Trees 2002	Saplings 2002	Seedlings 2002	F3,93	P
Palatable						
Melicytus ramiflorus	129 ± 29	127 ± 27	3 ± 1	260 ± 93	3.5	0.494
Weinmannia racemosa	175 ± 29	102 ± 26	22 ± 11	399 ± 200	13.0	<0.001
Unpalatable						
Beilschmiedia tawa	231 ± 47	310 ± 59	806 ± 156	5677 ± 1080	13.7	<0.001
Hedycarya arborea	91 ± 32	131 ± 38	144 ± 50	1580 ± 445	3.0	0.936
Pseudowintera colorata	152 ± 78	237 ± 93	328 ± 133	3611 ± 1244	1.3	1.000
Quintinia serrata	120 ± 54	85 ± 42	20 ± 14	399 ± 348	6.1	0.026
All species	1332 ± 110	1528 ± 130	2323 ± 278	27743 ± 2862	5.0	0.003

Although *Prumnopitys ferruginea* (2002 = 38 ± 16 tree stems ha^{-1}, 0.7 ± 0.3 m^2 ha^{-1}) increased in density by 63% between surveys ($F_{3, 93}$ = 6.2, P = 0.026), it had far lower tree density and basal area in 2002 than other common species such as *Hedycarya arborea* (1.7 ± 0.5 m^2 ha^{-1}), *Melicytus ramiflorus* (2.3 ± 0.6 m^2 ha^{-1}), *Pseudowintera colorata* (1.1 ± 0.5 m^2 ha^{-1}) or *Weinmannia racemosa* (1.7 ± 0.4 m^2 ha^{-1}). There was a 42% decline in the tree stem density of *W. racemosa*, particularly since 1981, and *Quintinia serrata* declined in stem density by 29%. Increases in *Beilschmiedia tawa* and *Prumnopitys ferruginea* stem density contributed to an overall increase in tree stem density of 15% for all 58 tree species recorded in the overstorey between 1975 and 2002 surveys. *Dacrydium cupressinum* (34 ± 26 stems ha^{-1}, 3.7 ± 1.9 m^2 ha^{-1})*, Dacrycarpus dacrydioides* (10 ± 7 stems ha^{-1}, 1.1 ± 1.0 m^2 ha^{-1})*, Elaeocarpus dentatus* (44 ± 10 stems ha^{-1}, 2.8 ± 0.9 m^2 ha^{-1}) and *Prumnopitys taxifolia* (15 ± 11 stems ha^{-1}, 2.2 ± 1.5 m^2 ha^{-1}) were also important in terms of basal area in 2002 (total of all 28 common species = 38.6 ± 3.3 m^2 ha^{-1}), but did not change in density between surveys (P = 1.000).

Three tree species (*Beilschmiedia tawa*, *Hedycarya arborea* and *Pseudowintera colorata*) known to be unpalatable to deer (Nugent et al. 1997; Forsyth et al. 2002), with high tree stem densities in 2002, had clear signs of successful regeneration. These three species had much higher seedling and sapling densities than tree stem densities, which would allow for stem mortality as cohorts age (Table 2). In contrast, two other species (*Melicytus ramiflorus* and *Weinmannia racemosa*) that are palatable to deer and one species generally avoided by deer (*Quintinia serrata*; Forsyth et al. 2002) had low seedling densities, and very low sapling densities, in comparison with their respective tree stem densities.

There was little overall change in understorey species composition between 1981 and 2002. Overall sapling density of all 60 tree and shrub species present as saplings did not vary significantly between 1975 and 2002. The only species with significant change was *Prumnopitys ferruginea*, which declined by 66% in sapling density between 1975 and 2002 (2002 = 35 ± 12 saplings ha^{-1} ± SE; $F_{3,93}$ = 8.7, P = 0.001). In the seedling tier *Beilschmiedia tawa* increased by 53% in seedling density between 1975 and 2002. This contributed to an overall 64% increase in seedling density of all 80 tree and shrub species that were recorded as seedlings in permanent plots.

Discussion

Despite intensive goat culling and recreational deer hunting over the past three decades there has been little change in northern Pureora Forest Park forest understory and overstorey species composition between 1974 and 2003. In contrast, within fenced deer and goat exclosure plots located in canopy gaps, there were large, rapid and consistent increases in the density of saplings and trees of highly palatable species such as *Coprosma grandifolia*, *Elaeocarpus dentatus*, *Griselinia littoralis*, *Melicytus ramiflorus*, *Schefflera digitata* and *Weinmannia racemosa*. This was not observed in adjacent unfenced plots, providing strong evidence that the intensity of ungulate browsing at Pureora Forest during this study has been sufficient to favour recruitment of unpalatable tree species. Comparisons of size class structures between common palatable and unpalatable species in permanent plots supports evidence from the exclosure plots of suppressed regeneration of palatable tree species. Results from this study contrast with other exclosure plot studies in New Zealand, which have shown less change in overstorey composition despite increases in palatable seedling density (e.g. Allen et al. 1984; Bellingham & Allan 2003; but see Husheer et al. 2005). The increase in sapling and tree density of palatable species was so rapid in fenced plots that any initial change in seedling composition was not observed. Ongoing changes in seedling composition appear to have been suppressed within fenced plots, most likely due to competition from large-leaved shade-tolerant palatable saplings and trees in canopy gaps.

