ENVIRONMENTAL FACTORS INFLUENCING THE DOUGLAS FIR INVASION OF *NOTHOFAGUS* FOREST

A thesis submitted in partial fulfilment
of the requirements for the Degree
of Master of Science in Environmental Science

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Abstract

Douglas fir (*Pseudotsuga menziesii*) was introduced to New Zealand in 1859 for timber, and in the last few decades has been recognised as an invasive species, particularly into grassland. However, its potential to invade native forests is still poorly understood. I investigated the invasion of Douglas fir into mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest, particularly the factors limiting the spread, at Cora Lynn, near Arthur's Pass. Adjacent to the beech forest is an 80 ha Douglas fir and Corsican pine (*Pinus nigra*) plantation, whose invasive potential started to raise concerns in the late 1980s. The study was divided into three parts. The first consisted of resampling plots established on the site in 1989 to count Douglas fir seedlings spreading into *Nothofagus*. In the second part, I investigated the factors limiting the establishment of Douglas fir seedlings in the beech forest. To do this I established 400 points in the native forest, and at each point I assessed the light environment (via hemispherical photography), measured altitude, and distance to the nearest seedling. Lastly, I conducted a root competition and fertiliser-addition experiment to investigate the factors limiting the growth of the Douglas fir seedlings. I selected 544 naturally regenerating seedlings (30 to 70 cm tall) in the beech forest, and applied one of four treatments: fertiliser addition, root trenching, fertiliser addition plus root trenching, and control. Light environment and altitude at each seedling were measured.

The mean density of seedlings in the plots has increased 13-fold since the first measurement in 1989, from 11,267 seedlings/ha to 150,333 seedlings/ha in 2016. There is a widespread Douglas fir invasion of the mountain beech forest in progress – in only a single point out of 400 did I fail to find a seedling within a 10-m radius. Altitude had the strongest effect on the distance to the nearest seedling, with lower seedling density at higher altitudes. Although distance to the nearest seedling decreased with light, the seedlings were not restricted to light-wells or canopy gaps as generally presumed, but present throughout the native forest. Light had the strongest effect on seedling growth. At the experimental seedlings, light ranged from 3.01 to 10.29 mol m^{-2} d^{-1}, that is 8.12% and 27.8% respectively of full sunlight. Altitude had a negative effect on seedling growth. Nutrient availability was second to light as a growth limiting factor. Fertiliser addition had the largest effect on seedling growth across treatments, increasing it 18.3% above that of the control. Root trenching had a small negative effect on growth, while fertilizer plus trenching had a positive effect, but still smaller than expected.

I have demonstrated that Douglas fir is well able to invade *Nothofagus* forest, albeit slowly, and that the spread was affected by a complex relationship between light, nutrients, root competition, distance to the seed source, and altitude. In New Zealand, poor control of conifer invasions into grasslands and shrublands in the past has led to large environmental and economic impacts. The potential negative effects of the Douglas fir spread into native forest could be minimized by early control. I hope that my work will contribute to a better understanding of the Douglas fir's invasive potential, as well as draw attention to the need for managing the spread in progress.

CHAPTER 1
GENERAL INTRODUCTION

1.1 Biological invasions

The dispersal of organisms is a natural and important process of life on the planet. It is one of the drivers of evolution, and helps shape the distribution of plants and animals on Earth. There are many natural barriers for dispersal, like climate, habitat needs or geography. In the past, these barriers have also limited our species' ability to populate new territories. However, humans have gradually found ways to overcome most of these challenges such that, today, we inhabit all kinds of environments on land, from the frozen poles to the equator. One strategy that allowed our species to be successful at dispersing was taking along plants and animals to the new environment as resources. Therefore, many species were shuffled between habitats, continents and hemispheres following human migration. In recent years, both intended and unintended transport of organisms have escalated with international trading and globalization, leading to an increasing homogenization of the world's biota (Lodge 1993, Vitousek et al. 1997, McKinney and Lockwood 1999). Over time, the extent of the biota exchange has become impressive. In the Cook Islands, Hawaii, and New Zealand, non-native species represent more than 45% of the total number of species; in Bermuda, there are almost twice as many exotic species as there are native species (Vitousek et al. 1996). Although the percentage is greater on islands, the absolute number of invasive species on the continents is remarkable: 50,000 non-native species have been introduced into the United States alone (Pimentel et al. 2005). More than 120,000 species of microbes, plants and animals have been introduced to Australia, Brazil, India, South Africa, the United Kingdom, and the United States, causing US$336 billion per year in economic damages (Pimentel et al. 2001).

Species are broadly classified in regard to their distribution as *native* (also called indigenous, autochthonous) or *exotic* (nonindigenous, alien, allochthonous). A native species is recognised as such when it occurs in a given region or territory as a result of its own dispersal mechanisms. Conversely, a species is considered exotic when it has arrived in a new territory, aided by humans. But there are more complex cases; many plants may have been spread by humans before historic times, making it difficult to determine their original range. These are labelled *archeophytes* (Petit et al. 2004).

There are slightly different definitions to what biological invasion is, and some disagreement towards characterizing the phenomenon (Valéry et al. 2008). Two main criteria currently used to define biological invasion are the geographic (or biogeographic) criterion and the impact criterion. The geographic criterion suggests that a species must overcome a major geographical barrier, or traverse large distances to be termed "invasive" (Richardson et al. 2000b, Richardson and Pyšek 2004). But adopting this criterion implies that a native species would not be considered invasive even if, for instance, it began to dominate the community in its original range. Native species can, however, be invasive outside their original range in the country, as karaka (*Corynocarpus laevigatus*) in New Zealand, native to north of the North Island, and invasive in the south of the North Island. Davis and Thompson (2000) suggest that short dispersal distances are enough to consider a species invasive, although they note that declaring the dispersal distance short or long largely depends on both system and invading species. The impact criterion concerns the effects on the environment following the invasion. Davis and Thompson consider that significant community, ecological and/or economic impact must be identified in the new ecosystem to classify the introduced species as invasive. Conversely, other studies dispute the idea that the characterization of invasion must be associated to either positive or negative impacts (Rejmánek et al. 2002), mainly because identifying a "significant impact" is somewhat subjective and leaves room for interpretation (Daehler 2001). Richardson et al. (2000b) have a different view than the impact criterion, and suggest that it may be more useful to look at the reproductive and spread potential of the species. Both geographic and impact criteria have limitations to characterizing invasive species, but are the best approach available as they deal with the key aspects of biological invasion. In this study I am going to use the definition proposed by Davis and Thompson.

Invaders can have deep impacts on the recipient ecosystems, such as altering primary productivity, decomposition, hydrology, geomorphology, nutrient cycling or natural disturbance regimes (Vitousek et al. 1996). One good example is the introduction of the zebra mussel (*Dreissena* spp.) to North America in the 1980s via ballast water of ships. The species rapidly spread in the new environment, establishing in rivers and lakes. Consequences of the zebra mussel population boom in the affected regions was a decline in native algae population and biological productivity, with subsequent eutrophication in entire ecosystems (Vitousek et al. 1996). Invasive species can reduce local biodiversity directly by competing for resources with natives, by predation, by acting as disease vectors, or by altering abiotic conditions which then lead to diversity decline, such as the introduction of the European cheatgrass (*Bromus tectorum*) in the steppes of North America. More than 410,000 km^2 of native sagebrush (*Artemisia* spp.) steppe have been dominated by the annual cheatgrass (Mack 1981). The introduced species increased the availability of fine fuel and the frequency of fires from every 60 to 110 years to less than 5 years, leading to a decrease in species richness (Whisenant 1990).

Biological invasions are normally considered one of the main causes of extinction (Vitousek et al. 1996, Mooney and Cleland 2001). One of the most iconic cases of extinction following the introduction of predators is the island of Guam. The wildlife in the small island of Guam in Micronesia was decimated after the brown tree snake (*Boiga irregularis*) was accidentally introduced (Rodda et al. 1997). The population of snakes reached the density of 100 individuals/ha (Rodda et al. 1992), extinguishing nearly all bird, reptile and mammal species of the island. Similarly, approximately 200 native fish species in Lake Victoria, East Africa, went extinct or became endangered following the introduction of the Nile Perch, with subsequent negative effects on the food web and primary productivity of the ecosystem (Witte et al. 1991).

There is evidence, however, that in many cases invasive species in aquatic systems are not detrimental to the recipient ecosystem (Moyle and Light 1996). Gurevitch and Padilla (2004) go as far as saying that, although the impacts of biological invasions are clear, there is still not enough evidence to characterize invasive species as a major cause of extinction. According to their rationale, only 6% of the threatened taxa in the IUCN Red List are threatened by exotic species, and less than 2% of extinctions were due to biological invasion. Furthermore, most species classified as threatened by aliens are also threatened by some direct human action, meaning it is difficult to separate the effect of invasive species on the community from other environmental pressures. For instance, they argue that in some cases, the disappearance of native species is primarily linked to other human-sourced impacts, such as deforestation, and that the biological invasion is in fact the result of this primary impact. In other words, both the decline of native species and establishment of alien species would be consequences of the habitat alteration. A quick response came from Clavero et al. (2005), who counterargued that the way Gurevitch and Padilla filtered the information from the IUCN database resulted in misleading conclusions. Clavero and others noted that only 5.1% of extinct species in the IUCN classification system include the cause of extinction; for example, none of the 129 extinct birds have been assigned an extinction cause, even though many of these cases are well known to be the consequence of biological invasions. So Gurevitch and Padilla's arguments do not seem particularly helpful, once they appear to misrepresent the causes of extinction.

New Zealand was subject to one of the most recent events of colonization, with the European settlement in the early 19th century. This was the entry way for thousands of exotic plant and animal species, brought to the country to replicate the resources that the settlers were familiar with (McDowall 1994). Although around 25,000 plant species have been introduced to New Zealand (Williams et al. 2002), it was the introduction of relatively fewer animal species that caused the greatest impact on wildlife. Invasions of animals include 34 species of land mammals, 33 species of land birds, three species of reptiles and amphibians, 20 species of freshwater fish, and approximately 1,500 insect species (Atkinson 2001). Mammal predators, in particular, arrived to a new ecosystem where the native animals were vulnerable prey due to the absence of mammalian predator pressure during their evolution (Lee et al. 2006).

1.2 Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco)

Douglas fir (Pinaceae) is a conifer of great ecological and economic importance. Native to Western North America, it is one of the largest tree species in the world, reaching 100 m tall, 4–5 m in diameter at breast height, and living for 800–1000 years (Farjon 2010). Conifers play a critical role in the ecosystem. They provide habitat through the complex spatial structure of the forest, and biomass from the young foliage and decaying wood for numerous organisms in the food web (Farjon 2008). This makes Douglas fir an important species, as it forms large pure stands and dominates vast areas of its natural range (Low 1994, Eckenwalder 2009). Two varieties are recognised for the species: *Pseudotsuga menziesii* var. *menziesii* and *Pseudotsuga menziesii* var. *glauca*. The main difference is their distribution and size. The first, taller variety occurs along the coast in the Pacific Northwest from near sea level to 1,000 m altitude. The second and smaller variety, *glauca,* grows further inland in the Rocky Mountains, ranging from British Columbia to Central Mexico at altitudes as great as 3,350 m (Farjon 2010).

Considered as the most economically important tree species in North America (Farjon 2008, 2010), and even in the world (Eckenwalder 2009), Douglas fir grows relatively fast, tall, and produces large volumes of quality wood per hectare. This resulted in the species being introduced in many temperate regions, especially in the southern hemisphere, as a significant component of the forestry sector.

Douglas fir was introduced to New Zealand in 1859. Large-scale plantings started as early as 1896, and research on productivity began in the 1950s (Low 1994). It is an important species for the forestry sector in New Zealand, representing 6% (105,000 ha) of total plantation area, and being second to Radiata pine (Ministry for Primary Industries 2015). But not all trials had good results early on; several nurseries and plantations on the South Island produced seedlings with symptoms of chlorosis, which decreases growth and the survival rate of the plants (Gilmour 1958). Gilmour attributed such deficiency to inadequate mycorrhizal development on the seedlings. The later introduction of mycorrhizae to New Zealand (Richardson et al. 2000a, Vellinga et al. 2009) meant that this constraint was removed, but also enabled Douglas fir to become potentially invasive.

The attributes that make it a good forestry tree also make it potentially invasive in new territories (Farjon 2008). Some life-history traits for which conifers are used in monocultures, such as fast growth rate, small seed mass, short juvenile stage, and short intervals between large seed crops, give them a competitive edge in the environment (Richardson et al. 1994, Rejmánek and Richardson 1996). The introduced tree species that have gradually spread outside the plantations by their own dispersal mechanisms are referred to as “wildings” (Ledgard 2004).

In the northern hemisphere, Douglas fir naturally regenerates in large areas and in several stand types in the Black Forest, Germany, where it was introduced. Its seedlings were found successfully establishing and competing with common native species such as silver fir (*Abies alba*), European beech (*Fagus sylvatica*), and Norway spruce (*Picea abies*) (Schmid et al. 2014). Douglas fir occurs in 27 of 160 forest reserves in Bavaria; however, spread into closed forests is unusual (Schmid et al. 2014). In Argentinian Patagonia, Douglas fir invades steppe areas and woodlands dominated by a native conifer canopy species *Austrocedrus chilensis* (Cupressaceae) (Sarasola et al. 2006). Sarasola and others drew attention to a potential large-scale invasion in the short term. Peña et al. (2007) highlighted the invasive potential of Douglas fir, given its absence of natural diseases, its capacity to tolerate shade, and its wide economic use. Douglas fir was found to be capable of developing under native *Nothofagus* forest with canopy cover below 65% in the Malalcahuello National Reserve. Some impacts of exotic conifers, either in plantations or as wildings, on biodiversity in South America include: decrease in species richness of understorey vascular plants, arthropods, and birds; loss of rare and specialist species; displacement of endemic species; and increase in exotic plant species (Simberloff et al. 2010).

In Europe, Douglas fir is the introduced conifer that has naturalised in most countries – 12 out of 54 – (Carrillo et al. 2010). The ecological consequences of its cultivation, and its uncontrolled spread, are still a matter of debate. Schmid et al. (2014) argued that although negative effects for plants, arthropods, and birds have been registered, such consequences appear to be minimal, and sometimes even mutualistic relationships can be created. According to them, Douglas fir does not interact with the environment very differently from native tree species, and the plant and arthropod communities associated with Douglas fir are similar to those associated with Norway spruce.

1.3 Assessing the light environment beneath the canopy

Solar energy is one of the most important components of plant growth and survival. In forest ecosystems, most of this energy is captured by the canopy species. A smaller fraction of sunlight penetrates the canopy and reaches the layers of vegetation beneath it. The light environment in the understorey varies in time and space, as the canopy structure, the geographic position, and the time of the year all influence the amount of light reaching the plants at the forest floor. Therefore, accurately assessing the light penetration in the understorey is crucial to understanding invasions of forests by introduced trees.

There are several established methods to assess light penetration in the understorey. They range from simple instruments such as light-sensitive paper (Friend 1961), and densiometer (Strickler 1959), to high-end technology such as quantum sensors, and LIDAR (light detection and ranging) (Riaño et al. 2004, Morsdorf et al. 2006, Jensen et al. 2008). To determine the most suitable methodology, I considered the goals of the study, the level of precision and accuracy desired, the spatial and temporal scale of the data collection, and the resources available.

Photosensitive papers are a direct measure of light irradiance, but they provide relatively low-precision data. They consist of light-sensitive chemicals embedded in paper sheets which bleach when exposed to light. The irradiance can be quantified by the number of bleached sheets (Lieffers *et al.* 1999). The densiometer is an easy-to-use instrument, portable and non-electronic. It has a curved mirrored surface carrying 96 dots. Essentially, recording the number of dots covered by the image of the canopy renders a percentage cover. However, it lacks the precision desired for this project. Quantum sensors can provide direct instantaneous measurements of light penetration or structural data such as canopy openness – the area of the sky hemisphere that is not obstructed by vegetation (Frazer et al. 1997) – or leaf area index (LAI) – one half of the total green leaf area per unit ground surface area (Chen et al. 1997). They can operate in the waveband used by plants for photosynthesis (400 to 600 nm), and are regarded as the most accurate technique in short time-scale sampling (Pearcy 1989). Although a very precise method, the use of quantum sensors also has complications. Light conditions vary significantly over time, such that two measurements taken at different locations beneath the canopy, even a few minutes apart, cannot be properly compared without a reference measurement out in the open, under direct sunlight. The LIDAR technology uses pulses from an airborne laser that hit the ground and reflect back to the sensor (Reutebuch et al. 2005). LAI can be estimated from the resulting signal.

1.3.1 Hemispherical photography

Another approach for assessing light is using hemispherical photography. Hemispherical photography is a technique that essentially involves photographs taken with a fisheye (very wide-angle) lens – generally around 180°, so imaging a hemisphere – to characterize plant canopies and calculate light penetration (Anderson 1964). Photographs can be taken facing upwards from beneath the canopy (Figure 1.1), or downwards from above the canopy, although the latter is used more for crops. Some of the earliest uses of hemispherical photographs were for nonecological studies: in a lengthy book, Wood (1911) used it to investigate the physical nature of light; Hill (1924) applied it to meteorological studies. Evans and Coombe (1959), and Anderson (1964) were pioneers in applying hemispherical photography to study the light environment beneath forest canopies. Today, this technique is widely used in ecology (Rich 1990, Rich et al. 1993, Whitmore et al. 1993, Chianucci and Cutini 2012, Sawada et al. 2016). Based on the criteria that I established to select the best method, I decided to use hemispherical photography.

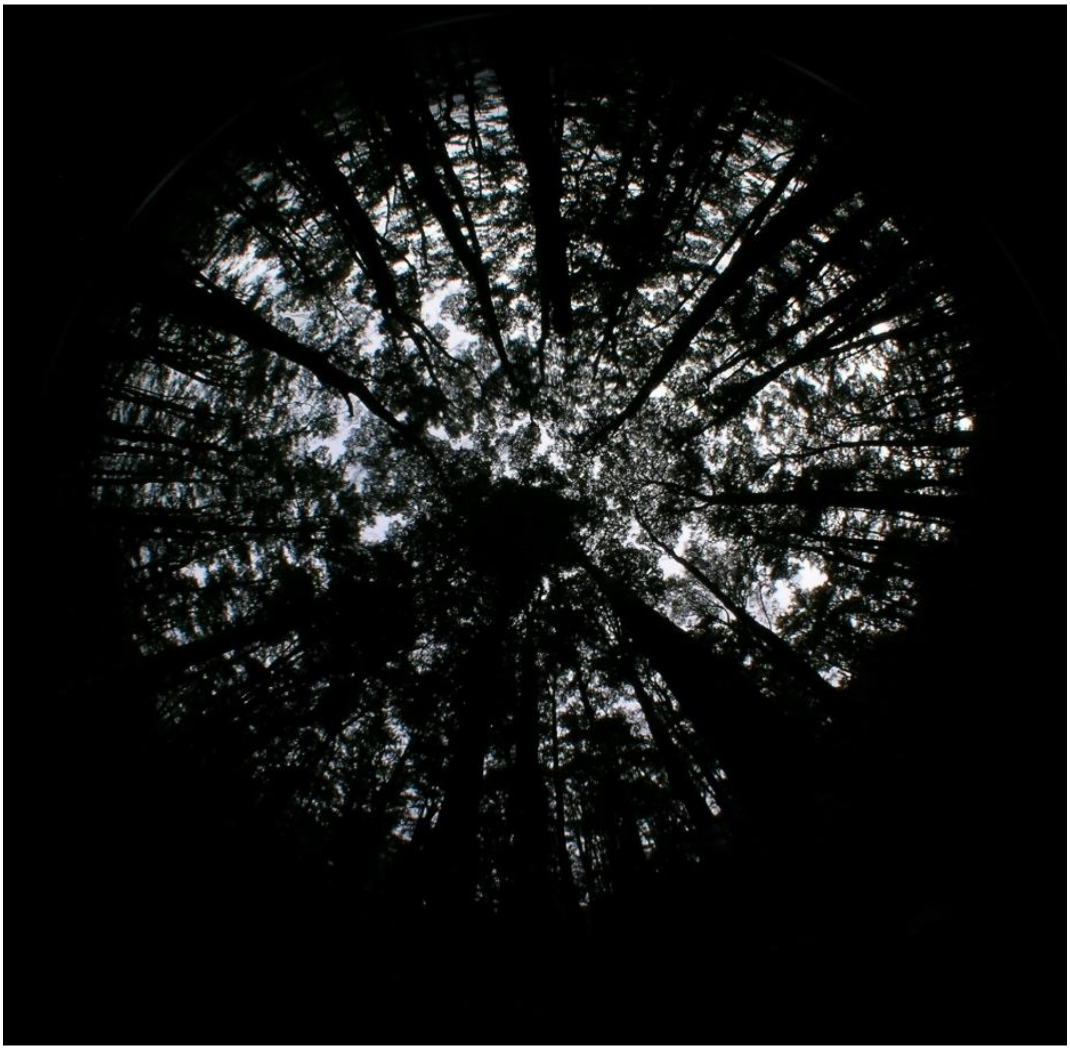

Figure 1.1 Example of a hemispherical photograph used to determine canopy geometry and solar regimes. Photo taken looking upwards beneath the *Nothofagus* canopy using a fisheye lens (Nikon Fisheye lens FC-E9 attached to a digital camera Nikon Coolpix E5400) on Burnt Face.

