Effects of red deer on tree regeneration and growth in Aorangi Forest, Wairarapa

Sean W. Husheer[1*], Q.W. (Joe) Hansen[2] and Stephen C. Urlich[3, 4]

[1] New Zealand Forest Surveys, 15 McElwee Street, Napier, New Zealand
[2] Department of Conservation, P.O. Box 191, Masterton, New Zealand
[3] Department of Conservation, P.O Box 5086, Wellington, New Zealand
[4] Current Address: Land Information New Zealand, Private Bag 4721, Christchurch, New Zealand
* Author for correspondence (E-mail: shusheer@clear.net.nz)

Abstract: New Zealand forests have been substantially modified by introduced red deer over the past century. New Zealand's indigenous forest managers need to know if regeneration of palatable tree species can be restored following control or eradication of browsing ungulates. Aorangi Forest, Wairarapa, suffered dramatic changes in forest understorey composition by the 1950s after more than seven decades of colonisation by red deer (*Cervus elaphus*), feral goats (*Capra hircus*) and pigs (*Sus scrofa*). Since then feral goats have been eradicated, but red deer and pigs persist throughout Aorangi Forest despite ongoing recreational hunting. This study uses data from paired fenced and unfenced plots established at seven sites in Aorangi Forest between 1981 and 1987, and re-measured in 2004, to show the effects of ungulates on tree (≥ 2 cm diameter at breast height) regeneration and growth. Our results show that browsing by red deer has prevented regeneration of kanono (*Coprosma grandifolia*), a highly palatable, fast-growing sub-canopy hardwood tree. Deer reduced the growth of mahoe (*Melicytus ramiflorus*) trees, probably by directly browsing epicormic shoots. The regeneration of other less palatable sub-canopy trees (e.g. porokaiwhiri, *Hedycarya arborea*), and slower-growing canopy species (e.g. hinau, *Elaeocarpus dentatus* and rewarewa, *Knightia excelsa*) appears to have been unaffected by deer browsing. Accordingly, tree species composition does not appear to have been greatly affected by browsing from deer populations in Aorangi Forest over the past two decades.

Keywords: *Cervus elaphus*; herbivory; regeneration; browsing; forest collapse; tree populations; long-term plots

Introduction

The invasion of New Zealand forests by deer, and the effects of deer on tree regeneration, is well-documented (e.g. Veblen and Stewart, 1982; Coomes *et al.*, 2003). Within three decades of deer colonisation into a forest, deer populations increase to high levels before declining again to more moderate levels, as deer survival and natality decline following reductions in food availability (Caughley, 1983; 1989). At this point, palatable hardwood tree species such as kanono (*Coprosma grandifolia*[1]), karamu (*Coprosma robusta*), mahoe (*Melicytus ramiflorus*) and tarata (*Pittosporum eugenioides*) are almost eliminated from the browse tier (< 2 m tall; e.g. Allen, Payton and Knowlton, 1984; Stewart and Burrows, 1989; Smale, Hall, and Gardner, 1995; Bellingham and Allan, 2003). Following the

decline in food availability, and intensive government and commercially funded deer culling in the second half of last century, deer numbers were reduced to less than 5 km^2 throughout New Zealand (Nugent and Fraser, 1993). Lower deer populations are now maintained in many New Zealand forests by litter-fall from mature trees (Nugent, 1990; Nugent, Fraser and Sweetapple, 2001). As trees producing palatable litter-fall reach senescence, they are likely to be replaced by less-palatable trees (e.g heketara, *Olearia rani*; kawakawa, *Macropiper excelsum*; horopito *Pseudowintera colorata*) (Forsyth *et al.*, 2002; Husheer, Coomes and Robertson, 2003), and at this point food available as litter-fall to deer must inevitably decline over many decades. This means that even without intensive deer culling deer densities may decline, or alternatively, deer may browse more intensively on remaining food supplies.

[1]Nomenclature follows Parsons, Douglass and Macmillan (1995).

