The effects of disturbance and deer herbivory on plant invasions

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Abstract

Despite the negative impacts invasive plants can impose on forest communities and the potential for these impacts to increase with global change, little has been done in New Zealand to examine what facilitates the establishment and spread of these species within native beech *(Nothofagus solandri)* forest. This study examines the role which forest canopy gaps and deer herbivory have on the dispersal, germination, establishment and spread of invasive plant species within the *Nothofagus* forests of the Hopkins and Huxley valleys, near Twizel, New Zealand. Propagule dispersal was enhanced by the presence of a gap in the above canopy, resulting in an increased number of seeds being caught on the sticky traps in these plots (159 compared to only 2 in the control plots). Seed bank samples were assessed by germination in a glasshouse for one year. The invasive seed bank was larger in the fenced plots and conversely to the other results of this study, the presence of a canopy gap had no effect on the size of the seed bank. Aboveground cover of these invasive plants was primarily driven by the existence of a canopy gap, suggesting that canopy gaps are the main cause of plant invasions into *Nothofagus* forest (9% mean cover in the gap plots compared to 0% in the control and fence plots). However, there was a further increase in the aboveground cover of these invasive plants where a deer exclusion fence was situated around the perimeter of an open canopy plot (27.5% mean cover in the gap fence plots compared to 9% in the gap plots). Thus, suggesting that deer herbivory could be decreasing the abundance of invasive plants in areas of forest where gaps have been created. The canopy gaps allowed invasive plants to spread back into the forest away from the openings but only for a short distance, as in all cases invasive plants were absent by 6-7m from the plot edge. This localised establishment and spread of invasive plants where canopy gaps have been created could pose a threat to New Zealand's native *Nothofagus* forests, as many small populations spread out across a landscape can cause more ecosystem adversity than larger single populations. If not kept in check these invaders could increase further with global change however, if herbivory is assisting in the control of plant invasions management strategies for both invasive plants and introduced deer may need to be revised.

Acknowledgements

Thesis content

Chapter 1: Introduction

1.1 What makes a weed a weed?

Whether these 'undesirable' species are referred to as weeds, exotics, noxious or nuisance species it is all due to the fact that they are present in a community or environment at a density where they are seen by humans as undesirable (Civeyrel and Simberloff, 1996; Davis and Thompson, 2001; Colautti and MacIsaac, 2004). However, there is a more scientific approach to this question, and in this research all introduced, 'undesirable' species will be referred to as invasive species.

Invasive species must go through a series of processes or 'filters' before they can be classified as invasive species (Figure 1.1) (Colautti and MacIsaac, 2004). Firstly, for an invasive species to become invasive it must originate from propagules residing in a region outside the one that is going to be invaded, this region is called the "donor" region (Colautti and MacIsaac, 2004). The propagules must then survive the dispersal or transportation event to the site of invasion, either by individual dispersal mechanisms or human transportation. Once the propagules are successfully released into the introduced environment they have the potential to establish as an invasive species and increase in abundance (Colautti and MacIsaac, 2004). The final classification of the invasive species is determined by how abundant and widely distributed the species becomes in the introduced environment (Richardson *et al.,* 2000). According to Colautti and MacIsaac (2004) an invasive species can either be localised and numerically rare (III), widespread but rare (IVa), localised but dominant (IVb) or widespread and dominant (V). Colautti and MacIsaac (2004) also suggest there are three determinants affecting the probability that a potential invader will pass through each filter: (A) propagule pressure; (B) physicochemical requirements of the potential invader; and (C) community interactions. These determinants may positively (+) or negatively (–) affect the number of propagules that successfully pass through each filter (Figure 1.1) (Colautti and MacIsaac, 2004).
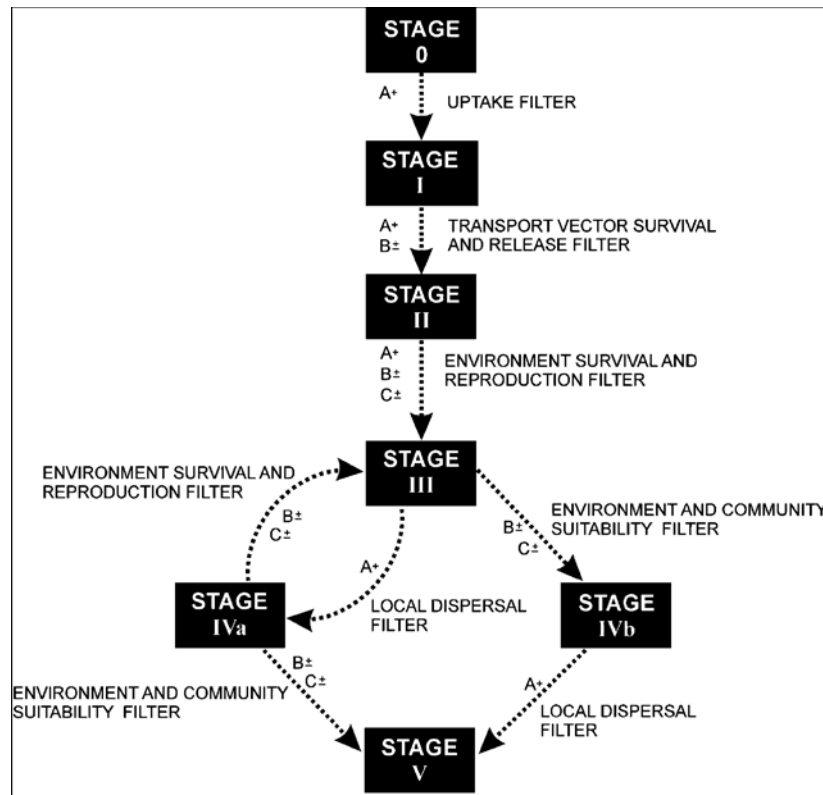
Figure 1.1. The filters a species must pass through to establish as an invasive species ending at stage III-V depending on its final distribution and abundance in the introduced environment (after Colautti and MacIsaac, 2004).

1.2 Biological invasion, a global phenomenon

Biological invasions occur at varying scales from the large global invasions, for example the world wide spread of ungulates from their native range (Nugent *et al.,* 2001a) right through to localised invasions, for example the invasion of small forest remnants by an invasive plant species (Ohlemüller *et al.,* 2006). Each biological invasion has ecological effects on the environment or community being invaded and in most circumstances the effects will be negative. For example, the invasion of a species can increase the susceptibility of resident native species to biocontrol agents (Rand and Louda, 2004) or more commonly will increase the competition displaced on a native species (Ohlemüller *et al.,* 2006). Contrary to this, there are situations where positive or beneficial effects can be associated with biological invasions. These positive effects can be directly related to the invasion, for example native plants increase resilience to herbivory in response to an

invasive herbivore (Bee *et al.,* 2007). Indirect effects can also occur in response to biological invasions, for example a herbivore prefers an invasive species over a native species, therefore releasing the native species from herbivory (Piasentier *et al.,* 2007).

Invasive plants have historically been viewed as nuisance species that readily invade anthropogenically disturbed areas such as roadsides, croplands, and overgrazed pastures (Keeley *et al.,* 2003). This biological phenomenon is prevalent all over the world with even the most geographically isolated countries, such as New Zealand, displaying multiple examples of plant invasions (Webb *et al.,* 1988; Timmins and Williams, 1991; Treskonova, 1991; Jesson *et al.,* 2000; Ohlemüller *et al.,* 2006). In recent decades there has been greater world-wide focus on invasions of natural communities, where invasive species are increasingly recognised as threats to ecosystem structure and function (Vitousek, 1990; Mooney and Hobbs, 2000).

1.3 Invasive species, high priority to New Zealand conservation

It is becoming increasingly important for resource managers to be able to predict which species are likely invaders, which communities are most at risk, and how land management practices influence the invasion process (Keeley *et al.,* 2003). Hence, in New Zealand it has been suggested that a comprehensive biodiversity management system be designed and made available to policy makers about the status of New Zealand's forest biodiversity (Allen *et al.,* 2003). There are three main reasons for constructing this type of system: assessing the effectiveness of management, reporting on the status of biodiversity under national and international requirements, and improving our knowledge of ecosystem dynamics for designing effective management systems (Allen *et al.,* 2003).

This type of management is highly relevant and important to the conservation of New Zealand's biodiversity. The native biodiversity of this geographically isolated country that evolved for centuries without any invasive species has had to cope with increased competition and predation from a biologically diverse group of invasive species

3

(Caughley, 1984). Examples of native species having to cope with both invasive plant and animal species are present in the literature (e.g., Rand and Louda, 2004; Dolman and Waber, 2008). This 'forcing' is due to the multiple human introductions of species with native ranges outside of New Zealand, for example the many species of ungulates that are now widespread throughout New Zealand (Allen *et al.,* 1984; Wardle *et al.,* 2001).

Over time, the accumulation of these invasive species in New Zealand has altered biological communities and interactions, especially increasing the negative impacts on native species (Jane, 1994; Nugent *et al.,* 2001b; Rooney, 2001). Conservation management in New Zealand has had to adapt to this increase of negative impacts on native species, by implementing strategies that attempt to minimise these impacts (Ministry of Conservation, 2007). There are many examples some that are unique to New Zealand, such as the widespread control of possums *(Trichosurus vulpecula)* to minimise their impacts on native tree species or the widespread control of mustelids, especially stoats (*Mustelia erminea)* in an attempt to minimise their impacts on native avifauna (www.doc.govt.nz).

Along with the concerns involving deer and other mammals, the number of invasive plant species now present in New Zealand and the potential negative impacts associated with these plants to native biodiversity is also of great concern (Mack *et al.,* 2000). For example, the latest survey shows there are over 30,000 introduced plant species in New Zealand of which 2,500 have naturalised in New Zealand, meaning they have established and are reproducing in the wild. Of these naturalised plants more than 300 plants have become environmental weeds meaning they impact detrimentally on the structure, functions or composition of New Zealand's indigenous plant communities, waterways and fauna (New Zealand Plant Conservation Network, 2008).

However, there are two conservation management strategies that are directly relevant to this research. Firstly, the management of invasive plant species in environments of high conservation importance, for example the management of Old Mans Beard *(Clematis vitalba)* in conservation national parks such as Kahurangi National Park. Secondly, the

management of introduced red deer *(Cervus elaphus)* in regions such as the Ruataniwha Conservation Park (RCP) where conservation of native tree species is of high importance. These examples illustrate how invasive species management is of high priority to conservation management in New Zealand, due to the threat they pose for native species. The management of deer in New Zealand is also evidence that conservation management has had to adapt over time with the change in status of particular species (Parkes *et al.,* 1996; Nugent *et al.,* 2001b).

1.4 The history of deer in New Zealand

The deer family (Cervidae) is now considered to consist of a complex group of about 57 species and almost 200 subspecies (Whitehead, 1993). There are seven deer species (red deer *(Cervus elaphus scoticus)*, wapiti deer *(Cervus elaphus nelsoni)*, sika deer *(Cervus nippon)*, sambar deer *(Cervus unicolor)*, rusa deer *(Cervus timorensis)*, fallow deer *(Dama dama)*, white-tailed deer *(Odocoileus virginianus)* from two subfamilies (Cervinae and Odocoilinae) present in New Zealand (Nugent *et al.,* 2001a).

Since being introduced in the 1850s, red deer are the most abundant and widespread species in New Zealand, having established multiple populations throughout New Zealand (Figure 1.2) (Nugent, 1992; Fraser *et al.,* 2000). However, all introduced deer species appear to be colonising new areas and establishing new populations, with fallow deer establishing 42 new populations and sika deer establishing 27. By comparison, the minor species (wapiti, sambar, rusa, and white-tailed deer) comprise only 9% of 166 new deer populations identified during the 1990s. Most of these new populations have resulted from farm escapes (38%) and illegal liberations (26%), whereas natural dispersal accounts for relatively few (5%) new populations (Fraser *et al.,* 2000).

Figure 1.2. Geographical distribution of the long established red deer populations in New Zealand (the shaded areas represent the presence of deer), from Fraser *et al.* (2000).

Although many deer populations had increased to high levels in many areas by the mid 1900s, various combinations of government-funded deer control, helicopter-based commercial harvesting, and recreational hunting have consequently reduced most deer populations by 75-95% (Caughley, 1983; Challies, 1985; Nugent, 1992; Parkes *et al.,* 1996). Despite this intensive control, red deer populations continued to expand in range in the last decade of the 20th century. They occupy around 120 000 km2, including

scattered areas of Northland, Auckland, Taranaki and the western King Country where red deer had not previously been recorded (Figure 1.2) (Fraser *et al.,* 2000).

The total breeding population of wild deer in New Zealand in the late 1980s was estimated at 250,000, of which some 81% were red deer (Nugent and Fraser, 1993). Most deer are now confined by helicopter-based hunting to around 60,000 km^2 of taller shrubland or forest, suggesting a national average density of 3-4 red deer/ km^2 (Nugent *et al.,* 2001a). Deer densities appear to be lower in the South Island (typically 2-5 deer/km^2) than in the North Island (more often 5-15 deer/km^2) (Nugent *et al.,* 2001a). Most of the large-scale variation is inversely correlated with the extent and continuity of forest cover, which in turn determines vulnerability to helicopter-based commercial hunting (Nugent and Sweetapple, 1989; Challies, 1991).

Today there is ongoing importation of new genotypes that continues to broaden the genetic base of New Zealand's red deer populations. Recent introductions have included eastern European red deer and all the principal strains of North American wapiti. Within the commercial deer farming industry, cross-breeding between red deer and wapiti is a common practice (Pearse and Goosen, 1999). With numerous deliberate releases and accidental escapes of farmed deer into the wild (Fraser *et al.,* 2000), and the recent reduction in large scale helicopter harvesting, it is inevitable that the genetic composition of wild red deer in New Zealand will gradually be modified (Nugent *et al.,* 2001a).

1.5 Background of canopy gap and exclosure experiments

The use of exclosure experiments to examine the impacts of grazing mammals on the regeneration of tree species is a method that has been used since the late 1940s (New Zealand Forest Service, 1984; Rose and Burrows, 1985; Wardle *et al.,* 2001). This method, which fully excludes ungulates from particular parts of forest, is now widely used both globally and in New Zealand, by fencing off areas usually around 10m x 10m (Kraft *et al.,* 2004; Webster *et al.,* 2008) or 20m x 20m (Stewart and Burrows, 1989;

Smale *et al.,* 1995)*,* however*,* in some circumstances this area can be on the scale of square kilometers (Kumar *et al.,* 2006).

The herbivore species that are being excluded will depend on what type of fence is set up which depends on what species are present and in some cases the aim will be to exclude more than one species, whether it is wild deer, goats or even grazing sheep and cattle (Kay and Bartos, 2000; Webster *et al.,* 2005). For example, the aim of an experiment conducted in Utah, USA was not only to examine the impact of both grazing livestock and big-game browsing on the decline of aspen *(Populus tremuloides),* but also to be able to distinguish the varying impacts from the different species. Therefore, five of the exclosures consisted of a total-exclusion portion, a livestock-exclusion portion, and a no-exclusion portion which permitted the effects of deer *(Odocoileus hemionus)* and elk *(Cervus elaphus)* herbivory to be measured separately from those of livestock (Kay and Bartos, 2000).

In contrast, the aim of the experiment may be to examine the effects of a single species. For example, a study examined the impacts of white-tailed deer *(Odocoileus virginianus)* (the only deer species present on Stewart Island) on the regeneration of the coastal conifer-broadleaved hardwood forests of Stewart Island, New Zealand. Permanent 20m x 20m quadrats were established in 1979 on deer-free Bench Island, matching quadrats were also established inside deer exclosures on Stewart Island. The quadrats were monitored for six years, after which the vegetation inside each quadrat was remeasured in 1985 (Stewart and Burrows, 1989).

The above examples both illustrate reasons why this method has been effective when used to study the impacts of browsing and/or grazing animals on the regeneration of vegetation. This method has been successful and widely used as it can be designed to fit the required time frame of the species that is being measured, whether it is a relatively short (Stewart and Burrows, 1989; Stroh *et al.,* 2008), intermediate (Smale *et al.,* 1995; Webster *et al.,* 2008) or an extremely long period (Husheer *et al.,* 2005).

Plant growth is highly variable between high and low light environments making light intensity a major factor in relation to the establishment of invasive plants in forested environments (Chacon and Armesto, 2005). Canopy gaps are a major source of this light variation in forested environments, therefore should be considered in regeneration experiments (Makana and Thomas, 2005).

Studies involving canopy gaps have been published as far back as the 1970s, however the idea of factoring canopy gaps into plant regeneration studies appeared slightly later in the 1980s (Chacon and Armesto, 2005; Makana and Thomas, 2005). Since these primary studies involving canopy gaps, there are now extensive examples in the literature. For example, a study conducted in the tropical forests of Africa which aimed to identify the factors that affected the regeneration of timber species after logging, found light to be a significant factor in enhancing regeneration of five out of six of these timber species (Makana and Thomas, 2005). More advanced studies have not only investigated the effect of the presence of light gaps in the canopy but also the size of these gaps (Baret *et al.,* 2008). In their study Baret *et al.* (2008) examined how canopy gap size influenced the establishment success of particular species. They found that although plants could persist in the shade, a germination experiment revealed that canopy gaps were essential for seedling establishment and larger gaps increased the abundance of these species (Baret *et al.,* 2008). This provides evidence that canopy gaps are an important driving factor and must be considered in canopy understory regeneration experiments (Kondani, 2001; Lof *et al.,* 2007).

1.6 Related research

As stated above in section 1.5 the use of exclosure experiments has been around since the late 1940's and tree gap experiments are slightly newer starting to be used in the 1980s. However, experiments that combine these two methods when investigating the regeneration of a species are rare in the literature. This rarity is due to the fact that globally, the idea of the interaction between canopy gaps and herbivory on forest regeneration is a relatively new concept, therefore has only been studied in recent times

in a small number of studies (Castleberry *et al.,* 2000; Holladay *et al.,* 2006). Of studies that have considered these two driving factors to interact, the majority have been conducted in America (Holladay *et al.,* 2006) or Switzerland (Smit *et al.,* 2006). For example, a study performed in South Carolina, USA examined the interactive effects of overstory gap size, canopy openness, herb layer competition, and mammalian (deer, swamp rabbits) herbivory on emergence and seedling bank formation of cherrybark oak, *(Quercus pagoda)* in experimental gaps created by mechanised logging. They concluded that canopy gaps had a larger effect on seedling regeneration than did mammalian herbivory (Collins, 2003).

There is one New Zealand example where both canopy gaps and herbivory have been considered when investigating the regeneration of a species. In 1989 an experiment conducted on Stewart Island, New Zealand concluded that after deer exclusion, numbers of treeferns and tall seedlings of hardwoods increased, especially in treefall gaps and areas of partial canopy dieback. Under the influence of deer, tall seedlings of hardwood trees and shrubs were rare and were being eliminated by browsing (Stewart and Burrows, 1989). This study did consider the interaction between canopy gaps and mammalian herbivory but failed to measure the effect of canopy gaps using a balanced factorial design. A more opportunistic approach was adopted by taking measurements where canopy gaps happened to be present within the study site (Stewart and Burrows, 1989).

Although there have been experiments that have considered the interaction between these two factors, they have all focused on how these affect the regeneration of native species (Stewart and Burrows, 1989; Tripler *et al.,* 2005). However, there are overseas studies that have investigated how the presence of canopy gaps affects the establishment of invasive species, but no New Zealand studies have examined this phenomenon. For example, a study performed on the volcanic island of Rèunion in the Indian Ocean investigated how gap dynamics in a tropical rain forest affected plant invasions. They found that the highest abundance of invasive species was beneath the larger of the examined canopy gaps (Baret *et al.,* 2008).

Therefore, this study set out to study the combined effects of canopy gaps and herbivory on the establishment of invasive plants. This was achieved by a balanced factorial design that considered the large scale interaction of canopy gaps and mammalian herbivory on the establishment and spread of invasive plant species in New Zealand native beech (*Nothofagus)* forest. Forty six percent of New Zealand's native forest is pure *Nothofagus* forest with another 22% being mixed *Nothofagus*, podocarp, angiosperm forest (Kelly *et al.,* 2008). *Nothofagus* has a natural mortality rate of around 360 years (Wardle, 1984); this along with natural wind throw creates gaps in the forest canopy. If browsing mammals such as deer are present and suppress the natural regeneration of this species, this will present an opportunity for invasive species to establish in the forest understory (Coomes *et al.,* 2003).

It follows on from above that, (1) canopy gaps have been found to be major driving factors of plant invasion into native forests, (2) there are a large number of invasive plants that have naturalised in New Zealand, and (3) deer which are established and widespread throughout New Zealand have altered the composition and structure of vegetation substantially (Coomes *et al.,* 2003). These three factors make New Zealand increasingly vulnerable to the establishment and spread of invasive plants in to native forest, making this present study highly important to New Zealand's native ecosystems and biodiversity.

1.7 The DOC experiment; how this present study was made possible

The Department of Conservation (DOC) proposed a nation-wide experiment to examine if canopy gaps and deer herbivory are significantly affecting the growth and regeneration of *Nothofagus* forests. Part of this involved the construction of 32 randomly located 10m x 10m plots in the Hopkins (16) and Huxley (16) valleys situated in the Ruataniwha Conservation Park, near Twizel, New Zealand (RCP) (Figure 1.3). The location of these plots was achieved by randomly generating global positioning system (GPS) coordinates that were within the boundary of the study site. There are four treatments being used; 8 of the plots were left alone (controls), 8 had 2m high fences put around the outside (fence),

8 had 12m x 12m light gaps created in the above canopy by cutting down the canopy trees (gap) and 8 had fences and light gaps (gap fence). Each of the 32 plots was assigned a treatment (4 of each treatment in each valley) to control for the fact that deer were being managed in the Hopkins valley and not the Huxley. With the use of helicopters the fences were flown in to ground crews waiting at the forest plots and the experiment was constructed in 2006/07.
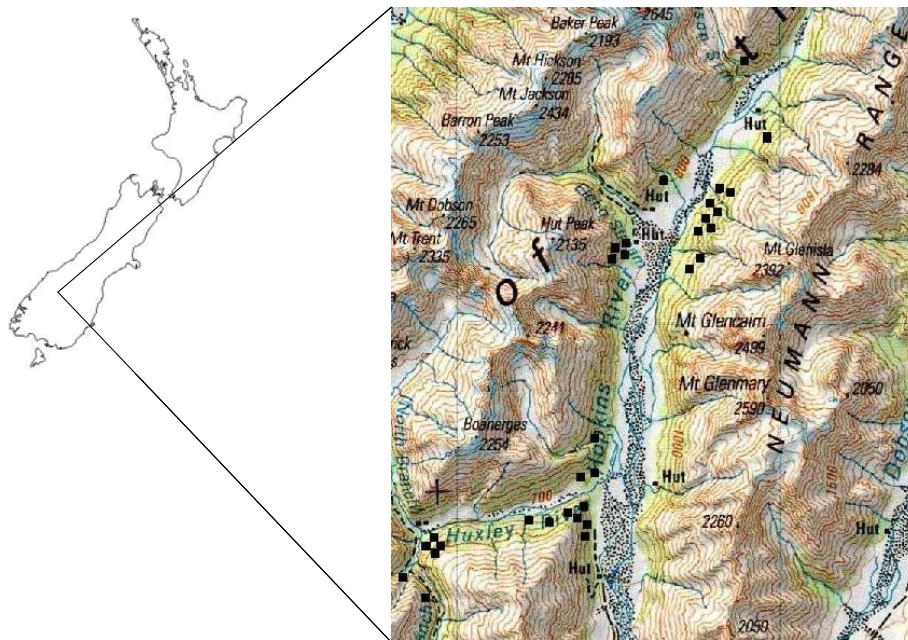
Figure 1.3. Topographic map displaying the 32 randomly located 10m x 10m plots (the large black squares) situated within the Hopkins and Huxley valleys in the Ruataniwha Conservation Park, near Twizel, New Zealand. The grid lines are at 10km spacings.

This presented a rare opportunity for me to design and work on an experiment of this scale, as without DOC and Landcare research this would have been far too expensive and time consuming to set up within the time constraints of a Masters of Science (MSc). I proposed to examine if these two factors (canopy gaps and deer herbivory) could affect the establishment and spread of invasive plants in *Nothofagus* forests by using the same plots.

Before their experiment was constructed, DOC and Landcare Research conducted vegetation and site characteristic surveys on the parts of forest that were going to be used

for their experiment. These data were made available to me so I could compare the 32
plots to examine if there was any significant variation between them before my
experiment began.

1.8 Research aims

The aim of this research was to investigate if canopy gaps and herbivory by red deer
significantly affect the abundance of invasive plants in New Zealand's native *Nothofagus*
forests, this was achieved by testing four hypotheses (Figure 1.4). Secondly, if there is a
significant effect, is it due to only one of these factors (canopy gaps or herbivory) or is
there an interaction between them? This is in attempt to ultimately increase scientific
knowledge on how to protect native forests from the negative impacts of invasive species.
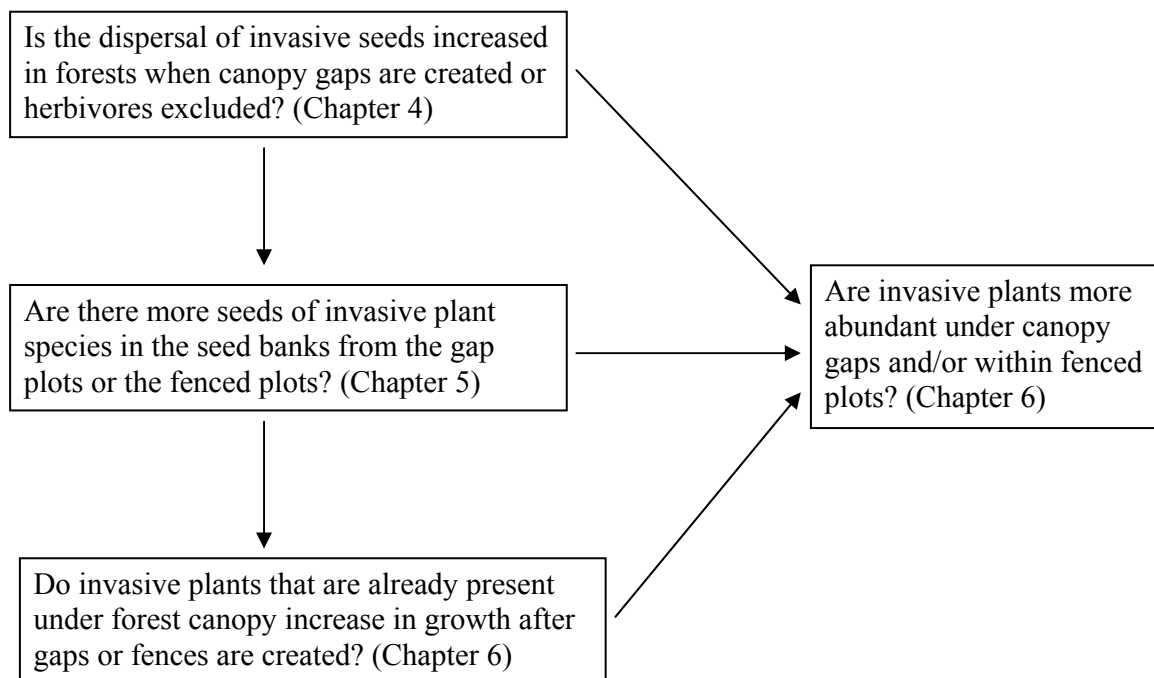
Figure 1.4. Diagrammatic representation of the four hypotheses tested in this present
study that were used to answer the main aims of this study.

How this was achieved is described in the following chapters:

1. Chapter 2 gives the history of the Ruataniwha Conservation Park (RCP) (where this present study was conducted) in relation to forest structure (canopy height, average tree diameter at breast height (dbh) and tree density) and vegetation composition, before this present study was set up. This information was used to establish a baseline for measuring changes during the course of the experiment.

2. Chapter 3 measured the climatic conditions (relative humidity, ambient air temperature and soil temperature) of open and closed canopy plots to investigate if canopy openness significantly affected these climatic variables that have the potential to influence the establishment and growth of invasive plant species.