1.3.1.1 Canopy openness versus light penetration

There are different parameters through which forest canopies and the light environment below it can be analysed when using hemispherical photography. Some of them are structural, for example, canopy openness or leaf area index, while others relate to the light environment, such as photosynthetically-active radiation (PAR), which can be expressed in photon or energy terms (Alados et al. 1996). Structural and solar parameters can provide different answers; thus, knowing what to use is key to correctly address the questions. For instance, in the southern hemisphere, a gap in the canopy north of the sampling point would allow more light to reach the forest floor than a gap south of the point. This is due to the relative movement of the sun in the sky throughout the year. Two hypothetical sites, both with 20% canopy openness, can have different amounts of incident light at ground level, depending on the structure of the canopy above. Therefore, using solar parameters is a better way to estimate how much light reaches a given point in the understorey.

1.3.1.2 Resolution and exposure

The region of canopy represented near 0° zenith is much closer to the camera than that near 90° zenith, which causes the gaps around the edge of the image to have less definition than at the centre. Thus, high image resolution is important to minimize such effects and to avoid mixed pixels and consequently misclassification during thresholding (Jonckheere et al. 2004). The right exposure is also important to classify the images. Under- or overexposure can contribute to overrepresentation of large gaps, and underrepresentation of small openings (Rich 1990). Macfarlane et al. (2014) suggested taking photos using one stop of underexposure below the reference reading from the light meter under the canopy, while Chen et al. (1991) found best results using either 4–5 stops below the reading from under the canopy or 1–2 stops above the reference exposure outside the stand, under overcast conditions. Zhang et al. (2005) suggests using 1 stop above the reference from outside the stand.

1.3.1.3 Image thresholding

Although every step in the process of hemispherical photography is important to successfully extract data, thresholding is a critical one (Jonckheere et al. 2004, Nobis and Hunziker 2005). This is the step in which the foliage area is distinguished from the sky area during the image analysis. The images are converted from continuous-tone (greyscale) into black (leaf) and white (gap) pixels according to a threshold that must be established either manually or automatically. Manual thresholding can be a source of errors and biases, especially for large sets of images, given it is a rather arbitrary method, and performance varies between observers (Rich 1990, Nobis and Hunziker 2005). Therefore, automatic thresholding is preferred for its consistency, objectivity and reproducibility (Jonckheere et al. 2005, Nobis and Hunziker 2005). Jonckheere et al. (2004) argued that the development of a software program to process a series of images and reduce intervention of the operator was required. This is precisely what ImageJ software (Schneider et al. 2012) does – it uses algorithms to process images in batches free from the observer’s bias. The threshold can be computed as a single value for the whole image or as multiple values for different regions of the image (Landini et al. 2016). Multiple thresholds can be particularly useful when the vegetation is not evenly illuminated on the image, meaning that a single threshold would likely over- or under represent some parts of the canopy.

1.3 Objective of the thesis

The overall objective of the thesis was to investigate the invasion of Douglas fir into mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest in New Zealand, as well as the environmental factors influencing the spread. The specific objectives are presented in each chapter.

1.4 Study site

The study described in all chapters was conducted on Burnt Face (43°06'S 171°31'E), within Craigieburn Forest Park, Canterbury. The park was established in 1967 with the primary function of conservation of water and soil for protection of land and other values, according to the Craigieburn Forest Park Management Plan. At the park's climate station (914 m elevation; 43°09′10″S 171°42′56″E), mean annual temperature is 8°C, and mean annual precipitation is 1,447 mm (McCracken 1980). The predominant soil is Allophanic Brown with underlying greywacke rock (New Zealand Forest Service 1981, Hewitt 2010). Mountain beech dominates the forest structure and ranges from 650 m altitude to 1,370 m in inland Canterbury (Wardle 1984). It is the only canopy species, being also one of the most abundant species in the understorey as saplings or seedlings. (New Zealand Forest Service 1981).

CHAPTER 2
CAN DOUGLAS FIR INVADE MOUNTAIN BEECH FOREST?

2.1 Introduction

Plots to measure Douglas fir seedling density on Burnt Face were established in 1989, and remeasured in 1996 and 2001 by other authors, and by me for this study in 2016. In this chapter I will review data collected on the study site by previous studies, and present my own results from a follow-up on these studies.

Until the 1970s, very little was known about the extent of conifer invasion nationwide, such that the Forest Research Institute did a survey to gather information on the spread of introduced trees into native bush in New Zealand (Chavasse 1979). Questionnaires involving identification of species, habitat and area of invasion were sent to conservators around the country, who would then consult with staff from reserves and national parks on the matter. At the time, introduced conifers had only invaded native forests following some sort of disturbance such as fire, grazing, logging or erosion. No evidence of invasion into beech forest was reported, and Douglas fir was mentioned only once in the survey, invading scrubland in Whakarewarewa State Forest Park.

The single reference to *P. menziesii* in the survey by Chavasse suggests that the species had little invasive potential in the past, which can be partially explained by its need for suitable mycorrhizae (Davis et al. 1996). Gilmour (1958) investigated the causes of chlorosis in Douglas fir plantations in the South Island of New Zealand – a condition in which seedlings appear moribund, yellow-coloured, and with low survival prospects – to find the symptoms were indeed related to lack of mycorrhizal development. Eventually this became less of a barrier, with the introduction of exotic fungi to the country, whether unintentional by importing plant material with contaminated soil, or purposely to inoculate *Pinus* spp. seedlings for forestry (Richardson et al. 2000a, Vellinga et al. 2009). Trappe (1977) estimates that around 2000 species of fungi are potentially associated with *P. menziesii* in its native range. Research has shown that the species can also establish novel associations with the native fungi in New Zealand (Moeller et al. 2015). In addition, introduced mammals like the European red deer (*Cervus elaphus*) and Australian brushtail possum (*Trichosurus vulpecula*) can assist the invasion by acting as fungi dispersers (Wood et al. 2015). Therefore, the opportunities for Douglas fir to establish mycorrhizal partnerships are many.

One characteristic that makes Douglas fir more likely than other conifers to invade forests and woodlands is its shade tolerance (Carter and Klinka 1992, Bond et al. 1999). The spread of Douglas fir into mountain beech forest was first documented in the 1980s. In the Ben Lomond Reserve, Queenstown, Cleary (1982) found Douglas fir seedlings establishing in windthrow gaps in the *Nothofagus* forest, and growing at a faster rate than mountain beech seedlings.

Although a segregation of the genus *Nothofagus* into three genera (*Fuscospora*, *Lophozonia*, and *Trisyngyne*) has been proposed (Heenan and Smissen 2013), the revised nomenclature is not yet widely applied (Hill et al. 2015), therefore, I will use *Nothofagus* in this study.

2.1.1 A brief history of Burnt Face

Burnt Face lies on the north-facing slopes of Mount Bruce, between Bruce Stream and Broad Stream, in Craigieburn. It became known as such after a fire in early 1900s consumed around 90 ha of mountain beech forest. After the fire, part of the exposed soil was then covered with grassland and leased for grazing to Cora Lynn until 1964 when the land was retired due to excessive erosion. There are, however, records of sheep grazing in Burnt Face until the 1980s (McKelvey 1995).

Years before, in 1947, the New Zealand Forest Service had started small-scale revegetation trials in Craigieburn using exotic conifers and a few native species (McKelvey 1995). The results of these trials were to guide which species to use in the large-scale plantings in the following decades. Douglas fir was selected for its fast growth results in the early trials, in addition to being considered noninvasive. Between 1965 and 1971, 80 ha of Douglas fir and Corsican pine (*Pinus nigra*) were planted on the north-west slopes of Burnt Face from 780 m up to 1370 m altitude. By 1986 the reforestation on Burnt Face had successfully stopped the erosion and produced a 39-year-old forest, averaging 25 m in height and 44 cm in diameter (McKelvey 1995).

The efforts to halt soil erosion via forestry development, however, created novel environmental problems at Burnt Face.

The mature 80 ha plantation represented a major source of Douglas fir seeds to the adjacent *Nothofagus* forest. Dispersal by wind is an advantage to tree species that are taller than the surrounding habitat (Willson and Traveset 2000), such as Douglas fir in Craigieburn. The prevailing north-west wind and the characteristics of the topography facilitate the dispersal of seeds far over the native forest. In late 1980s, the Forest Research Institute (FRI) was commissioned by the Department of Conservation (DOC) to investigate the extent of Douglas fir spread into the neighbouring mountain beech forest on Burnt Face.

2.1.2 Establishment of old plots

Ledgard (1989) performed a survey on Burnt Face in October 1989 to investigate the spread of Douglas fir into native mountain beech forest. The survey consisted of three permanently marked 100 m^2 plots (50 m x 2m) established beneath the beech canopy, starting at the margin of the Douglas fir plantings (Figure 2.1). According to the report, Plot 1 was at 700 m altitude, Plot 2 at 780 m, and Plot 3 at 900 m. However, the altitudes measured more accurately with a GPS in 2016 were 752 m, 814 m, and 939 m. The plots were divided into 10 subplots (5 m x 2 m) within which all Douglas fir seedlings were counted, aged by counting the number of segments on the main stem (see Section 4.2.3 for Douglas fir's development characteristics), and had their heights measured. The geographic coordinates of the western ends of the plots, from 1 to 3, are 43°02′13″S 171°38′03″E, 43°02′19″S 171°38′05″E, and 43°02′33″S 171°38′14″E.

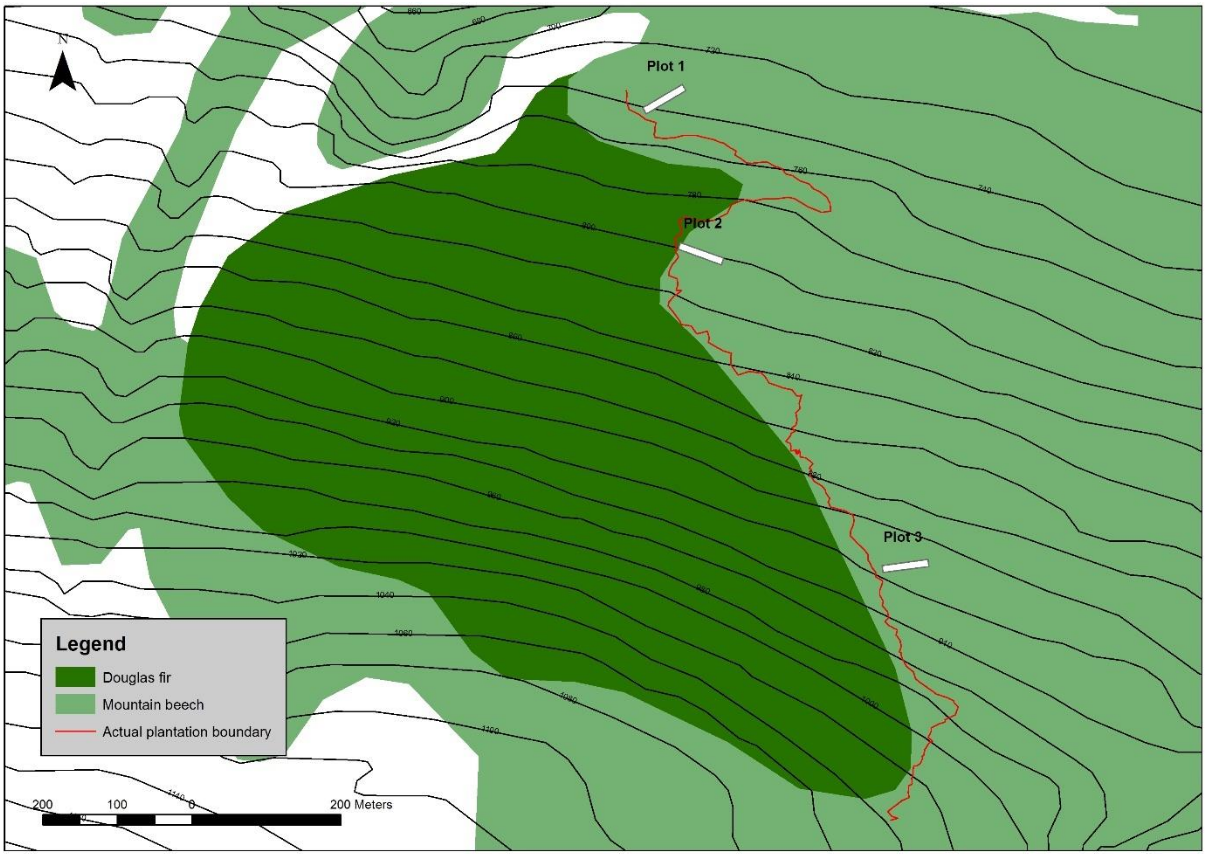

Figure 2.1 Map of the study site showing a representation of the three plots established by Ledgard (1989) beneath the *Nothofagus* canopy on Burnt Face, Craigieburn. Plots were 100 m^2 (50 m x 2m). Actual plantation (Douglas fir) boundary was tracked via manual GPS (see Section 3.2.4 for details).

Ledgard found a mean density of 11,267 seedlings/ha (Table 2.1). More than 80% of the seedlings were aged between 1 and 3 years, with the oldest being 6 to7 years old. Most of the seedlings were less than 5 cm tall; the tallest were 40 cm. In the Craigieburn Range, Douglas fir is expected to start reproducing from year 10 to year 12. Thus, by 1989, the oldest lots of the plantation had been producing seeds for 12 to 14 years. The investigation revealed an early stage of invasion of the native forest, and a trend of decreasing density with increasing distance from the seed source (Figure 2.2). Although there was a large decrease in number of seedlings between Plots 1 (low) and 3 (high altitude), the effect of altitude was not clear because the highest counts were recorded at Plot 2. Ledgard (1989) concluded that Douglas fir was able to spread into established mountain beech forest on Burnt Face; however, Corsican pine – also planted in the area – represented virtually no threat of invasion.

The three plots were remeasured in 1996 by Nick Ledgard. The mean seedling density had increased approximately 5-fold to 60,833 seedlings/ha during the 7-year period. In this second survey, a trend of decreasing seedling density with altitude became clearer, as the seedling counts decreased continuously from the lowest to the top plot (Table 2.1). The negative effect of distance to the plantation on seedling density was again identified (effects are shown in the Section 2.3).

In 2001, the plots were measured for the third time by Dickson (2001). The overall trend was still consistent: a mean density increase in seedlings/ha. Plot 2, however, had an increase of only 11 seedlings over 5 years, while Plots 1 and 3 together added 1,128 seedlings. It is possible that changes in the canopy, such as gaps created by tree fall, might have overexposed parts of Plot 2 to sunlight, the excessive heat consequently killing the seedlings (Helgerson 1989). Although there were fewer seedlings in the upper plot than at Plot 1, the gradual density decrease with altitude was no longer a clear trend.

Table 2.1 Douglas fir seedling counts per plot by Ledgard (1989, 1996) and Dickson (2001) on Burnt Face. Plots were 100 m^2, starting at the edge of Douglas fir plantings towards the *Nothofagus* forest. Seedling density per hectare is the mean of all three transects for each year.

	1989	**1996**	**2001**
Plot 1	109	840	1516
Plot 2	196	569	580
Plot 3	33	416	868
Density (seedlings / ha)	**11,267**	**60,833**	**98,800**

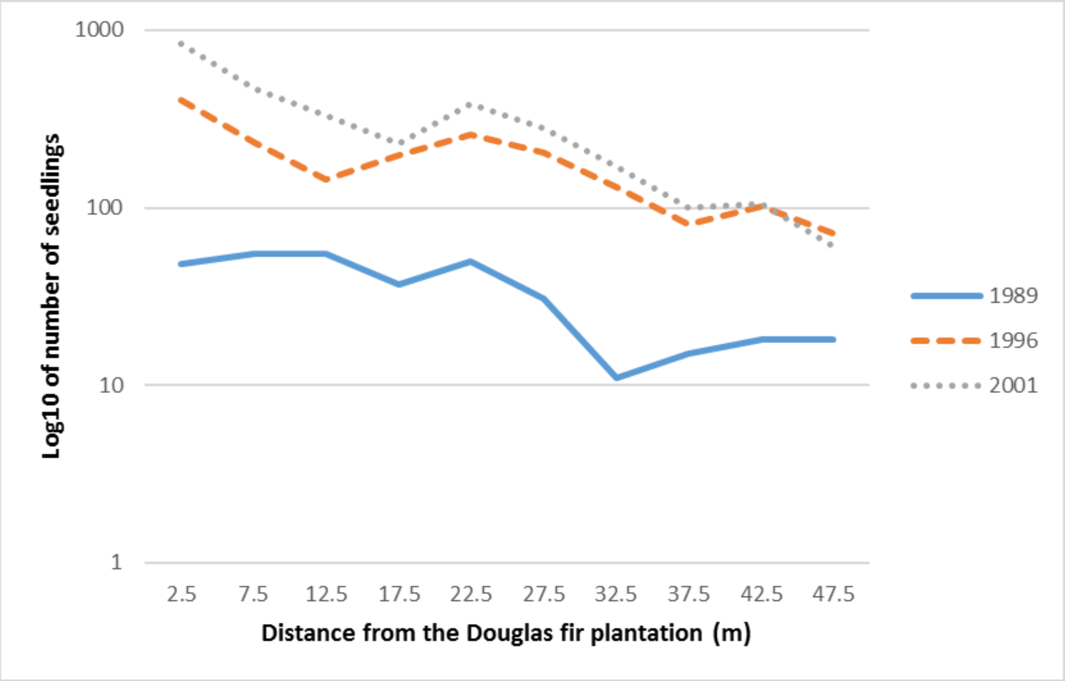

Figure 2.2 Log$_{10}$ of seedling density plotted against distance to the seed source. Distances are from the midpoint of each subplot to the edge of the Douglas fir plantings. Measurements made in 1989, 1996 and 2001.

2.1.3 Objectives

The objectives of this part of the study were to measure the Douglas fir seedling density in the plots 27 years after their establishment, and document growth rates over time, including the effects of altitude and distance from the Douglas fir plantation.

2.2 Methods

2.2.1 Remeasuring the old plots

The plots were found with the help of Nick Ledgard. I remeasured the density of Douglas fir seedlings in the plots established by Ledgard (1989) using the same methods as in the original study, with the difference being that I did not age the seedlings or measure their height. I chose not to do so because it would be time-consuming, and our main goal could be achieved without it.

2.2.2 Data analysis

The data from 1989 and 1996 was derived from the original field notes provided by Nick Ledgard. I used the figures present in his field notes rather than the respective reports due to some discrepancies between them. The data from the 2001 measurement was obtained through Dickson’s unpublished thesis available at the library of the University of Canterbury.

The seedling counts were compiled to calculate total and individual plot density increases, and to estimate density increase per year, and yearly seedling recruitment. Total density increase was calculated as the density ratio between 2016 and 1989. The same calculation was applied for each plot individually. Density increase per year assuming geometric increase was estimated using the ratio of density between two measurements and the number of years between two measurements, for instance:

$$\left(\frac{density_{year\ i}}{density_{year\ 0}}\right)^{\left(\frac{1}{year\ i\ -\ year\ 0}\right)}$$

To estimate the mean seedling recruitment per year in each plot, the yearly increase of the plot was calculated using the same equation as above. Then I multiplied the number of seedlings (actual seedling counts from a given plot and year, e.g., 109 seedlings in Plot 1 in 1989) by the yearly increase to obtain the mean number of new seedlings/year between one measurement and the next.

A generalized linear model (GLM) in RVersion 0.99.903 (R Core Team 2016)   was used to investigate the relationship between seedling counts and distance to the plantation and year using subplots (each 5 x 2 m) as replicates. The value used as “distance to plantation” was the distance from the edge of the forest to the centre of each subplot, according to Ledgard (1996). A generalised linear model with interacting effects was built as follows:

$$glm(seedling\ counts \sim distance * years, family = poisson)$$

I predicted that there would be no interaction between distance and years, but significant and strong effects of both distance and years on seedling counts.

A multipanel scatterplot – via xyplot() in lattice package (Sarkar 2008) – was used to compare the relationship between distance to the plantation and seedling density across years. The slopes of each year were measured with the function coef() to compare the effect size between years. I predicted that there would not be large differences in the effect of distance between years, but the seedling counts were expected to increase from one year of measurement to the next.

