Impacts of deer on Kaimanawa beech forests

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Contribution of others to study

While this PhD thesis is substantially my own work there has been considerable input from others, particularly assistance with fieldwork and reviewing of manuscripts. Several hundred permanent plots have been repeatedly measured for this study. Typically, each plot took a team of four people a full day to establish or re-measure. After data collection took place there was an equally large amount of effort required to enter data into databases, and then to check and correct errors. The sampling design for fenced and unfenced plots used in chapter five was devised by Chris Ward (East Coast/Hawkes Bay Conservancy), and sites were selected and plots established by Department of Conservation staff from Tongariro/Taupo and the East Coast/Hawkes Bay Conservancies.

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Abstract

Extensive mountain beech (*Nothofagus solandri* var. *cliffortioides*) canopy collapse has been apparent for decades in the Kaimanawa Region, central North Island of New Zealand. In most other unlogged mountain beech forests prolific seedling regeneration follows canopy collapse, but in the central North Island regeneration has been impeded by red (*Cervus elaphus*) and sika deer (*Cervus nippon*) browsing. The primary objective of this study was to determine relative impacts on mountain beech regeneration of red and sika deer, and the impacts of deer in general on Kaimanawa Region beech forest composition. Previous international research has shown that herbivores can drastically modify seedling species composition, but the ongoing consequences of herbivory for canopy composition and competitive interactions between plants on a landscape-scale are still poorly understood. This PhD uses short and long-term monitoring of vegetation to examine the effects of herbivory on forest regeneration and successional processes. In an attempt to restore mountain beech regeneration, high intensity deer culling was initiated in October 1998 to reduce deer densities. A further objective of this study was to determine the effect of deer culling on deer densities and mountain beech seedling growth.

Data from 20 m x 20 m permanent plots are used to relate the impacts of sika and red deer to changes in mountain, red (Nothofagus fusca) and silver (Nothofagu*s menziesii*) beech forest composition and regeneration. Plots were established on randomly located transects over two decades ago and were re-measured periodically since. Mountain beech seedling abundance is compared among areas with different sika deer colonisation histories to determine impacts of sika deer over time. Comparisons are also made with areas outside the region, where no sika deer were present.

At ten subjectively located sites, paired fenced and unfenced plots were established in a high-intensity deer culling area between 1997 and 1999, to monitor benefits of deer culling for mountain beech seedling growth. To provide comparisons, paired plots were also established at eleven sites in areas with low- and medium-intensity deer culling.

Results show that sika deer have widespread impacts on Kaimanawa beech (*Nothogagus* spp.) forest regeneration and composition. Where sika deer have been dominant over red deer for more than a decade, mountain beech seedling regeneration has been suppressed in comparison to areas without sika deer. This is particularly evident at stands which had low occupancy by trees, and where prolific seedling regeneration is expected due to increased nutrient and light availability.

Mountain beech forest composition in the Kaimanawa Region has undergone shifts towards browse-tolerant and browse-resistant species over the last two decades. In red and silver beech forests there was an increase in the stem densities of species of small trees that are unpalatable to deer. Analysis of seedling densities indicates that deer-palatable *Weinmannia racemosa* and *Griselinia littoralis* trees were failing to recruit into the >75 cm height class. In the southern part of the Kaimanawa study area understorey composition shifted over two decades towards browse-tolerant turf forming herb, fern, grass and bryophyte communities, which may have been due to the presence of deer.

Analysis of seedling growth rates from paired fenced and unfenced plots provides strong evidence that mountain beech seedling growth increased once deer browsing was removed through fencing, and to a lesser extent following reductions in deer abundance through high-intensity deer culling.

I established two experiments to examine the relationships between herbivory and competition between mountain beech seedlings and other turf-forming plant species. These experiments showed that the composition of turf communities had little effect on mountain beech seedling establishment, but their complete removal increased mountain beech seedling growth and survivorship. There was no immediate compositional response of turf communities to the removal of deer browsing, so the reversibility of deer-induced impacts are unclear.

CHAPTER ONE

Introduction, aims and literature review

The impacts of introduced deer on indigenous vegetation communities is likely to be one of the most difficult and contentious issues facing New Zealand conservation managers in the future. This is because deer impacts are spatially and temporally complex (Stewart and Harrison 1987), interest groups represent a diversity of conflicting opinion (Brash 1997), large-scale control techniques are expensive and need further development (Sweetapple 1997) and responses of vegetation following deer control are difficult to predict (Coomes et al. *In Press*). Recent research has shown that while deer impacts hinder forest processes in New Zealand, they are still inadequately understood (Nugent, Fraser and Sweetapple 1997; Forsyth, Coomes and Nugent 2001). In contrast, the recreational and economic benefits of a large recreational hunting industry are more readily apparent (Nugent and Fraser 1993). Balancing the ecological, social, economic and political pressures related to deer impacts provides unique challenges. Consequently, any deer management undertaken needs to be based on robust science. The purpose of this PhD is to provide increased understanding of herbivore impacts on indigenous vegetation, particularly impacts on mountain beech (*Nothofagus solandri* var. *cliffortioides*)[1] regeneration from sika (*Cervus nippon* Temm.) and red deer (*Cervus elaphus* L.) in the central North Island.

Red deer were first introduced into the central North Island in 1883 at Matapiro in Hawkes Bay (Elder 1962) and sika deer in 1905 (Davidson 1973). In the Kaimanawa Ecological Region (MacEwen 1987), which includes Kaimanawa and Kaweka Forest Parks, sika deer are becoming increasingly dominant over red deer (Davidson and Fraser 1991), and may have a far greater impact on vegetation (Fraser 1996). Even in moderate numbers, deer can have a dramatic effect on the understorey of New Zealand forests by preventing the regeneration of palatable plants so that less palatable species become more common (Allen, Payton, Knowlton 1984; Nugent, Fraser and Sweetapple 1997). Of greater concern is the possibility that sika deer browsing on regenerating beech species (*Nothogagus*) could induce compositional changes in canopy trees or the transformation of tall forest into shrub-land (Wardle 1979; Apthorp 1983; Fleury 1993).

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[1] See appendix II for nomenclature

A recent study of deer impacts on Kaweka Forest Park mountain beech forest showed that at some sites deer browse was preventing seedling regeneration to the extent that maintenance of a forest canopy was unlikely (Allen and Allan 1997). Several authors have stated in the past that sika deer prevent mountain beech canopy regeneration (Wardle 1979; Jenkins 1982; Apthorp 1983) while others have argued that beech regeneration is generally not threatened by sika deer in Kaimanawa Forest Park (Brabyn 1988; Fraser and Speedy 1997; Speedy 1992). Although these studies showed that beech species were intensively browsed by deer, and that this reduced seedling abundance, their conclusions were based on observations of beech regeneration at some stands. These observations were often in conflict of results that were overlooked in discussions. For instance, Fraser and Speedy (1997) concluded that mountain beech forest regeneration was adequate to maintain a canopy without any investigation of population demography. Their own data show intensive browsing by deer on mountain beech, particularly at sites infrequently visited by hunters, and Speedy (1992) reached the same conclusions although his results show that mountain beech seedlings were only present within a fenced plot and not an adjacent unfenced plot.

1.1 Structure of thesis

Literature reviews in this chapter provide background on deer impacts, *Nothofagus* forest dynamics and plant competition. Four quantitative studies examine the impacts of red and sika deer on mountain beech regeneration, relate changes in the composition and structure of two Kaimanawa beech forests to long-term deer browsing, show the effects of three levels of deer culling on deer abundance and deer impacts and relate deer impacts to plant competition and resource availability. Finally, the relevance of the four studies for the study of herbivory, plant competition and for deer management are discussed in a concluding chapter (chapter seven).

1.2 Aims of PhD

This PhD thesis is divided into four discrete but related quantitative studies, that are intended to provide five papers to be published in refereed journals. Individual chapters have been reformatted to maintain consistency and wording has been altered to reduce repetition. Studies 1 (chapters two and three) and 2 (chapter four) in this thesis relate to aims 1 and 2 respectively (section 1.2). These studies present analysis of large amounts of data from seven vegetation surveys in Kaweka and Kaimanawa Forest Parks, Kaimanawa

Ecological Region. Study 1 focuses on mountain beech forest regeneration in Kaweka Forest Park and how deer browsing reduces the seedling pool and prevents recruitment of seedlings into saplings and trees. I also relate the abundance of palatable and unpalatable plant species to the impacts of deer browsing using new and permanent vegetation plots, historical deer exclosure plots and aerial photographs. Also in study 1, mountain beech regeneration is contrasted with areas outside the Kaimanawa Ecological Region where sika deer are not present, and between areas with different histories of colonisation by sika deer. Study 2 focuses on changes in composition of red *Nothofagus fusca*, silver *Nothofagus menziesii* and mountain beech forests over the last two decades. Study 3 (chapter five) uses 10 m x 10 m exclosure plots established between 1997–1999 to show the effects of three deer culling treatments and deer exclusion on seedling growth. Two experiments on the relationships between natural and planted seedlings, herbivory and competing vegetation comprise study 4 (chapter six) and address the fourth aim of the PhD. The first experiment in study 4 examines how deer browsing, vegetation composition and site characteristics affect the establishment, growth and survival of naturally occurring mountain beech seedlings. Experimental plots were established at sites dominated by turf communities and browse-tolerant woody shrubs. The second experiment uses transplanted mountain beech seedlings to show the effects of light and nutrient resource limitation on seedling growth. Simulated herbivory is used to show how browsing interacts with plant competition to limit plant growth.

The aims of the PhD are to:

1. determine the effects of deer, and sika deer in particular, on mountain beech forest regeneration and structure in the Kaimanawa Region (chapters two and three);
2. relate the influence of deer on changes in mountain, red and silver beech forest structure and species composition in Kaimanawa Forest Park over two decades (chapter four);
3. examine the response of mountain beech seedling growth to three intensity levels of deer culling and exclusion of deer (chapter five);
4. show the influences of herbivory and resource availability on mountain beech regeneration through experimental studies of seedlings and their competitive interactions with other plants (chapter six).

1.3 New Zealand beech ecology

New Zealand beeches belong to the genus *Nothofagus* and the cosmopolitan family Fagaceae along with *c.*1000 species in eight genera. The distribution of fossil records and extant species of *Nothofagus*, entirely in the southern hemisphere, suggests a Gondwanan origin. Some taxonomists place the *c.* 34 species of *Nothofagus* into a separate southern hemisphere family, Nothofagaceae (Wilson 1993). Ecology of *Nothofagus* has been reviewed by Veblen, Hill and Read (1996), *Nothofagus* in New Zealand by Wardle (1984) and Poole (1987) and mountain beech by Wardle (1970a, b, c and d). The four New Zealand species (Table 1.1) together form a dominant or major component of > 60% of the remaining indigenous forest in New Zealand, and of that *c.* 20% consists of mountain beech dominated forest (Wardle 1984).

Table 1.1. Common and scientific names of New Zealand *Nothofagus* species.

Common name	Scientific name
black beech	*Nothofagus solandri* var. *solandri*
mountain beech	*Nothofagus solandri* var. *cliffortioides*
hard beech	*Nothofagus truncata*
red beech	*Nothofagus fusca*
silver beech	*Nothofagus menziesii*

All *Nothofagus* are woody trees or shrubs with alternate, stipulate leaves and small, usually wind-pollinated unisexual flowers that produce a nut (generally heavy) enclosed in a hardened cupule. *Nothofagus* are generally regarded as rain-forest trees, able to grow on sites with poor fertility, harsh temperature extremes and are able to form pure stands at those more stressful sites. *Nothofagus* is a poor disperser, with nuts seldom travelling further than the height of parent trees (Ogden, Stewart and Allen 1996).

Mountain beech (*Nothofagus solandri* var. *cliffortioides*) rarely grows over 20 m high or 1.0 m in diameter. It has ovate, entire leaves with no domatia. Leaves are dark green, thick and coriaceous and rarely longer than 20 mm. Branchlets are finely pubescent. In young trees the bark is smooth but becomes fibrous with age. Mountain beech is found only in New Zealand between latitudes 38° and 46°, usually at higher altitude and often forming a mono-specific stand at the treeline. Black, red and silver beech replace mountain beech at lower altitudes. Sometimes *Podocarpus hallii*, *Libocedrus bidwillii* and *Griselinia littoralis* are associated with mountain beech as canopy trees, and at wetter, high-altitude sites silver beech (*Nothofagus menziesii*) often replaces mountain beech (Wardle 1984). Leathwick and Austin (2001) used *Nothofagus* to show that competitive effects with other species were strongly related to temperature, and less strongly related to soil moisture deficit. Environmental optima for species that co-occur with *Nothofagus* were lower compared to *Nothofagus* species at colder, less fertile sites suggesting that *Nothofagus* is adapted to more stressful environments. Nevertheless, experimental evidence suggests that mountain beech seedlings perform best with only moderate restrictions on resource availability. Wardle (1970a) found that light shade and trenching improved seedling growth while moisture deficits increased seedling mortality.

Mountain beech flowering occurs in spring and early summer in irregular mast years, usually following a warm summer (Poole 1955; Connor 1966) at intervals of three to five years (Ogden, Stewart and Allen 1996). Seed-fall occurs from autumn through to spring and seed viability is usually highest during years with high seed production (Allen and Platt 1990). *Nothofagus* forests rely on external disturbance for regeneration (Wardle and Allen 1983; Ogden 1988). Storms, disease and earthquakes are major sources of disturbance in *Nothofagus* (Vittoz, Stewart and Duncan 2001). Rapid regeneration usually follows disturbance induced canopy collapse due to increased availability of water, nutrients and light for seedlings. *Nothofagus* forest can collapse on large scales after disturbances such as snow-fall (Wardle and Allen 1983), wind-fall (Hosking and Hutchinson 1988) insect attack (Wardle 1970a), drought (Skipworth 1981) or earthquake (Harcombe et al. 1998). While large collapse events can be very conspicuous, single tree-gap mortality is more common, and is therefore a more important mechanism initiating regeneration (Ogden, Stewart and Allen 1996). *Nothofagus* is unusual in that it generally replaces itself in the early stages of primary succession, as well as secondary succession, such as after single tree-fall gaps (Wardle 1984). Fertile, well-drained microsites are important for regeneration. Burrows (1977) and Gerdes (2000) found that mountain beech seedlings were more abundant on mounds when compared to pits. This is similar for red and silver beech for which seedling establishment, survivorship and density are greater on raised micro-sites (June 1974; June and Ogden 1975). Gerdes (2000) related this to the thinner litter depth, better drainage and soil moisture content.

1.4 Impacts of deer in New Zealand

Studies on the impacts of deer on New Zealand forests have tended to use one of two approaches. The animal-centric view is to look at the characteristics of deer herbivory on a relatively coarse, landscape-scale (e.g. Caughley 1983; Nugent, Fraser and Sweetapple. 1997; Forsyth, Parkes and Hickling 2000). This is a natural viewpoint to take given the mobility of animals and their ability to mask out spatial interactions between herbivores and plant communities at a fine-scale. In contrast, the plant-centric view is to study the effects of deer on a finer, stand-scale (e.g. Veblen and Stewart 1982; Allen, Payton and Knowlton 1984; Stewart, Wardle and Burrows 1987; Stewart and Burrows 1989; Allen and Allan 1997).

Using the first approach, animal ecologists often study the effects of deer browse from the perspective of deer food supply and deer abundance. This is also not surprising given the large influence that food supply has on a deer population (Krebs 2002). To understand deer impacts on forest communities it may be more appropriate to sample individual stands, then attempt to understand spatial and temporal complexities within and among these stands. Recent work examining fine-scale vegetation characteristics and the impact of deer herbivory is lacking in New Zealand (but see Wardle et al. 2001). The effect that these spatial complexities have on animal behaviour would also provide an interesting topic for research that has not been followed in New Zealand. Deer population dynamics may also vary on smaller scales than previously thought. Conradt, Clutton-Brock and Guinness (1999) showed that in Scotland two separate red deer sub-populations had quite different demographic characteristics because of the reluctance of hinds to move out of the territory in which they were born. This was the case even in situations where immigration would have led to better forage quality. I will review studies on the impacts of deer on New Zealand forests from both research approaches using unpublished reports from the New Zealand Department of Conservation, and its predecessors, as well as key research from the published literature.

1.4.1 History of deer in New Zealand

Soon after the liberation of deer into New Zealand in 1861 (Logan and Harris 1967) the potential for modification of forest composition was realised (Walsh 1892; Cockayne 1926; Holloway 1950; Riney et al. 1959; Caughley 1983). Although Cockayne (1908) reported that species vulnerable to deer browse such as *Coprosma tenuifolia* and *N. solandri* had abundant seedlings and saplings at sites where collapse or dieback had occurred, his observations may have been at a stage well before deer populations reached high abundance. Even at this early stage it was realised that introduced browsing ungulates provided browsing pressures that New Zealand plants were not adapted to. New Zealand's flora evolved in the absence of mammalian browsers and instead were likely to have developed defence mechanisms to avoid or tolerate browsing from moas (Aves: Dinornithiformes), that became extinct through human hunting probably around AD 1400 (Caughley 1989, Holdaway and Jacomb 2000). The effects of moa browsing on New Zealand plants is likely to have been quite different than that of introduced browsing mammals, particularly ungulates (McGlone and Clarkson 1993), because moa had no teeth and browsed using sight and not smell to identify plants (Atkinson and Greenwood 1989).

During the expansion of red deer the time between initial colonisation of an area and deer population crash was 25-30 years. In this time there was usually a substantial decline in the abundance of deer-palatable plant species (Caughley 1983). By the 1940's and 50's deer had increased to high levels throughout New Zealand's forests and grasslands (Challies 1985; Parkes, Nugent and Sweetapple 1997). Since that time, deer populations decreased by 75-95% due to a combination of widespread government-funded and commercial deer culling, and natural population decline. By the 1980's there were probably *c.* 250,000 wild deer in New Zealand (Nugent 1993).

While there is general acceptance that deer populations reduced the abundance of palatable plant species in forests (e.g. *Coprosma grandifolia*, *Griselinia littoralis*, *Hebe stricta*, *Pseudopanax colensoi;* Conway 1949, Wallis and James 1972, Jane and Pracy 1974, Smale, Hall and Gardner 1995), the ongoing relationships between post-irruptive deer populations and forest regeneration is less clear. Nugent, Fraser and Sweetapple (1997) concluded that deer generally have a strong regulating effect on their food supply that for some plant species was not linearly related to deer abundance. They reached this conclusion using a conceptual model originally proposed by Nugent (1990) utilising concepts described in Schmidt and Sinclair (1997). Nugent, Fraser and Sweetapple (2001) reviewed the applicability of Schmidt and Sinclair's (1997) consumer-resource model of the interaction between deer and their food supply in forests. In Nugent, Fraser and Sweetapple's (1997) model there is a non-linear gradient of impact for individual plant species depending on their palatability. Highly preferred species are reduced in abundance even at low deer densities and low palatability species gain competitive advantage, until deer density becomes very high. At this point moderately palatable species will also be browsed intensively. According to Nugent, Fraser and Sweetapple (1997), species of moderate palatability can tolerate moderate deer abundance with no decline in abundance. This is consistent with studies that have found that even moderately palatable species such as *Weinmannia racemosa* may be prevented from regenerating at some sites when deer are abundant (Nugent and Challies 1988; Stewart and Burrows 1989). Nevertheless, Veblen and Stewart (1982), Wardle (1984) and later, Forsyth, Coomes and Nugent (2001) argued that these simplistic animal-centric models need to be developed further by incorporating important mechanisms driving ecosystems. These mechanisms affecting spatial and temporal complexities might include gradients of productivity, climate, disturbance and altitude.

Nugent, Fraser and Sweetapple (2001) provide two different scenarios of what might happen to a highly deer-modified forest if deer are completely removed. After browsing pressure is eliminated, a substantial increase in the abundance of palatable plants could be expected. Alternatively, if deer have allowed slow-growing, long-lived, light-demanding plants with good defences to herbivory (e.g. *Podocarpus hallii*) to become more competitive and more abundant, then cohorts of these plants will be present for a long time even if deer browse is eliminated. Coomes et al. (*In Press*) further develop this idea of irreversibility or retarded recovery by considering the effect of changes in ecosystem processes, and a lack of seed source of highly palatable plants. Some changes alter conditions sufficiently to effect seedling establishment and growth. Conflicting with this argument of irreversibility is evidence from many sites of rapid responses by highly light- and nutrient-demanding palatable plant species once deer browse is removed in exclosure plots (Wardle et al. 2001).

1.4.2 Deer impacts in Podocarp forests of the Waikato region

A series of reports on forests in lower altitude forests (<600 m) in the Waikato Region in the northern-central North Island (Clegg 1986; Clegg 1987; Broome and Clegg 1990; Clegg 1991; Broome 1995) showed that deer at moderate densities can prevent palatable species from regenerating, which results in large shifts in canopy composition. In northern Pureora Forest Park, a mixture of constant count plots established in 1974/75 using the method of Batcheler (1971), 20 m x 20 m permanent plots and nine paired exclosure plots established in 1984 (Eadie 1985) were used to assess deer impacts. All plots were remeasured in 1992/93. In these forests the highly palatable *Coprosma grandifolia* decreased in abundance between surveys, while the unpalatable *Pseudowintera colorata* and *Hedycarya arborea* increased in abundance. Less preferred species such as *Blechnum* *fluviatile* were browsed more heavily in 1993 than 1981. There was no change in the abundance of the low palatability canopy tree *Beilschmiedia tawa* and evidence of very low regeneration of more palatable species such as *Alseuosmia macrophylla*, *Coprosma lucida*, *Coprosma robusta*, *Fuchsia excorticata*, *Geniostoma rupestre*, *Griselinia littoralis*, *Melicytus ramiflorus*, *Pseudopanax arboreus*, *Raukaua simplex*, *Schefflera digitata* in the sub-canopy and *Weinmannia racemosa* in the canopy. These species tended to increase in abundance inside fenced deer exclosure plots. These reports concluded that there was probably insufficient regeneration to ensure persistence of palatable species in the absence of deer control. Many plots had a complete absence of deer-palatable plants in the browse tier, with an overall decline of understorey stem density. There was no increase in the abundance of herbaceous palatable plants inside fenced plots.

Deer abundance was estimated at between 5–10 deer km^{-2} in these forests since 1975 (Broome and Clegg 1990), although deer kill rates by recreational hunters were low in Pureora Forest Park. For instance, between 1987 and 1989 recreational hunter kill rates were approximately 0.1 kills day^{-1}, which Broome and Clegg (1990) concluded was insufficient to lower the abundance of the deer population. In southern Pureora Forest Park, a deer diet study showed that deer mostly ate the foliage of woody plants (70%) with ferns (17%) and grasses (10%) also important. Important woody species in the diet of deer were *Griselinia littoralis*, *Pseudopanax crassifolius*, *Elaeocarpus hookerianus* and *Weinmannia racemosa* (Nugent, Fraser and Sweetapple 1997), which are all broad-leaved, hardwood tree species. For the first three species, most leaves were sourced from leaf-fall, and were not available to deer as growing plants because they had been eliminated from the understorey. Nugent, Fraser and Sweetapple's (1997) study showed that the availability of deer-preferred plants was low in the browse tier compared to the potential for deer consumption. The concept that faster-growing, broad-leaved trees, which tend to grow on fertile sites, were more preferred by deer was further developed by Forsyth, Coomes and Nugent (2001). Their review of diet studies throughout New Zealand showed that highly-preferred species tended to have low lignin or indigestible fibre content. Plants that were less palatable had lower nitrogen content.

1.4.3 Deer impacts in the central North Island beech forests

At Rangataua Forest on southern Mount Ruapehu, the fast growing *Coprosma tenuifolia* was the most abundant understorey shrub in *Nothofagus* forest prior to colonisation of deer (Cockayne 1926), but by 1960 had almost disappeared from the deer browse tier (Atkinson 1962). During his 1960 survey, Atkinson observed that deer had changed forest composition and that red and silver beech were continually being browsed heavily by deer (Atkinson 1983). Atkinson's semi-quantitative plot measurement method could not be used to show the effect of deer browse on regeneration success because of a lack of demographic data collected. In Kaweka Forest Park, Allen and Allan (1997) concluded that deer were preventing canopy regeneration at sites where deer were abundant and where mountain beech was near its ecological limits. Fleury (1993) had earlier found evidence of mountain beech regeneration failure at one site in Kaweka Forest Park. Allen and Allan (1997) considered that the impact of deer was so high at some sites, for so long, that planting seeds or seedlings may be required to ensure forest regeneration. Because mountain beech seeds only remain viable in soil for two years or less, once natural stand thinning has occurred there is only a short window of opportunity for mountain beech regeneration before seed trees are lost through senescence. Allan (1997a) and Allan, Stewart and Allen (1997) measured the height, diameter, density and age of mountain beech seedlings in fenced and unfenced transects at two sites in Kaweka Forest Park. They concluded that deer had slowed seedling establishment and growth leading to low densities of predominantly old seedlings. They also found that seedlings growing in canopy openings, on raised microsites or protected from deer by logs or woody shrubs tended to be taller than seedlings more exposed to deer herbivory. Allan (1997a) and Allan, Stewart and Allen's (1997) studies predicted that it would take nine years on average for seedlings at two exclosure plot sites to grow above the browse tier.

Speedy (1992) reported on the 1991 re-measurement of paired exclosure plots in the mid reaches of Ecology Stream, southern Kaimanawa Forest Park and on Mt Ruatahuna in western Kaimanawa Forest Park. Both plots were established in mountain beech forest in 1983. He concluded that deer had a significant influence on the understorey at Ecology Stream that was related to lower hunting pressure compared to the Ruatahuna exclosure. Surprisingly, he also concluded that deer did not affect natural stand dynamics of mountain beech even though his results showed 33 times more seedlings in the fenced plot relative to the unfenced plot at Ecology Stream and eleven times more at Ruatahuna.

1.4.4 Deer impacts in the eastern North Island Podocarp-hardwood forests

Bishop et al. (1998) used 20 m x 20 m paired exclosure plots at four sites established between 1981, remeasured again in the mid 1980's and finally in 1997 to study deer impacts in an extensive tract of *Podocarp-hardwood* forest in Whirinaki Forest Park, eastern North Island. A paired exclosure plot site was established in 1979 using a 10 m x 10 m system, and was remeasured at the same time as the other four plots. The rigour of their study was limited by data loss, uncertain data quality from early plot measurements and a lack of information on wild animal abundance. Nevertheless, they concluded that deer were shifting seedling composition to the extent that would eventually lead to future shifts in forest structure and composition. In a similar study of five paired exclosure plots (ranging from 7.5 m x 7.5 m to 9 m x 9 m in size) in northern Te Urewera National Park, eastern North Island, established in 1980/81 and remeasured in 1997, Bockett (1998) concluded that large reductions in deer density would be required before impacts were reduced. Plots from the same area were remeasured earlier by Allen, Payton and Knowlton (1984) who had similar conclusions to Bockett (1998). All plots in Bockett's (1998) study were located in Podocarp/tawa forest. Palatable species in the understorey (*Alectryon excelsus, Coprosma grandifolia*, *Coprosma tenuifolia*, *Geniostoma rupestre*, *Knightia excelsa*, *Melicytus ramiflorus*, *Pittosporum tenuifolium* and *Schefflera digitata*) generally decreased in abundance in unfenced plots. In contrast, less palatable species (*Beilschmiedia tawa*, *Carpodetus serratus*, *Dacrycarpus dacrydioides*, *Nestegis lanceolata* and *Prumnopitys taxifolia*) either increased or did not change abundance. In fenced deer-exclosure plots palatable plant species generally increased in abundance. In a survey of 57 permanent 20 m x 20 m forest plots in the Waikare catchment, Urewera National Park, Beadel (1991) showed that the proportion of deer-palatable species decreased compared to unpalatable species between 1980/81 and 1985/86. She related this to increases in deer pellet density between 1980 and 1985 (Beadel 1988). In six paired exclosure plots, deer-palatable plants increased in density more in the fenced plot than in the unfenced plots.

1.4.5 Deer impacts in South and Stewart Islands

Cochrane (1994) showed that deer and goats induced the decline of *Carpodetus serratus*, *Griselinia littoralis*, *Melicytus ramiflorus* and *Myrsine australis* in the beech-podocarp forest understories at Isolated Hill Scenic Reserve in Marlborough. He reported higher plant diversity inside three exclosure plots established in 1985, and re-measured in 1994 and in 2000. No differentiation was made between red deer and goat impacts or abundance in the Reserve.

In the Taramakau catchment, South Island, Wardle and Hayward (1969) used temporary vegetation plots (sociological descriptions) to divide forests into six types. They found that forest types near treeline (mountain and silver beech forests and *Metrosideros umbellata – Podocarpus hallii* forest) were relatively resistant to deer browsing, while red beech and *Weinmannia racemosa* forests at lower altitude were more susceptible to deer impacts, and showed altered forest composition and demographic structure. They divided common trees, shrubs and ferns into classes of: highly susceptible to deer browse; intermediate susceptibility; and those tolerant of deer browse. Deer browsing appeared to prevent the regeneration of highly susceptible plants.

Internal botanical reports prepared in 1984 (cited in Johnson, Allen and Wardle 1986) from Otago and Westland covered the Arawhata, Cascade River mouth, mid Cascade valley, Haast-Arawata and Gorge River catchments. All concluded that deer were causing local to severe browsing damage. Deer had been present in the area since at least 1954, and in 1984 were present in "not low" numbers (Johnson et al. 1986).

Stewart, Wardle and Burrows (1987) surveyed the Doon, Wapiti and Glaisnock catchments in Fiordland in 1984 and 1985 to determine trends in the impacts of deer by re-measuring 148 variable area plots established in 1969, and twentyfour 20 m x 20 m plots established in 1975. They were able to compare the Wapiti, Doon and Glaisnock catchments where deer had reached high numbers by 1969, thereby causing the rarity of highly preferred woody species, with the Milford and Blyth catchments, where deer had always been rare or absent. After intensive aerial hunting had reduced deer densities by 80%, highly preferred plants increased in abundance by up to 400% in the Wapiti, Doon and Glaisnock. However, even by 1985, after nearly two decades of intensive commercial deer hunting, full understorey recovery had not occurred. They found that low-altitude seral communities and silver beech forests on fertile soils were more modified by deer than forest communities growing at high altitude or on poor soils. Stewart and Harrison (1987) used

526 variable area plots to show that the more preferred seral and low altitude silver beech forests tended to occur on unstable landforms such as debris cones, colluvial sideslopes and terraces with recent soils. They concluded that the high proportion of highly preferred plants at these sites were a result of the more fertile soils. Less preferred mountain beech and high altitude silver beech forests tended to occur on more stable bedrock sideslopes, ridges and poorly drained benches. In beech forest in the Blue Mountains, Otago, Nugent (1990) concluded from a study of fallow deer (*Dama* dama) diet that highly palatable species such as *Griselinia littoralis* were being prevented from regenerating but that regeneration of a *Nothofagus* forest canopy was generally not threatened. Without detailed study of *Nothofagus* population demographics Nugent's conclusions should be treated with some caution as Stewart (1988) found evidence of deer impeding the regeneration of silver beech.

In a study showing the potential of red deer to reduce forest food availability for takahe (*Porphyrio hochstetteri*), Burrows et al. (1999) concluded that even very low numbers of red deer could reduce the abundance of palatable forest species. In high altitude mountain and silver beech forest, seedling and sapling abundance had remained very low in the Murchison Mountains for three decades. This could be due to a naturally low abundance in this forest type (Stewart and Harrison 1987); to continued high deer impacts with only a small remnant deer population (Nugent, Fraser and Sweetapple 1997); or due to the inability of the forest understories to recover after modification by deer has already occurred (Coomes et al., *In press*).

In a 17-year study of three paired exclosure plots, Graeme (1996) concluded that white-tailed deer (*Odocoileus virginianus*) had caused large compositional shifts in the understorey of Chew Tobacco Bay, Stewart Island, forests. She found that only the ferns *Blechnum discolor* and *Histiopteris incisa* were successfully regenerating on the forest floor. Other palatable species such as *Carpodetus serratus, Coprosma areolata*, *Coprosma foetidissima*, *Coprosma lucida*, *Griselinia littoralis*, *Myrsine australis* and *Raukaua simplex* had regeneration limited to micro-sites not accessible to deer. This finding is consistent with diet studies (Nugent and Challies 1988) on Stewart Island and other studies of coastal forest regeneration (Stewart and Burrows 1989; Bellingham and Allan 2003), which have found that deer browsed on all palatable seedlings that were accessible to them, and on leaf-fall from trees that were above the browse tier. It is likely that these trees had grown through the browse tier before deer colonised the area.

1.4.6 Comparison of deer and possum impacts

In a three-year study of possum *(Trichosurus vulpecula)* and deer impacts in Pureora Forest Park, Nugent, Fraser and Sweetapple (1997) compared the density and diet of red deer and possums (*Trichosurus vulpecula*) with the abundance of common trees and shrubs. They concluded that deer had a far higher impact on forest regeneration than possums because they consumed a higher proportion of the available foliage production in the 0–2m tier. Possums consumed over twice as much foliage as deer but this was concentrated more on large trees and thus had a lower impact on forest composition and successional processes. Nugent, Fraser and Sweetapple (1997) considered that possum control would have little benefit on forest regeneration processes unless deer numbers were reduced to <2 deer km^{-2} from the estimated 6 deer km^{-2} during their study. In their study, although deer and possums mostly ate the same species, they did so in quite different proportions. Major components of possum diet that were largely absent from deer diet included *Aristotelia serrata*, *Myrsine salicina*, *Podocarpus hallii*, *Prumnopitys ferruginea* and *Rubus cissoides*. Deer ate *Blechnum fluviatile*, grasses, *Griselinia littoralis* and *Pseudopanax arboreus*, in far greater amounts than possums. Some species were consumed by both deer and possums, including *Carpodetus serratus*, *Elaeocarpus hookerianus*, and *Melicytus ramiflorus*.

1.4.7 Below-ground effects

The impacts of deer on below-ground process are rarely considered. In a unique study of 30 paired exclosure plots in a variety of forest types throughout New Zealand, Wardle et al. (2001) tested the hypothesis that browsing shifts the composition of vegetation in the browse tier towards unpalatable species thereby altering the species mix of litter and in consequence soil chemistry, which in turn effects the composition of soil fauna. They showed that browsing usually reduced overall vegetation density, particularly more palatable larger leaved species, and that small-leaved plants, ferns and ground-layer monocotyledonous plants often increased dominance. This in turn led to a significantly lower C:N ratio inside exclosure plots compared to paired control plots. Despite this, there was no consistent effect on microbes or microfauna. Although there was evidence that the removal of browsing led to an increase in mesofaunal and macrofaunal groups, there was no significant relationship between the magnitude of vegetation compositional shifts and the abundance of any soil biota. They concluded that browsing mammals have generally had predictable effects on the above-ground flora but that effects on the soil fauna were inconsistent among different sites. In conclusion, Wardle et al. (2001) suggest that deer impacts can cause fundamental changes at an ecosystem level that are difficult to predict.

1.4.8 Summary of deer impacts on New Zealand Nothofagus forests

This review has shown some general themes of deer impacts on *Nothofagus* forests. Firstly, selective browsing by deer has consistently shifted the composition of forest understories towards browse-resistant or browse-tolerant species. Species that have been identified as palatable to deer (e.g. *Griselinia littoralis*, *Pseudopanax arboreus* and *Raukaua simplex*) disappeared or reduced in abundance as seedlings, which has provided opportunities for less palatable and often slower-growing plant species (e.g. *Coprosma 'taylorae'*, *Neomyrtus pedunculatus, Phyllocladus alpinus* and *Pseudowintera colorata*) to increase in abundance. Most of these changes occurred within several decades of deer colonising an area. This PhD study will examine the influence of deer on ongoing changes in Kaimanawa beech forest composition in the post-irruptive phase of deer colonisation. Secondly, there is evidence of widespread impacts of browsing on *Nothofagus* canopy regeneration only in a few instances, and only when deer appeared to be at moderate- to high-abundance. This PhD will examine the effect of deer on mountain beech regeneration in the Kaimanawa Region in detail, and make comparisons with other New Zealand regions. Finally, deer appear to have the potential to adversely affect ecosystem processes through permanent shifts in competitive advantage. The relationships between the effects of browsing on mountain beech demographics and competition from other plant species will be determined by two experiments.