Despite this general understanding of deer-forest interactions, the ongoing effects of deer colonisation on tree dynamics are still poorly understood (Veblen and Stewart, 1982; Rogers and Leathwick, 1997; Nugent *et al.*, 2001; Coomes *et al.*, 2003). Researchers should aim to provide conservation managers with more accurate predictions on the effects of deer on palatable plant regeneration over gradients of hunting intensity, deer density, and forest productivity and composition (Côté *et al.*, 2004). An important question for conservation management is whether deer populations have been sufficiently lowered by reduced food availability and intensive hunting to allow regeneration of palatable species? Alternatively, can remaining deer populations consistently prevent regeneration of palatable tree species and induce irreversible shifts in the direction of forest succession?

One of the earliest colonisations of forest by ungulates in New Zealand was in Aorangi Forest (19 373 ha; 41°S, 175° E; 0-610 m a.s.l.; Fig. 1), southern

Figure 1. Locations of paired fenced and unfenced plots (■), transect lines (▬), huts (●), streams (—) and Aorangi Forest boundary (▬).

Wairarapa (Wardle, 1966; Druce, 1971). Feral goats (*Capra hircus*) and pigs (*Sus scrofa*) reached high population densities in Aorangi Forest by the late 19th century, after earlier coastal liberations by European explorers and whalers. Feral goats were removed from Aorangi Forest by government cullers in the 1960s, and have not re-colonised. Red deer (*Cervus elaphus*) were liberated in Featherston in 1863, were established in Aorangi Forest by 1880, and would have reached high densities by the end of the 19th century before declining in density in the mid 20th century (Jane and Pracy, 1974). By the 1950s Aorangi Forest was conspicuously devoid of palatable seedlings and saplings due to the browsing effects of introduced mammals, particularly red deer (Wardle, 1966; Druce, 1971; Jane and Pracy, 1974). Since the 1980s recreational hunting has been relied on to maintain low deer densities in Aorangi Forest.

Aorangi Forest has four forest associations common to other areas of New Zealand (Wardle, 1966). These are three beech associations (*Nothofagus fusca*, *N. menziesii* and *N. solandri* var. *cliffortioides*), and a low-altitude association of hinau (*Elaeocarpus dentatus*), rewarewa (*Knightia excelsa*), mahoe, mapou (*Myrsine australis*) and kaikomako (*Pennantia corymbosa*). This mix of common forest types, along with early ungulate colonisation and ongoing browsing effects, provides an opportunity to assess the likely future effects of deer browsing in the many other New Zealand forests where deer colonisation occurred more recently. Although the effects of introduced ungulates on the density of palatable plants in forest understories has been previously shown in New Zealand (e.g. Jane and Pracy, 1974; Allen *et al.*, 1984), few studies have considered the ongoing effects on tree regeneration and growth in the overstorey after a century of colonisation by deer.