2.3 Results

The mean density of seedlings increased over 13-fold, from 11,267 seedlings/ha in 1989 to 150,333 seedlings/ha in 2016; however, not all three plots showed the same trend over time: density increased consistently in Plots 1 and 3, but stabilized in Plot 2 from 1996 to 2001, and decreased from 2001 to 2016 (Figure 2.3). The rate of increase from 1989 to 1996 was 27.2% per year, slowing down to only 2.8% per year from 2001 to 2016. However, the seedling recruitment per year was relatively similar between the first and last measurements.

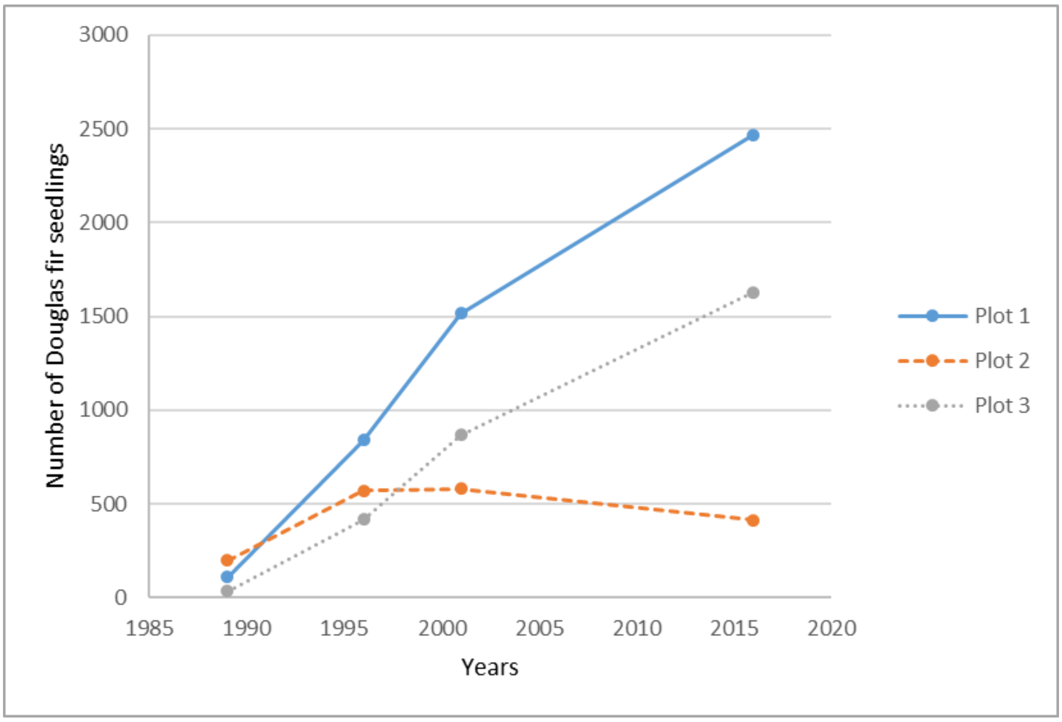

Figure 2.3 Number of Douglas fir seedlings in *Nothofagus* forest in 3 plots from 1989 to 2016 on Burnt Face. Measurements made in 1989, 1996, 2001 and 2016.

Table 2.2 Number of Douglas fir seedlings on each year of measurement on Burnt Face. 'Mean yearly increase' represents the percentage increase per year between one measurement and the next. 'Mean yearly seedling recruitment' is the average number of new seedlings per year between one measurement and the next. Negative values represent decrease in number of seedlings.

Year	No of seedlings	Mean yearly increase	Mean yearly seedling recruitment
		Plot 1	
1989	109	-	-
1996	840	33.87%	74
2001	1516	12.53%	101
2016	2470	3.31%	64
		Plot 2	
1989	196	-	-
1996	569	16.44%	42
2001	580	0.3%	2
2016	413	-9.77%	-11
		Plot 3	
1989	33	-	-
1996	416	43.62%	37
2001	868	15.85%	67
2016	1627	4.28%	51
		Average across all 3 plots	
1989	113	-	-
1996	608	31.31%	51
2001	988	9.56%	57
2016	1503	-0.73%	34

The GLM found that seedling counts decreased with distance to the plantation and increased with time (Table 2.3). The significant interaction between distance and time suggests that the effect of distance has varied between years. Because the interaction is negative, the effect of distance has increased from 1989 to 2016: that is, relatively fewer seedlings became established far from the plantation over time.

Table 2.3 Poisson generalised linear model showing the effects of distance to the plantation, year of measurement, and interaction between both on Douglas fir seedling counts on Burnt Face. Significant effects are in bold.

Coefficients:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	4.350	0.034	128.460	**<0.001**
Distance to plantation	-0.038	0.002	-24.579	**<0.001**
Year of measurement	0.062	0.002	37.223	**<0.001**
Distance:Year	0.000	0.000	-2.523	**0.012**

To understand how the distance effect varied between years, I did an additional GLM (Poisson) using the variable “years” as factors (Table 2.4). The slope of 1996 showed no significant difference from that of 1986. Conversely, the slopes of 2001 and 2016 were significantly steeper than 1989, with 2001 being the year with the strongest effect of distance to the seed source.

Figure 2.4 shows the plot equivalent to the GLM of Table 2.4. The coefficients of the slopes were -0.035, -0.029, -0.044, and -0.031 respectively for 1989, 1996, 2001, and 2016. This supports the coefficients in Table 2.4, showing that the effect of distance to the plantation was weakest in 1996 (flattest slope) and strongest in 2001 (steepest slope).

Table 2.4 Poisson generalised linear model showing the effects of each year of measurement (as a factor), and interaction between distance and each year on seedling counts on Burnt Face. Significant effects are in bold.

Coefficients:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.096	0.093	33.178	**<0.001**
Distance to plantation	-0.031	0.004	-7.671	**<0.001**
Year 1996	1.692	0.102	16.661	**<0.001**
Year 2001	2.487	0.098	25.409	**<0.001**
Year 2016	2.798	0.096	29.010	**<0.001**
Distance:1996	0.000	0.004	-0.070	0.944
Distance:2001	-0.018	0.004	-4.275	**<0.001**
Distance:2016	-0.012	0.004	-2.781	**0.005**

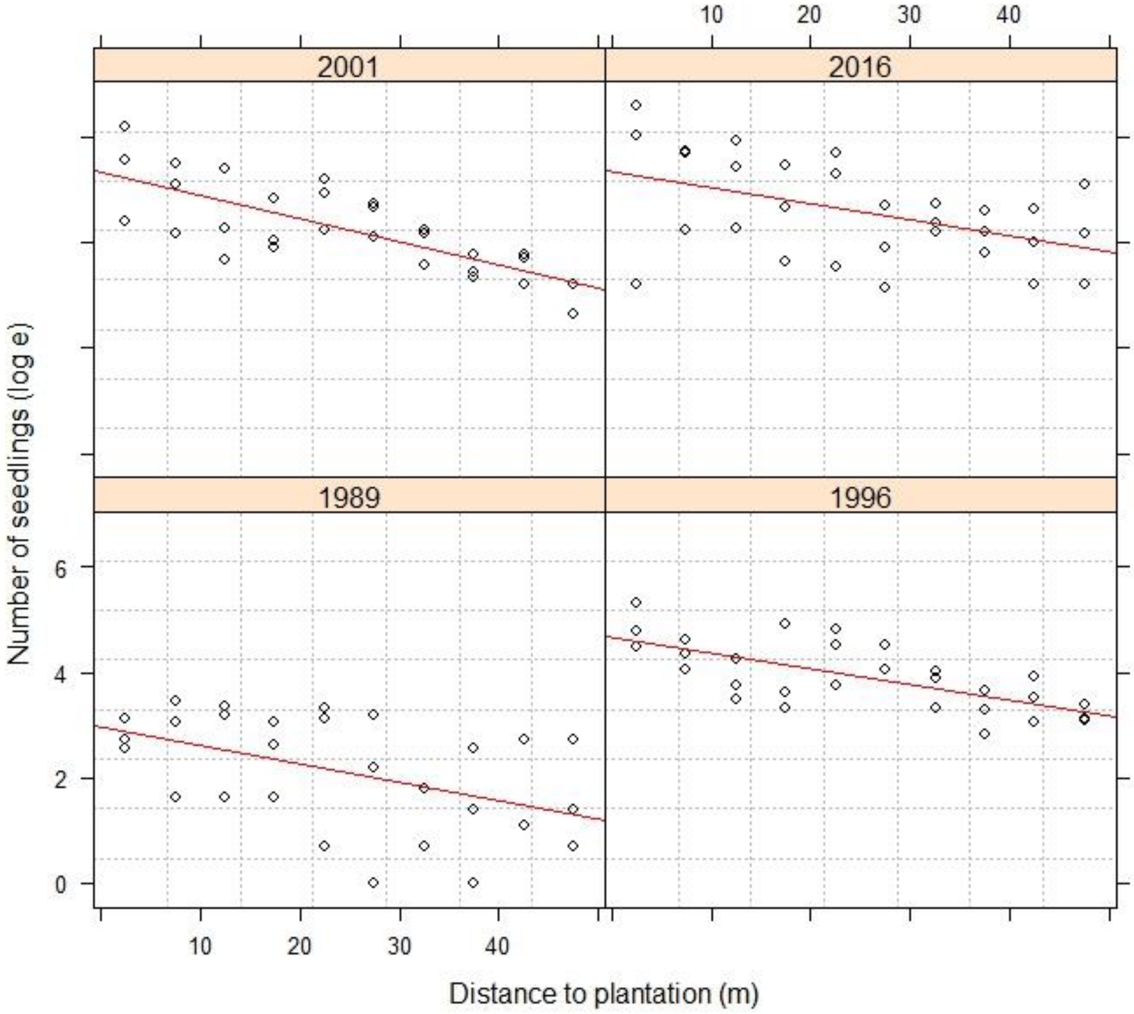

Figure 2.4 Distance to the plantation and number of Douglas fir seedlings (Log *e*) in the subplots in each year of measurement on Burnt Face. Best fit line in solid red line.

2.4 Discussion

This chapter demonstrates that Douglas fir (*P. menziesii*) is able to invade mountain beech (*N. solandri* var. *cliffortioides*) forest, although at a slow rate. In part, the ability of a seedling to outcompete the surrounding vegetation depends on the development stage of both seedling and competitors (Newton 1973). Ledgard (2002) suggests that Douglas fir can invade native forests following disturbance, and potentially dominate before the native vegetation recovers enough to supress the invasion, but that the risk of invasion of mature healthy forests is low. Chavasse (1979) made a similar conclusion when compiling reports from all over the country, i.e., with few exceptions, exotic trees invaded native forest only after disturbance. In Argentina, Sarasola et al. (2006) found no exotic conifer regeneration in the native forest where understorey cover was > 90%, and greater recruitment where disturbance was more intense. On the onset of the invasion on Burnt Face, the recovering understorey vegetation is likely to have facilitated the spread of Douglas fir.

Cleary (1982) investigated the spread of Douglas fir into mountain beech forest in Ben Lomond Reserve, Queenstown. He compared growth of *P. menziesii* and *N. solandri* var. *cliffortioides* seedlings (up to 2 m height) and found that the invaders had a significant advantage. Douglas fir had an average height growth of 39 mm/year beneath the *Nothofagus* canopy, whereas mountain beech had an average height growth of 15 mm/year. In the grassland, where mountain beech seedlings were absent, the average height growth of Douglas fir seedlings was 66 mm/year. Douglas fir grew faster than beech until around 15 years of age, when growth peaked and started to slow down. The fast early growth rate is possibly a competitive strategy, because in Douglas fir's original range, the density of conifer saplings in the understorey is relatively high. Cleary also recorded a decline in native species diversity following invasion of Douglas fir. The ability of *P. menziesii* to grow under high light, coupled with its faster growth rate gives it a competitive edge on windthrow gaps that are eventually created in the native forest.

Also in New Zealand, Douglas fir invasion of *Nothofagus* has been recorded in the Blue Mountains, Otago, and in Ashley Forest, Canterbury, where Douglas fir was planted alongside the native forest (Ledgard 2002). Densities were generally low, but in one site in the Blue Mountains, there was the equivalent to 200,000 seedlings/ha within 5 m of the plantation, similar figures to the highest density recorded on Burnt Face of 247,000 seedlings/ha in Plot 1 in 2016.

Sarasola et al. (2006) found Douglas fir invading the native Chilean cedar (*Austrocedrus chilensis*) forest in all 6 sites (native forests adjacent to plantations averaging 30 years old) that were surveyed in the Andean-Patagonian region. The seedling recruitment was largest in the downwind direction. The mean seedling density across all sites was 1,513 seedlings/ha, approximately 100 times lower than the average density on Burnt Face in 2016. However, Sarasola et al. (2006) used seedlings older than 4 years old to estimate density, and noted that 65% of seedlings were younger than 4 years old.

According to Ledgard (1989) there were no mycorrhizal seedlings – those seedlings which have established mycorrhizal partners – in 1989. Only 3.8% of the seedlings had become mycorrhizal in 1996, rising to 60.7% of total seedlings in 2001. Tree seedlings can persist for years waiting for mycorrhizal partners to boost their growth (Collier and Bidartondo 2009). This appears to have been the case on Burnt Face, as many seedlings classified as chlorotic in the survey of 1996 (Ledgard 1996) were found to be associated with mycorrhizae in the survey of 2001 (Dickson 2001). Thus, the barriers to survival are possibly becoming less important over time, consequently increasing the potential of Douglas fir to spread.

The shifting trend in Plot 2 from increasing density, then to stabilizing, to decreasing density is probably related to changes in the canopy structure between 1996 and 2001. A large gap resulting from a tree fall could overexpose the seedlings to the direct sunlight. Too much sun exposure and the excessive heat can kill tree seedlings (Helgerson 1989). Ledgard (1996) found fewer seedlings under large canopy gaps receiving many hours of full sunlight, which he attributed to moisture stress in summer and frosting in winter. The findings of Dickson (2001) support this hypothesis, as he observed that Plot 2 was under large canopy gaps, had sparse vegetation and exposed mineral soil. Gray and Spies (1996) studied the establishment of conifer seedlings under gaps in old-growth forests dominated by *P. menziesii* and *Tsuga heterophylla* and found greater emergence and survival of naturally regenerated Douglas fir seedlings in gaps than in closed-canopy areas. However, seedling survival decreased the closer the seedlings were to the sun-exposed edges of the gaps. Excessive solar radiation can cause hydric stress, and the collapse of tissues and conductive cells in xylem and phloem of Douglas fir seedlings (Smith and Silen 1963).

Despite the density decline observed in Plot 2, which is thought to be due to such local environmental conditions, the Douglas fir invasion still shows no sign of peaking. If looking at Plots 1 and 3, the rate of increase has been declining simply due to the large number of established seedlings in comparison to new ones.

Burnt Face has a history of fire and grazing, which severely impacted the plant community until the 1960s, and to a lesser extent until the 1980s. This past disturbance, coupled with the characteristics of the beech canopy and the understorey vegetation resulted in the area being more prone to invasion than other beech forests (Ledgard 1989). In addition, the prevailing Northwest winds blow Douglas fir seeds far into the *Nothofagus*. Sparse understorey vegetation at the onset of the spread must have facilitated the establishment of the Douglas fir seedlings. However, the invasion does not seem to be hindered at present, almost a century after the historic fire, and more than 30 years after sheep grazing has ceased. Given the maturity of the native forest, the formation of canopy gaps is likely to become increasingly frequent, thus creating more opportunities for the establishment of Douglas fir seedlings.

CHAPTER 3

WHAT LIMITS THE ESTABLISHMENT OF DOUGLAS FIR SEEDLINGS?

3.1 Introduction

Once it became clear that Douglas fir could invade *Nothofagus* forest, I proceeded to investigate the factors influencing the establishment of the seedlings. There are many biotic and abiotic factors that limit the spread of invasive plants into the recipient ecosystem. My focus in this section was the role of light, altitude and distance to the plantation on the spread of Douglas fir on Burnt Face.

3.1.1 Objectives

The aims of this part of the study were to investigate the effects of light penetration to the forest floor, altitude, and distance to the seed source on the establishment and survival of Douglas fir seedlings in *Nothofagus* forest, by recording naturally occurring seedlings near to 400 random points across the slope.

3.2 Methods

3.2.1 Marking the points

I established 400 points along 40 transects in the mountain beech forest (Figure 3.1). The transects were 90 m long with one point every 10 m, and started at least 50 m from the Douglas fir plantation, towards the *Nothofagus*. The lowest-altitude transect started at 742 m; the highest transect started at 1040 m. They were established at right angles to the plantation using GPS, compass, measuring tape and wood stakes. At each point I sampled the following: light reaching the forest floor, distance to the nearest Douglas fir seedling and its height, and distance to the nearest Douglas fir seedling > 0.7 m tall and its height. All points were recorded on GPS to derive each point's altitude and distance to the seed source. Transects were measured between 19 April and 6 May 2016 in approximately 97 hours of sampling effort. The gap between transects 12 and 13 was due to difficult terrain in that particular area.

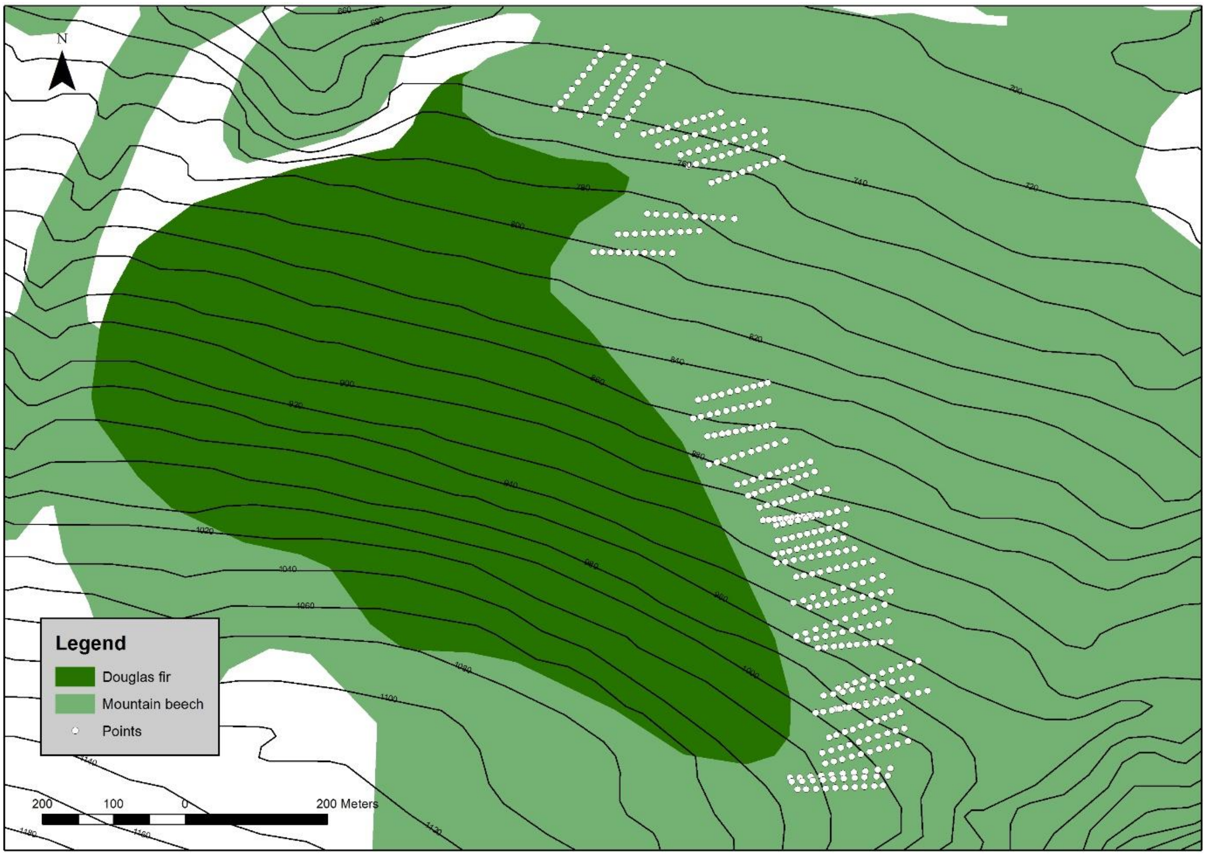

Figure 3.1 Study site showing location of the 400 points in *Nothofagus* forest on Burnt Face. Transects were 90 m long, with points every 10 m. Image made in ArcMap 10.4.

3.2.2 Distance to nearest seedling and height

Generally, the nearest seedling was close to the point and easily distinguished among the vegetation. When far away, I walked in circles around the point, increasing the radius of the circle until finding the nearest seedling. The distance between them was measured with a 30-m measuring tape. The height of the seedling was measured with the same tape. The same procedure was done for the nearest seedling taller than 70 cm, which are hereafter referred to as “tall seedlings”. Distance to nearest plants and their heights were measured for each point.

