

High-intensity deer culling increases growth of mountain beech seedlings in New Zealand

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Abstract. Browsing of mountain beech seedlings by introduced deer in the central North Island of New Zealand appears to have inhibited canopy regeneration over large areas. In 1998, a trial of high-, medium- and low-intensity deer-culling treatments was initiated in Kaimanawa and Kaweka Forest Parks to test whether mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest regeneration could be restored by removing deer. Paired enclosure plots (one plot fenced to exclude deer and the other unfenced) were established within a high-intensity culling area, to monitor the benefits of recreational, commercial and aerial deer culling. Paired plots were also established within low- and medium-intensity culling areas. Medium-intensity culling was allowed through recreational and commercial deer culling. In two low-intensity culling treatment areas, deer management remained substantially unaltered. Annual relative growth rates of tagged seedlings from spring 1998 to spring 2001 from low-, medium- and high-intensity culling areas provide strong evidence that mountain beech seedling growth increases once browsing by deer is removed through fencing. Faecal pellet data indicated that high-intensity deer culling reduced deer abundance by 67% in comparison to medium- and low-intensity culling areas. This apparent reduction in deer abundance appears to have led to a doubling in mountain beech seedling growth in the high-intensity culling area outside fences, in comparison to low- and medium-intensity deer culling areas where there was little or no evidence of benefits for seedling growth.

Introduction

It has been apparent for over two decades that browsing by deer has suppressed mountain beech (*Nothofagus solandri* var. *cliffortioides*¹) regeneration in the Kaimanawa region of the central North Island of New Zealand. Studies using permanent vegetation plots (some with deer-exclusion fencing) have suggested that beech regeneration is threatened by deer at critical sites in Kaweka (Allen and Allan 1997) and Kaimanawa Forest Parks (Husheer 2003), which constitute most of the Kaimanawa Ecological Region (MacEwen 1987). These critical sites are where natural death of canopy trees has occurred through episodic disturbance (Hosking and Hutcheson 1988) and where browsing by deer has reduced the growth rate of mountain beech seedlings so that canopy replacement is slowed or prevented (Allen and Allan 1997). In the past three decades extensive commercial deer culling appears to have restored canopy regeneration in many other forest areas in New Zealand (Coomes *et al.* 2003). Canopy decline normally creates opportunities for vigorous

seedling regeneration of mountain beech (Osawa and Allen 1993; Harcombe *et al.* 1998) through increased light (Stewart *et al.* 1991) and nutrient availability to seedlings (Allen *et al.* 1997). However, in the Kaimanawa region, densities of mountain beech seedlings are reduced through deer browsing. Forests are instead increasingly dominated by small-leaved shrubs (e.g. *Coprosma pseudocuneata*, *Coprosma* 'taylorae' and *Phyllocladus alpinus*) that are likely to be more browse-resistant than the less common beech seedlings and saplings (Husheer *et al.* 2003). Additionally, Husheer (2003) showed that suppression of mountain beech regeneration is widespread in the Kaimanawa Ecological Region, most likely because of intensive browsing by sika deer (*Cervus nippon*). Sika deer have been abundant in the Kaimanawa region for at least 50 years (Davidson 1976), and red deer (*Cervus elaphus*) since the 1930s (Elder 1963).

There has been a long history of deer culling² in the Kaimanawa Region, where records are available from 1958

¹ Nomenclature follows Parsons *et al.* (1995). *Coprosma* 'taylorae' is referred to by Eagle (1986) and *Phyllocladus alpinus* by Wilson and Galloway (1993).

² In New Zealand, the term 'deer culling' has been used for over five decades to describe widespread deer-hunting operations aimed at density reductions (e.g. Crump 1960; Bennet 1973; Caughley 1983).

until 1988 (Davidson and Fraser 1991). Following Allen and Allan's (1997) study on the suppression of mountain beech regeneration by deer, a working party of forest conservation, hunter and Department of Conservation representatives concluded that more intensive deer control was required to restore mountain beech regeneration, but no agreement could be reached on the best method of control. Options included increased recreational hunting, allowing access to commercial hunters, intensive aerial culling and ground-based fluoroacetate-laced gel poisoning.