Red deer are most likely to be responsible for the suppression of palatable tree recruitment in Pureora Forest, because unlike other ungulates present, red deer were not substantially reduced in density during the study. It is unlikely that feral goat or pig browsing had a major influence on results because intensive culling throughout the study reduced pig populations, and nearly eliminated goats from northern Pureora Forest Park (Clegg 1987; Broome & Clegg 1990). Brushtail possums and pigs could also access fenced plots, so if their impacts were significant there should have been no differences observed between fenced and unfenced plots.

The substantial influence of deer on overstorey forest composition is likely to have important effects on Pureora Forest ecosystem processes. It is generally accepted that palatable sub-canopy hardwood species rely on fast growth to reach beyond the height where ungulates can browse. Unpalatable species rely on chemical and morphological defences such as thick stems and high concentrations of foliar fibre to avoid being eaten (Bond et al. 2004; Forsyth et al. 2005). These defences can lower plant growth, so shifts towards unpalatable plant species composition may result in

lowered primary productivity (Grime 1979; Bryant et al. 1983; Crawley 1997). Because canopy trees such as *Weinmannia racemosa* account for a substantial amount of forest biomass and primary production, changes in overstorey species composition towards slow-growing chemically defended trees probably reduce forest biomass as well as leaf and litterfall quality. This will have important implications for invertebrate herbivores and their avian and invertebrate predators, and will influence soil nutrient cycling processes (Wardle et al. 2001, 2002). Trees such as *Coprosma grandifolia, Elaeocarpus dentatus, Griselinia littoralis*, *Melicytus ramiflorus* and *Schefflera digitata* are also important in the diet of kōkako *Callaeas cinerea* (Leathwick et al. 1983; Powlesland 1987) and New Zealand pigeon *Hemiphaga novaeseelandiae*, and reduction in food supplies could limit increases in folivorous bird populations where they are not already limited by predation (Meenken et al. 1994; Innes et al. 1999; Basse 2003; Smith & Westbrooke 2004).

Culling of deer populations needs to be sensibly implemented. Husheer and Frampton (2005) and Husheer et al. (2005) showed that deer culling in New Zealand has generally been unsuccessful in forests because deer are usually not sustained at sufficiently low levels to allow palatable plant regeneration for more than a decade. In the Murchison Mountains, palatable seedling densities doubled following intensive deer culling over several decades, but even at low densities deer appeared able to reduce seedling recruitment above 135 cm high (Coomes et al. 2006). Coomes et al. (2003b) showed that there has been a trend for small deer-palatable trees (2–5 cm dbh) to decline in density over the past two decades throughout New Zealand despite a general decline in deer density during this time, but it is unclear if ungulates can suppress canopy tree regeneration at a regional scale (Bellingham & Lee 2006; but see Husheer et al. 2006a). Even if deer populations are eliminated for several decades, palatable plant regeneration may not occur if deer have allowed slow-growing, long-lived, unpalatable plants (e.g. *Blechnum discolor*, *Dicksonia squarrosa*, *Beilschmiedia tawa* and *Pseudowintera colorata*) to dominate and competitively exclude palatable species (Nugent et al. 2001). Establishment of highly palatable plants can be prevented through a lack of seed source, or long-term ecosystem-level changes caused by dominance by unpalatable species (Coomes et al. 2003a).

Conflicting with this argument of lack of response to the removal of deer browsing is evidence from this and several other studies of rapid increases in the density of highly light- and nutrient-demanding palatable plants once deer browsing is reduced through fencing or culling (Jane & Pracy 1974; Husheer et al. 2003; Husheer & Robertson 2005; Husheer et al. 2006b; but see Allen

et al. 1984; Bellingham & Allan 2003). Idiosyncratic differences between sites may explain why there is such large and unpredictable variation in the response within New Zealand exclosure plots (Wardle et al. 2001). The rapid and consistent changes in overstorey composition at Pureora following exclusion of deer in fenced plots might be due to unique environmental characteristics, such as disturbance and edaphic processes. If mechanisms underpinning variability in herbivore impacts are better understood, predictions of forest responses to the presence or culling of deer would improve, and conclusions would be less speculative than in this study. To better inform decision making, future studies on the impacts of wild deer in New Zealand should compare a series of forests with contrasting management approaches and deer densities. This would address inadequacies in the poorly replicated sampling approach typically used in New Zealand, and help resolve uncertainties identified in this study.