The distance to nearest seedling – of any height, but typically they were shorter than 10 cm – is referred to as D1; distance to nearest tall seedling is referred to as D2. A maximum search distance (30 m) was set, beyond which, if no seedling were found, an arbitrary value of 31 m was attributed to the point. This was done to accommodate a feasible work load without compromising statistical analyses. No tall seedling was found within 30 m at 12 of the 400 points.

3.3.3 Estimating light

The light environment in all 400 points was assessed via hemispherical photography. I used a Nikon Fisheye lens FC-E9 attached to a digital camera Nikon Coolpix E5400 (image resolution = 2592 × 1944). The procedures involving image acquisition, image processing, and data extraction are described below.

The first step was the image acquisition. The camera was attached to a tripod with adjustable ball head, positioned at chest height (~1.5 m), oriented to true north using a compass (accounting for local magnetic deviation of 22° East), and levelled to 0° zenith using a circular bubble level attached to the camera's flash mount. Understorey foliage that was immediately above the camera was removed to avoid overestimating the canopy cover. Photos were taken under overcast condition or at dusk or dawn for even sky illumination, and consequently better contrast between foliage and sky (Rich 1990). The camera settings were set to ISO 100, and aperture fixed at *f*/5.6 (Frazer et al. 2001). At each point photos were taken at four different stops below the indicated automatic exposure (-1, -1.3, -1.7, and -2 f-stops) to be able to choose the one with the best contrast between vegetation and gaps (Chen et al. 1991, Macfarlane et al. 2014). This was done between 19 April and 6 May 2016.

To process the images, the photos were first analysed to find the exposures with the best contrast between sky and foliage. Exposure at -2 was the best for all points, which consequently added consistency to the process. Once a single photo per point was selected, the images were processed on ImageJ software (Schneider et al. 2012). Three coordinate points around the edge of the circular horizon of the image were recorded to be used as reference in the data extraction program. Images were split into RGB colour channels, and the blue channel was used for thresholding, while red and green were discarded (Nobis and Hunziker 2005). Different threshold methods were extensively tested for their accuracy in representing the original photo. Auto local threshold (Landini et al. 2016) using Bernsen's algorithm (Bernsen 1986) had the best results and was used to classify the images into black and white pixels. ImageJ was used to automatically threshold the images in batches, as discussed in Chapter 1.

The classified images were used to extract light penetration data in the CIMES package with the program PARCLR (Gonsamo et al. 2011). This program computes the photosynthetic photon flux density (PPFD) in the PAR waveband, intercepted and transmitted by canopies, under clear-sky conditions. It first extracts structural data, such as gap fraction, from the processed hemispherical photographs. Then it uses the structural data to estimate light penetration by taking into account the movement track of the sun in the hemisphere. Therefore, this is an indirect estimate of PAR, not a direct measure. I compared the fit of different parameters such as canopy openness to the Douglas fir distances data set, and PAR showed the best fit, i.e., the highest R-squared. I attribute this to the structural parameters alone not accounting for the sun track. CIMES does not have an interface, meaning that all usage of the software is done via command lines. The codes were written according to the manual instructions for the program PARCLR specifically. This program calculates PPFD for each Julian day written in the code. Because the program accepts only 25 days to the command line, I used the approximate midpoint of every month of the year, i.e., Julian days 16, 46, 76, 137, etc., as an average for the month. These monthly averages were used to obtain the mean daily PPFD for the period of one year. Thus, light penetration at each point was estimated as the mean number of moles of photons per square metre per day (mol m^{-2} d^{-1}). The full PPFD is estimated automatically by the program. To test if the full PPFD was correct, I ran a single completely white image separately in the program and both values matched. Canopy openness was estimated using the program OPENNESS in CIMES package (Gonsamo et al. 2011) for the purpose of characterizing the canopy only.

3.2.4 Distance to the seed source

To estimate the distance between each point and the seed source, I georeferenced the boundary of the plantation by walking alongside it with the GPS set to tracking mode. Distances were obtained by manipulating data in ArcMap 10.4. The shortest distance between the point and the boundary was used.

3.2.5 Data analysis

The distance between each point and its nearest seedling varies inversely with seedling density; therefore, shorter distances represented higher density, and longer distances represented lower density. Although this method does not return a comparable density value, e.g., individuals/ha, it allowed me to cover a large area while still providing data for several other analyses. This surrogate for density was the response variable, which was fitted against light, altitude, and distance to seed source. D1 and D2 were transformed to $\log_e$ (distance) to improve normality. All statistical analyses were carried out in R Version 0.99.903 (R Core

Team 2016), and analysis of variance was used to test the effect of the explanatory variables on seedling density.

To better understand the relationships between variables, I performed a regression using the “tree” package (Ripley 2016). Some of the benefits of the regression tree model are to make the most important variables stand out, to display the interactions between them, and to show the complexity of the behaviour of the explanatory variables (Crawley 2005).

Linear regressions were used to investigate the individual effects of each explanatory variable on seedling density. In addition to this, I performed a calculation to identify the largest amount of change (effect size) in the fitted values (Y) for density vs. light, density vs. altitude, and density vs. distance to seed source, using the following equations:

$$log(D1) = intercept\ estimate + (x) \times variable\ estimate$$

$$D1 = e^{log(D1)}$$

where *x* is the Y value at either extreme of the observed X range. For instance, to determine the effect size of altitude on seedling density, I used first ‘730’ as *x* (the lowest altitude in my data set), then ‘1040’, as *x* (the highest altitude). The ratio of the highest D1 value to the lowest D1 value was used to evaluate the variable’s importance. This was done with all three variables for both D1 and D2.

I tested the influence of the transects on the effect of altitude by running a multiple linear regression (Gaussian) with mixed effects using the package ‘lmerTest’ (Kuznetsova et al. 2016), which outputs p-values for the predictors. The transects were the random effects. The assumption in this case was that the variables were not completely independent. Although I do not believe this was the case, and will explore it further in the discussion, the decision to run a model with mixed effects was to accommodate the possibility of some influence of the transects on seedling density.

Finally, I explored the seedling survival using the logarithmic ratio between D2 and D1. The rationale was that in spots where more plants had survived, the distance between a tiny seedling and its nearest well-established seedling would be shorter. Therefore, the smaller the ratio, the greater the seedling survival. The formula I used was:

$$distance\ ratio = log\left(\frac{D2}{D1}\right)$$

This was done for all 400 points. The resulting values were tested in a linear regression against light, altitude, and distance to the seed source. ANOVA was used to evaluate the relationships.

I predicted that the distance ratio would be influenced by light and altitude, but not by distance to the seed source. Higher relative light availability should decrease the distance ratio (increase seedling survival), while altitude should increase the distance ratio (decrease survival).

3.3 Results

At 88% of the points I found a seedling within 1 m radius, 92% of which were under 10 cm height and chlorotic. Conversely, only 9% of the points had tall seedlings ($h > 70$cm) in the same radius, suggesting low post-germination survival rate. If considering a 10-m radius for the presence of seedlings, 99.7% of points were positive for seedlings of any height, and 74% were positive for tall seedlings. Twelve points (3%) had no tall seedlings within the 30-m threshold, and these were mostly concentrated at high altitude (>1000 m). Only one point had no seedlings within a 10-m radius. Light (PPFD) ranged from 2.39 to 10.96 mol m^{-2} d^{-1}, which are equivalent to 6.44% and 29.57% of the photosynthetic photon flux density in full sunlight, respectively. Mean light penetration was 5.67 mol m^{-2} d^{-1} (15.3% of full sunlight). Altitude ranged from 720 to 1040 m, and distance to the seed source ranged from 4.0 to 119.5 m.

Potential correlations between the predictors were investigated with the function “pairs()”. Altitude had a weak but significant negative effect on light (see Figure 3.2 for scatter plot, and ANOVA F and p values). There was no significant correlation between any other predictors.

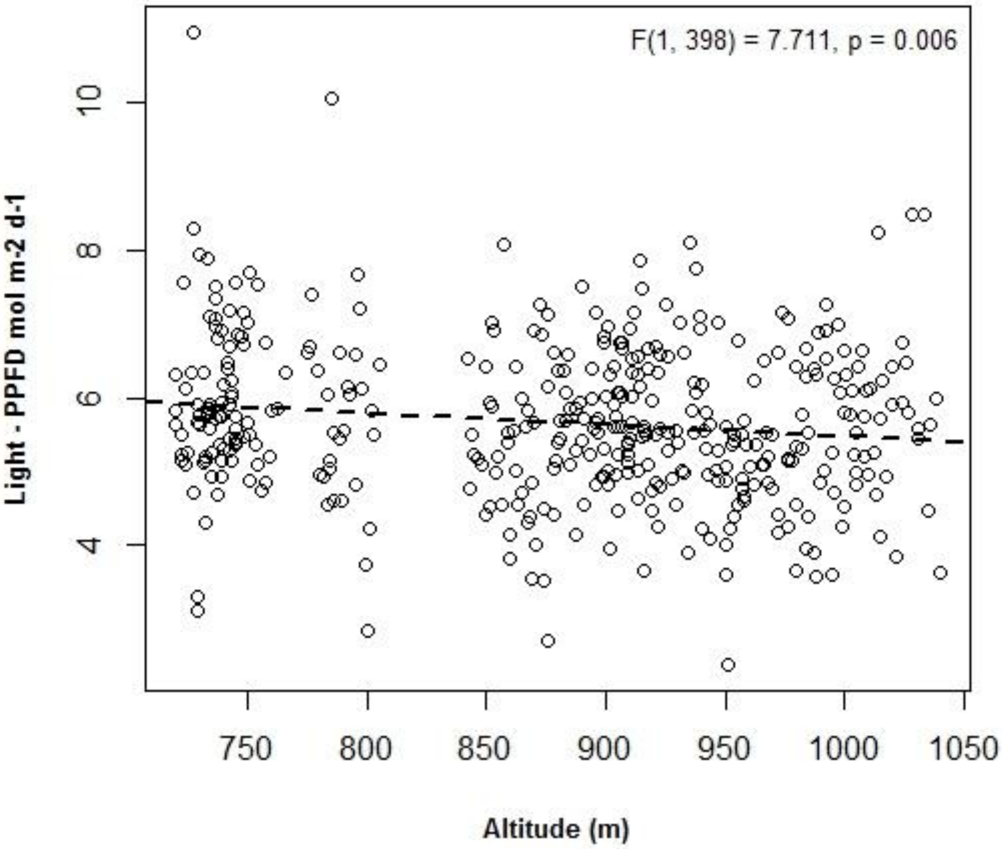

Figure 3.2 Relationship between light penetration to the forest floor and altitude in *Nothofagus* forest on Burnt Face. Scatter plot showing linear regression, fitted line, and F and p values of the ANOVA.

3.3.1 Nearest seedling (D1)

3.3.1.1 Effect of light

The distance to nearest seedling decreased as light availability increased. The fitted values of distance to nearest seedling were 0.36 m for x = 4 mol m^{-2} d^{-1}, and 0.17 m for x = 8 mol m^{-2} d^{-1}, a decrease of -52.05%. The results of the analysis of variance are presented in Table 3.1. Most of the points (78.5%) fell between 4.5 (12.14% of full PPFD) and 7 mol m^{-2} d^{-1} (18.88% of full PPFD). Only 10.3% of the points received more than 7 mol m^{-2} d^{-1}.

Table 3.1 Relationship between distance to the nearest seedling of any height (D1) and light availability (PPFD). Analysis of variance of linear regression (log(D1)~light). Significant relationship is in bold.

Response: $\log_e$ D1					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Light (PPFD)	1	15.44	15.442	11.707	**<0.001**
Residuals	398	524.98	1.319		

Distance decreased markedly from 2 to approximately 5 mol m^{-2} d^{-1}, then gradually decreased towards the maximum recorded light (Figure 3.3). This suggests that below around 5 mol m^{-2} d^{-1} (13.49% of full PFD) light becomes a limiting factor.

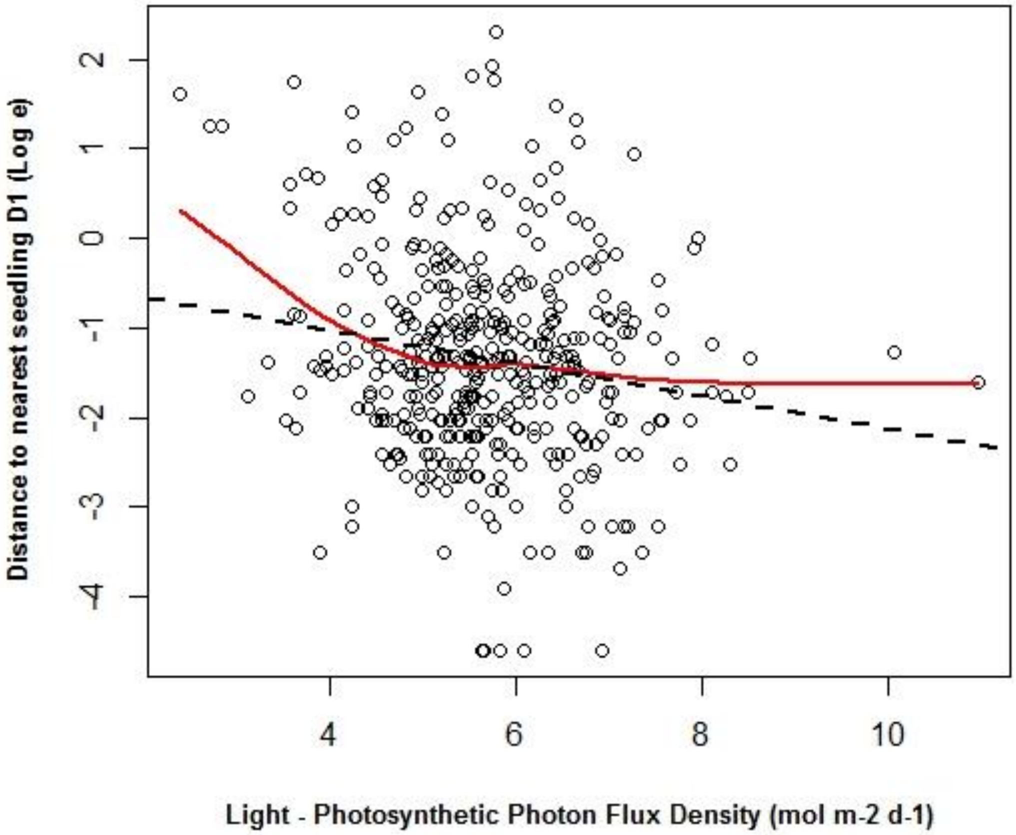

Figure 3.3 Distance (Log *e*) of the nearest seedling of any height (D1) to the point and light availability in *Nothofagus* forest on Burnt Face. Light is PPFD measured in mol m^{-2} d^{-1}. Scatter plot showing linear regression. Smoothed line in red, and best fit line in black dashed.

3.3.1.2 Effect of altitude

Altitude caused an increase in distance to the nearest seedling (D1) especially above 900 m, from which point D1 increased more steeply (Figure 3.4). The fitted values of distance to nearest seedling were 0.15 m for x = 730 m, and 0.47 m, for x = 1030 m: an increase of 212.8%. Table 3.2 shows the results of the analysis of variance.

Table 3.2 Relationship between distance to the nearest seedling (D1) and altitude. Analysis of variance of linear regression (log(D1)~altitude). Significant relationship is in bold.

Response: $\log_e$ D1	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Altitude	1	51.78	51.782	42.177	**<0.001**
Residuals	398	488.64	1.228		

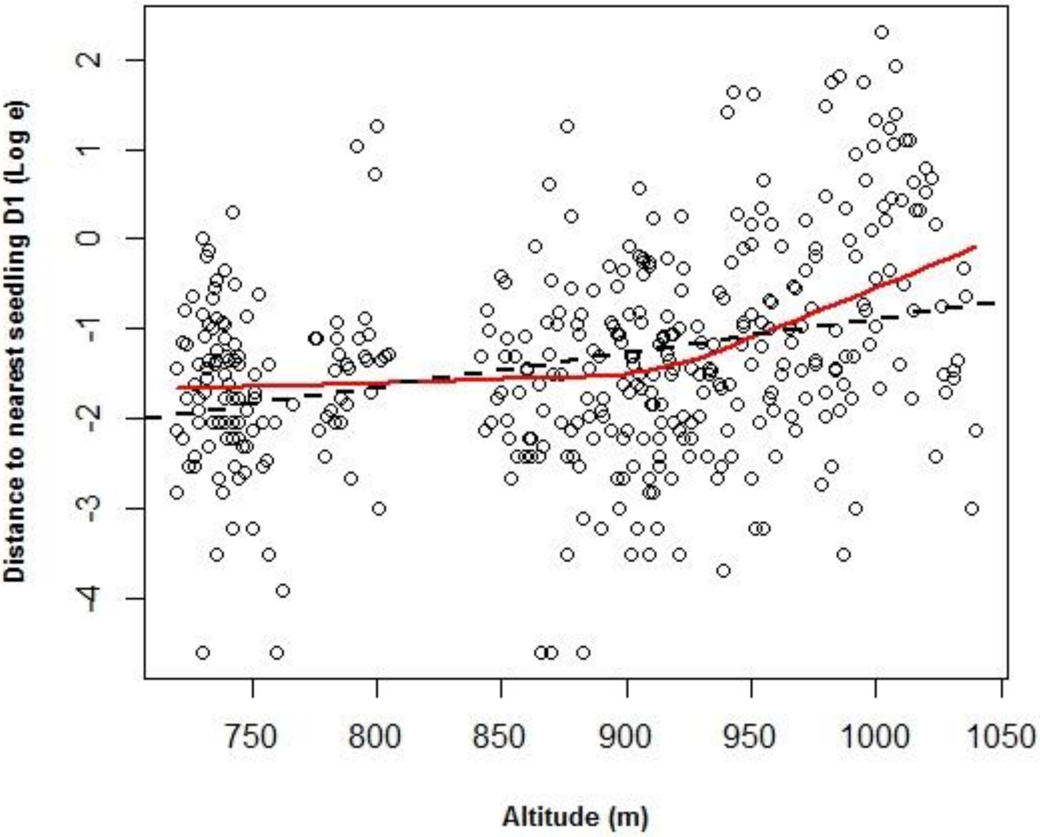

Figure 3.4 Distance (Log *e*) of the nearest seedling of any height (D1) to the point and altitude in *Nothofagus* forest on Burnt Face. There are no observations around the 830 m mark due to the difficult terrain. Scatter plot showing linear regression. Smooth line in red, and best fit line in black dashed line.

3.3.1.3 Effect of distance to the seed source

Distance to seedling D1 increased gradually as distance to the Douglas fir plantation increased. Such relationship was highly significant (Table 3.3) The effect of distance to seed source was slightly more pronounced within the first 50 m distance (Figure 3.5). The fitted values of distance to nearest seedling were 0.13 m for x = 10 m, and 0.51 m for x = 100 m, an increase of 290.4%.

Table 3.3 Relationship between distance to the nearest seedling (D1) and distance to the seed source. Analysis of variance of Linear Regression (log(D1)~dist.seed.source). Significant relationship is in bold.

Response: $\log_e$ D1	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Distance to seed source	1	64.54	64.542	53.979	**<0.001**
Residuals	398	475.88	1.196		

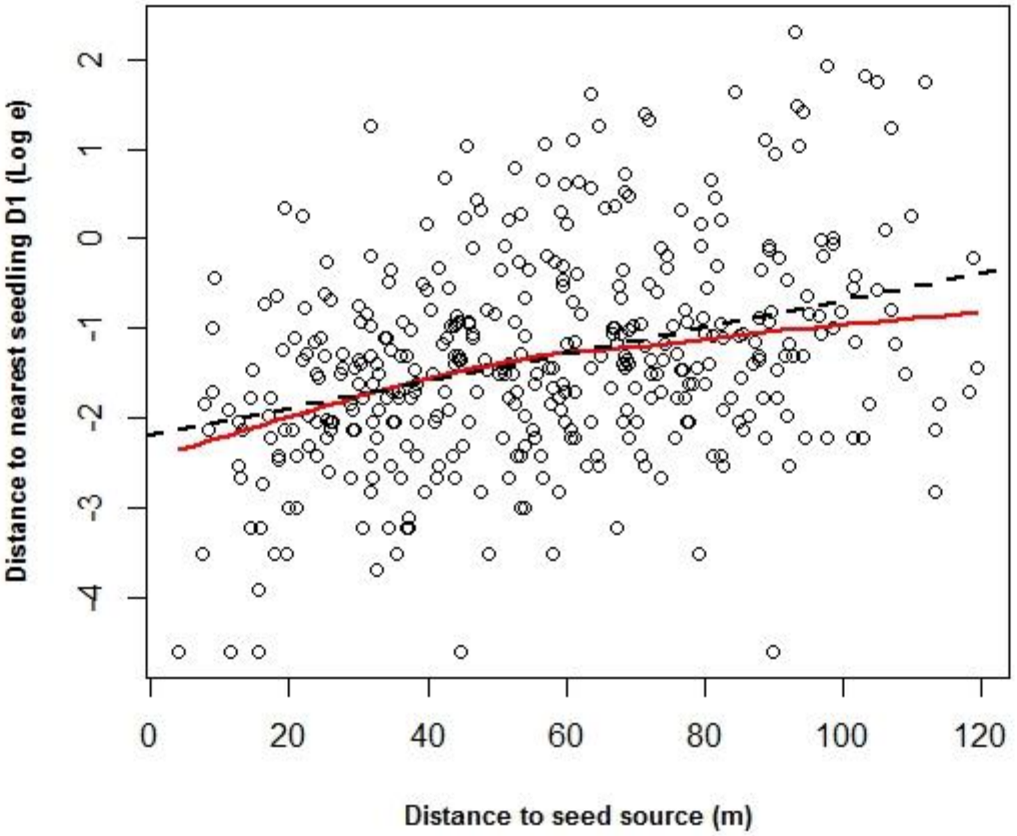

Figure 3.5 Distance (Log *e*) of the nearest seedling of any height (D1) to the point and distance to the seed source in *Nothofagus* forest on Burnt Face. Scatter plot showing linear regression. Smooth line in red, and best fit line in black dashed line.