In October 1998, high-intensity deer culling from helicopters was implemented in one treatment area within the Kaimanawa Ecological Region (Fig. 1). In this treatment area, and in another adjacent medium-intensity culling area, increased recreational and commercial hunting access was allowed to encourage a greater harvest of deer. Other adjacent areas in the Kaimanawa Region received no additional deer hunting, and acted as a low-intensity culling area. A monitoring program based on paired fenced and unfenced plots (10 m × 10 m) was established in these areas in the summer field seasons (October–March) of 1997/98 and 1998/99 to assess the effect of deer browsing on the growth of mountain beech seedlings.

The main objective of the present study was to determine whether intensive deer culling could reduce deer abundance, and the impact of deer browsing on the growth of mountain beech seedlings. To determine whether low-, medium- or high-intensity deer-culling treatments are effective, we com-

pared annual growth of mountain beech seedlings under these three culling regimes between paired fenced and unfenced plots over three summer growing seasons. We assumed that the growth of mountain beech seedlings in unfenced plots would approach the growth in fenced plots if deer densities could be reduced sufficiently, and that if these lowered deer densities could be sustained it should allow eventual replacement of the mountain beech canopy.

Methods

Description of the study area

The Kaimanawa and Kaweka mountains are located within Kaimanawa and Kaweka Forest Parks, Kaimanawa Ecological Region, in the central North Island of New Zealand (39°S, 176°E) (Fig. 1). These mountains are a series of ranges oriented north-east to south-west, and are formed predominantly from Jurassic folded greywacke with a schist belt in the north of Kaimanawa Forest Park. Elevations vary from a low of 340 m in the south of Kaweka Forest Park to a high of 1727 m in the south of Kaimanawa Forest Park. Terraces and flats are common in valley bottoms. Soils are derived from a combination of the greywacke bedrock or volcanic ash and ignimbrite flows from Taupo eruptions over the last two millennia (Wilson 1993).

Forests are dominated by the genus *Nothofagus* (southern beech). Mountain beech tends to occur above 1100 m elevation as it displaces red (*N. fusca*) and silver (*N. menziesii*) beech forests that dominate the valley floors. At some sites, beech forests have been replaced by *Chionochloa*- and *Poa*-dominated grasslands with patches of *Leptospermum scoparium* shrubland, probably due to repeated fires lit by Polynesian peoples (McGlone 1989). The understorey of the mountain beech forest has few woody species and these include *Coprosma taylorae* and *Gaultheria antipoda*. *Coprosma linariifolia* and *Coprosma microcarpa* are also important below 1100 m, but are