3. Chapter 4, by the use of sticky seed traps, recorded the abundance of invasive seeds arriving at each plot (dispersal), to determine how treatment influenced the abundance of invasive seeds that arrived at each of the 32 plots.

4. Chapter 5 compared the species diversity and individual abundance of seed bank samples taken from the 32 plots, under 'ideal' growing conditions (in the glasshouse). These results helped to determine how many invasive species had seeds present but dormant in the seed bank.

5. Chapter 6 describes the variation of aboveground invasive plant abundance from the 32 plots, in relation to treatment. This was done by recording the vegetation present in, and 50m either side of each plot, 12 and 24 months after the DOC experiment was set up. This helped to determine the effect of treatment on the establishment and spread of invasive plants in this New Zealand native forest.

6. The concluding chapter (chapter 7) links the various experiments together and explains how they all helped to answer the two main questions of this study.

Chapter 2: Site characteristics and history

2.1 Introduction

The Ruataniwha Conservation Park (RCP) is located at the north end of Lake Ohau in the Mackenzie Basin 300km south of Christchurch and encompasses two main valleys, the Hopkins and Huxley. Both valley floors are between 600-700m a.s.l, however, the altitudinal range of the 32 randomly located plots where this present study was performed, is between 680-1120m a.s.l, and the surrounding peaks reach 2590m. As the RCP is an eastern neighbour to the main divide of the Southern Alps it is comprised of steep, rugged terrain right from the valley floor up to the mountain tops above the tree line. The valley floors and riverbeds are farmed with grazing sheep and cattle as these components of the RCP are leased to the farmer by the crown.

The RCP features a diverse range of vegetation from valley-floor grasslands and wetlands to hillside beech forests and alpine herbfields. In the higher rainfall valleys close to the main divide, silver beech *(Nothofagus menziesii)* and mountain beech *(Nothofagus solandri* var. *cliffortioides)* are the dominant tree species while in the lower valleys mountain beech, subalpine shrublands and tussockland predominate. The beech forests in the Huxley, Dobson and Temple valleys are New Zealand's stronghold for the threatened tree *Pittosporum patulum* as well as some of the best sites for beech mistletoe *(Peraxilla* spp and *Alepis flavida)* in the country (www.doc.govt.nz).

The beech forests situated on the western side of the Mackenzie Basin form part of a floristic gradient that begins on the eastern side of the main divide and extends over to the western interior of the south island (Wardle, 2001). At the eastern end of this gradient where rainfall decreases and the temperature range increases the species-rich forests of the west shift towards pure mountain beech forest (Wardle, 1984). However, there is still albeit, a small diversity of other species present in these forests for example, *Phyllocladus alpinus, Podocarpus hallii* and a range of ferns in parts where there is an increase in water availability (Wardle, 1984).

The pattern of forest distribution in this district has been remarkably stable since European activity began in the 1850s, despite fire, grazing by domestic and feral mammals, and some exploitation for timber (Wardle, 2001). Although these influences continue, the greatest threat may now be competition from introduced plants, including herbaceous species that may have been encouraged by episodes of fertiliser use and increased stocking, and, especially, introduced trees that are hardier and more vigorous as pioneers than native trees (Wardle, 2001).

To accurately record the change of a study site over the duration of an experiment the initial state of that study site must be recorded before the experiment is constructed (Chacon and Armesto, 2005). The following data were collected before the DOC experiment was set up, which provided the information required to record the change of specific site characteristics over the duration of my present study. This initial recording of site characteristics is a method that is widely used (e.g. Smale *et al.,* 1995; Fownes and Harrington, 2004; Lof *et al.,* 2007; Seiwa, 2007) illustrating its importance in experiments that are involved with the change of communities over a certain time period. This information becomes increasingly important when the experiment involves the direct comparison of various plots within the study area (Ito and Hino, 2008). As the significant effect of this experiment was determined by the difference between these various plots; knowing if there was any significant difference between them before the experiment started was important.

The aim of this survey was to investigate if there was any significant pre-existing variation between the plots and to give a full description of the plots before the experiment was set up. This was achieved by attempting to answer the following questions:

1. What was the present vegetation composition and forest structure of the RCP before the present study began?
2. Before the construction of the DOC experiment was there any significant difference between the areas of forest that were going to be used, in regards to forest structure and vegetation composition?

2.2 Methods

2.2.1 Site descriptions

Before the experimental plots were constructed (in late 2006, early 2007) a description of the 32 sites was undertaken. These site descriptions were carried out by members of the Department of Conservation and Landcare Research. The site characteristics were recorded to test whether there was any significant variation between the plots before the present study was set up.

In total 18 site characteristics were recorded at each plot that were of interest to this present study and are separated in to three groups:

Geographical characteristics
- Altitude recorded with the use of a global positioning system (GPS)
- Aspect was recorded with the use of a GPS and compass
- The slope of each site was recorded by use of an abney level

Biological characteristics
- Ground cover composition of vegetation, moss, leaf litter, bare ground and rock were recorded in percentage cover of the plot area
- The mean top height of the canopy trees was calculated by measuring all the canopy trees within each 10m x 10m plot
- Estimations of canopy tree cover in the following height classes were also recorded
  - less than 30cm
  - 31cm to 1.99m
  - 2m to 4.99m
  - 4.99m to 12m
  - more than 12m

Geological characteristics

- The percent cover of broken rock and soil at each plot were recorded by visual estimation.
- Surface stability of each plot was recorded on a scale of 1-3, 3 being highly stable, this was dependant on what the surface was made up of whether it was broken rock, rock or *Nothofagus* forest floor comprised of soil and roots.

2.2.2 Statistical analysis

Firstly, I analysed in a principal component analysis (PCA) all 18 predictors that I considered to have the potential to produce any significant variation between the 32 plots, the PCA was performed in PC-ord4. The PCA compared all the 32 plots by the 18 predictors along two axes to produce a visual comparison of any variation between the plots (Figure 2.1). To investigate this further all 32 axis one and axis two scores for each plot were analysed in a single factor ANOVA to examine if there was significant variation between each treatment (control, fence, gap, gap fence) in regards to the 18 site variables (Table 2.1).

I then analysed the 5 most relevant predictors individually by the use of single factor ANOVAs, to investigate if any of these predictors were producing significant variation between the treatments (Table 2.2). This analysis was performed in R version 2.7.0.

2.3 Results

2.3.1 Principal component analysis

It is evident from the principal component analysis that there appears to be some original variation between the plots before the experiment began (Figure 2.1).
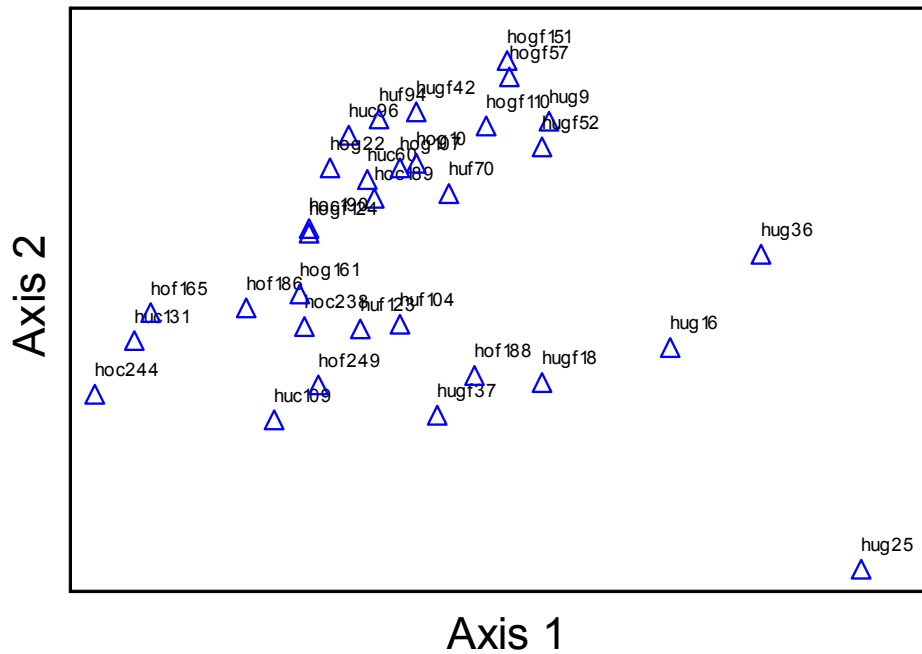
Figure 2.1. Principal component analysis (PCA) of the differences among the 32 plots randomly located in the Hopkins and Huxley valleys, using the 18 site variables described above in the methods section (2.2). Plot labels are formatted as follows, catchment (Hopkins (ho) or Huxley (hu), treatment (control (c) fence (f) gap (g) gap fence (gf) and plot number.

The two single factor ANOVAs comparing the axis one and axis two scores for all four treatments illustrated that there was no difference between all 32 plots along axis one and two (Table 2.1).

Table 2.1. Results from the two single factor ANOVAs comparing the axis one and axis two scores for each treatment from the above PCA to evaluate if there was significant variation between the four treatments regarding the 18 site characteristics recorded from the Hopkins and Huxley valleys, 2007.

Predictor	Df	Deviance	Residual Df	Residual Deviance	F-value	Pr(>F)
NULL axis1			31	87.17		
treatment	3	3.66	28	83.8	0.37	0.77
NULL axis2			31	158.28		
treatment	3	29.62	28	128.66	2.15	0.12

2.3.2 Similarity between the 4 treatments before this study began

In support from what is illustrated in the PCA, the results from five single factor ANOVAs conclude that there is no significant variation between the four treatments in relation to these five most relevant site characteristics (Table 2.2).

Table 2.2. Single factor ANOVA results that tested for significant variation between the four treatments in relation to the five most relevant site variables, from both the Hopkins and Huxley valleys, December 2007.

Predictor	Df	Deviance	Residual Df	Residual Deviance	F-value	Pr(>F)
NULL total cover			31	13215.5		
treatment	3	1380.8	28	11834.8	1.089	0.37
NULL native cover			31	9729.5		
treatment	3	1294.2	28	8435.2	1.43	0.25
NULL altitude			31	488732		
treatment	3	52065	28	436667	1.11	0.36
NULL slope			31	4538.9		
treatment	3	282.6	28	4256.2	0.62	0.61
NULL mean top height			31	751.6		
treatment	3	130.6	28	621	1.96	0.14

Vegetation cover, altitude and ground cover were all non-significant across the four treatments (Table 2.2). Figures 2.2 – 2.4 show the ranges for each of these variables across the four treatments at the start of this experiment.
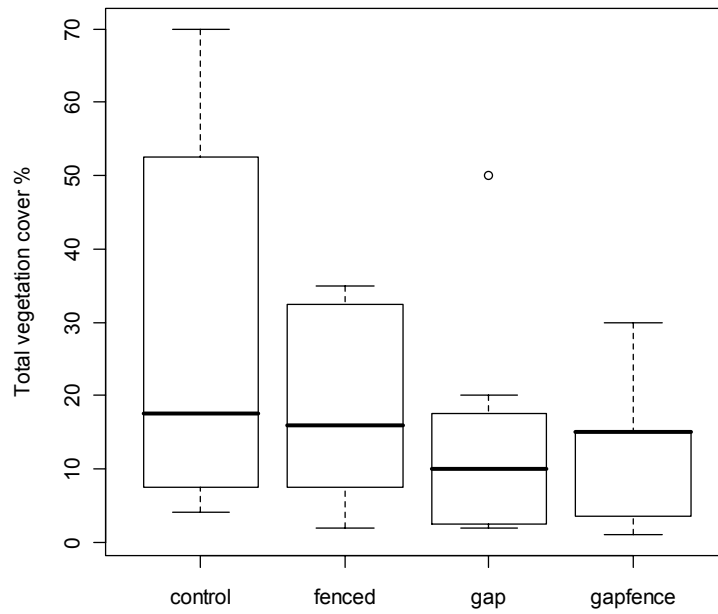
Figure 2.2. The variation in vegetation percent cover between the four treatments from both the Huxley and Hopkins valleys, December 2007.
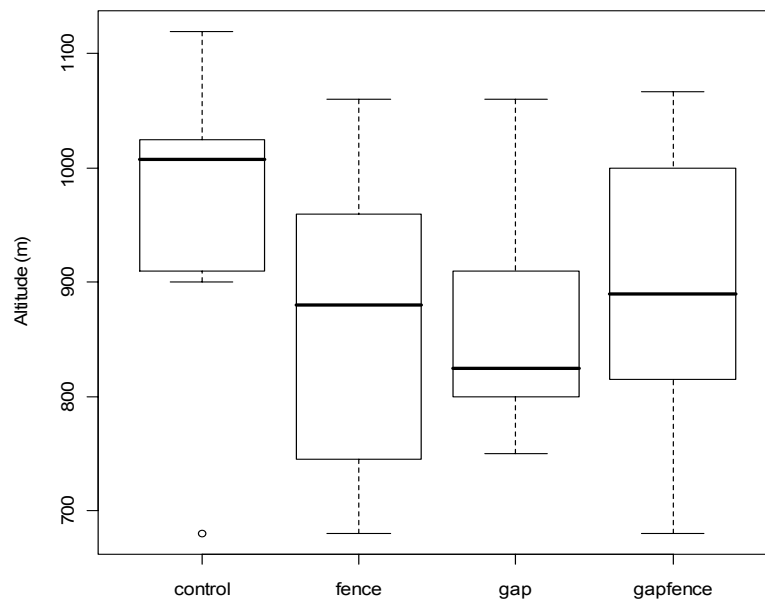
Figure 2.3. The variation in altitude between the four treatments from both the Huxley and Hopkins valleys, December 2007.
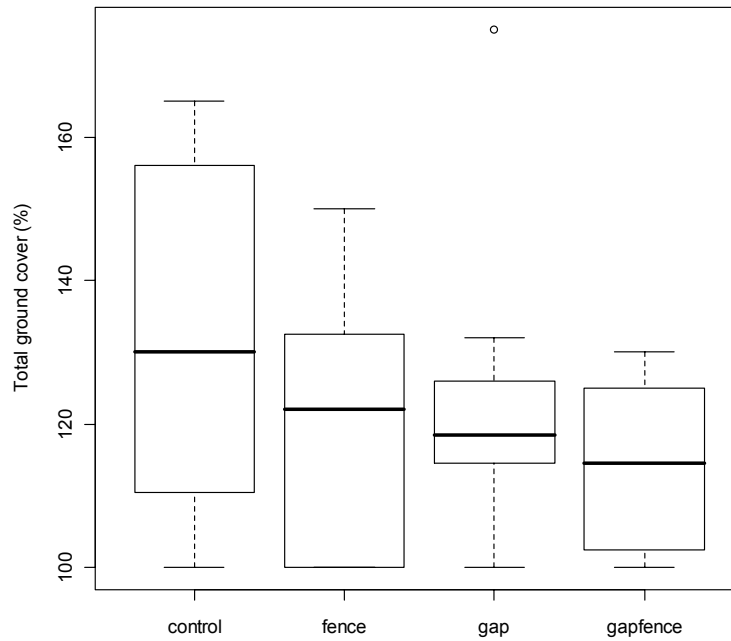
Figure 2.4. Total ground cover variation between the four treatments from both the Hopkins and Huxley valleys, December 2007.

2.4 Discussion

2.4.1 Similarity in site characteristics due to random site selection

When study plots are randomly selected and a wide range of site characteristics are considered such as, altitude or total vegetation cover it is highly likely that variation between plots will exist (Oheimb *et al.,* 2005). However, the use of random allocation of treatments to plots should usually ensure that there is no systematic difference among treatments before the experiment starts. Also, as stated above, compositionally speaking, *Nothofagus* forests in this region are quite homogeneous (Wardle, 1984). In this situation, the homogeneity of the forest in the RCP influenced these results more than the suggestion by Oheimb *et al.* (2005).

Although this present study considered a wide range of site characteristics, not exhaustive to vegetation composition, there was no significant variation between these site characteristics over 32 study plots (Table 2.1 and 2.2). This is fortunate as it ensures that any results found in this study will be due to the treatment at each plot and not an underlying factor that was not accounted for.

Even though it did not display significant variation, I thought the variation in altitude, had the potential to affect the final results of this study. However, there are two points to be made that provide evidence against this factor affecting the final results.

Firstly, in their study of species assemblages, Masaki *et al.* (1992) recognised the presence of site specialists and site generalists, where the site-specialist species occurred along ridges and at the bottom of the valley, while the generalists were not restricted in their site selection. As the invasive species recorded in this present study were site generalists that have very long distance dispersal (up to 18.5km from its origin) the effect of altitude was probably small in this regard (Richardson and Pysek, 2006). Secondly, the altitudinal range covered by all the plots was not large enough to exceed the altitudinal limits of the species being recorded (personal observation, 2008).

Therefore, the similarity between these 32 plots was due to the homogeneity of this *Nothofagus* forest in regards to vegetation composition as this was the most relevant or influential site characteristic to this present study. Lastly, the random location of the 32 plots resulted in a good representation of this forest as they all displayed similarities for the recorded site characteristics (Table 2.2).

2.4.2 Conclusions

1. The *Nothofagus* forests of this region are quite homogeneous in regards to the site characteristics recorded in this present study.

2. The random allocation of treatments to plots has ensured that there were no important pre-existing differences between treatments; this is concluded from the single factor ANOVAs in table 2.2.

3. The similarity between these plots before this study began helps to ensure that any variation found at the end of this study will be the result of the treatments applied to each of the plots.

Chapter 3: Microclimate comparisons between open and closed canopies

3.1 Introduction

The manner in which plant communities change through time and space has been a central concern of ecology, and the need to understand the patterns and processes in vegetation has, if anything increased in the face of ongoing and increasingly rapid environmental change. Projections of changing climate and incidence of climatic extremes in particular pose important questions in relation to likely ecosystem response (Easterling *et al.,* 2000; Klein Tank, 2002; Greenland *et al.,* 2003; Weltzin and McPherson, 2003; Hobbs *et al.,* 2007), especially when coupled with changes in land use and disturbance regimes (Chapin *et al.,* 2001). Davis (2005) recently suggested that contemporary ecology tends to consider vegetation change in a series of largely separate endeavors (for instance, succession ecology, invasion biology, gap/patch dynamics, and global change effects on plant communities) that focus on different causes of vegetation change, for example species introduced from other regions of the world, disturbances that create gaps and initi ate succession, and global change. In reality, all these influences are likely to be important to a greater or lesser extent and will interact within any particular plant community (Shaw *et al.,* 2002; Zavaleta *et al.,* 2003), and an understanding of these influences and interactions is essential if we are to understand, manage, and restore ecosystems more effectively in the future (Hobbs *et al.,* 2007).

The establishment of invasive species often compromises the biodiversity, ecological functioning and economic value of invaded ecosystems (Ross *et al.,* 2008; Mack *et al.,* 2000). Future global changes, such as climatic warming and an increased tendency towards human-dominated land use are likely to favour invasive species and exacerbate their impacts (Dukes and Mooney, 1999; Vilá *et al.,* 2006). Correlative models suggest that climate is a major constraint on the distribution of many invasive plant species (e.g. Kriticos *et al.,* 2005; Dunlop *et al.,* 2006). Whilst several studies have suggested likely range shifts based on such analyses (e.g. McDougall *et al.,* 2005; Thuiller *et al.,* 2005), independent measurement of the key climatic variables (light intensity and duration, air

and soil temperature and relative humidity) that assist in establishing invasive species has not been well covered in New Zealand *Nothofagus* forest. Thus, disentangling the relative importance of these climatic variables on the potential for invasion under a future warmer climate requires experimental rather than solely biogeographical (Thuiller *et al.,* 2005) or observational (Becker *et al.,* 2005; McDougall *et al.,* 2005) approaches (Ross *et al.,* 2008).

A study by Fernández and Fetcher (1991) concluded that different disturbances create different types of gaps, and these different gaps modify many abiotic factors. For example, in tropical environments where hurricanes occur frequently and create gaps, severe canopy damage defoliates the surrounding canopy which may result in higher solar radiation than would occur with a treefall gap. Fernández and Fetcher (1991) also suggest that landslides affect the distribution of litter by removing it from the upslope and concentrating it on the downslope area of the slide. These differences will impact both the temperature and moisture conditions present at each gap site depending on what environmental forces created the gap (Everham *et al.,* 1996).

An accurate way to simulate natural disturbance experimentally is to apply methods that have the potential to change the environmental microsite conditions of the forest for example, by admitting more light, increasing both the maximum and daily fluctuation in temperature and by altering the amount of relative humidity present at each microsite (Everham *et al.,* 1996). The resulting spatial/temporal heterogeneity of microsites as they function as germination cues, coupled with the known variation in species germination requirements, can show which climatic variables are important in determining the post-disturbance patterns of invasive species (Everham *et al.,* 1996).

Previous studies on canopy gaps have demonstrated that, over a diurnal period, due to the increase in sunlight availability, soil and air temperature increase in gaps and microclimate variation is greater within gaps compared to the forest understory (Phillips and Shure, 1990). The availability of light within gaps increases the soil temperature and air temperature which decreases the relative humidity (Barik *et al.,* 1992). In addition to

canopy cover, latitude has also been found to influence the distribution of light within gaps (Canham *et al.,* 1990). Interestingly, few studies have examined microclimate and vegetation patterns in the same experiment (Raymond *et al.,* 2006).

Therefore, this chapter set out to answer the following questions:

1. How did the canopy gaps created in 16/32 plots in *Nothofagus* forest at Lake Ohau affect climatic variables such as, relative humidity, soil temperature and air temperature?
2. If significant variation is detected, what specific climatic variables are producing this variation and how does this vary by time of day or season?
3. Also to help investigate what effect these climatic variables have on the abundance and composition of invasive plant species found at each plot.

3.2 Methods

The aim of this experiment was to test for any significant variation in the climatic conditions between the two treatments that were tested (open vs. closed canopies). Whether the plots were fenced or not was thought not to be relevant to this part of the study as the presence of a fence was assumed to have no effect on these three climatic variables.

3.2.1 Experimental design

The climatic variables that were of interest in this experiment were: air temperature ($^{\circ}$C), soil temperature ($^{\circ}$C) and percent of relative humidity (RH). To examine these variables I used a paired design, having one data logger placed in an open canopy plot and over the same 14 day period another data logger in a closed canopy plot nearby. After 14 days the data loggers were relocated to another pair of open and closed canopy plots. All three variables were recorded 8 times; twice in both treatments during autumn (11/4/2008 - 9/5/2008) and again in summer (18/12/2008 - 16/01/2009). This method produced four

replications for each of the two treatments, with eight plots being used to gather these data (Figure 3.1).
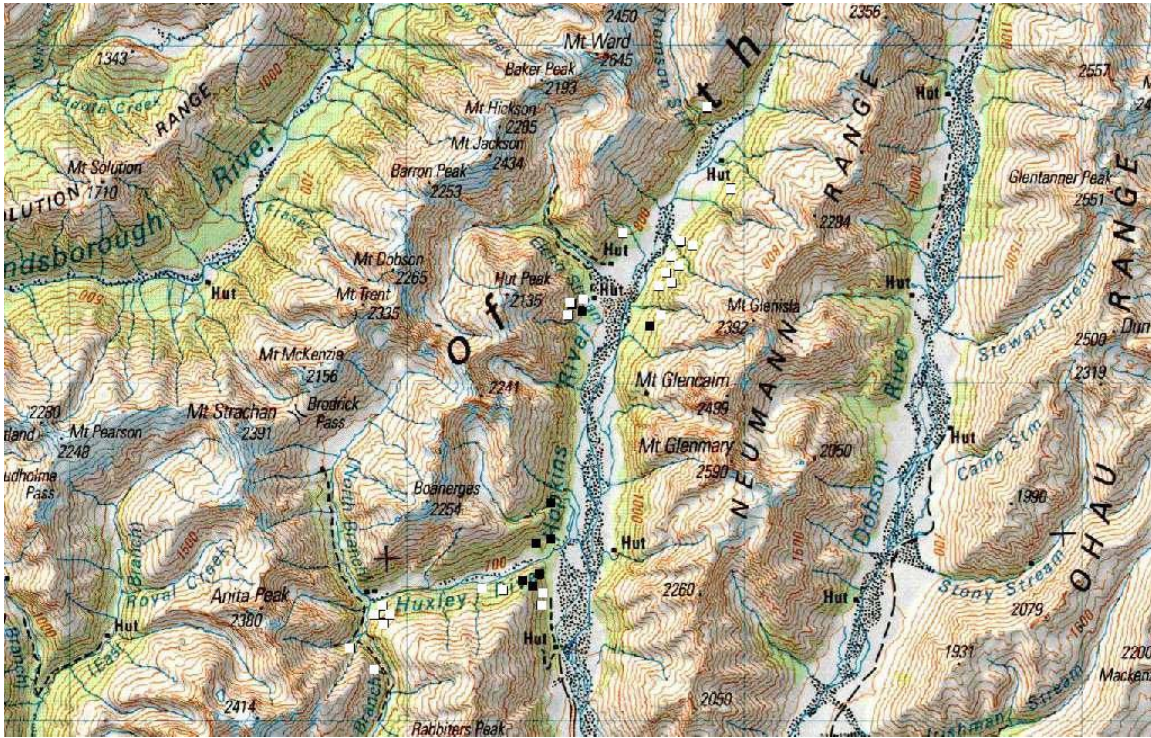
Figure 3.1. Topographic map of the 8 plots (black squares) used to record the climatic variables in the Hopkins and Huxley valleys during 2008 and 2009 (white squares illustrate the plots that were not used).

The three climatic variables were sampled at different intervals, because soil temperature and relative humidity (RH) were less variable than air temperature. Therefore, soil temperature and relative humidity were recorded once every 60 seconds and air temperature was recorded every 3 seconds. These individual values were used to produce a mean value for each variable for every hour and these hourly mean values were used for input into the analysis.

3.2.2 Data logger set up

Each data logger (CR10X measurement and control module from Campbell Scientific INC) had two recording instruments connected to it; a soil temperature probe (109SS-L

stainless steel temperature probe) and another probe that measured both RH and air temperature (Vaisala INTERCAP® humidity and temperature probe HMP50).

The depth of the soil temperature probe and the height of the air temperature/RH probe were kept constant. The soil probe was inserted into the ground, parallel to the soil surface at a depth of 3cm; as most seeds from wind dispersed invasive species germinate from the upper soil layers (Behenna and Vetter, 2008; Bond and Honig, 1999). The air temperature/RH probe was set at 1.4 metres (m) (breast height) from the ground to match the height of standard meteorological recording. An opaque plastic cover with small (0.5cm in diameter) holes in the side was placed over the air temperature/RH probe to allow air flow around the probe, to stop it from getting wet and to shield it from direct sunlight that may cause it to record incorrect measurements.

3.2.3 Statistical analysis

As the data were paired (one data logger in a closed canopy plot and another in a nearby open canopy plot at the same time) all three measured climatic variables (air and soil temperature and relative humidity) were analysed by the use of paired t-tests (paired two sample for means). The analysis compared the mean value between the open and closed canopy plots during the day (0600-1700) and night (1800-0500) in summer and again in autumn, from the Hopkins and Huxley valleys. These tests were performed in Microsoft Excel XP.

The day and night values were analysed separately due to the nature of the contrasting canopy structures (open vs. closed). Parts of forest that are under shade during the day will be cooler than parts that are exposed to direct sunlight, however at night this heat is allowed to escape faster where the canopy is open than from parts of the forest where the canopy is closed (Brooks and Kyker-Snowman, 2008; Jennings *et al.,* 1999). This contrast in diurnal heat cycling between open and closed canopies had the potential to produce opposite changes in temperature, this was controlled for by treating the day and night values separately.

The mean values that each paired t-test compared were derived from two sets of recordings each being 14 days in duration. The hourly recordings were used to generate mean values for every day and night that was recorded. This produced 28 values for both day and night in open and closed canopy plots during summer and autumn, 224 in total. These 12-hour means were averaged to give the final value for each climatic variable in a particular season (autumn or summer) at a given time (day or night) and specific treatment (open or closed canopy) (Table 3.1).