Acknowledgements

References

Allen RB 1993. A permanent plot method for monitoring changes in indigenous forests. Manaaki Whenua – Landcare Research, Lincoln, New Zealand. 35 p.

Allen RB, Payton IJ, Knowlton JE 1984. Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures. New Zealand Journal of Ecology 7: 119–130.

Atkinson IAE 2001. Introduced mammals and models for restoration. Biological Conservation 99: 81–96.

Atkinson IAE, Greenwood RM 1989. Relationships between moas and plants. New Zealand Journal of Ecology 20: 67–96.

Basse B, Flux I, Innes J 2003. Recovery and maintenance of North Island kokako (*Callaeas cinerea wilsoni*)

populations through pulsed pest control. Biological Conservation 109: 259–270.

Bellingham PJ, Allan CN 2003. Forest regeneration and the influences of white-tailed deer (*Odocoileus virginianus*) in cool temperate New Zealand rainforests. Forest Ecology and Management 175: 71–86.

Bellingham PJ, Lee WG 2006. Distinguishing natural processes from impacts of invasive mammalian herbivores. In: Allen RB, Lee WG eds Biological invasions in New Zealand. Berlin, Springer. Pp. 323–336.

Bellingham PJ, Wiser SK, Coomes DA, Dunningham A 2000. Review of permanent plots for long-term monitoring of New Zealand's indigenous forests. Science for Conservation 151. Wellington, Department of Conservation. 75 p.

Bond WJ, Lee WG, Craine JM 2004. Plant structural defences against bird browsers: a legacy of New Zealand's extinct moas. Oikos 104: 500–508.

Bradshaw RHW, Hannon GE, Lister AM 2003. A long-term perspective on ungulate–vegetation interactions. Forest Ecology and Management 181: 267–280.

Broome K, Clegg S 1990. Wild animals and their impact in the Rangitoto Range and the Waipapa Ecological Area. Hamilton, Department of Conservation.

Bryant JP, Chapin FS, Klein DR 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357–368.

Caughley G 1983. The deer wars. Auckland, Heinemann. 187 p.

Clegg S 1987. Resurvey of the forests of the Pureora north block. Auckland, Department of Conservation.

Coomes DA, Allen RB, Forsyth DM, Lee WG 2003a. Factors preventing the recovery of New Zealand forests following the control of invasive deer. Conservation Biology 17: 450–459.

Coomes DA, Duncan RP, Allen RB, Truscott J 2003b. Disturbances prevent stem size–density relationships in natural forests from following scaling relationships. Ecology Letters 6: 980–989.

Coomes DA, Mark AF, Bee J 2006. Animal control and ecosystem recovery. In: Allen RB, Lee WG eds Biological invasions in New Zealand. Berlin, Springer. Pp. 339–353.

Cowan PE 1990. Brushtail possum. In: King CM ed. The handbook of New Zealand mammals. Auckland, Oxford University Press. Pp. 68–98.

Crawley MJ 1997. Plant–herbivore dynamics. In: Crawley MJ ed. Plant ecology. Blackwell Science, Oxford, U.K. Pp. 401–474.

Elder NL 1956. North Island protection forests. New Zealand Journal of Forestry 7: 96–103.

Forsyth DM, Parkes JP, Hickling G 2000. A case for multi-species management of sympatric herbivore pest impacts in the central Southern Alps, New Zealand. New Zealand Journal of Ecology 24: 97–103.

Forsyth DM, Coomes DA, Nugent G, Hall GMJ 2002. The diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. New Zealand Journal of Zoology 29: 333–353.

Forsyth DM, Richardson SJ, Menchenton K 2005. Foliar fibre predicts diet selection by invasive Red Deer *Cervus elaphus scoticus* in a temperate New Zealand forest. Functional Ecology 19: 495–504.

Gill RMA 1992. A review of damage by mammals in north temperate forests 3. Impact on trees and forests. Forestry 65: 363–388.

Grime JP 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester.

Holloway JT 1950. Deer and forests of western Southland. New Zealand Journal of Forestry 6: 123–137.

Husheer SW, Frampton CM 2005. Fallow deer impacts on Wakatipu beech forest. New Zealand Journal of Ecology 29: 83–94.

Husheer SW, Robertson AW 2005. High-intensity deer culling increases growth of mountain beech seedlings in New Zealand. Wildlife Research 32: 273–280.

Husheer SW, Coomes DA, Robertson AW 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. Forest Ecology and Management 181: 99–117.

Husheer SW, Hanson QJ, Urlich SC 2005. The effects of red deer on tree regeneration in Aorangi Forest, Wairarapa. New Zealand Journal of Ecology 29: 271–277.