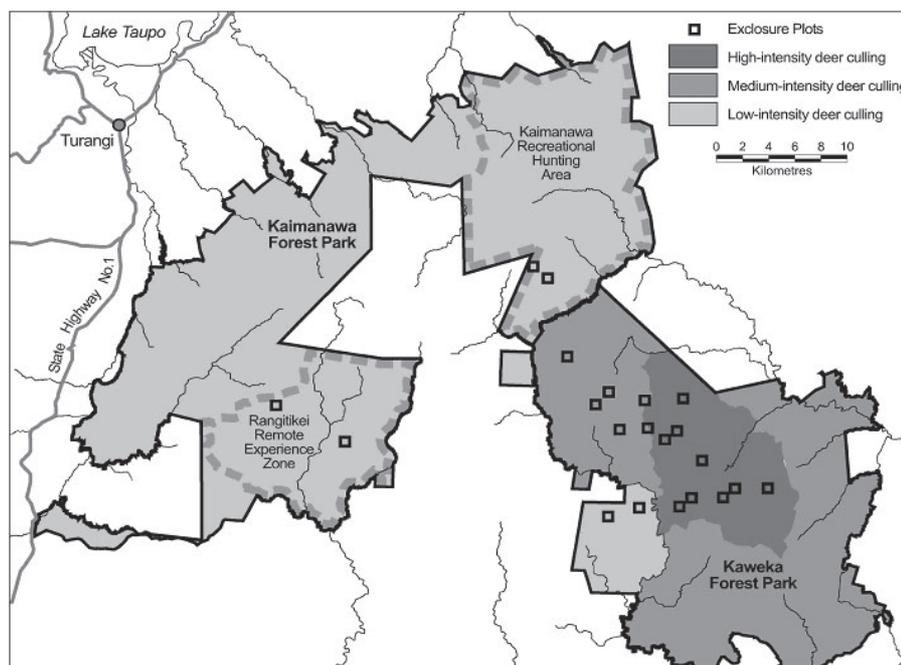


Fig. 1. The study site showing paired enclosure plot sites used for comparing growth of mountain beech seedlings in high-, medium- and low-intensity culling areas. The boundaries for Kaimanawa Recreational Hunting Area and Rangitikei Remote Experience Zone are also shown (dashed lines).

replaced by *Coprosma pseudocuneata*, *Phyllocladus alpinus* and *Podocarpus hallii* at higher elevations.

Descriptions of treatment areas

The high-intensity culling area (12 100 ha) comprises ~10 000 ha of *Nothofagus* forest, with large expanses of alpine grasslands and herb-fields on the numerous ridgelines and on the crest of the Kaweka range. This area was selected for intensive helicopter-based deer culling because it has extensive areas of open canopy, allowing deer to be seen and shot. Allen and Allan (1997) and Husheer (2003) showed that 10% of 20 m × 20 m plots throughout Kaweka Forest Park had low occupancy by canopy trees. Commercial venison recovery was limited to the alpine grassland areas where carcasses could be quickly recovered. Paired fenced and unfenced plots for monitoring seedlings were established at 10 sites in this area. Fences (1.8 m high) excluded red and sika deer (the only ungulates present), but allowed access for small herbivores such as common brushtail possums (*Trichosurus vulpecula*), which are not considered to extensively affect mountain beech regeneration (Rose *et al.* 1993; Pekelharing *et al.* 1998; Cochrane *et al.* 2003).

The medium-intensity culling area had enhanced, but unsubsidised, hunter access. This entailed the addition of four helicopter-access points established at campsites in 1998 to complement the existing five helicopter-access points at huts, and two at campsites. This area differs from the high-intensity area in that it has several tussock valley systems, is dominated more by mountain beech than by red and silver beech, and has fewer alpine grassland areas. Paired seedling-monitoring plots were established at five sites in this area.

One of the two low-intensity culling areas was located south-west of the Ngaruroro River in Kaweka Forest Park. Two helicopter-landing sites in this area enabled recreational, but not commercial, hunters to reach two huts from which to base their hunting activities. This area has modified alpine grasslands above the treeline, and less conspicuous canopy collapse. Paired seedling-monitoring plots were established at two sites in this area. Paired seedling-monitoring plots in the Kaimanawa Forest Park low-intensity culling area (76 500 ha) were located at two sites in the vicinity of Mt Maungaorangi in the Kaimanawa Recreational Hunting Area (24 000 ha) and at a further two sites in the heads of the Makomiko and Ecology streams in the Rangitikei Remote Experience Zone. Recreational hunters were allowed helicopter access to campsites in the Rangitikei Remote Experience Zone for six weeks each spring and to access two campsites and four huts in other areas of Kaimanawa Forest Park. Commercial venison-recovery operations were allowed in the southern and western part of Kaimanawa Forest Park. We assume that the relatively low numbers of deer reported killed by recreational hunters in spring in the Remote Experience Zone between 1993 and 1999 (290 deer killed; 0.2 deer day⁻¹) and by commercial hunters throughout Kaimanawa Forest Park (except for the Recreational Hunting Area) from 1 June to 1 October 2000 (177 deer recovered, 2.6 deer h⁻¹, 0.34 deer km⁻²) prior to the establishment of this study did not greatly alter deer numbers. In the areas where our paired seedling-monitoring plots were established in Kaimanawa Forest Park, it is probable that recreational and commercial hunters removed fewer than 1 deer km⁻² year⁻¹, which is unlikely to have significantly reduced deer abundance.