1.5 Plant competition, herbivory and resource availability

Understanding plant competition is paramount to developing predictive theory for vegetation dynamics, and to better understand interactions between herbivores and plant communities. A plant's performance, and its ability to compete with other plants, is influenced by its ability to adapt to its environment and to protect itself from herbivory. This section will review key studies on the relationship between plant competition and species richness, herbivory and site productivity. Potential site productivity can be measured by the availability of resources at that site, which is often closely associated with growth rates of individual plants and plant community biomass. Review of these relationships provides an important background to the quantitative parts of this PhD study. Variability in the intensity of deer impacts, and light and nutrient availability, are both likely to be important issues when determining the relative competitive abilities of plant species in Kaimanawa Region forests. Deer impacts in these *Nothofagus*-dominated forests may also vary with understorey community composition, species richness and site productivity.

Herbivores provide a common source of disturbance so the effects of herbivory can be closely related to theoretical studies of disturbance. According to the intermediate disturbance hypothesis (Connell 1978; Huston 1979) species richness reaches a maximum level at 'intermediate' levels of disturbance. Studies that have tested the hypothesis in the context of herbivory have shown that intermediate levels of disturbance created by herbivores lead to high species richness (e.g. rabbits: Zeevalking and Fresco 1979; periwinkles: Lubchenco 1978). In the U.S.A., moderate levels of grazing by cattle and bison increased plant diversity in grasslands (Collins 1987, Collins et al. 1998, Hartnett et al. 1996; Biondini, Patton and Nyren 1998; Milchunas, Lauenroth and Chapman 1990, 1992; Hart, 2001). Under very heavy grazing, diversity decreased on mixed-grass prairie (Biondini, Patton and Nyren 1998). Unfortunately, the hypothesis is potentially self-fulfilling because identification of the level of maximum species richness is often used to identify a medium level of disturbance. Defining a medium level of disturbance independent of the effects of disturbance is very difficult because different processes leading to increased species richness are often confounded at disturbed sites. Interpretations in such studies should be made with caution because different mechanisms (resource availability or decreases in inhibition from dominant species) may produce the effect of increased species richness.

Many authors relate plant species richness to the intensity of plant competition, associated with gradients of productivity (Wardle 2002). However, the ongoing debate on the intensity of plant competition along gradients of productivity and resource availability is still not resolved (Goldberg and Novoplansky 1997). This may be because of the complexity of relationships among species in communities, and the idiosyncratic relationships between productivity, resource availability and competition intensity in different habitats. Herbivory is also likely to influence species richness and primary productivity, but is not usually considered in studies considering influences on competition intensity. Grime (1973 and 1979) hypothesised that while competition is important at highly productive sites, it declines substantially at unproductive (or stressful) sites. This is because where plant biomass is limited by any environmental stress or a single limiting nutrient (including water), generally all nutrient requirements are low. This hypothesis has been supported by studies showing that unproductive environments are better suited to plants that have low capability to withstand competitive interactions, but a strong ability to withstand periods of low resource availability (Grime 1973). This in turn leads to increases in plant competition with increasing resource availability. Davis, Wrage and Reich (1998) explain the theory in terms of trade-offs in plant adaptation to competition, stress and disturbance (CSR hypothesis). In a contrasting school of thought, Tilman (1982, 1988) argued that the intensity of plant competition remains constant along fertility gradients, and only that its nature changes. Under this hypothesis, plant competition shifts from primarily below-ground for soil resources to more limited by competition for light as the availability of soil nutrients increases. Wilson and Tilman (1991) further developed the theory to suggest that the competitive ability of each plant species will be optimised for a particular ratio of nutrient-to-light availability. They tested competition intensity in a Minnesota old field and showed that above-ground competition was more important in fertilised treatments. Using similar reasoning, Newman (1973) had earlier predicted that plants will compete for light to the point of exclusion, but that competition for below-ground resources would not have the same effect. Aarssen and Epp (1990) argued that plants dominant at unproductive environments were superior competitors in this situation and therefore supported the "competition importance" hypothesis.

Grace (1995) has shown that the differences in the development of these hypotheses is due, in part, to the different use of relative and absolute definitions of competition intensity. Absolute measures of plant competition have bias because there is potential for greater growth rates at sites with high nutrient availability. Grace (1995) proposed that relative measures of competition should be used to overcome this problem. A further problem with the debate is that site productivity is not solely dictated by resource availability, yet some studies only address productivity (e.g. Grime 1973) and others only resource availability (e.g. Wilson and Tilman 1991). This means that contrasts between studies on gradients of productivity and resource availability should be made with caution.

The debate on the relationships between habitat productivity and plant species richness is similarly polarised (Wardle et al. 2000). Some authors support a positive linear relationship between productivity and species richness (e.g. Gurevitch and Unnasch 1989; Goldberg 1994), while others have shown where productivity reaches high levels, species richness begins to decline, forming a humpbacked curve. Grime (1979) interprets this as competitive exclusion at higher levels of nutrient availability. In an island archipelago study in Swedish boreal forest, Wardle et al. (1997) showed that plant species diversity was highest on larger, more frequently disturbed islands. Huston (1997) concluded that most studies on the relationship between productivity and species diversity do not provide evidence that increasing biodiversity improves ecosystem function.

Spatial scale is a critical factor underpinning the relationship between species diversity and productivity, which many studies have overlooked (Chase and Leibold 2002). In a study of aquatic species diversity Chase and Leibold (2002) showed that at a local, but not regional, scale there was a humpbacked (quadratic) relationship between productivity and aquatic species diversity. At the regional scale the relationship was linear. They also questioned if there is a temporal, as well as spatial, dependence for the relationship.

In conclusion, the relationship between species diversity, site productivity, resource availability and plant competition is still unclear across a variety of habitats. When the potential effects of herbivory are considered, the problem of understanding the mechanisms underlying species diversity becomes even more complex. Some authors consider that herbivory may be more important than plant competition in determining the diversity and composition of plant communities (Hulme 1996a). Consideration of herbivory may be a key to resolving the debates on changes in plant species richness and relative competition intensity along gradients of productivity and resource availability, because the intensity of herbivory is also likely to vary with productivity, and so act as a confounding factor.

Competition for resources with other plants, and the influence of herbivory, are the two main biotic stresses that plants need to contend with, so it is crucial to understand the interacting effects these factors have, in order to properly understand vegetation dynamics (Crawley 1993). Plant competition can have a similar level of impact on plant growth as herbivory (Hjältén, Danell and Ericson 1993), but there is still considerable uncertainty regrading their interactive effects. Both factors directly influence plant species composition and indirectly influence soil productivity. Stark, Strömmer and Tuomi (2002) showed negative effects of herbivores on soil nutrient pools and microorganisms, which decreased plant productivity (Grellmann *In press*). Herbivores can also directly influence plant species composition, and intuitively this could also influence ecosystem processes. Onipchenko, Makarov and Van der Maarel (2001) showed that *Cyperaceae* and *Asteraceae* in the Caucasus mountains tended to reduce nitrates in soil, whereas browse-tolerant *Gramminae* reduce phosphorous concentrations in soils. Reynolds et al. (1997) showed that inherent soil characteristics related to productivty controlled species competitive performance and composition, which in turn influenced nitrate levels in a Californian grassland. This shows strong feedback mechanisms between plant communities and their environment (Wardle 2002). Chapter six will examine if the impacts of deer on mountain beech establishement and growth in the central North Island vary along natural and experimental gradients of nutrient and light availablity, and if this interacts with the effects of herbivory.

Herbivores can indirectly decelerate nitrogen cycling by decreasing the abundance of nitrogen-rich plant species (Ritchie, Tilman and Knops 1998). This often results in increases in nitrogen-poor species, which are better defended but have poorer resource quality (Augustine and McNaughton 1998), ultimately causing retardation of soil processes (Stark, Strömmer and Tuomi 2002; but see De Mazancourt and Loreau 2000). The effects of herbivores on soil processes via the above mechanisms are increasingly recognised as important in influencing plant nutrition and plant growth, resulting in strong feed-back mechanisms between above-ground and below-ground ecosystem processes (McNaughton, Ruess and Seagle 1988; Wardle 2002). Consequently when deer are excluded from a site, such as in the paired exclosure plots reported in chapter six, shifts in plant composition and nutrient availability might be expected. On a longer temporal scale, browsing mammals preferentially feed upon plant species with a higher resource quality (Coley, Bryant and Chapin 1985; Grime et al. 1996).

Crawley (1983) stated that herbivores induce shifts of relative competition between plants, but rarely induce extinction. However, many studies in New Zealand have shown that introduced deer can cause localised extinctions of palatable species in the browse tier causing possibly permanent shifts in competitive interactions (reviewed in Coomes et al. *in press*).

Research results show conflicting evidence on the nature of the relationship between site productivity, plant competition and herbivory. Several theoretical models include the simple prediction that herbivory will reduce the competitive ability of fast- growing, potentially dominant species. This theory depends on dominant species being fast-growing and spending few resources defending themselves from herbivory. However, Louda, Keeler and Holt (1990) found no conclusive evidence of a consistent relationship between a plant's competitive ability and its palatability to herbivores. Conversely, if herbivory disadvantages inferior competitors, then competitively dominant species may become more abundant (Pacala and Crawley 1992). Hairston, Smith and Slobodkin (1960) hypothesised that plant competition in communities is negatively related to herbivory. They believed that plant communities reflect a shifting balance of the effects of competition and herbivory, so that herbivore impact is greatest at high and low productivity environments and plant competition most intense at intermediate productivity sites. Van de Koppel et al. (1996) showed that geese, hares and rabbits grazed most intensively at sites of intermediate productivity at their Schiermonnikoog study site in the Netherlands; while Van der Wal et al. (2000) showed that the impact of grazing at the same study area was highest at lower productivity.

More complex theoretical models have been developed by Grover (1995) and Huisman et al. (1999) to explain interactions between plant competition and herbivory. They predict that the pressure of grazing increases with increasing productivity. Grover (1995) predicts that herbivores reduce the competitive ability of usually competitive plants and thus shift competitive advantage towards plants that can tolerate grazing. In contrast, Huisman et al. (1999) believe that competition increases with grazing pressure. Palatable plants are usually reduced in height by grazing. Therefore, unpalatable plants increase in height and compete more effectively for light. They also suggest that high grazing can lead to an increase in overall biomass, and thus an increase in competition. As an extension of Tilman's (1982) hypothesis, Tilman and Pacala (1993) treat herbivory simply as a sink for resource availability, suggesting that it will have no effect on the overall intensity of plant competition, and only shift the competitive balance of individual species. Bonser and Reader (1995) used transplanted seedlings to show that both plant competition and herbivory had greater effects at sites with relatively high biomass.

Reader (1992) cautions on the use of seedlings over established plants in studies of herbivory and competition, because of the higher sensitivity of smaller seedlings to manipulative effects. Van der Wal et al. (2000) support this observation because in their experiment of levels of herbivory, neighbour plant competition and nutrient availability results for seedlings and mature plants differed. Effects of competition were more important for seedlings of *Triglochin maritime*, whereas grazing effects were most important for mature plants. Experiments that consider the relationship between stem and root biomass need to be carefully interpreted, because Cahill (2002) showed that root extraction efficiency varies with some treatments such as fertilisation and neighbour removal. Louda, Keeler and Holt (1990) suggested that specific types of studies are required to add to the large gaps in knowledge of the relationships between herbivory and plant competition. Firstly, they suggested comparative studies of herbivory among different plant populations, sites, habitats and regions. This in turn should lead to observational studies using animal density exclusion and measurements of plant responses to limiting resources promoting the development of specific hypotheses on the mechanisms underlying observations. Finally, phenomena identified in the comparative and observational studies need to be tested experimentally. They suggested manipulations of herbivore load (decreasing and increasing herbivory), resource availability and of plant competition intensity, preferably in the long-term.

1.6 Contribution of this thesis to understanding herbivory in the Kaimanawa Region

The review of the impacts of deer on New Zealand forests has shown gaps in the understanding of the long-term effects of deer on forest composition, competitive balances and plant demography. There are also gaps in the understanding of basic relationships between herbivores and plant responses and the environment. Plant composition is likely to be directly influenced by competitive balances and adaptations to plant competition intensity, nutrient availability and tolerance and resistance to herbivory. This PhD will address some of these gaps in understanding by exploring the influences of introduced deer on plant population demographic structure and community composition in the Kaimanawa Region, particularly influences on mountain beech regeneration. I will contrast competitive balances between plant species in *Nothofagus* forests known to be browse-tolerant or browse-resistant, with other species that are more palatable to deer. Most studies that were reviewed in section 1.4 from *Nothofagus* forest showed that if deer suppressed canopy regeneration, that it was generally not on a landscape scale. Some studies on deer impacts where deer populations were near the peaks in abundance following colonisation, did conclude that there was canopy regeneration failure. This study will explore the extent of any canopy regeneration failure in the Kaimanawa Region, determine the consequences for competitive balances of any regeneration failure and test the reversibility of these impacts. Finally, I will contribute to an increasing literature on relationships between herbivory, plant competition and resource availability.

The Harkness Valley from Tussock Hut, western Kaweka Forest Park

CHAPTER TWO

Mountain beech forest composition and structure in Kaweka Forest Park

2.1 Introduction

The aim of this study is to determine the effects of intensive browsing by introduced red and sika deer on mountain beech forest regeneration and stand structure in Kaweka Forest Park. Deer browsing is capable of preventing recruitment of seedlings into saplings and trees, but the long term consequences to plants with different levels of palatability are unclear. This study relates the relative abundance of palatable and unpalatable plant species to the impacts of deer browsing using new and permanent vegetation plots and historical deer exclosure plots. These results are then examined in the context of canopy gaps identified from aerial photographs, and the characteristics of vegetation in canopy gaps.

Conspicuous mountain beech canopy collapse has been evident for many decades in Kaweka Forest Park (Elder 1962), and is part of normal stand dynamic processes where most trees die in a collapsing stand within several decades (Hosking and Hutcheson 1988). In most mountain beech forests, abundant seedling regeneration is expected at sites where canopy collapse has occurred (Wardle 1984). This is not the case in mountain beech forest in Kaweka Forest Park where mountain beech seedling abundance is very low in both canopy gaps and intact forest, and is not related to measures of stand occupancy such as basal area (Allen and Allan 1997).

Red deer reached a high population density throughout Kaweka Forest Park by 1930 before declining in abundance as food resources were depleted (Elder 1962). Sika deer were liberated in the adjacent Kaimanawa Forest Park in 1905 (Davidson 1973), but probably colonised the Kaimanawa Region (MacEwen 1987) including Kaweka Forest Park much more slowly than red deer (Elder 1962). Davidson and Fraser (1991) suggested that sika deer may have colonised as quickly as red deer but that their spread may have gone undetected due to the denser habitat that sika deer often frequent. In Kaweka Forest Park, sika deer have become predominant in abundance over red deer since the 1950's (Davidson and Fraser 1991), and may have a far greater impact on forest composition due to a digestive morphology allowing them to browse on plants unpalatable to red deer (Fraser 1996). Previous studies have speculated on replacement of mountain beech seedling regeneration with browse-resistant small-leaved shrubs and dense browse-tolerant, disturbance-resistant turf layers of indigenous herbs, grasses and bryophytes (Wardle 1979; Allen and Allan 1997). Even in moderate numbers deer could have a dramatic affect on the understorey of Kaweka forests by preventing the regeneration of palatable plants so that less competitive unpalatable species become more common. This has been observed in lower altitude Podocarp–hardwood forests (Allen, Payton, Knowlton 1984; Nugent, Fraser and Sweetapple 1997). Recent research has shown that while deer impacts hinder normal forest regeneration processes, the complexities of impacts are still inadequately understood (Nugent, Fraser and Sweetapple 1997; Wardle et al. 2001). Of greatest concern in Kaweka Forest Park is the possibility that sika deer browse on regenerating mountain, red and silver beech forests could induce canopy compositional changes or the transformation of tall forest into shrub-land (Fleury 1993).

This study analyses and interprets data from 30 permanent plots that were selected in 1994 to be representative of Kaweka Forest Park mountain beech forest from a pool of 140 plots established between 1980 and 1982 by the New Zealand Forest Service. This subset of 30 plots were re-measured in January and February 1995 and again in January and February 2001. Results from the 1995 survey have already been reported by Allen and Allan (1997). In addition: data from two paired exclosure plots; 33 systematically selected plots at low basal area sites in western Kaweka Forest Park; and aerial photographs are also used to quantify deer impacts and the extent of canopy tree breakdown. In mountain beech forest, sites with recently lowered basal area (arbitrarily defined as <25 $m^2 ha^{-1}$ by Allen and Allan 1997) typically have increased seedling abundance and growth due to the release from competition for light and nutrients (Wardle 1984). Intensive analysis of low basal area sites and aerial photographs are used to determine the proportion of sites, and their characteristics, in western Kaweka Forest Park where canopy gaps occur and where regeneration failure is evident.

Although deer are likely to have modified forest understories prior to plot establishment, further compositional changes may have occurred with the continuing presence of red and sika deer. If this were so, understorey vegetation composition in Kaweka Forest Park is most likely to have become increasingly dominated by unpalatable woody species over the past two decades, whereas in plots fenced to exclude deer, a reversal of this trend should be evident. In unfenced plots, unpalatable species would make use of lowered levels of competition if palatable sub-canopy hardwood species, and the less palatable canopy dominant mountain beech, continue to decline in abundance. This study tests the hypothesis that deer are altering age class distributions of mountain beech populations by reducing recruitment of seedlings into trees. Changes in size class structure would also be evident in mortality rates, and changes in density and basal area of mountain beech.

2.2 Methods

This study was undertaken in Kaweka Forest Park, within the Kaimanawa Ecological Region, central North Island of New Zealand (39° South, 176° East). Forests in the Kaimanawa Region are dominated by the genus *Nothofagus*: silver, red, and mountain beech. All three species have relatively fast seedling growth in high light conditions and are important colonists after disturbance (Wardle 1970a). At some sites, beech forests have been replaced by *Chionochloa*- and *Poa*-dominated grasslands with *Leptospermum scoparium*, probably due to repeated Polynesian fires (McGlone 1989). *Nothofagus* is able to grow on drier and more exposed sites than many New Zealand trees but seedlings compete relatively poorly with more shade-tolerant species (Wardle 1970b). Consequently, at higher altitude and drier sites, southern beeches (*Nothofagus*) dominate. At lower altitudes the genus gives way to more competitive hardwoods such as *Weinmannia racemosa*. In areas of low fertility, poor drainage, low moisture or areas of recent forest disturbance, southern beech may dominate (Wardle 1991).

2.2.1 Permanent plots

Between January 1980 and February 1982 the New Zealand Forest Service established series of permanent forest monitoring plots throughout Kaweka Forest Park. The methods used to establish these plots follow a protocol used to establish over 5,000 permanent plots in New Zealand (Allen 1993). Thirty of these plots were selected in 1994 for re-measurement by the Department of Conservation to assess the impact of deer browsing on mountain beech regeneration, the adequacy of canopy regeneration and changes in mountain beech forest structure (Allen and Allan 1997). Of these 30 plots, 19 had been systematically located on randomly located transect lines, 40 m from transect origins and at 200 m intervals from the origin thereafter. The remaining 11 plots were subjectively located with unknown location selection criteria. During January and February 2001, 28 of the 30 plots were re-measured using the methods described by Allen (1992) and Allen (1993). One plot could not be re-located and was not remeasured in 2001. Another plot in the eastern part of the park was re-measured in March 2000 and was included in the 2001 data set. In this study the initial survey is referred to as the 1981 survey (called 1979 survey by Allen and Allan 1997), the first re-measure as the 1995 survey and the final survey as the 2001 survey. Details of plot locations are found in Allen and Allan (1997).

2.2.2 Pellet lines

Ninety-five randomly located transect lines were established in Kaweka Forest Park in 1979 (Allen and Allan 1997) or during the summer of 1981/82 (Taylor 1999) for monitoring deer and possum faecal pellets. The origins of these pellet lines were located in watercourses and were directed to the nearest ridgetop, peak or bushline. At intervals of 20 m the presence or absence of intact deer pellets (no sign of deterioration, mould or cracking) in 114 cm radius plots was recorded using the protocol described by Baddeley (1985). No differentiation was made between red or sika deer pellets. Pellet presence rates were determined by calculating the proportion of times that deer pellets were recorded in plots on individual transect lines. Between 1998 and 2000, 56 of these transects were re-measured. This study makes comparisons between the original (termed 1981 in this study) and 1998–2000 measurements (termed 2000 in this study). Prior to pellet line establishment ground-based deer culling had occurred since at least 1958 throughout the study area up until 1988.

2.2.3 Paired exclosure plots

Paired, permanent 20 m x 20 m exclosure plots have been established in Kaweka Forest Park on the northern end of Te Puke-O-Hikarua (established 1981 at 1260–1280 m.a.s.l) in the Mangatainoka catchment along with another pair of plots near Ihaka spur in the Koaro catchment (established 1983 at 1380 m.a.s.l). The Te Puke plot was remeasured in 1982, 1984, 1988 and 1992 (Fleury 1993), but these data have been lost along with establishment data. Fortunately, Fleury (1993) provides summary statistics from these data. The Ihaka spur exclosure was established in February 1983 and re-measured in March 2000. The Te Puke exclosure was re-measured in February 2001. Data is also available from the Ruatahuna paired exclosure (established in 1983 at 1250 m.a.s.l) in western Kaimanawa Forest Park and from another paired exclosure in Rangataua Forest (established in 1984 at 1200 m.a.s.l), southern Mt Ruapehu for comparisons with nearby mountain beech forests outside of Kaweka Forest Park. Both of these 20 m x 20 m exclosure plots were remeasured in 1991 and 1998.

2.2.4 Low basal area sites in western Kaweka Forest Park

In western Kaweka Forest Park intensive sampling was undertaken in 33 low basal area stands (<25 m^2 $^{ha-1}$) in 1999, systematically selected at 40 m intervals along twelve randomly selected transect lines in stands dominated in basal area by mountain beech. This area differs from the rest of Kaweka Forest Park in that it has several fire- or frost-induced tussock valley systems, is dominated more by mountain beech as opposed to red and silver beech and has fewer alpine grassland areas. Analysis of data from these sites concentrates on comparisons among plots of mountain beech density, vegetation composition and determines what factors are common to sites with low seedling abundance.

2.2.5 Plot measurement

Permanent 20 m x 20 m plot measurement procedures follow Allen (1992 and 1993). All saplings (individual plants, but not multiple stems, > 135 cm high) were counted and species identified in the 20 m x 20 m plot. All trees (stems over 20 mm – 30 mm DBH) were identified to species and the diameter over bark at breast height measured. Unfortunately, minimum stem size definitions for trees, and therefore maximum sapling size, varied between surveys in this study. In 1981 the minimum size was 20 mm, in 1995 25 mm, and in 2001 30 mm as recommended by Allen (1993). Complicating this is the fact that 55 previously tagged stems below 30 mm were remeasured in the 2001 survey. Because trees are counted as stems and saplings as individual plants, small trees (<30 mm) from earlier surveys cannot be counted as saplings without extensive raw data manipulation, which has not been undertaken. Where possible, tree stems <30 mm DBH were excluded from analysis.

Twenty four understorey subplots (49 cm radius) were systematically located within each 20 m x 20 m plot at 5 m spacings following Allen (1993). All woody seedlings (15–135 cm high) were identified to species level and counted in four height classes (15–45 cm, 46–75 cm, 76–105 cm, 106–135 cm) in each of the subplots. For the purpose of some analyses seedling data was pooled into one height class (15–135 cm). The presence of all small seedlings (<15 cm high) was also recorded and species identified. The presence of herbaceous plants was only recorded in the <15 cm height tier. Common bryophytes and lichens were identified in the 2001 survey.

In the western Kaweka low basal area plots, counts of mountain beech seedlings were only recorded in one height class (15–135 cm) and only the presence of other species was recorded. These data were then used to produce indices of herbaceous plant, fern, and monocotyledonous plant frequency occurrence by summing the frequency of occurrence of species in these categories.

2.2.6 Problems with permanent plot data set

The Kaweka Forest Park permanent plot system cannot be assumed to be fully representative of Kaweka forests. Of the 30 plots used in this study, eleven plots were subjectively located, with unknown establishment criteria, on the eastern side of the main Kaweka range. Ninety plots were supposedly systematically established on randomly selected transect lines. Unfortunately, field crews establishing the systematically located plots on random lines during the 1980–82 survey did not adhere to the system for establishment. Plots should have been established on the true left-hand side of random transects, 40 metres from transect origin and every 200 metres from transect origin thereafter. During plot re-measurement it was apparent that plots had often been established along transects up to 60 metres from correct locations, or on the right side of transects. This seemed to have occurred at sites where vegetation or site conditions made plot establishment difficult. This has had the effect of biasing plots towards, less steep, high basal area sites with an open understorey. Because low basal area sites are very important for *Nothofagus* forest regeneration, this problem was addressed by completing a survey of a representative selection of low basal area sites in western Kaweka Forest Park in 1999 (section 2.2.4).

2.2.7 20 m x 20 m plot data analysis

Common species found in Kaweka Forest Park were rated as palatable or unpalatable to deer based on Wardle (1984) and Table 4.1. Although mountain beech has been classified as only moderately palatable to deer in some previous studies (e.g. Nugent, Fraser and Sweetapple 1997) it appears to be palatable in Kaweka Forest Park to possums (Fleury 1993) and deer (Allen and Allan 1997) so was pooled with other palatable species for analysis (Table 2.1). Changes in the abundance of these species between 1981 and 2001 were summarised. Standing dead trees were not recorded in the 1981 or 1995 surveys and are not included in analysis of the 2001 Kaweka permanent plot survey. Seedling data was comparable between all surveys in terms of height definitions but accuracy in species identification probably differed. In 1981, 135 species were recorded in the understorey, this increased to 153 in 1995 and to 241 in 2001. This increase was largely due to better identification of bryophytes and herbaceous species in later surveys, making raw understorey data incomparable. There also appeared to be considerable inconsistencies in the identification of some woody species between surveys, particularly for small-leaved shrubs. Pooling of palatable and unpalatable woody species into two classes makes data generally comparable between surveys, but statistical tests are not undertaken individually for most species, and only changes in the composition of woody species are calculated in multivariate analysis. The abundance, basal area and demographics of the easily identified mountain beech and *Griselinia littoralis* are treated separately as it is most likely that these two species were consistently identified.

Table 2.1. Classification of plant species occurring in Kaweka Forest Park by palatability to deer based on Wardle 1984, Nugent, Fraser and Sweetapple 1997 and sources cited in Table 4.1.

Unpalatable to deer	Palatable to deer
Coprosma colensoi	*Carpodetus serratus*
Coprosma "taylorae"	*Coprosma grandifolia*
Coprosma pseudocuneata	*Coprosma tenuifolia*
Dracophyllum spp.	*Fuchsia excorticata*
Myrsine divaricata	*Griselinia littoralis*
Phyllocladus alpinus	*Melicytus ramiflorus*
Podocarpus nivalis	*Nothofagus solandri* var. *cliffortioides*
Nothofagus fusca	*Pseudopanax colensoi*
Coprosma ciliata	*Raukaua simplex*
Coprosma foetidissima	
Coprosma microcarpa	
Coprosma rhamnoides	
Leucopogon fasciculatus	
Neomyrtus pedunculatus	
Podocarpus hallii	
Pseudowintera colorata	
Nothofagus menziesii	

Plot values for mean stem or plant abundance were converted to means ha^{-1} or m^2 in SYSTAT (SPSS 2000), PC-Diam (Hall 1994a) or PC-Ustorey (Hall 1994b). Statistical tests were undertaken in SYSTAT or CANOCO (Ter Braak and Smilauer 1998). For western Kaweka Forest Park low basal plots, importance values were calculated using frequency of occurrence for understorey and density ha^{-1} for overstorey and were ordinated by Detrended Correspondence Analysis (DCA). When overstorey data was analysed a minimum tree diameter of 30 mm was selected.

2.2.8 Aerial photograph analysis

In 1998, an aerial work contractor provided a series of aerial photographs covering Kaweka Forest Park *Nothofagus* forests. Photographs were taken from approximately 3,500 m without fiducial reference markings, ground reference points or camera calibration. The relatively low, inconsistent and variable altitude and position of the aircraft where photographs were taken, means that scale differs considerably depending upon ground altitude and relative aircraft height above ground. Because of this deficiency and the lack of referencing and calibration, analysis techniques available are limited (Harley Betts, Landcare Research *pers. comm.*).

Analysis of aerial photographs was used to compare canopy cover at a scale of 20 m x 20 m with altitude and aspect. A systematic 1 km x 1 km grid was placed over photographs which provided 89 points at grid intersects within western Kaweka Forest Park. The relative intactness of plots was estimated on an equal interval scale of 0–9 by using a cluster of nine points, spaced at 10 m intervals, in a grid arrangement corrected to represent 20 m x 20 m on the ground. Estimates were then made of how many of these points covered tree canopies in *Nothofagus* forest. Nine clusters (of nine points at individual plots) were spaced at 100 m and 300 m intervals from the 89 grid-intersects in a cruciform arrangement. This gave a total of 705 20 x 20 m plots indexed, with a maximum of nine plots in a cluster around each intersect point including a plot at each of the 89 grid intersects. Plots were classified as dominated by mountain beech forest (n = 137), red and silver beech forest (n = 509) or unidentifiable (n = 59) from canopy appearance in photographs after ground referencing was undertaken. A total of 22 intersects had associated plots in forest that were identified as mountain beech forest. Multiple regression analysis on the effect of altitude and aspect on canopy cover was undertaken. Grid intersects (consisting of nine clusters or plots) were included as blocking factor in the model to remove the effect of spatial auto-correlation.

2.3 Results

2.3.1 Changes in tree and seedling abundance

The abundance of trees (>30 mm DBH) classified as unpalatable, more than doubled between 1981, 1995 and 2001 surveys (Table 2.2) in 30 permanent plots. This was primarily due to increases in *Pseudowintera colorata* and small-leaved species, particularly *Coprosma colensoi*, *C. microcarpa*, *C.* "taylorae", *Myrsine divaricata*, *Phyllocladus alpinus*, *Podocarpus hallii* and *Leucopogon fasciculatus*. There was little change in the abundance of unpalatable seedlings, or palatable seedlings or trees (including mountain beech). When palatable, unpalatable and unclassified species were combined (all species) there was no substantial difference in the abundance of seedlings and trees between surveys.

Table 2.2. Mean densities of unpalatable, palatable and all tree (>3cm DBH; stems ha^{-1}±SEM) and seedling (15–135 cm high; stems m^{-2}±SEM) species.

	1981	1995	2001
Unpalatable seedlings	3.4±0.5	3.0±0.5	2.8±0.5
Palatable seedlings	1.7±0.3	1.7±0.3	1.7±0.3
Unpalatable trees	199.2±73.6	398.3±73.6	485.3±74.8
Palatable trees	1315.8±198.6	1190.8±198.6	1260.3±202.0
All seedling species	5.3±0.8	5.2±0.8	6.2±0.8
All tree species	1525.8±190.6	1623.3±190.6	1795.7±193.8

Repeated measures ANOVA showed that mountain beech seedling density did not change significantly between 1981 (1.4 stems m^{-2}), 1995 (1.6 stems m^{-2}) and 2001 (1.6 stems m^{-2}) surveys (Wilks' Lambda (γ) = 0.912, F = 1.304, df = 2,27; P = 0.288). There was a significant increase in *Griselinia littoralis* seedling (15–135 cm high) abundance between 1981 (0.002 stems m^{-2}), 1995 and 2001 (0.030 stems m^{-2}; Wilks' $\gamma = 0.799$; $F = 3.397$; df = 2, 27; $P = 0.048$).

2.3.2 Composition of woody species in the understorey

Mean DCA plot scores for woody understorey data increased significantly between 1981 and 2001 surveys for Axis 1 (1981 = 1.5, 2001 = 2.5, t = 4.077, df = 25, $P < 0.001$) and Axis 2 (1981 = 1.5, 2001 = 2.1, t = 4.695, df = 25, $P < 0.001$). Eigenvalue analysis showed that the first axis of the DCA explained 42.7% of variation in species composition between plots. Analysis of DCA species scores for woody seedling species density data (Fig. 2.1) shows that increasing axis 1 and 2 plot scores were associated with dominance of the small-leaved trees *C. ciliata, C. colensoi, C. microcarpa, Gaultheria* spp., *Myrsine divaricata, Neomyrtus pedunculatus, Phyllocladus alpinus* and *Podocarpus hallii*. This is consistent with univariate results (section 2.3.1). The unpalatable *Coprosma foetidissima* and *Pseudowintera colorata* also had high axis 1 and 2 scores so may also have increased in importance between surveys in the understorey.

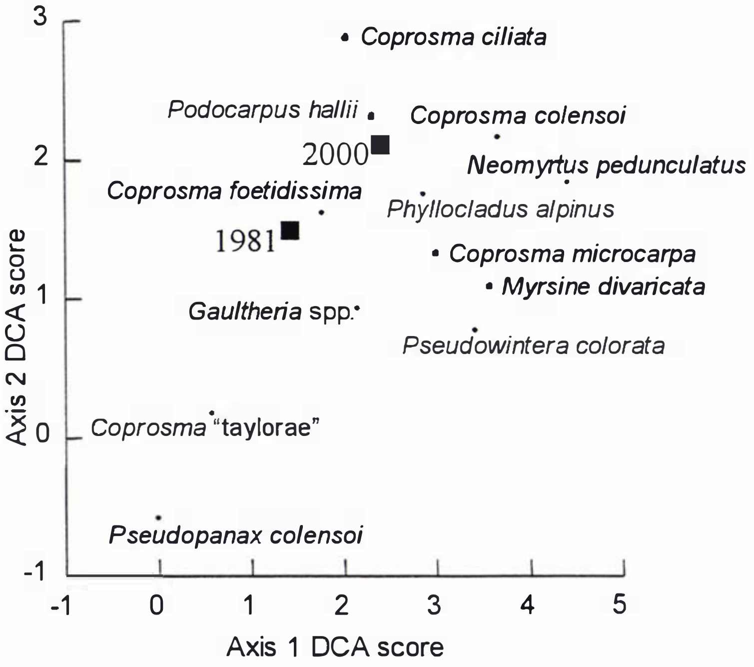

Fig. 2.1. Species scores from DCA ordination of woody seedling density in 30 permanent plots in Kaweka Forest Park measured in 1981/82, 1995 and 2001. Only species with axis weighting greater than the mean are displayed. Mean plot scores for 1981 and 2000 are also displayed (■).

2.3.3 Changes in overstorey basal area and abundance

Small-leaved, unpalatable or browse-tolerant species tended to increase in abundance between surveys (Table 2.3). *Leucopogon fasciculatus* and *Podocarpus hallii* increased by 50–60% between 1981 and 2001. *C. linariifolia, Myrsine divaricata* and *Phyllocladus alpinus* doubled in abundance, *Carpodetus serratus, C. microcarpa* and *Leptospermum scoparium* trebled in abundance between 1981 and 2001. *C. colensoi* and *C. pseudocuneata* quadrupled in abundance between 1981 and 2001. *C.* "taylorae" had increased more than tenfold by 2001. Of these species only *Phyllocladus alpinus* and *Podocarpus hallii* were relatively important (>0.5 m^2) in terms of basal area in 2001.

Podocarpus hallii appeared to increase in basal area between 1981 (0.91±0.47 and 2001 (1.37±0.65 m^2 ha^{-1}±SEM), as did *Phyllocladus alpinus* (1981 = 0.37±0.11; 2001 = 0.54±0.15 m^2 ha^{-1}±SEM). Despite the apparent increase in abundance in some plots, most of the increase in basal area of *Podocarpus hallii* was due to growth, particularly in the 5.0–9.9 cm tier (27.5%). Only 15.4% of basal area increase was due to recruitment into the 2.5–4.9 and 5.0–9.9 cm tiers. Overall, when data from all species were combined there was no significant difference in plot basal area (trees >30 mm DBH) between 1981 (41.6±2.5 m^2 ha^{-1}±SEM), 1995 (41.6±2.9 m^2 ha^{-1} ±SEM) and 2001 surveys (41.4±2.8 m^2 ha^{-1}±SEM; $F = 0.002$, df = 2, 86, $P = 0.998$).

Table 2.3. Overstorey summaries for tree stems (>20 mm DBH in 1981, >25 mm DBH in 1995 and 30 mm in 2001) in Kaweka Forest Park. Data is presented for the number of plots in which separate species are present and mean stem densities (stems ha^{-1}±SEM). Results are calculated with PC-DIAM (Hall 1994a).