The purpose of this study was to show the ongoing effects of introduced red deer, after a century of colonisation, on tree regeneration and forest succession. We compare tree density and growth inside and outside of ungulate exclosure fences established in the 1980s at seven sites in Aorangi Forest. We predicted that red deer would have continued to preferentially browse palatable tree species over the past two decades, reducing the growth and density of common tree species. This could have altered the direction of forest succession outside fenced plots towards dominance by unpalatable tree species. By removing the effects of browsing for two decades in fenced plots, tree species composition may have been restored to that more similar to pre-colonisation by deer, and in that case we would expect to see large compositional differences between fenced and unfenced plots and increases in species such as kanono, karamu, mahoe and tarata. Alternatively, if less palatable, slow-growing trees
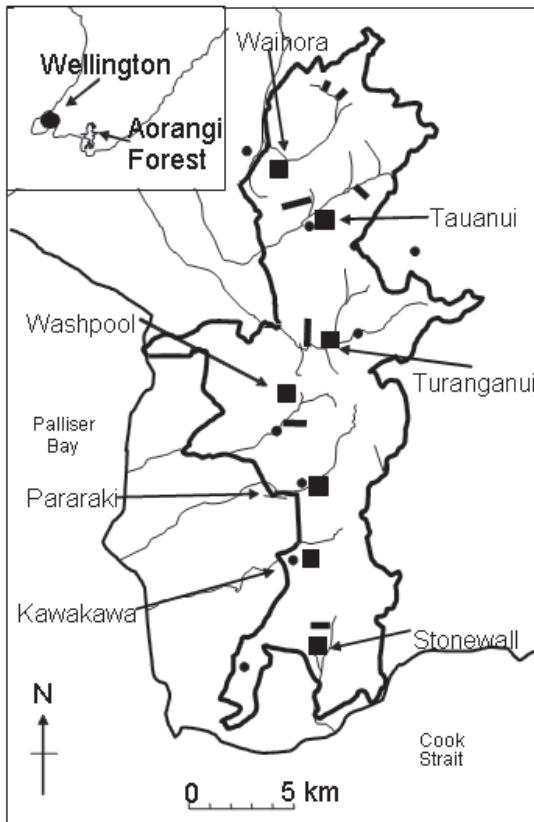
remain present or increase in density (Nugent, Fraser and Sweetapple, 1997; Husheer et al., 2003), then we would expect little evidence of different tree species composition between fenced and unfenced plots.

Methods

Plot measurement procedure

Forty-seven permanently marked 20 m × 20 m forest plots were measured in Aorangi Forest in January and February 1986, at 200-m intervals on seven randomly located transect lines. In each plot, all trees ≥ 2 cm diameter at breast height (DBH) were identified by species, tagged and measured to determine diameter over bark at breast height after Allen (1993). Paired fenced and unfenced plots, (fences were 2.2 m high and were designed to exclude all ungulates) were established annually over seven years (1981-1987), in each of the seven main river catchments in Aorangi Forest. Sites were subjectively selected to be representative of forest in that catchment and where a fence could be established around plots. Methods for tree measurement followed the same protocols used for permanent plots. At five paired plots sites, plot size was 20 m × 20 m plots, but at two sites paired plots were 15 m × 20 m (Tauanui and Kawakawa). Paired plots were re-measured in May and June 2004. In two fenced plots there was evidence that pigs had gained access (rooting, faecal pellets present), but at the fenced plots at Pararaki, Turanganui, Stonewall, Waihora and Washpool we are confident that red deer and pigs had been permanently excluded.

Data analysis

Summaries of tree species composition in paired and permanent plots measured in the 1980s were made using Detrended Correspondence Analysis (DCA) in CANOCO 4.0 (Ter Braak and Smilauer, 1998). Axis 1 and 2 DCA scores of subjectively located paired plots were compared with plots established in 1986 on randomly located transect lines using ANOVA in SYSTAT (SPSS, 2000) to test if paired exclosure plots were representative of Aorangi Forest, and if fenced and unfenced plots had similar species composition at the time of establishment. For these baseline comparisons, importance values were calculated using basal area summaries for all tree species. Three permanent plots with > 500 stems ha^{-1} of manuka (*Leptospermum scoparium*) were excluded from analysis, because shrub-dominated sites were not selected for exclosure plot establishment. DCA was also used to summarise tree species composition in paired fenced and unfenced plots in 2004 using importance values calculated from tree stem density.

Tree stem recruitment and mortality rates (McCune and Cottam, 1985), and average annual relative tree stem growth rates (RGR) were calculated for each species in each plot as,

Tree stem recruitment = $(1 + B_x)^{1/3} - 1$,

Tree stem mortality = $1 - (1 - Q_x)^{1/3}$,

$$\text{Tree stem relative growth rate} = \frac{\text{Log}_e \text{ stem diameter 2004} - \text{Log}_e \text{ diameter at plot establishment}}{\text{years between measurements}},$$

where B_x = proportion of new tree stems between measurements and Q_x = proportion of dead tree stems between measurements. Paired *t*-tests were used to test for differences in stem density of common tree species (occurring at ≥ 2 paired plot sites), DCA scores, and tree recruitment, mortality and RGR between fenced and unfenced plots. Tree basal area and stem density data were log_e transformed prior to analysis (Sokal and Rohlf, 1995). Deer-induced reductions in the density of palatable species can potentially retard nutrient cycling and lower the availability growth-limiting nutrients to trees (Wardle, 2002). To explore this possibility, the stem density of tree species that benefited from deer exclusion was compared with tree stem growth of common tree species using a series of linear regressions. Data can be accessed from the National Vegetation Survey databank (Wiser, Bellingham and Burrows, 2001).