Density of deer faecal pellet groups

As a relative measure of deer abundance, the densities of deer faecal pellet groups were indexed annually at 15 sites in Kaweka Forest Park (1998/99–2001/02). At each site, 160 2.2-m-radius subplots were spaced at 10-m intervals in a cruciform arrangement. Intact pellet groups centred within each of these subplots were counted. In the high-intensity culling area, faecal-pellet monitoring occurred at seven of the 10 sites where paired fenced and unfenced seedling plots were located. Faecal pellet monitoring occurred at all five sites with paired fenced

and unfenced plots in the medium-intensity culling area. In the low-intensity culling area in Kaweka Forest Park faecal-pellet monitoring was undertaken at both sites where paired seedling plots were established and at one additional site without paired seedling plots. Faecal-pellet monitoring was not undertaken in Kaimanawa Forest Park. For analysis, pellet data from the five sites in the medium-intensity area were pooled with data from three sites in the low-intensity treatment area because of low sample size.

Procedure and analysis of vegetation plot measurement

Seedling-monitoring plots were established between November 1997 and March 1999 at subjectively selected low-basal-area mountain beech forest sites with a variety of densities of mountain beech seedlings. Seedling densities in plots were 0.03–2.45 seedlings m⁻², compared to an average of <2 seedlings m⁻² (15–135-cm seedling height) throughout Kaweka mountain beech forest (Allen and Allan 1997). Sites were near the treeline with conspicuous deer browse damage on mountain beech seedlings. Allen's (1993) 20 m × 20 m permanent-plot method was used to measure the site's overstorey upon plot establishment to ensure that basal area was less than 35 m² ha⁻¹.

At the four seedling-monitoring sites under low-intensity culling in Kaimanawa Forest Park, and at three high-intensity culling sites, all mountain beech seedlings (5–160 cm high) were measured in each 10 m × 10 m plot. At the remaining 15 seedling-monitoring sites, where field crews determined that it was not practical to measure all mountain beech seedlings in the time available, seedlings were measured from only half of sixteen 2.5 m × 2.5 m subplots (systematically selected in a checkerboard pattern). When a seedling was sampled, a numbered aluminium tag was wired to its stem and its pull-up height was measured (in centimetres) to the end of the previous season's growth. This means that recent (<6 months) seedling growth was not measured in order to standardise height to the beginning of the new growing season. This was achieved by measuring to a point on a stem where light-coloured new-season's growth replaced darker-coloured old-season's growth. Measurements were undertaken in the spring or early summer of each season before substantial growth had occurred. In effect, the height of the seedling to the end of the previous growing season was recorded to avoid any bias between plots due to sampling dates. A consequence of this is that seedling-growth results correspond to deer abundance in the previous growing season. Winter browse of the previous season's growth will also negatively affect seedling height, as it cannot be allowed for in measurement.

Annual relative growth rates of mountain beech seedlings were calculated for each seedling for each of the 1998/99, 1999/2000 and 2000/01 summer seasons as:

$$(\log_e(\text{remeasured height}_{\text{year end}}) - \log_e(\text{initial height}_{\text{year beginning}})) / 1 \text{ year}$$

Relative growth rates of individual seedlings between 1998 and 2001 were also calculated. We used annual relative growth rates of seedlings (hereafter seedling growth) because this is a commonly used index of plant growth (e.g. Maranon and Grubb 1993; Broome *et al.* 1995; Swanborough and Westoby 1996; Oba *et al.* 2000; Walters and Reich 2000) that reduces bias in absolute growth rates of seedlings, which vary with seedling height. This was necessary because although there were no significant differences in initial seedling heights between fenced and unfenced plots ($F_{1,18} = 0.002$, $P = 0.964$), there were significant differences among treatment areas ($F_{3,8} = 5.982$, $P = 0.007$) likely to be due to environmental differences independent of deer density. Seedling heights in 1998/99 were highest in the low-intensity culling area (least-square mean height ± s.e.m. = 37 ± 2 cm), intermediate in the high-intensity culling area (33 ± 4 cm), and lowest in the medium-intensity culling area (30 ± 5 cm).

General linear models in SYSTAT (SPSS 2000) were used to examine the relationship between seedling growth at sites with paired

fenced and unfenced plots within different intensities of culling treatment. A hierarchical, nested design was employed and individual seedling growth was used as the response variable. Sites were nested within treatment areas, and fenced and unfenced plots nested within sites. Sites, treatments and fencing were treated as categorical variables. Hypothesis tests used an error structure of fencing interacting with sites nested within treatment areas. This avoided pseudoreplication between seedlings and plots at the same site.