3.3.1.4 Multiple regression in GLMM

I used a linear mixed-effects model to explore the influence of the transects, and all three fixed effects simultaneously, on the effect of altitude. This was done by fitting a random term for “transect”. The GLMM showed that the positive effect of light, and the negative effects of altitude and distance to the seed source, on distance to the nearest seedling D1 were significant (Table 3.4).

Table 3.4 Effect of light, altitude, and distance to seed source on distance to nearest seedling of any height (D1). Linear mixed effect model (lmerTest) with the transects as random effects. Significant effects are in bold

Random effects:			
Groups	Name	Variance	Std.Dev.
Transects	(Intercept)	0.1797	0.4239
Residual		0.8707	0.9331
Number of obs.: 400, groups: Transects, 40			

Fixed effects:	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	-4.488	0.849	52.6	-5.287	**<0.001**
Light (PPFD)	-0.147	0.048	394.9	-3.1	**0.002**
Altitude	0.004	0.001	38.8	4.08	**<0.001**
Distance to seed source	0.016	0.002	393.6	8.457	**<0.001**

Regression tree

The regression tree (Figure 3.6) shows that altitude explained most of the deviance; in other words, altitude was the most important factor influencing seedling density. Distance to the seed source was the second most important variable, and mattered at relatively low and high altitude. Light explained a small part of the variation in low altitude and in areas relatively far from the seed source, but not when close to it. Light is not of much importance according to this model, as it is represented in a short branch on the left-hand side of the tree, and not represented at all on the right-hand side of the tree.

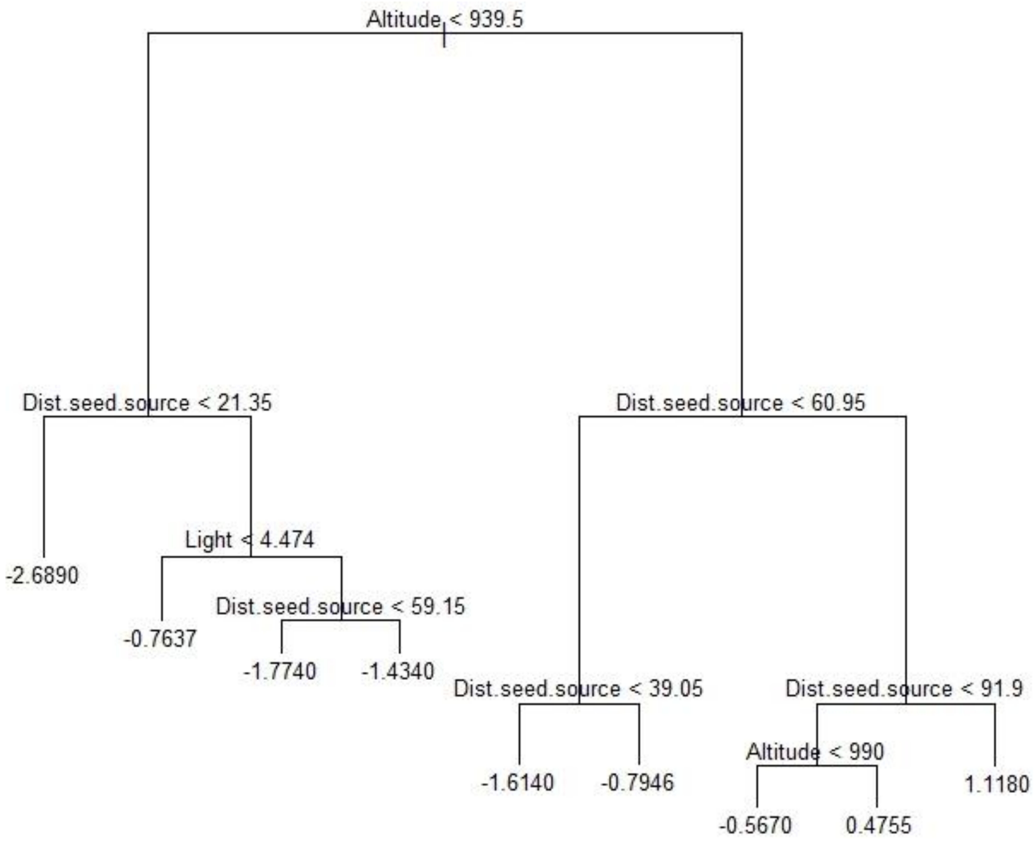

Figure 3.6 Regression tree showing the relationship of importance between distance to the nearest seedling (D1) and the three explanatory variables. The longer the branches in the tree, the greater the deviance explained. Altitude at the top is the most important variable. Figures to the right of the labels are the mean values of the variables calculated by the model. Left- and right-hand side of each branch represent conditions below and above the mean, respectively.

3.3.2 Nearest tall seedling (D2)

3.3.2.1 Effect of light

The relationship between tall seedling density (D2) and light was slightly more complex than for D1, and only just had statistical significance (Table 3.5). Nonetheless, distance generally decreased as light availability increased (Figure 3.7). There was an overall trend of decrease in distance towards sunnier spots. The fitted values of distance to nearest tall seedling were 6.01 m for x = 4 mol m^{-2} d^{-1}, and 3.80 m for x = 8 mol m^{-2} d^{-1} – a decrease of -36.77%.

Table 3.5 Relationship between distance to the nearest tall seedling (D2) and light availability. Analysis of variance of linear regression (log(D2)~light). Significant relationship is in bold.

Response: $\log_e$ D2

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Light (PPFD)	1	6.01	6.006	5.1219	**0.024**
Residuals	398	466.7	1.1726		

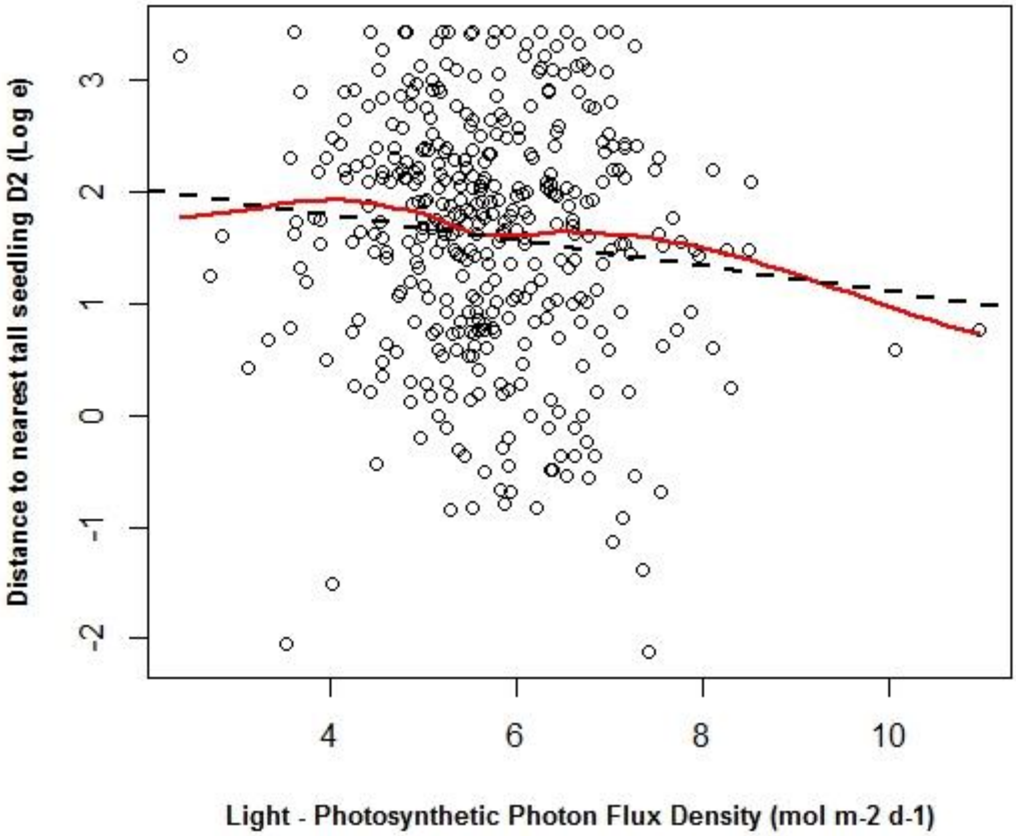

Figure 3.7 Distance (Log *e*) of the nearest tall seedling (D2) to the point vs. light availability in *Nothofagus* forest on Burnt Face. Light is PPFD measured in mol m^{-2} d^{-1}. Scatter plot showing linear regression. Smooth line in red, and best fit line in black dashed line.

I hypothesized that this effect was weak due to the larger distance between the point where light was measured, and where the nearest tall seedling was found (mean D2 was ~8 m), therefore less representative of the actual light environment above the seedling. I tested it by running a similar regression exclusively with tall seedlings within a 5-m distance, which resulted in a less good fit (ANOVA $F_{1,\,177} = 0.905$, $p = 0.342$) rather than a better fit. This suggests that there is no indication that the effect of light on D2 was hampered by the greater distance between measurement point and nearest tall seedling.

3.3.2.2 Effect of altitude

Altitude had the largest effect on distance to the nearest tall seedling among the variables (Table 3.6). D2 increased consistently along the entire range of altitude (Figure 3.8). The fitted values of distance to nearest tall seedling were 2.23 m for x = 730 m, and 11.20 m for x

= 1030 m, an increase of 401.8%. At 12 points no tall seedling was found within 30 m and were attributed the value of 31 m. All these points were at mid to high altitudes, and since the 31 m is likely to often be an underestimate of the true distance to the nearest tall seedling, the slope presented here is a conservative estimate of the true slope.

Table 3.6 Relationship between distance to the nearest tall seedling (D2) and altitude availability. Analysis of variance of linear regression (log(D2)~altitude). Significant relationship is in bold.

Response: $\log_e$ D2					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Altitude	1	103.57	103.568	111.67	**<0.001**
Residuals	398	369.14	0.927		

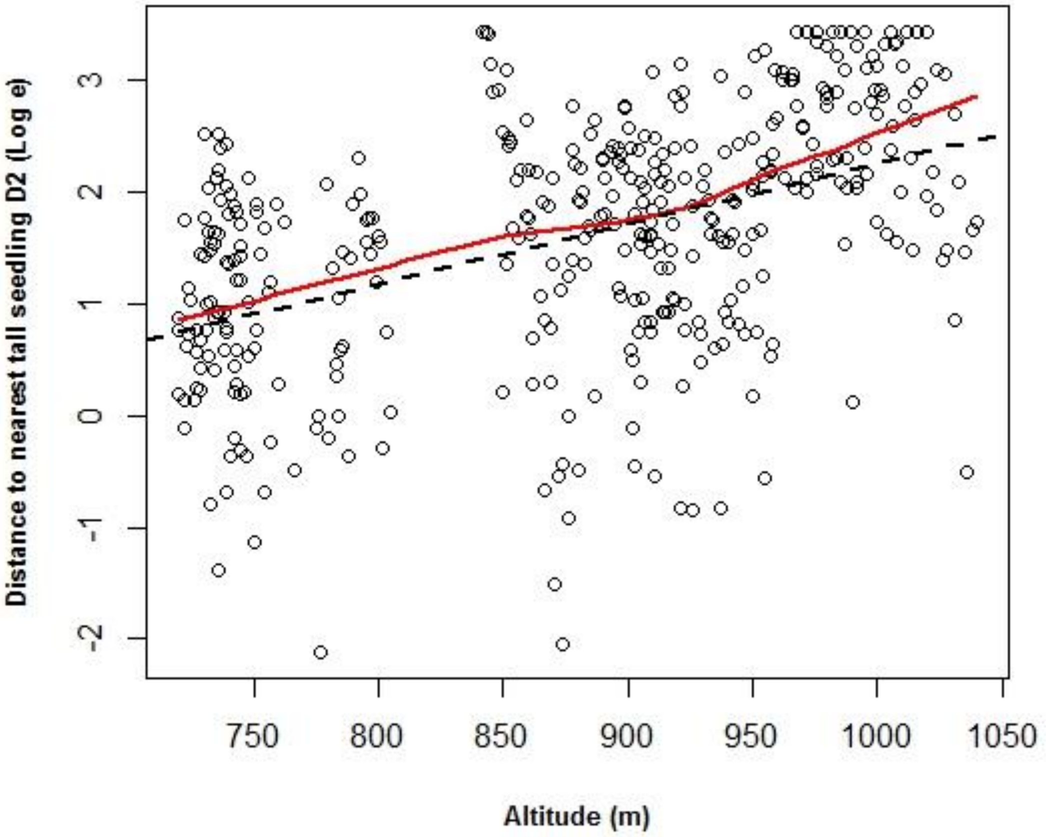

Figure 3.8 Distance (Log *e*) of the nearest tall seedling (D2) to the point and altitude in *Nothofagus* forest on Burnt Face. There are no observations around the 830 m mark due to the difficult terrain. If no seedling was found within 30 m the point was given the value of 31. Scatter plot showing linear regression. Smooth line in red, and best fit line in black dashed line.

3.3.2.3 Effect of distance to seed source

Distance to nearest tall seedling (D2) increased with distance to the Douglas fir plantation (Figure 3.9). The fitted values of distance to nearest tall seedling were 3.25 m for x = 10 m, and 7.36 m for x = 100 m, an increase of 126.9%. The results of the analysis of variance are presented in Table 3.7.

Table 3.7 Relationship between distance to the nearest tall seedling (D2) and distance to the seed source. Analysis of variance of linear regression (log(D2)~dist.seed.source). Significant relationship is in bold.

Response: $\log_e$ D2					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Distance to seed source	1	23.35	23.351	20.682	**<0.001**
Residuals	398	449.36	1.129		

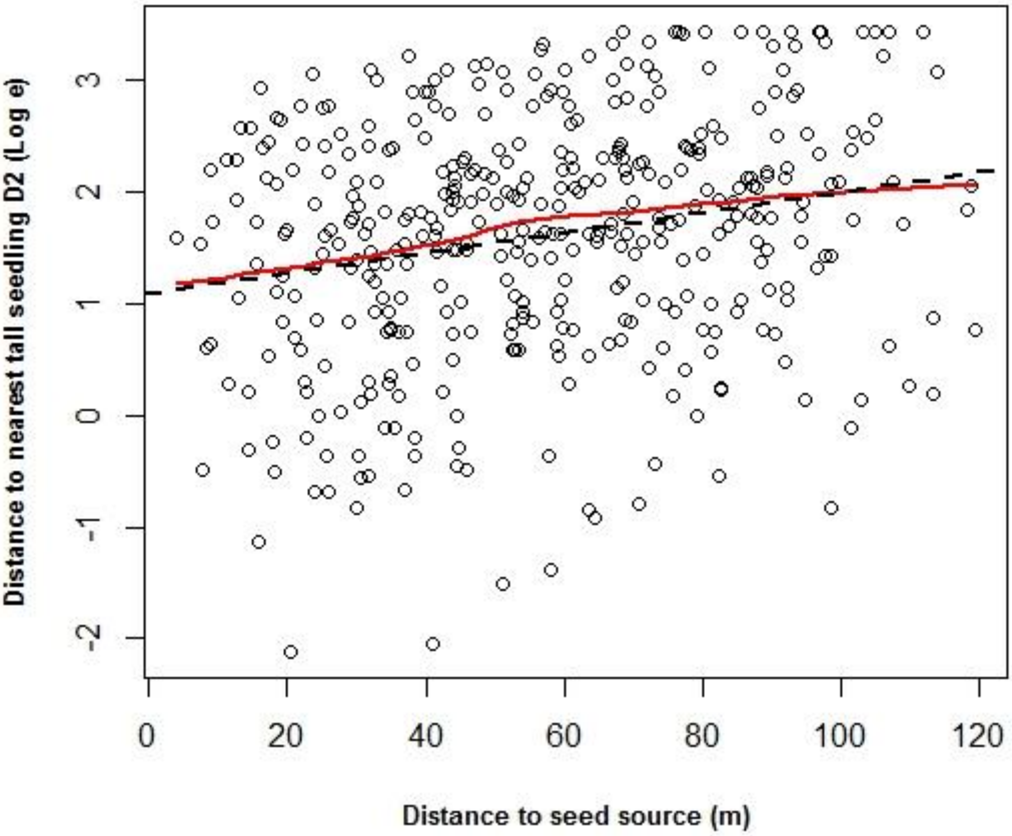

Figure 3.9 Distance (Log *e*) of the nearest tall seedling (D2) to the point and distance to the seed source in *Nothofagus* forest on Burnt Face. Scatter plot showing linear regression. Smooth line in red, and best fit line in black dashed line.

3.3.2.4 Multiple regression in GLMM

In the linear mixed model with the transects as random effects, altitude and distance to the seed source increased distance to the nearest seedling, and were statistically significant (Table 3.8). Light, on the other hand, decreased distance to the nearest seedling, but was not statistically significant. This is consistent with the weak effect of light on D2 (see Table 3.5; Figure 3.7)

Table 3.8 Effect of light, altitude, and distance to seed source on distance to nearest tall seedling (D2). Linear mixed effect model (lmerTest) with the transects as random effects. Significant effects are in bold

Random effects

Groups	Name	Variance	Std.Dev.
Transects	(Intercept)	0.1941	0.4406
Residual		0.6801	0.8247

Number of obs.: 400, groups: Transects, 40

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	-3.235	0.828	50.1	-3.907	**<0.001**
Light (PPFD)	-0.061	0.042	391.7	-1.435	0.152
Altitude	0.005	0.001	38.8	6.15	**<0.001**
Distance to seed source	0.010	0.002	392.4	5.963	**<0.001**

Regression tree

Altitude was the most important factor to influence the tall seedling distance (D2), and explained it here to a greater extent compared to D1 – the length of the top “Altitude” branch is more than half the length of the entire tree (Figure 3.10). The effect of altitude was so important that this variable also appeared as the second most important factor in relatively low and high altitude. Light had a similar result to D1 and is represented only on the left-hand side of the tree, i.e., at relatively low altitude.

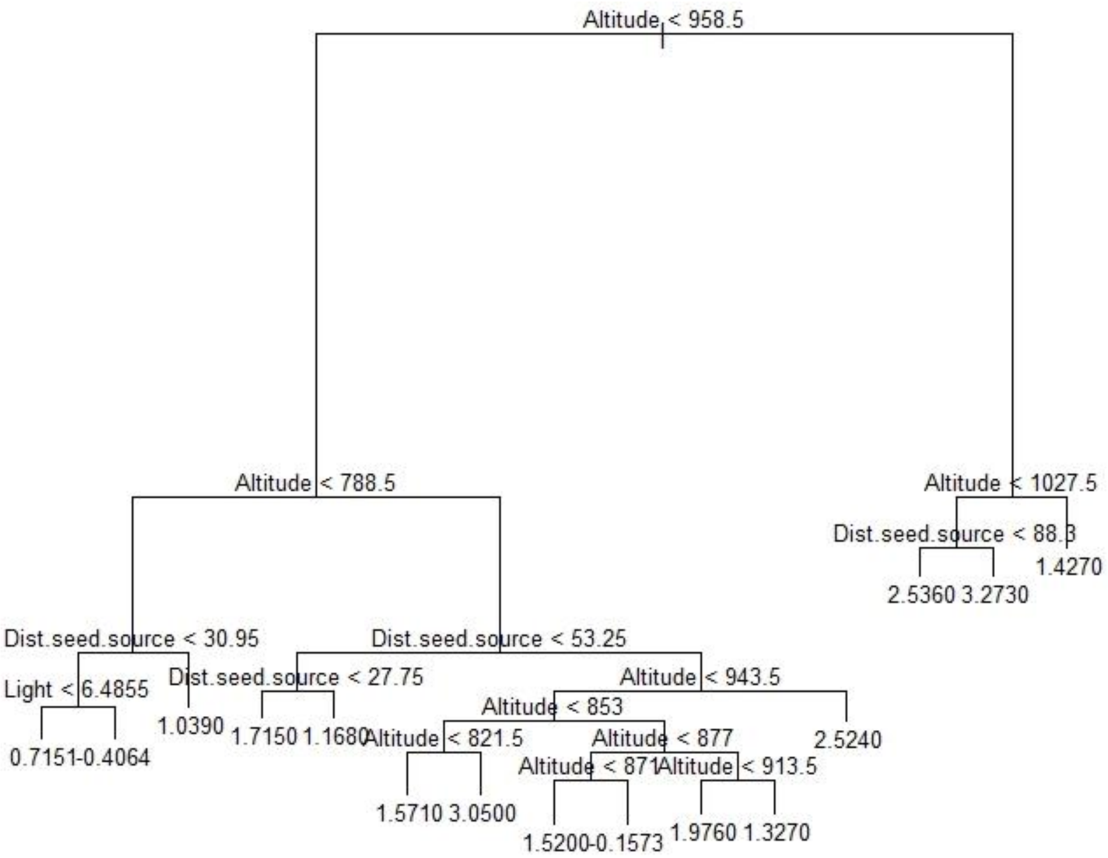

Figure 3.10 Regression tree showing the relationship of importance between distance to the nearest tall seedling (D2) and the three explanatory variables. The longer the branches in the tree, the greater the deviance explained. Altitude at the top is the most important variable. Figures to the right of the labels are the mean values of the variables calculated by the model. Left- and right-hand side of each branch represent conditions below and above the mean, respectively.