	Number of plots			Density 1981	Density 1995	Density 2001
Species	1981	1995	2001	stems ha^{-1} ±SEM	stems ha^{-1} ±SEM	stems ha^{-1} ±SEM
Carpodetus serratus	3	4	5	5 ±3	13 ±8	17 ±10
Coprosma ciliata	1	3	0	3 ±3	4 ±2	
Coprosma colensoi	6	13	14	9 ±4	32 ±10	37 ±11
Coprosma foetidissima	0	1	1		4 ±4	6 ±7
Coprosma linariifolia	3	3	3	9 ±7	15 ±9	18 ±10
Coprosma microcarpa	4	10	7	15 ±9	42 ±17	45 ±23
Coprosma parviflora	2	3	0	2 ±2	10 ±8	
Coprosma pseudocuneata	4	9	5	5 ±3	40 ±19	20 ±12
Coprosma spp.	3	1	0	4 ±2	< 1 ±1	
Coprosma "taylorae"	1	4	5	2 ±2	20 ±11	23 ±11
Coprosma tenuifolia	0	1	1		< 1 ±1	< 1 ±1
Elaeocarpus hookerianus	1	1	2	< 1	< 1 ±1	1 ±1
Griselinia littoralis	18	18	17	117 ±52	98 ±45	100 ±46
Hebe stricta	0	2	2		2 ±2	3 ±3
Kunzea ericoides	0	0	1			< 1 ±1
Leptospermum scoparium	2	5	5	5 ±4	13 ±8	15 ±10
Leucopogon fasciculatus	3	3	3	10 ±6	16 ±11	16 ±10
Myrsine divaricata	7	8	9	10 ±4	22 ±9	21 ±8
Neomyrtus pedunculatus	0	1	1		< 1 ±1	< 1 ±1
N. solandri	30	30	29	1186 ±244	1121 ±184	1133 ±170
N. fusca	3	3	3	9 ±7	10 ±8	11 ±9
N. menziesii	1	2	2	< 1	3 ±2	3 ±2
Olearia spp.	1	0	0	< 1		
Phyllocladus alpinus	16	20	20	104 ±39	197 ±59	218 ±65
Podocarpus hallii	9	9	9	85 ±32	127 ±48	131 ±50
Pseudowintera colorata	3	5	4	8 ±5	15 ±8	14 ±9
Pseudopanax crassifolius	1	1	1	< 1	< 1 ±1	< 1 ±1
Raukaua simplex	8	8	8	17 ±7	15 ±6	15 ±7
Total	30	30	29	1615 ±237	1831 ±171	1860 ±157

2.3.4 Size class distribution of mountain beech seedlings, saplings and trees

A Kolmogorov-Smirnov two sample test showed no significant difference ($P = 0.333$) in plant and stem distribution within the six seedling, sapling and tree size classes of mountain beech between 1981 and 2001 surveys (Fig. 2.2). While there appeared to be a decrease in the number of seedlings 15–45 cm high, this was compensated for by increases in 46–75, 76–105 and 106–135 cm height classes and could be explained by different seedling measurement technique employed between measurements (e.g. pull-up instead of resting height) as much as any real change in seedling height class distribution. Fig. 2.2 shows that sapling abundance was much higher in the 2001 survey and this is likely to be due in part to increases in maximum seedling diameter definitions.

2.3.5 Mountain beech and Griselinia littoralis stem diameter distributions

Tree recruitment from smaller size classes and mortality rates are relatively consistent among size classes, and in every size class recruitment rates do not compensate for mortality rates (Table 2.4). This is consistent with no changes in size class distributions. Kolmogorov-Smirnov two sample tests showed no significant difference between 1981 and 1995 DBH size class distributions ($P = 0.998$), 1981 and 2001 distributions ($P = 0.998$) and 1995 and 2001 distributions ($P = 1.00$).

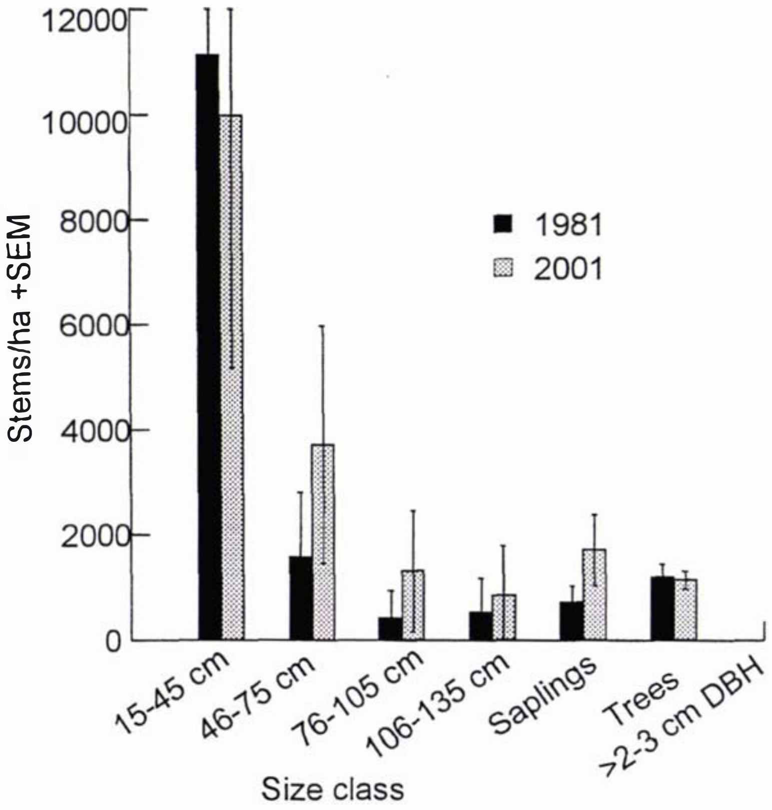

Fig. 2.2. Size class distribution of mountain beech var. *cliffortioides* seedling (15–135 cm high stems ha^{-1}), sapling (>135 cm high – <20 or <30 mm DBH stems ha^{-1}) and tree abundance (≥20 or ≥30 mm DBH stems ha^{-1}) from 30 plots measured in 1981 and 29 in 2001 (±SEM). A Kolmogorov-Smirnov two-sample test showed no significant difference between initial and final survey size class structures (P = 0.333).

Table 2.4. Recruitment and mortality of mountain beech trees (≥5cm DBH) between 1981 and 2001 calculated using PC-Diam (Hall 1994a).

DBH Class (cm)	New stems ha^{-1}	New stems (%)	Annual recruitment (%)	Dead ha^{-1}	Mortality (%)	Annual mortality (%)
5.0- 9.9	129.3	27.1%	1.3%	177.6	37.3%	2.4%
10.0- 14.9	7.8	2.5%	0.1%	87.9	28.6%	1.7%
15.0- 19.9	1.7	1.1%	<0.1%	28.4	18.6%	1.1%
20.0- 24.9	0.9	1.0%	<0.1%	18.1	21.4%	1.3%
25.0- 29.9				16.4	27.5%	1.7%
30.0- 34.9				12.1	25.5%	1.5%
35.0- 39.9				11.2	28.9%	1.8%
40.0- 44.9				6.9	23.5%	1.4%
45.0- 49.9				5.2	40.0%	2.6%
50.0- 54.9	0.9	7.10%	0.40%	1.7	14.3%	0.8%
> 55.0				6.0	33.3%	2.1%

Analysis of the highly palatable *Griselinia littoralis* shows almost a complete absence of young trees in all surveys. Of a total of 117 stems ha^{-1} of *Griselinia littoralis* recorded in the 1981 survey, only two stems ha^{-1} were under 5 cm DBH. By 2001, none of the 100 stems ha^{-1} recorded were under 5 cm DBH.

2.3.6 Altitude, plot basal area and mountain beech seedling abundance

Repeated measures ANCOVA showed that although there was no significant overall change in basal area between 1981 (41.9 m^2 ha^{-1}) and 2001 (41.4 m^2 ha^{-1} $F_{1,27} = 2.714$, $P = 0.111$) altitude did have a significant interactive effect on changes in mean plot basal area ($F_{1,27} = 5.865$, $P = 0.022$). Sites at high altitude tended to decrease in basal area, while some sites at low altitude showed a small increase (Fig. 2.3).

Comparisons of change in basal area with seedling abundance (Fig. 2.5) or change in basal area with change in seedling abundance (Fig. 2.6) may provide more useful results than comparisons of absolute abundance (Fig. 2.4).

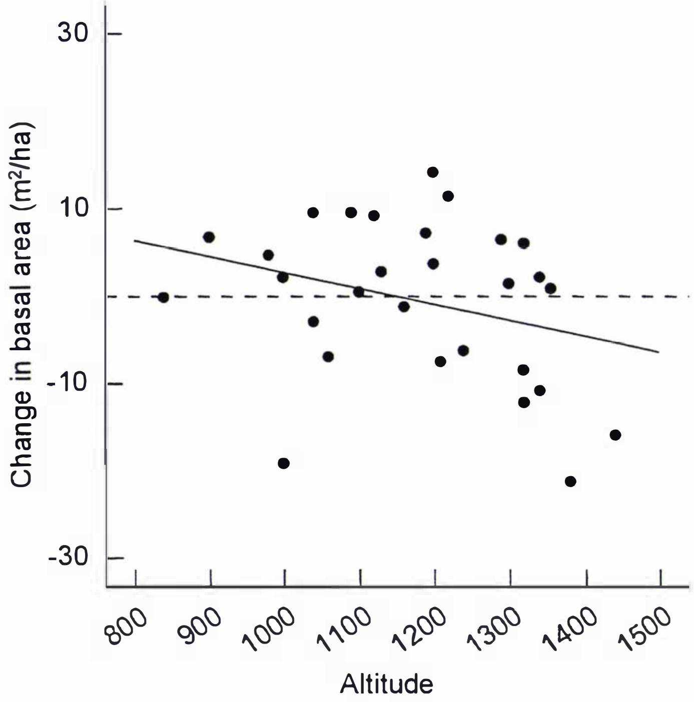

Fig. 2.3. Change in plot basal area between 1981 and 2001 against plot altitude with fitted regression line calculated in liner regression: change in basal area = 0.018*Altitude–20.9 ($R^2 = 0.180$, $F = 2.714$, $P = 0.111$).

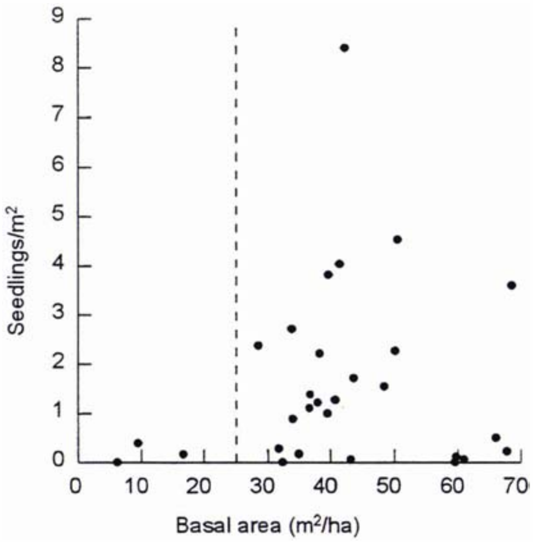

Fig. 2.4. The relationship between plot basal area and mountain beech seedling density in 2001. Regeneration is expected at low basal area sites (Wardle 1984), which were classified as < 25 m^2 ha^{-1}.

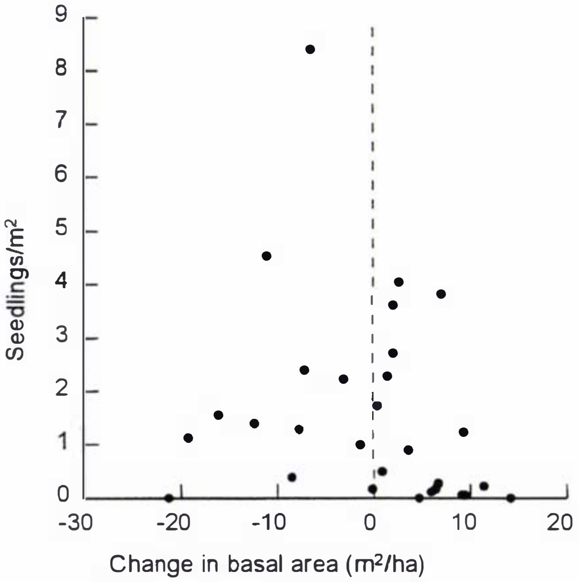

Fig. 2.5. The relationship between the change in plot basal area between 1981 and 2001 and mountain beech seedling abundance in 2001. Regeneration is expected in plots with declining basal area.

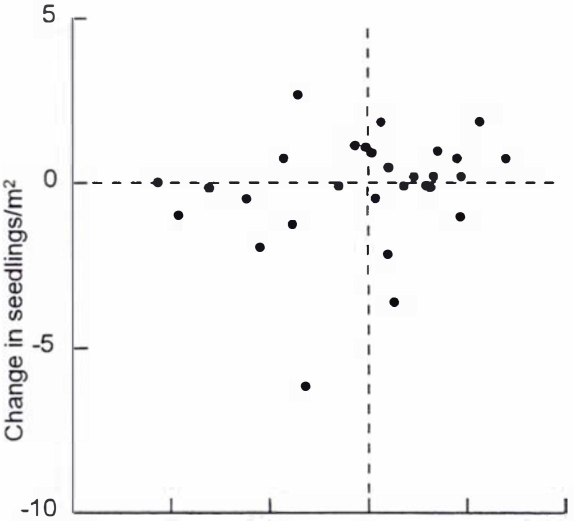

Fig. 2.6. The relationship between the change in plot basal area between 1981 and 2001 and change in mountain beech seedling abundance between 1981 and 2001. Strong negative correlation is expected between change in plot basal area and change in seedling abundance.

In mountain beech stands that have undergone disturbance events prolific regeneration is usually evident if sites are suitable. This means that low or decreasing plot basal area should be associated with high or increasing seedling abundance. Figs. 2.4, 2.5 and 2.6 show no relationship between 2001 seedling abundance and 2001 basal area (Pearson correlation $P = 0.115$), seedling abundance and change in basal area between 1981 and 2001 (Pearson correlation $P = 0.205$) or change in seedling abundance and change in basal area between 1981 and 2001 (Pearson correlation $P = 0.210$).

2.3.7 Pellet frequency of occurrence

A paired t-test showed no significant difference in deer pellet frequency of occurrence between 1981 (11.1 %) and 2000 (10.0%; $t = 0.612$, df = 55, $P = 0.543$).

2.3.8 Paired exclosure plots

Basal area at all four exclosure plot sites was initially high (46.5–74.8 m^2 ha^{-1}) and remained high (45.3–71.3 m^2 ha^{-1}) except at Te Puke where tree deaths resulted in low overstorey occupancy in both the fenced and unfenced plots in 2000 (11.2 m^2 ha^{-1}; Table 2.5). Basal area in the Ihaka spur fenced plot increased by 25% while it declined by 12% in the paired unfenced plot. This decline in basal area in the unfenced plot is explained by a single 6.5 m^2 ha^{-1} standing dead tree that was included in the 1983 data but not the 2000 data. Because original field sheets have been lost it is not possible to determine if this tree was dead or alive in 1983. The Ruatahuna fenced plot declined in basal area by 39% while there was 14% increase in the Ruatahuna unfenced plot and < 5% change in the fenced and unfenced plots at Rangataua.

Seedling abundance of mountain beech increased by over 250 times in the fenced plot at Ihaka spur between 1983 and 2000 while increasing by only 15 times in the unfenced plot (Table 2.5). At Te Puke, mountain beech seedling abundance was lower in the fenced plot compared to the unfenced plot in 2000. This can be explained by the competitive displacement of seedlings in the fenced plot by numerous saplings. Mountain beech saplings were nearly eight times more abundant in the Te Puke fenced plot compared to the unfenced plot. Fleury (1993) reported 1.1 saplings m^{-2} in the Te Puke exclosure in 1992, which increased to over 3 saplings m^{-2} in 2001. Because data has been lost it is unclear to what extent this increase is due to changes in methodology (sapling size definitions).

At Ihaka spur, saplings were also abundant in the fenced plot while not present at all in the unfenced plot. Mountain beech seedling abundance doubled in fenced plots and declined in unfenced plots at Ruatahuna. Mountain beech sapling abundance increased by 90% in the Ruatahuna fenced plot while declining in the paired unfenced plot by 80%. There were no mountain beech saplings in either the fenced or unfenced plot at Rangataua and little relative change (≈50%) in seedling abundance. In both the Ihaka spur and Te Puke exclosures, fenced and unfenced plots, small *Griselinia littoralis* seedlings (<15 cm high), were present in at least some of the seedling sub-plots in 2000. The presence was lower in the unfenced plot at Ihaka spur compared to the fenced plot and much lower in the unfenced plot at Te Puke compared to the fenced plot. Seedling (15–135 cm) abundance of *Griselinia littoralis* increased from zero to a high abundance of 2.82 stems m^{-2} in the Ihaka spur fenced plot while remaining at zero in the Ihaka spur unfenced plot. At Te Puke *Griselinia littoralis* 15–135 cm seedling density was high in the fenced plot and nearly eight times lower in the unfenced plot. *Griselinia littoralis* was present as seedlings in the Ruatahuna fenced seedling sub-plots and not present in the paired unfenced plot or at Rangataua.

Table 2.5. Plot basal area, and mountain beech and *Griselinia littoralis* seedling and sapling density (stems m^{-2}) in Ruatahuna, Rangataua, Ihaka spur and Te Puke paired exclosure plots from initial and final surveys (Ruatahuna: 1983 and 1998; Rangataua: 1984 and 1998; Ihaka: 1983 and 2000; Te Puke: 1981 and 2000). Raw data from Te Puke exclosure measures from 1981, 1982, 1984, 1988 and 1992 could not be found and are presumed lost. Data summaries for the initial Te Puke measurement were obtained from Fleury (1993). Original seedling sub-plot markers were removed from the Te Puke site between 1981 and 1982 by vandals, so were relocated for subsequent measures.

	Ruatahuna fenced	Ruatahuna unfenced	Rangataua fenced	Rangataua unfenced	Ihaka fenced	Ihaka unfenced	Te Puke fenced	Te Puke unfenced
Basal area initial (m^2 ha^{-1})	74.8	51.4	68.0	58.0	49.1	54.4	59.7	46.5
Basal area final (m^2 ha^{-1})	45.3	54.1	71.3	67.2	61.6	45.5	11.2	11.2
mountain beech basal area initial (m^2 ha^{-1})	69.6	37.3	68.0	58.0	49.0	54.4	59.4	46.5
mountain beech basal area final (m^2 ha^{-1})	37.9	40.2	71.3	67.2	58.0	39.0	11.2	11.1
mountain beech seedlings initial (stems m^{-2})	0.83	0.55	0.44	1.05	0.06	0.39	0.66	0.22
mountain beech seedlings final (stems m^{-2})	1.58	0.11	0.66	0.44	15.03	6.08	0.22	0.33
mountain beech saplings initial (stems m^{-2})	<0.01	0.05	<0.01	<0.01	0.0	<0.01	0.0	0.0
mountain beech saplings final (stems m^{-2})	0.12	0.02	<0.01	<0.01	3.15	<0.01	3.14	0.41
Griselinia littoralis seedlings initial (stems m^{-2})	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	–	–
Griselinia littoralis seedlings final (stems m^{-2})	2.84	<0.01	<0.01	<0.01	2.82	<0.01	0.6	0.0
Griselinia littoralis seedlings % <15 cm presence final	76.2	83.3	<0.01	4.2	79.2	50.0	41.7	8.3

2.3.9 Western Kaweka Forest Park low basal area sites

Only four seedling and sapling species were common at low basal area sites in western Kaweka Forest Park in 1999 (Table 2.6). These species were also important in a DCA summarising relationships between species in the understorey. Separate DCAs were used to summarise overstorey density (trees >3 cm DBH) and understorey frequency of occurrence (seedlings 15–135 cm) data to calculate DCA importance values. All vascular species other than mountain beech in the understorey were included in the analysis. An index of tree and shrub species abundance (including *C.* "taylorae", *Myrsine divaricata* and *C. microcarpa*) was positively associated with mountain beech seedling abundance in multiple regression (Table 2.7, Fig. 2.7). The same multiple regression found no relationship between mountain beech seedling density and understorey and overstorey DCA axis 1 and 2 scores, indices of herbaceous plant, fern, and monocotyledonous plant abundance, and altitude, aspect, slope and basal area. Other pairwise relationships may exist but these other variables gave no additional predictive power.

Table 2.6. Common (>0.05 stems m^{-2}) seedling and sapling species at low basal area sites (<25 m^2 ha^{-1}) in western Kaweka Forest Park.

Species	Seedling density (stems m^{-2}±SEM)	Sapling density (stems m^{-2}±SEM)
Coprosma "taylorae"	0.5±0.1	0.3±<0.1
Myrsine divaricata	0.3±0.1	0.1±<0.1
mountain beech	0.3±0.2	0.1±0.1
Coprosma microcarpa	0.1±0.1	<0.1±<0.1

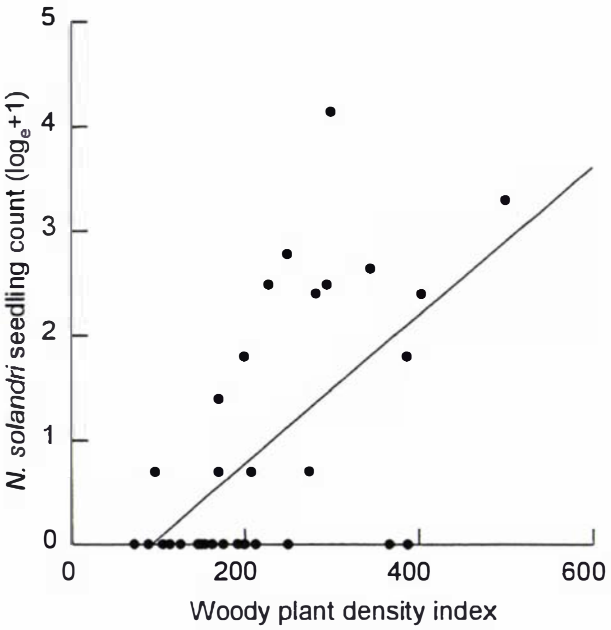

Fig. 2.7. The relationship between mountain beech seedling density and an index of tree and shrub seedling abundance (sum of % frequency occurrence of shrub species in 24 subplots from each plots) from 33 low basal (<25 m^2 ha^{-1}) area plots in western Kaweka Forest Park with a fitted regression line (mountain beech density = 0.007 x plant occurrence–0.648; R^2 = 0.3630, F = 17.671, df = 31, p<0.001).

Table 2.7. Results of multiple regression of factors influencing mountain beech seedling abundance (15–135 cm high stems ha^{-1} in 24 subplots) using a forward stepwise procedure with $P = 0.15$ to include and $P = 0.15$ exclude on 33 low basal area 20 m x 20 m plots (<25 m^2 ha^{-1}) in western Kaweka Forest Park.

Effect	Coefficient	*F*	*P*
In:			
Tree and shrub seedling abundance index	0.006	15.271	0.001
Out:			
Understorey DCA Axis 2	1.036	2.914	0.100
Overstorey DCA Axis 2	0.151	0.581	0.453
Herb index	0.085	0.182	0.674
Fern index	0.206	1.103	0.304
Monocot index	0.011	3.784	0.063
Understorey DCA Axis 1	0.190	0.932	0.344
Overstorey DCA Axis 1	-0.118	0.355	0.557
Altitude	0.204	1.085	0.307
Aspect	0.057	0.082	0.776
Slope	-0.161	0.668	0.421
Basal area	-0.194	0.982	0.331

2.3.10 Aerial photograph analysis

Multiple regression showed a statistically significant but weak relationships between altitude and aspect with canopy cover indexed on a 0–9 scale (Table 2.8; Figs. 2.8 and 2.9). Canopy cover declined with altitude, but with large variability. Graphical examination does not reveal a clear relationship between canopy cover and aspect. The effect of grid intercept was much stronger which shows a high level of clustering of stands with similar canopy cover scores around individual intersects. Most stands (62%) had high scores (>6) for canopy cover, 29.2% had scores from 3–6, and 8.8% had scores <3 (Fig. 2.10). This shows that intact canopies on a 20 m x 20 m scale are common in western

Kaweka Forest Park and that aerial photograph results are consistent with permanent plot data where three of thirty plots had low (<25 m^2 ha^{-1}) values for basal area.

Table 2.8. Results of multiple regression of intersect (clusters of stands), altitude and aspect on canopy cover scores at 136 20 m x 20 m stands identified from aerial photographs in western Kaweka Forest Park.

Effect	Coefficient	*P*
Constant	43.195	<0.001
Intersect (blocking)	-0.886	0.001
Altitude	-0.031	<0.001
Aspect	-0.126	<0.001
Intersect*altitude	0.001	0.002
Intersect*aspect	0.003	0.001
Altitude*aspect	<0.001	<0.001
Altitude*intersect*aspect	<0.001	0.001

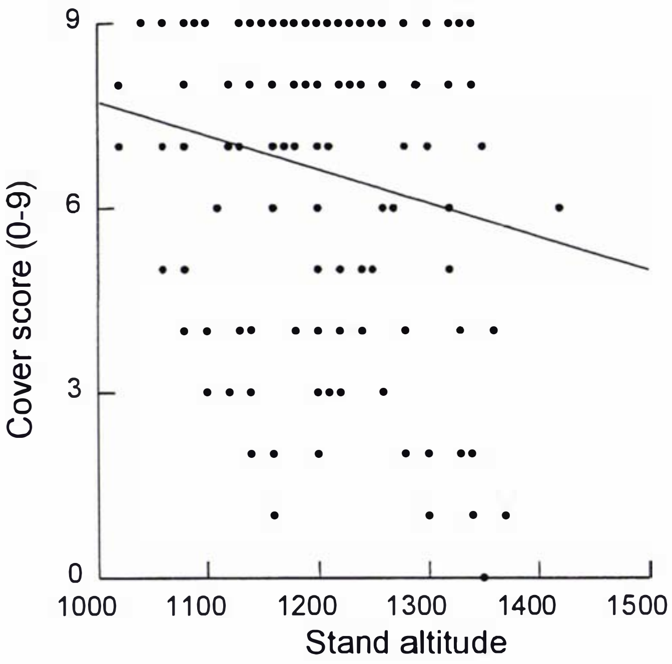

Fig. 2.8. The relationship between stand altitude and canopy cover scores for systematically located 20 m x 20 m stands on aerial photographs with a fitted line calculated in linear regression (Gap score = 13.201–Altitude x 0.005; R^2 = 0.033, F = 4.636, df= 135, P = 0.033).

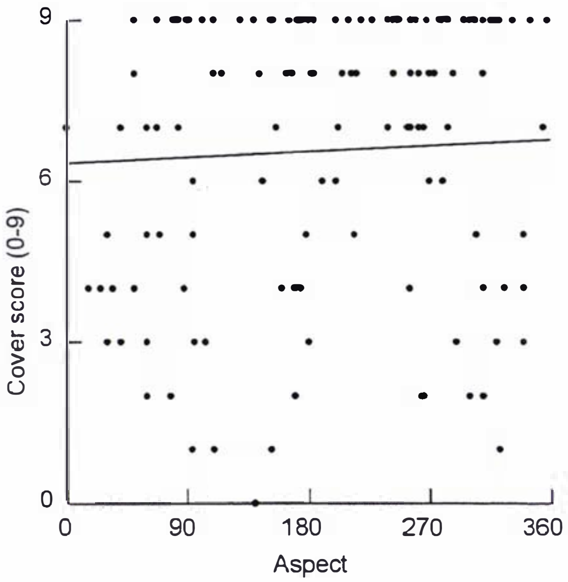

Fig. 2.9. The relationship between stand aspect and canopy cover scores for systematically located 20 m x 20 m stands on aerial photographs with a fitted regression line.

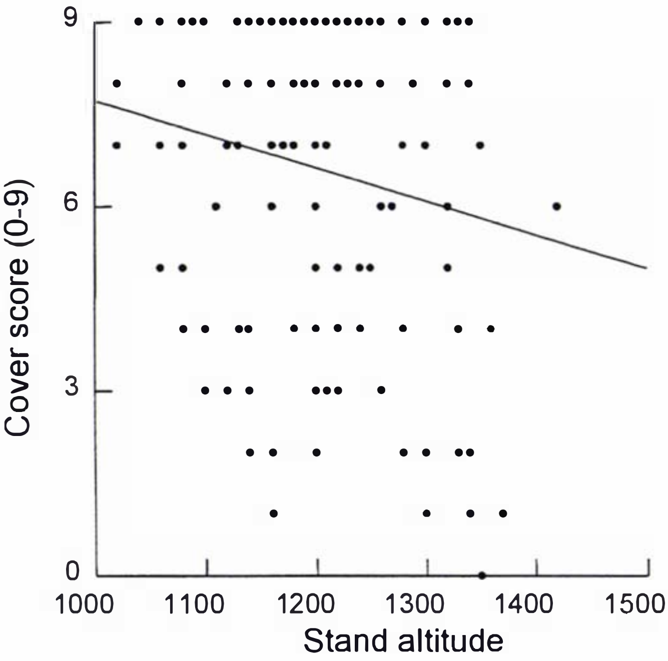

Fig. 2.8. The relationship between stand altitude and canopy cover scores for systematically located 20 m x 20 m stands on aerial photographs with a fitted line calculated in linear regression (Gap score = 13.201–Altitude x 0.005; $R^2 = 0.033$, $F = 4.636$, df = 135, $P = 0.033$).

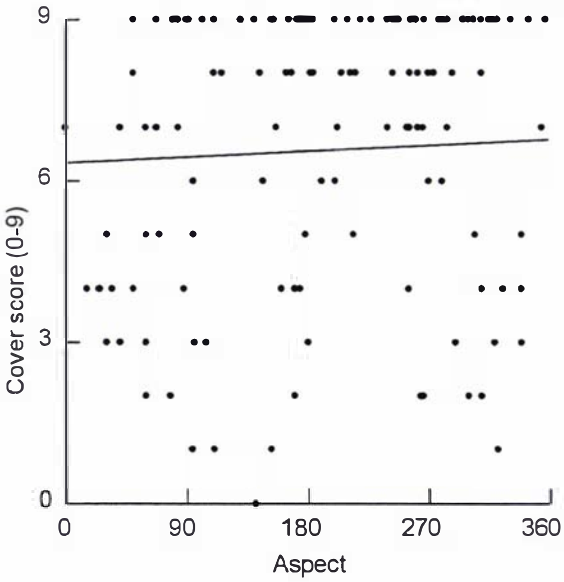

Fig. 2.9. The relationship between stand aspect and canopy cover scores for systematically located 20 m x 20 m stands on aerial photographs with a fitted regression line.

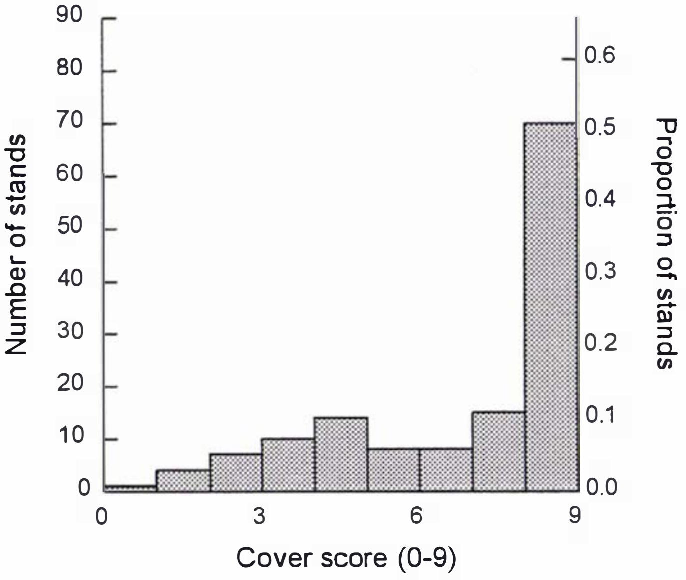

Fig. 2.10. Frequency occurrence of cover scores (0–9) estimated from aerial photographs of 20 m x 20 m mountain beech stands in western Kaweka Forest Park.

2.4 Discussion

This study shows that mountain beech forest in Kaweka Forest Park has retained its overall tree size-class structure, density and abundance over the past two decades. This is despite evidence of a lack of a regenerative response of the canopy dominant mountain beech in low basal area sites, and evidence of tree mortality exceeding recruitment. There is evidence from 20 m x 20 m plots and aerial photographs of the presence of canopy gaps, which should have created opportunities for mountain beech seedling regeneration (Osawa and Allen 1993; Harcombe et al. 1998). Instead, sites with low basal area were dominated by browse-resistant and browse-tolerant small leaved shrubs (*C. microcarpa*, *C.* "taylorae" and *Myrsine divaricata*) as seedlings and saplings. There is also evidence of an overall increase in abundance of tree species unpalatable to deer.

Of unpalatable tree species that increased in abundance only two (*Podocarpus hallii* and *Phyllocladus alpinus*) increased in basal area and were both relatively important in terms of occupancy (basal area >0.5 m^2). These results are similar to those of Allen and Allan (1997) who found that *Podocarpus hallii* and *Phyllocladus alpinus* increased in basal area and abundance between 1981 and 1995 in Kaweka Forest Park. Other unpalatable species that increased in abundance in the overstorey, such as *C. microcarpa*, *C. pseudocuneata*, *C.* "taylorae", *Leucopogon fasciculatus, Leptospermum scoparium* and *Myrsine divaricata*, were unimportant in terms of basal area compared to the canopy dominants. These small-leaved, unpalatable species increased in abundance as trees by between two- and ten-fold from 1981 to 2001, but these increases had little effect on overall basal area, which did not change significantly. This contradicts Allen and Allan's (1997) results which showed an overall decline in basal area in Kaweka Forest Park of 2.5% from 42 m^2 ha^{-1} to 41 m^2 ha^{-1} between 1981 and 1995. In their study, the reported decline may have been due in part to an increase in minimum tree size definition from $\geq$20 to $\geq$25 mm rather than real declines in basal area. There was no overall change in seedling or tree density between permanent plot surveys found in this study. This also contradicts Allen and Allan's (1997) results, which showed a small overall increase in stem density.

While there is evidence of compositional shifts towards less deer-palatable species in the overstorey in Kaweka mountain beech forest, changes are slow compared to red and silver beech forests at lower altitudes in nearby Kaimanawa Forest Park (chapter four), and did not have the same effect on overall composition. In the northern Kaimanawa red and silver beech forests, compositional shifts in the overstorey (trees $\geq$2 cm DBH) from deer-palatable towards deer-unpalatable species were found. Results from two paired exclosure plots in Kaimanawa Forest Park supported conclusions that deer browse is inducing shifts in understorey composition that is beginning to influence overstorey composition in Kaimanawa red and silver beech forest. A similar situation is likely to exist in Kaweka Forest Park red and silver beech forest. Unfortunately, data from Kaweka Forest Park red and silver beech forest permanent plots needs considerable error correction before would be of a satisfactory standard to make comparisons between 1981 and 1999 data sets (SWH personal observation).

Changes in the composition of woody species in Kaweka Forest Park understorey between 1981 and 2001 were detected. Detrended Correspondence Analysis (DCA) scores showed significant compositional shifts in the abundance of woody understorey species and explained most of the variation in species composition in the understorey overall. This analysis should be treated with caution: changes could be explained by the appearance of unimportant species in a few plots or changes in species identification (e.g. small leaved *Coprosma* spp., *Podocarpus* spp.) as much as any real change in understorey composition.

Results from Ihaka spur, Te Puke (eastern and western Kaweka) and Ruatahuna (western Kaimanawa) exclosure plots show that deer have largely prevented *Griselinia littoralis* and mountain beech from growing into the seedling or sapling tier at these sites over the past two decades, except where deer were excluded by fences. At all three sites ephemeral *Griselinia littoralis* and mountain beech seedlings (<15 cm high) were present so a lack of seed source is unlikely to explain differences in seedling abundance between fenced and unfenced plots. There was a substantial difference in the more palatable *Griselinia littoralis* between fenced and unfenced plots and this species did not appear to be successfully regenerating outside of the fenced plots in Kaweka Forest Park. The continued existence of *Griselinia littoralis* at these sites and throughout Kaweka Forest Park appears to be due to its longevity, as its regeneration appears to be severely effected by deer browse. Eventually, without a substantial increase in regeneration, this species will become uncommon in Kaweka Forest Park except at sites inaccessible to deer, and may be reliant upon epiphytic regeneration. At a high basal area site in Rangataua Forest, southern Ruapehu, where red deer are common but sika deer are only in the initial phases of colonisation, there was much less difference in the abundance of mountain beech seedlings inside and outside of the exclosure fence in comparison to the paired exclosure plots in Kaimanawa and Kaweka Forest Parks where sika deer are common. This suggests that sika deer are capable of having higher impacts on mountain beech regeneration than red deer.