Results

Deer culling

In the 1998/99 field season, 23 aerial deer culls were undertaken in the high-intensity culling area, totalling 45 h of flying time. After the first five culls, records of the numbers of deer seen were kept in addition to the numbers killed. Numbers of deer killed per hour were used as an index of culling success (Fig. 2). Of 355 deer seen on the last 18 culls, 306 (86%) were killed. Kill rates decreased by 10% during the 1999/2000 season when 32 culls were undertaken in 73 h of flying. Of a total of 636 deer seen, 88% were killed. In the 2000/01 season, kill rates reduced by a further 20%. Of 514 deer seen, 90% were killed in 30 culls during 76 h of flying. Overall, in the first three seasons, 93% of deer killed were identified as sika and 7% as red deer.

Commercial hunters removed 104 deer carcasses during the 1998 season (June–November), 15 in 1999, 23 in 2000 and 33 in 2001. All deer were shot and recovered using helicopters in the high- and medium-intensity culling areas.

Recreational hunters reported that 105 deer were killed in Kaweka Forest Park low-, medium- and high-intensity

culling areas in 1997, 225 in 1998, 367 in 1999 and 327 in 2000. However, the incidence of three-month hunting permit information being submitted for analysis by recreational hunters increased during this period from 11% of issued permits returned in 1997 to 14% in 1998, 17% in 1999, and 26% in 2000. Thus, the increase that was recorded in numbers of deer killed is likely related to increases in hunter permit returns rather than increasing numbers of deer killed, because kill per unit effort declined and successful hunters are more likely to return permits than unsuccessful hunters (Fraser and Sweetapple 1992). Reported kills per hunting day declined from 0.30 in 1997 to 0.26 in 1998, 0.23 in 1999, to 0.21 in 2000.

Pellet group density

The density of deer faecal pellet groups at 15 sites differed significantly among seasons and between the high-intensity culling area and the pooled low- and medium-intensity culling areas ($F_{3,11} = 5.084$, $P = 0.019$). In the 1998/99 and 1999/2000 seasons, pellet group densities were very similar between the high-intensity culling area and the low- and medium-intensity culling areas (Fig. 2). By the 2000/01 season, however, the density of pellet groups was 47% lower in the high-intensity culling area than in the low- and medium-intensity areas. By the 2001/02 season the density of pellet groups in the high-intensity culling area was 67% lower.

Seedling growth

Growth rates of mountain beech seedlings were consistently higher in fenced plots than in paired unfenced plots when all three growing seasons were considered individually ($F_{6,34} = 4.220$, $P = 0.003$) (Table 1). The size of this difference varied between the high-intensity culling area and the low- and medium-intensity culling areas ($F_{6,16} = 23.186$, $P < 0.001$) and between the medium- and low-intensity culling areas ($F_{6,34} = 6.078$, $P < 0.001$). By the third season in the high-intensity culling area there was very little difference in seedling growth between fenced and unfenced plots. In contrast, seedling growth in unfenced plots in the medium- and low-intensity areas was very low. There was some evidence that seedling growth was higher in the medium-intensity culling area than in the low-intensity areas. In the low-intensity culling area, seedlings declined in height in unfenced plots in the 1998/99 and 2000/01 growing seasons, but there was always positive seedling growth in the medium-intensity culling area even outside fences. Overall, from 1998 to 2001 there was significantly higher seedling growth in the high-intensity culling area than in the medium- and low-intensity culling areas ($F_{2,18} = 3.775$, $P = 0.043$) (Fig. 3).