Results

At the time of plot establishment in the 1980s there was no significant difference in DCA scores between the 47 permanent plots established on randomly selected lines (axis 1 mean ± S.E.M = 2.7 ± 0.2; axis 2 = 2.2 ± 0.1), fenced ungulate exclosure plots (axis 1 = 4.1 ± 0.4; axis 2 = 2.3 ± 0.3), and unfenced plots (axis 1 = 3.8 ± 0.4; $F_{2,54}$ = 2.879, P = 0.065; axis 2 = 2.0 ± 0.2, $F_{2,54}$ = 0.355, P = 0.703; Fig. 2). This confirms that at the time of establishment, subjectively selected paired exclosure plot sites were generally representative of Aorangi Forest, and that there was little difference in species composition between fenced and unfenced plots.

Paired *t*-tests of DCA scores calculated with tree stem density data show that there was no significant difference in species composition between fenced and unfenced plots in 2004 (Table 1). A series of paired *t*-tests of data from the 1980s showed no significant difference in the stem density of common tree species between fenced and unfenced plots (P ≥ 0.172). In 2004, only kanono showed significant differences in tree stem density and recruitment between fenced and unfenced plots. Over the two decades between plot establishment and re-measurement, mean kanono stem
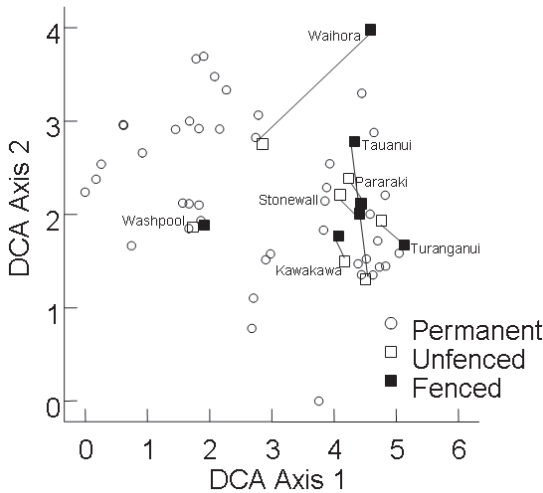
Figure 2. Tree (≥ 2 cm DBH) basal area ordination biplot scores from 44 permanent plots measured in 1986 (O), and from paired fenced (■) and unfenced (□) plots at seven sites, upon establishment in the 1980s. Paired plots at the same sites are linked (—).

density increased by forty times inside fenced plots, but was not present in paired unfenced plots upon establishment in the 1980s or at the time of re-measurement in 2004. In fenced plots, the annual tree stem recruitment rate of kanono was 0.030 ± 0.005 (mean ± S.E.M). In contrast, there was no recruitment in unfenced plots ($t_6 = 5.852$, $P = 0.001$). There was no significant difference between paired fenced and unfenced plots in tree stem density, stem recruitment ($P \geq 0.080$), or stem mortality ($P \geq 0.185$) in 2004 for the other twelve common tree species. Some species palatable to ungulates had very large standard error values for stem density in fenced plots in 2004 (e.g. karamu and tarata), indicating that there was a substantial increase in stem density at some sites, but little response to the removal of herbivory at other sites.