Husheer SW, Allen RB, Robertson AW 2006a. Suppression of regeneration in New Zealand mountain beech forests is dependent on species of introduced deer. Biological Invasions 8: 823–834.

Husheer SW, Coomes DA, Robertson AW, Frampton CM 2006b. Herbivory and plant competition reduce mountain beech seedling growth and establishment in New Zealand. Plant Ecology 183: 245–256.

Innes J, Hay R, Flux I, Bradfield P, Speed H, Jansen P 1999. Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. Biological Conservation 87: 201–214.

Jane GT, Pracy LT 1974. Observations on two animal exclosures in Haurangi Forest over a period of 20 years. New Zealand Journal of Forestry 1: 103–113.

Leathwick JR, Hay JR, Fitzgerald AE 1983. The influence of browsing by introduced mammals on the decline of North Island kokako. New Zealand Journal of Ecology 6: 55–70.

Meenken D, Fechney T, Innes J 1994. Population size and breeding success of North Island kokako in the Waipapa Ecological Area, Pureora Forest Park. Notornis 41: 109–115.

Moorcroft G, Speed HJ, Mathew H 2000. Summary of possum and rat control operations, Waipapa Restoration Project 1995–2000. Hamilton, Department of Conservation.

Moorhouse R, Greene T, Dilks P, Powlesland R, Moran L, Taylor G, Jones A, Knegtmans J, Wills D, Pryde M, Fraser I, August A, August C 2003. Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: reversing the decline of a threatened New Zealand parrot. Biological Conservation 110: 33–44.

New Zealand Forest Service 1981. Pureora Recreational Hunting Area wild animal control plan, 1982–1987. Auckland, New Zealand Forest Service.

New Zealand Meteorological Service 1973. Rainfall normals for New Zealand. Wellington, Government Printer.

Nugent G, Fraser KW, Sweetapple PJ 1997. Comparison of red deer and possum diets and impacts in podocarp-hardwood forest, Waihaha catchment, Pureora Conservation Park. Science for Conservation 50. Wellington, Department of Conservation. 61 p.

Nugent G, Fraser KW, Sweetapple PJ 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. Biological Conservation 99: 65–79.

Parsons MJ, Douglass P, Macmillan BH 1995. Current names list for wild gymnosperms, dicotyledons and monocotyledons (except grasses) in New Zealand. Lincoln, Manaaki Whenua Press.

Powlesland RG 1987. The foods, foraging behavior and habitat use of North Island kokako in Puketi State Forest, Northland. New Zealand Journal of Ecology 10: 117–128.

Russell FL, Zippin DB, Fowler NL 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. The American Midland Naturalist 146: 1–26.

Simberloff D 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? Biological Conservation 83: 247–257.

Smale MC, Hall GMJ, Gardner RO 1995. Dynamics of kanuka (*Kunzea ericoides*) forest on South Kaipara spit, New Zealand, and the impact of fallow deer (*Dama dama*). New Zealand Journal of Ecology 19: 131–141.

Smith ANH, Westbrooke IM 2004. Changes in bird conspicuousness at Pureora Forest. Notornis 51: 21–25.

Sokal RR, Rohlf FJ 1995. Biometry. New York, W.H. Freeman.

SPSS 2000. SYSTAT 10.0. Chicago, SPSS Inc.

Stewart GH, Burrows LE 1989. The impact of white-tailed deer *Odocoileus virginianus* on regeneration in the coastal forests of Stewart Island, New Zealand. Biological Conservation 49: 275–293.

Sweetapple PJ, Fraser KW 1997. Assessment of red deer and possum kills during an aerial 1080 control operation in the Rangitoto Range. Lincoln, New Zealand, Landcare Research.

ter Braak CJE, Šmilauer P 1998. CANOCO 4.0. Wageningen, The Netherlands, Centre of Biometry.

Wardle DA 2002. Communities and ecosystems: linking aboveground and belowground processes. Princeton, Princeton University Press.

Wardle DA, Barker MB, Yeates GW, Bonner KI, Ghani A 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71: 587–614.

Wardle DA, Bonner KI, Barker GM 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. Functional Ecology 16: 585–595.

Wardle P 1991. Vegetation of New Zealand. Cambridge, Cambridge University Press.

Wilson CJN 1993. Stratigraphy, chronology, styles and dynamics of late Quaternary eruptions from Taupo volcanoes, New Zealand. Philosophical Transactions of the Royal Society, London, Series A, 343: 205–306.

Wiser SK, Bellingham PJ, Burrows LE 2001. Managing biodiversity information: development of New Zealand's National Vegetation Surveys databank. New Zealand Journal of Ecology 25: 1–18.

Wodzicki KA 1950. Introduced mammals of New Zealand. DSIR Bulletin 98.