A high degree of variation in the ratio of seedling growth between unfenced and fenced areas is evident for different seasons (Table 1). Spatial and temporal variation in deer browse may explain these anomalies, as variation between sites

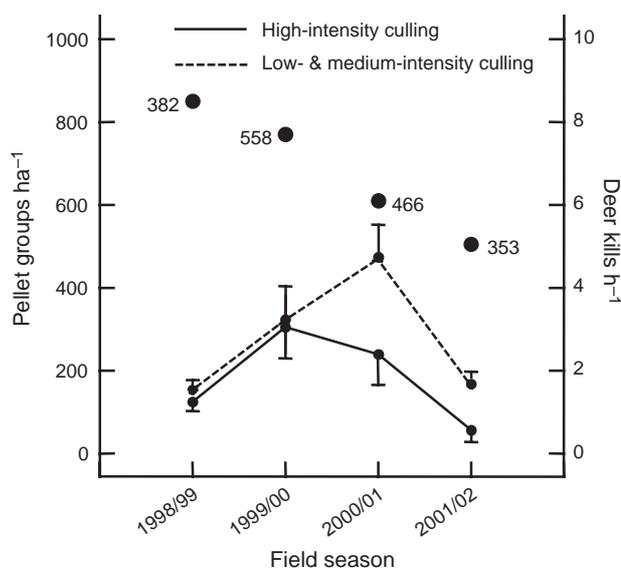


Fig. 2. Mean pellet group densities (\pm s.e.m.), comparing high-intensity deer culling ($n = 7$ sites) with medium- ($n = 5$) and low-intensity ($n = 3$) treatment areas. Data for medium- and low-intensity treatment areas were pooled because of low sample size. Also shown are the numbers of deer killed per hour (●) by aerial deer culling per season (labelled with numbers of deer killed in each summer culling season).

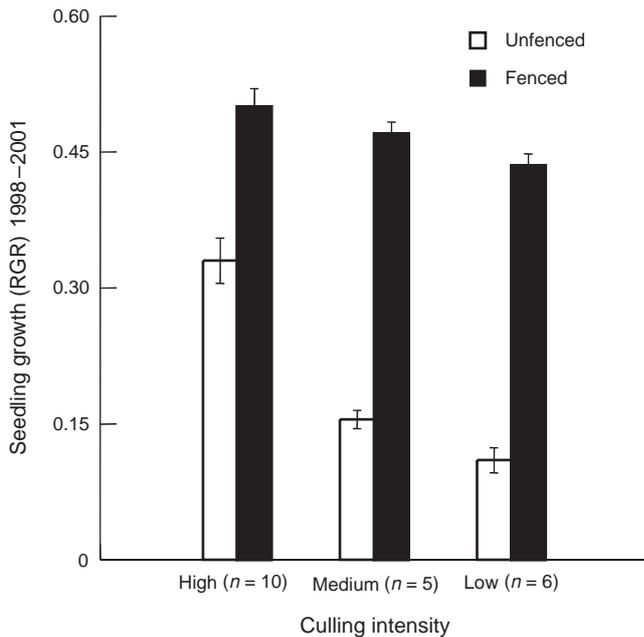


Fig. 3. Least-squares means of the relative growth rates of seedlings (1998–2001, \pm s.e.m) in fenced and unfenced plots with three levels of deer-culling intensity at 21 sites.

and growing seasons was much more pronounced in unfenced plots. Examination of raw data revealed that there was nearly twice the variance in seedling growth between 1998/99, 1999/2000 and 2000/01 in unfenced plots than in fenced plots.

Discussion

Changes in deer density

Our data suggest that three seasons of aerial hunting substantially lowered deer densities in the high-intensity culling area. Between October 1998 and February 2001 more than 11 deer km^{-2} were killed using helicopters in this area. With deer culling from recreational and commercial hunters included, >1600 deer may have been culled in the intensive-culling area (>13 deer km^{-2}) by June 2001. Aerial deer culling appears to have been the more effective form of control, while recreational and commercial hunters appear to have accounted for <1 deer km^{-2} year⁻¹ in that period. Density results for deer faecal pellet groups are consistent

with a 67% reduction in deer abundance over three years in the high-intensity culling area.

Pellet-recording techniques have been widely used to index deer abundance in New Zealand and elsewhere (Bennet *et al.* 1940; Riney 1957; Batcheler 1975; Focardi *et al.* 2002), but the potential for variability in decomposition rates between seasons (Aulak and Babinska-Werka 1990), between areas (Bayliss and Giles 1985) or amongst operators (Van Etten and Bennet 1965; Caughley *et al.* 1976) may affect estimates. Here, we assume that deer density was equal in the different treatment areas prior to the 1998/99 culling season; that decay and defecation rates, and definitions and identification of intact pellets were consistent among areas; that deer abundance outside the high-intensity area did not change substantially; and that there was a 1:1 relationship between changes in pellet group density and deer abundance. In this study, there was very little variation in pellet group densities between the high-, and medium- and low-intensity culling areas in the first two seasons, indicating that comparisons among treatment areas within seasons are reliable. Net immigration from one treatment area to another could also bias results, although reported immigration rates of sika deer are low (Davidson 1979).