3.3 Results

It is evident that the open canopy plots recorded higher soil and air temperatures. Therefore, relative humidity was lower in the open plots compared to the closed canopy plots as, in this forest environment, these two climatic variables are inversely correlated (Table 3.1). The following sections test whether these differences were significant.

Table 3.1. Comparison of the open and closed plots in relation to temperature and RH (%), during the day (0600-1700) and night (1800-0500), over autumn and summer, from the Hopkins and Huxley valleys. The night and day mean values have also been combined to produce season values, taking away the diurnal effect.

		Air temp Open	Air temp closed	Soil temp open	Soil temp closed	RH open	RH closed
Day	autumn	5.94	4.31	7.24	7.00	70.24	86.17
	summer	17.74	15.40	15.49	14.00	76.10	80.19
Night	autumn	4.91	3.50	7.32	7.18	74.07	88.19
	summer	16.90	14.55	15.34	13.85	77.91	82.00
Season	autumn	5.43	3.91	7.28	7.09	72.16	87.14
	summer	17.33	14.98	15.42	13.93	77.00	81.10

Paired t-test comparing air temperature between the open and closed canopy plots over night (1800-0500) and daily (0600-1700) periods illustrated that air temperature varied significantly between these treatments. During autumn there was no significant difference in air temperature, however in summer the air temperature was significantly higher in the open canopy plots over both day and night periods (Table 3.2).

Table 3.2. Paired t-tests comparing the average air temperature between the open and closed canopy plots in summer and autumn during the day (0600-1700) and night (1800-0500), from the Hopkins and Huxley valleys.

		d.f	t Stat	t critical two-tail	P(T<=t)
Night	autumn	54	1.59	2.005	0.117
	summer	54	2.21	2.005	**0.031**
Day	autumn	54	1.82	2.005	0.075
	summer	54	2.18	2.005	**0.034**

Soil temperature between the open and closed canopy plots over night (1800-0500) and daily (0600-1700) periods did not vary significantly between these treatments. During the summer soil temperature was slightly higher in the open canopy plots, however in autumn the opposite occurred where the closed canopy plots recorded higher soil temperatures than the open canopy plots during both the day and night periods (Table 3.3).

Table 3.3. Paired t-tests comparing the average soil temperature between the open and closed canopy plots in summer and autumn during the day (0600-1700) and night (1800-0500), from the Hopkins and Huxley valleys.

		d.f	t Stat	t critical two-tail	P(T<=t)
Night	autumn	54	0.35	2.005	0.774
	summer	54	1.76	2.005	0.085
Day	autumn	54	0.57	2.005	0.57
	summer	54	1.51	2.005	0.137

From the results of the paired t-tests that compared the relative humidity between the open and closed canopy plots over night (1800-0500) and daily (0600-1700) periods illustrated that relative humidity varied significantly between these treatments. During the summer relative humidity was slightly lower in the open canopy plots, however this difference was insignificant. In autumn significantly higher relative humidity was recorded in the closed canopy plots during both the day and night periods (Table 3.4).

Table 3.4. Paired t-tests comparing the average relative humidity between the open and closed canopy plots in summer and autumn during the day (0600-1700) and night (1800-0500), from the Hopkins and Huxley valleys.

		d.f	T Stat	t critical two-tail	P(T<=t)
Night	Autumn	54	-4.65	2.005	**<0.0001**
	Summer	54	-1.24	2.005	0.219
Day	Autumn	54	-4.21	2.005	**<0.0001**
	Summer	54	-0.87	2.005	0.388

3.4 Discussion

3.4.1 Is air temperature significantly affected by canopy gaps?

The presence of canopy gaps significantly affected the air temperature that was recorded between the open and closed canopy plots. However, differences in air temperature between the open and closed plots during the autumn (March – May) were non-significant. Therefore, during the summer (December – January) there was a positive relationship between canopy openness and increased air temperature during the day (0600-1700) and night (1800-0500) (Table 3.2). This result is due to the amount of sunlight reaching each plot as this is the only contrasting factor between the open and closed canopy plots. This is determined by the amount of shade cover present at each plot which is controlled by the canopy cover (Dai, 1996). A study by Everham *et al.* (1996) supports this result, as they found when comparing regeneration success of five tropical tree species, that canopy gaps had increased temperatures compared to other shaded (closed canopy) parts of the same forest.

De Freitas and Enright (1995) studied the microclimates situated within temperate rainforests of northern New Zealand. They compared microclimates that were present in the forest understory with parts of the forest where canopy gaps of varying sizes had formed. The mean daytime (0700-1700) air temperature in the gap sites was 84.3% greater than the air temperature recorded in the understory microclimates (de Freitas and Enright, 1995). They concluded this to be the direct result of the amount of sky exposure

present at each site, therefore increasing sunlight availability in the more exposed (gap) sites (de Freitas and Enright, 1995).

However, an American study on the responses of coastal Douglas fir *(Pseudotsuga menziesii)* to gap formation found that there were only slight increases in air temperature after the gaps were created (Gray *et al.,* 2002). To present stronger contrast to the general trend and further support to the previous finding, a study by Clinton (2003) on microclimate responses to small canopy gaps in the southern Appalachians, concluded that there was no significant difference in air temperature between the gap and non-gap sites. He went on to further suggest that topography, aspect and evergreen understory are the primary determinants of spatial and temporal heterogeneity in understory microclimates (Clinton, 2003).

The results from this present experiment have further importance to the whole study as it has been widely suggested that invasive plant abundance increases with an increase in temperature (Cicek and Tilki, 2006; Vilà *et al.,* 2006; Dukes and Mooney, 1999; Thompson *et al.,* 1997) even in artic tundra regeneration has been seen to increase with temperature (Hobbie and Chapin, 1998). Therefore, with canopy gaps increasing the air temperature of the surrounding microclimates, the increase of invasive diversity in to natural forests may be able to persist in the long term.

3.4.2 Do canopy gaps affect soil temperature?

There was no difference in soil temperature between the open and closed plots with the largest variation being less than two degrees celcius, which was recorded at night during the summer (Table 3.3). Therefore, illustrating that although the increase in sunlight availability significantly increased the air temperature it was not of high enough intensity to significantly increase the soil temperature (Table 3.3).

In a study involving the responses of herb layer species to experimental canopy gaps in a northern hardwood forest Collins and Pickett (1988) also detected no difference in soil

temperature between the gap and non-gap plots. They concluded that canopy height and density were the two major determinants influencing soil temperature between gap and non-gap plots, but also admit that this result could vary spatially over forests at a global scale.

However, studies have illustrated that canopy gaps can significantly change (decrease, increase or make more variable) present soil temperatures to that of the surrounding understory soil temperatures. For example, Sariyildiz (2008) who studied the effect of various gap size classes on long-term litter decomposition rates in northeast Turkey, concluded that the large (diameter of more than 30m) gaps significantly reduced litter decomposition rates by changing environmental conditions, especially by decreasing soil temperature (Sariyildiz, 2008).

In contrast, studies have illustrated the more obvious trends, for example where a canopy gap has been created and there is an increase in sunlight reaching the forest floor, therefore increasing the soil temperature compared to the neighbouring understory forest floor (Ewel *et al.,* 1998; Schmidt *et al.,* 1998). Another example is where canopy gaps have significantly increased the diurnal variability in soil temperature due to the exposed ground increasing in temperature during the day, resulting in more dramatic cooling at night (Abe *et al.,* 2002). Canopy gaps increase the heat of the forest floor from sunlight during the day but increase heat lose by night especially on calm, clear nights (Ritter *et al.,* 2005; Barik *et al.,* 1992). Therefore, cloud and wind can both reduce these effects, but overall canopy gaps have an increased temperature variation compared to closed canopy forest (Brooks and Kyker-Snowman, 2008).

3.4.3 Did relative humidity vary between the open and closed canopy plots?

During the summer the variance between the open and closed canopy plots was non-significant irrespective to whether it was day or night. However, in autumn relative humidity decreased significantly in the open canopy plots compared to the closed canopy plots, this variation was detected during both the night and day (Table 3.4).

Wang *et al.* (2008) when studying the thinning effects on the microclimate and ground vegetation in a Taiwan plantation forest also found a significant difference in relative humidity between the open and closed canopy plots. However, there is a slight difference between the results obtained by Wang *et al.* (2008) and the present study; as they stated that there was a very significant difference during the day, but no significant difference was found during the night among treatments (Wang *et al.,* 2008). Thus, suggesting a diurnal effect may influence the difference in relative humidity between open and closed canopy sites. Danehy and Kirpes (2000) agree with this suggesting when they compared the relative humidity gradients across riparian areas. They found that over 0-5m (0 being the stream edge or open area and 5 being 5m back into the forest) there were significant changes in relative humidity but by 10m from the stream edge relative humidity had returned to upland understory levels. One of their final conclusions was that the diurnal pattern of air temperature (increase during the day and decrease during the night) is the dominant driver of relative humidity in these eastside forests as these two climatic variables are inversely correlated (Danehy and Kirpes, 2000).

The findings from an earlier study by Zarnowiecki (1994) that estimated air humidity relations in the forest communities also found that the mean relative humidity in all the forest communities was greater than in the open areas. As Danehy and Kirpes (2000) concluded Zarnowiecki (1994) also put this variation down to the lower mean air temperature recorded in the forested plots, therefore increasing the relative humidity in these forest plots.

Brooks and Kyker-Snowman (2008) also found the effect of time of day on relative humidity to be significant. However, in contrast to the pre-mentioned findings they found there only to be quite small (generally <1%) differences in relative humidity between paired control and harvest sites. In fact, unlike my present study, they found the largest average differences in relative humidity occurred at the forest floor position in the afternoon of the summer. This result is in total contrast as, my present study found no significant difference in relative humidity between the open and closed canopy plots during the summer (Table 3.4).

3.4.4 What about light availability?

The other factor that must be considered is the increase in light availability at the open canopy plots and the decrease of light as distance from the forest edge increases back into the forest interior. This is crucial to the understanding of forest ecology especially when investigating the spread of invasive species into the forest interior (Valladares and Guzman, 2006).

Buckley *et al.* (2003) realised this importance and constructed a model using multi-level, mixed-effects statistics on growth, survival, fecundity and damage, incorporating intrinsic plant variables, environmental variables, herbivory and spatial and temporal stochasticity. They found that populations in shaded and open sites had different dynamics and responses to control strategies. Shaded populations took longer to reach infestation densities and were less affected by herbivory and reductions in survival than open populations. Open populations increased faster in response to increases in rainfall, but this was not so for shaded populations.

A more specific example comes from a study by Cole and Weltzin (2005) who investigated how light availability created the patchy distribution of an invasive grass in eastern American deciduous forests. They concluded that light reduction by the canopy was the environmental constraint that prevented establishment of *Microstegium vimineum* beneath the tree canopy. Whereas, overstory tree canopy apparently facilitates the establishment of this shade-tolerant grass, the interaction of overstory canopy with mid-story canopy interferes with *M. vimineum* by reducing the availability of sun flecks at the ground layer.

Although brief, these examples illustrate the importance of sunlight present in a given part of forest when investigating the establishment and spread of invasive plants in to native forests after the creation of gaps in the forest canopy (Raymond *et al.,* 2006).

3.4.5 Conclusions

After comparing the results of this research with the wider literature, the following conclusions can be made:

1. Canopy gaps significantly affected the air temperature that was recorded between the open and closed plots during the summer.
2. The difference in soil temperature between the open and closed plots was non-significant with the largest variation being less than two degrees celcius which was recorded at night during the summer.
3. In autumn relative humidity decreased significantly in the open canopy plots compared to the closed canopy plots.
4. The amount of sunlight that reaches a site is an important factor that must be considered when investigating the establishment and spread of invasive plants in to native forests, after a gap has been created in the forest canopy.

Chapter 4: Seed dispersal

4.1 Introduction

Causes and consequences related to the distribution of invasive vegetation have always been of high interest in ecology, especially when implementing management strategies to decrease the adverse effects on native species (Nuttle and Haefner, 2005). Seed dispersal is widely recognised to be a fundamental process shaping population and community dynamics and all subsequent ecological interactions (e.g., Schupp and Fuentes, 1995; Howe and Miriti, 2000; Nathan and Muller-Landau, 2000) and determining, to a large extent, local and regional patterns of vegetation (Hubbell, 2001; Tuomisto *et al.,* 2003).

Research to understand and predict the spread of invasive species has become increasingly urgent in recent decades, as the widespread effects of invasive species cause ever more prominent problems. Management planning and implementation require improved information to be effective, especially given the constraints of limited resources. However, studies of seed dispersal and population spread are relatively difficult to carry out, compared to localised demographic studies (Skarpaas and Shea, 2007).

The use of seed traps to examine the dispersal of seeds to a specific site can be difficult especially in alpine environments. Artificial traps are often not easily accessible in remote field sites when repeat visits are required and traps must withstand the harsh conditions if left out for long periods (Larsson, 2003). However, when performed accurately this approach is very effective at supplying quantitative data on which species are arriving at a site, the abundance of each species and the preference shown by species to particular sites for example, where canopy light gaps are present (Larsson, 2003). This last point is especially important and highly relevant to invasive species, as it is often advantageous for invasive species to disperse their seeds into light gaps where offspring mortality is lower and the growth of seedlings is enhanced (Augspurger and Franson, 1988). Although recognised, this 'dispersal advantage' has not been tested thoroughly

with the use of a well balanced design encompassing a large scale, in New Zealand beech forest.

A pioneering study by Augspurger and Franson (1988) examined the input of wind-dispersed seeds into light-gaps and forest sites in a tropical forest. They concluded that at the community level nearly twice as many wind-dispersed seeds were collected from light-gaps as from a comparable area of intact forest (Augspurger, 1988). At the other end of the time scale a study by Skarpaas and Shea (2007) examined the speed of invasion waves and related these to species traits and environmental conditions. They concluded that over a wide range of realistic conditions, mechanistic spread rate estimates were most sensitive to high winds and low seed settling velocities. However, there are limited examples of this type of research in New Zealand and the most relevant one to this study comes from work done by McAlpine and Jesson (2008). Their study aimed to understand the factors and processes influencing recruitment of the invasive species *Berberis darwinii* (Darwin's barberry). They examined both temporal and spatial patterns of seed dispersal, germination and seedling establishment and found that newly emerged seedlings largely reflected patterns of seed rain, but seedling survival was significantly affected by distance from the source population, seedling density and light environment, therefore concluding that recruitment of *B. darwinii* is dependent on dispersal of seeds to favourable microsites.

The aim of this part of my research was to investigate the invasive species seed composition arriving in each plot for all treatments (control, fence, gap, gap and fence), in an attempt to examine how the four treatments affect seed dispersal. We might expect canopy gaps to have a larger effect on dispersal than the wire netting fences, but the design of the experiment allowed both to be tested.

This was achieved by answering the following questions:

1. Is the abundance of seeds (from all present species) arriving at a site significantly increased when there is a gap in the above forest canopy or a fence around the plot?

2. Are seeds of invasive plant species widespread throughout New Zealand *Nothofagus* forest or do they disperse in when canopy gaps or 10m x 10m fences are created in these forests?

* "Of course, some of the seeds caught in seed traps may come from plants growing in the plots rather than from longer distance dispersal; this aspect will be examined in chapter 6."

4.2 Methods

4.2.1 Seed trap design

This experiment used sticky sheets placed flat on the ground surface to trap arriving seeds. The seed traps were constructed from a clear A4 acetate sheet (210 x 296mm) that was attached to a plastic frame (250 x 350mm) so the trap could be pegged to the ground (Figure 4.1). The acetate sheet was then painted with an adhesive substance called "Tanglefoot" that the seeds would fall on and get stuck to. This design was used as it produced a uniform method across all of the 32 plots independent of treatment type, and was thought to be the most suitable for the target species (small seeded wind dispersed species) (Larsson, 2003).
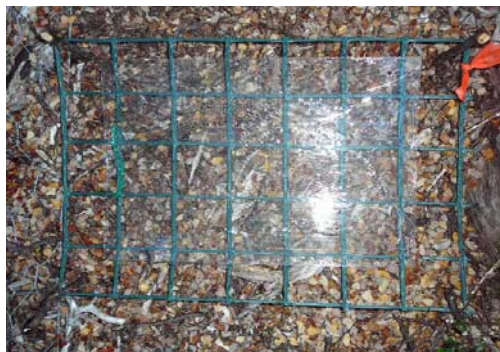
Figure 4.1. A seed trap attached to the plastic frame, coated in "Tanglefoot" and then pegged face up to the ground.

4.2.2 Seed trap layout

Each 10m x 10m plot contained two seed traps; one trap was placed half-way along the top edge and the other trap was placed half-way along the bottom edge (Figure 4.2). The 64 seed traps (2 traps x 32 plots) were set up and left out for a one month period from the 15th of April to the 15th May 2008, as autumn is the main period for seed dispersal.
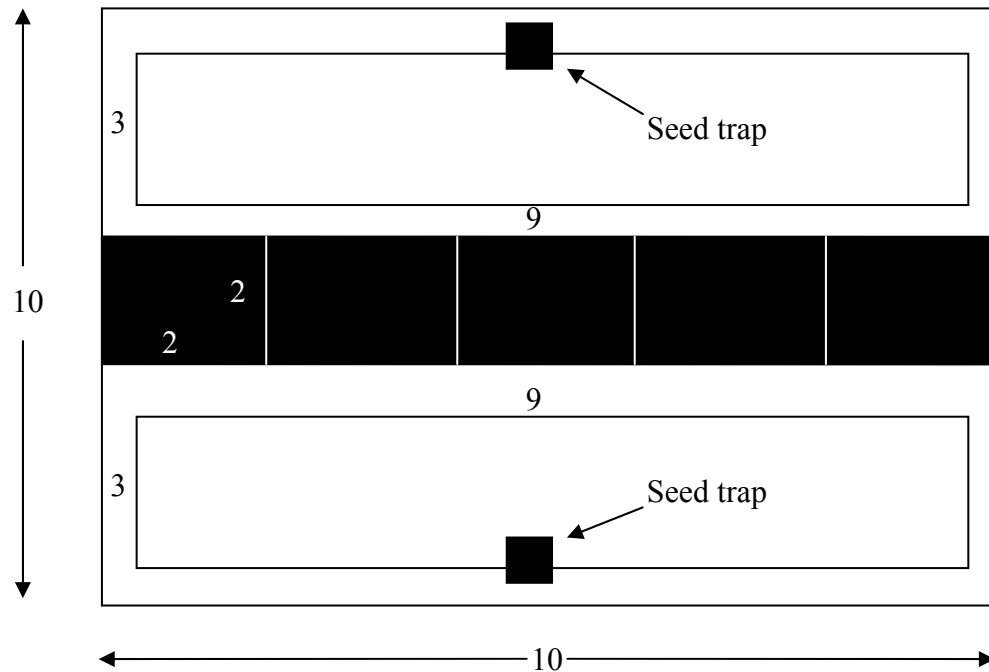
Figure 4.2. Diagrammatic representation illustrating the position of the two seed traps within the larger 10m x 10m plots. Traps were positioned to avoid disturbing the DOC experiment (black area across the middle).

4.2.3 Extracting and counting the seeds

After the one month period the seed traps were collected and brought back to the lab so the seeds could be extracted from the traps and counted. Each trap was placed under a large, well lit magnifying glass and each seed was then extracted with tweezers. Each trap was re-examined until it was evident that there were no seeds left on the trap. The seeds were then individually examined under a microscope so all seeds caught in each sticky trap could be identified, this was achieved with reference to the New Zealand seed atlas (Webb and Simpson, 2001)

The seeds caught in each plot were combined whether they were from the bottom trap or the top. This was done as the level of replication of interest was the 32 plots, not traps within plots

The analysis used two different approaches; seeds per square metre (m^2), calculated from the number of seeds from both seed traps, and the proportion of the total that was comprised of seeds from invasive species. To calculate the number of seeds per m^2, the total ground area over which the seeds were caught was calculated, this total area (1260 cm^2) was divided into $1m^2$ which equalled $0.1260m^2$, the seed totals from each plot were multiplied by this to give a m^2 value.

4.2.4 Statistical analysis

Poisson ANOVAs were used to analyse all the data that were generated from actual counts of seeds as these data displayed poisson distributions. Total seeds present for each treatment were analysed with gap, fence and the gap x fence interaction as the three predictors (Table 4.2). The total seed counts of the three most common species were also analysed separately with gap, fence, catchment and the gap x fence interaction (Table 4.6, 4.7 and 4.8). All statistics were performed in R version 2.7.0.

Catchment was not used in the analysis for the total seeds present in each treatment as it was only of interest which treatment was having an effect not if catchment was driving the seed abundance at each plot. However, this was important for the abundance of specific species to conclude whether each species found specific treatments more favourable or if they were just locally more abundant in one catchment compared with the other so catchment was included as a predictor.

The analysis of the highest proportion of invasive seeds used a linear mixed model as it is proportion data, but the estimated scale was too high (4.21 instead of close to 1), therefore the analysis type was changed to quasibinomial. The model tested these data against fence, gap and the fence x gap interaction (Table 4.4). This resulted in all three

predictors having a significant effect; the models were then run separately. Significance was tested between the models (fence only, gap only, gap and fence) by comparing the model with the predictor included with one from which the predictor had been removed. The best model was selected using a likelihood ratio test using the Akaike Information Criterion (AIC) and a Chi square statistic (Table 4.5).

4.3 Results

These results have been separated into three sections. The first section investigated what effect treatment had on the total number of seeds that were present at each plot. The second section examined what effect treatment had on the total proportion of invasive seeds found in each plot. Thirdly, I investigated how some species tend to favour one treatment over another. Section three examined the individual abundance of three more common species that had a high number of seeds caught over all the plots.

4.3.1 Total number of seeds (native and invasive) per plot across all treatments

The 64 sticky traps caught a total of 1012 seeds from 14 species, with only one species *(Nothofagus solandri)* being native. Thirteen of the 14 species that had seeds caught in these sticky traps were wind dispersed, the only species that is not wind dispersed was *(Solanum nigrum)*, note this species only had 2 seeds caught in all 64 sticky traps (Table 4.1).

Table 4.1. Summary of all the seeds (native and invasive) caught in 64 sticky traps (0.063m^2 exposed for one month) across all treatments, from both the Hopkins and Huxley valleys, April 2008.

	Control	Fence	Gap	Fence and Gap	**Grand totals**
Crepis capillaris	0	0	21	11	32
Carduus nutans	0	0	13	41	54
Echium vulgare	0	5	39	22	66
Cerastium glomeratum	0	0	0	5	5
Holcus lanatus	0	2	48	17	67
Agrostis capillaris	0	0	21	0	21
Senecio jacobaea	1	0	0	0	1
Urtica dioica	1	0	0	3	4
Hydrocotyle americana	0	0	0	13	13
Epilobium brachycarpum	0	0	0	7	7
Danthonia pilosa	0	0	0	38	38
Solanum nigrum	0	0	0	2	2
Agrostis gigantea	0	3	23	110	136
Nothofagus solandri	161	59	262	84	566
Total species	3	4	7	12	14
Total seeds	163	69	427	353	1012
Total invasive seeds	2	10	159	269	446
Invasive seeds/m^2	1.98	9.92	157.74	266.87	442.46
Percentage of invasives	1.23	14.49	37.24	76.2	43.48

The Poisson ANOVA on total number of seeds recorded for each treatment showed that the presence and absence of a canopy gap was the main predictor to significantly affect total seed catches, explaining most of the variation; however fence and the gap x fence interaction was also significant (Table 4.2). This suggests that when a gap is created in the above canopy it increases the number of seeds arriving at a site (Figure 4.3 and Table 4.2). These results were also found for the total number of invasive seeds recorded at each plot (Figure 4.4 and Table 4.3).
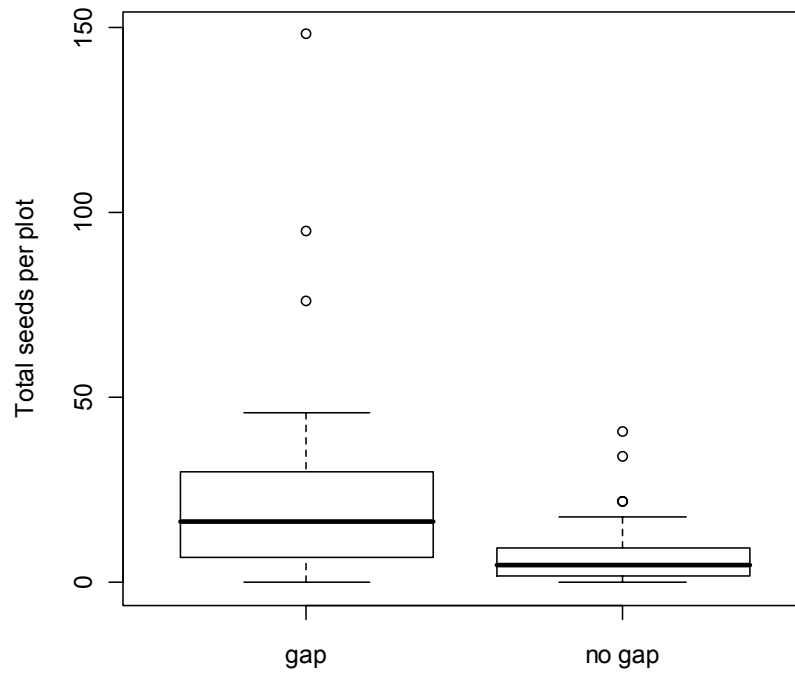
Figure 4.3. The total number of seeds caught from all 64 sticky traps (0.063m^2), exposed for one month in the 16 gap and 16 no gap plots, from both the Hopkins and Huxley valleys, April 2008.

Table 4.2. Poisson ANOVA on the total number of seeds caught in sticky traps from the 16 gap (gap and, gap fence) and the 16 no gap (control and fence) plots, from both the Hopkins and Huxley valleys, April 2008.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	1168.84	
gap	1	273.14	30	895.7	**< 0.0001**
fence	1	29.81	29	865.89	**< 0.0001**
gap:fence	1	34.11	28	831.78	**< 0.0001**
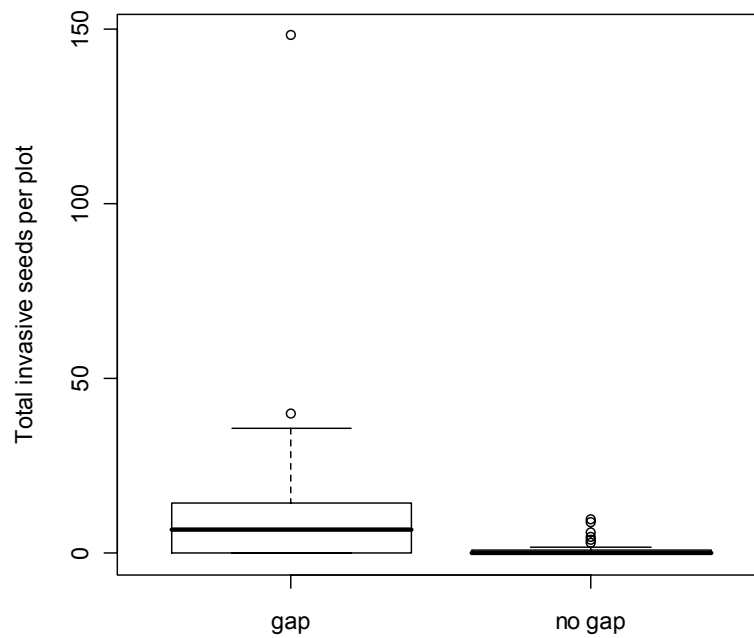
Figure 4.4. Total number of invasive seeds caught from all 64 sticky traps ($0.063m^2$), exposed for one month in the 16 gap and 16 no gap plots, from both the Hopkins and Huxley valleys, April 2008.