3.3.3 Seedling survival (distance ratio)

Following the rationale that the relative distance to large seedlings (D2) compared to the distance to any seedling (D1) should be shorter where survival of the seedlings was higher, I tested the log of the ratio D2/D1 on a multiple linear regression against light, altitude and distance to the seed source (see Table 3.9 for summary). Therefore, high ratios represented low survival; low ratios represented higher survival.

Table 3.9 Effect of light, altitude, and distance to the seed source on $\log_e$ (distance ratio). Linear regression. Estimate of survival is $\log_e$ of ratio D2/D1. Significant effects are in bold.

Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.233	0.721	1.71	0.088
Light (PPFD)	0.092	0.058	1.575	0.116
Altitude	0.002	0.001	2.618	**0.009**
Distance to seed source	-0.006	0.002	-2.482	**0.013**

Distance to the seed source decreased the log of ratio D2/D1, and altitude increased it (see Figure 3.11 for F and p values). Light did not have statistically significant effects.

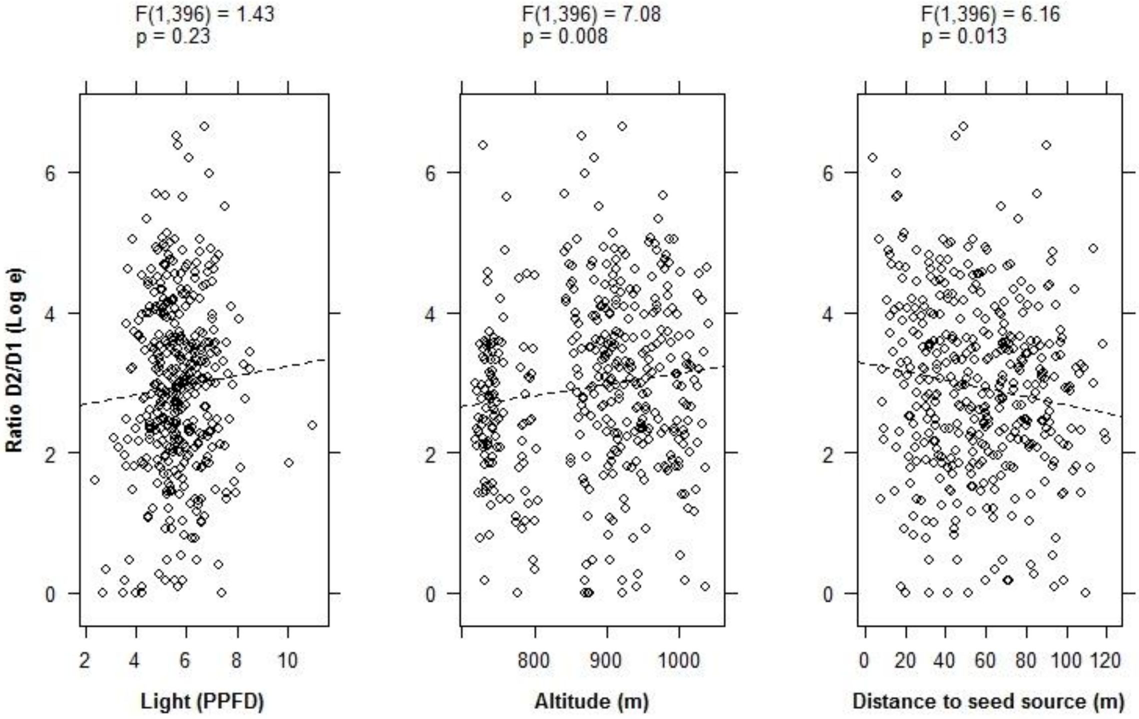

Figure 3.11 Regression analysis of the estimate of survival showing the relation between log of ratio D2/D1 and light, altitude, and distance to the seed source. F and p values of each ANOVA is shown on top of scatter plots.

3.4 Discussion

There is a widespread Douglas fir invasion of the mountain beech forest in progress – in only a single point out of 400 did I fail to find a seedling within a 10-m radius. Although seedling density was influenced by light, the seedlings were not restricted to light wells or canopy gaps as generally presumed, but were in fact establishing consistently throughout the native forest. Gray and Spies (1996) drew a similar conclusion, observing that the common perception that Douglas fir is unable to regenerate in the shade or on intact forest floor was not supported by their study. Holle and Simberloff (2005) demonstrated that the ecosystem's resistance to biological invasion can be overwhelmed by propagule pressure, reducing the importance of other environmental determinants of habitat invasibility. This may have some influence on the resulting Douglas fir spread in Burnt Face. Douglas fir is a much taller species than mountain beech, and the plantation is located west of the native forest. These two factors promote a large seed rain delivered hundreds of metres over the beech canopy every year by the prevailing north-west winds. The transects method shows that the Douglas fir seeds are reaching virtually all parts of the *Nothofagus* within 150 m from the plantation, and that they are successfully germinating. However, few of them survive past the early development stages. The large decline of points with tall seedlings (D2) in a 1-m radius, in comparison to D1, suggests a low survival rate.

Most of the nearest seedlings (D1) were under 10 cm tall and chlorotic, which suggests they had not yet formed mycorrhizal connection (Ledgard 2002) and potentially living off the energy reserves stored in the seed. Suitable mycorrhiza may not be widespread, which hinders the spread of Douglas fir into *Nothofagus*. The ongoing dispersal of fungi across the ecosystems (Wood et al. 2015) increases the potential for establishing mutualistic relationships. This could boost seedling survival and consequently the speed of invasion in the future. Bingham and Simard (2012) have shown that the establishment and survival of Douglas fir seedlings under pressure of competition from nearby trees can be increased by conspecific adult trees via the mycorrhizal network.

The analyses from the regression trees, the linear regressions, and the calculated range of change in the fitted values, all point to light as the least important variable to influence the seedling establishment, contrary to my expectations. Altitude had the largest overall effect, accounting for more than half (54.82%) of the total change in seedling density.

The lmer function tests random and fixed effects together to avoid overestimating a variable that is not independent. I considered a scenario in which the transects were not independent (random effects) to test their influence on the effect of altitude. Results were similar to the linear regressions performed without random effects, but with lower significance values for altitude. The largest difference was the absence of statistical significance for light in D2 when running the lmer. However, given how the transects were established, it is not my understanding that they represent a spatial pseudoreplication, i.e., several measurements taken from the same vicinity. The transects are evenly spread across the slope, apart from the gap between transects 12 and 13, and often the distance between two points from different transects is equivalent to that between two points of the same transect.

The mean light penetration to the forest floor found in this study (using light data of the 400 sampling points in this chapter only, as estimated using the CIMES software program on hemispherical photos) was 15.3% of full sunlight. In a study also in *Nothofagus* forest in New Zealand, Cleary (1982) found mean light penetration equivalent to 32.6% of full sunlight in the Ben Lomond Reserve, whereas Dehlin et al. (2008) found a smaller value of 5.1% of full light. The negative correlation between light and altitude was unexpected. This might be related to the slope aspect in the upper parts of the study site, where it is more east-facing than at around 700 m. The upper parts are shaded by the hill itself, such that, at sunset, I had a longer window of time to take the hemispherical photographs there than at the lower parts. Alternatively, it could be due to changes in the canopy structure at higher altitudes, or the angle at which the sunlight comes through the canopy in more steep slopes, resulting in less light penetrating the forest floor.

Ledgard (1989) noted that seedling densities tended to decline where canopy closure was greatest; however, this was based on personal observation only, as no light measurements were done. Gray and Spies (1996) studied the establishment of Pacific silver fir (*Abies amabilis*), Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterohylla*) seedlings in Douglas fir and western hemlock stands in the United States, and found an intricate relationship between gap size, within-gap position, and seedling establishment and survival. Generally, seedling establishment was greater in gaps than under closed-canopy areas; however, it was relatively low under large gaps that were too exposed to sunlight. Douglas fir seedlings survival decreased when positioned north of the gap – and therefore receiving more solar radiation – and survival increased when positioned south of the gap, sheltered from excessive sunlight by the canopy. On the other hand, growth of Douglas fir seedlings increased towards the north edge, and decreased towards the south edge of the gaps. Higher solar radiation decreased seedling survival, but those plants that survived benefited from increased height growth rate. In Argentina, (Sarasola et al. 2006) also found a trend of declining density in Douglas fir seedlings with distance to the seed source, similar to that found in the present study. Subsequently, they documented pockets of high density far from the plantation, which were associated with clearings or gaps in the native cypress forest. The maximum distance Douglas fir was found was 140 m from the seed source into the native forest. The potential of seed dispersal appears to be greater on Burnt Face, as in my cursory surveys in the study site I found Douglas fir seedlings well beyond 300 m distant from the plantation.

Douglas fir appears to be gradually overcoming the barriers to the invasion of *Nothofagus* forest on Burnt Face. This is worrisome as the constraints to this spread might be much reduced or even removed in the future, potentially escalating the invasion. Part of the success of an invasive tree species is its ability to compete for resources with the native vegetation in the new ecosystem. After finding the right conditions to germinate, the invading plants must, for example, be able to meet their demand for light and nutrients. Therefore, the Douglas fir's potential to survive and grow in the mountain beech forest is a determinant of the spread.

CHAPTER 4
WHAT INFLUENCES THE GROWTH OF DOUGLAS FIR SEEDLINGS?

4.1 Introduction

Light, nutrients, and water are the pillars of plant growth. In nutrient-poor soils, root competition tends to have a larger effect on the availability of nutrients (Coomes and Grubb 1998). In New Zealand's nutrient-poor environment, particularly *Nothofagus* forest, invading plants must possess traits that enable them to meet their demand for nutrients (Richardson et al. 2000a). Only one peer-reviewed journal article by Dehlin et al. (2008) has looked at growth of Douglas fir seedlings and below-ground competition from native vegetation in New Zealand. In this section of the study I have investigated the role of light, nutrients and root competition as limiting factors to the growth of Douglas fir seedlings on Burnt Face. I did not include analysis of the soil water content in my research because, due to the high rainfall rate at Craigieburn, I predicted that soil moisture was unlikely to be a growth limiting factor (see details in the Section 4.2.5).

4.1.1 Objective

The objective was to investigate with a manipulative experiment the effects of root competition, nutrient and light availability, and altitude on the growth of Douglas fir seedlings in the *Nothofagus* forest.

4.1.2 Hypotheses

1. The growth of Douglas fir seedlings will increase when root competition from mountain beech (*Nothofagus solandri* var. *cliffortioides*) is reduced by root trenching.
2. The growth of Douglas fir seedlings will increase when fertiliser is applied.
3. The growth of Douglas fir seedlings increases with more light penetration to the forest floor and decreases with altitude.

4.2 Methods

To test the hypotheses, an experiment involving the manipulation of root competition and nutrient availability to Douglas fir seedlings was designed. The light environment and altitude at each seedling were sampled. The study site was Burnt Face in the Craigieburn Forest Park, as in Chapter 3.

4.2.1 The treatments

The experiment was a factorial one with all four combinations of two treatments involving the application of fertiliser (yes/no), and root trenching (yes/no) around Douglas fir seedlings as follows:

Fertiliser (F): I added nitrogen (N) and phosphorus (P) to increase the nutrients available to plants. I chose N and P as the key nutrients following Coomes and Grubb (1998) and Platt et al. (2004) Fertiliser was applied between 28 November and 4 December 2015 as 15.7 g of calcium ammonium nitrate (equivalent to 555 kg/ha) and 39 g of superphosphate (equivalent to 1380 kg/ha), evenly spread in a 30-cm radius around each seedling. A second repeat application was done at the same rates on 19 – 20 January 2016. The interval between applications was to allow proper breakdown of the slow-release fertiliser pellets.

Trenching (T): I used root trenching to reduce competition from nearby trees on some Douglas fir seedlings. Trenching consisted of spade cuts in a circle, 40-cm radius out from the seedling at the centre of the circle, to a depth of 30 cm. Mountain beech’s lateral and fine roots are mostly concentrated in the upper layers of the soil, from 10 to 20 cm deep (Wardle 1991). The trenching was done between 28 November and 4 December 2015.

Fertiliser & Trenching (FT): The combined procedures of Fertiliser and Trenching treatments.

Control (C): No manipulation was done.

I predicted that (1) growth of the seedlings would increase with the treatments in the following order: Fertiliser & Trenching > Fertiliser > Trenching > Control; and (2) the response to fertiliser would be greater in high light conditions (i.e., a significant fertiliser × light interaction).

4.2.2 Selecting the plants for the experiment

I selected 544 Douglas fir seedlings from 30 to 70 cm in height (136 plants per treatment) naturally regenerating in the mountain beech forest (Figure 4.1). The seedlings were selected at random along the boundary of the plantation to approximately 150 m away from it, in the altitudinal range of 736 m to 1051 m. One treatment was assigned to each plant by intercalating treatments while marking the seedlings, e.g. C1, F1, T1, FT1, C2, F2, T2, FT2 and so on. Seedlings were individually labelled with flagging tape and mapped using a handheld GPS Garmin 60CSx between 10 and 22 November 2015.

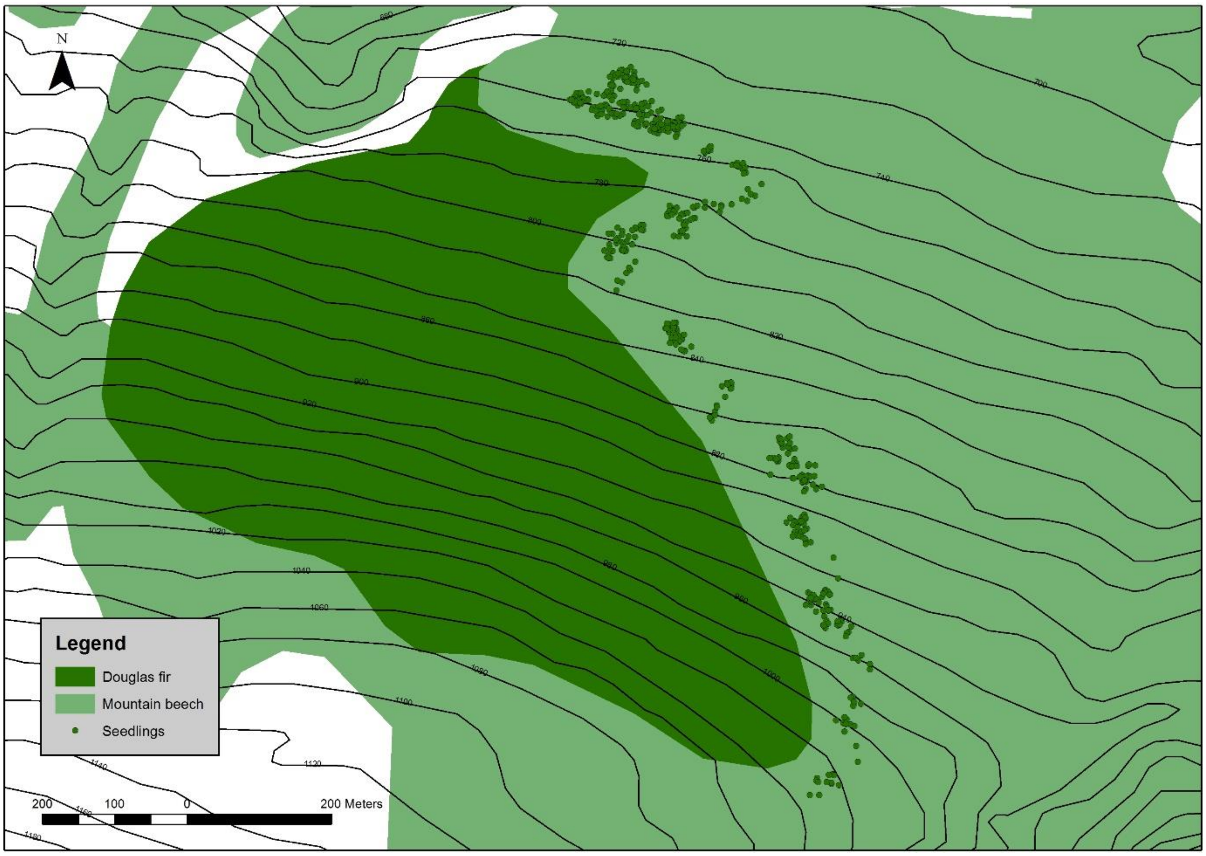

Figure 4.1 Image of study site showing the location of the seedlings (30 to 70 cm height) used in the experiment on Burnt Face. Image made in Arc Map 10.4.

4.2.3 Measuring relative growth

The characteristics of Douglas fir's development were important to determine the approach for measuring seedling growth. The shoots of a tree can be considered as a series of stem segments, each composed of a node and an internode (Doak 1935). Douglas fir has strongly seasonal growth, and develops in a very particular way, such that its shoots form obvious segments on the main stem (Figure 4.2). Each main-stem segment between side branches reflects one season's growth, allowing one to measure the seedling's age as well as the height growth in each previous season.

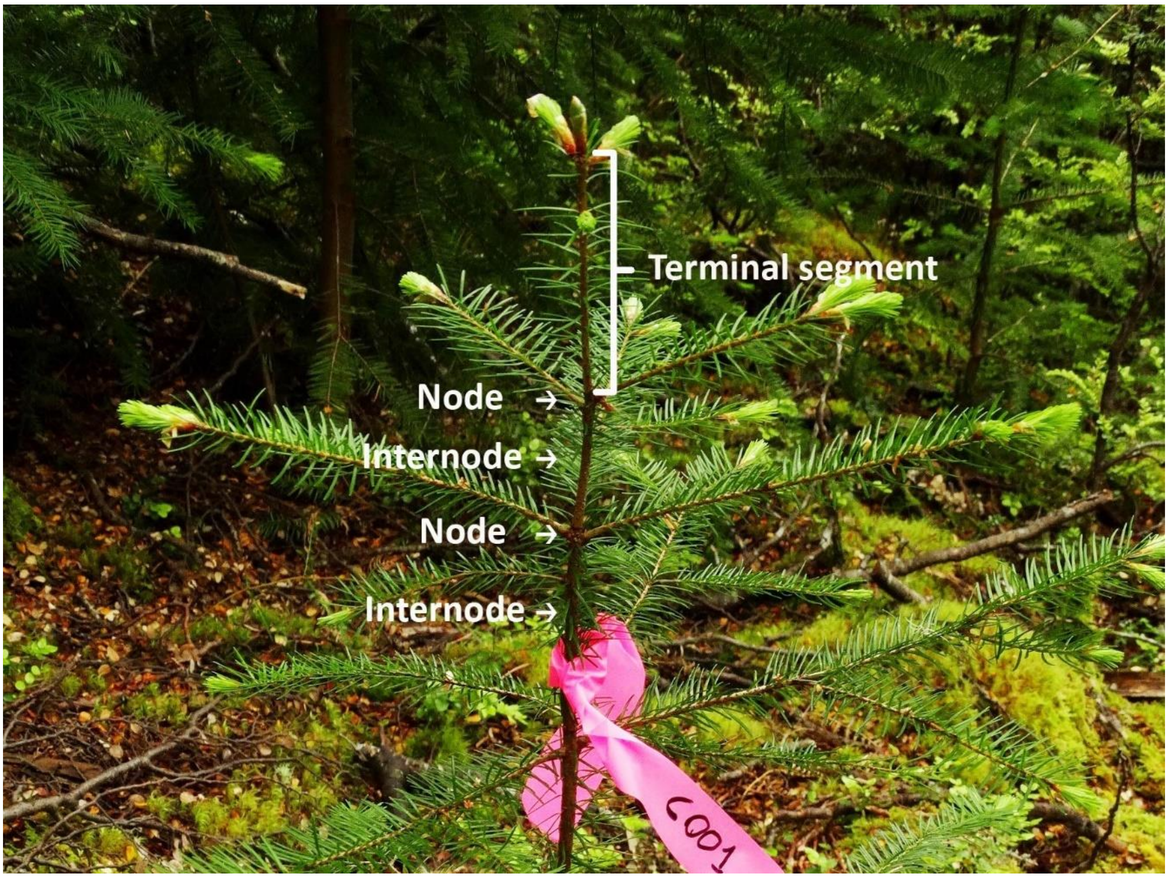

Figure 4.2 Picture of Douglas fir seedling showing the delimited segments on the main stem. The internodes are a reliable means to measure the plant's age and height growth of previous seasons. In this case the pink flagging tape is on the internode formed three seasons ago.