The estimated 67% reduction suggests that there were >2000 deer in the 12 100-ha high-intensity culling area (>16 deer km^{-2}) prior to the commencement of aerial culling. If no substantial demographic or immigration response had occurred in the high-intensity culling area, deer densities would have been reduced to <6 deer km^{-2} by the end of the 2000/01 culling season. In comparison, Batcheler (1975) estimated a density of ~2.5 deer km^{-2} in 1968 in the Cupola Basin, northern South Island. Nugent *et al.* (1987) estimated that there were ~3.5 deer km^{-2} in northern Fiordland, South Island. On predator-free Kinkazan Island in Japan where hunting was prohibited, sika deer density was estimated at 60 deer km^{-2} in *Fagus crenata*- and *Abies firma*-dominated forest (Takatsuki and Gorai 1994) and roe deer (*Capreolus capreolus*) density in a conifer-broadleaf forest in Dorset, England, varied between 34 and 76 deer km^{-2} between 1967 and 1980 (Gill *et al.* 1996). Thus, on an international scale, deer abundance in the Kaimanawa region is not exceptionally high, but compared to other New Zealand studies it is relatively high.

Table 1. Least-square means of annual relative growth rates of seedling (RGR \pm s.e.m), numbers of seedlings measured in 1998, 1999, 2000 and 2001 (*n*), seedling heights in 1998 (cm \pm s.e.m) and numbers of seedlings measured in 1998 in fenced and unfenced plots with three levels of deer-culling intensity at 21 sites

Culling intensity	RGR 98/99	RGR 99/00	RGR 00/01	<i>n</i>	Height 1998	<i>n</i> 1998
High, unfenced (10 sites)	0.134 \pm 0.020	0.072 \pm 0.016	0.125 \pm 0.016	850	32.9 \pm 1.7	946
High, fenced (10 sites)	0.181 \pm 0.016	0.170 \pm 0.013	0.147 \pm 0.012	1088	31.0 \pm 1.4	1188
Medium, unfenced (5 sites)	0.097 \pm 0.008	0.050 \pm 0.007	0.007 \pm 0.006	885	30.1 \pm 0.8	989
Medium, fenced (5 sites)	0.225 \pm 0.010	0.143 \pm 0.008	0.101 \pm 0.008	680	34.3 \pm 1.0	725
Low, unfenced (6 sites)	-0.005 \pm 0.011	0.117 \pm 0.009	-0.001 \pm 0.009	712	34.9 \pm 1.0	866
Low, fenced (6 sites)	0.141 \pm 0.010	0.203 \pm 0.008	0.096 \pm 0.008	811	30.6 \pm 1.0	930

Over the longer term, there has been a change in dominance from red to sika deer in the Kaimanawa region (Davidson and Fraser 1991), although overall deer abundance may not have varied substantially. Between the 1959/60 and 1967/68 deer-culling seasons, mean kill rates were 1.0 deer hunter⁻¹ day⁻¹. Between the 1968/69 and 1977/78 seasons kill rates were slightly higher (1.1 kills hunter⁻¹ day⁻¹). There was then a sharp decline in the 1980/81 season (0.5 kills hunter⁻¹ day⁻¹) followed by a generally increasing trend until the final season of deer culling in 1987/88 when kill rates were once again over 1 deer hunter⁻¹ day⁻¹ (Davidson and Fraser 1991).