Table 4.3. Poisson ANOVA on the total number of invasive seeds caught in sticky traps from 16 gap and 16 no gap plots, from both the Hopkins and Huxley valleys, April 2008.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	1029.81	
gap	1	358.82	30	670.99	**< 0.0001**
fence	1	15.49	29	655.49	**< 0.0001**
gap:fence	1	22.52	28	632.98	**< 0.0001**

4.3.2 The total proportion of invasive seeds per plot

The linear mixed model on the total proportion of invasive seeds present in each plot showed that gap, fence and the gap x fence interaction all had a significant effect (Table 4.4). The gap plots had a higher percentage of invasive seeds than the closed canopy plots with the gap and fence plot having the highest percentage overall (Figure 4.5).
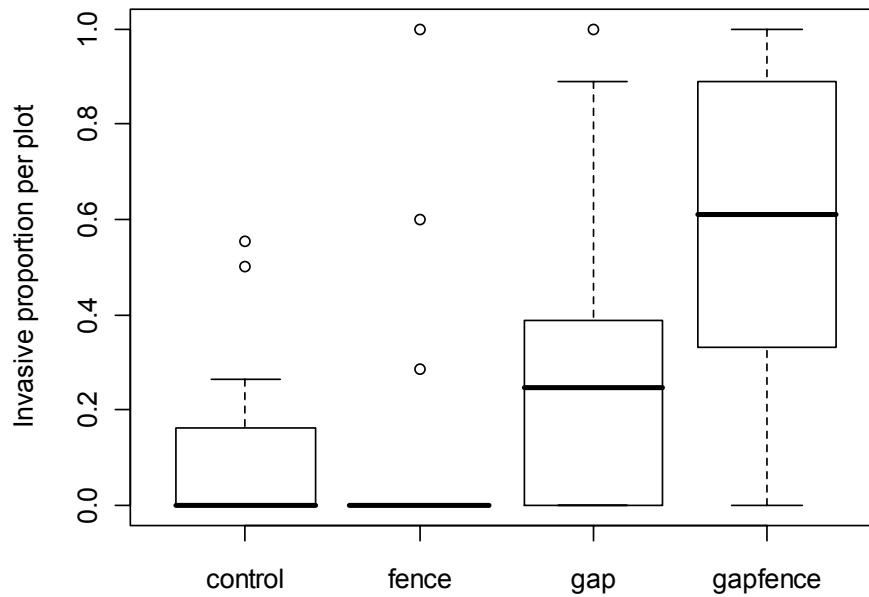
Figure 4.5. Total proportion of invasive seeds present in all plots across the four treatments from both the Hopkins and Huxley valleys, April 2008.

Table 4.4. The linear mixed model on which predictors increased the total proportion of invasive seeds present in each plot, from both the Hopkins and Huxley valleys, April 2008.

Predictor	Estimate	Std. Error	z value	P (>z)
fence	0.71	0.33	2.11	**< 0.035**
gap	1.59	0.29	5.44	**<0.0001**
fence:gap	1.47	0.42	3.51	**<0.0001**

Further analysis was performed on these data to determine which of these three predictors was most likely explaining this phenomenon (Table 4.5).

Table 4.5. Akaike Information Criterion test that compared all three models with each other to explain which predictor was driving the total invasive proportion of seeds caught in sticky traps from the 32 plots, from both the Hopkins and Huxley valleys, April 2008.

Model	Df	AIC	BIC	Chi square	P (>Chi)
fence	4	1513.53	1522.16		
gap	4	1498.85	1507.48		
fence:gap	6	1470.38	1483.33	47.151	**< 0.0001**

After comparison of the three models, it was evident that the model fence:gap had the lowest Akaike Information Criterion (AIC) score, therefore the model with fence, gap and fence x gap interaction was clearly best.

4.3.3 Trends of individual species

The last section of these results investigated if any predictors were driving the abundance of any specific individual species across the varying treatments. The raw data were observed for any trends where species may have been favouring one treatment over another and these species were investigated further (Table 4.1). The three species (*Carduus nutans* (8), *Echium vulgare* (8) and *Holcus lanatus* (9)) that occurred in the highest number of the 32 plots were tested to determine what was driving the increase in seed abundance from these 3 species (Figure 4.6, 4.7 and 4.8).

The number of *Carduus nutans* seeds were significantly increased by gap, fence and catchment (higher in Huxley), however the gap x fence interaction was non-significant (Figure 4.6, Table 4.6).

Figure 4.6. Total individual abundance of *Carduus nutans* seeds across the four treatments, from both the Hopkins and Huxley valleys, April 2008.

Table 4.6. Results summary from the Poisson ANOVA, displaying which predictors had a significant effect on the individual abundance of *Carduus nutans* seeds in each plot, from both the Hopkins and Huxley valleys, April 2008.
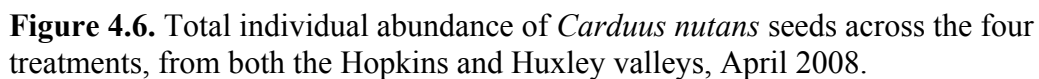
Predictor	Df	Deviance	Residual Df	Residual Deviance	P (>Chi)
NULL			31	237.93	
gap	1	74.86	29	147.82	**<0.0001**
fence	1	15.25	28	222.68	**<0.0001**
catchment	1	29.56	27	118.27	**<0.0001**
gap:fence	1	0	26	118.27	1.00

The number of *Echium vulgare* seeds recorded at each plot was significantly increased by canopy gaps and the gap x fence interaction; however fence and catchment had no effect (Table 4.7). There were no *E. vulgare* seeds recorded in the control plots and only 1 fence plot had *E. vulgare* seeds caught in the sticky traps (Figure 4.7).
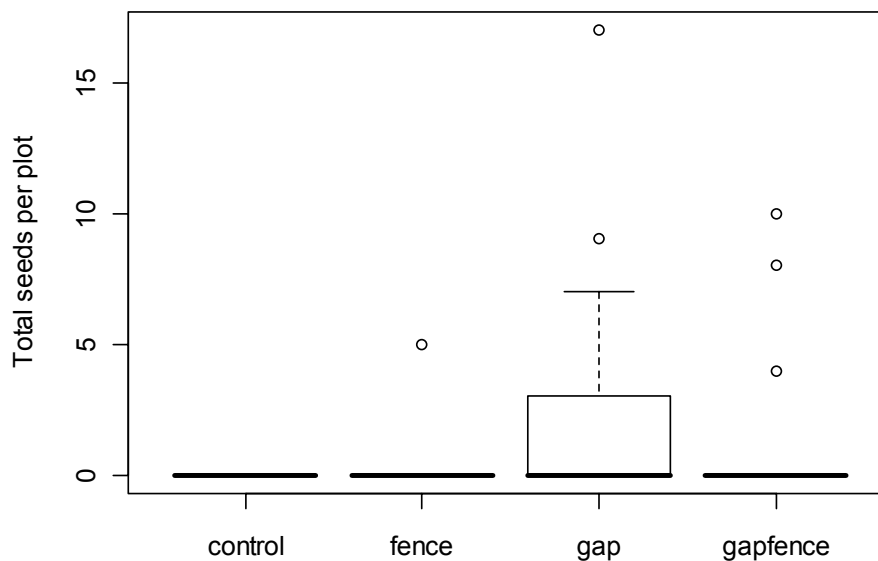
Figure 4.7. Total individual abundance of *Echium vulgare* seeds across the four treatments, from both the Hopkins and Huxley valleys, April 2008

Table 4.7. Results summary from the Poisson ANOVA, displaying which predictors had a significant effect on the individual abundance of *Echium vulgare* seeds in each plot, from both the Hopkins and Huxley valleys, April 2008.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	287.069	
gap	1	56.082	30	230.99	**< 0.0001**
fence	1	2.194	29	228.79	0.139
catchment	1	0.972	28	227.82	0.324
gap:fence	1	9.54	27	218.28	**0.002**

The number of *Holcus lanatus* seeds caught at each plot significantly increased with gap, fence and the gap x fence interaction (Figure 4.8 and Table 4.8). Catchment also had a significant effect on the abundance of *Holcus lanatus* seeds, as there were an increased number of seeds in the Huxley catchment compared to the Hopkins catchment (Table 4.8).
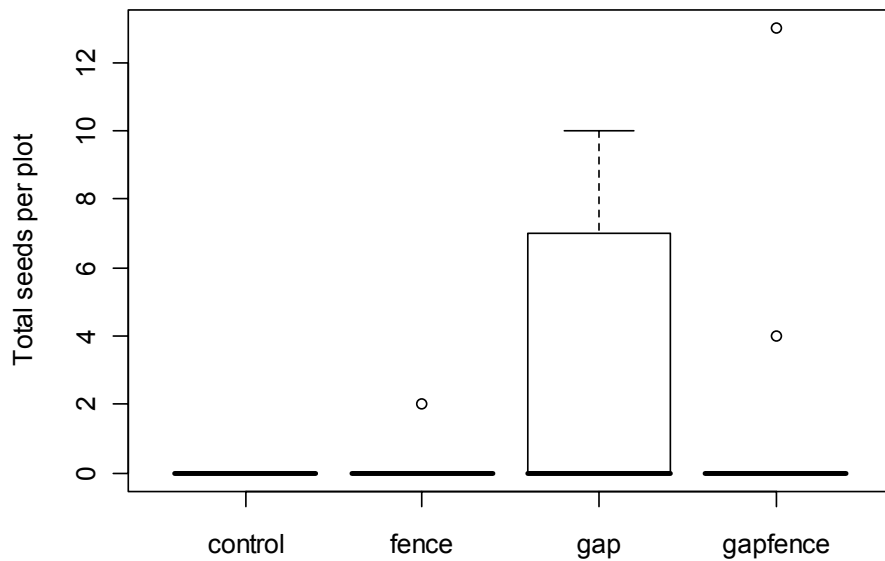
Figure 4.8. Total number of seeds caught per plot of *Holcus lanatus* seeds across the four treatments, from both the Hopkins and Huxley valleys, April 2008.

Table 4.8. Results summary from the Poisson ANOVA, displaying which predictors had a significant effect on seed abundance of *Holcus lanatus* in each plot, from both the Hopkins and Huxley valleys, April 2008.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	287.069	
gap	1	74.9	30	200.66	**< 0.0001**
fence	1	12.98	29	187.68	**< 0.0001**
catchment	1	14.91	28	172.77	**< 0.0001**
gap:fence	1	5.2	27	167.56	**0.023**

4.4 Discussion

4.4.1 The total number of seeds and the proportion of invasive seeds affected by treatment

4.4.1.1 Total number of seeds

There was a significant treatment effect in determining the total number of seeds and the total number of invasive seeds caught at each plot from the four treatments (Table 4.2). The total seed abundance increased where the plots contained a gap in the above canopy (all species by 3.36 fold and invasive species by 35.7 fold); compared to the closed canopy plots thus; illustrating the positive effect that canopy openness has on seed abundance (Figure 4.3). Furthermore, the total number of invasive seeds also increased when there was a gap in the above canopy (Figure 4.4).

This result has support in the wider literature; for example Augspurger and Franson (1988) found that nearly twice as many seeds were recorded from sites that were situated under canopy gaps compared to sites under intact forest. Twenty years ago their study hypothesised five explanations to describe this phenomenon: (1) the seed source is situated closer to gaps, (2) there maybe a greater fecundity associated with the individuals that are present in these high light environments, (3) seeds fall easily to the ground as there are no branches to catch them before they reach ground level, (4) gaps alter wind patterns (speed and direction) drawing seeds into gaps (Geiger, 1965) and (5) the aerodynamic properties of seeds make them unstable when encountering changing wind conditions, drawing seeds into gaps (Augspurger and Franson, 1988).

These are all plausible explanations, however the one of particular note is (4) that has gained support in the literature since the original study by Geiger (1965) (e.g. Augspurger and Franson, 1988; Nuttle and Haefner, 2005). A recent study by Panferov and Sogachev (2008) also confirms this theory, illustrating that this alteration can draw seeds into sites where canopy gaps are present (Figure 4.9). As the wind flow reaches the canopy gap the

wind changes sharply and moves in a downwards direction instead of continuing its normal path where it flows parallel to the forest canopy, thus drawing the seeds down to ground level, therefore increasing the abundance of wind dispersed seeds which settle into these closed canopy sites (Panferov and Sogachev, 2008).
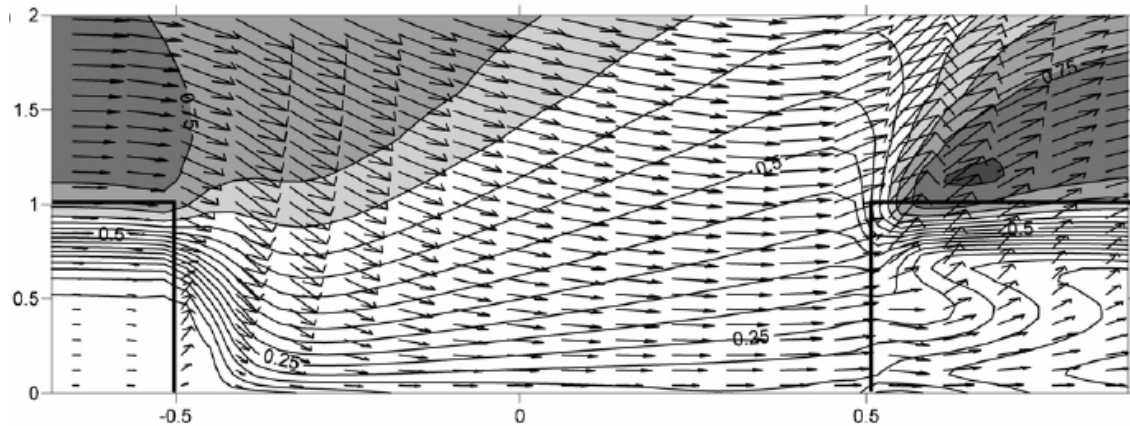
Figure 4.9. Systematic representation of the wind direction as it passes across a canopy gap, note the sharp downward movement as the wind encounters the canopy gap; drawing the seeds down to ground level. X-axis represents the horizontal dimension and the y-axis represents the height function. Solid black lines indicate the vegetation border and the grey zones indicate the areas of maximum wind force on the forest canopy (after, Panferov and Sogachev, 2008).

The majority of evidence supports this, however there is evidence that suggests updrafts occur where the leaf density and the height of the canopy is significantly decreased and this increases the distance seeds can disperse away from a site (Bohrer *et al.,* 2008). Although in this example the canopy may not be absent altogether it still illustrates the possibility that wind dispersed seeds may be carried further when released from these sites. From their results Bohrer *et al.* (2008) hypothesised this change in turbulence can affect seed travel and these sites where strong updrafts occur will increase the chance of long distance seed dispersal as the seeds have a greater chance of escaping the canopy, therefore travelling further. This suggests that the presence of a canopy gap is the key when determining if there is a sharp downwards change in the wind direction which draws these wind dispersed seeds down to the ground (Augspurger and Franson, 1988; Nuttle and Haefner, 2005).

4.4.1.2 Proportion of invasive seeds

The mean invasive proportion recorded for each treatment increased from 0.11 in the control plots to 0.56 in the gap fence plots (Figure 4.5). This is explained with reference to the above section; as the wind flow changes in a downwards direction when it encounters a canopy gap, therefore drawing wind dispersed seeds down to ground level (Geiger, 1965; Augspurger and Franson, 1988). Thus, 13 of the 14 invasive species recorded in the sticky traps were wind dispersed, so were likely to be more abundant at plots that were situated under canopy gaps.

4.4.2 Occurrence of the three most common species in relation to treatment

Carduus nutans, *Echium vulgare* and *Holcus lanatus* were the three species that had seeds caught in the highest number of sticky traps from the 32 plots. The number of seeds from these three species that were caught in the sticky traps was determined by gap, fence, catchment and the gap x fence interaction (Table 4.6, 4.7 and 4.8). I will discuss the reasons why fence, gap and catchment were the predictors that determined the number of seeds caught in the sticky traps from these three species (Table 4.9).

Table 4.9. Summary of which predictors were driving the number of seeds caught in the sticky traps for *Carduus nutans*, *Echium vulgare* and *Holcus lanatus*, from both the Hopkins and Huxley valleys in April 2008. The positive (+) symbols represent an increase in the number of seeds and a "0" where a predictor had no effect on the corresponding species.

	gap	fence	catchment	gap x fence
Carduus nutans	+	+	Huxley +	0
Echium vulgare	+	0	0	+
Holcus lanatus	+	+	Huxley +	0

Firstly, the presence of a canopy gap increasing the abundance of these species is directly related to what has been discussed in 4.4.1. As the wind flow reaches the canopy gap the wind changes sharply and moves in a downwards direction instead of continuing its normal path where it flows parallel to the forest canopy, thus drawing the seeds down to

ground level, increasing the abundance of wind dispersed seeds into these closed canopy sites (Bohrer *et al.,* 2008; Panferov and Sogachev, 2008; Webster *et al.,* 2005).

The reason for the presence of a fence increasing the abundance of these species is not clear, but may be explained by the fence deterring seed predators. Studies have illustrated that some predators are deterred by certain structures such as fences for example (Mayer and Ryan, 1991; Jackson, 2001). The deterrent can simply be because the structure prevents the predator from reaching the food source, for example a cage around a seed source will prevent birds reaching the seeds. Secondly, the seed predator may be unsure of the risk associated with the structure due to its unfamiliarity, therefore will stay away from it and gather resources from a less risky site (Mayer and Ryan, 1991; Jackson 2001). However, it is unlikely the seed predators present in the RCP, for example rodents and small avifauna would be deterred by the presence of the fence therefore this may be a spurious result.

Catchment was the third predictor that significantly affected the number of seeds that were caught in the sticky traps from these three species. The seeds of these species were more abundant in the Huxley valley compared to the Hopkins valley (*C. nutans* (46, 8) *E. vulgare* (37, 29) *H. lanatus* (47, 18)) respectively. As described in chapter 2 the two catchments encompass two separate valleys where the further most point can be over 15km from each other and differ in aspect.

There are three reasons why catchment can have an effect on the number of seeds caught in sticky traps: Firstly, varying conditions between the two catchments described in chapter 2 can drive the occurrence of these two species. As a study by Pyšek *et al.* (2005) illustrates that basic environmental and climatic conditions present at specific sites can drive the occurrence of certain species when the specific species find these conditions favourable (1). Secondly, as a recent study by Skarpaas and Shea (2007) and others (Nathan and Muller-Landau, 2000; Landenberger *et al.,* 2007) describes the combined importance of the parental seed source location (2) and relation to the prevailing wind (3) when explaining the occurrence of wind dispersed species. Therefore, the seed source of

these three species may have been situated closer to one catchment than the other or were positioned favourably in relation to the prevailing wind, thus increasing the number of seeds reaching the Huxley plots.

4.4.3 Conclusions

From the results of this research and evidence from the wider literature the following conclusions can be made:

1. There was a very low rate of arrival of invasive seeds into control plots, with only a single seed of each of 2 invasive species caught in the 8 plots over 1 month.
2. From all of the predictors tested, the presence or absence of a canopy gap directly above each plot was the main predictor driving the number and proportion of invasive seeds caught at each plot.
3. The presence of a fence was involved in explaining the high number of seeds caught in the sticky traps for the 3 species that were analysed, however this did not affect the total number of seeds caught in all 64 sticky traps.
4. Canopy gaps alter the local wind currents and seed movements in to forests; this form of disturbance has the potential to increase the number of seeds that arrive on the forest floor.

Chapter 5: Seed bank samples

5.1 Introduction

Many invasive species are able to grow in forests when a gap has been created in the forest canopy, either by dispersing in after the gap has been created, or by being present in a dormant state in the seed bank and germinating in response to increased light (Cone and Kendrick, 1986; Mancinelli, 1994; Buhler, 1997).

Two attributes are instrumental to the success of a plant population: (1) an early emergence time in relation to that of its competitor(s); and (2) to have a capacity to establish a large number of seedlings (Harper, 1977). These attributes are the reason why assessment of both timing and the extent of emergence are so important when studying the seed banks of invasive species (Benech-Arnold *et al.*, 2000). Temperature (as a function of light intensity, availability and duration), water availability and the gaseous environment are the important factors known to modulate or determine the emergence of invasive plants (Benech-Arnold *et al.*, 2000). When investigating the emergence (timing and composition) of invasive seed banks in a controlled environment (e.g. glasshouse) these factors can be measured and the quantity that is available to each seed bank can be considered when analysing the emergence of these invasive seed banks (Leon and Owen, 2004).

A study by Leon and Owen (2004) also makes note of the importance between using artificial (a known number of seeds sown into a growing medium) or natural seed banks (a soil sample taken directly from the study site, this was the method used in my research), stating that, "artificial weed seed banks are practical for studying seed bank depletion and weed seedling emergence because the number, depth, and species composition of seed banks can be managed". However, they concluded that the distribution of emergence with time differed (was lower) in the natural seed banks compared with the artificial seed banks (Leon and Owen, 2004). These differences were attributed to the artificial seed banks having a lower soil bulk density and greater

temperature fluctuation than the natural seed bank, therefore illustrating the importance of increased temperatures on the emergence of these invasive plant species (Leon and Owen, 2004).

With global climate change becoming a 'hot' topic over a relatively short time, it has generated considerable debate (e.g. Houghton and Woodwell, 1989; Mitchell, 1989; Schneider, 1990; Short and Neckles, 1999; Kriticos *et al.,* 2003). These impacts of increased atmospheric carbon dioxide, elevated land and sea temperatures, increasing sea level, increasing UV radiation and a host of secondary changes will alter the conditions for and rate of growth in both terrestrial and aquatic plants (Watson *et al.,* 1996).

Increasing temperature will directly affect plant metabolism and the maintenance of a positive carbon balance (Evans *et al.,* 1986; Marsh *et al.,* 1986; Bulthuis, 1987; Zimmerman *et al.,* 1989), which may result in changes in seasonal and geographic patterns of species abundance and distribution (McMillan, 1984; Walker, 1991). The direct effects of increased temperature will depend on the individual species' thermal tolerances and their optimum temperatures for photosynthesis, respiration, and growth (Short and Neckles, 1999). As invasive plant species have the potential to react positively to warmer temperatures by increasing seed emergence, compared to individuals situated in cooler environments. Global climate change has the credentials to increase biotic invasions, which have now been added to the list of important factors driving global change (Mack *et al.,* 2000).

This experiment was conducted to test the following question:

1. Is there a significant difference in the seed banks (diversity and abundance) of all invasive species, between the four treatments (control, fence, gap, gap and fence) from the Hopkins and Huxley valleys?

5.2 Methods

The aim of this chapter was to compare the variation in seed bank composition between the four treatments, to determine if treatment type significantly affected which species were present in the seed bank.

5.2.1 Sampling method

This seed bank sampling experiment was set up at the end of February 2008 with all the seed bank samples being taken from within the large 10m x 10m plots. Four seed bank samples were taken per plot; one sample half-way along each of the four edges (Figure 5.1). The size of each sample was kept uniform across the whole experiment by the use of a cylindrical core soil sampler. The soil sampler was 65mm in diameter, which equates to 33.2 cm^2 of soil surface area per sample equalling 132.8 cm^2 for each plot (33.2 per sample x 4 samples per plot); this is consistent with other studies of this nature (Rahman *et al.,* 1997; Bàrberi and Cascio, 2001; Funes and Basconcelo, 2003; Graham and Florentine, 2004). Each sample was removed from the ground and placed in a bag that was labelled with the plot number and a letter from A-D, this letter corresponded to the location in the plot where the sample had been taken from as all four samples were combined into a single trap for each plot (Figure 5.1).
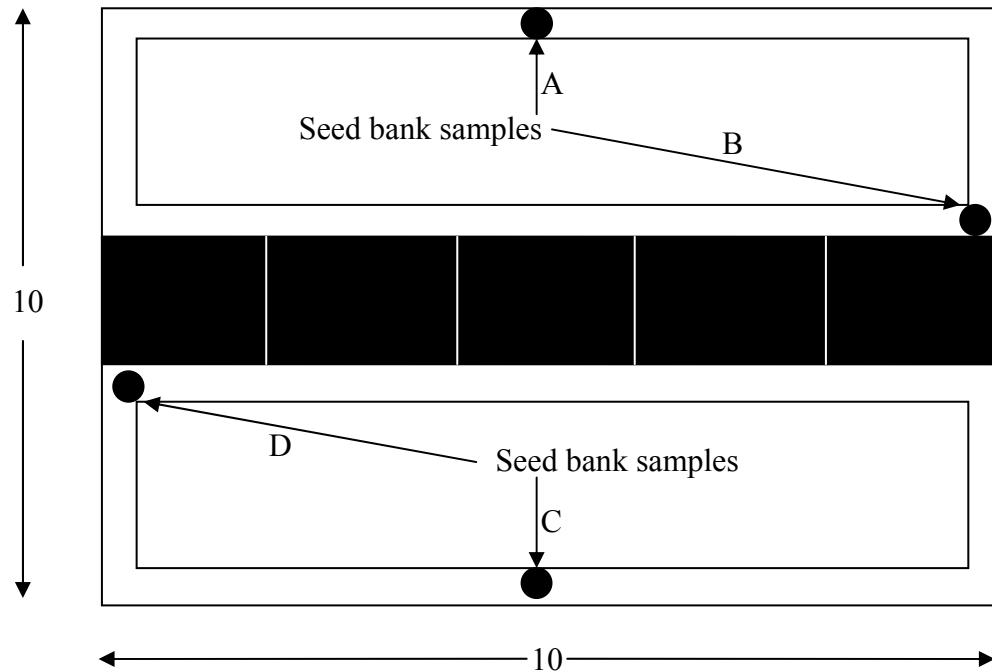
Figure 5.1. Diagrammatic representation illustrating the location of the four soil samples within the 10m x 10m plots. Note the soil samples are not drawn to scale as this makes it easier to see where they were taken from.

5.2.2 Set up in the glasshouse

The four samples from each plot were laid out in a plastic tray (22.5 x 29 x 6cm); non-fertilised potting mix was added to each container to increase the growing medium, so when the soil samples were added there was an average soil depth of 3.5cm. The trays were laid out in a glasshouse that had a diurnal temperature range of 18-21 degrees celcius ($^{\circ}$C) decreasing to 13 $^{\circ}$C over night (Figure 5.2). Instead of grouping the samples by treatment, they were arranged randomly to eliminate any possible differences in the sunlight duration received in the glasshouse by each sample. Control trays, containing only the potting mix used with the samples, were placed at each end of the seed bank samples (Figure 5.2). This was done to measure contamination by seeds being dispersed into the trays in the glasshouse.

(Figure 5.2). Photograph illustrating how the seed bank sample trays were set up in the glasshouse; note the glasshouse control tray at either end of the samples.

5.2.3 Data recording

For the first four months the sample trays were checked on a fortnightly basis, to observe when individuals started to grow above the soil surface. After the first four months (mid June 2008), seedlings were identified to species and counted for each sample tray. This was performed again at the eight month stage and finally at the end of the twelve month period. Throughout the chapter I will refer to "seeds" and the "seed bank", however this also includes all plants which emerged from the sample trays, including non-seed plants like ferns.

5.2.4 Statistical analysis

The individual abundance and the species diversity data were all analysed using Poisson ANOVAs. All statistics were performed in R version 2.7.0.

Poisson ANOVAs were used for the total individual counts as these data displayed poisson distributions, therefore violated the assumption of normally distributed data. The

mean individuals present within each tray were analysed with gap, fence, catchment and the gap x fence interaction (Table 5.2).

The species diversity data (number of species per tray) also displayed poisson distributions. This Poisson ANOVA analysed species diversity against catchment, gap, fence and the interaction between these two predictors (Table 5.3).

5.3 Results

Firstly, to note at the end of the experiment there were no plants in the blank trays that were positioned at either end of the sample trays, therefore concluding that there was no contamination of the sample trays.

From the summary table below it is evident that over the 12 month period there was low species diversity across all treatments (Table 5.1). However, the total number of seeds present in the seed banks was reasonably high with the gap fence treatment having a total of 170. At the species level, trends and contrasts are apparent for example, *Paesia scaberula* (an invasive fern native to New Zealand) was present in all treatments and both catchments, on the other hand *Craspedia* was only found in the Hopkins valley and *Cardamine hirsuta* was present only in the fence gap plots (Table 5.1).