In chapter three I compare mountain beech regeneration within the Kaimanawa region with four regions without sika deer, which supports this conclusion. In chapter five I also show that once deer browsing was removed through exclosure fencing or intensive aerial hunting that mountain beech seedling growth increased and chapter six shows that deer browsing also prevented the establishment of mountain beech seedlings at some sites. There may be other factors responsible for poor mountain beech seedling growth and establishment such as competition with other plants. Chapter six shows that dense turf communities present in the Kaimanawa Ecological Region were also capable of slowing seedling growth. Allen and Allan (1997) found unexpectedly low seedling and sapling abundance in plots with low basal area in Kaweka Forest Park and concluded that this was an indication of inadequate regeneration.

The main evidence in this study for deer impeding gap-phase canopy regeneration is the low seedling abundance of mountain beech in comparison to small-leaved shrubs at unfenced low basal area sites. This evidence, while being consistent with deer impeding forest canopy regeneration, by itself is circumstantial. Although other factors such as normal successional processes, and other herbivores such as possums and hares, cannot be discounted without data from replicated exclosure plots, comparisons with other areas, or from experimental manipulations there are several lines of evidence to support a conclusion that deer browsing is preventing canopy regeneration. This study showed no relationship between densities (and changes in densities) of seedling abundance with basal area (and changes in basal area). These results, along with the two exclosure plot results, provide evidence that there was a poor response of mountain beech seedlings at low basal area sites up to 2001. Without data on the site-specific growth, density dependence, mortality and recruitment of individual seedlings, and the potential of the site to support mountain beech forest, it is difficult to determine the scale at which regeneration is impeded in Kaweka Forest Park. Given the very low mountain beech seedling abundance throughout Kaweka mountain beech forest it is probable that deer are preventing maintenance of a forest canopy at most sites where canopy opening has occurred, but this needs further investigation to confirm. The lack of change in mountain beech seedling, sapling and tree abundance, basal area and overall size class structure between permanent plot measurements does not necessarily indicate that deer impacts are negligible, only that they have probably remained relatively constant over the past two decades. This is consistent with results from pellet data that show that deer numbers have remained similar over the same time.

Aerial photograph analysis showed that only *c.* 10% of plots had canopy gaps at a 20 x 20 m scale. These gaps were only weakly predicted by plot altitude and aspect. This estimate of gap occurrence is consistent with permanent plot data where only three of thirty sites had very low basal area (<25 m^2 ha^{-1}). Intense sampling of low basal area sites showed that *C. microcarpa*, *C.* "taylorae", *Myrsine divaricata* and mountain beech were important species dominating understorey composition at sites with low canopy cover. The density of mountain beech seedlings was positively related to the increasing importance of shrub communities, which suggests that they were both competing for the same resources. An alternative explanation is that mountain beech seedlings were provided refuge from deer by dense stands of unpalatable shrub species. Other predictors, such as basal area, altitude, aspect, slope, and indices of plant composition and abundance were also tested at low basal area sites and showed no association with mountain beech seedling abundance. While shrub density is the best predictor of mountain beech seedling abundance, other variables are not necessarily unrelated. Low basal area does not give additional predictive power, perhaps because shrub density is a better measure of regeneration potential than basal area. I conclude the balance of evidence supports a conclusion that intense browsing by sika deer is impeding canopy regeneration in Kaweka Forest Park.

Currently re-measurements of permanent plots in Kaweka Forest Park are scheduled on a five yearly rotation. Because of the slow rates of change in Kaweka mountain beech forest five yearly re-measurements of permanent plots may be more frequent than is necessary. Even in the faster growing red and silver beech and *Weinmannia racemosa* forests a five yearly re-measurement schedule may be excessive. A ten-year time interval between re-measurements may be sufficient to maintain plots and detect changes in Kaimanawa Ecological District forest composition. If management regimes are altered, particularly if high intensity-deer culling becomes widespread, it may be necessary to re-measure permanent plots more frequently to relate accelerated changes in forest composition to changes in management. In future, properly referenced aerial and satellite photograph data could be used to help determine the spatial complexities of Kaweka forest canopy composition, canopy structure and the effects of deer. Accurate remeasurement and analysis of permanent plots in red and silver beech forest in Kaweka Forest Park would help illustrate the impacts of deer in these vegetation types, in addition to the present study of mountain beech forest.

2.5 Conclusions

This study concurs with Allen and Allan's (1997) conclusions that deer browsing is having a widespread and detrimental effect on canopy replacement in Kaweka Forest Park. At low basal area sites with very low mountain beech seedling and sapling density, canopy replacement is unlikely. Instead small-leaved shrubs may increasingly dominate. While forest in Kaweka Forest Park is largely intact, canopy gaps occur at approximately 10% of sites at the 400 m^2 scale, and appear to be in locations that are largely unpredictable in terms of site altitude and aspect.

Mountain beech seedling abundance was not related to stand basal area. Instead, mountain beech seedling abundance at low basal area sites was positively associated with some shrub species such as *Coprosma* "taylorae", *Coprosma microcarpa* and *Myrsine divaricata*. These sites are likely to have increased resource availability following tree death leading to increased mountain beech seedling abundance and growth. In most mountain beech forests mountain beech seedlings appear to out-compete other plant species at such sites, instead in Kaweka Forest Park, other woody shrub species appear to compete more successfully against mountain beech in the presence of intense herbivory by deer.

There is no evidence of any change in deer abundance during the two decades of this study. Changes in plant species composition in the understorey or overstorey are limited to increases in tree species unpalatable to deer. There was no change in the abundance or structure of mountain beech populations. These results suggest that deer and disturbance induced changes in forest structure and understorey composition still occur, and are most likely to have taken place prior to the establishment of permanent plots.

Sika deer, Oamaru Valley, northern Kaimanawa Forest Park (DOC collection)

CHAPTER THREE

Suppression of mountain beech forest regeneration is dependent on the species of introduced deer

3.1 Introduction

The aim of this study is to contrast the impacts of sika and red deer on mountain beech regeneration by comparing the abundance of mountain beech seedlings in the Kaimanawa region where there has been progressive invasion by sika deer, to four other regions in New Zealand where red, but not sika, deer are present. To allow for differences in the effects of disturbance within and among areas and regions, the effects of stand basal area on seedling density are also considered. Because sika deer are rapidly colonising many countries it is essential that impacts of sika deer on vegetation are contrasted with other deer species. This ensures impacts at newly colonised sites are more accurately predicted, and that management objectives are more successfully met.

Disturbance and regeneration are central themes in the study of forest dynamics (Pickett and White 1989) because many tree species rely on canopy tree death for regeneration. Lowering stand occupancy increases the availability of light and nutrients for seedlings, permitting regeneration in tropical and temperate hardwood forests (e.g. Canham 1988, Peterson et al. 1990, Denslow, Ellison and Sanford 1998). Despite this, few studies have considered the impacts of herbivores on canopy replacement in temperate forests within a context of stand occupancy (but see Castleberry et al. 2000, Cornett et al. 2000). This is a critical omission because herbivory may be concentrated at sites where canopy tree death has occurred (Peterson and Picket 2000). At these sites resource availability is often higher, and so nutrient and light demanding plants more common (Kelly 2002). In New Zealand, previous studies on the impacts of deer in the widespread *Nothofagus* forests have found that canopy replacement was generally not affected by deer browse (e.g. James and Wallis 1969, Wardle 1984, Stewart and Harrison 1987, Stewart, Wardle and Burrows 1987, Nugent 1988; see also Conway 1949, Wardle 1962, Jane and Pracy 1974, Jane 1986). These studies have generally not specifically considered the influence of site basal area (frequently used as measure of stand occupancy by mature beech trees; but see Wardle and Guest 1977, Allen and Allan 1997) on deer impacts on regeneration.

After repeated introductions in the 19th century, red deer reached high population densities throughout many areas in New Zealand in the first half of the 20th century (Challies 1985).

Red deer caused a rapid decline in the abundance of palatable understorey herbs and shrubs as they increased in abundance (Caughley 1983). Sika deer were liberated into the central North Island in 1905 (Davidson 1979), but colonised much more slowly than red deer (Elder 1956), which have subsequently been steadily displaced by sika (Davidson and Fraser 1991). Because of this slower rate of dispersal there is a distinct history of colonisation of mountain beech forests by sika deer, followed by competitive displacement of red deer.

The primary objective of this study was to contrast mountain beech forest dynamics between regions with red deer and regions where sika deer have displaced red deer. The intensity of impact on forest regeneration is likely to vary with the species of herbivore, although past studies in New Zealand have often not differentiated between impacts of different species of introduced ungulate (e.g. Wardle et al. 2001, Bellingham and Allan 2003). This approach assumes that where one species of ungulate is already present, subsequent introductions of other species will have no additional impact. This assumption is unlikely to be met in many instances through either competition (Murray and Illius 2000) or facilitation between different species of ungulates (Arsenault and Owen-Smith 2002). Larger forest dwelling ungulates with relatively slow digestion, such as red deer, are better adapted to high cellulose diets (grazers or mixed-feeders). In comparison, ungulates such as sika deer with small mouths, bodies and rumens are likely to be better adapted to diets high in chemicals that interfere with rumen microbial activity (browsers) such as monoterpenes and phenols (Duncan, Hartley and Iason 1994, Hanley 1997). Sika deer are thought to have the ability to browse more intensively than red deer because of a different digestive morphology (Fraser 1996) and dietary versatility (Asada and Ochiai 1996). This suggests that sika deer are likely to have higher impacts on tree and shrub species that are only moderately palatable to red deer such as mountain beech (Tables 2.1 and 4.1). Observations of rumen contents from the central North Island suggest that beech species are more commonly browsed by sika deer than red deer (Fraser 1991, Personal observation SWH).

The second objective of this study was to determine if impacts of sika deer on mountain beech regeneration varied with basal area, or with time of colonisation. Previous studies in Japan have shown that where sika deer are present in high numbers for several decades, impacts on beech *Fagus crenata* forest regeneration can be intense (Takatsuki and Gorai 1994). If impacts of sika deer over time are cumulative, New Zealand species that are palatable to sika deer such as *Griselinia littoralis* and mountain beech might remain common in recently colonised areas, but be replaced by unpalatable shrubs such as small-leaved *Coprosma* in areas with longer histories of colonisation by sika deer. I used data from recent surveys to compare mountain beech seedling abundance in relation to respective histories of sika deer colonisation from four mountain beech forest areas with different distances from the point of liberation of sika deer. Deer impacts can also vary with site productivity or availability of nutrients to plants (John and Turkington 1997, Ball, Danell and Sunesson 2000, Virtanen 2000), and this might be more important than length of time since colonisation. In Japan, sika deer favour highly productive sites (Takada, Asada and Miyashita 2002). In New Zealand southern beech forests, the lowering of basal area following disturbance increases the availability of nutrients to seedlings and saplings (Allen, Clinton and Davis 1997) thereby increasing the nutrient content of plants in the deer browse tier (Davis, Allen and Clinton 2003). This is likely to allow faster-growing, palatable plants to increase in abundance in the browse tier at low basal area sites, influencing the attractiveness of the site to deer. Therefore, impacts of deer on mountain beech seedling abundance are likely to be highest at low basal area sites.

3.2 Methods

3.2.1 Kaimanawa Region study areas and sampling approach

The Kaimanawa Mountains constitute a series of ranges in the central North Island of New Zealand (39° South, 176° East) and are characterised by high relief, with often steep valley walls, valley bottoms often less than 500 m and a high point of 1727 m in the southern Kaimanawa. The geology is predominantly Jurassic folded greywacke and soils are either derived from this bedrock or from volcanic ash and ignimbrite flow from the Taupo eruption (*c.* 1800 years BP, Wilson 1993). The landscape is dominated by indigenous, unlogged southern beech forest. Mountain beech is able to grow on drier and more exposed sites than most New Zealand trees, but seedlings compete relatively poorly in dense stands with more shade-tolerant species (Wardle 1970a). Consequently, at higher altitude (>1000 m) and drier sites, mountain beech dominates up to the treeline, while at lower altitudes the species gives way to more competitive hardwoods such as red and silver beech, and *Weinmannia racemosa* (Wardle 1991). The small-leaved shrubs *Coprosma foetidissima, C. pseudocuneata, C.* "taylorae" and *Myrsine divaricata* are important in the understorey of Kaimanawa Ecological Region (MacEwen 1987) mountain beech forests.

Throughout the Kaimanawa Region, 108 survey plots were measured on 30 randomly located transect lines between January 1999 and April 2001. The plots were located in four contiguous areas that had established populations of red deer by 1930 (Elder 1962), but with different histories of colonisation by sika deer (Fig. 3.1). Northern Kaimanawa Forest Park (F.P.; 29 plots, 8 lines) was the closest area to the liberation point and sika deer became conspicuous here in the 1930's (Davidson 1973) following likely colonisation from their liberation point via the Oamaru Valley in the late 1920's.

Sika deer probably colonised western Kaweka F.P. (34 plots, 12 lines) in the 1940's and they had displaced red deer at some sites there in the 1950's (Davidson and Fraser 1991). Western Kaimanawa F.P. (10 plots, 2 lines) was probably colonised by sika deer through open grasslands and plantation forestry between Kaimanawa F.P. and Lake Taupo in the 1960's before being more commonly observed in the early 1970's (Davidson 1973). In southern Kaimanawa F.P. (35 plots, 8 lines) sika deer only became dominant over red deer through the mid 1990's (Personal observation SWH) and so probably colonised this area in the 1980's.

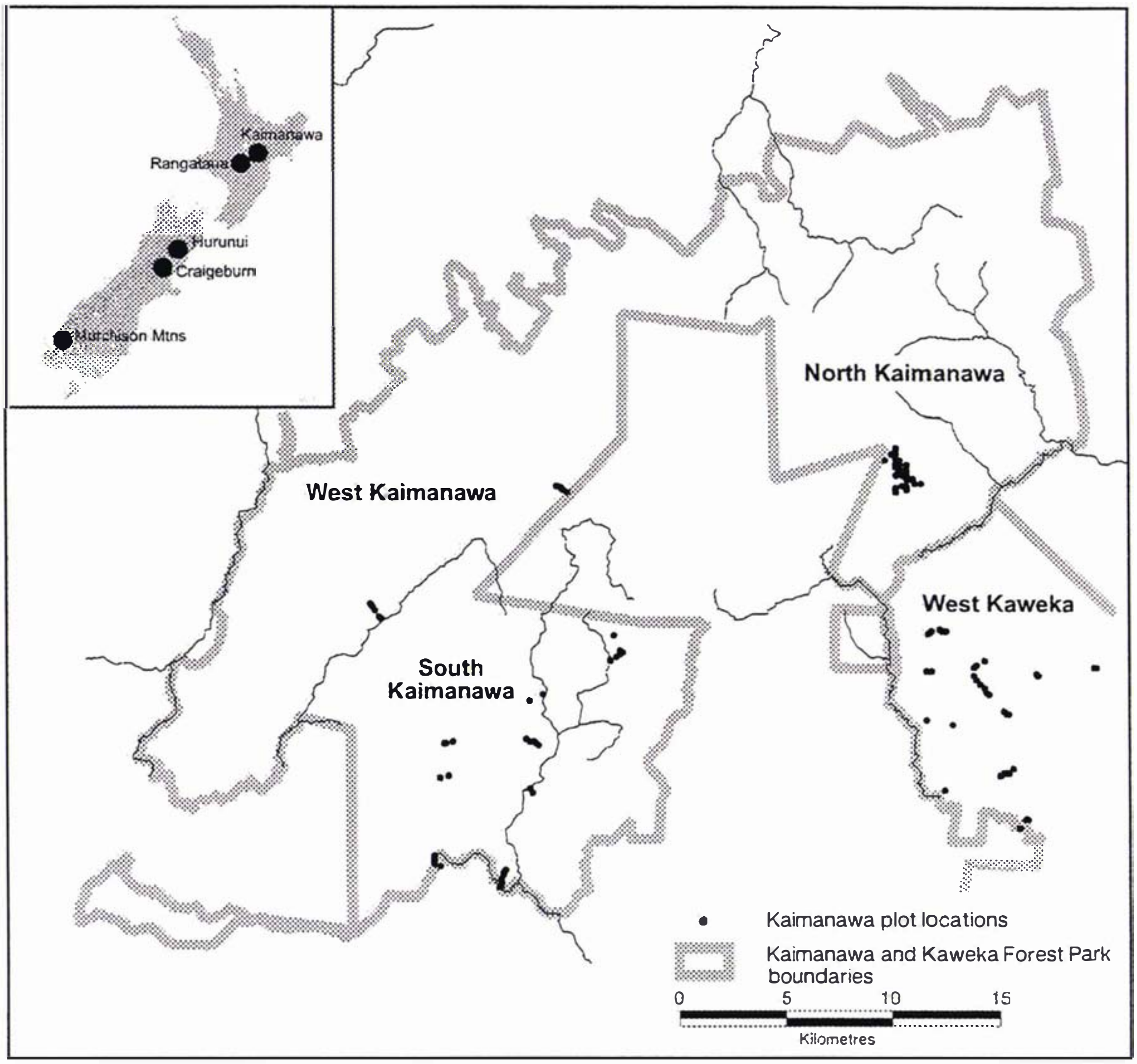

Fig. 3.1. Map of Kaimanawa Region plots on randomly selected transect locations. Inset are New Zealand's North and South Islands showing study areas in Kaimanawa, Rangataua, Hurunui, Craigieburn Regions and Murchison Mountains.

In all but the northern Kaimanawa F.P., lines started at randomly selected watercourses and terminated at the nearest highpoint or bushline. In northern Kaimanawa, transect origins were at randomly located points and followed randomly selected compass bearings. On each transect, plots were established 40 m from transect origins and at 200 m intervals from the origin thereafter. Only large (>100 ha) areas of mountain beech dominant forest were sampled (dominance was determined by basal area).

I searched the National Vegetation Surveys database (Wiser, Bellingham and Burrows 2001) for 20 m x 20 m plot (Allen 1993) surveys undertaken since 1998 of mountain beech forest throughout New Zealand. Data from plot measurements in four regions with no sika deer were compared to the regions colonised by sika deer. Surveys in these regions were undertaken by Landcare Research in the Craigieburn Range, Craigieburn F.P. (34 plots, 13 lines, 43° South 171° East), and by the New Zealand Department of Conservation in Rangataua Forest (13 plots, 5 lines, 39° South 175° East), Hurunui Valley, Lake Sumner F.P. (5 plots, 3 lines, 43° South 172° East), the Murchison mountains and Fiordland National Park (16 plots, 6 lines, 45° South 167° East). Surveys outside the Kaimanawa region used the same procedures for line and plot establishment as detailed below.

3.2.2 Plot measurement procedure

All eight surveys in this study used a protocol for 20 m x 20 m plot measurement described by Allen (1993) and in more detail in section 2.2.5. Briefly, in this study, for the overstorey, species of all trees >30 mm diameter over bark at breast height (DBH, 135 cm) rooted within plots were identified, and their stem diameter measured. Mountain beech seedlings were counted in the 15–135 cm height tier within twenty-four systematically located 0.49 m radius sub-plots within each plot. To summarise woody species composition in the understorey, the presence of tree and shrub (distinguished using the criteria of Poole and Adams 1994) seedlings were recorded in two height classes (<15 cm and 15–135 cm) in these sub-plots.

3.2.3 Data analysis

Data for mountain beech seedling abundance was $\log_e$ transformed to meet assumptions of ANOVA before comparisons between areas with and without sika deer were made using SYSTAT (SPSS 2000). Detrended Correspondence Analysis (DCA) in CANOCO 4.0 was used to produce plot ordination scores for under and overstorey composition (Ter Braak and Smilauer 1998). Importance values for the understorey were calculated from frequency of occurrence of seedlings (15–135 cm) in 24 sub-plots within each plot, and using relative live tree basal area for the overstorey. DCA scores, mean plot overstorey density, basal area, and understorey frequency of occurrence were compared using ANOVAs, Bonferroni-corrected for repeated measures (Sokal and Rohlf 1995). Because individual transect lines started in valley bottoms and ended at highpoints, or at treeline, there was a large variation in altitude within lines for most parameters. Hypothesis tests among areas and regions used an error term of lines nested within areas or regions, to allow for this variation and avoid pseudoreplication at the plot level.

3.3 Results

3.3.1 Contrasts between regions with and without sika deer

Mountain beech seedling abundance ($\log_e +1$) was higher in regions with no sika deer present (22,025 seedlings ha^{-1}, 24 lines 76 plots) compared to Kaimanawa Region areas where sika deer were present (664 seedlings ha^{-1}; $F_{1,51} = 18.096$, $P < 0.001$; 29 lines, 108 plots). Variation in stand occupancy between sites was allowed for by using basal area as a covariate, which had a significant effect ($F_{1,127} = 11.760$, $P = 0.001$). In regions without sika deer, linear regression showed a clear negative relationship between seedling counts and plot basal area ($F_{1,74} = 31.124$, $R^2 = 0.296$, $P < 0.001$), particularly for data from Rangataua and Craigieburn (Fig. 3.2). In contrast, the four Kaimanawa Region areas showed no such relationship ($F_{1,106} = 0.276$, $R^2 = 0.003$, $P = 0.600$; Fig. 3.3) demonstrating that seedling counts at low basal area sites where sika deer are present are particularly low in comparison to similar sites with no sika deer.

The Kaimanawa Region had lower overall basal area, mostly due to low mountain beech basal area from fewer large trees and low abundance of silver beech (Table 3.1). *Griselinia littoralis* and *Phyllocladus alpinus* had higher basal area in the Kaimanawa. For *Phyllocladus alpinus* this was due to differences in stem abundance more than the size of trees. These differences in the basal area of individual species did not result in significant differences in composition overall. Contrasts of first axis DCA scores, calculated using relative basal area, showed that there was no significant difference in overstorey composition between Kaimanawa areas with sika deer (mean score ± SEM = 0.75 ± 0.03) and regions without sika deer (mean ± SEM = 0.59 ± 0.02; $F_{1,52} = 3.002$, $P = 0.089$). Other than silver beech being more common in areas with no sika deer, there was no overall difference in tree stem density for species with >100 stems ha^{-1} between Kaimanawa and regions without sika deer.

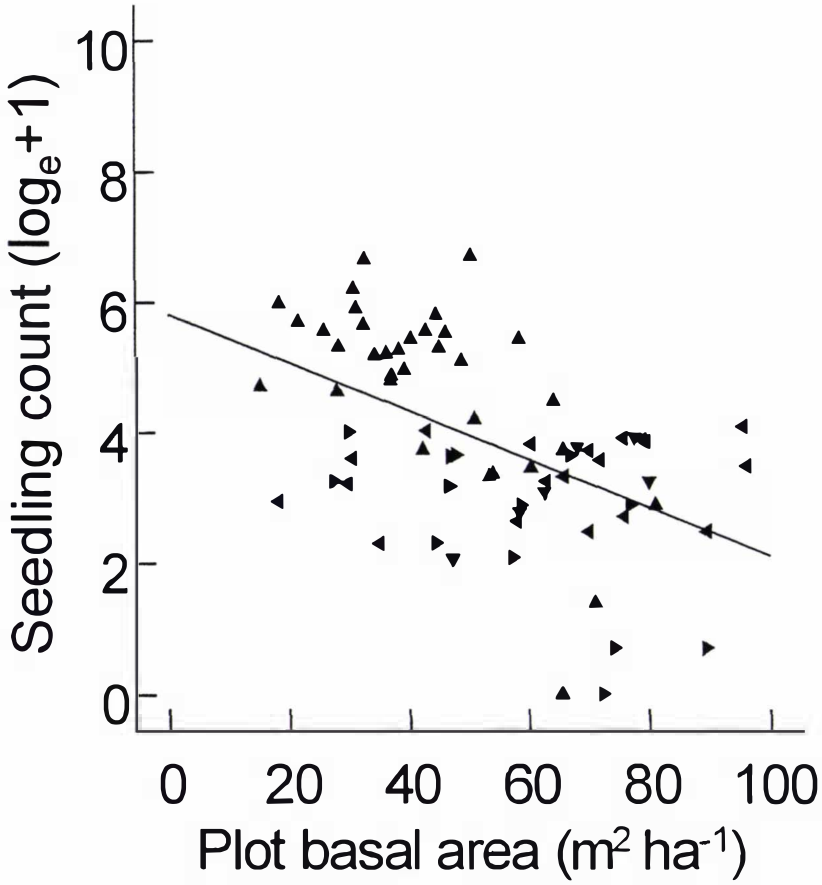

Fig. 3.2. The relationship between the number of mountain beech seedlings counted in twenty-four 0.75 m^2 subplots in each 20 m x 20 m plot ($\log_e$+1) and plot basal area (m^2 ha^{-1}) for 66 plots in five areas outside the Kaimanawa Region where sika deer are not present. These areas are Craigieburn (▲), Hurunui (▼), Murchison (◀) and Rangataua (▶). The regression equation is: seedling count ($\log_e$+1) = 5.814 – basal area x 0.037.

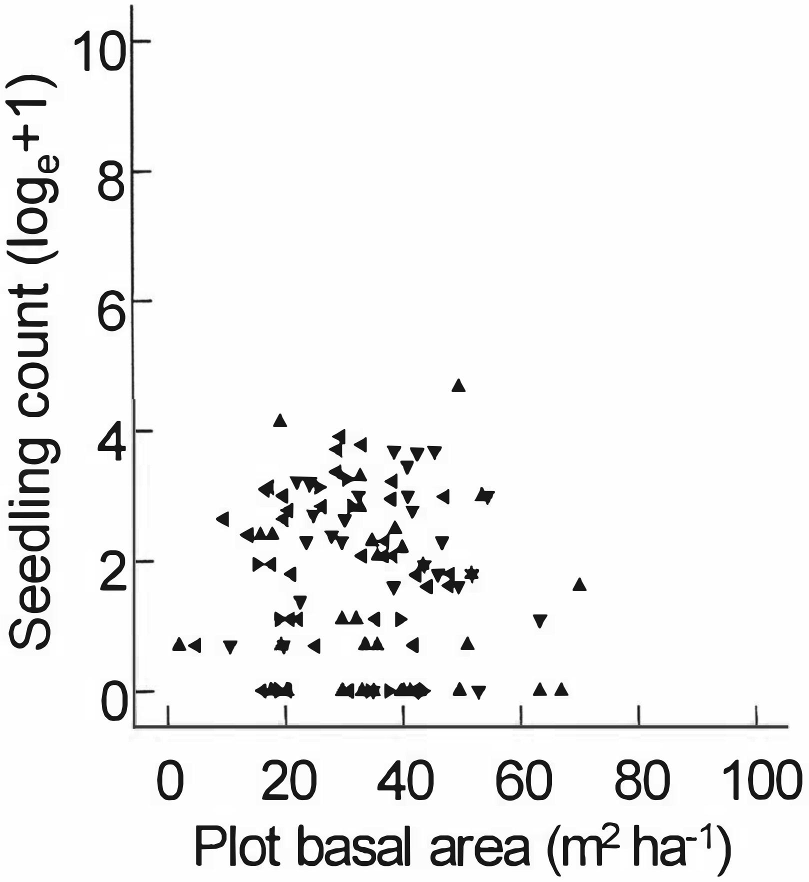

Fig. 3.3. The relationship between the number of mountain beech seedlings counted in twenty-four 0.75 m^2 subplots in each 20 m x 20 m plot ($\log_e$ +1) and plot basal area (m^2 ha^{-1}) in the Kaimanawa E.R. where sika deer are present. Data are from 108 plots in western Kaweka (▲), and northern (▼), western (◀) and southern Kaimanawa Forest Parks (▶).

Table 3.1. Means of plot basal area, relative basal area (for species with basal area > 1.0 m^2 ha^{-1}), tree stem density (for species with tree abundance >100 stems ha^{-1}) and frequency of occurrence of woody seedlings (for species with >10% occurrence in sub-plots) with Bonferroni adjusted *F*-tests. All tests contrast Kaimanawa region data with four regions without sika deer and use an error term of randomly located transect lines nested within regions. Contrasts of seedling frequency occurrence use plot basal area as a covariate.

	No sika deer	Sika deer	*F*	*P*
Basal area (mean m2 ha–1 ± SEM)				
Griselinia littoralis	0.1 ± 0.1	2.3 ± 0.3	16.913	<0.001
silver beech	6.9 1.7	0.4 ± 0.1	25.49	<0.001
mountain beech	46.1 ± 2.2	26.6 ± 1.3	47.717	<0.001
Phyllocladus alpinus	0.2 ± 0.1	1.0 ± 0.1	8.455	0.020
All species	55.8 ± 2.5	33.1 ± 1.3	87.819	<0.001
Relative basal area (% of mean plot relative basal ● SEM)				
Griselinia littoralis	0.2 ± 0.1	8.0 ± 1.2	15.312	0.001
silver beech	9.5 ± 2.0	3.0 ± 1.2	20.805	<0.001
mountain beech	86.0 ± 2.3	78.4 ± 2.2	0.850	1.000
Phyllocladus alpinus	0.4 ± 0.2	3.4 ± 0.5	11.469	0.005
Tree density (mean stems >30 mm ha–1 ± SEM)				
C. "taylorae"	58 ± 23	281 ± 46	0.725	1.000
silver beech	257 ± 57	31 ± 12	16.36	<0.001
mountain beech	1704 ± 152	1219 ± 113	0.27	1.000
Phyllocladus alpinus	58 ± 23	244 ● 30	4.109	0.110
All species	2267 ± 168	2248 ● 139	4.281	0.095
Seedling frequency of occurrence in sub-plots (% frequency ± SEM)				
C. foetidissima	4 ± 1	12 ± 2	0.705	1.000
C. pseudocuneata	9 ± 2	16 ± 2	1.324	1.000
C. "taylorae"	9 ± 3	33 ± 2	23.488	<0.001
Myrsine divaricata	3 ± 1	16 ± 2	8.976	0.016
mountain beech	57 ± 4	18 ± 2	47.599	<0.001
Mean of plot totals	113 ± 9	154 ± 9	0.335	1.000

Total tree and shrub seedling (15–135 cm high) frequency of occurrence did not differ between Kaimanawa and regions without sika deer, but some individual species did differ in frequency of occurrence between the regions. Mountain beech had over twice the frequency of occurrence in regions without sika deer, which is consistent with seedling abundance comparisons of this species. Conversely, the frequency of occurrence of seedlings of the browse-resistant small-leaved shrubs *C.* "taylorae" and *Myrsine divaricata* was *c.* five times higher in the Kaimanawa compared to regions without sika deer. These differences led to significant differences in woody seedling composition, calculated using frequency of occurrence at plots with woody species present, between areas with sika deer (mean axis 1 DCA score ± SEM = 2.51 ± 0.6) and regions without sika deer (mean axis 1 DCA score ± SEM = 0.99 ± 0.8, $F_{1,49} = 53.745$, $P < 0.001$). Basal area was used as a covariate but did not have a significant effect on DCA scores for woody seedling frequencies of occurrence ($F_{1,115}=0.521$, $P = 0.472$).

3.3.2 Contrasts among areas with different histories of sika deer colonisation

There was no significant difference in basal area among Kaimanawa areas in the stand dominants (*Griselinia littoralis*, mountain and silver beech, and *Phyllocladus alpinus*; Table 3.2). Differences in the abundance of *C. pseudocuneata* and *Phyllocladus alpinus* did not appear to be related to the history of colonisation by sika deer. There was no significant difference in mountain beech seedling density (stems ha^{-1}, $\log_e + 1$) among the four Kaimanawa areas when plot basal area ($\text{m}^2\ \text{ha}^{-1}$) was used as a covariate ($F_{3,26} = 1.423$, $P = 0.259$) and therefore, no indication that the different colonisation history of the four areas influenced mountain beech seedling density once basal area was allowed for.

Table 3.2. Basal area (for species with basal area >1 m^2 ha^{-1}) and tree stem density (for stems >30 mm DBH densities >100 stems ha^{-1}) from a total of 108 plots from western Kaweka, and northern, western and southern Kaimanawa Forest Parks. Bonferroni corrections for multiple comparisons have been applied and decades when sika deer probably became dominant over red deer are listed.

Species	North Kaimanawa (n = 30)	West Kaweka (n = 35)	West Kaimanawa (n = 10)	South Kaimanawa (n = 35)	F	P
Sika dominance	≈ 1930's	≈ 1950's	≈ 1970's	≈ 1990's		
Basal Area (m^2 ha^{-1} ± SEM)						
mountain beech	29.1±3.0	30.8±2.8	23.1±4.3	24.72±2.5	1.232	1.000
Griselinia littoralis	1.5±0.7	3.4±0.7	1.7±1.0	2.01±0.6	0.751	1.000
silver beech	1.3±0.5	<0.1±<0.1	0	0	3.618	0.130
Phyllocladus alpinus	0.9±0.3	1. 1±0.3	2.3±0.4	0.8±0.3	2.308	0.495
All 26 species	32.6±2.8	36.0±2.7	27.6±4.0	27.7±2.4	1.621	1.000
Tree stem density (stems ha^{-1} ± SEM)						
mountain beech	1197.1±257.0	644.4±243.3	1785.0±367.0	1529.4±218.0	5.158	0.042
C. pseudocuneata	378.0±49.8	21.7±47.1	177.5±70.9	140.9±42.2	8.266	0.003
Phyllocladus alpinus	209.6±69.2	258.3±65.4	532.5±98.6	206.6±58.7	2.971	0.343
C. "taylorae"	123.1±97.4	291.2±92.1	575.0±139.0	187.2±82.6	1.567	1.000
Griselinia littoralis	67.0±34.3	125.4±32.4	52.5±48.8	103.5±29.1	0.391	1.000
Myrsine divaricata	<0.1±22.7	68.2±21.5	185.0±32.3	10.4±19.2	22.962	<0.001
All 26 species	2105.9±319.0	1586.8±301.2	3412.5±454.0	2418.0±270.0	4.928	0.049

3.4 Discussion

This study has shown high mountain beech seedling abundance at low basal area sites, but only in the absence of sika deer. This confirms the importance of low basal area sites for mountain beech regeneration (Wardle 1970a, Ogden, Stewart and Allen 1996), and is likely to be due to increasing nutrient availability following disturbance (Allen, Clinton and Davis 1997, Clinton, Allen and Davis 2002). Where sika deer have colonised mountain beech seedling abundance is now relatively low, and does not show increases at low basal area sites. This implies that sika deer have suppressed mountain beech regeneration throughout the Kaimanawa Region.

Conclusions are limited by having only one locality with sika deer from which to obtain data. Studies on the impacts of invasive organisms often suffer from this problem of replication because independent introductions of species into new ranges in a replicated manner are rare. Consequently, as Oksanen (2001) points out, observational studies such as this one are often the only possible approach to take, but the causes of observed effects are never completely irrefutable. Alternative explanations for the low level of mountain beech regeneration apparent in the Kaimanawa Region could include fundamental differences in forest regeneration dynamics in comparison to regions without sika deer, an idiosyncratic response to red deer browsing, or climatic differences between regions with and without sika deer. However, differences in the abundance of individual trees of some species (silver beech, *Griselinia littoralis* and *Phyllocladus alpinus*) between regions with and without sika deer represent a relatively small variation in the overstorey of mountain beech-dominant forest, and are unlikely to explain the large differences observed in the Kaimanawa understorey. Intense browsing by red deer and brushtail possums, which are the only other widespread introduced herbivore in the Kaimanawa can not explain low mountain beech regeneration because red deer are now relatively uncommon in areas colonised by sika deer within the last five decades (Davidson and Fraser 1991), and brushtail possums are not regarded as intensive browsers of mountain beech (Pekelharing, Frampton and Suisted 1998, Rose et al. 1993). Environmental and climatic differences are also unlikely to explain the low level of mountain beech regeneration observed with sika deer presence because there is more variation in altitude, latitude and rainfall among areas with no sika than there is between the Kaimanawa and areas without sika deer. Previous studies have shown that southern beech regeneration can vary between sites at fine scales (June and Ogden 1975, Allen and Platt 1990, Allen, Reif and Hall 1991, Cuevas 2002), but not with such strong contrasts and on such a large scale as in this study. In this study, differences in the level of regeneration between areas with and without sika deer were so profound on a landscape scale that the impacts of sika deer appear to be the most plausible explanation. Although the limits of interpretative power of this study must be recognised, there are three lines of reasoning that support a conclusion that sika deer are capable of suppressing mountain beech regeneration.