There was no evidence that hinau, rewarewa, and kawakawa trees grew faster in fenced plots in comparison to trees growing in paired unfenced plots (Table 1). Mahoe grew significantly slower outside fenced plots in comparison to inside fenced plots. A series of linear regressions failed to show any significant effect of tree stem density of kanono on RGR for hinau ($R^2 = 0.015$, d.f. = 3, $P = 0.844$), porokaiwhiri ($R^2 = 0.252$, d.f. = 3, $P = 0.389$), rewarewa ($R^2 = 0.056$, d.f. = 4, $P = 0.653$) or mahoe ($R^2 < 0.001$, d.f. = 3, $P = 0.989$) in fenced plots.

Table 1. Tree stem densities in 2004 (≥ 2 cm DBH), 2004 DCA scores and annual stem growth common species (mean ± S.E.M of species occurring at ≥ 2 sites) in paired fenced and unfenced plots. Results of paired *t*-tests comparing DCA scores and stem densities ($\log_e + 1$) between paired plots in 2004 are displayed in order of unfenced stem density. Numbers of plots for which tree growth data could be calculated is also displayed.

Maori name (common name)	Botanical name	Tree stem densities (stems/ha ± S.E.M.)				Tree stem growth (RGR ± SEM)			
		Unfenced	Fenced	t_6	P	Unfenced (n)	Fenced (n)	t	P
Kanono	*C. grandifolia*	0	357.1 ± 118.7	13.477	< 0.001	— (0)	0.005 (1)		
Tarata (lemonwood)	*P. eugenioides*	0	92.9 ± 58.4	2.022	0.090	— (0)	0.002 (1)		
Karamu	*C. robusta*	0	67.9 ± 52.0	2.047	0.087	— (0)	— (0)		
Hinau	*E. dentatus*	21.4 ± 11.5	60.7 ± 20.3	1.183	0.282	0.002 ± <0.001 (3)	0.003 ± 0.002 (5)	0.609	0.652
Kaikomako (ducksfoot)	*P. corymbosa*	32.1 ± 28.2	39.3 ± 23.1	1.276	0.249	0.013 (1)	0.012 ± 0.006 (2)		
Mapou	*M. australis*	32.1 ± 24.8	10.7 ± 7.4	0.303	0.772	0.003 ± 0.001 (2)	— (0)		
Heketara (tree daisy)	*O. rani*	35.7 ± 20.3	28.6 ± 19.2	1.099	0.314	0.003 ± 0.002 (3)	0.002 (1)		
Kawakawa (peppertree)	*M. excelsum*	39.3 ± 24.9	164.3 ± 99.2	1.418	0.206	0.008 ± 0.004 (2)	0 ± 0.003 (2)	8.171	0.078
Rewarewa (honeysuckle)	*K. excelsa*	100.0 ± 35.8	92.9 ± 26.6	0.346	0.742	0.011 ± 0.003 (6)	0.007 ± 0.002 (6)	1.116	0.315
Mahoe (whiteywood)	*M. ramiflorus*	160.7 ± 52.6	221.4 ± 76.3	0.384	0.715	0.003 ± 0.001 (6)	0.005 ± 0.001 (5)	5.977	0.004
Porokaiwhiri (pigeonwood)	*H. arborea*	292.9 ± 105.9	282.1 ± 90.9	0.128	0.902	0.002 ± 0.001 (5)	0.002 ± <0.001 (5)	0.070	0.947
DCA axis 1 stems/ha		0.733 ± 0.512	0.656 ± 0.281	0.312	0.766				
DCA axis 2 stems/ha		1.104 ± 0.227	1.031 ± 0.300	0.245	0.815				