Table 5.1. Summary table of the total invasive individuals and diversity recorded over the 12 month period from the seed banks collected from 32 plots, with 132.8 cm^2 of soil surface sampled per plot, from the Huxley and Hopkins valleys in February 2008.

Species	Native or Exotic	Control Hopkins	Control Huxley	Fence Hopkins	Fence Huxley	Gap Hopkins	Gap Huxley	Gap and Fence Hopkins	Gap and Fence Huxley	Total individuals
Paesia scaberula	Native	6	24	16	76	2	42	8	74	248
Epilobium ciliatum	Exotic	4	0	2	4	4	2	16	16	48
Lepidium africanum	Exotic	0	4	0	0	0	0	14	0	18
Craspedia sp	Native	0	0	2	0	0	0	14	0	16
Juncus articulatus	Exotic	0	4	0	0	4	0	6	0	14
Carduus nutans	Exotic	0	0	0	0	0	0	10	0	10
Cardamine hirsuta	Exotic	0	0	0	0	0	0	4	2	6
Agropyron repens	Exotic	0	2	0	0	0	0	2	2	6
Urtica diocia	Exotic	0	0	0	0	0	0	0	2	2
Epilobium sp	Exotic	0	0	0	2	0	0	0	0	2
Echium vulgare	Exotic	2	0	0	0	0	0	0	0	2
Total individuals per treatment			46		102		54		170	372
Individuals per m^2			4.89		10.85		5.75		18.01	39.58
Species per treatment			6		4		3		9	

5.3.1 Total invasive individuals in the seed bank samples

The seed banks from the two fenced treatments (fence and gap fence) displayed an increase compared to the unfenced treatments (control and gap) (Figure 5.3). The total number of invasive individuals per tray (plot) was significantly increased by the fence plots and which catchment the samples were taken from. However, in contrast to expectations the gap plots had no effect on the total number of invasive individuals present in the seed banks (Table 5.2).
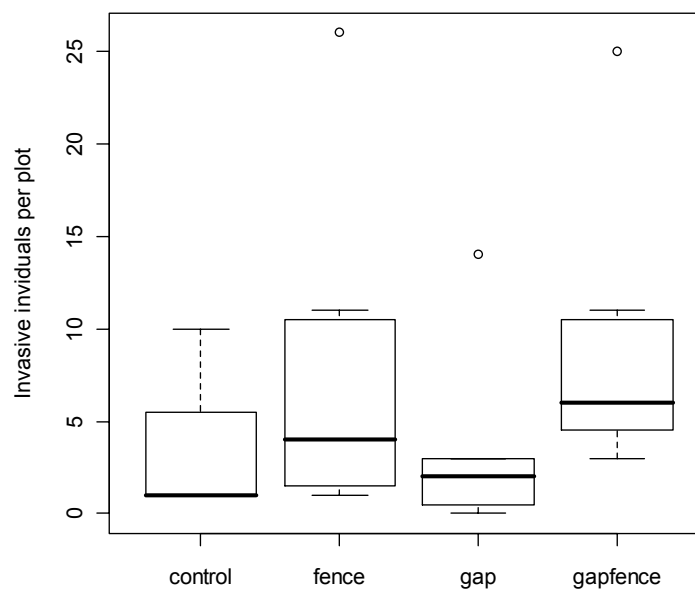
Figure 5.3. The number of invasive individuals per plot for each treatment, from the seed bank samples that were taken from both the Huxley and Hopkins valley in February 2008.

Table 5.2. Results from the poisson ANOVA on the number of invasive individuals in the seed bank sample for each plot in relation to gap, fence, catchment and the gap x fence interaction, from the 32 plots from both the Huxley and Hopkins valleys, February 2008.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	187.32	
gap	1	0.56	30	186.76	0.46
fence	1	34.95	29	151.82	**<0.0001**
catchment	1	26.34	28	125.48	**<0.0001**
gap:fence	1	0.4	27	125.07	0.53

5.3.2 Species diversity of the seed bank samples

There was no difference in species diversity between the 4 treatments as all of the treatments displayed low diversity over the 12 month period (Figure 5.4). This was reinforced by the ANOVA analysis that illustrated the species diversity within the seed bank samples was not significantly affected by gap, fence, catchment or the gap x fence interaction (Table 5.3).
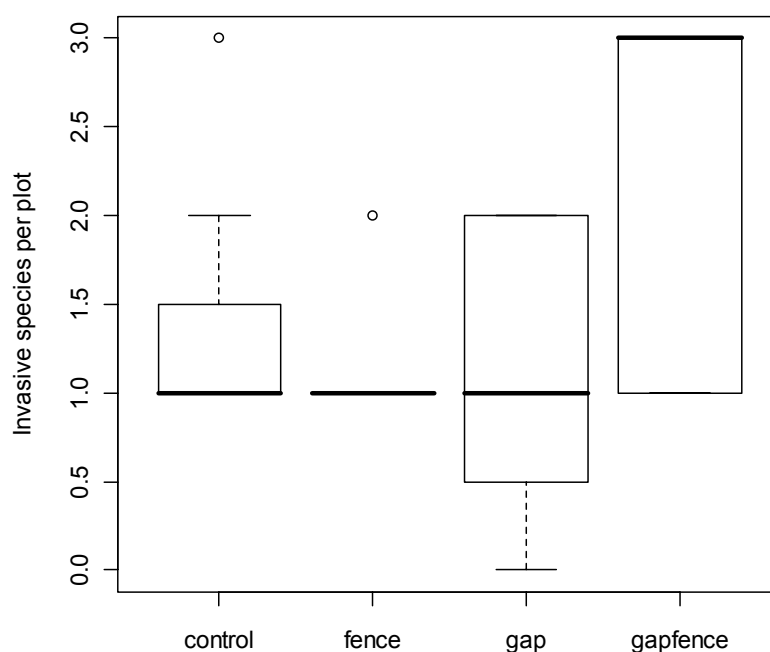
Figure 5.4. The number of invasive species per plot from the seed bank samples for each of the four treatments, taken from both the Huxley and Hopkins valley in February 2008.

Table 5.3. Poisson ANOVA results on the number of invasive species per plot, recorded from the seed bank samples for gap, fence catchment and the gap x fence interaction, from both the Huxley and Hopkins valleys, February 2008.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	17.28	
gap	1	1.05	30	16.23	0.31
fence	1	1.05	29	15.19	0.31
catchment	1	0.19	28	14.99	0.66
gap:fence	1	2.21	27	12.78	0.14

This non-significant result is also determined by the generally low number of species recorded across the 32 plots, for example the most species recorded in a sample tray for a single plot was three from a gap fence plot (Figure 5.4).

5.4 Discussion

5.4.1 Total number of invasive individuals

The total number of invasive individuals in each seed bank was significantly affected by fence and catchment (Table 5.2). The seed banks from the two treatments that had fences around each plot (fence and gap fence) displayed an increase compared to the treatments without fences around the plots (control and gap) (Figure 5.3). This result can also be observed visually from the actual seed bank sample set up in the glasshouse (Figure 5.5).

Figure 5.5. Visual comparison of the seed bank samples, from left to right; 4 months, 8 months and 12 months at the top, with typical forest plot examples of the four different treatments (control, fence, gap, gap fence) underneath from the Huxley and Hopkins valleys, 2008.

As fences are not known to increase the size of the forest seed bank the reason as to why an increased number of invasive individuals was recorded in the fence plot seed banks is unclear. Although, as shown in figure 4.5 the proportion of invasive seeds

was high and variable across all treatments, thus illustrating that invasive plant species are well dispersed and can be found in the seed banks of open and closed canopy plots. However, at the same time if deer are consuming the seed heads of these plants (for the increased nutritional value) this would decrease the amount of seeds present in the unfenced plots, thus increasing the effect the fences are having on the seed bank (Table 5.2).

The larger seed banks in the gap fence plots might be caused by a combination of factors. Firstly, as illustrated in figure 4.9 inward dispersal is increased when canopy gaps are created, thus allowing an increased amount of seeds to reach the forest floor when there is a gap in the above canopy (Augspurger and Franson, 1988; Panferov and Sogachev, 2008). Secondly, the micro-environmental factors (e.g. space availability) of the gap plots can be different to the closed canopy plots (Gray and Spies, 1997) and even soil conditions could differ significantly (Wright *et al.,* 1998). Species that can adapt to these heterogeneous micro-environmental factors, with different characteristics of regeneration and dispersal (Grubb, 1977; Grime, 2001) can be present in these varying environments with different proportions or increases in individuals (Zang *et al.,* 2008). For example, Zang *et al.* (2007) found species belonging to different functional groups existed in the forest community with different densities and distribution patterns, dispersing seed rains that produced different densities across the entire gap zone (Zang *et al.,* 2007). Thus, resulting in a higher number of individuals in the seed banks of the gap plots compared to the closed canopy plots (Zang *et al.,* 2007).

5.4.2 Invasive species diversity

There was no difference in the invasive plant species diversity between the four treatments (Table 5.3). The gap fence treatment produced the highest diversity with 9 while the gap treatment recorded the lowest diversity of 3 species from the 8 sample trays, and the combined number of invasive species from all treatments was only 11 (Table 5.1). Therefore, even at both extremes of the scale, the species diversity across all treatments was generally low and this result may be responsible for the non-significant variation between the four treatments.

So why was there such low species diversity in the seed banks? Firstly, did I sample an area large enough to produce an accurate representation of the forest seed bank? This is important to consider as the area taken from all the plots may not have been enough to collect all the invasive seeds present in the forest seed bank. However, according to other studies of this nature the area sampled was sufficient to produce an accurate representation of the forest seed bank (Bàrberi and Cascio, 2001; Funes and Basconcelo, 2003; Graham and Florentine, 2004). Therefore, the fact that there is relatively low invasive species diversity throughout most of New Zealand's *Nothofagus* forest and the pattern of forest distribution has been remarkably stable since European activity began in the 1850s must also be considered (Wardle, 2001).

The second factor to consider is the breaking of the dormancy in the seed bank samples. This suggests that these seed bank samples have the potential to produce higher species diversity if the dormancy of all the species present in these samples was broken. A study by Benech-Arnold *et al.* (2000) suggested that changes in dormancy during burial of seeds have been reported for a number of species. In some studies, seeds were in primary dormancy at the moment of burial. In the course of one year, the seeds passed through a pattern of change in dormancy that started with alleviation of dormancy followed by a period of germinability under several test conditions and was concluded by a re-induction of dormancy (secondary dormancy). Seasonal fluctuations in dormancy were observed in both summer and winter annuals. Seeds of some summer annuals are dormant in autumn, lose dormancy in winter, and recover it in summer, whereas some winter annuals pass through these stages in spring, summer and winter, respectively (Benech-Arnold *et al.,* 2000).

Moreover, adverse incubation conditions (constant temperature and low water content) can induce secondary dormancy in invasive seeds. Martinez-Ghersa *et al.* (1997) concluded when seeds were incubated at temperatures high enough for a high emergence rate, 70% of seeds that were incubated in open boxes emerged before the soil reached a condition that would cause the seeds to wilt. Thus, leaving almost one third of the seeds dormant even in optimal germination conditions, if this is correct it appears slightly on the contrary to the previous result in section 5.4.1.

5.4.3 Conclusions

After comparing the findings form this research with the wider literature the following conclusions can be made:

1. Species diversity of the seed bank in February 2008 was not affected by treatment (control, fence, gap and gap fence).
2. Total number of invasive individuals from the seed bank samples did vary significantly in respect to which treatment the samples were taken from.
3. The presence of a fence surrounding the plot from where the seed bank samples were taken was the main predictor driving an increase in the number of invasive individuals in each seed bank, however the number of invasive individuals also increased in the gap fence plots.

Chapter 6: Vegetation surveys

6.1 Introduction

The spread of invasive plants into native forests provides an environmental problem in most regions of the world; increased human mobility over the last three hundred years has led to an alteration of the biosphere, increasing the exchange of species between biogeographically separated habitats and has increased their susceptibility to invasion (Weber, 1998). Invasive species are viewed in the context of global change drivers as they have the potential to reduce biodiversity and alter community structure and functioning (D'Antonio and Vitousek, 1992).

The spread and range expansion of invasive plants can be rapid compared with natural large-scale plant migrations (Perrins *et al.,* 1993). However, the mechanisms driving successful plant invasions are poorly understood and the prediction of a successful invasion remains difficult (Crawley, 1986). Therefore, studying the establishment and spread of these species will help to understand the success of the species in particular landscapes. This allows for predictions about future spread rates, thus assisting management strategies that attempt to decrease the spread of invasive species (Weber, 1998).

The number of invasive plants that will establish is proportional to the probability of propagules finding safe sites and the number of founder populations (Weber, 1998). Auld and Tisdell (1986) have shown that the increase in total area occupied by a species increases faster when several small populations are expanding compared with a single large population. Besides genetic and ecological attributes of an invader (Baker, 1974; Crawley, 1986), opportunity and timing of introduction and dispersion by man make an equal, if not more important, contribution to the success of an invasion (Mack, 1986; Di Castri, 1989). The natural and anthropogenic factors determine whether an invasive species will spread quickly or slowly, and whether it will achieve a large or small range (Weber, 1998).

The spread of an invasive plant species into an area where it was absent before its introduction consists both of ecological and biogeographical components. There are

four steps that can be distinguished: (1) the arrival of the species and the local introduction of individuals in a habitat, (2) the formation of a persistent founder population by growth and reproduction, (3) deriving of new populations by transport of propagules to safe sites and (4) range expansion by increases in the number and sizes of populations (Weber, 1998). Thus, to detect these invasions over time it is important to accurately record the arrival of invasive species into forests where previously they did not exist.

This particular research focused on stages 2 and 4 which are outlined in chapter 1 (Figure 1.4). These processes (plant establishment and spread) can be examined by performing accurate measurements of the vegetation present over a given time period (1 year). Secondly, these processes were deemed to be the most important processes to measure when attempting to investigate the establishment and spread of invasive plant populations into New Zealand's native *Nothofagus* forest.

This chapter aims to answer the following questions:

1. Are invasive plants present in native beech forest and if so, are there established populations that have the potential to spread within these forests?
2. Is the percent cover of these invasive plants affected by canopy openness and deer exclosures?
3. If present, does the percent cover of these invasive plants increase significantly over the 1 year period?
4. Is red deer *(Cervus elaphus)* herbivory significantly decreasing the abundance of these invasive plants and if so does this present management implications for both of these invasive groups?
5. If these invasive plants are establishing how far are they spreading into the forest and does canopy openness affect the spread of these species?

6.2 Methods

This experiment is comprised of two parts: Firstly, the plot vegetation surveys that were performed inside the 10m x 10m plots (Figure 6.1) and secondly, the transect vegetation surveys that were performed outside the plots along a 50 x 1m transect that extended perpendicular on each side of the 10m x 10m plots (Figure 6.2).

6.2.1 Plot vegetation surveys

The aim of the first part of this experiment was to record all the invasive species present in each plot; twelve and 24 months after the plots had been created. This was performed to examine the effect treatment had on the establishment of invasive species.

6.2.1.1 Plot design and location

The plot vegetation survey experiment was conducted within two 9m x 3m sub plots which were situated within the larger 10m x 10m plots. The reason for the vegetation survey plots being 9m x 3m is due to the experimental design of the 10m x 10m plots (Figure 6.1). The two metre section across the middle of the plot that is divided up in to five 2m x 2m sub plots is being used by the Department of Conservation (Figure 6.1). Therefore, the vegetation survey plots were designed to keep a half metre gap between these sub plots and the boundary of the 10m x 10m plot. The two 9m x 3m sub plots were placed at either end of each 10m x 10m plot so there was one sub plot at the bottom and one sub plot at the top (Figure 6.1). To avoid pseudo-replication the data from these two sub plots were combined so there were a total of 32 (one for each 10 x 10m plot); 4 treatments (control, fence, gap, gap fence) x 4 replicates x 2 catchments = 32 plots.
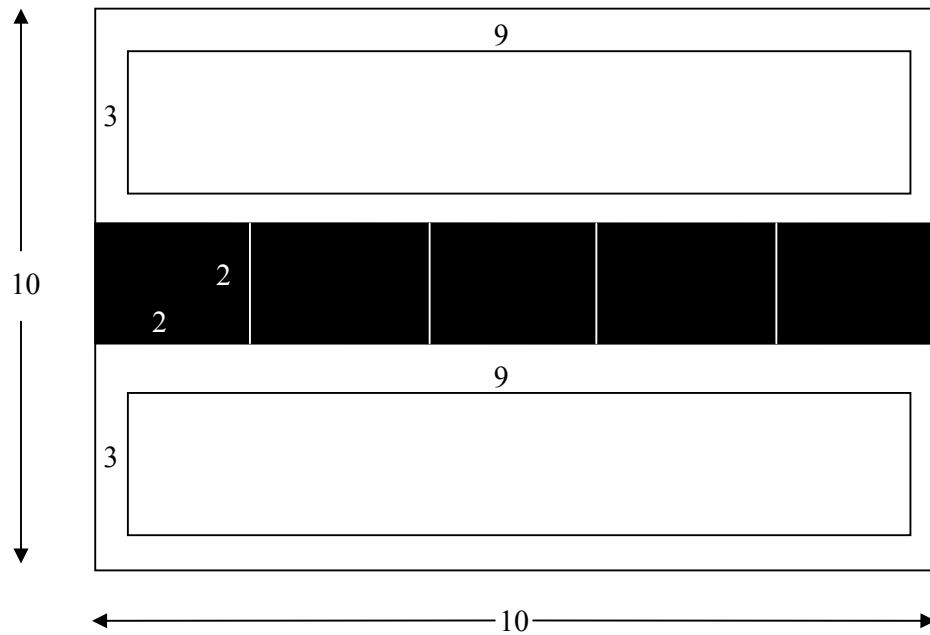
Figure 6.1. Diagrammatic representation of the plot design and the location of the 9m x 3m sub plots; note the section across the middle is the part being used by the Department of Conservation for seedling monitoring.

6.2.1.2 Recording the invasive species in each plot

Once the vegetation sub plots had been marked out, all the invasive species present in these sub plots were recorded. Each invasive species was recorded in two ways: Firstly, each species that was present in the vegetation plot was recorded for individual abundance (number of individuals per 9m x 3m plot) and clonal species were recorded by defined clumps present in each sub plot. Secondly, the total cover percentage of each species (percentage area of the 9m x 3m plot occupied by each species) was recorded. These two measurements were taken twice; the first was from 25th-29th of February 2008 and the second was conducted at the beginning of January 2009. These two methods were used as they are the most effective methods for detecting any trends in the establishment and spread of plant species within a defined area over a defined time period (Dullinger *et al.,* 2007).

6.2.2 Transect vegetation surveys

The second part of this experiment aimed to examine the effect each treatment had on the spread of invasive species from the plot edge into the forest understory, and to determine whether the source of any invaders inside the plots was from plants already growing out in the undisturbed forest.

6.2.2.1 Transect design and location

For this part of the experiment only the two side edges of each 10m x 10m plot were used (Figure 6.2). This was to ensure the measurements were taken across the slope and not up and down the slope, in attempt to eliminate any variation in the vegetation that may have been caused by any changes in gradient or altitude. Each transect started half-way down the side of each plot (5m from both corners) on the plot edge, extending out perpendicular from this edge 50m into the forest (Figure 6.2). This method was chosen as it was thought to produce the best representation of the undisturbed vegetation near each plot beyond where the experiment was set up.
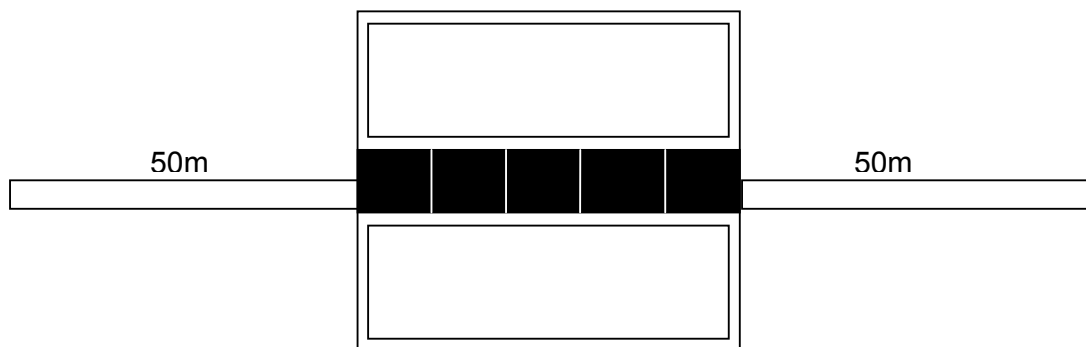
Figure 6.2. Diagrammatic representation (not to scale) of the 50 x 1m transect design and location used at each of the 10m x 10m plots.

6.2.2.2 Recording the invasive species along each transect

To record the invasive species cover along this 50 x 1m transect it was divided up into the following sections:

- 1m x 1m sections for the first 6 metres
- 2m x 1m sections from 6 metres to 10 metres (6-8m, 8-10m)

- 5m x 1m sections from 10 metres to 20 metres (10-15m, 15-20m)
- 10m x 1m sections from 20 metres to 50 metres (20-30m, 30-40m, 40-50m)

The size of each section increased with distance from the plot edge due to the decrease in invasive plant abundance. At each section of transect, the total cover percentage for all invasive species was recorded. This was performed on both transects and the data was recorded separately under left or right transect. As for the plot vegetation surveys the 2 transects from each 10 x 10m plot were then combined to avoid pseudo-replication giving a total of 32 replicates.

6.2.3 Statistical analysis

The total percent cover of invasive plants present inside the 32 plots in 2008 and 2009 were analysed separately using poisson ANOVAs. The abundance of invasive plants recorded outside the 32 plots was analysed using a generalised linear model (GLM). All statistics were performed in R version 2.7.0.

Poisson ANOVAs were used to analyse the invasive plant percent cover data that was recorded inside the 32 plots because the data were very non-normal with many zeros. The 2 years of measurement (2008 and 2009) were analysed separately because an attempted repeated measures analysis including both years proved to be unstable. Plant cover for each plot was analysed with gap, fence, catchment and the gap x fence interaction. The data on the abundance of invasive plants in relation to the transects were analysed in a generalised linear model (GLM). The transects were separated into two categorical groups; either close (0-7m) and far (7-50m) however, as all far values were 0 only the close values were analysed. Like the percent cover data these data also displayed a poisson distribution, so a poisson GLM was used. This GLM analysed the abundance data against five predictors; percent cover of invasive plants inside each plot, gap, fence, catchment and the gap x fence interaction (Table 6.5).

6.3 Results

Invasive plant species were more abundant in the plots that had open compared to closed canopies (Table 6.1). In fact there were no invasive plants recorded in any of the 16 plots without a canopy gap. It is also evident that while most species did not change in abundance over the two years, some species increased in abundance while some even decreased in abundance for example, *Carduus nutans* decreased from 16 to 12% in the gap and fence sites (Table 6.1).

Table 6.1. Summary table of the mean percent cover per plot of all invasive species for the 4 treatments, from both the Hopkins and Huxley valleys, summer 2008 and 2009 (both years are displayed in the same box and are separated by a comma i.e. 2008, 2009).

Species	Treatment				Catchment	
	Control	Fence	Gap	Gap and Fence	Huxley	Hopkins
Crepis capillaris	0,0	0,0	2,2	15,15	14,14	3,3
Trifolium repens	0,0	0,0	11,11	3,3	3,3	11,11
Carduus nutans	0,0	0,0	8,8	16,12	7,3	17,17
Echium vulgare	0,0	0,0	6,6	13,13	7,7	12,12
Cerastium glomeratum	0,0	0,0	6,6	12,12	1,1	17,17
Holcus lanatus	0,0	0,0	9,9	10,10	5,5	14,14
Agrostis capillaris	0,0	0,0	3,3	14,14	3,3	14,14
Senecio jacobaea	0,0	0,0	2,2	3,3	2,2	3,3
Hordeum sp	0,0	0,0	1,1	12,12	1,1	12,12
Alopecurus aequalis	0,0	0,0	10,10	8,8	4,4	14,14
Urtica diocia	0,0	0,0	1,1	9,9	2,2	8,8
Hydrocotyle americana	0,0	0,0	1,1	11,11	0,0	12,12
Epilobium brachycarpum	0,0	0,0	3,3	15,15	9,9	9,9
Danthonia pilosa	0,0	0,0	1,1	13,13	3,3	11,11
Solanum nigrum	0,0	0,0	0,0	3,5	2,4	1,1
Pseudognaphalium luteoalbum	0,0	0,0	0,0	2,2	1,1	1,1
Lagenifera sp	0,0	0,0	0,0	7,7	5,5	2,2
Agrostis gigantea	0,0	0,0	8,8	32,33	0,1	40,40
Taraxacum officinale	0,0	0,0	0,0	0,14	0,14	0,0
Bromus willdenowii	0,0	0,0	0,0	0,5	0,5	0,0
Mean percent cover per plot	0	0	9	27.5	11.4	25.13

6.3.1 Invasive plant abundance in relation to treatment over the two years

Poisson ANOVAs on the total cover percentage of invasive plants in relation to treatment illustrated that the abundance of invasive plants in all plots was significantly determined by gap, fence and catchment, in both 2008 and 2009 (Table 6.2 and 6.3). The presence of a gap explained most of the variation that increased the abundance of the invasive plants. There was no difference in the abundance of these invasive species between the two years for all four treatments (Figure 6.3 and Table 6.4).
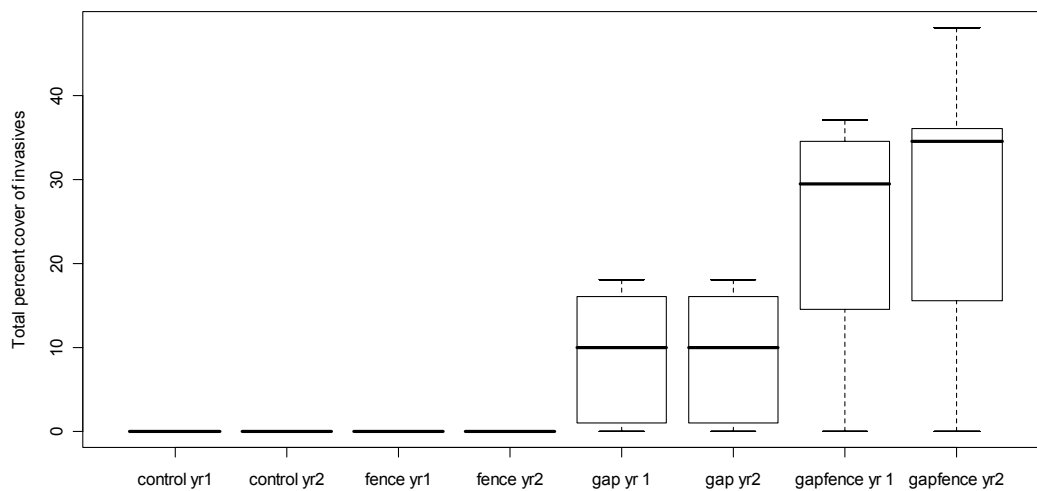
Figure 6.3. Total percent cover of all invasive species in relation to treatment, from both the Hopkins and Huxley valleys, for 2008 (yr1) and 2009 (yr2).

Table 6.2. Poisson ANOVA results on the percent cover of all invasive species in relation to gap, fence, catchment and the gap x fence interaction, from both the Hopkins and Huxley valleys in 2008.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	596.94	
gap	1	368.75	30	228.18	**<0.0001**
fence	1	58.1	29	170.08	**<0.0001**
catchment	1	72.93	28	97.15	**<0.0001**
gap:fence	1	0.00004	27	97.15	1

77

Table 6.3. Results from the poisson ANOVA on the percent cover of all invasive species in relation to gap, fence, catchment and the gap x fence interaction, from both the Hopkins and Huxley valleys in 2009.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	670.95	
gap	1	404.8	30	266.16	**<0.0001**
fence	1	78.61	29	187.55	**<0.0001**
catchment	1	42.48	28	145.07	**<0.0001**
gap:fence	1	0.00004	27	145.07	1

It is evident that gap, fence and catchment had a significant effect on the percent cover of all invasive species; in both 2008 and 2009 these three predictors produced highly significant results (Table 6.2 and 6.3). The two analyses are not independent, as some of the same plants were counted in both surveys, but both are presented to show the pattern did not change greatly over the year between surveys, this is also shown in table 6.4.