Firstly, the morphology of sika deer provides this species with the potential to browse more intensively than red deer (Fraser 1996, Hanley 1997) enabling them to maintain high reproductive rates, associated with better physiological condition, in depleted habitats (Asada and Ochiai 1996). This may allow sika deer to suppress mountain beech seedling regeneration where red deer would not, and to maintain higher population densities than red deer, even under intense hunting pressure. In chapter five I estimate that there were >17 deer km^{-2} in an area adjacent to the western Kaweka F.P. area in 1998, whereas Nugent and Fraser (1993) estimated that deer had an average population density throughout New Zealand forests of *c.* 4 deer km^{-2} in 1988. Even though sika deer are *c.* half the size of red deer, this difference in biomass still represents considerably more potential browsing pressure. Because sika deer are smaller than red deer, the conclusion that sika deer browse more intensively than red deer is consistent with theory that smaller deer species graze less on plants that are high in fibre and cellulose, and are better able to digest tree and shrub seedlings (Hanley 1997). Previous studies have shown that deer impacts can differ between hinds and stags through differential browsing (Staines, Crisp and Parish 1982, Padmalal and Takatsuki 1994, Clutton-Brock et al. 2002), and there is also evidence from studies of sika deer in Japan relating body size to dietary preferences. Sika deer from northern study sites in Japan tend to be larger and to graze graminoids more than the smaller sika deer from southern study areas, which tend to browse on herbs (Asada and Ochiai 1996, Jayasekara and Takatsuki 2000). Deer in the south of Japan also occur in habitats with a relatively stable food supply, whereas in the north there is considerable seasonal variation in the quality of food. This places dietary stress on animals during winter (Takatsuki and Ikeda 1993, Asada and Ochiai 1999) when unpalatable plants are increasingly browsed (Takahashi and Kaji 2001). In contrast, Hester et al. (1999) showed that red deer and sheep have similar grazing behaviour in moorlands dominated by *Calluna vulgaris*. The ability of sika deer to occupy small range sizes may also contribute to their potential to more intensively browse forests (Endo and Doi 1996).

Secondly, exclosure plot studies in the Kaimanawa sika deer range have shown that once deer browse was removed, mountain beech seedling growth increased dramatically after only one year (chapter five). Moreover, exclosure plots established during the 1980's at Kaimanawa sites with sika deer showed that mountain beech seedling and sapling abundance was 2–25 times higher inside fenced plots compared to paired unfenced plots (Chapters one and four). In contrast, in regions with only red deer, there was little difference (<50%) in the density of mountain beech seedlings and saplings between fenced and unfenced plots (Hurunui, Wardle et al. 2001; Murchison Mountains, Burrows et al. *unpublished manuscript*; Rangataua, chapter two).

Finally, two small-leaved shrubs (*C.* "taylorae" and *Myrsine divaricata*), that are considered to be browse-resistant, high in lignin and low in nitrogen content (Wardle 1984, Nugent, Fraser and Sweetapple 1997, Coomes et al. *In Press*) were more common as seedlings in the Kaimanawa compared to other regions. This result is consistent with sika deer shifting competitive advantage away from palatable mountain beech seedlings (chapter four) towards species less tolerant of temperature extremes, and low nutrient and water availability than mountain beech (Wardle 1970b, Adams 1976), but also less vulnerable to browsing by sika deer. It is unlikely that *C.* "taylorae" and *Myrsine divaricata* are more competitive than mountain beech in the absence of intense herbivory because neither of these species has responded to the exclusion of deer in fenced plots in the Kaimanawa Region to the same extent as mountain beech.

The hypothesis that areas where sika deer had colonised most recently would show fewer signs of intense browsing by sika deer, in comparison to areas colonised first, was not supported. There were only minor differences in abundance and basal area of overstorey species among Kaimanawa areas, and there was no significant difference in mountain beech seedling abundance. Intensive browsing of mountain beech seedlings appears to occur during the early stage of sika colonisation, quickly reducing seedling abundance, particularly at low basal area sites. These low basal area sites may be preferentially selected by deer due to higher productivity, following increased nutrient and light availability after tree death. Studies on the Isle of Rum in Scotland (Virtanen, Edwards and Crawley 2002) and in a Swedish Boreal forest (Ball, Danell and Sunesson et al. 2000) have shown that productive sites are more attractive to deer. Alternatively, some studies (e.g. Olofsson 2001, Moen and Oksanen 1998) have shown that at unproductive sites, herbivores are food limited and therefore have greatest impacts there (Oksanen 1990).

Absolute impacts of deer may be greatest at highly productive sites, and relative impacts may be greatest at sites of lower productivity where the ability of plants to respond to browsing damage is limited by the restriction of nutrients and light.

The likely ability of sika deer to browse more intensively than red deer, and their increased difficulty to control due to heightened alertness and preference for dense forest habitats (Kiddie 1962), has important management implications where red and sika deer are sympatric. Sika deer have been introduced into Great Britain, the Czech Republic, Ireland and the United States of America (Goodman et al. 1996). If they are able to suppress regeneration of forests there, then sika deer may pose a serious problem for forest and indigenous deer managers (Kelly 2002). In Great Britain and Ireland red deer are regarded as having the ability to adversely affect woodland regeneration (Gong, Swaine and Miller 1991, Scott et al. 2000). Sika deer may have greater impacts on species that red deer are known to periodically browse such as European beech *Fagus sylvatica* L. (Ammer 1996), sitka spruce *Picea sitchensis* Carr. (Duncan et al. 2001), Scots pine *Pinus sylvestris* L. (Scott et al. 2000) and Norway spruce *Picea abie* Karst. (Gill 1992). Regeneration of these species in forests recently colonised by sika deer needs to be monitored, particularly at productive sites where the magnitude of impact may be greatest. In Scotland, sika appear to be able to competitively displace red deer, and reach higher densities (Chadwick, Ratcliffe and Abernethy 1996) over an increasing large area (Rose 1994). Moreover, by preferring forest or shrub habitats (Marques et al. 2001) sika may suppress forest regeneration in Europe where red deer do not (Goodman et al. 1996). If sika deer are able to have higher levels of impacts on forest regeneration than red deer then the same may be true for widespread sika–red hybrids (Abernethy 1994). This may pose additional management problems where red and sika deer are sympatric in Britain, Czech Republic, Ireland and New Zealand. Because this study has highlighted the intense impacts of sika deer in newly colonised mountain beech forests, it is essential that other forest types and more recently colonised areas (e.g. Tararua Forest Park) are monitored for the abundance of sika deer and their impacts.

Ecology Stream exclosure, southern Kaimanawa Forest Park

CHAPTER FOUR

Long-term influences of introduced deer on the composition and structure of Kaimanawa beech forests

4.1 Introduction

This study infers the influences of deer on changes in mountain, red and silver beech forest structure and species composition in Kaimanawa Forest Park over two decades. Previous studies outside and within New Zealand have shown that deer induce compositional changes in forest understories (section 1.4), but few have shown what flow-on effects these changes in forest understories have on forest overstories. Therefore, this study focuses on the long-term effects of deer on changes in forest composition throughout several forest tiers.

Deer were introduced into New Zealand in the 19th century and are now considered a serious threat to conservation of forests administered by the Department of Conservation (Holloway 1993; Nugent and Fraser 1993). It was soon noticed that deer were reducing the density of understorey vegetation in some forests and altering composition by preferentially browsing certain species (Walsh 1892; Cockayne 1926; Caughley 1983; chapter one). New Zealand forests evolved with avian and invertebrate herbivores, in the absence of mammalian herbivores until approximately 150 years ago (Greenwood and Atkinson 1977). Invertebrate and avian herbivores have different feeding characteristics than mammalian herbivores, particularly ruminants, so introduced deer imposed a novel selective pressure. Avian herbivores have no teeth, simple stomachs, and probably quite different feeding behaviour that exerts unique selective pressures on plants (Cooper et al. 1993). Many of these avian herbivores became extinct several hundred years ago, soon after the arrival of Polynesians to New Zealand (Fleming 1969). Since this time, vertebrate herbivory would have been relatively unimportant until the introduction into New Zealand of the brushtail possum in 1837 and deer in 1861 (Logan and Harris 1967).

The short-term effects of deer invasion are well documented, but the ongoing effects on forest dynamics in the post-irruptive phase of colonisation are still poorly understood (Rogers and Leathwick 1997; Lee 1998; Forsyth, Coomes and Nugent 2001; Nugent, Fraser and Sweetapple 2001). To understand ongoing impacts of deer it is important to know if forests have been shifted into an alternative state by deer browsing, from which further directional change is unlikely to occur, or whether deer browsing may continue to induce further shifts in vegetation composition. There are three main reasons for the ongoing lack of understanding about long-term changes: firstly, deer only browse on the lowest two-metre tier of forests so their impact on overstorey composition may take decades to become apparent in the structurally dominant trees (chapter one); secondly, it is difficult to partition deer browsing from the effects of other agents of change such as spatially complex disturbance events and other herbivores (Veblen and Stewart 1982; Coomes et al., *In Press*); thirdly, reduction in seedling densities may not result in reduced adult density if browsing simply replaces some of the mortality that would have occurred anyway by the process of self-thinning (Westoby 1984). Many studies have investigated the influences of deer in temperate forests of the northern hemisphere, where ungulate herbivores have been present for hundreds of thousands of years (e.g., Gill 1992; Gonzalez-Hernandez and Silva-Pando 1996; Hobbs 1996; Reimoser and Gossow 1996; Motta 1996; Duncan, Hartley and Iason 1998). Most forest stands in the northern hemisphere regenerated in the presence of deer, so the influence of deer herbivory on forest composition can be difficult to ascertain. In contrast, New Zealand's *Nothofagus* (southern beech) forests provide an opportunity to understand the influence of mammalian herbivory on temperate forest composition because invasion was so recent that directional responses of forests to introduced deer might still be occurring (Veblen and Stewart 1982). Because of the long-time scale over which deer impacts act, long-term monitoring of forest structure and composition provides an important method of observing the impacts of invasive organisms (Wiser et al. 1998), and forms the basis of this study.

This study examines the influence of introduced deer on long-term shifts in under- and overstorey composition in mountain, red and silver beech forest vegetation in Kaimanawa Forest Park (Fig. 4.1). Red deer reached a high population density throughout Kaimanawa Forest Park by 1930 after dispersing from liberations in 1896 at nearby Tongariro to the west, and in 1883 at Matapiro to the south-east (Elder 1962). Similar patterns were observed following deer introductions in other parts of New Zealand, where deer numbers typically reached irruptive peaks within two to three decades of establishment (Challies 1985). Sika deer were liberated in Kaimanawa Forest Park in 1905 (Davidson 1973) but colonised the study area much more slowly (Elder 1962). They only colonised northern Kaimanawa Forest Park in the 1950s (Davidson 1973) and southern Kaimanawa Forest Park during the 1980s. Sika deer are thought to have the ability to browse more intensively than red deer because of a different digestive morphology (Fraser 1996). In Japan, sika deer eat unpalatable plants and litterfall when preferred food sources are not available (Hiroshi and Koichi 2001). Reproductive rates of both deer species were initially high until carrying capacity was exceeded and deer numbers crashed, or were reduced through intensive commercial and Government-funded hunting (Caughley 1983). Recreational, and ground and aerial based commercial hunting is the most commonly used management technique chosen to control deer in New Zealand (Parkes, Nugent and Warburton 1997). During the period of this study, deer management in Kaimanawa Forest Park was restricted to recreational hunting.

Common New Zealand tree species have been classified by a number of authors for their palatability to deer, using a variety of methods including observed signs of browse, changes in abundance following deer colonisation and studies of deer diet (McKelvey 1959; Wallis and James 1972; Jane and Pracy 1974; Veblen and Stewart 1980; Veblen and Stewart 1982; Allen, Payton and Knowlton 1984; Wardle 1984; Stewart and Harrison 1987; Stewart, Wardle and Burrows 1987; Nugent and Challies 1988; Stewart and Burrows 1989; Nugent, Fraser and Sweetapple 1997; Fraser and Speedy 1997). A general consensus has now been reached on most species. I reviewed these studies and arbitrarily classified each species into unpalatable, moderately palatable, palatable and highly-palatable classes, and this has been used in this study to determine an overall classification, based on subjectively assessed common agreement (Table 4.1). I hypothesised that under the presence of intense deer browsing, seedlings and saplings of palatable species such as *Coprosma tenuifolia*, *Weinmannia racemosa* and *Griselinia littoralis* are generally expected to decline in abundance, followed in turn by moderately palatable species such as *Nothofagus* spp. (Nugent, Fraser and Sweetapple 1997). I also hypothesised that unpalatable woody species such as *Leucopogon fasciculatus, Neomyrtus pedunculatus, Phyllocladus alpinus* and *Pseudowintera colorata* would increase significantly in abundance due to competitive release, along with unpalatable ferns, and browse tolerant grasses and herbs with prostrate growth.

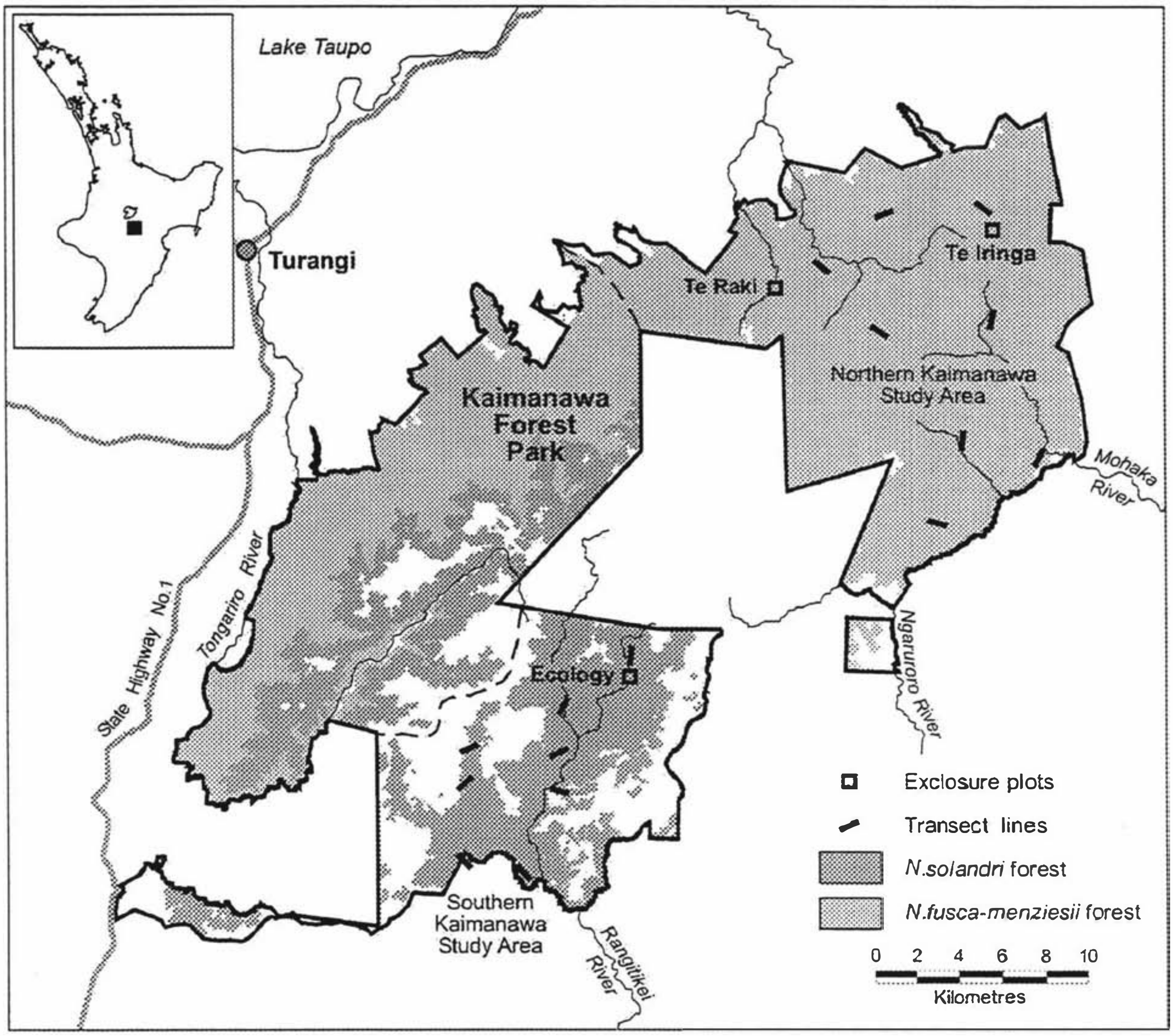

Fig. 4.1. Northern and southern Kaimanawa Forest Park study areas showing exclosure plots and random permanent plot monitoring lines.

Table 4.1. Results of a literature search on common species found in northern and southern Kaimanawa Forest Park. Species were subjectively rated as highly palatable (HP), palatable (P), moderately palatable (MP) and unpalatable (UP). For this study a consensus of these ratings was used to assign a palatability score to each species based on the most common ratings of previous studies.

Species	Source													
	1	2	3	4	5	6	7	8	9	10	11	12	13	This Study
Carpodetus serratus					P	MP			HP	HP	HP	P	HP	HP
Coprosma linariifolia													MP	MP
C. microcarpa	P			P									MP	P
C. pseudocuneata							MP						UP	MP
C. "taylorae"	P			P			MP					UP	MP	MP
C. tenuifolia	P			P		HP								P
Griselinia littoralis					P		HP	P	HP	HP	HP	P	HP	HP
Leucopogon fasciculatus			UP			UP							UP	UP
Neomyrtus pedunculatus	UP						UP		UP	UP		UP	UP	UP
red beech		MP					MP						MP	MP
silver beech		MP					MP		MP				MP	MP
mountain beech							MP					MP	MP	MP
Phyllocladus alpinus							UP							UP
Pseudowintera colorata	UP					UP	UP	UP	UP	UP		UP	UP	UP
Weinmannia racemosa	P	HP			P	P	P		MP	HP	MP	P	HP	P

Sources: 1 McKelvey 1959; 2 Wallis and James 1972; 3 Jane and Pracy 1974; 4 Veblen and Stewart 1980; 5 Veblen and Stewart 1982; 6 Allen, Payton and Knowlton 1984; 7 Wardle 1984; 8 Stewart and Harrison 1987; 9 Stewart, Wardle and Burrows 1987; 10 Nugent and Challies 1988; 11 Stewart and Burrows 1989; 12 Nugent, et al. 1997; 13 Fraser and Speedy 1997.

4.2 Methods

4.2.1 Study Site Description

Kaimanawa Forest Park is located within the Kaimanawa Mountains, which form the bulk of the Kaimanawa Ecological District, and are made up of a series of ranges running north-east to south-west in the central North. Altitudes in Kaimanawa Forest Park vary from a low point of 560 m in the north to the high point of 1727 m in the south. Geology in the northern and southern study areas is predominantly Jurassic folded greywacke with a schist belt in the north. 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 millennia.

The northern study site is co-dominated by red and silver beech with mountain beech at higher altitudes. Silver beech is the main species from about 1100 m altitude to the crests of the ridges, while red beech dominates below 1100 m, with silver beech often forming a sub-canopy. At lower levels, *Carpodetus serratus, Griselinia littoralis* and *Raukaua simplex* form an open sub-canopy with occasional *Podocarpus hallii* and sometimes *Weinmannia racemosa.* The shrub layer is dominated by *Myrsine divaricata, Neomyrtus pedunculata, Pseudowintera colorata* and *Coprosma microcarpa, C.* "taylorae", *C. tenuifolia,* and *C. foetidissima.*

In the southern Kaimanawa study area, mountain beech is the dominant tree species over large areas, especially between 1100 m and the upper timberline, which varies between 1375 and 1430 m. The understorey 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 replaced by *C. pseudocuneata, Phyllocladus alpinus* and *Podocarpus hallii* higher up. The southern area has high relief (valley bottoms 800–1000 metres; ridgetops 1500–1700 metres) and is steep (mean plot slope 34°). Mean plot altitude is 1117 m in the south and 843 m in the north and is less steep (18°).

4.2.2 Permanent plot establishment and re-measurement

Detailed data were collected for overstorey, understorey and environmental variables from 57 20x20 m permanent plots in northern Kaimanawa Forest Park, that were established between January 1979 and January 1980. Forty of the more eastern plots were re-measured between November 1987 and January 1988. All 57 were re-measured once again between July and December 1998. In the southern Kaimanawa 35 permanent plots were established between November 1981 and January 1982 and were re-measured between November 1999 and March 2000, using the same protocols used in the northern survey. Plots were systematically located (at 200 m intervals from line origins except for the first plot which was 40 m from origin) on randomly located transect lines that ran from streams or valley floors to the nearest ridgetop (Fig. 4.1). There were eleven transects in the northern study area and eight in the south.

4.2.3 Paired exclosure plot establishment and re-measurement

Three pairs of 20 x 20 m plots (one of the pair fenced to exclude deer) were established at two sites in the north and one in the south (Fig. 4.1). The Te Raki Stream paired exclosure (altitude 760 m, aspect 300°, and slope 5°) was in mixed red and silver beech forest. It was established in May 1985, and re-measured in March 1993 and August 1998. Most trees at Te Raki are silver beech with some red beech, *Weinmannia racemosa*, *Neomyrtus pedunculatus* and *Pseudowintera colorata* stems. The Te Iringa exclosure (established in April 1983 and re-measured in February 1991 and August 1996; altitude 1000 m, aspect 70°, slope 20°) is in silver beech forest with some *Griselinia littoralis*, *Raukaua simplex*, *Pseudowintera colorata* and *Myrsine divaricata* stems in the sub-canopy. The Ecology Stream exclosure (established in October 1983 and re-measured in June 1991, March 1996, and January 2000; altitude 1020 m, aspect 300°, slope 20°) had an overstorey almost completely dominated by mountain beech (>98% of basal area) with 13 stems of *Phyllocladus alpinus*, *Griselinia littoralis,* and *Myrsine divaricata* found in the two plots at this site.

4.2.4 Plot measurement procedure

Identical methods were used for all measurements of permanent and paired exclosure plots following Allen (1992 and 1993) and described in section 2.2.5. In each 20 m x 20 m plot, the species of all trees over 20 mm diameter at breast height (DBH = 1.35 m) were identified. In the original southern Kaimanawa survey, all dead trees were included in the measurement, but in other surveys only live trees were measured. All saplings (≤20 mm DBH, >135 cm high) were counted and species identified. Circular understorey subplots (n = 24; 49 cm radius) were systematically located according to Allen (1993) within each plot, as described in section 2.2.5. Altitude was estimated to the nearest 5 m using map references; slope was estimated with a Suunto inclinometer to the nearest 5° and aspect to the nearest 5° using a compass. For analysis, aspect was converted to degrees from true north. Plots were not established at two sites in the southern study area where plot slope was >60°.

4.2.5 Data analysis

Upon re-measurement in 1998, errors and omissions were found for 1979–80 and 1987/88 understorey and tree tag data from the northern Kaimanawa. No herbarium specimens were collected so corrections could not be made to understorey species identifications. Consequently, only data from easily recognised species in the understorey in these two surveys are reported here (red and silver beech, *Weinmannia racemosa* and *Griselinia littoralis*). Secondly, calculation of recruitment and mortality was limited to the southern Kaimanawa where the fates of individual trees were followed more reliably than in the north.

Basal area is a good descriptor of canopy structure because it serves as an indicator of site occupancy with a clear link to regeneration in *Nothofagus* forests (chapter three, Wardle 1970b). Basal areas and density of stems per hectare were calculated in SYSTAT (SPSS 2000) before statistical analysis was undertaken. Recruitment and mortality rates for southern Kaimanawa mountain beech were calculated according to McCune and Cottam (1985) using PC-Diam (Hall 1994a).

$$\text{Recruitment} = (1+\mathrm{B}_x)^{1/x}-1, \text{ where } \mathrm{B}_X = \text{proportion of new stems for period } x \qquad (1)$$

$$\text{Mortality} = 1-(1-\mathrm{Q}_x)^{1/x}, \text{ where } \mathrm{Q}_X = \text{proportion of dead stems for period } x. \qquad (2)$$

An audit re-measurement of four randomly selected plots from the 35 plots in the southern Kaimanawa that were re-measured in 1999/2000 showed that field standards for overstorey re-measurement and understorey species identification were high. Audits of mean diameter measurements were within 4% of survey measurements and there was 96% agreement of species identifications. Counts of seedlings and saplings were more variable (43.6% more seedlings and 10.9% more saplings in the audit than in the original measurement). I assumed that error was not biased and thus was included as random error in statistical tests. Where possible, statistical tests on understorey data used frequency presence data and not seedling counts.

Statistical comparisons of univariate data were made with student t-tests (e.g., change in stem density over time) or step-wise regressions (e.g., relationship between stem density and environmental variables). Multivariate comparisons were made using General Linear

Models in SYSTAT 10 (SPSS 2000) and with Canonical Correspondence Analysis (CCA) in CANOCO 4.0 (Ter Braak and Smilauer 1998). An automatic forward selection procedure was used in CCA to test for the effect of time between surveys, altitude, aspect and slope on overstorey species composition of stand dominants (> 100 mm DBH) in northern and southern Kaimanawa and vascular understorey composition in southern Kaimanawa. Because randomly located permanent plots were repeatedly measured and I expected large spatial variation because of variability in deer impacts and normal successional processes, plots were treated as blocks to reduce unexplained variation in analysis. Abundance values (stems ha^{-1}) were used for overstorey analysis and in the understorey importance values were calculated from the relative occurrence of vascular plants (<135 cm high) in 24 sub-plots in each plot. The presence of uncommon species can have a large influence on CCA results so these were down-weighted in analysis using an option in CANOCO.

4.3 Results

4.3.1 Changes in stand basal area and tree abundance in northern Kaimanawa

In the northern Kaimanawa red and silver beech forests there was no significant difference in plot basal area between 1979–80 (63.3 m^2 ha^{-1}) and 1998 (63.7 m^2 ha^{-1}; *paired* $t = 0.160$, df =56, $P = 0.874$). Total tree stem density (≥20 mm DBH) for all northern Kaimanawa plots increased from 1347.8 stems ha^{-1} in 1979–80 to 2340.4 stems ha^{-1} in 1998 (*paired* $t = 5.965$, df = 56, $P < 0.001$). A series of paired t-tests showed that this overall increase in abundance was mainly due to increases in unpalatable and browse-resistant small trees (20 mm to 100 mm DBH) but these only had a small effect on stand basal area. No correction was made for multiple comparison of species, so interpretation of these results needs to be made with caution for species with marginally significant differences in abundance between years. The palatable *Carpodetus serratus* and the unpalatable *Leucopogon fasciculatus, Neomyrtus pedunculatus,* and *Pseudowintera colorata* increased significantly in abundance in the 20 mm to 100 mm DBH size class; in the same size class the highly palatable *C. tenuifolia* and *Weinmannia racemosa* decreased significantly in abundance (Table 4.2).

Although there was no significant change of the highly palatable *Griselinia littoralis* in this size class, this species decreased in abundance in the >100 mm size class between 1979–80 (23.7 stems ha^{-1}) and 1998 (15.4 stems ha^{-1}; *paired* $t = 2.595$, df = 56, $P = 0.012$) while *Carpodetus serratus* increased in abundance between 1979–80 (39.5 stems ha^{-1}) and 1998 (66.5 stems ha^{-1}; *paired* $t = 3.153$, df = 56, $P = 0.003$). Increases in the abundance of *Pseudowintera colorata, Neomyrtus pedunculatus* and *Leucopogon fasciculatus* were influenced by recruitment into plots where they were not found in the initial measurement as well as by increases in density in plots where they were initially found.

Table 4.2. Mean density of stems in the 20 mm to 100 mm diameter size class from 57 plots in northern Kaimanawa recorded in 1979–80 (initial) and 1998 (final) surveys, and from 35 plots in southern Kaimanawa 1981/82 (initial) and 1999/2000 (final) surveys. For each species the palatability rating and number of plots where it occurred in respective surveys (N) are given. Changes in density are tested with paired t-tests. Data are displayed by palatability rating for species with significant changes (P <0.05) or species that had stem densities in the initial or final survey of >100 stems ha^{-1}.

Species	Palatability	Initial tree density	N initial	Final tree density	N final	t-value	*P*
Northern Kaimanawa							
Carpodetus serratus	Highly palatable	28.5±8.0	24	46.1±12.0	27	2.196	0.032
Coprosma tenuifolia	Palatable	6.6±3.4	7	2.6±1.8	3	2.260	0.028
Weinmannia racemosa	Palatable	75.4±23.1	19	48.2±16.4	12	3.360	0.001
silver beech	Moderately palatable	148.2±44.8	41	296.5±93.3	45	1.636	0.108
red beech	Moderately palatable	44.3±19.5	21	58.8±16.1	21	0.744	0.460
Pseudowintera colorata	Unpalatable	511.0±120.3	41	1088.6±201.8	46	5.424	<0.001
Neomyrtus pedunculatus	Unpalatable	97.4±21.4	30	335.1±65.5	32	4.558	<0.001
Leucopogon fasciculatus	Unpalatable	3.1±1.9	3	12.7±4.8	11	2.543	0.014
All other species		94.3±19.1	57	81.1±13.9	57	0.787	0.435
Southern Kaimanawa							
Griselinia littoralis	Highly palatable	70.7±27.7	13	45.0±16.8	13	2.038	0.049
C. microcarpa	Palatable	21.4±8.9	12	49.3±17.7	12	2.039	0.049
mountain beech	Moderately palatable	925.0±169.7	35	1465.0±285.1	34	2.384	0.023
C. pseudocuneata	Moderately palatable	249.3±75.1	19	267.1±84.0	19	0.302	0.764
C. linariifolia	Moderately palatable	67.1±27.9	11	127.9±46.4	11	2.161	0.038
C. "taylorae"	Moderately palatable	372.9±110.9	28	327.9±90.3	25	0.988	0.330
Phyllocladus alpinus	Unpalatable	146.4±41.5	25	208.6±56.4	25	2.650	0.012
All other species		298.6±67.5	35	255.7±44.3	35	0.964	0.342

Decreases in *Coprosma tenuifolia*, *Weinmannia racemosa* and *Carpodetus serratus* were influenced by these species disappearing from some plots. Paired t-tests showed no significant difference in abundance of other overstorey species at the 95% level of confidence in the 20 mm to 100 mm or the >100 mm size classes. Of the species that had densities >100 stems ha^{-1}, red and silver beech, *C.* "taylorae" and *C. pseudocuneata* are the only species without significant changes in abundance.

Multiple regression, using a forward stepwise procedure, showed that changes in the abundance of unpalatable *Pseudowintera colorata* was significantly related to aspect (Fig. 4.2, df = 2,44; $R^2 = 0.336$, $P = 0.014$) while changes in density of unpalatable *Neomyrtus pedunculatus* (df = 1,33; $F = 4.9$, $P = 0.035$) was positively related to altitude.

Changes in the abundance of the palatable *Weinmannia racemosa* were negatively related to altitude (df = 7,1, $F = 6.8$, $P = 0.048$). Canonical Correspondence Analysis showed no significant shifts in species composition using data from all size classes (trees > 20 mm DBH) with time ($P = 0.055$) or aspect ($P = 0.635$) but there were significant effects of altitude ($P = 0.005$) and slope ($P = 0.005$). *Griselinia littoralis*, *Neomyrtus pedunculatus*, *Pseudowintera colorata* and *Weinmannia racemosa* had highly significant changes in abundance detected in univariate analysis and were also most strongly influenced by environmental variables and time in CCA. These three species had >15% of their CCA scores explained by time and environmental variables, whereas all other species had <15% of variation explained. Although *Carpodetus serratus*, *Coprosma tenuifolia* and *Leucopogon fasciculatus* had moderately significant changes in abundance detected by univariate tests, they had <15% of variation explained by time and environmental variables.

4.3.2 Changes in stand basal area and tree abundance in southern Kaimanawa

In the southern Kaimanawa, overstorey dead trees contributed considerably to basal area (5.9 m^2 ha^{-1} of a total of 31.7 m^2 ha^{-1} for live and dead stems combined). There was a significant increase in the mean overall basal area (all tree species) between the 1981/82 and 1999/2000 surveys from 25.8 m^2 ha^{-1} to 29.2 m^2 ha^{-1} (*paired* $t = 3.593$, df = 34, $P = 0.001$). Most of this increase was due to increases in the basal area of mountain beech (Table 4.3).

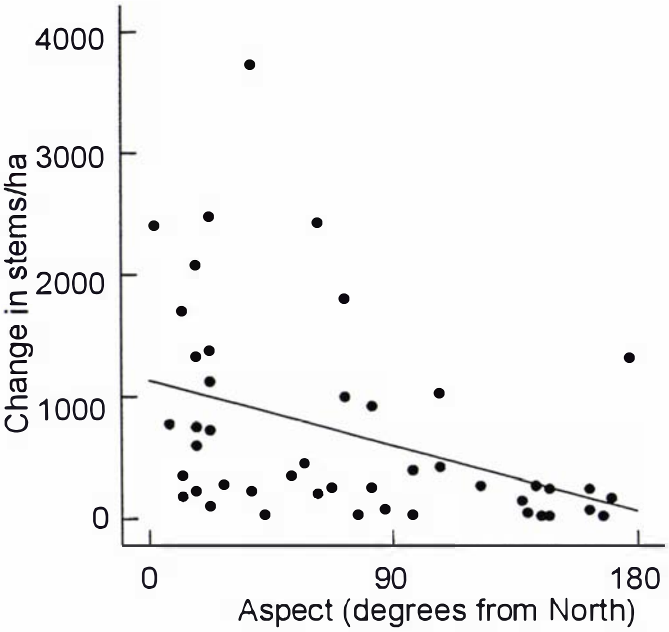

Fig. 4.2. The relationship between the change in tree stem density of *Pseudowintera colorata* and plot aspect from 47 plots in northern Kaimanawa, where the species was present as a tree in the 1979–80 or 1998 surveys. The line of best fit, calculated in linear regression, is change = 1135.977–5.924*Aspect ($R^2 = 0.007$, $P = 0.007$).

Table 4.3. Basal area (m^2 ha^{-1}±SEM) of tree species which exhibited significant changes over time ($P < 0.05$) in 35 plots in southern Kaimanawa. Statistics from paired t-tests are displayed.

Species	Tree basal area 1981/82	Tree basal area 1999/2000	*t*-value	*P*
mountain beech	22.45±1.99	25.60±2.07	2.926	0.006
Griselinia littoralis	1.46±0.43	1.82±0.50	2.140	0.040
Coprosma microcarpa	0.01±0.005	0.034±011	2.781	0.009
All other species	0.706±0.218	0.375±0.065	1.711	0.096

Coprosma linariifolia, C. microcarpa and *Griselinia littoralis* also increased in basal area between 1981/82 and 1999/2000, but contributed little to total increases. The abundance of *C. linariifolia*, *C. microcarpa*, mountain beech and *Phyllocladus alpinus* trees (>20 mm to 100 mm DBH size class) increased significantly between surveys, whereas *Griselinia littoralis* tree abundance decreased significantly in this size class (Table 4.2). Changes in the abundance of *C. linariifolia*, *C. microcarpa* and *Phyllocladus alpinus* were in part due to increases in the number of plots these species were found in (2, 4 and 5 additional plots for each species respectively). These statistical tests need to be treated with caution because their P values were all moderately significant and were not corrected for multiple comparisons. No other significant changes in abundance were detected in the southern Kaimanawa overstorey in the >20 mm to 100 mm or the >100 mm size classes between surveys. Mountain beech showed considerable recruitment into the smaller size classes (<220 mm = 1.9% recruitment), particularly the smallest size class (<70 mm = 2.5% recruitment; Table 4.4). In comparison, annual mortality rates were nearly half that of recruitment at 1% overall, and remained between 0.7 and 3.0% through all age classes.

A stepwise multiple regression showed no significant relationship between mountain beech stem density and mountain beech mortality at the 400 m^2 plot scale (df = 1,27; $F = 2.867$, $P = 0.122$). The same multiple regression showed that mountain beech mortality decreased with plot altitude ($F = 24.381$, $P = 0.004$; Fig. 4.3) and plot basal area ($F = 9.344$, $P < 0.001$).

Table 4.4. mountain beech tree recruitment and mortality between 1981/82 and 1999/2000 surveys by DBH size classes in 35 plots, southern Kaimanawa.