Changes in seedling growth

Fenced plots had consistently higher growth of mountain beech seedlings than unfenced plots, which provides strong evidence of the negative effect that deer have on seedling growth at low-basal-area sites. By 2000/01, there was little difference in relative seedling growth rates between unfenced and fenced plots in the high-intensity culling area. This suggests that deer impacts on seedling growth were much reduced after three seasons of aerial deer culling. In contrast, differences in growth between unfenced and fenced plots remained consistently greater in the medium- and low-intensity culling areas. At some sites in these treatment areas there was no growth, or seedlings were actually reduced in height outside fences. These results show that both medium- and low-intensity culling treatments were ineffective at restoring seedling growth. These conclusions are consistent with the deer-culling and pellet data, which show a reduction in deer abundance in the high-intensity culling area but not in the medium- and low-intensity culling areas. These results also provide the main support for our conclusion that high-intensity culling, primarily aerial deer-culling, has led to a reduction in the intensity of deer browsing and a corresponding increase in growth of mountain beech seedlings.

To reliably determine the adequacy or deficiency of mountain beech regeneration, data on recruitment and mortality as well as seedling growth rates are required. This information is available from another study that used the same 10 m × 10 m paired plots used in the present study. Husheer (2003) showed no significant difference in annual mortality or recruitment of seedlings (5–135 cm) between fenced and unfenced plots at seven sites. However, there were significantly more small seedlings (<5 cm high) established in fenced plots (mean ± s.e. = 196.0 ± 111.0 seedlings plot⁻¹) than in unfenced plots (mean ± s.e. = 16.9 ± 10.0 seedlings plot⁻¹). This relates to the effects of deer on seedling establishment and survival after a beech mast seeding in autumn 1999. Further research is required to develop full demographic models predicting how long deer numbers need to be reduced for successful mountain beech regeneration, and whether increases in seedling abundance will lead to more recruitment into larger size classes in

fenced plots. Any model used to predict canopy replacement therefore appears to be more dependent on measures of seedling establishment and growth than on recruitment and mortality. Thus, we cautiously assume that relative growth rate data from the present study can be used as an index of canopy replacement in the absence of a complete demographic model. Because there was sustained seedling growth over the three years in unfenced plots in the high-intensity culling area, regeneration is likely to be sufficient there to maintain a canopy while deer numbers remain low. In other areas without aerial deer culling, growth of mountain beech seedlings at low-basal-area sites is unlikely to be sufficient for canopy replacement, although this study does not reveal the threshold deer density required to ensure canopy regeneration across the landscape.

There was considerable variation in seedling growth within culling areas, particularly among unfenced plots, which may be due to plot-scale variation in deer density and carrying capacity interacting with biotic and environmental variables at the ecosystem level (Wardle *et al.* 2001). This variation means that models of canopy replacement need to include not only the demographics of mountain beech seedlings but also the effects of deer carrying capacity because deer browsing may impede canopy regeneration more where carrying capacity is lowest. Although productive sites can be more attractive to deer, increasing the absolute effects of browsing (Ball *et al.* 2000; Virtanen *et al.* 2002), limitations of food supply at unproductive sites will not only lower carrying capacity but will also lead to greater relative impacts (Oksanen 1990; John and Turkington 1997; Moen and Oksanen 1998).

If deer-induced regeneration failure is allowed to continue in our study area, mountain beech forest may be transformed into shrubland dominated by a turf of browse-tolerant herbs, sedges and grasses along with small-leaved, browse-resistant shrubs such as *C. 'taylorae'* and *Phyllocladus alpinus*. Husheer *et al.* (2003) showed that these turf-forming species have increased their dominance in mountain beech forest in southern Kaimanawa Forest Park. These turfs compete with mountain beech seedlings and can suppress canopy regeneration at some sites even after deer densities are reduced (Husheer *et al.* in press). In Europe there are instances where deer browsing has maintained semi-natural grasslands (Eriksson *et al.* 1995; Hellström *et al.* 2003) and grazing lawns (Olf *et al.* 1999). A case of deer indirectly preventing regeneration of canopy species has also been recorded in North America, where deer browsing induced a dense cover of ferns (de la Cretaz and Kelty 2002).

On the basis of the available evidence, we conclude that deer abundance has been significantly lowered and, as a result, seedling growth significantly increased in the high-intensity culling area by three seasons of aerial deer culling. This provides support for aerial deer culling as an effective technique for restoring mountain beech growth at sites with

open canopies. In contrast, there is only a small benefit for seedling growth from medium-intensity deer culling by unsubsidised recreational and commercial hunters.

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