Table 6.4. Results from the poisson ANOVA comparing the invasive species percent cover in the 32 plots from 2008 with the invasive species percent cover from 2009, from the Hopkins and Huxley valleys.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			63	1269.1	
year	1	1.21	62	1267.89	0.27

6.3.2 Invasive plant abundance outside each plot in relation to treatment (gap and fence) and distance from the plot edge

A generalised linear model (GLM) on the total percent cover of invasive plants outside each plot illustrated that the cover of invasive plants inside each plot, gap and catchment had a highly significant effect on invasive plant abundance (Table 6.5). The cover inside each plot accounted for the majority (72%) of the deviance and gap accounted for the majority of the rest (Table 6.5). Overall, the gap and gap fence plots were the only ones that had invasive species outside of the plots. However, the abundance of these invasive species decreased as distance from the plot edge increased, with every transect having zero values by 6-7m (Figure 6.4). Therefore,

only the close (0-7m) section of each transect was analysed and these results are displayed in table 6.5.
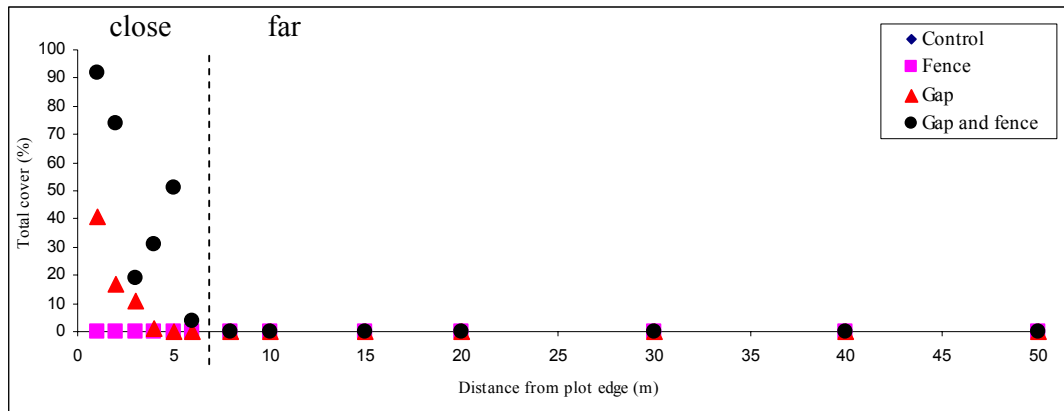
Figure 6.4. Total percent cover of invasive plants in relation to distance from the plot edge, for each treatment (control, fence, gap and gap and fence), from both the Hopkins and Huxley valleys for 2008 and 2009.

Table 6.5. GLM results explaining the percent cover of invasive plants outside each plot (along transects) in relation to the invasive plant cover inside each plot, gap, fence, catchment and the gap x fence interaction, from both the Hopkins and Huxley valleys in 2008 and 2009.

Predictor	Df	Deviance	Residual Df	Residual Deviance	P (> Chi)
NULL			31	811.15	
cover inside plot	1	582.1	30	229.05	**<0.0001**
gap	1	113.37	29	115.68	**<0.0001**
fence	1	2.82	28	112.86	0.09
catchment	1	61.59	27	51.27	**<0.0001**
gap:fence	1	0.00005	26	51.27	1

6.4 Discussion

6.4.1 Is the percent cover of invasive plants within each plot affected by treatment?

There was a significant treatment effect that determined the total percent cover of invasive plants recorded at each plot in 2008 and 2009 (Table 6.2 and 6.3). The percent cover of invasive plants increased where there was a gap in the canopy directly above the plot, thus illustrating a positive relationship between canopy

openness and increased invasive plant abundance (Figure 6.3). Dickinson *et al.* (2004), found as canopy openness increased, the proportion of individuals that occurred in these felled gaps also increased, however most of the individuals were shade-intolerant species.

In clear-felled gaps (similar to the gaps used in this study), this effect can be ascribed to increased canopy openness because the proportion of the ground area that was disturbed did not increase with gap size (Dickinson *et al.,* 2004). In contrast to felling gaps, natural gaps displayed no relationship between the proportion of new individuals and canopy openness (Dickinson *et al.,* 2004). The absence of a significant relationship in natural gaps is likely related to a combination of low levels of understory and substrate disturbance and a lack of large gaps with high canopy openness (Dickinson *et al.,* 2004). Invading individuals must also contend with the negative competitive effects by larger seedlings and pre-existing individuals. Soil disturbance, litter removal and the creation of dispersal barriers for native vegetation have been described as key conditions to assist invasive plants trying to establish from seed (Brandani *et al.,* 1988; Raich and Christensen, 1989; Denslow, 1995; Grubb, 1996) and may also contribute to increased abundances of shade intolerant species in felled gaps (Dickinson *et al.,* 2004).

With (2001) hypothesised that canopy gaps or 'fragmentation' may affect plant migration rates more through a reduction in source strength of the native vegetation (the number of propagules produced) than through the creation of dispersal barriers, once some threshold is exceeded (Malanson and Cairns, 1997). Thus, landscape effects on demography involve factors that affect the fecundity or survivorship of invasive species (population vital rates), which may affect establishment and govern the rate of invasion. For example, consider how landscape structure might affect population vital rates in plants; habitat destruction and fragmentation may increase resource availability (such as light) that can be exploited by invasive species directly or indirectly by mediating competition with native plants (Luken *et al.,* 1997). This in turn may increase the performance of invasive species in disturbed areas such as, canopy gaps by increasing germination, growth, or seed set.

6.4.2 The "spill over" of invasive plants in to the forest from the open canopy plots

There was no relationship between invasive plant abundance and distance from the plot edge at the closed canopy plots (Figure 6.4). This result is purely due to the absence of any invasive species at these plots, illustrated in (Figure 6.3 and 6.4) and discussed in 6.4.1. However, at the open canopy plots (12m x 12m light gaps), the abundance of invasive plants decreased exponentially as distance from the plot edge (into forest with less canopy openness) increased (Figure 6.4). Also the invasive plant cover inside each plot significantly affected the invasive plant cover outside each plot (Table 6.5). Therefore, illustrating the "spill over" of these invasive species into the native forest until the canopy structure returns to a more undisturbed state where the spread of these invasive plants decreases to zero (Figure 6.5).
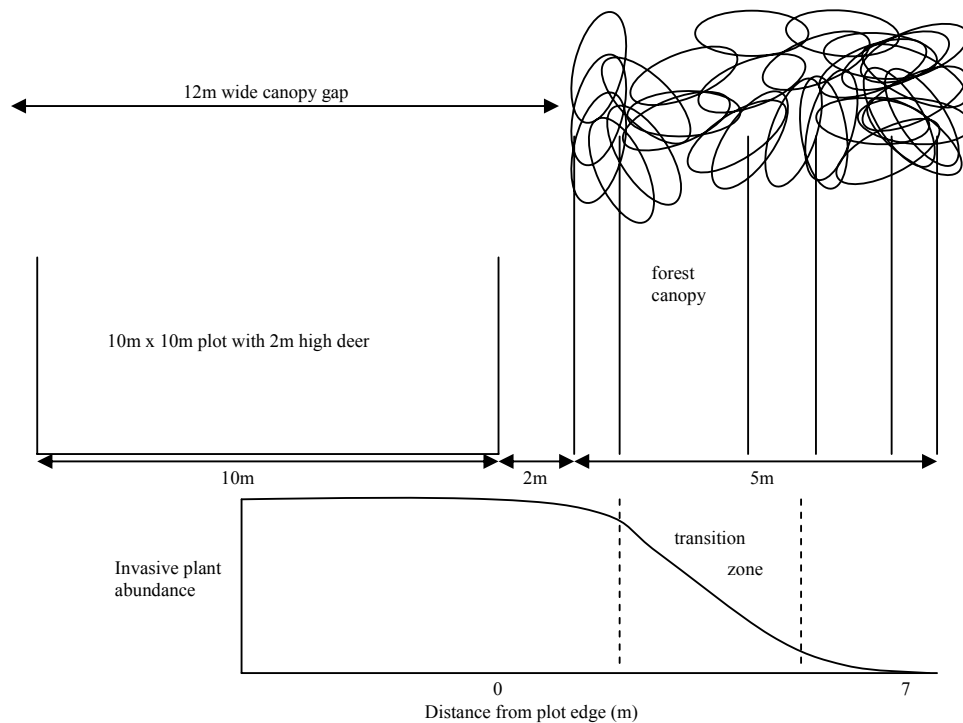
Figure 6.5. Diagrammatic representation, illustrating the abundance or "spill over" of invasive plants from the edge of a gap (open) and fence plot with distance back in to *Nothofagus* forest; note the decrease in abundance through the "transition zone".

There are two reasons why this "spill over" of invasive plants into the undisturbed forest that is near the canopy gaps is suggested instead of invasive plants colonising

this undisturbed part of forest from a longer distance. This suggestion has been made because there is zero density of invasive plants in all non-gap plots and there is zero density of invasive plants in all transect sections >7m from a plot edge (Figure 6.4). If invasive plants are in the undisturbed forest (as would be required for them to be a source of invasion into new nearby clearings) they are at undetectably low densities. Therefore, it seems much more likely they disperse into the gap from a further distance, grow there and 'spill over" into the first 7m from the plot edge (Figure 6.4 and 6.5).

This result agrees with the findings of a study by Lambrinos (2006), who found that the abundance of the invasive tussock grass *Cortaderia jubata* decreased exponentially as distance from the edge back into closed canopy increased. His findings were very clear and occurred over a very short distance of only two metres (Figure 6.6).
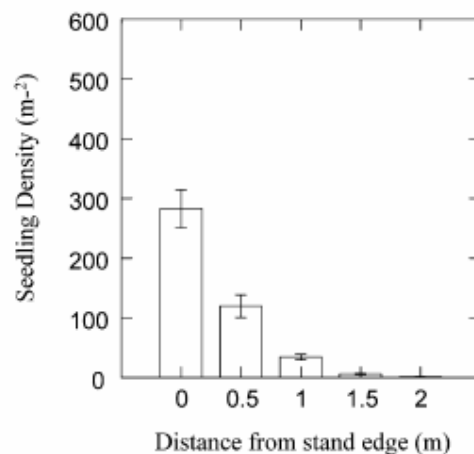
Figure 6.6. The exponential decrease in seedling density of the invasive tussock grass *Cortaderia jubata*, as distance from the stand edge back into closed canopy forest increased (from Lambrinos, 2006).

Lambrinos's result was due to the flux of the invasive propagules reaching the soil surface being a lot greater along the edge than under the stand canopy due to the contrasting environments. A study by Cadenasso and Pickett (2001) that investigated the flux of propagules from invasive species into the forest interior from the forest edge also recorded very similar findings. In some examples from Cadenasso and Pickett (2001), propagules decreased from 20 per transect to 0 within 17m from the forest edge. As with the study by Lambrinos (2006), Cadenasso and Pickett (2001)

also concluded that the abrupt decrease in invasive abundance over such short distances from the forest edge was in response to the presence of the forest edge and canopy.

In support of these results a study by Buckley *et al.* (2003) comparing populations of the invasive plant *Hypericum perforatum* in shaded environments with populations in open environments found the shaded populations took longer to reach infestation densities and were less affected by herbivory and reductions in survival than open populations. Open populations had higher densities and increased faster in response to increases in rainfall, but this was not so for shaded populations, showing that population size increased more rapidly in open environments (Buckley *et al*., 2003).

6.4.3 Is herbivory decreasing the abundance of these invasive plants?

The abundance of these invasive plants increased further when a 2m deer fence was surrounding plots that already had a gap in the above canopy (Figure 6.3). In fact with reference to table 6.1 there are 12 out of 20 species (10 all palatable to deer) that increase in percent cover by 5 fold or more from the gap to the gap fence plots. Not only does this result reinforce the positive relationship between canopy openness and invasive plant abundance, but it also introduces the question of; are some of these invasive plant species being limited by herbivores?

A study by Carpenter and Cappuccino (2005) found that the invasive species present at their study sites were less damaged than their native counterparts. However, plant origin, native or exotic, explained only a small (5.6%) percentage of the variance in herbivore damage. Although some invasive species were virtually damage-free, others suffered more leaf damage than any of the native plants. The large variance in herbivory corresponded to expectations, given the mixed results of previous tests examining the enemy release hypothesis (Keane and Crawley, 2002; Agrawal and Kotanen, 2003). Therefore, invasive plants were not expected to enjoy a strong advantage in terms of escaping from herbivory (Carpenter and Cappuccino, 2005). In contrast, from the same study, Carpenter and Cappuccino (2005) also found that, less invasive plants always displayed some form of leaf damage resulting from herbivory. They suggested the high level of leaf herbivory on the less invasive plants is a result

of the herbivores contributing to the control of these plants and preventing them from becoming more abundant in natural areas (Carpenter and Cappuccino, 2005).

The result from figure 6.3 gains further support from a study by Fagan and Bishop (1999) with their research, that involved long-term demographic studies of Mount St. Helens lupins (*Lupinus lepidus* var. *lobbii*). They documented extreme levels of herbivory and accompanying depression of population growth rates in some portions of the lupin population since 1986 and in the edge of the lupin population since 1990 (Bishop and Schemske, 1998). In the context of classical theories of biological invasions, herbivore-mediated decreases in lupin population growth rate in the edge region would translate into decreased rates of lupin spread across the landscape, which they quantified using diffusion models.

As mentioned on page 82, more recent support of the result from figure 6.3 comes from a study by Lambrinos (2006). His study illustrated that herbivory posed a strong barrier to the establishment of the invasive tussock grass *Cortaderia jubata*. Part of this resistance was provided by generalist mammalian herbivores. In their study, the herbivores reduced the establishment success of transplants to zero, mirroring the same result obtained in a previous experiment conducted in an adjacent stand of maritime chaparral (Lambrinos, 2002). Spatial variation in herbivore resistance, rather than resource competition with native shrubs, appeared to be the principal factor influencing the distribution of *C. jubata* at this site. When transplants were protected from herbivory, the spatial differences in survival disappeared further supporting the evidence towards herbivore mediated distribution and survival of this species (Lambrinos, 2006).

6.4.4 Conclusions

After comparing the results of my present study with the wider literature, the following conclusions can be made:

1. No invasive plants were detected inside or outside any of the non-gap (control and fence) plots or along any transect more than 7m from a gap (gap and gap fence) plot.

2. Where there was a canopy gap above the plot, the abundance of invasive plants increased significantly within the plot compared to the closed canopy plots.

3. When there was a 2m deer fence surrounding an open canopy plot the abundance of invasive plants increased further. Notably however, plots with a fence but no gap did not result in any invasive plants being present, thus suggesting that some of these invasive species are being consumed by herbivores.

4. The best predictor of invasive plant cover outside a plot was invasive plant cover inside the plot, this and zero abundance in all areas away from a gap suggests "spill over" outside the gap plots spreads from within the plots and not in the other direction.

5. The dominant predictor of plant invasions in these plots is the creation of a canopy gap, with the protection from herbivores being a secondary predictor.

Chapter 7: Overview and main findings of this study

7.1 Which invasive species were recorded in each experiment?

This research conducted three experiments in attempt to detect and record the invasive species that are present (arriving, dormant and actually growing) in the forests of the Huxley and Hopkins valleys in 2008 and 2009 (Figure 1.4). These experiments were designed to answer four hypotheses that are all linked to one another in relation to propagule dispersal, germination and population establishment and spread (Figure 7.1).
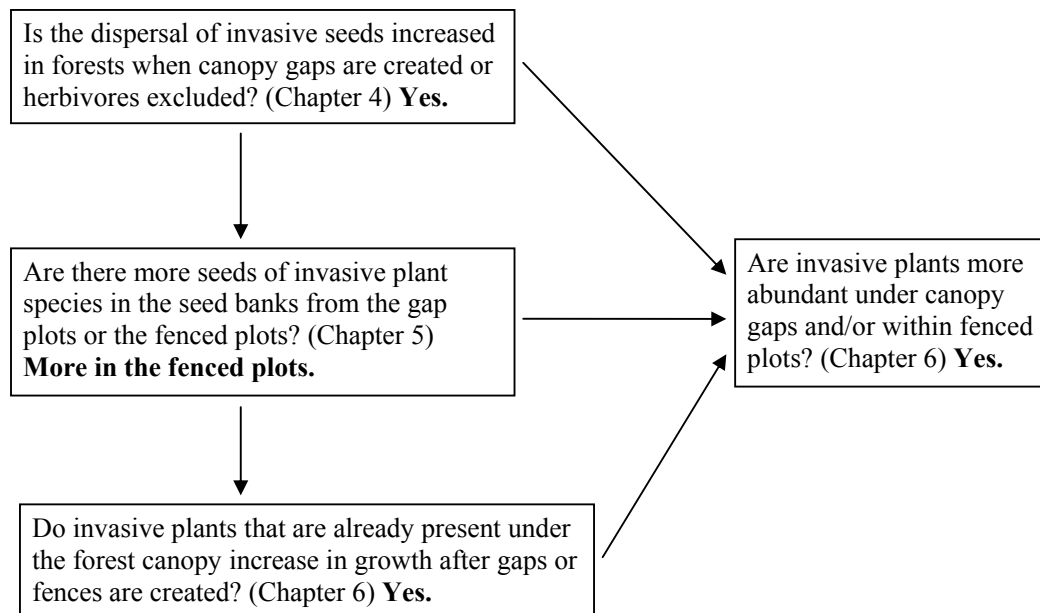
Figure 7.1. Diagrammatic representation of the four hypotheses and the answers to these hypotheses from the results of this present study.

Firstly, seed traps were set to record which species were dispersing propagules into and around these forests (arriving). Secondly, seed bank samples were taken to observe which species had seeds in the soil dormant, waiting for good germination conditions. Lastly, vegetation surveys were conducted, once at the beginning of this research and again after one year, to monitor species diversity and individual abundance over this time frame (spreading). Some species were present in all three experiments; however there were various species present in more than one experiment and some interesting trends became apparent (Table 7.1).

Firstly, the most interesting result is the fact that all 13 species that had seeds in the seed traps were also recorded in the vegetation surveys, yet not all in the same plots. However, only 4 of these 13 species were also present in the seed bank samples, making these the 4 most ubiquitous species (first four species listed in table 7.1). Secondly, there were 7 species that were not present in the seed traps or vegetation surveys but were recorded in the seed bank samples. This suggests that, some species that disperse seeds into these forests need more 'optimal' conditions to germinate, thus being the species that would benefit most from climate change (Kriticos *et al.,* 2003). The last group from this table is the 8 species that were present only in the vegetation surveys (Table 7.1). Therefore, the seeds of these species were not caught in any of the seed traps and were not found in the seed bank but they were growing within the forest plots (Table 7.1). The only plausible explanation for this result is that, these species are present within the Hopkins and Huxley valleys at such a low density that the seeds were not picked up in the seed traps or the seed bank samples. This explanation is supported with reference to the raw data on the vegetation surveys which displays that these species had very low numbers of individuals per plot (Appendix 1).

Table 7.1. Summary table of the species recorded in each of the three experiments. The absence of a species is illustrated by a blank square and presence by a 'P', for the vegetation surveys each year is separated by a comma (2008, 2009).

Species	Seed traps	Seed banks	Vegetation surveys
Carduus nutans	P	P	P,P
Echium vulgare	P	P	P,P
Epilobium brachycarpum	P	P	P,P
Urtica diocia	P	P	P,P
Agrostis capillaris	P		P,P
Agrostis gigantean	P		P,P
Cerastium glomeratum	P		P,P
Crepis capillaries	P		P,P
Danthonia pilosa	P		P,P
Holcus lanatus	P		P,P
Hydrocotyle americana	P		P,P
Senecio jacobaea	P		P,P
Solanum nigrum	P		P,P
Cardamine hirsute		P	
Craspedia sp		P	
Epilobium ciliatum		P	
Juncus articulatus		P	
Cynodon dactylon		P	
Lepidium africanum		P	
Paesia scaberula		P	
Alopecurus aequalis			P,P
Danthonia pilosa			P,P
Hordeum sp			P,P
Lagenifera sp			P,P
Pseudognaphalium luteoalbum			P,P
Trifolium repens			P,P
Bromus willdenowii			,P
Taraxacum officinale			,P
Total species 28	13	11	21

7.2 Which treatment and experiment recorded the highest diversity of invasive species?

Invasive plant abundance increased significantly where a gap was present in the above canopy but increased further when a fence was also present at plots that had a gap in the above canopy (Table 7.2). This result occurred throughout the three vegetation

experiments illustrating the positive influence the fence and gap plots had on the abundance of the invasive species (Table 7.2).

Table 7.2. Results table summarising the statistical analyses from the three vegetation experiments, illustrating which treatments had no effect (>0.05) (NS), a significant effect (<0.05) (**S**) or a highly significant effect (<0.0001) (**HS**) in each experiment.

	fence	gap	fence gap
Seed traps	**S**	**HS**	**HS**
Seed banks	**HS**	NS	NS
Plant cover within plots	**HS**	**HS**	NS
Plant cover outside plots	NS	**HS**	NS

The experiment that recorded the highest number of species was the vegetation surveys, recording almost double the diversity in both the gap and 'gap fence' plots (Table 7.3). Furthermore, note the zeros in the 'control' and 'fence' columns for the vegetation surveys, which for obvious reasons coincide with the results from chapter 6; zero abundance equals zero diversity.

Table 7.3. Summary table of the invasive species diversity found in each experiment for each of the four treatments, from the Hopkins and Huxley valleys from 2008-2009.

	control	fence	gap	fence gap
Seed traps	2	3	6	11
Seed banks	6	4	3	9
Vegetation surveys	0	0	15	20
Total species diversity	**5**	**4**	**22**	**27**

Firstly, these summary results suggest one finding not intended to be presented, this being that, vegetation surveys recorded up to twice as many species when investigating invasive plant establishment and spread in specific forests (Table 7.3) (Meentemeyer and Moody, 2000; Vittoz and Guisan, 2007). These summary results also support the previous findings from chapters 4, 5 and 6, that all suggest that invasive species will become more prevalent (abundant or diverse) when a gap is created in the above canopy (Table 7.3). This was the main driver of invasive abundance due to the opening of the canopy that increased the dispersal of invasive propagules and increased the above ground growth of invasive plants in the gap plots

(Figure 7.2) (Panferov and Sogachev, 2008). In addition, they also give further support to the results that suggest these invasive species become even more prevalent when there is a deer exclusion fence around the plot, thus presenting the idea that deer may be consuming some of these plants.

Undisturbed forest (control plots)
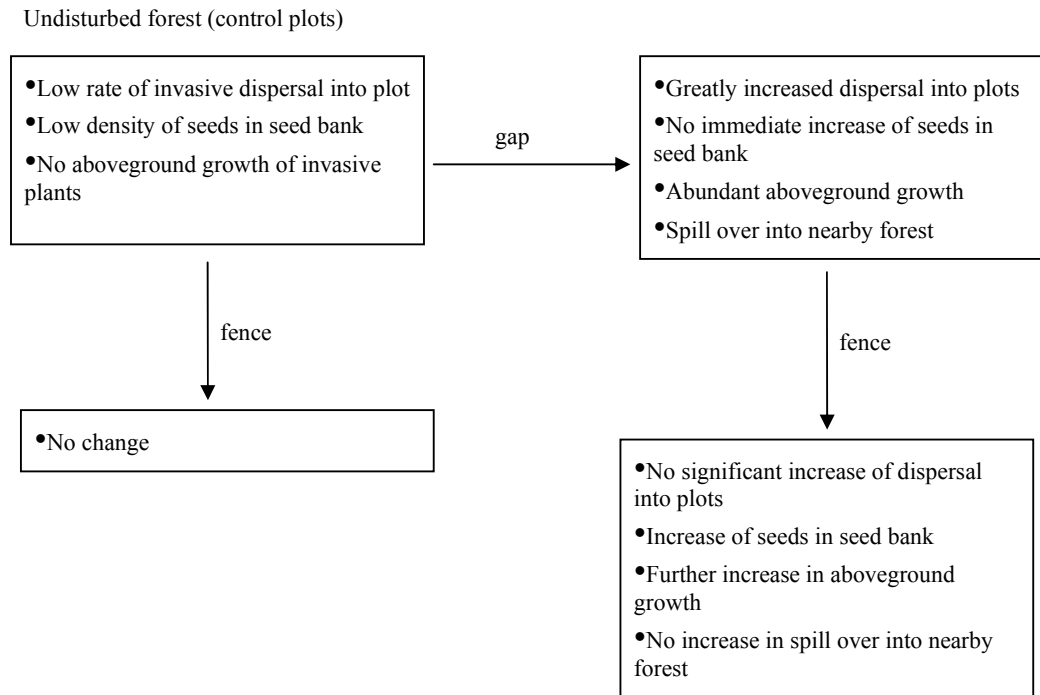
Figure 7.2. Diagrammatic representation of how the dispersal, seed banks and above ground growth of invasive plants change when a gap is created in the forest canopy and a 10 x 10 x 2m wire fence is constructed in the Hopkins and Huxley valleys.

7.3 Disturbance, one main driver of global change relevant to this study

Definitions of disturbance vary, from Grime's (1979) view of disturbance as a process removing or damaging biomass, to White and Pickett's (1985) definition of "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment". Petraitis *et al.* (1989) expand the definition further to include any "process that alters the birth and death rates of individuals present in the patch, by directly killing individuals or by affecting resource levels, natural enemies, or competitors in ways that alter survival and fecundity". Temporal and spatial scale are also important when recognising the "discreteness" of a disturbance event, as nearly any ecological or biogeochemical process might fall under the last, most inclusive definition. Pickett *et*

al. (1989) define a disturbance as a change in structure caused by factors external to the hierarchical level of the system of interest; this is necessary to distinguish disturbance from other changes in the system. Therefore, disturbances to plant communities include such events as earthquakes, fires, storms, and floods; but other changes such as altered grazing regimes or light and nutrient inputs would also be classed as disturbance if they affected resource levels and demographic processes (Hobbs and Huenneke, 1992).

Preservation of natural communities has historically consisted of measures protecting them from physical disturbance, for example the harvesting of native timber and grazing of livestock are usually excluded from preserves (Hobbs and Huenneke, 1992). This is not to ignore that many forms of disturbance are important components of natural systems. Many plant communities and species are dependent on disturbance, especially for regeneration (Pickett and White, 1985). However, in native plant or forest communities, disturbance acts in another way, by promoting the establishment of invasive plants (Ewel, 1986; Hobbs, 1991). Forest fragmentation or more specifically to this present study, the removal of the forest canopy in random locations, is one disturbance that can promote the establishment of these invasive plants. By influencing edge effects and the likelihood of movement of nutrients, propagules, and fauna from adjacent patches, fragmentation affects disturbance regimes in forests and remnant patches of vegetation (Hobbs, 1987; Saunders *et al.* 1991).

But how can such a relatively small disturbance (12m x 12m canopy gap) have any effect on a large forest? If the part of forest that has been disturbed is small does this necessarily constrain the diversity of species that might invade the disturbed part of forest (Hobbs and Huenneke, 1992)? Quinn and Robinson (1987) and Robinson and Quinn (1988) used an experimental approach to this question, subdividing annual grassland into fenced patches separated by heavily grazed zones; species richness was substantially higher in the more subdivided treatments. Single species frequently came to dominate single plots, so if a region (or forest) has a greater number of patches (or canopy gaps) it can support both more dominant species (alternate dominants in different plots) and more edge species (growing where the forest and the open environment meet). Therefore, the point that fragmentation will lead to an

increase of invasive species is important (Hobbs and Huenneke, 1992). From a conservation management perspective, one would want to know just which species are being favoured by edge effects. High total species richness could be primarily due to an increased number of invasive species of low conservation value to a high number of legitimate community members (Hobbs and Huenneke, 1992).