Class (mm)	New ha^{-1}±SEM	%New	%New pa	Dead ha^{-1}±SEM	%Mortality	%Mortality pa
20–69	889.3±196.3	55.0	2.5	197.1±33.0	12.2	0.7
70–119	77.1±25.4	21.2	1.1	122.1±44.0	33.6	2.3
120–169	7.1±4.0	4.5	0.2	36.4±11.6	23.1	1.5
170–219	2.1±1.2	2.2	0.1	15.0±4.2	15.3	0.9
220–269				7.9±2.2	15.9	1.0
270–319				5.7±2.1	15.4	0.9
320–369				9.3±2.5	37.1	2.6
370–419				5.0±1.7	23.3	1.5
420–469				3.6±1.5	29.4	1.9
470–519				3.6±1.8	41.7	3.0
>520				1.4±1.0	33.3	2.2
Total	975.7±211.3	40.8	1.9	407.1±73.4	17.0	1.0

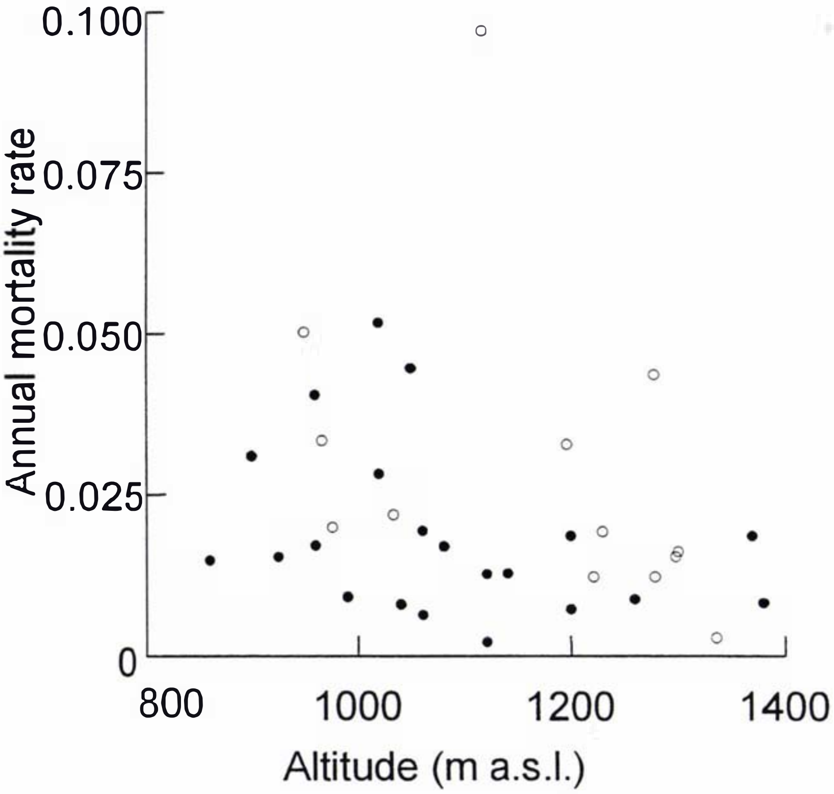

Fig. 4.3. The relationship between mountain beech mortality rate (proportion of tree deaths/annum) and altitude (m a.s.l.) in 35 20x20 m low (○<25m^2 ha^{-1}) and high basal area (● ≥25m^2 ha^{-1}) plots from southern Kaimanawa.

Canonical Correspondence Analysis (CCA) showed no significant shifts in tree species composition in the overstorey with time ($P = 0.170$), or any significant effects of altitude ($P = 0.430$), aspect ($P = 0.655$) or slope ($P = 0.115$).

4.3.3 Changes in seedling abundance

Visual inspection of the height-class distributions in northern Kaimanawa of palatable *Weinmannia racemosa* and highly palatable *Griselinia littoralis* showed distinct gaps in the regeneration of taller seedlings (>45 cm high), whereas the moderately palatable red and silver beech showed no distinct gaps (Fig. 4.4). Seedling abundance of red beech increased by approximately fifteen times and silver beech by three times in the northern Kaimanawa study area (Table 4.5).

Table 4.5. Mean (±SEM) numbers ha^{-1} of red and silver beech seedlings (stems within 15–135 cm height class) in 1979–80, 1987/88 and 1998 surveys from 40 plots in northern Kaimanawa, tested using repeated measures ANOVA. Means for density of red beech seedlings for north (17 plots) and south (23 plots) aspects are also presented.

Species	1979/80	1987/88	1998	Wilks' γ	df	*F*	*P*
silver beech	14±14	1764±555	3000±675	0.663	2, 38	9.643	<0.001
red beech	83±51	2111±733	2181±517	0.667	2, 38	9.476	<0.001
Aspect							
red beech north	0	3301±1605	1275±461				
red beech south	145±87	1232±4432	2850±812				

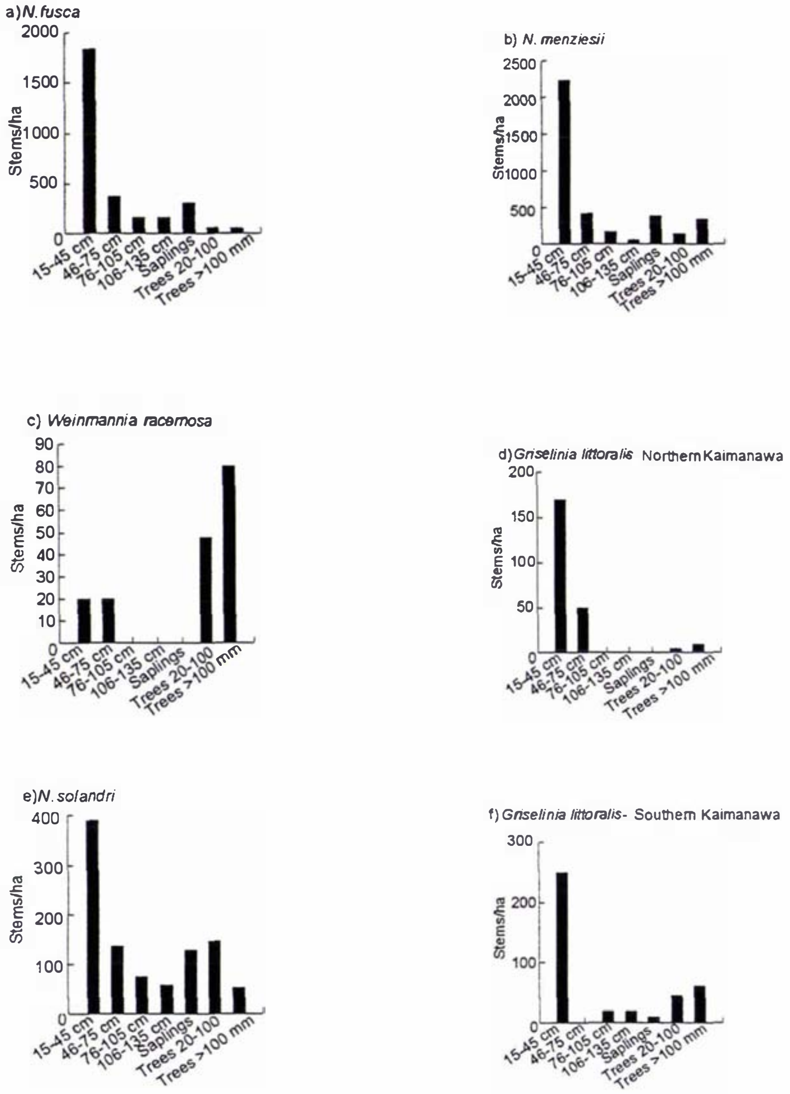

Fig. 4.4. Mean numbers of seedlings (height classes of 15–45 cm, 46–75 cm, 76–105 cm, 106–135 cm), saplings (>135 cm high and less than 20 mm DBH), small trees (≥20–100 mm DBH) and large trees (>100 mm DBH) of a) red beech, b) silver beech, c) *Weinmannia racemosa*, d) *Griselinia littoralis* in northern Kaimanawa, 1998, and e) mountain beech and f) *Griselinia littoralis* in southern Kaimanawa, 1999/2000.

These increases in seedling density were not related to changes in plot basal area (classified as low, ≤ 25 m^2 ha^{-1}; medium, 25–50 m^2 ha^{-1}; or high, ≥ 50 m^2 ha^{-1}), plot aspect (closer to true north or south) or altitude (classified into low, <= 900 m or high, >900 m). Changes in the abundance of red beech were significantly related to plot aspect (Table 4.5; Wilks' $\gamma = 0.847$, $F = 3.348$; df = 2,37; $P = 0.048$) but no other exploratory tests of the effect of altitude or basal area produced significant results.

There was no overall change in mountain beech seedling abundance in the southern Kaimanawa between 1981/82 (8603 seedlings ha^{-1}) and 1999/2000 surveys (6634 seedlings ha^{-1}; *paired t* = 1.202, df = 34, $P = 0.238$). This overall pattern of a decline of 2500 seedlings ha^{-1} masked considerable variation among plots as is shown by the high standard deviation of 9900 seedlings ha^{-1}. Seedling density tended to increase in plots at high altitude and decrease in plots at lower altitude (Fig. 4.5).

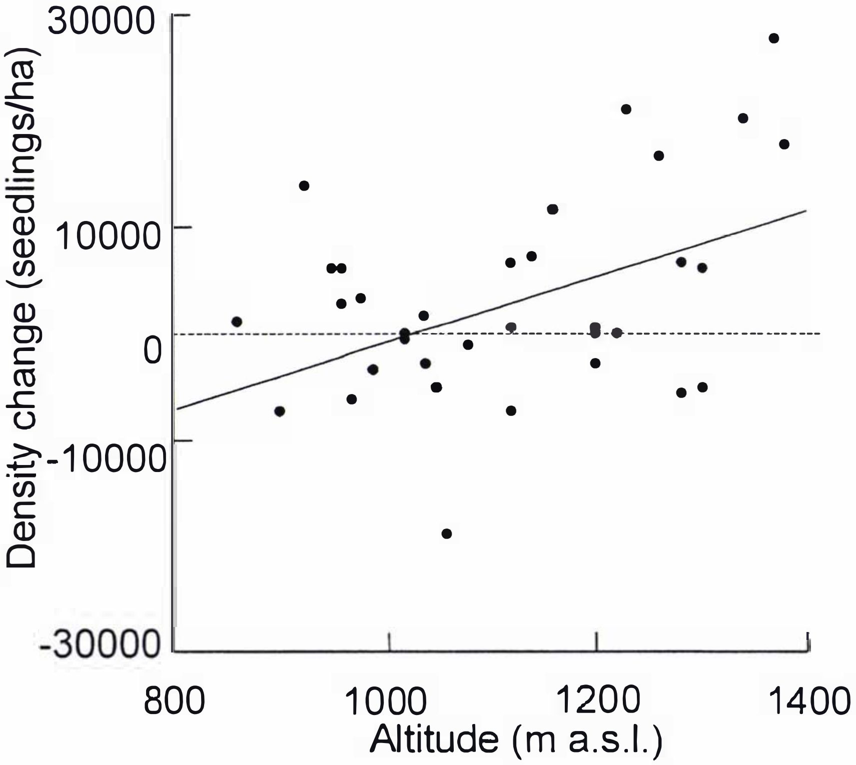

Fig. 4.5. The relationship between changes in mountain beech seedling (15–135 cm high) abundance between 1981/82 and 1999/2000 and plot altitude (m a.s.l.) in 35 plots in southern Kaimanawa. A line of best fit from linear regression is: change in seedling density = 32.7*Altitude–34559.7; R^2=0.189, $P = 0.009$.

4.3.4 Exclosure plots

Little difference in seedling (15–135 cm high) abundance was apparent between three paired fenced and unfenced plots in the first ten years after establishment in 1983–1985 (Fig. 4.6). By the 1996/1998 re-measurements, fenced plots had greater densities of *Nothofagus* seedlings while there was little or no change in adjacent unfenced plots. By 1996 at Te Raki, red beech seedling abundance in the fenced plot had increased moderately to >1000 seedlings ha^{-1} and silver beech increased to >1500 seedlings ha^{-1}. By 1998 in the Te Iringa fenced plot silver beech densities had increased to >10,000 seedlings ha^{-1}, while density of mountain beech had increased to >40,000 seedlings ha^{-1} in the Ecology Stream fenced plot by 1998.

Some of the changes in seedling numbers could have arisen from the chance creation of canopy gaps in fenced plots, but not in neighbouring unfenced plots. Plot basal area in the Ecology Stream exclosure declined from 73.5 m^2 ha^{-1} in 1983 to 41.9 m^2 ha^{-1} in 2000, whereas the paired unfenced plot increased from 48.9 m^2 ha^{-1} to 51.9 m^2 ha^{-1}. At Te Iringa, basal area increased in both the exclosure (93.6 m^2 ha^{-1} to 99.5 m^2 ha^{-1}) and unfenced (69.2 m^2 ha^{-1} to 74.1 m^2 ha^{-1}) plots between 1983 and 2000. At Te Raki Stream, basal area in the exclosure plot declined substantially from 101.1 m^2 ha^{-1} in 1985 to 58.1 m^2 ha^{-1} in 1998 after one large red beech tree died (basal area 40.5 m^2 ha^{-1}) between plot establishment and the first re-measurement in 1993. There was an increase in basal area in the unfenced plot from 72.3 m^2 ha^{-1} in 1985 to 78.8 in 1998.

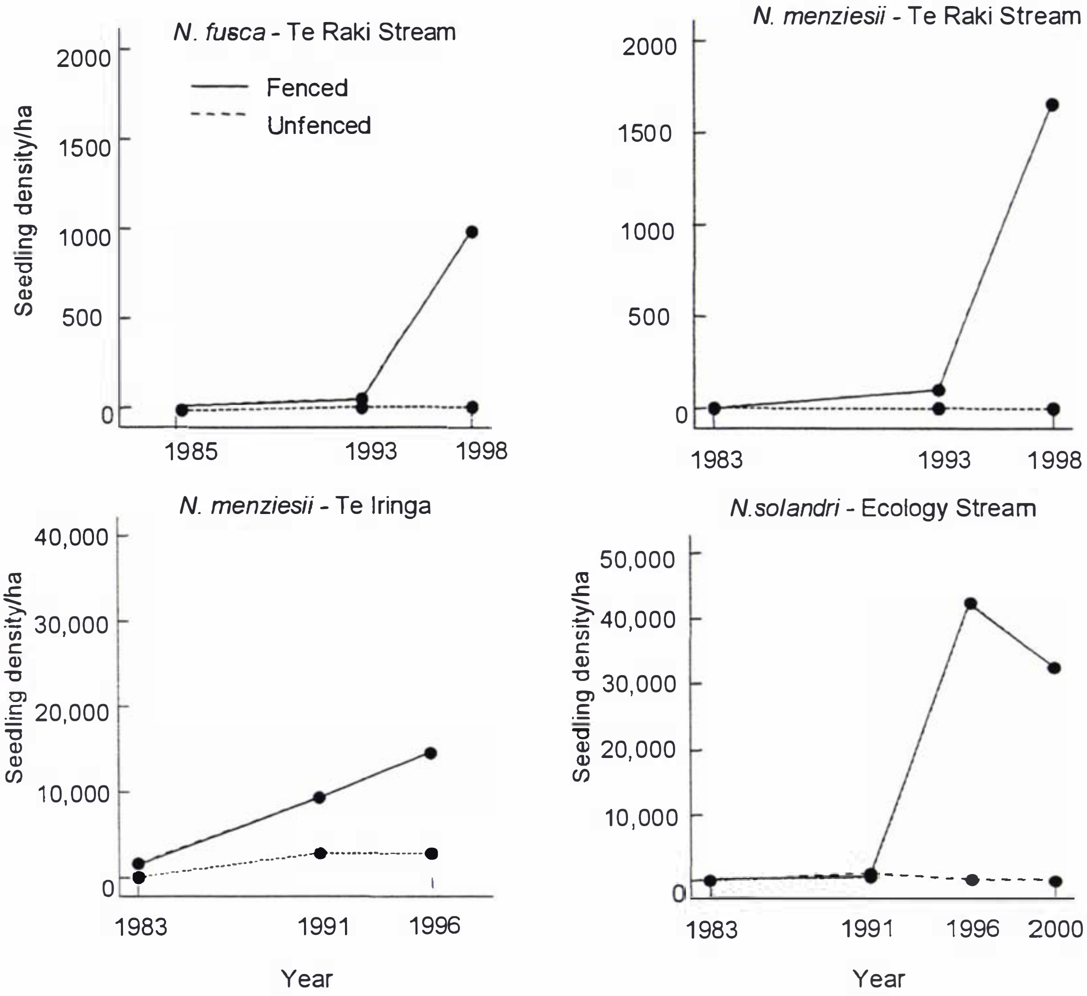

Fig. 4.6. *Nothofagus* seedling (15–135 cm high) abundance in three paired exclosure plots, Kaimanawa Forest Park.

4.3.5 Analysis of understorey community composition in the southern Kaimanawa

Canonical Correspondence Analysis (Table 4.6, Fig. 4.7) showed significant changes in understorey species composition, shifting away from woody species towards herbaceous species and ferns (many of which can form prostrate 'mats'). The shrubs and small tree species that became less common included *Coprosma* spp., *Cyathodes fraseri, Cyathodes juniperina, Dracophyllum recurvum, Fuchsia excorticata, Gaultheria antipoda, Leptospermum scoparium, Neomyrtus pedunculatus, Olearia furfuracea* and *Olearia nummularifolia*, and the other species in decline included the fern *Sticherus cunninghamii*, the climber *Rubus cissoides*, and *Lycopodium* species. The herbaceous species that increased their dominance, and had >15% variation in their CCA scores explained by environmental variables, included *Chiloglottis cornuta*, *Corybas trilobus*, *Epilobium* *pedunculare*, *Gnaphalium ruahinicum*, *Hydrocotyle moschata*, *Lagenifera pinnatifida*, *Lagenifera strangulata* and *Sagina procumbens* and the increases in fern species included *Grammitis billardieri*, *Histiopteris incisa* and *Hymenophyllum* species. A rush (*Juncus novaezelandiae*) also increased its dominance. When prostrate and rosette-forming herbaceous plants such as *Epilobium*, *Hydrocotyle*, *Lagenifera* and *Viola cunninghamii* are in high abundance they tend to form mat-like turfs. *Caladenia lyallii*, *Coprosma pseudocuneata*, *C. foetidissima* and mountain beech increased their importance over time with increasing site slope and decreasing altitude and all had >15% variation in their CCA scores explained by environmental variables.

Table 4.6. CCA on vascular understorey species composition from 35 permanent plots established in 1981/82 and re-measured in 1999/2000 in southern Kaimanawa. Importance values for each plot were calculated using frequency occurrence in 24 sub-plots. Factors of time, altitude aspect and slope (and their interactions) are displayed in order of their inclusion in the forward selection procedure. The variance each factor explains (γ marginal), the additional variance explained at the time each factor was included (γ conditional) and the significance of the variable at that time (*P*) are shown. Eigenvalue analysis showed that the first four axes explained 36.6%, 34.4%, 18.3% and 10.7% respectively.

Variable	γ marginal	γ conditional	*F*	*P*
Year	0.07	0.07	2.64	0.005
Slope	0.04	0.04	1.69	0.030
Year-Aspect-Altitude	0.04	0.04	1.24	0.655
Aspect	0.03	0.02	1.00	0.465
Year-Aspect	0.02	0.03	1.21	0.155
Altitude	0.02	0.03	0.80	0.525
Year-Altitude	0.02	0.03	1.48	0.035
Year-Slope	0.02	0.02	0.74	0.775

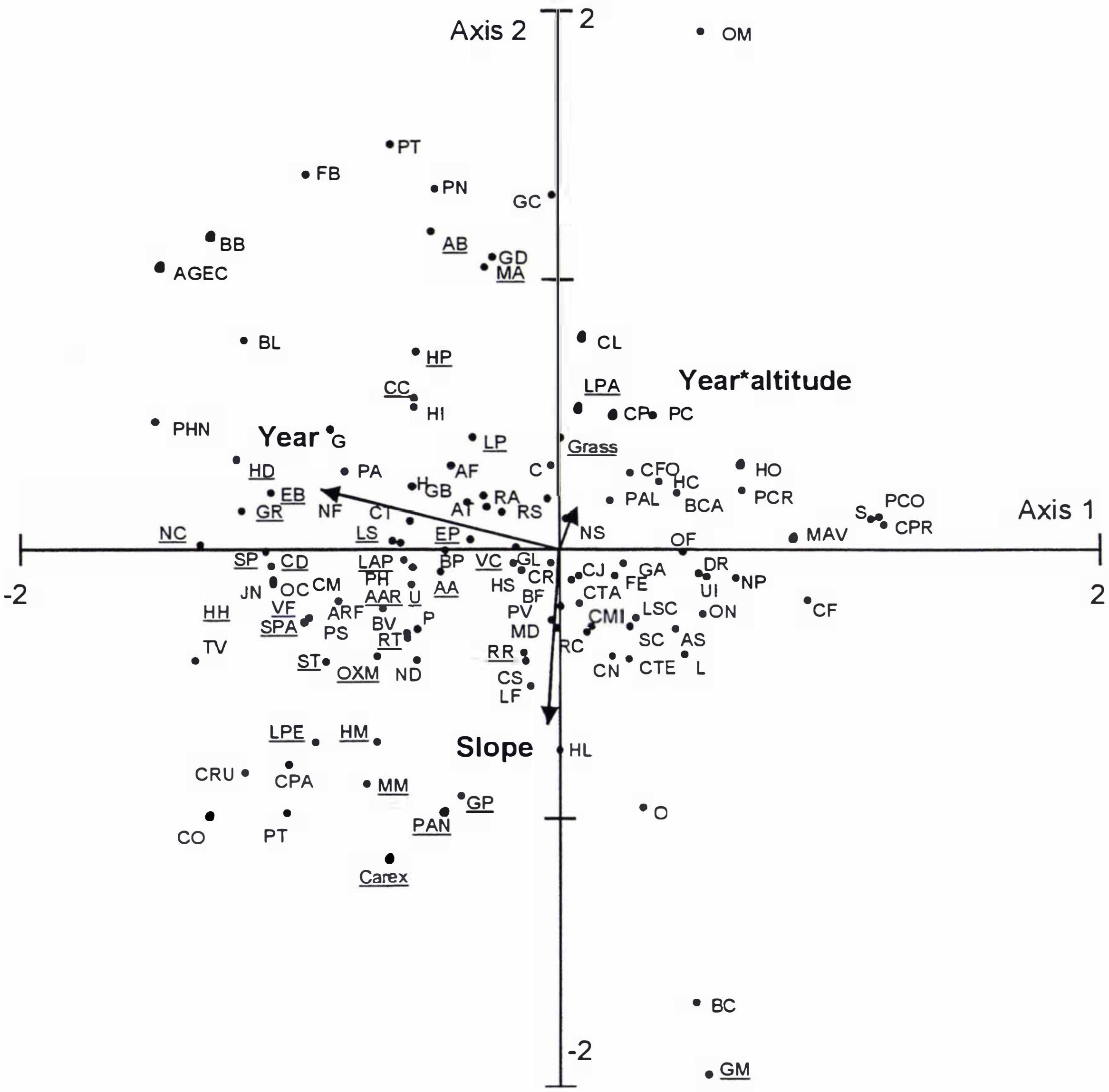

Fig. 4.7. CCA of southern Kaimanawa understorey composition. Significant environmental factors are displayed. Axis 1 explained 36.6% of total variation and axis 2 34.4%. Species positions are shown using abbreviations (full names are listed in appendix 1). Turf-forming species are underlined.

4.4 Discussion

This study has shown significant temporal changes in the abundance of smaller trees (20–100 mm DBH) in Kaimanawa Forest Park and changes in understorey composition in southern Kaimanawa Forest Park, similar to some of the changes described in chapter two. Despite these changes there was no evidence from ordination analysis of an overall change in overstorey composition. Previous studies throughout New Zealand indicated that there would have been a substantial shift in understorey composition within a decade of deer reaching an irruptive peak in Kaimanawa Forest Park (e.g., Jane and Pracy 1974; Stewart and Burrows 1989). These historical shifts favouring unpalatable seedling regeneration now seem to have been translated into shifts in the abundance of small trees. If this trend continues it is likely that the composition of stand dominants will be affected in the future. Although there are several alternative explanations for the changes observed in this study, including normal successional processes or browsing by invasive brushtail possums, ongoing browsing by introduced deer is the single most plausible explanation. Four main lines of evidence support an explanation of deer-induced forest modification in Kaimanawa Forest Park. Firstly, there was a general trend for the stem density of small trees of deer-unpalatable species to increase while deer-palatable species decreased in density. Secondly, there was structural evidence of very little regeneration of the most palatable sub-canopy and canopy species. Thirdly, three paired deer exclosure plots showed increases in *Nothofagus* seedling abundance in fenced plots while unfenced plots had low seedling abundance (see also results from Ruatahuna exclosure, section 2.3.8). Finally, there was evidence of a shift in southern Kaimanawa understorey composition towards herbaceous, turf-forming species.

Unpalatable trees capable of forming a sub-canopy such as *Neomyrtus pedunculatus* and *Pseudowintera colorata* increased in abundance by between two and four times between the northern Kaimanawa 1979–80 and 1998 surveys. Increases of *Pseudowintera colorata* tended to be associated with warmer, north-facing sites, which might be more favoured, by deer as well as having increased light availability. There was some evidence that *Carpodetus serratus* also increased in abundance. Although this species is palatable to deer it has a divaricating growth form that makes it tolerant to browsing as deer may find its small leaves protected by numerous branches. In contrast, seedlings of the palatable *Griselinia littoralis* and *Weinmannia racemosa* did not appear to be recruited into the > 75 cm height tier. There were signs that lack of regeneration was affecting the abundance of these species as small trees.

Canonical Correspondence Analysis (CCA) failed to show any shift towards a browse-resistant community in the overstorey, even though some individual unpalatable species increased in dominance as small trees while some palatable species declined. In the future this apparent imbalance may be translated through to compositional changes in stand dominants, but this is not yet apparent. This could be because only some sites are vulnerable to deer impacts and therefore large shifts in composition at all sites cannot be expected. Without data on deer abundance at individual plot sites or deer abundance trends over time and with season it is not possible to show this conclusively. Compositional shifts could occur at a subset of vulnerable sites, to a set of key species, and not be detected by ordinations. CCA might not detect these types of changes if most species in most plots do not change in abundance, and if key species that do change in abundance do not occur at the same sites.

Levels of resource availability and productivity may affect plant competitive interactions and responses of some species to herbivory (Van der Wal et al. 2000). Results from chapter three suggest that absolute deer impacts might be higher at potentially more productive, low basal area sites. In New Zealand, palatable woody plants tend to be small tree species limited to more productive low-altitude, high-fertility sites (Wardle 1984; Coomes et al., *In Press*) and tend to have high nitrogen and low lignin concentrations in their foliage. *Weinmannia racemosa* is a notable exception to this generalisation (Forsyth, Coomes and Nugent 2001). This may mean that highly productive sites with fast-growing plants are most vulnerable to modification by ungulates, as well as being more attractive to deer because of the high levels of nutrients in plants at these sites. Thus, if deer are affecting forest regeneration then the problem is likely to be more serious at sites on the potentially more productive lower slopes and river terraces, such as the Ecology Stream exclosure site where conspicuous regeneration occurred once deer were excluded (Fig. 4.8). Such findings are reported by McShea and Rappole (2000) in the U.S.A. and Smale, Hall and Gardner (1995) in New Zealand.

The three exclosure plots showed that once deer browse was removed, all three *Nothofagus* species present increased in abundance through increased growth or survivorship. In the Ecology stream exclosure, within two decades seedling abundance increased from what is typically found in the Kaimanawa Region (664 stems ha^{-1}; section 3.3.1 and Fig. 3.3) to what is typically found in mountain beech forests without sika deer present (22,025 stems ha^{-1}; section 3.3.1 and Fig. 3.2). This reinforces the view that sika deer could affect the regeneration of *Nothofagus* species in northern and southern Kaimanawa Forest Park as has been found in other exclosure plot studies in *Nothofagus* forests (Wardle 1984). If this occurs at sites critical for canopy regeneration, canopies could shift away from beech dominance towards shrubs and small trees that are resistant to deer browse (such as *Leucopogon fasciculatus, Neomyrtus pedunculatus, Phyllocladus alpinus* and *Pseudowintera colorata*). This evidence of deer impact was confounded by disturbance (measured through changes in basal area), which differed between fenced and unfenced plots, and a lowering of seedling abundance between 1996 and 2000 at Ecology Stream. Lowered basal area is usually associated with increased nutrient and light availability and so lowering of basal area is likely to increase seedling growth. *Nothofagus* seedling abundance increased significantly between surveys in the northern Kaimanawa but without replicated exclosures and longer-term monitoring it is not possible to determine if this increasing abundance is sufficient to maintain a forest canopy at all sites. Overall, red beech seedlings increased in abundance in the northern Kaimanawa over the study but were at approximately half the abundance on north aspects compared to south aspects in the 1998 survey. This may be because deer have higher browsing impact on the north-facing sites or because of competitive exclusion from plants better suited to these warmer sites. Because of the high spatial variation in seedling abundance it is most likely that some sites have sufficient seedling regeneration to maintain a canopy while others do not. This might be related to high spatial and seasonal variation in deer abundance at a stand scale. Evidence for deer-induced regeneration failure is also found in South American *Nothofagus* forests; Veblen, Hill and Read (1989) showed that red deer introduced between 1911 and 1936 were impeding the regeneration of *Nothofagus dombeyi* in Argentina.

The low basal area, conspicuous tree-fall, and high proportion of standing dead trees recorded in the 1981/82 southern Kaimanawa survey show that a large disturbance event, probably a tropical cyclone, is likely to have occurred in the study area less than two decades prior to plot establishment. In this area there was little evidence of density-dependent tree mortality despite evidence of disturbance and recruitment into the 20–120 mm size classes. Deer-induced mortality could be replacing natural stand thinning processes but this is impossible to determine without replicated exclosure plots. There was evidence of increased tree mortality at lower altitude sites, and stands of lower basal area in the southern Kaimanawa. It would be expected that canopy opening through disturbance would increase opportunities for regeneration but in fact there was a decrease in mountain beech seedling abundance at low altitude sites. This may exacerbate any canopy replacement problem associated with increased tree mortality at these sites.

In southern Kaimanawa, CCA shows evidence of compositional shifts in the understorey in the last two decades, away from shrubs and towards unpalatable ferns and browse-resistant herbaceous species capable of forming turf communities. The most plausible explanation for this is that ongoing deer browsing is capable of replacing palatable shrub species with browse-tolerant herbaceous turf communities in Kaimanawa Forest Park. In nearby Urewera National Park an exclosure plot study demonstrated deer-induced compositional shifts from palatable to unpalatable shrub species (Allen, Payton and Knowlton 1984) as did Wardle et al. (2001) at other New Zealand exclosure plots. This study is the first to show clear compositional shifts from shrubs to herbaceous species across extensive areas of New Zealand forest. These turf species, while being palatable to deer, are often tolerant of browse due to their prostrate growth form which allows them to be grazed to a low, dense turf. Instead of increases in turf communities being a response to herbivory it is possible that this is a response to increasing basal area and overstorey tree abundance following storm damage prior to plot establishment. Although it seems unlikely that increased competition for nutrients and light associated with increasing basal area would favour turf-forming herbs (Fredericksen et al. 1999), this possibility cannot be dismissed without further evidence from stands from which deer are excluded for a number of years following a canopy disturbance event. The competitive relationships between these turf communities and mountain beech regeneration will be explored in more detail in chapter six.

Deer-induced compositional shifts might be largely irreversible, even after deer are removed, if slower-growing, unpalatable or browse-tolerant species are able to gain an advantage once the faster growing palatable species are removed (Wardle et al. 2001). Permanent plot data suggests that shifts towards unpalatable or browse-tolerant species have occurred in the northern Kaimanawa red and silver beech forest, and that the induction of a vegetative turf has occurred in the southern Kaimanawa mountain beech forest. If this turf does impede woody seedling establishment, then compositional shifts may not be completely reversible at these sites, even in the absence of deer browse. In contrast, exclosure plot data showed recovery in *Nothofagus* seedling growth and abundance once deer browse was removed, in comparison to adjacent unfenced plots.

Closer examination of the data showed that tree deaths in two of the exclosures potentially confounded this interpretation of recovery following deer exclusion. In the long term, deer might shift successional pathways by removing otherwise competitive indigenous plants and encourage the establishment of unpalatable species. If deer browse prevents regeneration of some species for long enough, local seed sources may be eliminated and this could prevent their re-establishment. As the seed sources of important food plants for deer, such as *Griselinia littoralis* (Nugent 1988; Nugent and Challies 1988) are removed through lack of regeneration, food availability for deer might decline. The consequences of this on forest impacts are difficult to predict. Deer impacts might increase as deer switch to more unpalatable food sources. Alternatively, impacts might decrease if deer populations decline considerably.

Long-term data on plant population and community changes are an essential resource for conservation management but the interpretation of such data is speculative because the information is not derived from experimental manipulation. Other possible causes of compositional and structural change are successional processes and the impacts of other introduced herbivores such as brushtail possums. Nevertheless, I believe that deer browse is the main factor influencing structural and compositional shifts observed in this study. Successional processes are likely to favour palatable species that in New Zealand, and sometimes in other temperate hardwood forests, tend to be large-leaved and adapted to low light environments, or fast-growing species that are more competitive in gaps (Grime 1979; Coomes et al. *In Press*). In this study, fast-growing and larger-leaved palatable species declined in abundance. The dietary preferences of arboreal brushtail possums mean that they are also unlikely to explain the compositional changes observed in this study (Owen and Norton 1994).

In conclusion, there is evidence of ongoing tree abundance and structural changes in the northern Kaimanawa overstorey consistent with deer affecting the regeneration of palatable species. Less-palatable species appear unaffected, or to be increasing in abundance. There is some evidence in the southern Kaimanawa of compositional shifts away from shrubs to herbaceous plants in the understorey. While exclosure plots showed that deer were likely to be reducing *Nothofagus* seedling abundance, there was no evidence in this study that this had yet affected the stand dominants. Findings could have been strengthened if there was information on deer abundance and nutrient availability. Future monitoring studies of this type should use replicated exclosures and collect serial information on soil fertility, water availability, light availability and deer abundance to show the relationship between these important environmental variables and changes in species composition through time. Individually tagging seedlings and saplings would also be worthwhile, compared to the counts used in this study, as they also provide information on seedling growth, mortality and recruitment as well as probably more accurate measures of abundance. Tagged seedlings are used in chapter five to monitor the growth of mountain beech seedlings with and without the presence of deer.

If the changes observed in this study reflect the impact of two post-irruptive introduced deer populations and not natural forest succession following disturbance, then Kaimanawa Forest Park conservation managers will need to implement intensive deer control to reduce deer impacts. With time, compositional changes may become increasingly irreversible if deer have shifted competitive balances between plants, altered successional pathways and ecosystem processes, or eliminated seed sources.

This study has demonstrated the value of monitoring vegetation using permanent plots established by the New Zealand Forest Service. Similar selected permanent plot networks previously established in other forests (ca. 6,500 plots; Wiser, Bellingham and Burrows 2001) should also be remeasured in a prioritised manner and results contrasted with this study. The establishment of more paired exclosure plots in the Kaimanawa Region using a randomised procedure would provide evidence of deer impacts in the future with fewer potentially confounding effects of natural forest succession. Future permanent plot monitoring in Kaimanawa Forest Park should examine deer impacts in the local context of primary production, soil chemical and biotic characteristics, and light availability.

Northern Arm exclosure, Mt Maungaorangi, northern Kaimanawa Forest Park

CHAPTER FIVE

Deer culling and mountain beech seedling growth

5.1 Introduction

It has been apparent for over two decades that browsing by deer has suppressed mountain beech regeneration in the central North Island of New Zealand (Wardle 1979; Jenkins 1982; Apthorp 1983; Fleury 1993; Allan 1997a; Allan, Stewart and Allen 1997; chapter two). This is due to the intense browsing of sika deer (chapter three) which has altered forest composition in the Kaimanawa Region (chapter four). The aim of this study is to determine if the suppression of mountain beech regeneration by deer can be reversed through deer culling and deer exclusion. I use a series of 10 m x 10 m exclosure plots established between 1997-1999 to show the effects of three deer culling treatments and deer exclusion on seedling growth. Studies using permanent vegetation plots (some with deer exclusion fencing) in Kaweka (Allen and Allan 1997; Allan 1997a; Allan, Stewart and Allen 1997; chapter three) and Kaimanawa Forest Parks (Apthorp 1983; chapter four but see Brabyn 1988; Fraser and Speedy 1997) have suggested that beech regeneration is threatened by deer at critical sites. These are sites where natural canopy tree death has occurred through episodic disturbance (Hosking and Hutcheson 1988) and where browsing by deer has reduced the growth of mountain beech seedlings. Canopy decline normally creates opportunities for vigorous mountain beech seedling regeneration (Osawa and Allen 1993; Harcombe et al. 1998) through increased light (Stewart, Rose and Veblen 1991) and nutrient availability to seedlings (Allen, Clinton and Davis 1997). However, in the Kaweka and Kaimanawa mountains, low basal area sites are now dominated by browse-resistant and browse-tolerant small-leaved shrubs (e.g. *Coprosma* "taylorae", *Myrsine divaricata* and *Phyllocladus alpinus*; chapters two and three) rather than by young beech trees. Chapter three showed that mountain beech regeneration failure was widespread in the Kaimanawa Ecological Region due to intensive browsing by sika deer, and there is also evidence of an overall increase in the dominance of browse-resistant, turf-forming species as ground cover in southern Kaimanawa mountain beech forest over the last two decades (chapter four).