Discussion

Kanono regeneration prevented by red deer

This study has shown a rapid increase in the tree stem density of kanono in fenced deer exclosure plots that was not observed in paired unfenced plots, providing evidence that browsing by red deer has prevented regeneration of kanono at Aorangi Forest over the past two decades. Changes in tree stem density of species less palatable than kanono such as porokaiwhiri, mahoe and tarata, and of canopy tree species such as hinau and rewarewa (Forsyth *et al.*, 2002), varied considerably among sites, but were not significantly different between fenced and unfenced plots. One explanation is that deer populations were sufficiently large to consistently prevent regeneration of kanono, while being low enough to have allowed regeneration of less palatable species at some sites. It is unlikely that feral goat browsing had an influence on kanono regeneration, because intensive culling undertaken before plots were established eliminated feral goats from Aorangi Forest (Handford, 1991; QWH pers. obs.). The effect of pigs on tree regeneration is less clear. Pigs were able to access two fenced plots in Aorangi Forest and may have been able to reduce the density of small seedlings in fenced plots to similar levels observed in unfenced plots. Brushtail possums (*Trichosurus vulpecula*) were also present throughout the study area and may have influenced forest regeneration and succession (Thomas *et al.*, 1993). Because brushtail possums could access both fenced and unfenced plots their browsing effects do not explain the results observed in this study.

Effects of deer on forest succession

Tree species composition in Aorangi Forest was not significantly affected by the suppression of kanono regeneration over the past two decades. In contrast, Jane and Pracy (1974) found that by the 1960s red deer had a massive effect on Aorangi Forest sapling species composition. After a century of occupation, red deer appear to be continuing to suppress the regeneration of kanono. This is consistent with some previous studies in New Zealand, which have shown increased densities of palatable seedlings after deer exclusion (e.g. Allen *et al.*, 1984; Bellingham and Allan, 2003). While kanono and other palatable species did not reach sufficient densities in all fenced plots to affect tree species composition, the continued absence of individual palatable species may have indirect influences on future forest composition. Tree species palatable to deer are likely to also to provide important nutrients in the diet of bird species (Leathwick, Hay and Fitzgerald, 1983). Some folivorous bird species such as the New Zealand pigeon (*Hemiphaga novaeseelandiae*) act as seed dispersers, and if their densities are limited through reduced food availability, seed bank composition may be altered. Reductions in kanono density could also affect nutrient cycling. Reductions in the biomass of palatable plants and their litter-fall, which are likely to contain high levels of nutrients, can result in reductions in the amount and quality of organic matter in the soil (Pastor *et al.*, 1993; Sirotnak and Huntly, 2000). This could shift competitive balances between plants altering tree species composition, but this is rarely assessed in the field. Nevertheless, in Aorangi Forest, the lack of compositional change in fenced plots supports the view that the direction of forest succession can be permanently altered towards a highly modified but stable state by a century of deer browsing (Coomes *et al.*, 2003). Red deer may have prevented some tree species from establishing for long enough in Aorangi Forest to lead to an absence of seeds at some sites. This may help to explain why tree recruitment of palatable trees within fenced plots was inconsistent among sites, although variation in disturbance, nutrient cycling and species composition are also likely to be important factors affecting tree regeneration.

Mahoe tree growth reduced

Tree growth rates of mahoe were significantly reduced by the presence of deer, most likely due to deer eating foliage. Mahoe frequently produces epicormic shoots and branches palatable to deer, which if browsed intensively could reduce tree stem growth. The growth of larger tree species (hinau, porokaiwhiri and rewarewa; which have less foliage growing in the browse tier in Aorangi Forest than shorter sub-canopy species such as mahoe) did not appear to be affected by deer browsing. An alternative explanation is that mahoe growth was indirectly reduced through ecosystem level effects of deer. Deer-induced reductions in the density of palatable species such as kanono might have reduced the quality of litter fall, thereby lowering the availability growth-limiting nutrients to trees (Wardle, 2002). Wardle *et al.* (2001) and Wardle, Bonner and Barker (2002) showed that the quality of litter fall is indirectly affected by herbivores at some sites in New Zealand, but they did not address the possibility that the growth of canopy trees is reduced where herbivores have reduced nutrient inputs into soils. Kanono is a fast-growing palatable species and so is likely to produce high quality litter-fall that, following its decomposition, might be expected to result in higher nutrient availability to trees (Wardle *et al.*, 2002). This study showed no relationship between the stem density of kanono and growth of other tree species, and therefore provides no evidence that reductions in the densities of palatable tree species can reduce the quality of litter fall, nutrient availability and tree growth.