Disturbance, thus presents a conundrum to conservation management: the continued existence of particular species or communities often requires disturbance of some type and hence disturbance regimes must be integrated with management plans but disturbance may simultaneously lead to the degradation of natural communities by promoting invasions (Hobbs and Huenneke, 1992).

7.4 Deer: facilitators or obstacles to invasive plants?

The negative impacts of introduced deer on forests around the world and more specifically to this study, the native forests of New Zealand are well documented throughout the literature (Wallis and James, 1972; Allen *et al.,* 1984; Jane, 1994; Husheer *et al.,* 2003; Dolman and Waber, 2008). However, the idea that these introduced ruminant species could actually play a positive role in the native *Nothofagus* forests of New Zealand has to my knowledge, not been suggested before. Yet the results from experimental research carried out in this study suggest this some what controversial idea is possible. As the results from the vegetation surveys in chapter 6, illustrate an increase in invasive plant cover within the plots where there was a gap in the above canopy and a 2m deer exclusion fence around the outside of the forest plot (Figure 6.3).

Since the cover of these invasive species increased in these plots it prompted the suggestion that red deer could be keeping the abundance of these species in check in these specific parts of *Nothofagus* forests. So could these ruminants be 'gardeners' of canopy gaps in New Zealand's *Nothofagus* forests? To my knowledge the only similar New Zealand example comes from a study by Lord (1990) who examined the maintenance of a short tussock *(Poa cita)* grassland by sheep *(Ovis aries)*, however more relevant examples from the wider literature are present. Maron and Vilà (2001) when studying how herbivores affect plant invasions, presented evidence from

California, USA of deer consuming the introduced iceplant *(Carpobrotus edulis)* where 90% of the seedlings and almost 40% of experimentally transplanted cuttings were consumed (Vilà and D'Antonio, 1998). Further support comes from a recent Argentinean example, Nuñez *et al.* (2008) when examining the invasion of two conifers (*Pseudotsuga menziesii* and *Pinus ponderosa*) concluded that the low rates of invasion currently observed can result from high densities of exotic deer, which, despite consuming native species as well, can prevent the establishment of invasive species.

It may be that by dispersing seeds, changing competitive interactions and creating soil disturbance, some herbivores have more of a facilitating than inhibiting affect on exotic plant invasion (Schiffman, 1997). On the other hand are these negative affects outweighed by the consistent consumption of invasive plant species decreasing the spread of these species into native forests that if not kept in check, could increase over time along with the positive effects of climate change (Buckland *et al.*, 2001)? My results from chapter 6 suggest the net impact of introduced deer decreases the spread of invasive plants from parts of forest where a canopy gap has been created, however further research is required to definitively understand the possibility of this controversial idea (Schiffman, 1997).

7.5 What are the potential effects of climate change on the spread of invasive plant species in New Zealand's *Nothofagus* forests?

The pattern of New Zealand forest distribution has been remarkably stable since European activity began in the 1800s (Wardle, 2001), despite fire, grazing by domestic and feral mammals, and some exploitation for timber. Although these influences continue, the greatest threat may now be climate change in conjunction with competition from introduced plants, including herbaceous species that may have been encouraged by episodes of fertiliser use and increased stocking, and, especially, introduced trees that are hardier and more vigorous as pioneers than native trees (Wardle, 2001).

Alterations in atmospheric chemistry and changes in climate have long been recognised as major components of global change (Kriticos *et al.*, 2003). More

recently, biotic invasions have been added to the list of important factors driving global change (Mack *et al*., 2000). This along with an increased frequency of mild winters, droughts, storms and floods provides compelling evidence of global climate change. As a result, concerns are developing about the potential impacts on both agriculture (Hanson *et al.,* 1993; Chakraborty *et al.,* 1998) and wildlife (Markham, 1996; Coley, 1998). In particular, where climate is known to govern the distribution of plants and animals (Pigott and Huntley, 1981; Beerling, 1993), climate change is likely to alter current limits of distribution (Buckland *et al.*, 2001).

An example of this comes from a study by Kriticos *et al.* (2003) who investigated the potential distribution of the invasive plant, *Acacia nilotica* in relation to climate change. Global climate change is likely to increase markedly the potential distribution of *A. nilotica* in Australia, significantly increasing the area at risk of invasion. The driving factors are the expected increases in water-use efficiency of *A. nilotica* due to increased atmospheric CO_2 concentrations, allowing it to invade more xeric sites further inland and increased temperatures, allowing it to complete its reproductive life cycle in more southern locations (Kriticos *et al.,* 2003).

More specifically, a New Zealand study by Leathwick (2001) presents the other issue that must be addressed to successfully protect the longevity of New Zealand's *Nothofagus* forests. This study examined New Zealand's potential forest pattern as predicted from current species-environment relationships and presented two conclusions relevant to this discussion. Firstly, *Nothofagus* is much more dominant in cooler environments, as in the forests of the North Island's central volcanoes and main axial ranges (Elder, 1962, 1965; Franklin, 1969) and of the South Island (Wardle, 1974; Wardle *et al.,* 1973). Secondly, much less *Nothofagus* forest survives in the drier eastern parts of New Zealand due to the warmer temperatures and the decrease in soil moisture availability. These are two changes that are said to occur in the face of climate change (Mackey, 1997; Short and Neckles, 1999; Kriticos *et al.,* 2003), thus illustrating the significance of climate change to the native *Nothofagus* forests of New Zealand in two ways; one is the decrease in abundance of *Nothofagus* in drier, warmer climates and secondly, the fact that invasive species increase in abundance and spread in these such climates (Mack *et al.,* 2000).

7.6 Management implications and future research

Understanding the effects of red deer browsing on a range of plant communities is important for formulating guidelines for the management of forestry plantations, nature reserves and deer hunting enterprises (Clutton-Brock and Albon, 1989), each of which may have different objectives (Virtanen *et al.,* 2002). In nature reserves (such as the Ruataniwha conservation park used in my present study), where the regeneration of trees is desirable, deer browsing is generally regarded as having a negative effect (Scott *et al.*, 2000), and deer proof fences or culling are implemented to achieve low deer densities and encourage tree recruitment (Booth, 1984; Gong *et al.,* 1991). However, on the contrary some browsing by deer can help maintain species diversity and keep the spread of invasive plant species in check (Ball, 1974; Crawley, 1997).

But when is enough, enough, as, when deer densities are too high they may also be detrimental to nature conservation (Virtanen *et al.,* 2002). Modeling studies of Buckland *et al.* (1996), suggest achieving a sustainable stag harvest may be possible with much lower overall deer densities (achieved through increased hind culls). Thus, conflicts in management objectives between deer-stalking enterprises and other land uses (e.g. nature conservation) may be reconciled (Virtanen *et al.,* 2002).

One of the concerns associated with the exclusion of herbivores or reduced herbivore densities in upland plant communities is a reduction in plant species richness and increased dominance of a few species (Ball, 1974; Wood, 2000). A study by Virtanen *et al.* (2002) indicates that this is a valid concern in productive communities (e.g. *Agrostis–Festuca* grasslands) but of less importance in unproductive communities (e.g. *Calluna–Molinia* wet heath), where effects of exclusion are small. There has also been concern that very high grazing pressure by deer or other domestic livestock can have negative impacts on plant biodiversity. However, a study by (Virtanen *et al.,* 2002), illustrated that the high deer densities of an unculled deer population were not associated with negative impacts on plant biodiversity they also found that none of the herbivore exclusion or culling policies had any measurable effect on tree regeneration.

What about the invasive plants? The success of plant invasions, may not only depend on the absence of specialist natural enemies in the invaded ecosystem, but also on available resource niches, competition with neighbouring plants and the grazing intensity of generalist herbivores (Shea and Chesson, 2002; van Ruijven *et al.,* 2003; Huston, 2004).

According to the enemy-release hypothesis, specialist herbivores should be more abundant in native plant populations than in uncontrolled populations in the invaded range (Keane and Crawley, 2002). Therefore, key insights into the role of natural enemies on the population dynamics of the plant, and their potential for biological control, could be gained from examination of the population dynamics in the native range (Jongejans *et al.,* 2006). Most studies of the population dynamics of invasive plants in general (Lonsdale *et al.,* 1995; Buckley *et al*., 2005), have, however, focused on the invaded range (Jongejans *et al.,* 2006). Native range studies, in this context, have been pioneered by Paynter *et al*. (1998) and Grigulis *et al*. (2001), and recent reviews have called for more such studies (Hinz and Schwarzlaender, 2004; Hierro *et al.,* 2005).

Where should future research effort be directed, to increase the management efficiency of these invasive species? First and foremost, the idea that red deer could be playing a beneficial role towards the management of invasive plants in New Zealand's forests needs to be compared with the known adverse effects of this species to found out if the negatives outweigh the positives. Once this is achieved, a precise management plan can be formulated to determine what density, deer must be kept at, to maximise native biodiversity. Importantly, this must be done in a manner that allows everyone who uses these resources to be involved (including hunters, landowners and the wider public) and in depth discussions are undertaken to insure all parties are satisfied with the final outcome. Implementing this approach will help to improve the relationship between government departments and the wider public, a relationship that has deteriorated over time and needs serious attention.

Obviously nothing can be done to stop trees falling down and creating canopy gaps in the forests, however decreasing the establishment success of any invasive species can to a degree, be mitigated. As suggested by Jongejans *et al*. (2006), specific studies at a

species level on the invasive plants of these forests need to be carried out. More specifically, the investigation of the population dynamics that occur in the native range of these species should be performed in attempt to decrease the adverse effects these species have on New Zealand's native *Nothofagus* forests.

References

Abe, M., Izaki, J., Miguchi, H., Masaki, T., Makita, A., Nakashizuka, T. 2002. *The effects of sasa and canopy gap formation on tree regeneration in an old beech forest.* Journal of Vegetation Science, 13 (4), 565-574.

Agrawal, A.A., Kotanen, P.M. 2003. *Herbivores and the success of exotic plants: a phylogenetically controlled experiment.* Ecology Letters, 6, 712–715.

Allen, R.B., Payton, I.J., Knowlton, J.E. 1984. *Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures.* NZJ Ecol, 7, 119-130.

Allen, R.B., Bellingham, P.J., Wiser, S.K. 2003. *Developing a forest biodiversity monitoring approach for New Zealand.* NZJ Ecol, 27 (2), 207-220.

Augspurger, C.K., Franson, S.E. 1988. *Input of wind-dispersed seeds into light-gaps and forest sites in a neotropical forest.* Journal of Tropical Ecology, 4 (3), 239-252.

Auld, B.A., Tisdall, C.A. 1986. *Impact assessment of biological invasions.* In: Groves, R.H., Burdon, J.J. Ecology of Biological Invasions. Cambridge University Press, Cambridge, 79-88.

Baker, H.G. 1974. *The evolution of weeds.* Annual Review of Ecology and Systematics, 5, 1-24.

Ball, M.E. 1974. *Floristic changes on grasslands and heaths on the Isle of Rum after a reduction of exclusion of grazing.* Journal of Environmental Management, 2, 299-318.

Bàrberi, P., Cascio, B.L. 2001. *Long-term tillage and crop rotation effects on weed seedbank size and composition.* Weed Research, 41 (4), 325-340.

Baret, S., Cournac, L., Thébaud, C., Edwards, P., Strasberg, D. 2008. *Effects of canopy gap size on recruitment and invasion of the non-indigenous **(Rubus alceifolius)** in lowland tropical rain forest on Réunion.* Journal of Tropical Ecology, 24, 337-345.

Barik, S.K., Pandey, S.N., Tripathi, R.S., Rao, P. 1992. *Microenvironmental variability and species diversity in treefall gaps in a sub-tropical broadleaved forest.* Vegetatio, 103 (1), 31-40.

Becker, T., Dietz, H., Billeta, R., Buschmann, H., Edwards, P.J. 2005. *Altitudinal distribution of alien plant species in the Swiss Alps.* Perspectives in Plant Ecology, Evolution and Systematics, 7, 173–183.

Bee, J.N., Kunstler, G., Coomes, D.A. 2007. *Resistence and resilience of New Zealand tree species to browsing.* Ecology, 95, 1014-1026.

Beerling, D.J. 1993. *The impact of temperature on the northern distribution limits of the introduced species **Fallopia japonica** and **Impatiens glandulifera** in North-west Europe.* Journal of Biogeography, 20, 45-53.

Behenna, M.,Vetter, S. 2008. *Viability of alien and native seed banks after slash and burn: Effect of soil moisture, depth of burial and fuel load.* South African Journal of Botany, 74 (3), 454-462.

Benech-Arnold, R.L., Sánchez, R.A., Forcella, F., Kruk, B.C., Ghersa, C.M. 2000. *Environmental control of dormancy in weed seed banks in soil.* Field Crops Research, 67, 105-122.

Bishop, J.G., Schemske, D.W. 1998. *Variation in flowering phenology and its consequences for lupines colonizing Mount St. Helens.* Ecology, 79, 534-546.

Bohrer, G., Katul, G.G., Nathan, R., Walko, R.L., Avissar, R. 2008. *Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds.* Journal of Ecology, 96, 569-580.

Bond, W.J., Honig, M. 1999. *Seed size and seedling emergence: An allometric relationship and some ecological implications.* Oecologia, 120 (1), 132-136.

Booth, T.C. 1984. *Natural regeneration in the native pinewoods of Scotland: a review of principles and practice.* Scottish Forestry, 38, 33-42.

Brandani, A., Hartshorn, G.S., Orians, G.H. 1988. *Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest.* Journal of Tropical Ecology, 4, 99-119.

Brooks, R.T., Kyker-Snowman, T.D. 2008. *Forest floor temperature and relative humidity following timber harvesting in Southern New England, USA.* Forest Ecology and Management, 254, 65-73.

Buckland, S.T., Ahmad, S., Staines, B.W., Gordon, I.J., Youngson, R.W. 1996. *Estimating the minimum population size that allows a given annual number of mature red deer stags to be culled sustainably.* Journal of Applied Ecology, 33, 118-130.

Buckland, S.M., Thompson, K., Hodgson, J.G., Grime, J.P. 2001. *Grassland invasions: effects of manipulations of climate and management.* Journal of Applied Ecology, 38, 301-309.

Buckley, Y.M., Briese, D.T., Rees, M. 2003. *Demography and management of the invasive plant species **Hypericum perforatum**. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies.* Journal of Applied Ecology, 40, 494-507.

Buckley, Y.M., Rees, M., Sheppard, A.W. Smyth, M.J. 2005. *Stable coexistence of an invasive plant and biocontrol agent: a parameterized coupled plant–herbivore model.* Journal of Applied Ecology, 42, 70-79.

Buhler, D.D. 1997. *Effects of Tillage and Light Environment on Emergence of 13 Annual Weeds.* Weed Technology, 11 (3), 496-501.

Cadenasso, M.L., Pickett, S.T.A. 2001. *Effect of edge structure on the flux of species into forest interiors.* Conservation Biology, 15 (1), 91-97.

Canham, C.D., Denslow, W.J., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S. 1990. *Light regimes beneath closed canopies and treefall gaps in temperate and tropical forests.* Canadian Journal of Forest Research, 20, 620-631.

Carpenter, D., Cappuccino, N. 2005. *Herbivory, time since introduction and the invasiveness of exotic plants.* Journal of Ecology, 93, 315-321.

Castleberry, S.B., Ford, W.M., Miller, K.V., Smith, W.P. 2000. *Infuences of herbivory and canopy opening size on forest regeneration in a southern bottomland hardwood forest.* Forest Ecology and Management, 131, 57-64.

Caughley, G. 1983. *The deer wars.* Heineman, Auckland, New Zealand.

Caughley, G. 1984. New Zealand plant-herbivore systems: Past and present. NZJ Ecol, 12 (supplement), 3-10.

Chacon, P., Armesto, J.J. 2005. *Effect of canopy openness on growth, specific leaf area, and survival of tree seedlings in a temperate rainforest of Chiloé Island, Chile.* NZJ Botany, 43, 71-81.

Chakraborty, S., Murray, G.M., Magarey, P.A., Yonow, T., O'Brien, R.G., Croft, B.J., Barbetti, M.J., Sivasithamparam, K., Old, K.M., Dudzinski, M.J., Sutherst, R.W., Penrose, L.J., Archer, C., Emmett, R.W. 1998. *Potential impact of climate change on plant diseases of economic significance to Australia.* Australasian Plant Pathology, 27, 15-35.

Challies, C.N. 1985. *Establishment, control, and commercial exploitation of wild deer in New Zealand.* In: Fennessey, P.F., Drew, K.D. Biology of deer production. Royal Society of New Zealand, Wellington, New Zealand, 22, 23-26.

Challies, C.N. 1991. *Status and future management of the wild animal recovery industry.* New Zealand Forestry, 36, 10-17.

Chapin, F.S.I., Sala, O.E., Huber-Sanwald, E. 2001. *Global biodiversity in a changing environment: scenarios for the 21st century.* Springer, New York, USA.

Cicek, E., Tilki, F. 2006. *Effects of temperature, light and storage on seed germination of **Ulmus glabra** Huds. and **U. laevis** Pall.* Pakistan Journal of Biological Sciences, 9 (4), 697-699.

Civeyrel, L., Simberloff, D. 1996. *A tale of two snails: Is the cure worse than the disease?* Biodiversity and Conservation, 5, 1231-1252.

Clinton, B.D. 2003. *Light, temperature, and soil moisture responses to elevation, evergreen understory, and small canopy gaps in the Southern Appalachians.* Forest Ecology and Management, 186, 243-255.

Clutton-Brock, T.H. Albon, S.D. 1989. *Red deer in the highlands.* BSP Professional Books, Oxford, UK.

Colautti, R.I., MacIsaac, H.J. 2004. *A neutral terminology to define invasive species.* Diversity and Distributions, 10, 135-141.

Cole, P.G., Weltzin, J.F. 2005. *Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests.* Biological Invasions, 7, 477-488.

Coley, P.D. 1998. *Possible effects of climate change on plant/herbivore interactions in moist tropical forests.* Climatic Change, 39, 455-472.

Collins, B. 2003. *Ground layer competition and herbivory effects on cherrybark oak (Quercus pagoda Raf.) regeneration in experimental canopy gaps.* Journal of the Torrey Botanical Society, 130 (3), 147-157.

Collins, B.S., Pickett, S.T.A. 1988. *Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest.* The Journal of Ecology, 76 (2), 437-450.

Cone, J.W., Kendrick, E. 1986. *Photocontrol of seed germination.* In Kendrick, R.E., Kronberg, G. Photomorphogenesis in Plants. Dordrecht, Netherlands, 443-462.

Coomes, D.A., Allen, R.B., Forsyth, D.M., Lee, W.G. 2003. *Factors preventing the recovery of New Zealand forests following control of invasive deer.* Conservation Biology, 17 (2), 450-459.

Crawley, M.J. 1986. *What makes a community invasible?* In: Gray, A.J. Colonization, succession and stability. Blackwell Scientific Publication, Oxford, 429-453.

Crawley, M.J. 1997. *Plant–herbivore dynamics.* In: Crawley, M.J. Plant Ecology. Blackwell Science, Oxford, UK, 401-474.

Dai, X. 1996. *Influence of light conditions in canopy gaps on forest regeneration: a new gap light index and its application in a boreal forest in East-central Sweden.* Forestry Ecology and Management, 84, 187-197.

Danehy, R.J., Kirpes, B.J. 2000. *Relative humidity gradients across riparian areas in Eastern Oregon and Washington forests.* Northwest Science 74 (3), 224-233.

D'Antonio, C., Vitousek, P. 1992. *Biological invasions by exotic grasses, the grass/fire cycle, and global change.* Annual Reviews of Ecology and Systematics, 23, 63-87.

Davis, M.A. 2005. *Vegetation change - a reunifying concept in plant ecology.* Perspectives in Plant Ecology, Evolution, and Systematics, 7, 69-76.

Davis, M.A, Thompson, K. 2001. *Invasion terminology: should ecologists define their terms differently than others? No, not if we want to be of any help.* ESA Bulletin, 82-206.

De Freitas, C.R., Enright, N.J. 1995. *Microclimatic differences between and within canopy gaps in a temperate rainforest.* International Journal of Biometeorology 38 (4), 188-193.

Denslow, J.S. 1995. *Disturbance and diversity in tropical rain forests: the density effect.* Ecological Applications, 5, 962-968.

Di Castri, F. 1989. *History of biological invasions with special emphasis on the old world.* In: Drake, J.A. Biological invasions, a global perspective. John Wiley, Chinchester, 1-30.

Dickinson, M.B., Whigham, D.F., Hermann, S.M. 2004. *Tree regeneration in felling and natural treefall disturbances in a semideciduous tropical forest in Mexico.* Forest Ecology and Management, 134, 137-151.

Dolman, P.M., Wäber, K. 2008. *Ecosystem and competition impacts of introduced deer.* Wildlife Research, 35, 202-214.

Dukes, J.S., Mooney, H.A., 1999. *Does global change increase the success of biological invaders?* Trends in Ecology Evolution 14, 135-139.

Dullinger, S., Kleinbauer, I., Pauli, H., Gottfried, M., Brooker, R., Nagy, L., Theurillat, J.P., Holten, J.I., Abdaladze, O., Benito, J.L., Borel, J.L., Coldea, G., Ghosn, D., Kanka, R., Merzouki, A., Klettner, C., Moiseev, P., Molau, U., Reiter, K., Rossi, G., Stanisci, A., Tomaselli, M., Unterlugauer, P., Vittoz, P., Grabherr, G. 2007. *Weak and variable relationships between environmental severity and small-scale co-occurrence in alpine plant communities.* Journal of Ecology, 95, 1284-1295.

Dunlop, E.A., Wilson, J.C., Mackey, A.P. 2006. *The potential geographic distribution of the invasive weed **Senna obtusifolia** in Australia.* Weed Research, 46, 404-413.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O. 2000. *Climate extremes: observations, modelling, and impacts.* Science, 289, 2068–2074.

Elder, N.L. 1962. *Vegetation of the Kaimanawa Ranges.* Transactions of the Royal Society of New Zealand (Botany), 2, 1-37.

Elder, N.L. 1965. *Vegetation of the Ruahine range: an introduction.* Transactions of the Royal Society of New Zealand (Botany), 3, 13-66.

Evans, A.S., Webb, K.L., Penhale, P.A. 1986. *Photosynthetic temperature acclimation in two coexisting seagrasses **Zostera marina** and **Ruppia maritima**.* Aquatic Botany, 24, 185-198.

Everham, E.M., Myster, R.W., Van De Genachte, E. 1996. *Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico.* American Journal of Botany, 83 (8), 1063-1068.

Ewel, J. 1986. *Invasibility: lessons from South Florida.* In H.A. Mooney., Drake, J.A. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, 214-230.

Ewel, K.C., Zheng, S., Pinzon, Z.S., Bourgeois, J.A. 1998. *Environmental effects of canopy gap formation in high-rainfall mangrove forests.* Biotropica, 30 (4), 510-518.

Fagan, W.F., Bishop, J.G. 1999. *Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens.* The American Naturalist, 155 (2), 238-251.

Fernández, D.S., Fetcher, N. 1991. *Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico.* Biotropica 23 (4a), 393-399.

Fownes, J.H., Harrington, R.A. 2004. *Seedling response to gaps: separating effects of light and nitrogen.* Forest Ecology and Management, 203, 297–310.

Franklin, D.A. 1969. *The synecology of the Tararua indigenous forests.* Forest Research Institute Technical Paper, 53.

Fraser, K.W., Cone, J.M., Whitford, E.J. 2000. *A revision of the established ranges and new populations of 11 introduced ungulate species in New Zealand.* Journal of the Royal Society of New Zealand, 30 (4), 419-437.

Funes, G., Basconcelo, S. 2003. *Seed bank dynamics in tall tussock grasslands along an altitudinal gradient.* Journal of Vegetation Science, 14 (2), 253-258.

Geiger, R. 1965. *The climate near the ground.* Harvard University Press, Cambridge, England.

Graham, R.A., Florentine, S.K. 2004. *The germinable soil seedbank of **Eucalyptus victrix** grassy woodlands at Roy Hill Station, Pilbara District, Western Australia.* Rangeland Journal, 26 (1), 17-33.

Gray, A., Spies, T.A. 1997. *Micorsite controls on tree seedling establishment in conifer forest canopy gaps.* Ecology 78, 2458–2473.

Gray, A.N., Spies, T.A., Easter, M.J. 2002. *Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests.* Canadian Journal of Forest Research, 32 (2), 332-343.

Greenland, D., Goodin, D.G., Smith, R.C. 2003. *Climate variability and ecosystem response at long-term ecological research sites.* Oxford University Press, New York, USA.

Grigulis, K., Sheppard, A.W., Ash, J.E., Groves, R.H. 2001. *The comparative demography of the pasture weed **Echium plantagineum** between its native and invaded ranges.* Journal of Applied Ecology, 38, 281-290.

Grime, J.P. 1979. *Plant strategies and vegetation processes.* Wiley, New York

Grime, J.P. 2001. *Plant strategies, vegetation processes and ecosystem properties.* John Wiley & Sons, Chichester.

Grubb, P.J. 1996. *Rainforest dynamics: the need for new paradigms.* In: Edwards, D.S. Tropical Rainforest Research - Current Issues. Kluwer Academic Publishers, Dordrecht, Netherlands, 215-233.

Grubb, P.J. 1977. *The maintenance of species richness in plant communities: the importance of the regeneration niche.* Biological Reviews, 52, 107-145.

Hanson, J.D., Baker, B.B., Bourdon, R.M. 1993. *Comparison of the effects of different climate change scenarios on rangeland livestock production.* Agricultural Systems, 41, 487–502.

Harper, J.L. 1977. *Population biology of plants.* Academic Press, London.

Hierro, J.L., Maron, J.L., Callaway, R.M. 2005. *A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range.* Journal of Ecology, 93, 5-15.

Hinz, H.L., Schwarzlaender, M. 2004. *Comparing invasive plants from their native and exotic range: what can we learn for biological control?* Weed Technology, 18, 1533-1541.

Hobbie, S.E., Chapin, S.F. 1998. *An experimental test of limits to tree establishment in Arctic tundra.* Journal of Ecology, 86, 449-461.

Hobbs, R.J. 1987. *Disturbance regimes in remnants of natural vegetation.* In Saunders, D.A., Arnold, G.W., Burbidge, A.A., Hopkins, A.J.M. Nature conservation: the role of remnants of native vegetation. Surrey Beatty, Chipping Norton, Australia, 233-240.

Hobbs, R.J. 1991. *Disturbance as a precursor to weed invasion in native vegetation.* Plant Protection Quarterly, 6, 99-104.

Hobbs, R.J., Huenneke, L.F. 1992. *Disturbance, diversity, and invasion: Implications for conservation.* Conservation Biology, 6 (3), 324-337.

Hobbs, R.J., Yates, S., Mooney, H.A. 2007. *Long-term data reveal complex dynamics in grassland in relation to climate and disturbance.* Ecological Monographs, 77 (4), 545-568.

Holladay, C.A., Kwit, C., Collins, B. 2006. *Woody regeneration in and around aging southern bottomland hardwood forest gaps: effects of herbivory and gap size.* Forest Ecology and Management, 223, 218-225.

Houghton, R.A., Woodwell, G.M. 1989. *Global climatic change.* Scientific American, 260, 36-44.

Howe, H. F., Miriti, M.N. 2000. *No question: seed dispersal matters.* Trends in Ecology and Evolution, 15, 434-436.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography: monographs in population biology.* Princeton University Press, Princeton, USA.

Husheer, S.W., Coomes, D.A., Robertson, A.W. 2003. *Long-term influences of introduced deer on the composition and structure of New Zealand **Nothofagus** forests.* Forest Ecology and Management, 181, 99-117.

Husheer, S.W., Hansen, Q.W., Urlich, S.C. 2005. *Effects of red deer on tree regeneration and growth in Aorangi Forest, Wairarapa.* NZJ Ecol, 29 (2), 271-277.

Huston, M.A. 2004. *Management strategies for plant invasions: manipulating productivity, disturbance, and competition.* Diversity and Distributions, 10, 167-178.

Ito, H., Hino, T. 2008. *Effects of deer and mice on seedling survival in a temperate mixed forest of Japan.* Forest Ecology and Management, 256, 129-135.