The growth of the seedlings during one season (2015/2016) was used as a measure of response to the treatments. The initial height of the seedlings (length of main stem) was measured before applying the treatments between 28 November and 4 December 2015. At the time, some plants had already started the spring growth as the bud breaks indicated, especially at lower altitudes. The manipulations could not be done earlier due to constraints of the academic year. The final height of the seedlings, as well as the length of the terminal segment (equivalent to the full season's growth) were measured between May and June 2016. The main stem height was measured with a 1 m wooden ruler, the terminal segment with a 30-cm ruler.

I attempted different ways to calculate relative growth. My first method used the initial and final height (as measured at my initial and final visits, in other words growth between my sampling dates) of the seedlings as follows:

$$measured\ growth = \frac{final\ height - initial\ height}{initial\ height}$$

My second method used the terminal segment's length divided by the initial height (worked out from the final height minus the terminal segment's length, so representing the full growth during the 2015/16 season) as follows:

$$season's\ growth = \frac{length\ of\ terminal\ segment}{final\ height - length\ of\ terminal\ segment}$$

I tested both approaches and found that the first method (measured growth) caused some discrepancies in the data analysis, for two reasons. First, no two height measurements of the same plant had precisely the same results. This was because on an uneven surface such as the forest floor, the measured height varied slightly with the position of the ruler, and the amount of pressure used on the ruler against the ground. Also, often the seedlings were bent, and the extent to which they were straightened to be measured had an influence on resulting height. As the seedling growth during one season was generally small (sometimes less than 1 cm), the lack of precision from this approach caused some final height values to be shorter than the initial height. Second, the early growth of some plants before the first measurement in November/December underestimated the full-season seedling growth, especially at lower altitude. This became evident when I compared the difference between the measured and the season's growth to the altitude, and found a trend of decreasing difference with altitude. The measured growth also masked the effect of altitude on growth. For instance, when looking at the relative growth of the seedlings as a function of altitude, results indicated that growth increased with altitude, because more of that season's growth was captured at high altitudes than at lower altitudes.

The second method (season's growth) was more consistent as there was only one measurement of height, thus eliminating errors between two measurements. In addition, using the terminal segment as measure of response to the treatments accounted for the growth of the entire season, and solved the issue of plants that started spring growth earlier than others.

I tested if taller plants produced longer terminal shoots and whether it had any influence on the results. I used a linear regression with the terminal shoot as a function of initial height and found a strong positive and significant correlation (ANOVA $F_{1, 535} = 80.76$, $p < 0.001$) between the two variables: taller plants tended to have longer terminal shoots. Then I looked at the relative growth as a function of initial height, and there was no correlation (ANOVA $F_{1, 535} = 2.93$, $p = 0.088$): relative growth was equal across initial height values. Finally, I used analysis of variance to test the initial height as a function of the treatments, which showed that there was no significant difference in initial height between the four treatments (ANOVA $F_{1, 535} = 0.11$, $p = 0.95$). Therefore I decided to use the season’s growth as the method for measuring relative growth.

4.2.4 Estimating light availability and altitude

The light environment was characterized for all 544 seedlings using the same hemispherical photography methodology as described in Chapter 3. The hemispherical photographs were taken between 2 March 2016 and 17 April 2016. The images were processed with ImageJ software (Schneider et al. 2012), and analysed using the programs PARCLR and OPENNESS in the CIMES package (Gonsamo et al. 2011), as in Chapter 3. The estimated parameters were canopy openness and photosynthetic photon flux density (PPFD), calculated for the midpoint of every month of the year and used to obtain the mean daily PPFD for the period of one year. Altitude at each seedling was derived from the GPS data.

4.2.5 Data analysis

All statistical analyses were done in R Version 0.99.903 (R Core Team 2016). The response variable (growth) was $\log_e$ transformed before all analyses, to improve normality. The response of the seedlings to the experiment was analysed using a generalized linear model (Gaussian family including F-test. In the data set, I created two columns named “fertiliser” and “trenching”, and the observations “0” and “1” indicating absence or presence of either fertiliser addition of root trenching. This was done to test their effects across treatments. I used the $\log_e$ of growth as a function of fertiliser and trenching plus their interaction as follows:

$$glm(log(seedling\ growth) \sim fertiliser * trenching, family = gaussian, test = "F")$$

I investigated how well the model fitted the data by plotting the residuals against the fitted values, the explanatory variables, the sequence of data collection, and standard normal deviates (Crawley 2005).

An analysis of covariance was used to analyse the combined effects of light, altitude and treatments, and their interaction on seedling growth, as follows:

$$lm(\log(seedling\ growth) \sim fertiliser * trenching + fertiliser * light + altitude)$$

A linear regression was used to analyse the effect of light on seedling growth, and the effect of altitude was tested similarly.

To test the response to fertiliser under different light levels I created a separate data set including exclusively Control and Fertiliser data. In this data set, a column named “fertiliser” was added with the observations “0” for Control, and “1” for Fertiliser. This was used to fit a GLM as follows:

$$glm(log(seedling\ growth) \sim light * presence\ of\ fertiliser, test = "F"$$

To test my prediction that soil moisture was not a growth limiting factor due to the high rainfall at the study site, I measured the soil water content at 90 experimental seedlings using a Theta probe (Delta-T devices), which is a time domain reflectometry instrument (Gaskin & Miller 1996, Davie 2008). I randomly selected seedlings from all four treatments, and performed three probing per seedling (to average them) within a 15-cm radius from the main stem. I used analysis of variance to test the $\log_e$ of growth against soil moisture. The analysis of variance showed that there was no relationship between seedling growth and soil moisture (ANOVA $F_{1,88} = 0.023$, $p = 0.88$), thus supporting my prediction.

Finally, I checked the interactions between the explanatory variables and their relative importance on growth of the seedlings by fitting a regression tree with the tree() package (Ripley 2016). I created a separate data set including only $\log_e$ of relative growth, light, altitude and two columns for presence (1) or absence (0) of fertiliser and trenching.

4.3 Results

Five Fertiliser & Trenching and two Trenching seedlings were left out of the analysis because they were broken or too damaged at the top to differentiate the terminal segments from other segments. There were no signs of this being a result of the treatments, however. The canopy openness ranged from 5.2% to 14.4% of hemisphere unobstructed by vegetation. Light ranged from 3.01 to 10.29 mol m^{-2} d^{-1}, respectively 8.12% and 27.8% of PPFD above the canopy. Altitude ranged from 736 to 1051 m. The seedling with the largest relative height increase was a Control plant with 50.8% growth (initial height = 33.3 cm), and the smallest was a Fertiliser & Trenching with 2% growth (initial height = 46 cm).

4.3.1 Seedling response to the treatments

Mean relative growth under Control treatment was 14.4%, against 17.1% for Fertiliser, 14.2% for Trenching and 15.7% for Trenching & Fertiliser. Fertiliser had the largest effect on seedling growth (Figure 4.3), increasing it 18.3% above that of Control. Contrary to the prediction, trenching had a small negative effect on growth, while Fertiliser & Trenching had a positive effect, but still less than expected. The response to the treatments was analysed using a generalised linear model (Gaussian). Fertiliser increased relative growth when applied to the seedlings regardless of whether the target plant was trenched, whereas trenching did not increase relative growth even when fertiliser was applied (neither the trenching effect or fertiliser × trenching interaction were significant). The difference between treatments was statistically significant. The coefficients for all treatments are presented in Table 4.2.

Table 4.1 Response of the seedlings to the treatments. Analysis of deviance of Gaussian generalised linear model including F-Test ((log(growth)~fertiliser*trenching), test="F"). Significant relationship is in bold.

Response: $\log_e$ growth						
	Df	Deviance	Resid. Df	Resid. Dev	F	Pr(>F)
NULL			536	123.2		
Fertiliser	1	2.768	535	120.43	12.312	**<0.001**
Trenching	1	0.301	534	120.13	1.339	0.248
Fertiliser:Tenching	1	0.273	533	119.86	1.2151	0.271

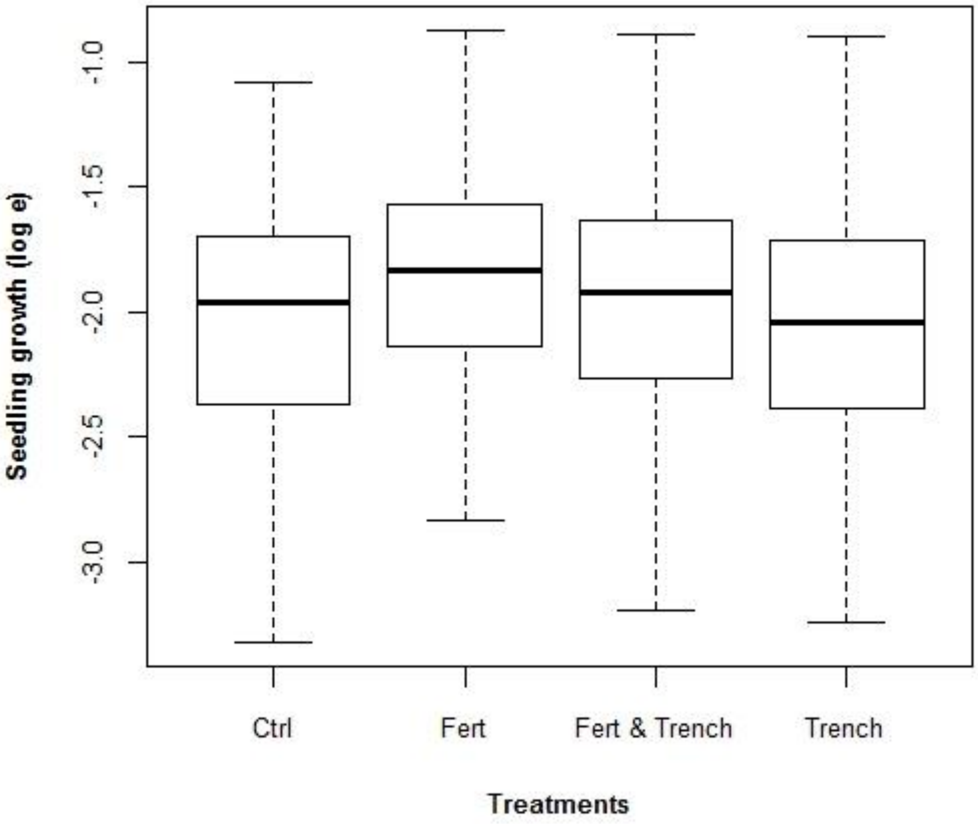

Figure 4.33 Growth (log *e*) of naturally regenerated Douglas fir seedlings in all four treatments. "Ctrl" = Control; "Fert" = Fertiliser; "Trench" = Trenching; "Fert & Trench" = Fertiliser & Trenching. Effects of treatments were statistically significant (see Table 4.1).

Table 4.2 Effects of the fertiliser addition, trenching, and their interaction on relative seedling growth. Gaussian generalised linear model including F-Test ((log(growth)~fertiliser*trenching), test="F"). Significant effects are in bold.

Coefficients:	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-2.050	0.041	-50.410	**<0.001**
Fertiliser	0.188	0.058	3.267	**0.001**
Trenching	-0.003	0.058	-0.043	0.965
Fertiliser:Trenching	-0.09	0.082	-1.102	0.271

The root system of younger and shorter plants tends to be closer to the surface than older and taller seedlings. I checked whether this could have resulted in better uptake of nutrients in the Fertiliser treatment. This was done by fitting a linear regression using $\log_e$ of relative growth as a function of the initial height of fertilised seedlings only. The test did not support the hypothesis of different response to fertiliser from seedlings of different heights (ANOVA $F_{1,134} = 0.008$, $p = 0.93$).

4.3.2 Analysis of covariance (ANCOVA)

The combined effects of light, altitude, fertiliser addition, and trenching on $\log_e$ of relative growth of Douglas fir seedlings were tested with an ANCOVA. Light, fertiliser addition, and altitude had statistically significant effects, with light being the factor with the largest significance (highest F-value), and causing the largest percentage increase on seedling growth (Table 4.3; see next section for details on effect size). There was no significant effect from root trenching. The interactions between fertiliser application and light, and fertiliser application and trenching were also not significant.

Table 4.3 Relative seedling growth against light, altitude, fertiliser addition, and trenching, including terms for interaction fertiliser:light, and fertiliser:trenching. Analysis of covariance (log(growth)~fertiliser*trenching+fertiliser*par+alt). Significant relationships are in bold.

Response: $\log_e$ growth					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Light (PPFD)	1	3.493	3.493	16.194	**<0.001**
Fertiliser	1	2.769	2.769	12.834	**<0.001**
Altitude	1	2.043	2.042	9.47	**0.002**
Trenching	1	0.301	0.301	1.396	0.238
Fertiliser:Light	1	0.02	0.019	0.09	0.764
Fertiliser:Trenching	1	0.241	0.241	1.119	0.291
Residuals	530	114.332	0.216		

4.3.3 Effect of light on seedling growth

Light had a large positive effect on seedling growth and was statistically significant (Table 4.1). The fitted values of relative growth were 12.3% for x = 4 mol m^{-2} d^{-1}, and 16% for x = 8 mol m^{-2} d^{-1}, an increase of 30.7% (see Table 4.2 for coefficients). The smooth line shows that the seedling growth increased at a relatively constant rate from 3 to approximately 8 mol m^{-2} d^{-1} (Figure 4.4). From this point onwards, growth ceased to increase with more available light, suggesting the light saturation point (where more light does not result in more growth) at around 8 mol m^{-2} d^{-1}, equivalent to 21.6% of full PPFD, although there are very few data points above 8 mol m^{-2} d^{-1}.

Table 4.4 Relationship between seedling growth and light availability. Analysis of variance of linear regression (log(growth)~light). Significant relationship is in bold.

Response: $\log_e$ growth					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Light (PPFD)	1	3.456	3.456	15.441	**<0.001**
Residuals	535	119.743	0.224		

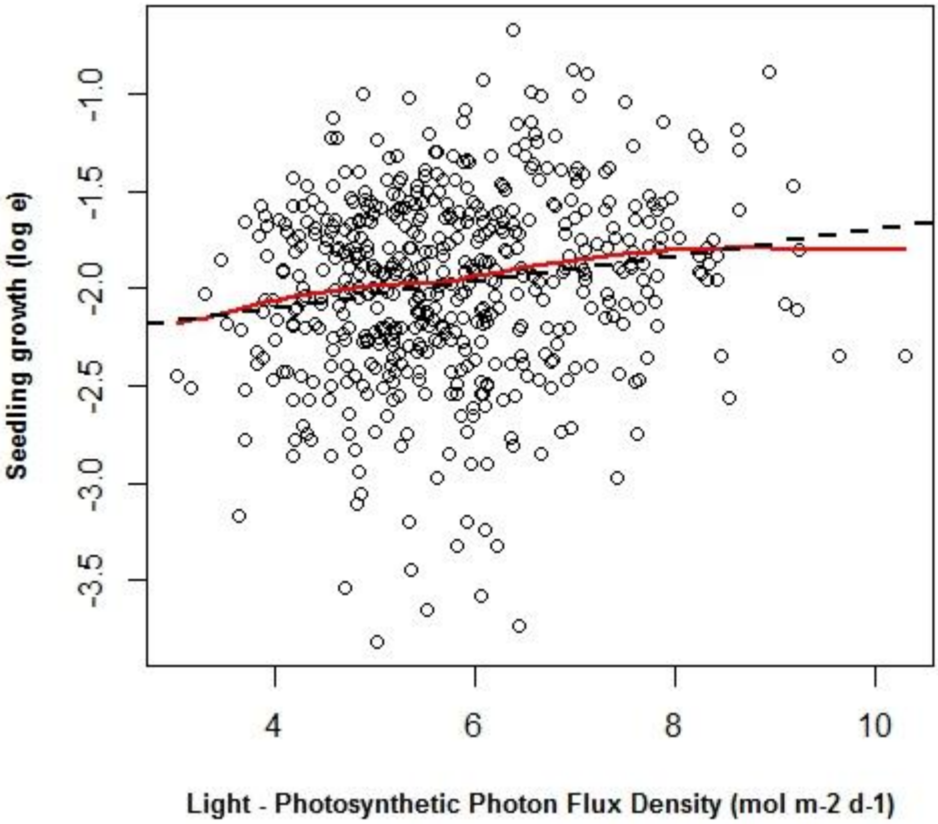

Figure 4.4 Growth (log *e*) of naturally regenerated Douglas fir seedlings and estimated PPFD (mol m^{-2} d^{-1}) in *Nothofagus* forest on Burnt Face. Scatter plot showing linear regression with best fit line (black dashed line). Solid red line is a smooth curve computed by LOESS.

4.3.4 Effect of altitude on seedling growth

The seedling growth decreased significantly with altitude (Table 4.5; Figure 4.5; see Table 4.4 for coefficients). The fitted values of relative growth were 14.6% for x = 750 m, and 12.4% for x = 1000 m, a decrease of 14.8%.

Table 4.5 Relationship between relative seedling growth and altitude. Analysis of variance of linear regression (log(growth)~altitude). Significant relationship is in bold.

Response: $\log_e$ growth					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Altitude	1	1.598	1.598	7.029	**0.008**
Residuals	535	121.601	0.227		

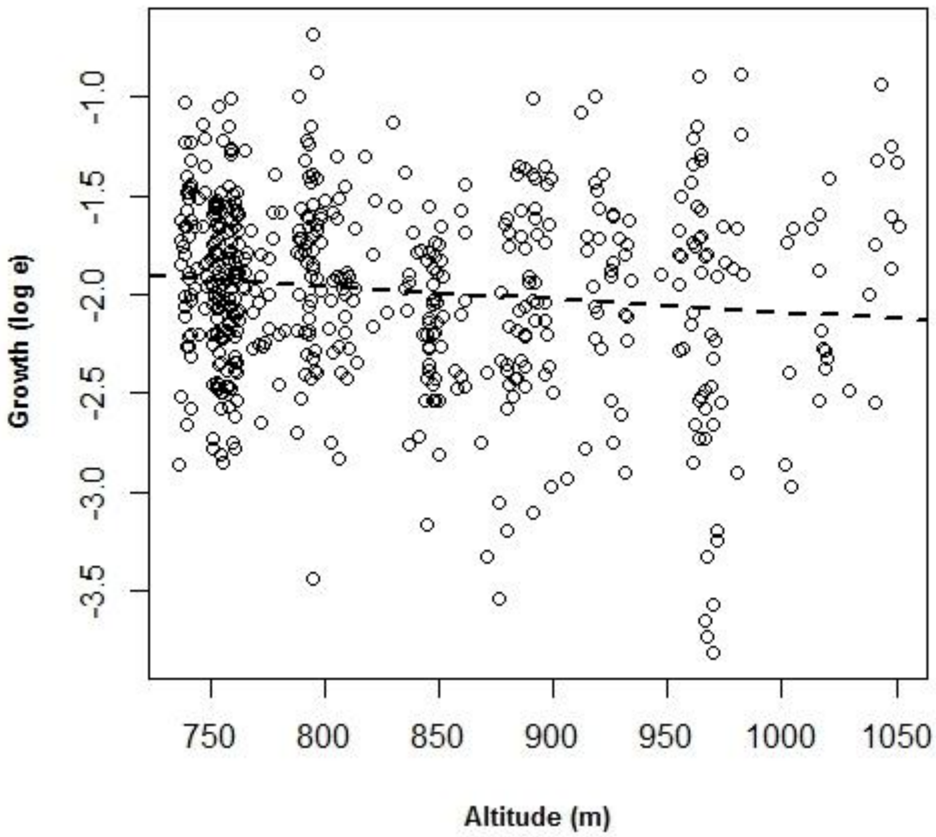

Figure 4.5 Growth ($\log_e$) of naturally regenerated Douglas fir seedlings versus altitude in *Nothofagus* forest on Burnt Face. Scatterplot showing linear regression with best fit line.