Management implications and conclusions

It appears that deer hunting over the past two decades in Aorangi Forest has been ineffective at reducing deer densities to sufficiently low levels to allow regeneration of palatable species such as kanono. Deer densities were low enough to ensure regeneration of less palatable species such as porokaiwhiri, mahoe and kawakawa. Previous studies have shown that intensive commercial culling can reduce deer densities by 80% (Nugent, Parkes and Tustin, 1987) and lead to increases in cover of palatable plant species in alpine grasslands (Rose and Platt, 1987; Mark, 1989). Intensive culling has also resulted in restoration in the regeneration of palatable plant species for short periods in beech forests (Stewart, Wardle and Burrows, 1987; Husheer and Robertson, 2005), but there is no published evidence of deer culling having benefits for palatable species in New Zealand's indigenous forests for more than a decade. This study contributes to an increasing body of recent research showing that palatable plant species will generally not regenerate in New Zealand beech and low altitude hardwood forests unless deer populations are maintained at very low densities (e.g. Husheer and Frampton, 2005; Nugent *et al.*, 2001), although there is large variation in the responses of plants to deer browsing both within and among different forests (e.g. Wardle *et al.*, 2001; Bellingham and Allan, 2003). Management responses to deer will therefore need to be targeted to areas where deer populations can be maintained at very low levels over several decades. Management that does not lower deer populations to very low levels is less likely to result in the regeneration of palatable plant species.

Acknowledgements

References

Allen, R.B. 1993. *A Permanent Plot Method for Monitoring Changes in Indigenous Forests.* Landcare Research, Lincoln, N.Z. 35 pp.

Allen, R.B.; Payton, I.J.; Knowlton, J.E. 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.

Bellingham, P.J.; Allan, C.N. 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.

Caughley, G. 1983. *The Deer Wars.* Heinemann, Auckland, N.Z. 187 pp.

Caughley, G. 1989. New Zealand herbivore–plant systems: past and present. *New Zealand Journal of Ecology 12:* 3–10.

Coomes, D.A.; Allen, R.B.; Forsyth, D.M.; Lee, W.G. 2003. Factors preventing the recovery of New Zealand forests following the control of invasive deer. *Conservation Biology 17:* 450-459.

Côté, S.D.; Rooney, T.P.; Tremblay, J.-P.; Dussault, C.; Waller, D.M. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics 35:* 113-147.

Druce, A. P. 1971. The flora of the Aorangi Range southern Wairarapa with notes on the vegetation. *Bulletin of the Wellington Botanical Society 37:* 4-30.

Forsyth, D.M.; Coomes, D.A.; Nugent, G.; Hall, G.M.J. 2002. The diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. *New Zealand Journal of Zoology 29:* 333-353.

Handford, P. 1991 (unpublished). *The distribution and abundance of introduced browsing animals in Haurangi Forest Park.* Department of Conservation, Wellington, N.Z. 69pp.

Husheer S.W.; Coomes D.A.; Robertson A.W. 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, S.W.; Frampton, C.M. 2005. Fallow deer impacts on Wakatipu beech forest. *New Zealand Journal of Ecology 29:* 83-94.

Husheer, S.W.; Robertson, A.W. 2005. High-intensity deer culling increases growth of mountain beech seedlings in New Zealand. *Wildlife Research 32:* 273-280.

Jane, G.T.; Pracy, L.T. 1974. Observations on two animal exclosures in Haurangi Forest over a period of 20 years. *New Zealand Journal of Forestry 1:* 103-113.

Leathwick, J.R.; Hay, J.R.; Fitzgerald, A.E. 1983. The influence of browsing by introduced mammals on the decline of North Island kokako. *New Zealand Journal of Ecology 6:* 55-70.

Mark, A.F. 1989. Responses of indigenous vegetation to contrasting trends in utilisation by red deer in 2 southwestern New Zealand National Parks. *New Zealand Journal of Ecology 12:* 103-114.