There has been a long history of deer control in central North Island beech forests, where deer culling records are available from 1958 (Davidson and Fraser 1991). During the 1970's the New Zealand Forest Service became increasingly concerned at apparent deer-induced regeneration failure and continued to undertake government-funded ground-based deer culling (Wardle 1979), which lapsed in 1988. Following the production of Allen and Allan's (1997) report on mountain beech regeneration, a working party of conservation, hunter and Department of Conservation representatives concluded that increased deer control was again required to address the problem of failure of mountain beech to regenerate, but no agreement could be reached on the best method of control. Options included increased recreational hunting, allowing access to commercial hunters, government-funded aerial culling and ground-based 1080-laced gel poisoning (Sweetapple 1997). In 1998, a combination of government-funded aerial deer culling was implemented, along with increased recreational and commercial hunting access. A monitoring system was established at this time to determine the effects of these management options.

The main objective of this study was to determine if intensive deer culling could lower indices of deer abundance and reduce the impact of deer browsing on mountain beech seedling growth. To determine if low-, medium- or high-intensity deer culling treatments are effective, I compared seedling growth under these hunting regimes between paired fenced and unfenced plots over three summer growing seasons.

5.2 Methods

This study is based on four treatment areas, and low-, medium- and high-intensity deer culling intensity levels. All three levels of treatment were applied in Kaweka Forest Park, with an additional low-intensity level within adjacent Kaimanawa Forest Park (Fig. 5.1). In October 1998, a trial of government-funded aerial deer culling was initiated in central Kaweka Forest Park by shooting deer from helicopters, along with a relaxation of restrictions for unsubsidised commercial hunters (high-intensity culling). Unsubsidised recreational hunters were also provided with additional helicopter access points in this area.

A monitoring program based on paired fenced and unfenced 10 m x 10 m plots was established at ten sites in this area in the summer field seasons (October – March) of 1997/98 and 1998/99 to assess the effect of intensive management on mountain beech seedling growth. Fences (1.8 m high) were used to exclude red and sika deer, the only ungulates present, but allowed access for small herbivores such as the brushtail possum (*Trichosurus vulpecula*) which is not considered to affect mountain beech regeneration (Rose et al. 1993, Pekelharing, Frampton and Suisted 1998).

In north-western and eastern Kaweka Forest Park, unsubsidised recreational and commercial hunters were encouraged to kill deer through provision of additional helicopter landing sites (medium-intensity culling). Five pairs of fenced and unfenced plots were established in north-western Kaweka Forest Park to monitor this form of deer culling.

In western Kaweka Forest Park, ease of hunter access was not changed, with helicopter access restricted to two landing sites for recreational hunters (low-intensity culling). Paired plots were also established at two sites in this area. In Kaimanawa Forest Park, paired plots were also established at four sites where commercial hunting was not permitted and helicopter access for recreational hunting was restricted to six weeks in November and December (low-intensity culling).

5.2.1 Treatment area descriptions

The high-intensity culling area (12,100 ha) has approximately 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 (Fig. 5.1). This area was selected for intensive helicopter-based deer culling because it has extensive areas of forest collapse allowing deer to be seen and shot. Allen and Allan (1997) estimated that *c.* 10% of 20 m x 20 m stands throughout Kaweka Forest Park had low occupancy by canopy trees. Commercial venison recovery tended to be limited to the open mountain top areas where carcasses could be quickly recovered.

The medium-intensity culling area had improved, 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 as opposed to red and silver beech, and has fewer alpine grassland areas. In chapter two, analysis of 20 m x 20 m plots and aerial photographs shows that in this area *c.* 10% of mountain beech stands had significant canopy breakdown and low seedling numbers.

The Kaweka low-intensity culling area is located south-west of the Ngaruroro River. Two helicopter landing sites in this area enable recreational, but not commercial, hunters to access two huts to base their hunting activities. This area has extensive modified alpine grasslands and less conspicuous canopy collapse.

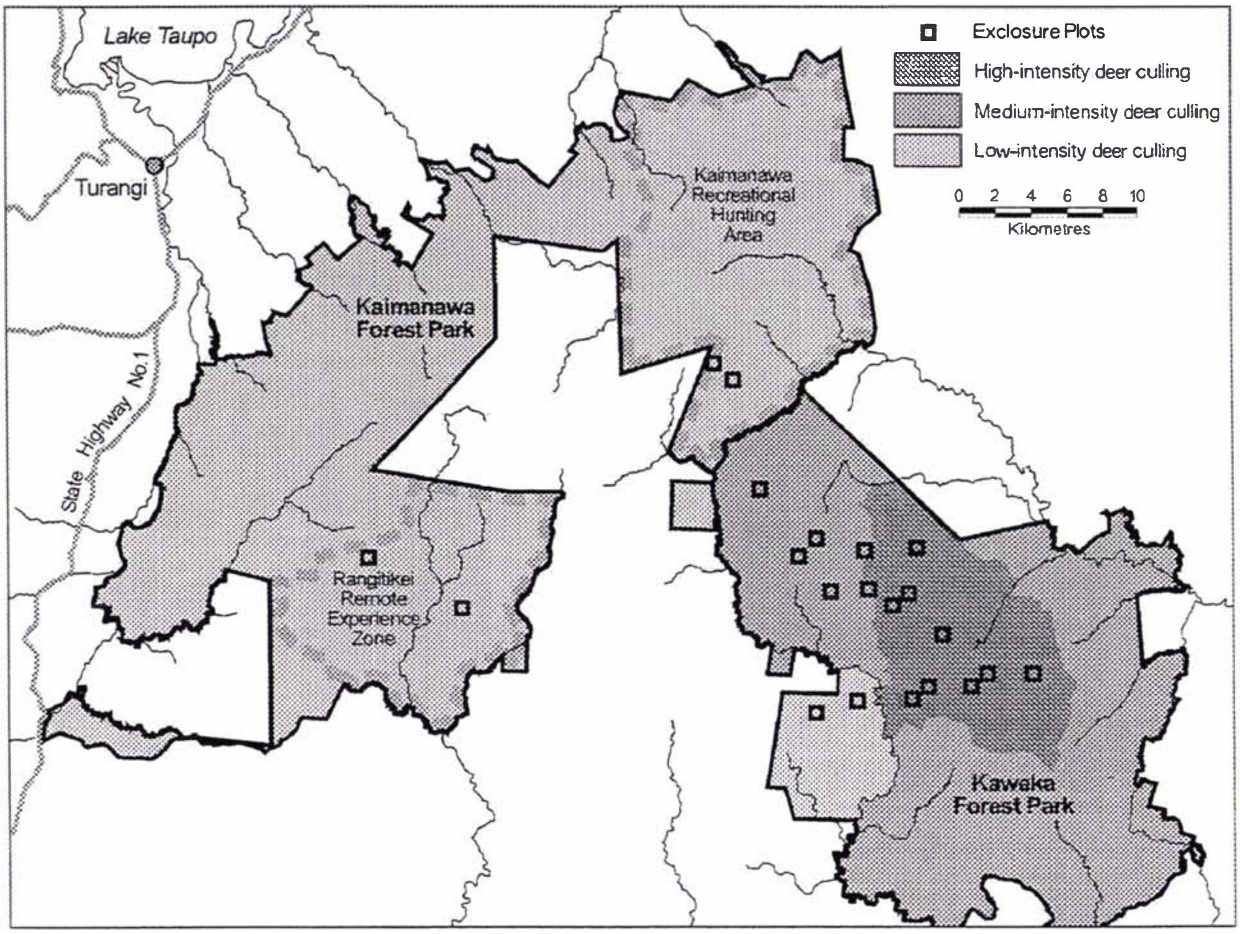

Fig. 5.1. Study site showing paired exclosure plot locations used for mountain beech seedling growth comparisons, in high-, medium- and low-intensity culling areas. Boundaries for Kaimanawa Recreational Hunting Area and Rangitikei Remote Experience Zone are also displayed.

Plots in the Kaimanawa Forest Park low-intensity culling area (76,500 ha) are located in the vicinity of Mt Maungaorangi in the Kaimanawa Recreational Hunting Area (24,000 ha) and in the heads of the Makomiko and Ecology streams in the Rangitikei Remote Experience Zone. Commercial venison recovery operations and spring helicopter access by recreational hunters were allowed in the southern and western part of Kaimanawa Forest Park. I assume that the relatively low numbers of deer reported shot by spring recreational hunters in the Rangitikei catchment between 1993 and 1999 (290 deer shot; 0.2 deer day^{-1}) and by commercial hunters throughout Kaimanawa Forest Park (except for Recreational Hunting Area) from 1st June to 1st October 2000 (177 deer recovered, 2.6 deer hour^{-1}, 0.34 deer km^{-2}) prior to the establishment of this study did not greatly alter deer numbers. In the areas where exclosure plots were established in Kaimanawa Forest Park, it is probable that recreational and commercial hunters removed less than 1 deer km^{-2} year^{-1}, which is unlikely to have reduced deer abundance.

5.2.2 Frequency of occurrence of deer faecal pellets and pellet group density

As a relative measure of deer abundance, deer pellet group density was indexed annually at fifteen sites in Kaweka Forest Park. At each site, one hundred and sixty 2.2 m radius plots were spaced at 10 m intervals in a cruciform arrangement according to Taylor (1999). Intact pellet groups centred within each of these plots were counted. Fourteen of these sites were adjacent to paired fenced and unfenced plots. The presence or absence of intact deer pellets was also recorded within one hundred and sixty 1.14 m radius plots (milli-acre) according to Baddeley (1985). The proportion of these plots occupied by at least one intact pellet was determined for each site. I have used pellet frequency of occurrence in this study (along with pellet group counts) to allow comparison with other central North Island studies and because it is easier to consistently apply by only requiring a decision on whether intact pellets are present or absent in a 4 m^2 plot rather than a count of discrete pellet groups in a 15 m^2 plot. The advantage of pellet group count techniques is that deer abundance can be estimated if deer defecation rates and rates of pellet deterioration are known.

5.2.3 Vegetation plot measurement procedure and analysis

Allan (1997b) and Ward (1997) describe the vegetation sampling strategy adopted and Taylor (1999) provides a full description of methods used to select and measure 10 m x 10 m fenced and unfenced plots. Plots were established between November 1997 and March 1999 at subjectively selected low-basal area mountain beech forest sites with a variety of seedling densities. Allen's (1993) 20 m x 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 m^2 ha^{-1} (section 2.2.5). Sites tended to be in areas of extensive forest collapse, and often near the treeline with conspicuous deer browse on mountain beech seedlings. Seedling (5–160 cm high) density in plots varied between 0.03 and 2.45 seedlings m^{-2}. This compares with a mean value of 1.6 seedlings m^{-2} (15–135 cm) throughout Kaweka mountain beech forest (chapter two).

At the four Kaimanawa Forest Park, and at three high-intensity culling sites, all seedlings (5–160 cm high) were measured in each 10 m x 10 m plot. At the remaining 15 sites, where field crews determined that it was not practical to measure all seedlings in the time available, seedlings were measured from only half of the 16 sub-plots (systematically selected based on Allen 1993). When a seedling was sampled, a numbered aluminium tag was wired to its stem and its pull-up height was measured in cm 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 the growth results correspond to deer abundance in the previous growing season. Winter browse of the previous season's growth will also affect seedling height, as it can not be allowed for in measurement.

Annual seedling relative growth rates were calculated for each seedling for each of spring 1998, 1999, 2000 and 2001 seasons as:

$$(\log_e \text{re-measured height} - \log_e \text{initial height})/\text{year}$$

I used annual relative growth rates of seedlings (hereafter seedling growth) because this is a commonly used index of plant growth (e.g. Broome, Mendelssohn and McKee 1995; Swanborough and Westoby 1996; Oba, Mengistu and Stenseth 2000; Walters and Reich 2000) that reduces bias in seedling absolute growth rates with varying seedling heights. This was necessary because although there were no significant differences in initial seedling heights between fenced and unfenced plots (F=0.002; df = 1,18; P = 0.964) there were significant differences among treatment areas (F=5.982; df = 3,18; P = 0.007). Seedling heights in 1998/99 were highest in the low-intensity culling area (least square mean height ± SEM = 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 were used to examine the relationship between seedling growth between fenced and unfenced plots and 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 pseudo-replication between seedlings and plots at the same site.

5.3 Results

5.3.1 Deer control

In the 1998/99 field season, 23 aerial deer culls were undertaken in the intensive culling area, totalling 45 hours of flying time. After the first five culls, records of the numbers of deer seen were kept in addition to the numbers shot. Of 355 deer seen on the last 18 hunts, 306 were shot of those seen (86%). Kill rates reduced by 10% during the 1999/2000 season when 32 culls were undertaken in 73 hours flying (Fig. 5.2). Of a total of 636 deer seen (88%) were shot. In the 2000/2001 season kill rates reduced by a further 20%. Of 514 deer seen, 90% were shot in 30 culls during 76 hours flying. Overall, in the first three seasons 93% of deer killed were identified as sika and 7% as red deer. Kill rates continued to decline in the 2001/2002 season, although this reduction in deer abundance would have had little effect on pellet counts or seedling growth rate data collected from that season, because most pellet and seedling sampling had occurred prior to the most intensive culling activity in late January and February.

Commercial hunters removed 104 deer carcasses during the June to November 1998 season, 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. Notably, reported kills per hunting day declined from 0.30 in 1997, 0.26 in 1998, 0.23 in 1999, to 0.21 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, 14% in 1998, 17% in 1999, and 26% in 2000. Thus, the increase that was recorded in numbers of deer shot is likely to be related to increases in hunter permit returns rather than increasing numbers of deer killed as kill per unit effort has declined.

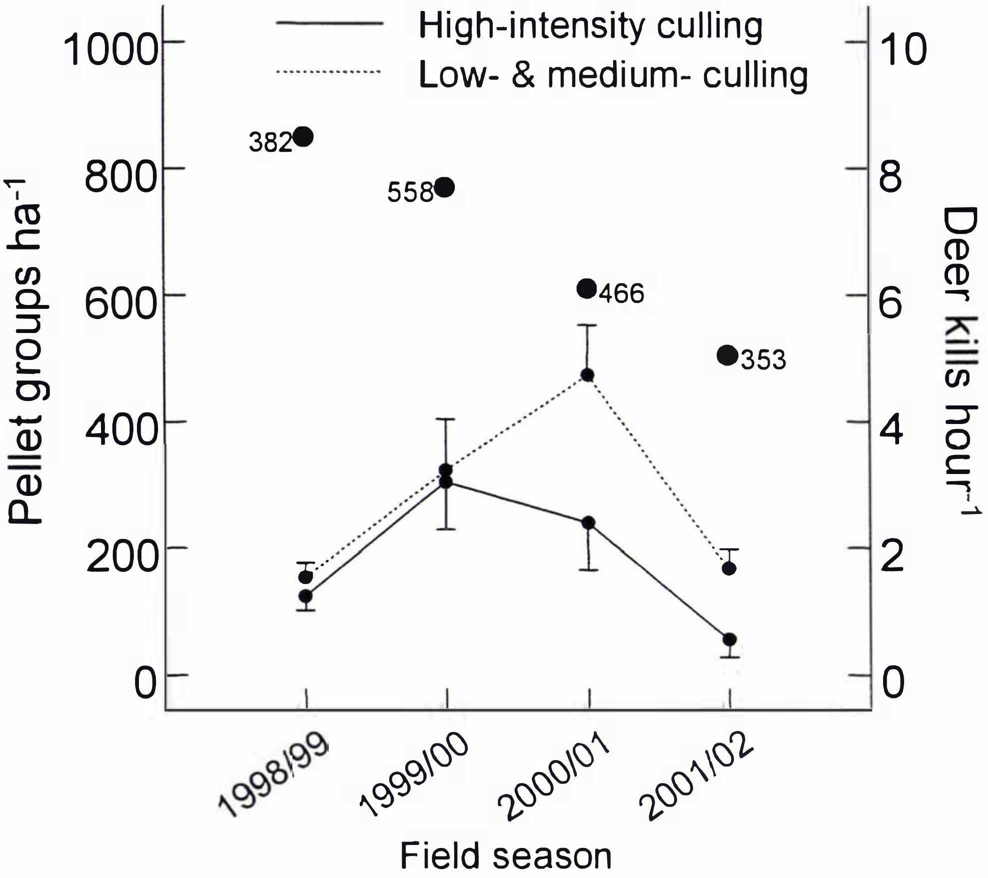

Fig. 5.2. Mean pellet group counts (± SEM), comparing high-intensity deer culling (n = 7 sites) with medium- (n = 5) and low-intensity (n =3) treatment areas. Data for medium- and low-intensity treatment areas was pooled because of low sample size. Also displayed are the numbers of deer killed per hour (●) by aerial deer culling (labelled with numbers of deer killed) in each summer culling season.

5.3.2 Pellet frequency of occurrence and pellet group density

Pellet frequency of occurrence at 15 sites differed significantly among years and varied between the high-intensity culling area and the pooled low- and medium-intensity culling areas (Table 5.1; $F_{3,11} = 4.453$; $P = 0.028$). Results for pellet group densities were generally consistent with trends for pellet frequency of occurrence. There were significant differences in pellet group densities 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. 5.2). By the 2000/2001 season however, there was 47% lower pellet group densities in the high-intensity culling area compared to the low- and medium-intensity areas. By the 2001/2002 season, pellet group densities in the high-intensity culling area were 67% lower.

Table 5.1. Deer faecal pellet frequency of occurrence (%) from 15 sites and four field seasons.

Culling intensity	1998/99 ± SEM	1999/2000± SEM	2000/01± SEM	2001/02± SEM
High	11.9 ± 1.8	22.4 ± 3.6	20.8 ± 4.5	6.6 ± 2.7
Medium and low	12.0 ± 1.9	20.3 ± 3.9	33.1 ± 4.8	16.9 ± 2.9

5.3.3 Seedling growth

Mountain beech seedling growth rates were consistently higher in fenced plots compared to paired unfenced plots in all three growing seasons (Table 5.2; $F_{6,34} = 4.220$; $P = 0.003$). 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 ($F_{6,34} = 6.078$; $P < 0.001$). In the high-intensity area annual growth rates were generally high, particularly for fenced sites. 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 in comparison to fenced plots. Overall from 1998 to 2001 there was significantly higher seedling growth rates in the high-intensity culling area compared to the medium- and low-intensity culling treatments (Fig. 5.3; $F_{2,18} = 3.775$, $P = 0.043$). There was also some evidence that seedling growth was higher in the medium-intensity culling area compared to the low-intensity areas. In the low-intensity culling area, seedlings declined in height in unfenced plots in the 1998–1999 and 2000–2001 growing seasons, but there was always positive seedling growth in the medium-intensity culling area even outside fences.

A high degree of variation in the ratio of unfenced to fenced seedling growth is evident for different seasons' (Table 5.2). Spatial and temporal variation in deer browse may explain these anomalies, as variation between sites and growing seasons was much more pronounced in unfenced plots. Examination of raw data revealed that there was nearly twice the mean variation in seedling growth between 1998-1999, 1999-2000, and 2000-2001 in unfenced plots compared to fenced plots.

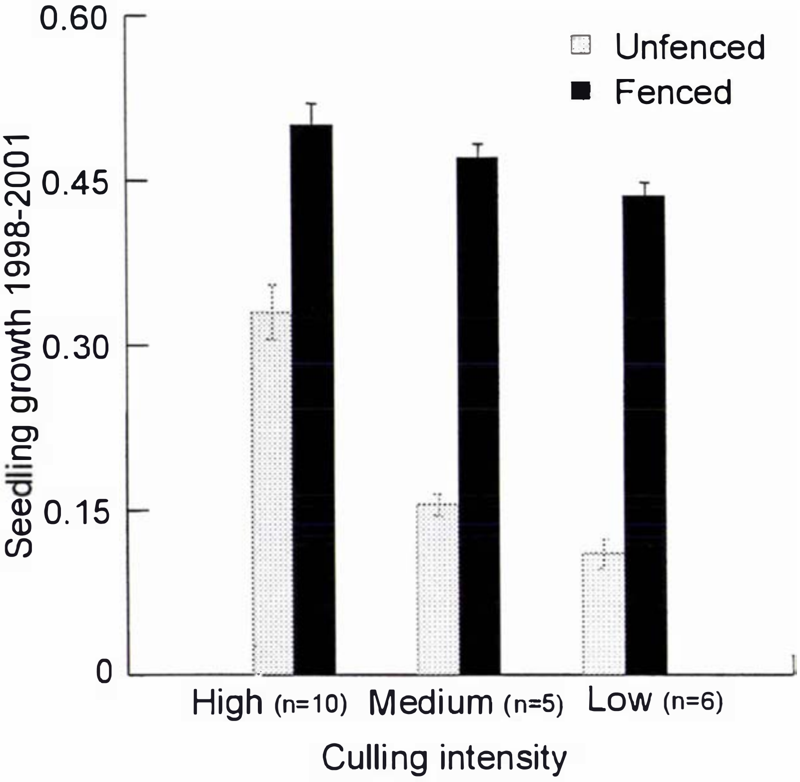

Fig. 5.3. Least square means of seedling relative growth rates (1998 – 2001 ± SEM) in fenced and unfenced plots with three levels of deer culling intensity at 21 sites.

Table 5.2. Least square means of annual seedling relative growth rates (RGR ± SEM), numbers of seedlings measured in 1998, 1999, 2000 and 2001 (N), seedling heights in 1998 (cm ± SEM) 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 ± SEM	RGR 99/00 ± SEM	RGR 00/01 ± SEM	N	Height 1998 ± SEM	1998 N
High unfenced (10 sites)	0.134 ± 0.020	0.072 ± 0.016	0.125 ± 0.016	850	32.9 ± 1.7	946
High fenced (10 sites)	0.181 ± 0.016	0.170 ± 0.013	0.147 ± 0.012	1088	31.0 ± 1.4	1188
Medium unfenced (5 sites)	0.097 ± 0.008	0.050 ± 0.007	0.007 ± 0.006	885	30.1 ± 0.8	989
Medium fenced (5 sites)	0.225 ± 0.010	0.143 ± 0.008	0.101 ± 0.008	680	34.3 ± 1.0	725
Low unfenced (6 sites)	-0.005 ± 0.011	0.117 ± 0.009	–0.001 ± 0.009	712	34.9 ± 1.0	866
Low fenced (6 sites)	0.141 ± 0.010	0.203 ± 0.008	0.096 ± 0.008	811	30.6 ± 1.0	930

5.4 Discussion

5.4.1 Changes in deer density

Between October 1998 and February 2001 more than 11 deer km^{-2} were shot using helicopters in the high-intensity culling 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. In contrast, recreational and commercial hunters appear to have accounted for < 1 deer km^{-2} $year^{-1}$. Thus, aerial deer culling is likely to have substantially reduced deer abundance compared to recreational and commercial hunting.

Pellet frequency of occurrence and pellet group density results are consistent with large reductions in deer abundance over three years in the high-intensity culling area, compared to low- and medium-intensity culling areas. Pellet group density suggests a 67% reduction in deer density over the three seasons, but this relies on several important assumptions. These include: 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 between areas; that deer abundance outside of 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. Net immigration from one treatment area to another would also bias results, although this is likely to be minimal because of low immigration rates of sika deer (Davidson 1976, 1979). Although reliable information is not available on how many deer were shot by recreational and commercial hunters in the intensive culling area, their influence on deer herd demographics is likely to be minimal. The estimated reduction suggests that there were 2098 deer in the 12,100 ha culling area (> 17 deer km^{-2}) prior to the commencement of aerial culling. If no substantial demographic or immigration response has occurred in the aerial culling area, deer densities were apparently reduced to < 6 deer km^{-2} by the end of the 2000/2001 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, Parkes and Tustin (1987) estimated that there were ≈ 3.5 deer km^{-2} in northern Fiordland, South Island. In the Tararua ranges pellet frequency of occurrence rates were used to estimate a deer density of 12 deer km^{-2} in 1959 (27% faecal pellet frequency of occurrence), which declined to 3 deer km^{-2} by 1975 (9 %), while deer culler kill rates were < 1 deer hunter day^{-1} between 1968 and 1975 for a harvest of between 0.3 and 1.1 deer km^{-2} (Bell 1976). Handford (1989 and 1991) estimated that in the late 1980's in the Aorangi, Tararua and Ruahine ranges, North Island there were $<$ 10 deer km^{-2}. 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 *Caperolus capreolus* in a conifer-broadleaf forest in Dorset, England varied between 34–76 deer km^{-2} between 1967–1980 (Gill et al. 1996). Thus, on an international scale, deer abundance in my central North Island study area is not exceptionally high, but compared to other New Zealand studies it is relatively high. This helps to explain why deer impacts in the central North Island are also high compared to other beech forests in New Zealand (Allen and Allan 1997; chapter three).

Over the longer term, there has been a change from red to sika deer dominance in my study site (Davidson and Fraser 1991), while 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 kills/hunter day. Between the 1968/69 and 1977/78 seasons kill rates were slightly higher (1.1 kills day^{-1}). There was then a sharp decline in the 1980/81 season (0.5 kills 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 one deer per hunter day. Data from 56 randomly located pellet presence transect lines supports kill rate information and show that deer numbers have remained steady between 1979 (11.1% frequency of occurrence) and 2000 (10.0% frequency of occurrence) in Kaweka Forest Park (chapter two). In comparison, this level of pellet presence is much lower than found by other authors in northern Kaimanawa Forest Park Recreational Hunting Area where two monitoring sites are located (Fleury 1979, 24.0%; Thomas 1985, 30.0%; Speedy 1986, 37.5%; Brabyn 1988, 35.2%; but see Whiteford 1983, 3.0%).

Pellet recording techniques have been widely used to index deer abundance (Bennet, English and McCain 1940; Riney 1957; Batcheler 1975; Focardi, Isotti and Tinelli 2002), but 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, Sinclair and Scott-Kemis 1976) have been suggested. However, in this study there was very little variation in pellet frequency of occurrence or group densities between the high-, and medium- and low-intensity culling areas, indicating that comparisons between treatment areas within seasons may be more reliable in the first two seasons.

5.4.2 Changes in seedling growth

Results show that fenced plots had consistently higher mountain beech seedling growth compared to 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 seedling growth between unfenced and fenced plots in the high-intensity culling area. This shows that deer impacts on seedling growth were much less after three seasons of aerial deer culling. In contrast, the difference in growth between unfenced and fenced plots remained consistently greater in the medium- and low-intensity culling areas. At some sites in these treatment area there was no growth, or seedlings actually were 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 provide the main evidence supporting the 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 mountain beech seedling growth.

To reliably determine the adequacy or deficiency of regeneration, data on recruitment and mortality as well as seedling growth rates are required, which will be undertaken for a sub-set of sites in chapter six. Chapter six shows no significant difference in annual mortality or recruitment of seedlings between fenced and unfenced plots. However, there were significantly more small seedlings (< 5 cm) high established in fenced plots compared to unfenced plots, which is likely to relate to differences in seedling establishment and survival after a beech mast seeding in autumn 1999. It remains to be seen whether this increase in seedling abundance will lead to more recruitment into larger size classes in fenced plots. Annual recruitment and mortality rates for established mountain beech seedlings (> 5 cm high) have not so far been affected by the complete removal of deer browse through 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, I assume that relative growth rate data from this study can be used as an index of canopy replacement in the absence of a complete demographic model. Because there was little reduction in seedling growth rates 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, seedling growth at canopy gap sites is unlikely to be sufficient for canopy replacement.

If deer-induced regeneration failure is allowed to continue in the study area, at many sites mountain beech forest may be transformed into shrub-land dominated by associations of herbs and grasses such as *Acaena anserinifolia, Hydrocotyle moschata, Lagenophora strangulata, Poa breviglumis, Ranunculus reflexus, Nertera dichondrifolia* and *Viola filicaulis* along with small-leaved, browse-resistant species such as *C.* "taylorae" and *Phyllocladus alpinus*. Chapter four showed that these browse-tolerant, turf-forming species have increased their dominance in mountain beech forest in southern Kaimanawa Forest Park. If regeneration failure also occurs in the lower altitude red- and silver-beech forest, unpalatable species such as *C.* "taylorae", *Neomyrtus pedunculatus* and broad-leaved species such as *Pseudowintera colorata* are also likely to dominate at sites where the stand dominants have collapsed. In addition to direct browsing pressure, mountain beech seedling growth and mortality are also affected by competition from the deer-induced small-leaved shrub (chapter three) and turf communities (investigated in chapter six). Thus, it seems likely that continuation of intact forest canopies may be retarded at some sites even after deer browse is removed. A similar case of deer indirectly preventing regeneration of canopy species has been recorded in North America after deer have induced a dense cover of ferns (Cretaz and Kelty 2002).

Based on the available evidence, I 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 strong support for sika deer culling as an effective technique for restoring mountain beech growth at sites with past canopy collapse. In contrast, the results show only a small benefit for seedling growth of medium-intensity deer culling by unsubsidised recreational and commercial hunting.

While this study has shown that impacts of deer browsing can be reversed through intensive culling, it is still unclear to what level deer densities need lowering to before responses in vegetation can be expected. Intensive deer culling at more regions in New Zealand would help to confirm the benefits for vegetation of deer population reductions, but intensive experimentation is required to determine the functional response of different plant species at different sites to deer abundance. This relationship is likely to be related to the probability of deer browsing individual seedlings of different species on a site-by-site basis. Therefore, future research needs to integrate studies of deer behaviour along with soil biota, and environmental and vegetative characteristics at a variety of scales.

Heavily browsed mountain beech seedlings and herbaceous turfs, southern Kaimanawa

CHAPTER SIX

Herbivory and plant competition reduce mountain beech seedling growth and establishment

6.1 Introduction

The aim of this study is to examine the relative importance of herbivory, resource availability and interspecific competition on mountain beech seedling demographics. An exclosure plot experiment examines how deer browsing, vegetation composition and site characteristics affect the establishment, growth and survival of naturally occurring mountain beech seedlings. A second experiment uses transplanted mountain beech seedlings to show the effects of light and nutrient resource limitation on seedling growth and survival. Simulated herbivory is used to show how browsing interacts with plant competition to limit plant growth. Previous theoretical, observational and experimental research on herbivory has tended to focus on seed herbivores and biomass removal by grazers rather than on seedling herbivory (Hulme 1996a). This is despite recognition that, compared to herbivory on seeds or adult plants, seedling herbivory has greater influence on plant demography (Harper 1977; Crawley 1983; Crawley 1988; Crawley 1992; Hulme 1996b). Seedling demographics are also strongly influenced by intra-specific competition and resource availability (Goldberg and Barton 1992), but even fewer studies have addressed relationships between herbivory, plant competition and resource availability (Van der Wal et al. 2000; Kullberg and Welander 2003). Some studies on the ability of seedlings to tolerate herbivory along gradients of resource availability have supported the view that individual plants in highly productive environments are best able to recover from herbivory (e.g. Coley 1983; McNaughton 1983; Maschinski and Whitham 1989; Louda, Keeler and Holt 1990; Rosenthal and Kotenen 1994; Bazzaz 1996; Crawley 1997; Meyer 2000). Other studies have shown that individual seedlings are better able to cope with herbivory in low- or medium-productivity environments (e.g. Hilbert et al. 1981; McNaughton and Chapin 1985; Van Auken and Bush 1989; Schmid, Miao and Bazzaz 1990; Bonser and Reader 1995; Van der Wal et al. 2000), or that resource availability is not important (Wandera, Richards and Mueller 1992). The ability of plants to successfully respond to herbivory can also vary with plant species or functional type (Hicks and Reader 1995). For instance in environments with high-resource availability monocotolydonous species may recover better and be more competitive under intense grazing, in comparison to dicotyledonous species (Hawkes and Sullivan 2001).

Studies that address the effects of competition and herbivory on plant communities along gradients of productivity and resource availability also provide conflicting conclusions (for reviews see: Swank and Oechel 1991; Belsky 1992; Goldberg and Barton 1992; Reader 1992; Cebrián and Duarte 1994; Gough and Grace 1998). Several studies have shown that plant communities best cope with herbivory in low productivity environments where resources are restricted (e.g. Hairston, Smith and Slobdkin 1960; Grime 1979; Van der Wal et al. 2000; Virtanen 2000; but see Van de Koppel et al. 1996) or that plant competition increases with increased herbivory (Huisman et al. 1999). Chase et al. (2000) concluded that the effects of herbivores in high productivity situations are diminished because of amelioration through increased species turnover. Relationships between herbivory, browse-tolerance, resource availability and productivity need to be better understood in order to develop fundemental rules for vegetation dynamics (Di Tommaso and Aarssen 1989; Louda, Keeler and Holt 1990).

Because New Zealand forests evolved with invertebrate, and recently extinct avian herbivores, many plant species are poorly adapted to the browsing strategies of mammalian herbivores (Greenwood and Atkinson 1977). This provides unique opportunities to study rapid responses of seedlings to herbivory and plant competition along gradients of resource availability.

In the Kaimanawa Region intense browsing by sika deer has suppressed mountain beech forest regeneration (chapter three), through reducing seedling growth (chapter five). At some sites deer browsing also appears to have induced compositional shifts in ground cover composition towards browse-tolerant, turf-forming communities (chapter four). It is possible that these turf communities prevent mountain beech canopy regeneration through competitive exclusion. For instance, Wiser, Allen and Platt (1997) showed that beech seedlings established under shrub species but not with the presence of turfs, and Zmafir (2000) showed in a greenhouse experiment that bryophytes and lichens are capable of inhibiting or facilitating grass seedling emergence. However, in a review of the effects of herbivory on succession, Davidson (1993) found that herbivory tended to accelerate compositional shifts from herbs to woody plants. Competitive interactions between plants can also vary with interactions of resource availability and the intensity of herbivory (Gedge and Maun 1994) .

The objective of this study was to determine the importance of interactions of resource availability, natural and simulated deer herbivory and competition between mountain beech seedlings and established turf communities. A deer exclusion experiment on regenerating mountain beech seedlings tested if the effects of eliminating browsing by deer varied with light availability, potential soil productivity and competition with other plants. In an ongoing debate, one school of thought contends that plant competition intensity is low in stressful environments, and increases with productivity (Grime 1973; Keddy 1989). Proponents of an opposing school of thought contend that competition intensity is constant along gradients of resource availability, but shifts from predominantly below-ground for nutrients at unproductive sites to above-ground for light and space with higher productivity potential (Newman 1973; Wilson and Tilman 1991). The effects of herbivory on seedling establishment, growth and survivorship might also increase, decrease or remain constant with increasing productivity governed by resource availability. A second experiment explores the effects of competition from herbaceous plants and simulated herbivory on transplanted mountain beech seedling growth and survival. The effects of herbivory and plant competition on mountain beech regeneration could be: 1) multiplicative, where increased herbivory results in increased plant competitive effects, thereby reducing seedling growth and survivorship; 2) negative, where increased herbivory reduces plant competitive effects; or 3) neutral or simply additive, where there is no is evidence of interactive effects between plant competition and herbivory on seedling demographics (Tilman 1987).

6.2 Methods

Between September 1998 and March 1999 twelve sites were subjectively selected in mountain beech dominant forest. Data from these sites were also used in chapter five, and all sites had low basal area (< 30 m^2 ha^{-1}), were at altitudes (1300–1430 m) near timberline, and were where mountain beech seedling growth appeared to be suppressed through deer browsing or competition with turf, shrub or fern species. In regions outside of the Kaimanawa low basal area sites showed increased abundance of mountain beech seedlings (chapter three). Two plots (10 m x 10 m understorey, 20 m x 20 m overstorey) were established at each site, and one of the pair was fenced to exclude ungulates.