4.3.5 Influence of light on the response to fertiliser

The response to fertiliser under different light conditions was tested using a generalised linear model (with a data set including only Control and Fertiliser), looking specifically at the interaction between light and fertiliser. The response of the seedlings to fertiliser addition was higher with more light, as the fitted lines in Figure 4.6 suggest, but not significantly so, as the interaction light × fertiliser shows (Table 4.6). Both light and fertiliser had separately significant effects.

Table 4.6 Influence of light on seedling response to fertiliser. Analysis of deviance of Gaussian generalised linear model including F-Test ((log(growth)~light*fertiliser), test="F"). Significant relationships are in bold.

Response: $\log_e$ growth						
	Df	Deviance	Resid. Df	Resid. Dev	F	Pr(>F)
NULL			271	63.465		
Light (PPFD)	1	1.641	270	61.824	7.427	**<0.001**
Fertiliser	1	2.399	269	59.425	10.855	**0.001**
Light:Fertiliser	1	0.199	268	59.226	0.901	0.343

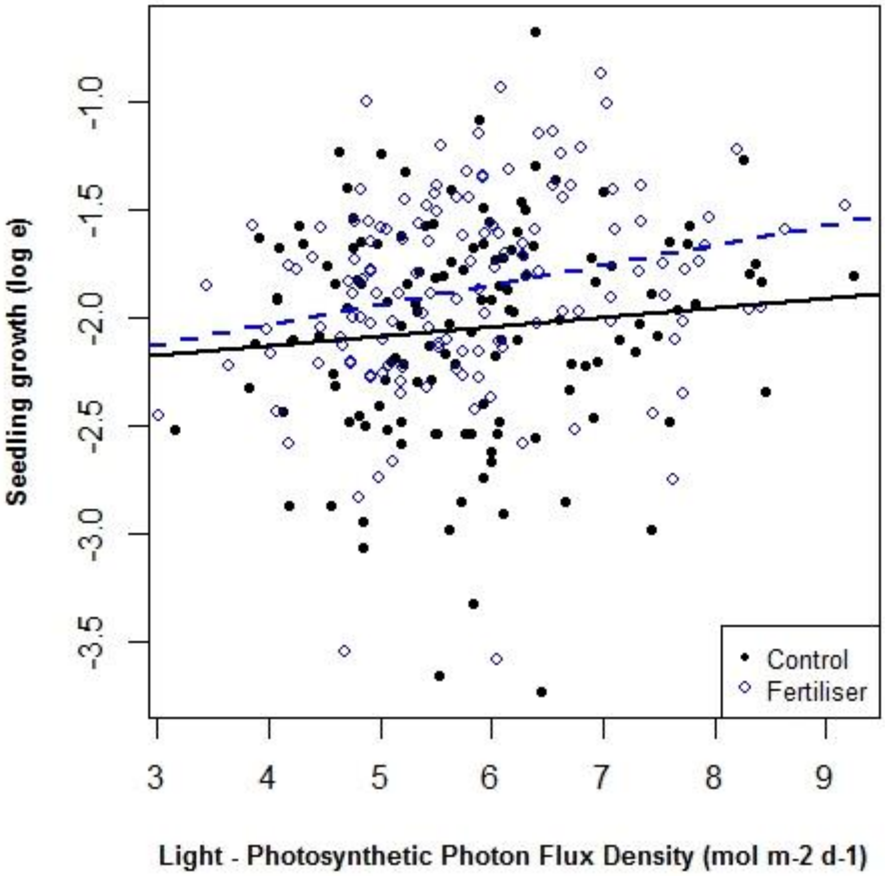

Figure 4.6 Scatterplot showing growth of Control and Fertiliser across the light gradient. Mean growth of Fertiliser increased with light more than Control did; however, the relationship was not significant. Best fit line of Control in black solid; Fertiliser in blue dashed.

4.3.6 Regression tree

Overall, light was the most important factor to affect growth, as predicted (Figure 4.7). In a high light environment there was no other variable causing a significant effect on growth. The mean seedling growth under high light availability was 15.85% ($\log_e{}^{-1.841} = 0.1585$). Altitude was important at relatively low light spots. The treatments had the least important effect. Fertiliser addition is shown in a small branch, low in the tree, indicating a small relative importance to seedling growth. Trenching did not meet the threshold for being represented in the model.

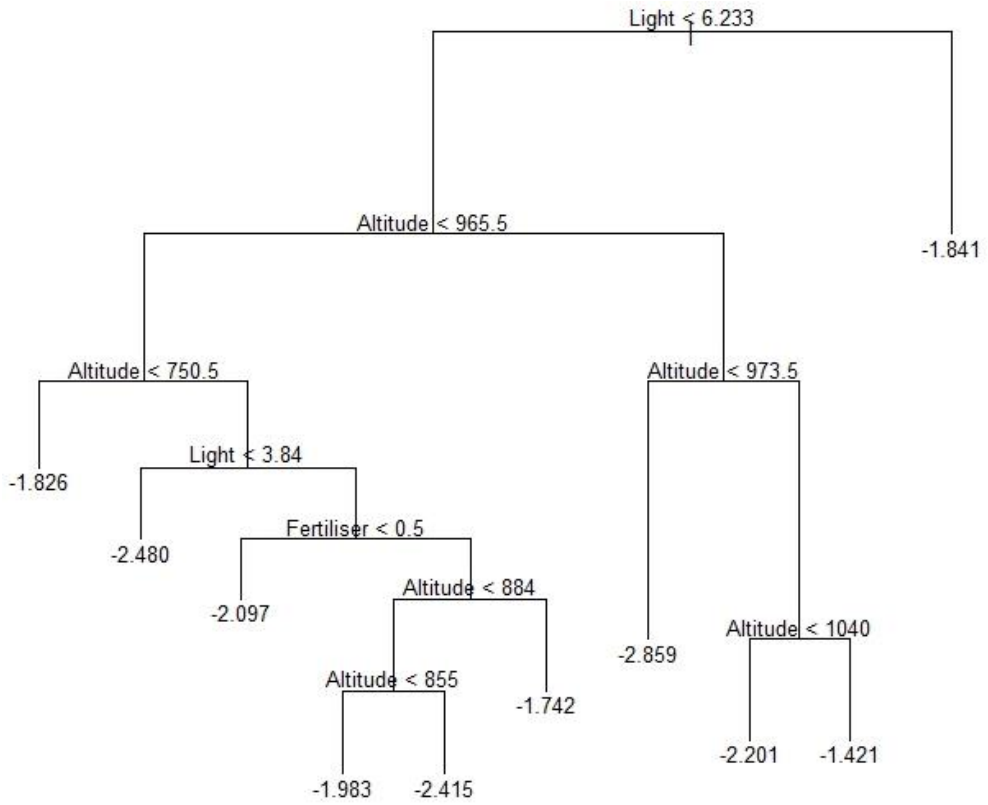

Figure 4.7 Regression tree showing the relationship of importance between seedling growth and the three explanatory variables. The longer the branches in the tree, the greater the deviance explained. Light at the top is the most important variable. Figures to the right of the labels are the mean values of the variables calculated by the model. Left- and right-hand side of each branch represent conditions below and above the mean, respectively.

4.4 Discussion

There was a complex relationship between light, nutrients, root competition, and altitude, all affecting the growth of Douglas fir seedlings in *Nothofagus* forest on Burnt Face. Light availability is considered the most important resource to limit plant growth in the tropics (Chazdon et al. 1996), and was the main factor to increase growth in this experiment. Interestingly, light was the least important factor to limit the seedling density, as shown in Chapter 3. Better growth should increase survival and thus positively affect density, but this indirect effect of light on the establishment of the seedlings was not measured. Therefore, the importance of light to the seedling density might have been slightly underestimated. Nutrient availability was second to light on growth-limiting factors. The effect of root competition was somewhat unclear as the results of trenching were opposite those I predicted. Trenching was intended to decrease root competition effects on the Douglas fir seedlings from the native vegetation, and thus test the effects of below-ground competition on the growth of Douglas fir. However, the seedlings had a negative response to trenching, decreasing growth relative to Control plants, although this was not statistically significant. Altitude, on the other hand, had clear results limiting growth of the seedlings.

Plants use environmental cues such as temperature to start the spring growth. At higher altitude, the necessary temperature to trigger the season’s growth is reached later in the year than at lower altitudes. Wardle (1971) noted that the growth season becomes shorter as altitude increases on Craigieburn Range. The effect of altitude demonstrated in this study is consistent with that found by Wardle (1985) when testing survival and growth of mountain beech and exotic conifer species seedlings across an altitudinal range in Craigieburn. Survival and growth of mountain beech, and *Picea engelmannii* seedlings decreased with altitude, whereas *Pinus contorta* experienced decline in growth alone.

4.4.1 Light and nutrients

There is a minimum irradiance required for woody plants to respond to nutrient addition. This varies between species and can range from 2–4% to more than 45 % of full daylight (Latham 1992, Grubb et al. 1996). For instance, Coomes and Grubb (1998) working in Amazonian rain forest with 14 species found that application of fertiliser only increased growth of the seedlings in gaps, but not in the understorey; Gill and Marks (1991) recorded small effects of increased light in untrenched plots, but large effects in trenched plots. Such a threshold was not identified in the present study, however. I did not find a statistically significant difference between the response of Control and Fertiliser across the light gradient, even though the slope of Fertiliser was steeper. This suggests that there may be a modest influence of light on the response of the seedlings to fertiliser addition, but my sample size, although large, was not enough to show the interaction was present.

Light was more important than nutrients to Douglas fir seedling growth. Pinard et al. (1998) found no difference in growth between trenched and untrenched *Shorea parvifolia* (Dipterocarpaceae) seedlings in Malaysia, but growth was positively correlated with canopy openness. Holl (1998) found that aboveground clearing had a larger effect than trenching on *Calophyllum brasiliense* (Calophyllaceae) seedling growth in Costa Rica. Using different tree species (*Simarouba amara, Gustavia superba, Tachigali versicolor*, and *Aspidosperma cruenta*) in the Panamanian rain forest, Barberis and Tanner (2005) also found light to have greater importance on seedling growth than manipulation of root competition on fertile soil. Little response to trenching is expected from seedlings when nutrients are not scarce.

However, on the nutrient-poor soil of Craigieburn, the response was expected to be positive and large.

The estimated percentages of full PPFD were higher than measures from Dehlin et al. (2008) at Craigieburn using flux meters. However, the values that I obtained via the CIMES package are reliable to compare the light environment between different spots in the forest, and to correlate the relative light penetration with the establishment and growth of the seedlings.

4.4.2 Below-ground competition

Below-ground competition for water and nutrients plays an important role on the development of plants in forests and woodlands, however, its dynamics are still not well understood (Coomes and Grubb 2000, Barberis and Tanner 2005). This is partially due to the complexity of accurately isolating the effects of root competition. For instance, Berendse (1983) points to the difficulty in separating the effect of ceased competition from the natural nutrient increase of decaying roots after trenching. Conversely, McLellan et al. (1995) argue that any potential benefit to target plants from release of nutrients by dead roots is small when compared to the massive influence of manipulating root competition. But most of the root-competition researchers agree that Berendse’s point should not be of major concern since the nutrient supply by decaying roots is small during the time period in which most experiments are conducted; and the observed increase in growth of trenched plants is usually rapid, while the release of nutrients by severed roots is much slower (Coomes and Grubb 2000).

The hypothesis that the growth of Douglas fir seedlings would increase when root competition from mountain beech was reduced by root trenching was not supported by the results. Trenching had a very weak negative but not significant effect on seedling growth. This weak negative effect is also suggested by the results of Fertiliser, and Fertiliser & Trenching treatments – if trenching were neutral, then the plants under Fertiliser & Trenching would have responded similarly to Fertiliser, not worse. This result was contrary to the increase in seedling growth most experiments have found in temperate forests (Cameron 1960, Machado et al. 2003, Platt et al. 2004, Petriţan et al. 2011) and tropical forests (Gerhardt 1996, Coomes and Grubb 1998, Holl 1998, Lewis and Tanner 2000, Barberis and Tanner 2005). Fewer studies found no response of tree seedlings to trenching in nutrient-poor soils in the tropics (Pinard et al. 1998) and temperate forests (McVean 1956, Dehlin et al. 2008). Horn (1985) found significant but small increase in seedling growth for *Acer rubrum*, and no effect for *Cornus florida* and *Oxydendron arboreum*. McVean (1956) actually pointed out that the control seedlings had better growth than the trenched seedlings, although not significant, as in the present study. In what is possibly the most comprehensive review of root competition experiments, Coomes & Grubb (2000) found that 40 out of 47 root-trenching studies recorded positive plant response.

There are two potential explanations for the lack of positive effect from trenching. The first and most obvious is damage done to the seedlings' roots with the shovel. If some roots of the Douglas fir seedlings were unintentionally severed by trenching, then a negative effect could be expected, as the plants would suffer from biological stress and have their potential to absorb water and nutrients reduced. In this case, I used a distance of 40 cm around the seedlings for the trenching so it is possible that some roots were damaged. The second and more interesting possible reason is that trenching cut the mycelium around the seedlings, thus reducing the size of the mycorrhizal network which the seedlings were connected to. Research has shown that Douglas fir (*Pseudotsuga menziesii*) and paper birch (*Betula papyrifera*) seedlings can exchange carbon isotopes via the mycorrhizal network (Simard et al. 1997a), and that naturally regenerated Douglas fir seedlings can enhance survival rates and benefit from resource transfer from host trees (Teste et al. 2009). In old-growth paper birch and Douglas fir forest, Simard et al. (1997b) found that the net photosynthetic rate, and height: diameter ratio of Douglas fir seedlings were greater in untrenched than in trenched treatment, which they attributed to differences in mycorrhizal partners. However, Dehlin et al. (2008) compared the seedling growth of three species (including Douglas fir) in monodominant stands at Craigieburn and found slightly higher percent of mycorrhizal root tips on seedlings in trenched plots than in untrenched plots. They concluded that the stand type had more effect on growth than trenching or mycorrhizae.

Also in the Craigieburn Range, Platt et al. (2004) examined the response of mountain beech seedlings to trenching and fertiliser addition in *Nothofagus* forest. Trenching had a greater effect on growth of the seedlings than fertiliser, and fertiliser addition only caused significant effect when combined with trenching. The mycorrhizal network of the seedlings might not have been fully severed, given the experimental design – the seedlings were not individually trenched, instead, they trenched the edges of 1 m^2 plots each containing 10 seedlings from 10 to 24 cm height – thus potentially preserving the mycorrhizal connections between seedlings.

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

I have demonstrated that the Douglas fir invasion of *Nothofagus* forest on Burnt Face is influenced by abiotic factors, above and below ground, such as light, altitude, distance to the seed source, and nutrient availability. All these have an effect on the establishment and/or growth of the Douglas fir seedlings. The invasion (measured by seedling density in the *Nothofagus*) has increased over 13-fold since 1989. The establishment of the seedlings was unexpectedly more limited by altitude than by light, while the opposite was true for seedling growth – the largest constraint to height growth was light. The relative importance of fertiliser addition to growth was small. Now that suitable mycorrhizae have established, the invasion of *Nothofagus* is constrained by light gaps and thus disturbance, which might be different from 40 years ago, before the fungi needed by Douglas fir were widespread. And since there is constant disturbance in forests (Wardle 1984, Allen et al. 1999), opportunities for the establishment of the seedlings are likely to be created regularly.

Although biological interactions were not in the scope of my study, they are important to the success of conifer invasions (Davis et al. 1996, Richardson et al. 2000a, Dickie et al. 2010, Moeller et al. 2015). There are no indications that the ongoing spread of fungi across and within ecosystems is going to slow down. Therefore, the relative importance of suitable mycorrhizae as a limitation to the Douglas fir invasion on Burnt Face is likely to decrease with time, consequently increasing the relative importance of factors such as light, altitude, and nutrient availability.

There is a conflict of interest between the economic benefits from commercial plantings and the negative economic and environmental impacts associated with tree invasions. According to Velarde et al. (2015), the current annual cost of controlling wilding conifers in New Zealand is $5.8 million, and the estimate of economic losses due to the ongoing infestation between 2015 and 2035 is $1.2 billion. Harrington et al. (2003) argued that the forestry industry should take a proactive role in identifying the threats of invasive species and working to reduce their potential hazards, although they acknowledged that many actions have already been taken towards these goals. There is a large effort from the government, the forestry sector, and independent groups to control wilding conifers in New Zealand. Institutions such as the Ministry of Primary Industries, the Department of Conservation, SCION and the New Zealand Wilding Conifer Management Group work to identify and map invasions, to research forms of control, and to mitigate impacts. Some of these efforts being made today are in fact remedying invasions that should have been dealt with sooner, for example, the conifers at Flock Hill – which came from plantings by the defunct Forest Service, and began to spread widely in the 1990s but were not actively controlled until about 2010 – and those at Mt Barker, the Amuri Range, and Mid Dome.

It is clear that the invasion on Burnt Face must be controlled, but how to control it is less obvious. There are several methods for control of wilding conifers, including burning, pulling, ring-barking, using tools such as chainsaw and scrub-bar, machinery such as a mulcher or dozer, and chemicals (Ledgard and Paul 2008). However, most of these are not suitable for control of wildings in forest ecosystems. Herbicide application from helicopters directly onto the target plants as applied in New Zealand (Gous et al. 2015) is unsuitable in this case, as is the use of heavy machinery to remove wildings. On Burnt Face, control would have to be done locally and manually, with the aid of tools. Volunteers are often used in wilding control in New Zealand, mainly to pull out small seedlings, as handling tools such as machetes or chainsaws raise potential safety issues. This leaves few choices for managing the spread on Burnt Face and similar areas. Harrington et al. (2003) suggested replacing highly invasive species with less invasive ones in commercial plantings. This is a sensible idea, but may not be necessary in the case of Douglas fir invasion of native forest. Ledgard (2002) presented two relatively simple strategies to minimize the risk of such invasion: to plant a less spread-prone species in between the Douglas fir and the native forest to serve as a barrier for the seeds; and to avoid planting Douglas fir on exposed sites, upwind of the native forest. Also, the strong negative effect of altitude on the establishment of the Douglas fir seedlings found in this study could help guide future plantings – such as to avoid plantings in lower altitudes.

There may be negative environmental effects on Burnt Face, however, even if the management of the spread is successful. Dickie et al. (2014) found that changes in the soil nutrients and soil community – such as shifts in the nutrient cycling, N and P availability, and ectomycorrhizal species – persisted at least three years after removal of lodgepole pine invasion in the grassland/shrubland ecosystem in Craigieburn. This promoted the subsequent invasion of the clear land by exotic plants, rather than regeneration of native plant species, which was still absent nine years after removal. Therefore, managing the legacy of the invaders in the ecosystem is often required in addition to removal of the invasive organisms (Wardle and Peltzer 2017).

There is a need to identify and control biological invasions early. Braithwaite and Timmins (1999) called for early detection of weeds in New Zealand to minimize potential negative impacts of the unwanted spread. The frequency of surveys to detect weeds are dependent on the species growth rate, the ability to detect them, and the costs associated with control of the weed (Brown et al. 2004). Naturally, Douglas fir is well known as a weedy species in grasslands and shrublands in New Zealand, but its invasive potential in forest ecosystems, especially in undisturbed forests, has not been well understood. At present, 35 years after the start of the invasion on Burnt Face, Douglas fir is still spreading relatively slowly into the mountain beech forest. However, plant invasions tend to take off after the lag phase, leading to a rapid population growth and range expansion (Kowarik 1995). This adds to the need for early management of the spread on Burnt Face.

The general assumption is that conifers are more likely to invade forests following disturbances in the plant community, and that the seedlings would normally establish under canopy gaps, as discussed in Chapter 2. The past disturbance on Burnt Face did indeed contribute to the spread of Douglas fir into the *Nothofagus*. However, more than thirty years have passed since then, and the establishment of the seedlings has not been halted. More importantly, the Douglas fir seedlings are establishing throughout the forest, not under obvious canopy gaps only. Given that *Nothofagus* forests are subject to natural disturbances such as wind storms, snow damage, earthquakes, and insect damage (Harcombe et al. 1997, Allen et al. 1999, Cullen et al. 2001), it may be a sensible idea to reconsider the circumstances under which Douglas fir can invade forest ecosystems. If we consider that all beech forests adjacent to Doulas fir plantations are potentially subject to invasion, the next step is to identify how many of these cases exist in New Zealand.

The established seedlings can eventually grow taller than the *Nothofagus* canopy and start to disperse seeds even further into the beech forest (I found scattered saplings up to 10 m tall). The minimum control strategy for Burnt Face would be to cut down any Douglas fir trees visible above the canopy. A transformation of the native *Nothofagus* forests through the gradual replacement of the dominant native trees by Douglas fir would have major environmental, economic and cultural consequences. In New Zealand, nonexistent or poor control of conifer spread in the past has led to a large scale invasion of grassland and shrublands across the country. However, a different outcome in regard to the invasion into forests is still possible, as long as control is done early. I hope that my research can contribute to the invasion ecology field, particularly to the conservation of the pristine *Nothofagus* forests in New Zealand.

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