McCune, B.; Cottam, G. 1985. The successional status of a southern Wisconsin Oak woods. *Ecology 66:*

1270-1278.

Nugent, G. 1990. Forage availability and the diet of fallow deer (*Dama dama*) in the Blue Mountains, Otago. *New Zealand Journal of Ecology 13:* 83-95.

Nugent, G.; Fraser, K.W. 1993. Pests or valued resources? Conflicts in management of deer. *New Zealand Journal of Zoology 20:* 361-366.

Nugent, G.; Fraser, K.W.; Sweetapple, P.J. 1997. Comparison of red deer and possum diets and impacts in podocarp-hardwood forest, Waihaha catchment, Pureora Conservation Park. *Science for Conservation 50,* Department of Conservation, Wellington, N.Z. 61pp.

Nugent, G.; Fraser, K.W.; Sweetapple, P.J. 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.

Nugent, G.; Parkes, J.P.; Tustin, K.G. 1987. Changes in the density and distribution of red deer and wapiti in northern Fiordland. *New Zealand Journal of Ecology 10:* 11-21.

Parsons, M.J.; Douglass, P.; Macmillan, B.H. 1995. *Current names list for wild gymnosperms, dicotyledons and monocotyledons (except grasses) in New Zealand*. Manaaki Whenua Press, Lincoln, N.Z. 206 pp.

Pastor, J.; Dewey, B.; Naiman, R.J.; McInnes, P.F.; Cohen, Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology 74:* 467–480.

Rose, A.B.; Platt, K.H. 1987. Recovery of northern Fiordland alpine grasslands after reduction in the deer population. *New Zealand Journal of Ecology 10:* 23-33.

Rogers, G.M.; Leathwick, J.E. 1997. Factors predisposing forest to canopy collapse in the southern Ruahine Range, New Zealand. *Biological Conservation 80:* 325-338.

Sirotnak, J.M; Huntly, N.J. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology 81:* 78–87.

Smale, M.C.; Hall, G.M.J.; Gardner, R.O. 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.

Sokal, R.R.; Rohlf, F.J. 1995. *Biometry.* W.H. Freeman, New York, U.S.A. 887 pp.

SPSS. 2000. SYSTAT 10.0. SPSS inc, Chicago, U.S.A.

Stewart, G.H.; Burrows, L.E. 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.

Stewart, G.H.; Wardle, J.A.; Burrows, L.E. 1987. Forest understorey changes after reduction in deer numbers, northern Fiordland. *New Zealand Journal of Ecology 10:* 35-42.

ter Braak, C.J.E.; Smilauer, P. 1998. *CANOCO 4.0.* Centre of Biometry, Wageningen, The Netherlands. 95 pp.

Thomas, M.D.; Hickling, G.L.; Coleman, J.D.; Pracy, L.T. 1993. Long-term trends in possum numbers at Pararaki: evidence of an irruptive fluctuation. *New Zealand Journal of Ecology 17:* 29-34.

Veblen, T.T.; Stewart, G.H. 1982. The effects of introduced wild animals on New Zealand forests. *Annals of the Association of American Geographers 72:* 372-397.

Wardle, D.A. 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton, U.S.A. 392p.

Wardle, D.A.; Bonner, K.I.; Barker, G.M. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology 16:* 585-595.

Wardle, D.A.; Barker, G.M.; Yeates, G.W.; Bonner, K.I.; Ghani, A. 2001. Introduced browsing mammals in natural New Zealand forests: aboveground and belowground consequences. *Ecological Monographs 71:* 587-614.

Wardle, J. 1966. Vegetation of the Aorangi Range, southern Wairarapa. *New Zealand Journal of Botany 5:* 22-48.

Wiser, S.K.; Bellingham, P.J.; Burrows, L.E. 2001. Managing biodiversity information: development of New Zealand's National Vegetation Surveys databank. *New Zealand Journal of Ecology 25:* 1-18.