Sites selected for paired exclosure plot establishment in this study had a groundcover of dense herbaceous turf and bryophyte communities. These turf communities appear to form grazing lawns that are both maintained by and attractive to herbivores. Studies in other countries have shown that grazing lawns that are induced by herbivory, and consist of browse-tolerant herbs or grasses, can have increased productivty and nutrient content making them highly attractive to herbivores (McNaughton 1984; Posse, Anchorena and Collantes 2000). Turf communities in the Kaimanawa Region typically include bryophytes (e.g. *Bryum billiardierei, Dicranoloma robustum, Dendroligotrichum dendroides, Ptychomnion aciculare*), herbs (e.g. *Acaena anserinifolia, Hydrocotyle moschata, Lagenophora strangulata* and *Nertera dichondrifolia*), and grasses or sedges (e.g. *Poa breviglumis, Rytidosperma gracile, Microlaena avenacea, Uncinia filiformis*).

6.2.1 Natural seedling experiment

The heights of all established mountain beech seedlings (5–135 cm high) were measured when plots were established during the austral summer of 1998/1999 in paired plots at seven of the twelve sites. A numbered aluminium tag was wired to each seedling's stem and its pull-up height was measured in cm to the end of the previous season's growth. Each 10 x 10 m seedling plot was divided up into sixteen 2.5 m x 2.5 m sub-plots and centred within 20 x 20 m overstorey plots (tree stems ≥ 3 diameter at breast height, 135 cm). In the austral summer of 2001/2002 all seedlings still alive were relocated and their heights remeasured. Any seedlings that had grown above 5 cm since the 1998/1999 survey were also measured. At the same time all species of vascular plants, bryophytes and lichens growing in mineral soil were identified and estimates of cover were made for each sub-plot, in two tiers (<15 cm; 15–135 cm), using a six point inverse log scale (1 < 2% cover, 2 = 2–5 %, 3 = 6–25 %, 4 = 26–50 %, 5 = 51–75 %, 6 = 76–100 %; Mueller-Dombois and Ellenberg 1974). Lichens and bryophytes were not identified when they had a cover < 2%. Bare ground with no plant cover was estimated using the same scale. Slope was measured at each sub-plot to the nearest 5° using a Suunto inclinometer, and aspect was measured to the nearest 5° using a compass. For analysis, aspect was converted to degrees from true north. Soil samples (200–250 ml) were taken from each sub-plot and were transported to a glasshouse for bioassay based on the method of Lee and Fenner (1989). Ryegrass was sown in these soil samples, harvested after four months and dried until weight stabilised. The leaf dry weight (g) was measured using a four decimal place scale and this weight was used as an index of soil productivity. A black and white hemispherical photograph was captured at 135 cm above the centre of each sub-plot using a Nikon 990 digital camera. This image was used to calculate the percentage of transmitted light available at each sub-plot using GLA 2 software (Frazer et al. 1999). Images captured with digital cameras under dense canopies and broken skies can produce variable results, but digital images captured under relatively open canopies and overcast skies (such as in this study) are generally more reliable (Frazer et al. 2001).

6.2.2 Transplanted seedling experiment

At eight of the twelve subjectively located sites, 80 mountain beech seedlings (40–306 mm high) were planted within deer fences, but outside 10 m x 10 m plots, in sixteen 20 cm radius replicate plots (five seedlings within each replicate). Replicate plots were systematically located with < 25% cover of woody plant species and were centred > 1 m apart. A shade tunnel designed to shade 80% of available light provided a whole-plot treatment of shading. Fertilisation, turf removal and simulated herbivory treatments were randomly applied in a 2 x 2 x 2 randomised design within the shade tunnel and adjacent unshaded replicate plots. Fifty grams of slow release fertiliser (Osmocote 12 month; 15% N, 3% P, 9.1% K, 1.2% Mg) was sown over selected 0.126 m^2 replicate plots at the time of establishment. This level of fertilisation provided 60 g of N m^{-2} and is consistent with other studies: Cahill (1999) sowed 60 g m^{-2} Osmocote 3 month (14%N, 14%P, 14%K) for 2.8 g of N m^{-2} which he considered to be low; Wilson and Tilman (1991) used 5.4 g and 17.0 g of N m^{-2} $year^{-1}$ to promote positive growth responses; and Coomes and Grubb (1998) used 1.4 and 3.2 g N^{-1} m^{-2} in an experiment to test below ground competition in a very low fertility Amazonian caatinga forest. Replicate plots selected for turf removal in this study had all herbs and woody seedlings removed prior to planting of seedlings and at six-month intervals thereafter. All stems and branches > 1.5 mm diameter of seedlings selected for herbivory were clipped in winter 2001 with scissors to simulate browsing by deer. This reduced clipped seedlings in height by a mean of 30.0% (s.d. = 16.3%).

Vascular plant, bryophyte and lichen cover was estimated for each replicate plot without turf removal using a six-point scale (Mueller-Dombois and Ellenberg 1974; section 6.2.1). Transplanted seedling heights were measured immediately after planting in 2000, when simulated herbivory was applied in 2001 (from root–stem intersection to apical bud), and immediately prior to being uprooted and removed for weighting of roots, stems and leaves in the winter of 2002. Roots, stems and leaves were sorted prior to drying to a stable weight and weighed to the nearest mg.

6.2.3 Data Analysis

Natural mountain beech seedling annual recruitment, annual mortality rates (McCune and Cottam 1985), mean relative growth rates (RGR) and the percentage of established seedlings surviving from 5 cm to 135 cm were calculated for each 10 m x 10 m plot. Vegetation and environmental variables were summarised in SYSTAT (SPSS 2000) for each sub-plot and plot before statistical analysis was undertaken. The numbers of small seedlings (<5 cm high) counted in each plot were log transformed to meet assumptions of ANOVA.

$$\text{Recruitment} = (1+B_x)^{1/3} - 1, \text{ where } B_X = \text{proportion of new seedlings for 3 years}$$

$$\text{Mortality} = 1 - (1 - Q_x)^{1/3}, \text{ where } Q_X = \text{proportion of dead seedlings for 3 years}$$

$$\text{RGR} = (\text{Log}_e \text{ seedling height 2001} - \text{Log}_e \text{ seedling height 1998}) / 3 \text{ years}$$

$$\text{Survivorship from 5–135 cm (\%)} = (-\text{ mortality } (\log_{\text{exp.}} 135 \text{ cm} / 5 \text{ cm}) / \text{RGR}) \times 100 \times \text{exp.}$$

For the transplant experiment, the relationship between individual transplanted seedling root and stem biomass was calculated using linear regression through the origin. Residual error values were then used as an index of the relationship of individual plant stem–root weights. This approach limits scaling error inherent in alternative ratio based indices (Atchley, Gaskins, and Anderson 1976). Mean transplanted seedling heights, mean stem–root index and the mean number of seedlings with living leaf material remaining in each replicate plot 2002 were calculated before the effect of experimental manipulations on means were tested with a split-plot ANCOVA in SYSTAT (SPSS 2000) using sites identified as a blocking variable. Transplanted seedling heights in the year 2000 were used as a covariate and means adjusted accordingly in ANCOVA.

Constrained ordination methods were used in CANOCO 4.0 (Ter Braak and Smilauer 1998) to determine the effect of the experimental manipulations on turf community species composition. For the natural seedling experiment sites were treated as blocks in a randomised Canonical Correspondence Analysis (CCA) to reduce unexplained variation between sites. An automatic forward selection procedure was used to test for the effect of deer exclusion fencing, total transmitted light, soil productivity and slope on <15 cm species composition in 2001/2002 in each plot. Importance values were calculated from the mean cover value in each sub-plot. For the transplant seedling experiment I used a split-plot, partially constrained CCA to show differences in < 5 cm high tier species composition in 2002 within 20 cm radius, replicate plots where turfs had not been removed. A forward stepwise procedure was used to test for the significance of shading treatments as a main-plot effect. A separate stepwise procedure was then used to test for the split-plot effects of herbivory, turf removal and fertilisation and their interactions. Baseline species composition was allowed for by using Detrended Correspondence Analysis (DCA) of 2000 compositon to calculate axis 1, 2, 3 and 4 scores and using these as constraining covariates in the CCA. Sites were also treated as blocking covariates in analysis.

6.3 Results

6.3.1 Effects of deer exclusion on natural seedlings

When fences were established and initial baseline measurements of seedling heights made in 10 m x 10 m plots in 1998, nearly all mountain beech seedlings present were browsed in both fenced and unfenced plots in all four height classes (5–9 cm, 10–19 cm, 20–49 cm, 50–135 cm; Table 6.1). Counts of mountain beech seedlings were also similar in these height classes in fenced and unfenced plots for the 5 – 9 cm, 10–19 cm height classes, but in the 20–49 cm and the 50–135 cm height classes seedlings were 30 and 84 % higher in unfenced plots respectively, although high standard deviations showed considerable baseline variation within fenced and unfenced plots. I also summarised the comparability of fenced and unfenced plots for key environmental variables measured in 2001/02 and found that paired plots had similar means for aspect, slope, total transmitted light, indices of plant cover in the ground cover tier (< 5 cm), bare-ground cover, understorey composition (axis 1 DCA scores) and soil productivity.

Naturally occurring mountain beech seedlings were commonly browsed by deer at the experimental sites. In unfenced plots, 408 browsed established seedlings (5–135 cm) had significantly lower relative growth rates (Mean RGR ± S.E. = 0.01±0.01) than the 23 established seedlings that showed no signs of browsing (Mean RGR±S.E. = 0.05±0.02; F = 7.582, P = 0.006), suggesting that deer browsing was capable of inhibiting seedling growth. Furthermore, established seedlings that were not exposed to deer browsing after 1998 in fenced plots had higher mean relative growth rates than seedlings in unfenced plots (paired t_5 =3.14. P = 0.026).

The natural seedling experiment showed that deer browsing inhibited the establishment and survival of small seedlings (<5 cm high). In 2001, there were significantly more small seedlings in fenced plots (LS mean±S.E. = 196.0±111.0 seedlings plot^{-1}) compared to unfenced plots (LS mean±S.E. = 16.9±10.0 seedlings plot^{-1}; paired t_6 =3.18. P = 0.019). There was no difference in mortality (t_6 =0.49, P = 0.643, Type 2 P = 0.061), recruitment (t_6 =0.28, P = 0.786, Type II P = 0.053) or survivorship of seedlings (5–135 cm; t_5 =0.87, P = 0.423, Type II P = 0.086) between fenced and unfenced plots.

Variance decomposition of ANOVA on small seedling (< 5 cm) abundance between the seven fenced plots showed that there was considerable variation among (variance = 1.7; min = 8, max = 348) 10 m x 10 m plots as well as variation in seedling counts among 2.5 m x 2.5 m sub-plots (variance = 0.87, min = 0, max = 146). Therefore I investigated in more detail the factors responsible for variation in small seedling counts (< 5 cm, $\log_e$+1) at the plot and sub-plot scale. At the plot level there was no significant effect on small seedling counts of mean total transmitted light, mean soil productivity index (g), mean sub-plot slope (°), mean bare-ground (1–6) or ground cover plant composition (mean axis 1 DCA) as shown by a multiple regression ($P > 0.067$). At the sub-plot level a randomised block ANOVA showed no significant effect of these same variables on seedling counts (df = 6, 98; $P > 0.224$). A randomised block CCA showed that ground cover species composition did not significantly vary with the exclusion of deer ($\gamma = 0.08$, $F = 0.52$, $P = 0.865$), or with mean soil productivity ($\gamma = 0.19$, $F = 1.29$, $P = 0.225$), total transmitted light ($\gamma = 0.13$, $F = 0.93$, $P = 0.510$) or plot slope ($\gamma = 0.11$, $F = 0.71$, $P = 0.715$).

Table 6.1. Summary means of baseline (± S.D.) and post-experimental measurements (± S.E.) for natural seedling experiment. Baseline measurements are the mean proportion of seedlings browsed and mean numbers of seedlings counted in 10 m x 10 m plots in four height classes upon plot establishment and fencing in 1998/99. Mean plot aspect, slope, total transmitted light, bare ground cover, soil productivity and DCA axis 1 scores were estimated from sampling in 2001/2002. Final measurements are the effects of fencing on mean seedling relative growth rates, mortality, recruitment and survivorship from 1998–2002.

Parameter	Fenced	Unfenced
Baseline (1998)		
Browse 5-9 cm	1.0 ± <0.1	0.9 ± 0.2
Browse 10-19 cm	0.9 ± 0.2	0.9 ± 0.1
Browse 20-49 cm	1.0 ± <0.1	1.0 ± <0.1
Browse 50 - 135 cm	1.0 ± 0.1	1.0 ± <0.1
Seedling counts 5-9 cm	9.7 ± 9.5	7.9 ± 12.4
Seedling counts 10-19 cm	24.3 ± 23.4	19.4 ± 32.8
Seedling counts 20-49 cm	20.7 ± 23.3	26.9 ± 37.5
Seedling counts 50-135 cm	10.4 ± 12.4	19.1 ± 22.7
Baseline (2002)		
Aspect (mean ° from true north)	126.8 ± 48.9	124.7 ± 42.4
Slope (°)	23.5 ± 10.9	26.1 ± 10.8
Total transmitted light (mean %)	52.0 ± 15.4	59.1 ± 15.5
Bare ground (mean 0–6)	1.1 ± 1.0	0.9 ± 0.4
Soil productivity (mean g)	1.3 ± 0.2	1.2 ± 0.2
Mean axis 1 DCA Scores	2.4 ± 0.8	2.5 ± 0.8
Final measurement (2002)		
Mean relative growth 98-01 5-135 cm	0.19 ± 0.03	0.08 ± 0.03
Mean annual mortality 98-01 5-135 cm (%)	6.8 ± 2.6	5.6 ± 1.7
Mean annual recruitment 98-01 >5 cm (%)	11.2 ± 4.4	10.8 ± 4.4
Mean of seedlings surviving to 135 cm (%)	31.3 ± 12.1	20.1 ± 16.2

6.3.2 Effects of shading, clipping, fertilisation and turf removal on transplanted seedlings

Mean stem height in 2002 for transplanted seedlings in replicate plots with turf removal was significantly higher (mean±SE = 194±3.9 mm) than means for seedlings without turf removal (mean height±SE = 176±4.1 mm, Table 6.2). Seedlings that had undergone clipping were significantly lower (mean ± SE = 168±4.0 mm) in 2002 than unclipped seedlings (mean±SE = 201±4.0 mm). There were no significant effects of interactions of shading, fertilisation, turf removal or clipping on stem heights in 2002. ANCOVA showed that height in 2002 was significantly related to seedling height in 2000.

Seedlings in fertilised plots had three times higher mean stem–root index values (mean ratio±SE = 1.2±0.7) than in unfertilised plots (mean±SE = 0.4±0.7), showing that fertilisation treatments led to increased stem weight relative to root weight. Clipping and turf removal treatments had the opposite effect. Clipped seedlings had nearly five times lower mean stem-root index values (mean±SE = 0.4±0.7) compared to seedlings that had not undergone herbivory (mean±SE = 1.9±0.8) and seedlings with turf removal had nearly three times lower (mean±SE = 0.4±0.8) mean stem-root index than seedlings without turf removal (mean±SE = 1.2±0.7). There were no significant effects of interactions of shading, fertilisation, turf removal, or simulated herbivory on stem–root means.

There were significantly fewer seedlings with living leaf material remaining in fertilised replicate plots (mean number±SE = 2.9±0.1) compared to unfertilised seedlings (mean±SE = 3.9±0.1). Seedling survivorship was higher when turfs were removed (mean number±SE = 3.7±0.1) compared to seedlings without turf removal (mean±SE = 3.1±0.1). There was no difference in survivorship between seedlings in plots with clipping or shading and plots without these effects or second order treatment interactions.

There was no significant effect of shading as a main-plot effect on <5 cm tier species composition in replicate plots without turf removal in 2002 ($\gamma = 0.10$, $F = 1.02$, $P = 0.785$). A separate stepwise procedure showed no significant effects on species composition of mountain beech seedling clipping ($\gamma = 0.07$, $F = 0.97$, $P = 0.130$), fertilisation ($\gamma = 0.11$, $F = 1.14$, $P = 0.055$) or second and third order interactions of shading, fertilisation and clipping within split-plots ($P > 0.420$).

Table 6.2. Transplanted seedling split-plot ANOVA of the of treatments of shading, fertilisation, turf removal, and simulated herbivory on mean seedling height (mm) in 2002, mean stem–root index and mean number of live seedlings remaining in each plot. Second order interactions of treatments are included in one term. Seedling height 2000 (mm) is treated as a covariate for calculation of seedling height 2002 and stem–root index adjusted means.

	Height 2002				Stem-root index				Survival			
	df	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*
Main plot												
Shade	1	1269	0.128	0.731	1	0.016	1.615	0.244	1	7.508	1.538	0.255
Blocks	7	12816	14.018	<0.001	7	0.009	1.819	0.094	7	21.660	15.197	<0.001
Main plot error	7	9876			7	0.010			7	4.883		
Split plot												
Fertiliser	1	1326	1.450	0.231	1	0.024	4.735	0.032	1	31.008	21.755	<0.001
Turf removal	1	9391	10.272	0.002	1	0.045	8.896	0.004	1	14.445	10.135	0.002
Simulated herbivory	1	34254	37.466	<0.001	1	0.033	6.419	0.013	1	0.008	0.005	0.941
Interactions	6	1100	1.203	0.312	6	0.009	1.867	0.096	6	0.852	0.598	0.731
Seedling height 2000	1	75042	82.081	<0.001	1	0.031	6.099	0.015				
Split plot error	94	914			86	0.005			103	1.425		

6.4 Discussion

It is widely accepted that herbivory is generally detrimental to plants (e.g. Darwin 1872; Pacala and Crawley 1992; but see Coley, Bryant and Chapin 1985) and that it reduces the competitive ability of poorly defended species (e.g. Herms and Mattson 1992; Baldwin and Hamilton 2000; Crawley 1993), which shifts community composition towards browse-tolerant or -resistant species (Louda, Keeler and Holt 1990; Crawley 1997; Collins et al. 1998). But, does herbivory have an affect on the overall intensity of plant competition, and does this vary with habitat productivty? In this study natural and simulated deer herbivory directly reduced mountain beech seedling growth, but there was no evidence for strong interactive effects between the intensity of competition between mountain beech seedlings and neighbouring turf communities. The effects of browsing and clipping did not vary with composition of competing plants, light availability or soil productivity for naturally occurring seedlings, or with fertilisation, shading and turf removal for transplanted seedlings. This implies that the effects of herbivory did not interact with changes in plant competition or with resource availability, which supports Tilman's (1987) hypothesis that the impact of herbivory on plant competition does not vary along gradients of productivity. Kullberg and Welander (2003) also found that water limitation did not significantly interact with simulated herbivory on beech seedlings in Sweden, which also supports Tilman's (1987) neutral hypothesis, where there is no evidence of multiplicative or negative interactions between plant competition and herbivory on seedling demographics. Other studies have reached contrasting conclusions, particularly for gramminoids. Swank and Oechel (1991) found strong interactive effects of herbivory, nutrient and water addition and root trenching on plant survival and growth in North American Chaparral. Cahill (1999) found that in a Pennsylvanian grassland that the interactive effects of above- and below-ground competition became multiplicative with fertilisation. Interactive effects were also found by Van der Wal et al. (2000) where herbivory mitigated increasing competition with increased productivity. An additive hypothesis has been proposed by Oksanen et al. (1981), Grover (1995) and Leibold (1996) where herbivore impacts increase with productivity. Since there are no natural predators of deer in my study area, I could explore this hypothesis where productivity and herbivory interact without the confounding effects of predators. There was no evidence in my study to support multiplicative relationships between deer impacts and productivity, which does not contradict Oksanen et al.'s (1981) additive hypothesis. Cebrián and Duarte (1994) reviewed studies testing this hypothesis and found that the effects of herbivory appeared to be independent of ecosystem productivity and were more closely linked to the growth rate of plants. Virtanen (2000) expressed concern that Cebrián and Duarte (1994) had not considered studies of slow growing plants in low-productivity, high-latitude sites that showed considerable impacts of herbivores (Leader-Williams, Smith and Rothery 1987).

In the transplanted seedling experiment, removal of herbs increased growth of plants overall, and particularly of roots, showing that competition for nutrients limited growth. Results show that mountain beech seedlings invest more resources on leaf and stem growth in comparison to root mass when competition for light is intense, whereas more resources were spent on root-mass growth when nutrients were limited. Increased stem growth with fertilisation shows that increasing nutrient availablity appeared to shift plant competition above-ground, where shading treatments showed no evidence of the effect of light limitation. None of these changes in competitive ability in mountain beech varied with simulated herbivory, which is a similar result to that of Wandera, Richards and Mueller (1992). Thus, there is no evidence from this study that the resilience of mountain beech seedlings or turf communities to herbivory varied with productivity. Other studies have found evidence that the tolerance of plants to herbivory can vary along gradients of productivity. In a review, Bryant, Chapin and Klein (1983) concluded that grasses can tolerate severe grazing in low- and high-productivity environements through below-ground storage of carbon and nutrients, whereas woody plants are more likely to use browsing-resistant strategies, particularly in low nutrient environments. McNaughton, Banyikwa and McNaughton (1998) showed that even under intense herbivory from large ungulates below-ground productiveiy and biomass was not inhibitied in a Serengeti grassland. In a study using a Serengeti sedge (*Cyperaceae*) and a grass (*Poaceae*) species McNaughton and Chapin (1985) found that simulated herbivory had greatest effects with high nutrient levels. McLaren (1996) found that simulated moose browsing on naturally browsed balsam fir had a greater effect at more shaded sites in his Michigan study site. He interpreted that this was because both shade and herbivory provided additional stress that caused additive effects on branch growth (Maschinski and Whitham 1989).

Because the results of this study show simple and direct effects of deer herbivory on mountain beech seedling growth, managers can take a direct approach to deer control. If this study had found interactive effects between herbivory and plant competition, more complex responses of mountain beech to deer control might be expected and these responses could be strongly influenced by the composition and occurrence of turf communities. Although the presence of turf communities also reduces mountain beech seedling growth this issue can be considered separately to the direct impacts of deer on mountain beech regeneration.

Future experiments examining plant competition and herbivory could make use of natural gradients of resource availability and vegetation productivity. New Zealand's diverse environment has strong gradients of altitude, soil development and rainfall which provides unique opportunities to examine relationships between biological productivity, nutrient and light availability, plant competition and herbivory.

CHAPTER SEVEN

Synthesis, conclusions and management implications

The four studies making up this PhD show that deer, and sika deer in particular, can influence forest regeneration and succession at plant population, community and landscape scales. Deer have suppressed the regeneration of palatable plant species occurring throughout the Kaimanawa landscape, which has modified the composition and structure of beech forest communities. A variety of scales and levels of deer impact were examined in this PhD: between the Kaimanawa Region and other regions in New Zealand without sika deer; through manipulation of deer abundance within the Kaimanawa Region; through complete exclusion of deer at individual stands; and by monitoring the growth and survival of individual plants. This approach has provided information on the impacts of deer at these different scales, which I will briefly summarise.

Deer densities have been at relatively high levels in the Kaimanawa Region for several decades despite ongoing ground-based deer culling, and this has led to relatively high impacts on beech forest regeneration and composition in comparison to other regions. At a plant population scale, deer decrease the growth and abundance of mountain beech seedlings at low basal area sites, but this appears to be reversible when deer are reduced in density or are completely excluded. In contrast, browse-tolerant turf communities, which have become more common, did not change in composition when deer were excluded for two years. The extent to which the abundance of mountain beech seedlings can be increased is also unclear, because it appears that under the influence of deer browsing less palatable small-leaved shrubs have increased in abundance. It is also possible that compositional changes observed in red and silver beech forest will permanently influence the direction of forest succession and future composition of these forests, which are increasingly dominated by unpalatable tree species. Overall, I conclude that the presence of deer has had a considerable influence on plant populations and community composition throughout the Kaimanawa landscape, which is likely to continue to dominate the ecology of the region's beech forests for many decades, even where the immediate impacts of deer are reduced through intensive deer culling.

7.1 Study one - sika deer suppress mountain beech regeneration

The first study in this thesis shows a paucity of mountain beech seedlings at sites with low occupancy by trees, measured using stand basal area, throughout the Kaimanawa

Ecological Region. This departs from the normal situation following canopy collapse, where vigorous regeneration is expected (chapters two and three). In four other New Zealand regions where red, but not sika deer, were present there was evidence of just such a response to canopy gap creation, and for the presence of an advanced-growth seedling bank in intact stands. Although there are likely to be differences among these four regions and the Kaimanawa Region that influence the regeneration of mountain beech such as climatic and geological characteristics, the single most plausible reason for this difference is the high abundance and intensive browsing of sika deer in the Kaimanawa region. When compared to larger deer species, sika deer have a digestive morphology allowing greater dietary versatility (Fraser 1996), which may allow them to impede forest regeneration where red deer do not (Hanley 1997). Sika deer are extending their range through natural dispersal and ongoing introductions, and where established appear to be able to displace red deer (Davidson and Fraser 1991). Forest managers should be concerned about the ability of sika deer to have a high level of impact, and their heightened difficulty to control with unsubsidised recreational and commercial hunting in comparison to red deer.

Permanent plot and aerial photograph data indicates that *c.* 10 % of sites in mountain beech forest in western Kaweka Forest Park have undergone canopy collapse within the last few decades, on a 20 m x 20 m scale. Instead of increased seedling density at these sites, there appears to be increasing dominance of browse-resistant shrubs such as *Coprosma* "taylorae" and *Myrsine divaricata.* This compositional change is likely to induce permanent changes to ecosystem function that may increase or decrease nutrient availability to plants depending on site characteristics (Wardle 2002).

When the western Kaweka and three other areas in the Kaimanawa Region with different histories of deer colonisation were compared in chapter three, there was no clear relationship between the date of colonisation by sika deer and mountain beech seedling abundance or understorey composition. This suggests that sika deer browsing quickly suppresses canopy regeneration and shifts successional pathways. Low basal area sites appear to suffer the largest reductions in abundance of mountain beech seedlings in absolute terms, while stands with fuller occupancy had large reductions in abundance in relative terms. Because low basal area sites, that have undergone recent adult tree death, are likely to have increased nutrient and light availability (Allen, Clinton and Davis 1997) and so be potentially more productive, this study supports theory suggesting that deer impacts are greatest in absolute terms at highly productive sites and greatest in relative terms at least productive sites (McNaughton 1984).

7.2 Study two - forest compositional changes are consistent with deer impacts

In chapter four, data from plots across a range of basal areas are used to show changes in species composition of forests dominated by red and silver beech and *Weinmannia racemosa*. There was an expansion in the stem densities of highly unpalatable species of small trees (stems ≥20 mm diameter at breast height) over two decades. Numbers of stems of the unpalatable *Pseudowintera colorata* increased on north-facing slopes, and the unpalatable *Neomyrtus pedunculatus* and *Leucopogon fasciculatus* increased in number at many sites. In the understorey, the palatable *Weinmannia racemosa* and *Griselinia littoralis* are failing to recruit into the >75 cm height class. Exclosure plot data show that deer have prevented increases of red and silver beech seedling densities, but representative permanent plot data show no corresponding decline in tree or seedling abundance in two decades. In the southern Kaimanawa mountain beech forests, understorey composition shifted towards increasing dominance of browse-tolerant turf forming communities comprising bryophyte, fern, grass, herb, rush and sedge species.

7.3 Study three - reduction in deer abundance increases mountain beech seedling growth

Data from exclosure plots reported in chapter five provide strong evidence that once deer browsing was removed through fencing, mountain beech seedling growth increased substantially. There is also evidence that intensive aerial deer culling more than halved deer abundance over three years, and that this led to increases in mountain beech seedling growth comparable to fenced plots. This provides evidence of the success of high-intensity deer culling at reducing deer abundance and increasing the growth rates of seedlings at stands of low basal area. As well as data on seedling and sapling growth rates, models used to predict canopy replacement also need to be parameterised for establishment of new seedlings, recruitment of new seedlings into height classes occupied by established seedlings and mortality of established seedlings and saplings. Representatively collected data on seedling demographics at more sites are required to construct a mathematical model to determine if intensive deer culling has lowered deer abundance sufficiently to ensure maintenance of a forest canopy on a landscape scale. Results from seven subjectively located sites in chapter six shows that there is much less impact of deer on seedling mortality and recruitment, than on seedling establishment and growth. Therefore in chapter five I assume that relative growth rate data can be used as an index of canopy replacement at sites with a large number of existing seedlings with high survivorship. This assumption needs to be more rigorously tested once appropriate data are obtained. Nevertheless, my conclusion is that intensive deer culling appears to be effective at restoring mountain beech regeneration at low basal area sites.

7.4 Study four - herbivory and plant competition reduce seedling growth, but in a non-multiplicative manner

At twelve sites where dense turf communities were present, I investigated in detail in chapter six the potential of herbivory and turf communities (that form a grazing lawn) to reduce seedling growth, establishment and survival. At these sites competitive exclusion from turf communities may prevent enough seedlings from establishing to the extent that the seedling growth is not the critical parameter for predicting canopy replacement.

Although composition of turfs communities had little effect on mountain beech seedling establishment, complete turf removal increased transplanted seedling growth. Deer browsing reduced the establishment and growth of naturally occurring seedlings, but this did not vary with turf community composition or light and nutrient availability. Mortality was not significantly affected by herbivory, which suggests that the key parameters for predicting mountain beech regeneration in the presence of deer browsing are seedling growth and establishment.

Increased nutrient availability appears to reduce below-ground competition, and more surprisingly decrease transplanted seedling survival, but there was no effect of changing levels of light on seedling growth or survival. These results show simple and direct effects of deer browsing and competition from turf communities on mountain beech seedling growth. There was no evidence of interactions between herbivory, plant competition and resource availability, which suggests that these factors do not have multiplicative effects on mountain beech seedling regeneration. In order to ensure regeneration of mountain beech forest in the central North Island, conservation managers should focus on restoring seedling growth and establishment on a landscape scale, through intensive deer control.

7.5 Synthesis and future research

This thesis has shown that intensive browsing by sika deer has had long-term impacts on beech forest canopy regeneration, plant populations and communities. For mountain beech populations these impacts appear to be reversible, but the responses of plant communities to the removal of deer browsing are less evident. It appears that deer browsing has induced shifts in competitive balances between plants that favour browse-resistant and browse-tolerant species, particularly at sites with low occupancy by trees. At low basal area sites in mountain beech forest there was evidence of a compositional shift towards browse-resistant, small-leaved shrubs. This may be linked to more intensive deer browsing associated with increased nutrient and light availability following canopy tree death at these sites. This issue needs further exploration: are increased deer impacts at these sites, and accelerated changes in forest composition, linked to resource availability and primary productivity?

In this PhD I have focused on deer impacts on plant populations and communities but have overlooked impacts on ecosystem processes, which may be very important (Wardle 2002), and could be considered in future studies of deer impacts. Deer induced changes in plant communities can influence the composition of soil chemistry and biota in a complex manner (e.g. Wardle et al. 2001; Stark, Strömmer and Tuomi 2002). This may have flow-on effects that influence forest dynamics, and therefore deer populations.

Chapter five showed a growth response from mountain beech seedlings after deer abundance was lowered in the Kaimanawa Region. Seedling growth and establishment appear to be key demographic parameters in determining the effects of deer on the regeneration of mountain beech. However, it is important that data is collected in the Kaimanawa Region to develop models of mountain beech replacement. Managers also need to know the level that deer abundance needs to be held at to ensure viability of populations of species such as red and silver beech, *Griselinia littoralis* and *Weinmannia racemosa*. This important question could be explored through a combination of adaptive management in a variety of habitats, and observational and experimental studies relating deer browsing to seedling mortality at different scales.

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Appendices

Appendix 1. Species list from southern Kaimanawa Forest Park understorey plots

AGEC: *Wahlenbergia pygmaea, Gentiana bellidifolia, Euphrasia cuneata, Coprosma cheesemanii, Coriaria pteridoides*

AA: *Acaena anserinifolia*

AAR: *Anisotome aromatica*

AB: *Anaphalioides bellidioides*

AF: *Astelia fragrans*

ARF: *Aristotelia fruticosa*

AS: *Aristotelia serrata*

AT: *Asplenium terrestre*

BB: *Brachyglottis bidwillii*

BC: *Blechnum chambersii*

BCA: *Blechnum capense*

BF: *Blechnum fluviatile*

BL: *Brachyglottis lagopus*

BP: *Blechnum penna-marina*

BV: *Blechnum vulcanicum*

C: *Celmisia* spp.

CC: *Chiloglottis cornuta*

CD: *Cardamine debilis*

CF: *Cyathodes fraseri*

CFO: *Coprosma foetidissima*

CJ: *Cyathodes juniperina*

CL: *Caladenia lyallii*

CM: *Corybas macranthus*

CMI: *Coprosma microcarpa*

CN: *Coprosma linariifolia*

CO: *Corybas orbiculatus*

CP: *Coprosma pseudocuneata*

CPA: *Clematis paniculata*

CPR: *Coprosma propinqua*

CR: *Coprosma rhamnoides*

CRU: *Coprosma rugosa*

CS: *Carpodetus serratus*
CT: *Corybas trilobus*
CTA: *Coprosma* “taylorae”
CTE: *Coprosma tenuifolia*
DR: *Dracophyllum recurvum*
EB: *Epilobium brunnescens*
EP: *Epilobium pedunculare*
FB: *Forstera bidwillii*
FE: *Fuchsia excorticata*
G: *Gentiana* spp.
GA: *Gaultheria antipoda*
GB: *Grammitis billardieri*
GC: *Gaultheria colensoi*
GD: *Gaultheria depressa*
GL: *Griselinia littoralis*
GM: *Geranium microphyllum*
GP: *Galium propinquim*
GR: *Gnaphalium ruahinicum*
H: *Hymenophyllum* spp.
HC: *Hebe corriganii*
HD: *Hydrocotyle dissecta*
HI: *Histiopteris incisa*
HL: *Helichrysum lanceolatum*
HM: *Hydrocotyle moschata*
HO: *Hebe odora*
HP: *Hieracium pilosella*
HS: *Hebe stricta*
JN: *Juncus novaezelandiae*
L: *Lycopodium* spp.
LAP: *Lagenifera pinnatifida*
LF: *Leucopogon fasciculatus*
LP: *Luzula picta*
LPA: *Luzula parviflora*
LPE: *Lagenifera petiolata*
LS: *Lagenifera strangulata*
LSC: *Leptospermum scoparium*

MA: *Muehlenbeckia axillaris*
MAV: *Microlaena avenacea*
MD: *Myrsine divaricata*
MM: *Mycelis muralis*
NC: *Nertera ciliata*
ND: *Nertera dichondrifolia*
NF: *Nothofagus fusca*
NP: *Neomyrtus pedunculatus*
NS: *Nothofagus solandri*
OC: *Ophioglossum coriaceum*
OF: *Olearia furfuracea*
OM: *Ourisia macrophylla*
ON: *Olearia nummularifolia*
OXM: *Oxalis magellanica*
P: *Pterostylis* spp.
PA: *Pseudopanax arboreus*
PAL: *Phyllocladus alpinus*
PAN: *Pratia angulata*
PC: *Pseudowintera colorata*
PCO: *Pseudopanax colensoi*
PCR: *Pseudopanax crassifolius*
PH: *Podocarpus hallii*
PHN: *Podocarpus hallii* x *nivalis*
PN: *Podocarpus nivalis*
PS: *Paesia scaberula*
PT: *Pittosporum tenuifolium*
PV: *Polystichum vestitum*
RA: *Raukaua anomalus*
RC: *Rubus cissoides*
RR: *Ranunculus reflexus*
RS: *Raukaua simplex*
RT: *Raoulia tenuicaulis*
S: *Senela* spp.
SC: *Sticherus cunninghamii*
SP: *Sagina procumbens*
SPA: *Stellaria parviflora*

ST: *Schizeilema trifoliolatum*

TV: *Trichomanes venosum*

U: *Uncinia* spp.

UI: *Urtica incisa*

VC: *Viola cunninghamii*

Appendix 2. Nomenclature

Nomenclature follows Galloway (1985), Beever, Allison, and Child (1992), Parsons, Douglass and Macmillan (1995), Edgar and Connor (2000), and Brownsey and Smith-Dodsworth (2000). *Raukaua simplex* is described by Mitchell, Frodin and Heads (1997). *Coprosma* "taylorae" is referred to by Eagle (1986), and *Phyllocladus alpinus, Podocarpus hallii* and *Podocarpus nivalis* by Wilson and Galloway (1993).