Jackson, D.B. 2001. *Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland.* Journal of Applied Ecology, 38, 802-812.

Jane, G.T. 1994. *The impact of browsing animals on the stand dynamics of monotypic mountain beech **(Nothofagus solandri)** forests in Canterbury, New Zealand.* Australian Journal of Botany, 42, 113-124.

Jennings, S.B., Brown, N.D., Sheil, D. 1999. *Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures.* Forestry, 72 (1), 59-73.

Jesson, L., Kelly, D., Sparrow, A. 2000. *The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand.* NZJ Botany, 38, 451-468.

Jongejans, E., Sheppard, A.W., Shea, K. 2006. *What controls the population dynamics of the invasive thistle **Carduus nutans** in its native range?* Journal of Applied Ecology, 43, 877-886.

Kay, C.E., Bartos, D.L. 2000. *Ungulate herbivory on Utah Aspen: assessment of long-term exclosures.* Journal of Range Management, 53 (2), 145-153.

Keane, R.M., Crawley, M.J. 2002. *Exotic plant invasions and the enemy release hypothesis.* Trends in Ecology and Evolution, 17, 164–170.

Keeley, J.E., Lubin, D., Fotheringham, C.J. 2003. *Fire and grazing impacts on plant diversity and alien plant invasions in the Southern Sierra, Nevada.* Ecological Applications, 13 (5), 1355-1374.

Kelly, D., Koenig, W.D., Liebhold, A.M. 2008. *An intercontinental comparison of the dynamic behavior of mast seeding communities.* Population Ecology, 50 (4), 329-342.

Klein Tank, A.M.G. 2002. *Daily dataset of 20th-century surface air temperature and precipitation series for the European climate assessment.* International Journal of Climatology 22, 1441-1453.

Kondani, J. 2001. *The effects of canopy gaps on seedling emergence and growth of two deciduous broad-leaved species (**Cornus controversa** and **Prunus grayana**) in a **Cryptomeria japonica** plantations.* Journal of Forest Research, 6, 303-305.

Kraft, L.S., Crow, T.R., Buckley, D.S., Nauertz, E.A., Zasada, J.C. 2004. *Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA.* Forest Ecology and Management, 199, 219-230.

Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.W., Maywald, G.F. 2003. *Climate change and the potential distribution of an invasive alien plant: **Acacia nilotica ssp. Indica** in Australia.* Journal of Applied Ecology, 40, 111-124.

Kriticos, D.J., Yonow, T., McFadyen, R.E. 2005. *The potential distribution of **Chromolaena odorata** (Siam weed) in relation to climate.* Weed Research 45, 246-254.

Kumar, S., Takeda, A., Shibata, E. 2006. *Effects of 13-year fencing on browsing by sika deer on seedlings on Mt. Ohdaigahara, central Japan.* Journal of Forestry Research, 11, 337-342.

Lambrinos, J.G. 2002. *The variable invasive success of **Cortaderia** species in a complex landscape.* Ecology, 83, 518-529.

Lambrinos, J.G. 2006. *Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass.* Oecologia, 147, 327-334.

Landenberger, R.E., Kota, N.L. 2007. *Seed dispersal of the non-native invasive tree **Ailanthus altissima** into contrasting environments.* Plant Ecology, 192, 55-70.

Larsson, E.L., 2003. *Two ways of trapping seeds in alpine environments, Lapland, Sweden.* Nordic Journal of Botany, 23 (3), 333-343.

Leathwick, J.R. 2001. *New Zealand's potential forest pattern as predicted from current species-environment relationships.* NZJ Botany, 39, 447-464.

Leon, R.G., Owen, M.D.K. 2004. *Artificial and natural seed banks differ in seedling emergence patterns.* Weed Science, 52 (4), 531-537.

Lof, M., Karlsson, M., Sonesson, K., Welander, T.N., Collet, C. 2007. *Growth and mortality in underplanted tree seedlings in response to variations in canopy closure of Norway spruce stands.* Forestry, 80 (4), 371-384.

Lonsdale, W.M., Farrell, G., Wilson, C.G. 1995. *Biological control of a tropical weed: a population model and experiment for **Sida acuta**.* Journal of Applied Ecology, 32, 391-399.

Lord, J.M. 1990. *The maintenance of Poa cita grassland by grazing.* NZJ Ecology, 13, 43-49.

Luken, J.O., Kuddes, L.M., Tholemeier, T.C., Haller, D.M. 1997. *Comparative responses of **Lonicera maackii** (amur honeysuckle) and **Lindera benzoin** (spicebush) to increased light.* American Midland Naturalist, 138**,** 331-343.

Mack, R.N. 1986. *Alien plant invasions into the Intermountain West: a case history.* In: Mooney, H.A., Drake, J.A. Ecology of biological invasions of North America and Hawaii. Springer, New York, 191-213.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F. 2000. *Biotic invasions: causes, epidemiology, global consequences and control.* Ecological Applications, 10, 689-710.

Mackey, A.P. 1997. *The biology of Australian weeds 29. **Acacia nilotica** sp. **indica** (Benth) Brenan.* Plant Protection Quarterly, 12, 7–17.

Makana, J.R., Thomas, S.C. 2005. *Effects of light gaps and litter removal on the seedling performance of six African timber species.* Biotropica, 37 (2), 227-237.

Malanson, G.P., D.M. Cairns. 1997. *Effects of dispersal, population delays, and forest fragmentation on tree migration rates.* Plant Ecology, 131, 67-79.

Mancinelli, A.L. 1994. *The physiology of phytochrome action.* In Kendrick, R., Kronberg, G. Photomorphogenesis in Plants. 2nd ed. Kluwer Academic, Netherlands, 211-269.

Markham, A. 1996. *Potential impacts of climate change on ecosystems: a review of implications for policy makers and conservation biologists.* Climate Research, 6, 179-191.

Maron, J.L., Vilà, M. 2001. *When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses.* Oikos, 95, 361-373.

Marsh Jr., J.A., Dennison, W.C., Alberte, R.S. 1986. *Effects of temperature on photosynthesis and respiration in eelgrass **(Zostera marina L.)**.* Journal of Experimental Marine **Biology and Ecology,** 101, 257-267.

Martinez-Ghersa, M.A., Satorre, E.H., Ghersa, C.M. 1997. *Effect of soil water content and temperature on dormancy breaking and germination of three weeds.* Weed Science, 45 (6), 791-797.

Masaki, T., Suzuki, W., Niiyama, K., Iida, S., Tanaka, H., Nakashizuka, T. 1992. *Community structure of a species-rich temperate forest, Ogawa Forest Reserve, Central Japan.* Vegetatio, 98, 97-111.

Mayer, P.M., Ryan, M.R. 1991. *Electric fences reduce mammalian predation on piping plover nests and chicks.* Wildlife Society Bulletin, 19 (1), 59-63.

McAlpine, K.G., Jesson, L.K. 2008. *Linking seed dispersal, germination and seedling recruitment in the invasive species **Berberis darwinii** (Darwin's barberry).* Plant Ecology, 197, 119-129.

McDougall, K.L., Morga, J.W., Walsh, N.G., Williams, R.J. 2005. *Plant invasions in treeless vegetation of the Australian Alps.* Perspectives in Plant Ecology, Evolution and Systematics, 7, 159-171.

McMillan, C. 1984. *The distribution of tropical seagrasses with relation to their tolerance of high temperatures.* Aquatic Botany, 19, 369-380.

Meentemeyer, R.K., Moody, A. 2000. *Rapid sampling of plant species composition for assessing vegetation patterns in rugged terrain.* Landscape Ecology, 15, 697-711.

Ministry of Conservation. 2007. *Managing numbers of deer, chamois, tahr and pigs; A discussion document.* Game animal panel, Christchurch, New Zealand.

Mitchell, J.F.B. 1989. *The greenhouse effect and climate change.* Revolutionary Geography, 27, 115-139.

Mooney, H.A., Hobbs, R.J. 2000. *Global change and invasive species: where do we go from here?* In: Mooney, H.A., Hobbs, R.J. Invasive species in a changing world. Island Press, Covelo, California, USA, 425-434.

Nathan, R., Muller-Landau, H.C. 2000. *Spatial patterns of seed dispersal, their determinants and consequences for recruitment.* Trends in Ecology and Evolution, 15, 278-285.

New Zealand Forest Service. 1984. *Deer control and vegetation response on Stewart Island.* What's New in Forest Research, 126. Forest Research Institute, Rotorua, New Zealand.

New Zealand Plant Conservation Network. 2008. www.nzpcn.org.nz/exotic_plant_life_and_weeds/index.asp

Nugent, G. 1992. *Big-game, small-game and game bird hunting in New Zealand: Hunting effort, harvest and expenditure in 1988.* New Zealand Journal of Zoology, 19, 1-16.

Nugent, G.; Fraser, K.W. 1993. *Pest or valued resource: conflicts in game management.* New Zealand Journal of Zoology, 20, 361-366.

Nugent, G., Fraser, K.W., Asher, G.W., Tustin, K.G. 2001a. *Advances in New Zealand mammalogy 1990-2000: Deer.* Journal of the Royal Society of New Zealand, 31 (1), 263-298.

Nugent, G., Fraser, W., Sweetapple, P. 2001b. *Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand.* Biological Conservation, 99, 65-79.

Nugent, G., Sweetapple, P.J. 1989. *The impact of three deer hunting regimes in North-Eastern Fiordland.* NZJ Ecol, 12, 33-46.

Nuñez, M.A., Relva, M.A., Simberloff, D. 2008. *Enemy release or invasional meltdown? Deer preference for exotic and native trees on Isla Victoria, Argentina.* Austral Ecology, 33, 317-323.

Nuttle, T., Haefner, J.W. 2005. *Seed dispersal in heterogeneous environments: bridging the gap between mechanistic dispersal and forest dynamics models.* The American Naturalist, 165 (3), 336-349.

Oheimb, G., Westphal, C., Tempel, H., Härdtle, W. 2005. *Structural pattern of a near-natural beech forest **(Fagus sylvatica)** (Serrahn, North-east Germany).* Forest Ecology and Management, 212, 253-263.

Ohlemüller, R., Walker, S., Wilson, J.B. 2006. *Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species.* Oikos, 112, 493-501.

Panferov, O., Sogachev, A. 2008. *Influence of gap size on wind damage variables in a forest.* Agricultural and Forest Meteorology, 148 (11), 1869-1881.

Parkes, J.P., Nugent, G., Warburton, B. 1996. *Commercial exploitation as a pest control tool for introduced mammals in New Zealand.* Wildlife Biology, 2, 135-141.

Paynter, Q., Fowler, S.V., Memmott, J., Sheppard, A.W. 1998. *Factors affecting the establishment of **Cytisus scoparius** in Southern France: implications for managing both native and exotic populations.* Journal of Applied Ecology, 35, 582-595.

Pearse, A.J., Goosen, D.G. 1999. *Hybridisation and species/strains in the New Zealand deer industry.* Deer Branch of the New Zealand Veterinary Association. Proceedings of a Deer Course for Veterinarians, 16, 167-174.

Perrins, J., Fitter, A., Williamson, M. 1993. *Population biology and rates of invasion of three introduced **Impatiens** species in the British Isles.* Journal of Biogeography, 20, 33-44.

Petraitis, P.S., Latham, R.E., Niesenbaum, R.A. 1989. *The maintenance of species diversity by disturbance.* Quarterly Review of Biology, 64, 393-418.

Phillips, D.L., Shure, D.J. 1990. *Patch-size effects on early succession in southern Appalachian forests.* Ecology, 71, 204-212.

Piasentier, E., Saccà, E., Bovolenta, S. 2007. *Dietary selection and ingestive behaviour of fallow deer and sheep grazing on adjacent monocultures of white clover and tall fescue.* Small Ruminant Research, 71, 222-233.

Pickett, S.T.A., Kolasa, J., Armesto, J.J., Collins, S.L. 1989. *The ecological concept of disturbance and its expression at various hierarchical levels.* Oikos, 54, 129-136.

Pickett, S.T.A., White, P.S. 1985. *The ecology of natural disturbance and patch dynamics.* Academic Press, Orlando, Florida.

Pigott, C.D., Huntley, J.P. 1981. *Factors controlling the distribution of **Tilia cordata** at the northern limit of its geographical range. III. Nature and cause of seed sterility.* New Phytologist, 87, 817–839.

Pyšek, P., Jarošik, V., Chytry M., Kropáč, Z., Tichy, L., Wild, J. 2005. *Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats.* Ecology, 86 (3), 772-785.

Quinn, J.F., Robinson, G.R. 1987. *The effects of experimental subdivision on flowering plant diversity in a California annual grassland.* Journal of Ecology, 75, 837-855.

Rahman, A., James, T.K., Waller, J.E., Grbavac, N. 1997. *Soil sampling studies for estimation of weed seedbanks.* Proceedings of the 50th New Zealand Plant Protection Conference, 447-452.

Raich, J.W., Christensen, N.L. 1989. *Malaysian Dipterocarp forest: tree seedling and sapling species composition and small-scale disturbance patterns.* National Geographic Research, 5, 348-363.

Rand, T.A., Louda, S.M. 2004. *Exotic weed invasion increases the susceptibility of native plants to attack by a biocontrol herbivore.* Ecology, 85 (6), 1548-1554.

Raymond, P., Munson, A.D., Ruel, J., Coates, K.D. 2006. *Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood – white pine stands.* Canadian Journal of Forest Research, 36 (3), 639-651.

Richardson, D.M., Pysek, P. 2006. *Plant invasions: merging the concepts of species invasiveness and community invasibility.* Progress in Physical Geography, 30 (3), 409-431.

Richardson, D.M., Pysek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J. 2000. *Naturalization and invasion of alien plants: concepts and definitions.* Diversity and Distributions, 6, 93-107.

Ritter, E., Dalsgaard, L., Einhorn, K.S. 2005. *Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark.* Forest Ecology and Management, 206, 15–33.

Robinson, G.R., Quinn, J.F. 1988. *Extinction, turnover and species diversity in an experimentally fragmented California annual grassland.* Oecologia, 76, 71-82.

Rooney, T.P. 2001. *Deer impacts of forest ecosystems: A North American perspective.* Forestry, 74 (3), 201-208.

Rose, A.B., Burrows, L.E. 1985. *The impact of ungulates on the vegetation.* In: Davis, M.R., Orwin, J. Report on a survey of the proposed wapiti area, West Nelson. New Zealand Forest Service, FRI Bull, 84, 210-34.

Ross, L.C., Lambdon, P.W., Hulme, P.E. 2008. *Disentangling the roles of climate, propagule pressure and land use on the current and potential elevational distribution of the invasive weed **Oxalis pes-caprae** L. on Crete.* Perspectives in Plant Ecology, Evolution and Systematics , 10, 251–258.

van Ruijven, J., De Deyn, G.B., Berendse, F. 2003. *Diversity reduces invasibility in experimental plant communities: the role of plant species.* Ecology Letters, 6, 910-918.

Sariyildiz, T. 2008. *Effects of gap-size classes on long-term litter decomposition rates of beech, oak and chestnut species at high elevations in Northeast Turkey.* Ecosystems, 11, 841-853.

Saunders, D.A., Hobbs, K.J., Margules, C.R. 1991. *Biological consequences of ecosystem fragmentation.* Conservation Biology, 5, 18-32.

Schiffman, P.M. 1997. *Animal-mediated dispersal and disturbance: driving forces behind alien plant naturalization.* In: Luken, J.O. Thieret, J.W. Assessment and Management of Plant Invasions. Springer, Verlag, 87-99.

Schmidt, M.G., Ogden, A.E., Lertzman, K.P. 1998. *Seasonal comparison of soil temperature and moisture in pits and mounds under vine maple gaps and conifer canopy in a coastal western hemlock forest.* Canadian Journal of Soil Science, 78 (2), 291-300.

Schneider, S.H. 1990. *The global warming debate: Science or politics?* Environmental Science and Technology, 24, 432-435.

Schupp, E.W., Fuentes, M. 1995. *Spatial patterns of seed dispersal and the unification of plant population biology.* Ecoscience, 2, 267-275.

Scott, D., Welch, D., Thurlow, M., Elston, D.A. 2000. *Regeneration of **Pinus sylvestris** in a natural pinewood forest in NE Scotland following reduction in grazing by **Cervus elaphus**.* Forest Ecology and Management, 130, 199-211.

Seiwa, K. 2007. *Trade-offs between seedling growth and survival in deciduous broadleaved trees in a temperate forest.* Annals of Botany, 99, 537-544.

Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A., Field, C.B. 2002. *Grassland responses to global environmental changes suppressed by elevated CO2.* Science, 298, 1987-1990.

Shea, K., Chesson, P. 2002. *Community ecology theory as a framework for biological invasions.* Trends in Ecology and Evolution, 17, 170-176.

Short, F.T., Neckles, H.A. 1999. *The effect of global change on seagrasses.* Aquatic Botany, 63, 169-196.

Skarpaas, O., Shea, K. 2007. *Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles.* The American Naturalist, 170 (3), 421-430.

Smale, M.C., Hall, G.M.J., Gardener, R.O. 1995. *Dynamics of Kanuka **(Kunzea ericoides)** forests on South Kaipara spit, New Zealand, and the impact of fallow deer **(Dama dama)***. NZJ Ecol, 19 (2), 131-141.

Smit, C., Gusberti, M., Müller-Schärer, H. 2006. *Safe for saplings; safe for seeds?* Forest Ecology and Management, 237, 471-477.

Stewart, G.H., Burrows, L.E. 1989. *The impact of white-tailed deer **Odocoileus virginianus** on regeneration in the coastal forests of Stewart Island, New Zealand.* Biological Conservation, 49, 275-293.

Stroh, N., Baltzinger, C., Martin, J.L. 2008. *Deer prevent western redcedar **(Thuya plicata)** regeneration in old-growth forests of Haida Gwaii: Is there a potential for recovery?* Forest Ecology and Management, 255, 3973-3979.

Thompson, A.J., Jones, N.E., Blair, A.M. 1997. *The effect of temperature on viability of imbibed weed seeds.* Annals of Applied Biology, 130, 123-134.

Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O., Rouget, M. 2005. *Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale.* Global Change Biology, 11, 2234-2250.

Timmins, S.M., Williams, P.A. 1991. *Weed numbers in New Zealand.* NZJ Ecol, 15, 153-162.

Treskonova, M. 1991. *Changes in the structure of tall tussock grasslands and infestation by species of **Hieracium** in the MacKenzie country, New Zealand.* NZJ Ecol, 15, 65-78.

Tripler, C.E., Canham, C.D., Inouye, R.S., Schnurr, J.L. 2005. *Competitive hierarchies of temperate tree species: Interactions between resource availability and white-tailed deer.* Ecoscience, 12 (4), 494-505.

Tuomisto, H., Ruokolainen, K., Yli-Halla, M. 2003. *Dispersal, environment, and floristic variation of Western Amazonian forests.* Science 299, 241-244.

Valladares, F., Guzman, B. 2006. *Canopy structure and spatial heterogeneity of understory light in an abandoned Holm oak woodland.* Annals of Forest Science, 63 (7), 749-761.

Vilà , M., Corbin, J.D., Dukes, J.S., Pino, J., Smith, S.D. 2006. *Linking plant invasions to environmental change.* In: Canadell, J., Pataki, D., Pitelka, L. Terrestrial Ecosystems in a Changing World. Springer, Berlin, 115-124.

Vilà, M., D'Antonio, C.M. 1998. *Fitness of invasive **Carpobrotus** (Aizoaceae) hybrids in coastal California.* Ecoscience, 5, 191-199.

Virtanen, R., Edwards, G.R., Crawley, M.J. 2002. *Red deer management and vegetation on the Isle of Rum.* Journal of Applied Ecology, 39, 572-583.

Vitousek, P.M. 1990. *Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies.* Oikos, 57, 7-13.

Vittoz, P., Guisan, A. 2007. *How reliable is the monitoring of permanent vegetation plots? A test with multiple observers.* Journal of Vegetation Science, 18 (3), 413-422.

Walker, D.I. 1991. *The effect of sea temperature on seagrasses and algae on the Western Australian coastline.* Journal of the Royal Society, 74, 71-77.

Wallis, F.P., James, I.L. 1972. *Introduced animal effects and erosion phenomena in the Northern Urewera forests.* New Zealand Journal of Forestry, 17, 21-36.

Wang, D.H., Tang, S.C., Liu, C.K. 2008. *Four-year monitoring of thinning effects on the microclimate and ground vegetation in a Taiwania plantation in the Liukuei Experimental Forest, Taiwan.* Taiwan Journal of Forest Science, 23 (2), 191-198.

Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I., Ghani, A. 2001. *Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences.* Ecological Monographs, 71(4), 587–614.

Wardle, J. 1974. *Influence of introduced mammals on the forest and shrublands of the Grey River headwaters.* New Zealand Journal of Forestry Science, 4, 459-486.

Wardle, J.A. 1984. *The New Zealand beeches; ecology, utilisation and management.* New Zealand Forest Service, Caxton Press, Christchurch.

Wardle, J., Hayward, J., Herbert, J. 1973. *Influence of ungulates on the forests and scrublands of South Westland.* New Zealand Journal of Forestry Science, 3, 3-36.

Wardle, P. 2001. *Distribution of native forest in the upper Clutha district, Otago, New Zealand.* NZJ Botany, 39, 435-446.

Watson, R.T., Zinyowera, M.C., Moss, R.H. 1996. *Climate change 1995 - Impacts, adaptations, and mitigation of climate change: Scientific-technical analysis.* Contribution of working group II to the second assessment report of the intergovernmental panel on climate change. Cambridge University Press, NY.

Webb, C.J., Simpson, M.J.A. 2001. *Seeds of New Zealand: gymnosperms and dicotyledons.* Manuka press, Christchurch, New Zealand.

Webb, C.J., Sykes, W.R., Garnock Jones, P.J. 1988. *Flora of New Zealand. Vol. IV.* Christchurch, Botany Division, DSIR.

Weber, E. 1998. *The dynamics of plant invasions: a case study of three exotic goldenrod species (Solidago L.) in Europe.* Journal of Biogeography, 25, 147-154.

Webster, C.R., Jenkins, M.A., Rock, J.H. 2005. *Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA.* Biological Conservation, 125, 297–307.

Webster, C.R., Rock, J.H., Froese, R.E., Jenkins, M.A. 2008. *Drought–herbivory interaction disrupts competitive displacement of native plants by Microstegium vimineum, 10-year results.* Oecologia, 157 (3), 497-508.

Weltzin, J.F., McPherson, G.R. 2003. *Changing precipitation regimes and terrestrial systems.* University of Arizona Press, Tuscon, Arizona, USA.

White, P.S., Pickett, S.T.A. 1985. *Natural disturbance and patch dynamics: an introduction.* In Pickett S.T.A., White, P.S. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, 3-13.

Whitehead, K.C. 1993. *The Whitehead encyclopedia of deer.* Shrewsbury, Swan Hill Press.

With, K.A. 2001. *The landscape ecology of invasive spread.* Conservation Biology, 16 (5), 1192-1203.

Wood, B. 2000. *Room for nature? Conservation management of the Isle of Rum, UK, and prospects for large protected areas in Europe.* Biological Conservation, 94, 93-105.

Wright, E.F., Coates, K.D., Bartemucci, P. 1998. *Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position.* Canadian Journal of Forest Research, 28, 1352-1364.

www.doc.govt.nz/upload/documents/science-and-technical/Sfc200b.pdf.

Zang, R.G., Ding, Y., Zhang, W.Y. 2008. *Seed dynamics in relation to gaps in a tropical montane rainforest of Hainan Island, South China: (II) Seed Bank.* Journal of Integrative Plant Biology, 50 (5), 513-521.

Zang, R.G., Zhang, W.Y., Ding, Y. 2007. *Seed dynamics in relation to gaps in a tropical montane rain forest of Hainan Island, South China: (I) Seed rain.* Journal of Integrative Plant Biology, 49, 1565-1572.

Zarnowiecki, G. 1994. *The estimation of air humidity relations in the forest communities.* Przeglad Geofizyczny. 39 (2), 179-184**.**

Zavaleta, E.S., Shaw, M.R., Chiariello, N.R., Thomas, B.D., Cleland, E.E., Field, C.B., Mooney, H.A. 2003. *Responses of a California annual grassland community to three years of experimental climate change, elevated CO2, and N deposition.* Ecological Monographs, 73, 585-604.

Zimmerman, R.C., Smith, R.D., Alberte, R.S. 1989. *Thermal acclimation and whole-plant carbon balance in **Zostera marina** L. (eelgrass).* Journal of Experimental Marine Biology and Ecology, 130, 93-109.

Appendix 1 – raw data from the vegetation surveys for 2008 and 2009

catchment	plot	treatment	fence	gap	cover 08	cover 09	crecap	trirep	carnut	echvul	cerglo	taroff	browil	agrcap	hollan
huxley	hu96	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu109	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu131	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu60	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu104	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu94	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu123	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu70	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu36	gap	control	gap	2	2	0	0	1	0	0	0	0	0	0
huxley	hu9	gap	control	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu16	gap	control	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu25	gap	control	gap	5	5	1	1	0	1	0	0	0	1	1
huxley	hu52	gapfence	fence	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu18	gapfence	fence	gap	1	1	0	0	0	0	0	0	0	0	1
huxley	hu42	gapfence	fence	gap	29	48	11	1	2,6	3	1	0,10	0,5	1	3
huxley	hu37	gapfence	fence	gap	28	35	2	1	0	3	0	0,4	0	1	0
hopkins	ho238	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho190	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho244	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho189	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho249	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho186	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho165	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho188	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho9	gap	control	gap	17	17	1	0	1	5	0	0	0	0	7
hopkins	ho22	gap	control	gap	18	18	0	10	6	0	0	0	0	0	0
hopkins	ho161	gap	control	gap	15	15	0	0	0	0	5	0	0	0	1
hopkins	ho107	gap	control	gap	15	15	0	0	0	0	1	0	0	2	0
hopkins	ho57	gapfence	fence	gap	30	30	0	0	0	0	0	0	0	10	0
hopkins	ho124	gapfence	fence	gap	37	37	1	0	1	0	10	0	0	0	1
hopkins	ho110	gapfence	fence	gap	35	35	1	1	7	7	1	0	0	0	0
hopkins	ho151	gapfence	fence	gap	34	34	0	0	2	0	0	0	0	2	5

catchment	plot	treatment	fence	gap	senjac	horspp	aloaeq	urtdio	hydame	epibra	danpil	solnig	pselut	lagspp	agrgig
huxley	hu96	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu109	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu131	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu60	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu104	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu94	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu123	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu70	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
huxley	hu36	gap	control	gap	1	0	0	0	0	0	0	0	0	0	0
huxley	hu9	gap	control	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu16	gap	control	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu25	gap	control	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu52	gapfence	fence	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu18	gapfence	fence	gap	0	0	0	0	0	0	0	0	0	0	0
huxley	hu42	gapfence	fence	gap	1	1	4	1	0	0	0	0	0	0	0
huxley	hu37	gapfence	fence	gap	0	0	0	1	0	9	3	2,4	1	5	1
hopkins	ho238	control	control	closed	0	0	0	0	0	0	0	0	0	0	0,1
hopkins	ho190	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho244	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho189	control	control	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho249	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho186	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho165	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho188	fence	fence	closed	0	0	0	0	0	0	0	0	0	0	0
hopkins	ho9	gap	control	gap	0	0	0	0	1	1	0	0	0	0	1
hopkins	ho22	gap	control	gap	0	0	0	1	0	0	1	0	0	0	0
hopkins	ho161	gap	control	gap	1	1	5	0	0	2	0	0	0	0	0
hopkins	ho107	gap	control	gap	0	0	5	0	0	0	0	0	0	0	7
hopkins	ho57	gapfence	fence	gap	0	0	0	0	0	0	10	0	0	0	10
hopkins	ho124	gapfence	fence	gap	0	10	0	0	1	0	0	0	1	0	12
hopkins	ho110	gapfence	fence	gap	2	0	4	0	0	0	0	0	0	2	10
hopkins	ho151	gapfence	fence	gap	0	1	0	7	10	6	0	1	0	0	0